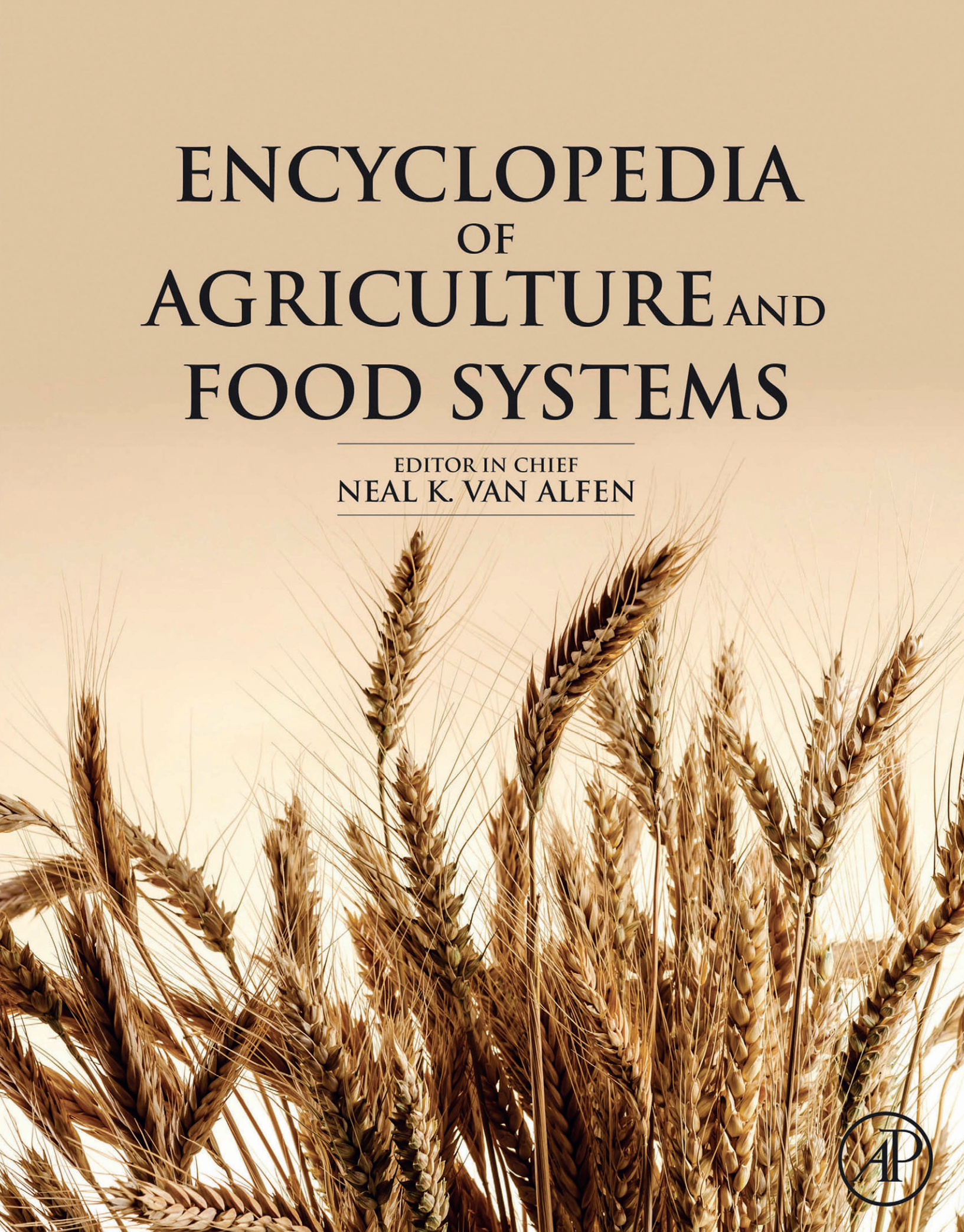
ENCYCLOPEDIA OF AGRICULTURE AND FOOD SYSTEMS

EDITOR IN CHIEF
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ENCYCLOPEDIA OF AGRICULTURE AND FOOD SYSTEMS

VOLUME 1

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GUIDE TO USING THE ENCYCLOPEDIA

Structure of the Encyclopedia

The material in the encyclopedia is arranged as a series of articles in alphabetical order.

There are four features to help you easily find the topic you're interested in: an alphabetical contents list, cross-references to other relevant articles within each article, and a full subject index.

1 Alphabetical Contents List

The alphabetical contents list, which appears at the front of each volume, lists the entries in the order that they appear in the encyclopedia. It includes both the volume number and the page number of each entry.

2 Cross-References

Most of the entries in the encyclopedia have been cross-referenced. The cross-references, which appear at the end of an entry as a See also list, serve four different functions:

i. To draw the reader's attention to related material in other entries.
ii. To indicate material that broadens and extends the scope of the article.
iii. To indicate material that covers a topic in more depth.
iv. To direct readers to other articles by the same author(s).

Example

The following list of cross-references appears at the end of the entry Critical Tracking Events Approach to Food Traceability.

> *See also*: Agribusiness Organization and Management. Food Chain: Farm to Market. Food Labeling. Food Law. Food Packaging. Food Security: Development Strategies. Food Security: Food Defense and Biosecurity. Food Security, Market Processes, and the Role of Government Policy. Food Security: Postharvest Losses. Global Food Supply Chains. Government Agricultural Policy, United States. Regulatory Conventions and Institutions that Govern Global Agricultural Trade

3 Index

The index includes page numbers for quick reference to the information you're looking for. The index entries differentiate between references to a whole entry, a part of an entry, and a table or figure.

4 Contributors

At the start of each volume there is list of the authors who contributed to that volume.

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Agricultural Cooperatives
Agricultural Ethics and Social Justice
Agricultural Finance
Agricultural Labor: Demand for Labor
Agricultural Labor: Gender Issues
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PREFACE

Food is absolutely necessary for human existence, yet for most in wealthy nations it is largely taken for granted because of its abundance. Sufficient food is a concern, however, for about 1 billion of the earth's inhabitants today who often go to bed hungry. Food security in a broad sense is becoming a worry of the future for those who understand the limitations of our earth's ecosystems. Malthusian prophecies have so far been wrong, but there is growing concern that we are rapidly reaching the point where feeding the world's growing and richer population will be at the cost to our environment that is unacceptable. In the next few decades we face the challenge of growing more food, with less water, with less fertilizer on less land – because of the growth of urban areas on prime agriculture land. We also face the largely unknown consequences that global warming will have on agricultural production. During the last century agricultural scientists were able to bring cutting-edge science into traditional agricultural practices and increase food production sufficiently to prevent global food shortages. The hope that new scientific discoveries will provide the means to keep ahead of world food demand is complicated by a growing public discomfort with biotechnology being applied to food production.

The concept of services being provided by the ecosystems of the earth is a fairly recent attempt to understand and place value on functions of natural lands that have historically been assumed to have few limits. In the past, if more food was needed, new lands were converted from forests or steppe lands into farm land and new water systems developed to provide the water needed for agriculture. When human populations were low our activities were largely buffered by the abundance of forest and steppe, but too late, we are beginning to understand that these provisioning services of our ecosystems are being overused and are no longer buffered by the abundance of wild lands and waters. We are rapidly losing our planet's biodiversity, irreplaceable ground water is being unsustainably consumed, and major river systems are being overused and polluted. Our oceans, the last place on the planet that still support our hunter and gathering traditions may not be able to sustain these activities into the future. And, food production and processing activities contribute to the greenhouse gas emissions that are rapidly warming our planet. Agriculture is the single greatest user of the earth's land and water resources. In the concept of ecosystem services, provisioning or providing food for all organisms is one of the services provided by ecosystems. Human population growth has and will continue to overtax the ecosystems we inhabit. The ultimate outcome of this major diversion of nature's resources into provisioning the human species is unknown, but it is critically important for us to understand what we must do to sustain our planet.

The breakthrough discovery about 10 000 years ago that plants and animals could be bred to provide a more abundant and secure food source was the foundation upon which all other human activities were able to flourish. Activities other than finding food now became possible and our diverse cultures were able to develop because of agriculture. Until fairly recently, however, the majority of the population of most nations was still directly involved in producing food. Mechanization of agriculture and continued improvements in genetics, fertilizers, and pesticides made food production very efficient in developed nations. In the United States, the leading nation in value of agricultural exports, less than 2% of the workforce is currently employed in producing food. The United States, however, is alone among the most populous nations of the world in having such a small population employed as farmers. In countries such as China, India, Indonesia, and Nigeria the majority of people are rural and involved in agriculture either directly or indirectly. But, as food production becomes more efficient in these countries, and as wages increase in other sectors, a major shift is occurring from rural to urban occupations. This revolution is potentially as important in affecting our cultures and community structures as was the development of agriculture. Many nations are currently experiencing a very rapid transition from rural to urban living with all of the social and logistic problems associated with such rapid structural changes. While this transition in our social and cultural structures is a broad subject, it does have significant impacts on agriculture and our food systems. To mention just a few, agriculture labor, food transport, food safety, and access to healthy food.

There is genuine concern among agricultural scientists that human populations and changing diets are outpacing our ability to meet the increasing food needs of the planet. In the first iteration by Academic Press in 1994 of the *Encyclopedia of Agricultural Science*, Noble Prize Winner Normal Borlaug wrote in its forward:

> Had the world's 1990 food production been distributed evenly, it would have provided an adequate diet (2350 calories, principally from grains) for 6.2 billion people – nearly one billion more than the actual population. However, had the people in Third World countries attempted to obtain 30% of their calories from animal products – as in the United States, Canada, or European Economic Community countries – a world population of only 2.5 billion people could have been sustained – less than half of the present world population.

The issue raised by Dr. Borlaug is probably the most important challenge we face. Human behavior and the food choices of consumers will determine the outcome of the race between food supply and population. Population control has been advocated for decades, and in some cases has become part of national policy, but the world's population continues to grow. Science breakthroughs cannot solve our food security and environmental quality challenges if consumers reject food that is not traditionally produced. Likewise, if meat products and other inefficiently produced food continue to be in high demand by consumers, there will be increased pressure on our food production systems. As supplies become short, prices rise. While this may be good for farmers, high food prices and food shortages will probably undermine our efforts to preserve the

world's remaining arable land as natural lands. We must change human behavior to solve the problems we face.

Food choices, nutrition, diets, food cultures, water and air quality, GMOs, global warming, food security, and similar topics are daily in the news throughout the world. We are all concerned about these issues, yet with all of the information easily available in the popular media about food there seems to be too little informed discussion on these various topics. In planning the *Encyclopedia of Agriculture and Food Systems* the editorial committee chose to organize the topics primarily by issues, rather than to focus on a traditional topic approach. We organized the issues that would be discussed in the chapters around the broad topics of Agriculture and People, Agriculture and the Environment, Agricultural Products, Plant Health Management, Animal Health Management, and Agriculture and Science. The issues raised in this preface are the ones that we felt needed to be addressed in this encyclopedia.

The associate editors joined me in the development of topics for the encyclopedia and were responsible for working with the authors – they deserve particular recognition. I was fortunate to be joined by a very distinguished group of colleagues who, I hope, are still friends. They spent much more time and effort in bringing this project to completion than any of us anticipated. I want to thank our authors who while overly committed and overworked, fulfilled their commitments to contribute to this work. I have been impressed with the quality of their contributions. The editorial staff of Elsevier have had the professionalism and patience to work with scientists who do not work under the same time and budget constraints that the staff work. I want to particularly thank Kristi Gomez, Donna de Weerd-Wilson, and Simon Holt who, each in succession, oversaw this effort, and I especially thank the project managers, who worked directly with me, and the associate editors, Kate Miklaszewka-Gorczyca, Will Bowden-Green, and Sam Mahfoudh.

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Glossary

Clone A cell, group of cells, or organism that is produced asexually from and is genetically identical to a single ancestor.
Genetic marker Gene or other identifiable portion of deoxyribonucleic acid (DNA) whose inheritance can be followed.
Marker-assisted selection (MAS) The use of DNA markers to improve response to selection in a population. The markers will be closely linked to one or more target loci, which may often be QTL.
Nuclear transfer A laboratory procedure in which a cell's nucleus is removed and placed into an oocyte with its own nucleus removed so the genetic information from the donor nucleus controls the resulting cell. Such cells can be induced to form embryos.
Quantitative trait loci (QTL) Stretches of DNA containing or linked to the genes that underlie a quantitative trait.
Quantitative traits Traits that vary continuously and are affected by multiple genes or loci. Examples include height and weight.
Recombinant DNA A m1olecule formed by joining DNA of interest to vector DNA.
Single nucleotide polymorphism (SNP) A DNA sequence variation at only one base pair between synonymous pieces of DNA.
Transgenics Organisms that have foreign DNA stably integrated into their genome.
Xenotransplantation The act of transplanting or grafting tissue or organs from an individual of one species into an organism of another species, genus, or family. A common example is the use of pig heart valves in humans.

What is Animal Biotechnology?

Animal biotechnology is any technological application that utilizes animals to make or modify products. The practice of animal biotechnology began more than 8000 years ago when humans began domesticating and selectively breeding animals. The modern era of animal biotechnology arrived following the discovery of the genetic code in the mid 1950s. Today new tools including increased computing power, genomic sequencing, cloning, regenerative medicine and direct gene insertion, and manipulation have given people the potential to dramatically alter animals for a broad range of purposes, including food production, medical, and scientific research. Modern biotechnology represents the intersection of man's manipulation of the environment and the emergence of molecular and computing technologies. These advances, as well as the US Supreme Court ruling that designed life could be patented, have spawned new ways of expediting the use of animals in serving society.

Earliest Animal Biotechnology

Prehistoric humans were originally hunter-gatherers who nourished themselves by following the migration of animals and ripening of foods such as wild fruits and berries. Hunter-gatherer communities could not support high population densities in part, because food resources were not steady or predictable. It is believed that the end of the ice age approximately 10 000 BC created conditions suitable for the transition from a hunter-gatherer lifestyle to farming communities. This transition, known as the Neolithic Revolution, marked the beginning of early agriculture. The Neolithic Revolution is believed to have occurred independently in seven to nine major centers, including Mesopotamia, China, Mesoamerica, and East and West Africa (Von Baeyer, 2010). Most accounts identify Mesopotamia, also known as the Fertile Crescent, as the origin of early agriculture. Owing to its impact on civilization, the transition from hunter-gatherer to farmer has been described as the most important technological development

Table 1 Domestication centers of the world

Center of domestication	*Dates (years ago)*
Near East/'Fertile Crescent'	11 000
Northern China	9 000
Southern China	8 000
Central Mexico	5 750
Peruvian Andes	5 250
Papau New Guinea	6 000–9 000
West Africa	4 500
Eastern North America	4 000

Source: Origins of agriculture by Lewis Foote on Prezi. Available at: prezi.com/uczfibsijcj7/origins-of-agriculture/ (accessed 06.05.13).

ever to occur in human history. By becoming farmers, humans were able to gather in greater numbers, have better and more consistent nutrition and develop technology. **Table 1** shows the major centers of domestication in the world.

Scientists believe crop domestication preceded the earliest domesticated animals by approximately 1000 years. In East Asia, rice, millet, and soy were domesticated; in sub-Saharan Africa, millet, sorghum, and African rice were domesticated; and in the Americas potato, sweet potato, corn, squash, and beans were domesticated (Floros *et al.*, 2010). The domestication of cattle, sheep, and goats took place 8000, 11 000, and 10 000 years ago, respectively, whereas buffalos, horses, asses, and camels were domesticated approximately 5000 years ago (Hirata, 2004). These animals were considered suitable for domestication because of their docile temperament, willingness to be dominated, and ability to live in large groups.

As humans became sedentary, they began caring for and controlling wild animals and plants for food production, transportation, protection, production of valuable commodities (cotton, silk, or wool), warfare, and companionship. Domesticated animals that we commonly use today, including dogs, cats, sheep, geese, camels, cattle, pigs, and horses started as wild animals but were changed over time through domestication practices (Zeder *et al.*, 2006; Andersson, 2011).

Domestication is not an instantaneous event. It is a cumulative process characterized by changes in which partner populations become interdependent over time (Zeder *et al.*, 2006). This process is also shaped by the particular environmental, biological, and behavioral profiles of the target species, as well as the cultural context of the human societies involved. The typical changes caused by the domestication process can be external or internal morphological changes, such as modifications in body size, decreased brain size, physiological changes, developmental changes, and behavioral changes, such as reduced fear (Jensen, 2006).

Although domestication initially had a small influence on the economies of human societies, which were originally based on hunting and gathering, it enabled these societies to grow in size and to expand into new and more-challenging environments. For example, the domestication of plants and animals enabled human population to grow by providing a food surplus. Moreover, domesticated dogs and sheep enabled human societies to become pastoral. Farming and raising livestock permitted the creation of permanent communities in place of the temporary ones prevalent in migratory hunter-gatherer groups, and the building of permanent shelters to house livestock and store harvested crops. In addition, new farming tools and technologies were developed once people started to grow their own crops (Zeder *et al.*, 2006; Jensen, 2006).

Fewer than 20 animal species have been successfully domesticated (Diamond, 1997), only 7 of which (cats, dogs, cattle, sheep, goats, pigs, and horses) are found worldwide. As pointed out by Hale (1969) and Diamond (1997), animals that have been successfully domesticated and farmed share and exhibit a unique combination of characteristics. They are relatively docile, flexible in their dietary habits, grow, and reach maturity quickly on an herbivorous diet, and breed readily in captivity. They also have hierarchical social structures that permit humans to establish dominance over them and are adapted to living in large groups. They do not include species that generally have a tendency to be fearful of humans or disturbed by sudden changes in the environment. Our ancestors no doubt based their selection methods for improving their herds and flocks on how easy the animals were to farm, as well as on potential agricultural value. In turn, the animals adapted to thrive in a domesticated environment.

Dogs (*Canis lupus familiaris*) were the first animal species to be domesticated, probably in East Africa and Asia. According to archeological evidence, dogs first began to show differences in appearance compared to wolves approximately 15 000 BCE. Many researchers believe that dogs essentially domesticated themselves by scavenging near human camps. Humans then bred them to bark in warning and for reduced aggression compared to wolves (Gray *et al.*, 2009; Skoglund *et al.*, 2011).

Sheep (*Ovis aries*) were probably first domesticated approximately 15 000–11 000 BCE. Their remains have been found at a wide range of sites of early human habitation in the Middle East, Europe, and Central Asia (Chen *et al.*, 2006; Chessa *et al.*, 2009). According to deoxyribonucleic acid (DNA) and mitochondrial DNA (mtDNA) studies of European, African, and Asian domestic sheep, it is believed that they descended from at least three different subspecies of the wild mouflon (*Ovis gmelini* spp.) and that there are three major and distinct lineages: Type A or Asian, Type B or European, and Type C, which has been identified in modern sheep from Turkey and China. Initially sheep were domesticated mainly for meat production. Later, these animals were also used to provide milk, wool, and leather. Nowadays, sheep continue to be important agricultural animals, as well as model organisms for scientific research (Chen *et al.*, 2006; Chessa *et al.*, 2009; Pedrosa *et al.*, 2005).

Goats (*Capra hircus*) were domesticated for their milk and meat, as well as materials for clothing and building (hair, bone, skin, and sinew). Their dung was also used for fuel. They are thought to have been domesticated in Iran and neighboring countries approximately 10 000–11 000 BCE. Recent mtDNA research has shown that all modern goats probably descended from a wide range of animals and may have been domesticated in a variety of different places (Fernández *et al.*, 2006; Luikart *et al.*, 2001).

Pigs (*Sus scrofa domesticus*) have mostly been domesticated for meat production; however their bones, hide, and hair are also used for items such as weapons and brushes. Domestic pigs, especially pot-bellied pigs, are also kept as pets. Archeological studies have shown that the domestic pig was domesticated from wild boars approximately 13 000 BCE in

the Tigris basin. However, remains of domesticated pigs have been found in southeast Anatolia dated to earlier than 13 000 years BCE (Vigne *et al.*, 2009). According to DNA evidence from Neolithic pigs, domesticated pigs were brought west to Europe. Zooarchaeological evidence suggests the domesticated pig was also brought east to China from the Near East, in addition to a separate domestication in China that took place approximately 10 000 years ago. These findings have led to the conclusion that pig domestication occurred independently in several places across Eurasia (Larson *et al.*, 2007; Chen *et al.*, 2007).

Cattle (*Bos primigenius*) have been domesticated since at least the early Neolithic for their meat, milk, leather, dung for manure or fuel, and for use as load-bearers and to pull plows. According to archeological records and modern genetics research for the domestication of wild forms of cattle, the process occurred independently from as few as 80 aurochs (the now-extinct predecessor of cattle) in Mesopotamia approximately 10 500 years ago near the villages of Çayönü Tepesi in southeastern Turkey and Djade al-Mughara in northern Iraq (Allan and Smith, 2008; Ajmone-Marsan *et al.*, 2010; Beja-Pereira *et al.*, 2006).

In addition, several other animal species also went through a process of domestication, such as farmed fowl (chickens, geese, and turkeys), horses, aquatic animals, and some insects. All of them, like those mentioned above, are of great importance to humans, providing products and inputs used routinely.

Assisted Reproductive Technology

Since animals were first domesticated, many technologies have been developed to select for desirable qualities, make breeding easier, and make animals produce more offspring. Many of those technologies, including artificial insemination, *in vitro* fertilization (IVF), embryo flushing, and cloning, involve the manipulation of animal reproduction.

Artificial Insemination

History of artificial insemination

Artificial insemination refers to the introduction of semen and viable sperm into the female reproductive tract via artificial means. Lazzaro Spallanzani, a French physiologist, was the first person to successfully demonstrate artificial insemination in animals, when he artificially impregnated a dog in 1784. However, the use of artificial insemination for commercial purposes began in 1937, when the first artificial insemination cooperative was established in the US. Artificial insemination is still widely practiced today; approximately 60% of dairy cows in the US are bred by artificial insemination.

Spermatozoa extraction and storage

Although many different animals require different methods of artificial insemination, the basic premises remain the same. First semen must be extracted from the male. There are a variety of extraction techniques; however, most often a mechanical breeding mount containing an artificial vagina is used. In the case of dairy cattle, the bull is allowed to first mount a live cow, which is known as the teaser animal. The bull is allowed to repeatedly mount the teaser animal without ejaculating. After a few live mounts, the bull is now directed to an artificial vagina and ejaculation is allowed to take place. The teaser animal serves to increase the amount of viable sperm per ejaculation. After ejaculation, the sperm is collected and sperm sorting may be applied. The sperm is sorted into a male and female population by a flow cytometer, and is typically 90–98% accurate for most breeding species. Sperm sorting is primarily reserved for industries where one sex is more valuable, such as the dairy industry where females are required for milk production. Because one ejaculation contains exponentially more sperm than is necessary for fertilization, an extender solution is added to the semen for dilution and freezing purposes. Depending on the fate of the semen, the extender can be composed of a variety of ingredients. Extenders typically contain milk or egg yolk to protect against cold shock, cryoprotectants such as glycerol, buffers to protect against pH changes, and energy sources for the sperm such as glucose. It is also common for extenders to contain antibiotics to protect against contamination. Once the extender is added to the semen, the semen is frozen down in multiple plastic tubes known as straws. The straws are stored in liquid nitrogen at −196 °C until they are needed for insemination. These advances in cryopreservation of semen have greatly advanced the practice and prevalence of artificial insemination.

Insemination procedure

The female's estrous cycle must be continuously monitored to detect when the animal reaches her estrus phase and thus is ready for the insemination procedure. This estrus phase is also referred to as the 'heat phase' of the female because she is sexually receptive to males. Many behavioral and physical signs indicate the animal is in estrus. The most prominent sign is the standing position the animal assumes, which is referred to as 'standing heat.' This is a natural position the female assumes to be mounted by the male. Other physical indicators of estrus are swelling and reddening of the vulva, discharge of mucous from the vagina, and increased affectionate behavior toward other animals. Because ovulation occurs at the end of the estrus phase, the most efficient and effective time for sperm deposition is 12–26 h after the onset of estrus. This ensures that the sperm are viable in the uterus before ovulation occurs, which leads to a higher conception rate. To make breeding more efficient and simple, many cattle farmers practice estrus synchronization. Estrus synchronization is the practice of synching a female population's estrus cycles through the injection of natural and artificially synthesized hormones. Once the animal is ready for insemination the sperm must be properly thawed and loaded into the insemination catheter or gun. For most species, the sperm should be thawed to 36.7 °C for optimal results. It is also crucial that the sperm not be thawed for more than 10 min, as exceeding this threshold leads to infertile sperm. There are a variety of insemination techniques, and the ideal location for sperm deposition varies between species. Generally, depositions in the uterus lead to a higher conception rate versus deposition in the vagina and cervix (Dalton, 1999). Transcervical insemination is a common technique used among many animals and is

preferred because it does not require surgery. Transcervical insemination utilizes an endoscope to locate the cervix and then a catheter is passed through the cervix into the uterus for sperm deposition.

Advantages of artificial insemination

Artificial insemination has opened numerous doors for animal biotechnology in the past 80 years. Perhaps the greatest advantage conferred by artificial insemination is the ability to quickly pass desirable traits to many offspring. Artificial insemination is also extremely cost-efficient, as sperm can be collected and shipped all across the world. This reduces the need for many breeding grounds to house and maintain male animals. Not only does this reduce costs, but it also provides a safer environment because males can be aggressive and become a safety threat. Other advantages include higher conception rates, the elimination of many genital diseases, and more comprehensive records of animals.

In Vitro Fertilization

History of in vitro fertilization

IVF refers to the fertilization of an ovum by a spermatozoon outside of the body. Research on the possibilities of animal IVF began in the late 1800s, whereas the first attempts at animal IVF began in the early 1930s (Bavister, 2002). The first attempts used rabbit oocytes and spermatozoa, but were unsuccessful. In 1951 the discovery of sperm capacitation by researchers Austin and Chang explained why those initial experiments failed: Spermatozoa need to develop and undergo changes in the female reproductive tract before fertilization can occur (Bavister, 2002). This discovery enabled Chang to successfully fertilize rabbit oocytes *in vitro* using sperm that was capacitated *in vivo*. This led to the first mammalian IVF birth, a rabbit born in 1959 (Brackett, 2001). However, it was approximately 20 years later when the first successful mammalian IVF was performed using spermatozoa capacitated *in vitro*. Today, IVF is still being heavily researched and the full extent of its promises for animal biotechnology has not been reached. However, it has already greatly increased researchers' knowledge of animal reproductive mechanisms. Commercially, the bovine industry has seen the greatest impact from IVF. Hundreds and thousands of bovine embryos created via IVF are sold and exchanged worldwide each year.

Oocyte extraction and fertilization

Like every assisted reproductive technique, the actual mechanics will vary among species. Regardless of which technique is employed, five basic steps define IVF. They are (1) superovulation of the oocyte donor, (2) immature oocyte collection, (3) oocyte maturation *in vitro*, (4) mature oocyte fertilization, and (5) embryo development and growth *in vitro*. Superovulation is achieved in the donor animal through the injection of gonadotropins. Immature oocytes are typically collected in the form of cumulus–oocyte complexes (COCs) either from a live animal or from the ovaries at a slaughterhouse. If the immature oocytes come from a live donor animal, this is most often performed by a procedure called transvaginal oocyte recovery. Transvaginal oocyte recovery is a nonsurgical technique that employs an ultrasound probe, a vacuum pump, and a needle aspiration system to collect the COCs. Once the COCs are collected, they are placed into an oocyte maturation medium, which can contain numerous hormones and other reagents. This medium mimics the *in vivo* environment that induces meiosis of the oocytes, thus arresting them in metaphase II and preparing them for fertilization. Once the oocytes have matured, they are ready for fertilization. The oocytes must be washed before fertilization to ensure that all hormones and unwanted reagents from the maturation medium are removed. Likewise, the spermatozoa must also be purified from the extender and cryopreservation reagents if it came from a frozen straw. Finally, the spermatozoa are screened to ensure they are motile, and a capacitance-inducing medium is added to the spermatozoa. The prepared spermatozoa can be added to the mature COCs to initiate fertilization.

Culture of embryos

Once fertilization occurs, there are a number of different methods to culture the fertilized oocytes. Some species require that the 2–8-cell stage embryos be transferred to the oviduct of a live animal (Havlicek *et al.*, 2005). For *in vitro* culturing, there are numerous protocols that can be used. One method frequently used is a coculture in which the medium contains oviduct cells to replicate *in vivo* conditions. A sequential medium method is also commonly used, where the components of the media are changed depending on the cell stage of the embryos, mimicking the different chemical environments embryos experience as they mature *in vivo*. Many factors affect the development of embryos, including temperature, pH, and gas concentrations. Depending on the researchers' needs the embryos may be used for embryo transfer, the implantation of embryos into viable females, or cryopreserved for shipping or future use.

Embryo transfer in vitro fertilization

After being cultured for 7 days the embryos reach the blastocyst stage and are ready to be transferred to a recipient animal. It is crucial that the recipient animal's estrous cycle be synchronized to the current stage of the embryo. That is, if the embryo is 7 days old, the recipient animal must be close to her 7th day of estrous (Senger, 2003). This ensures that the environment of the uterus is suitable for attachment of the embryo and that proper embryonic development occurs. Embryos can be transferred into the recipient by surgical or nonsurgical means. Nonsurgical methods are preferred because they are quicker and less expensive. The most common form of nonsurgical embryo transfer utilizes a transfer pipette or loading gun to insert the embryo into the uterine horn. When transferring into a cow, the technician often reaches through the rectum to grasp the cervix to help guide the loading gun through. Epidural anesthesia is often used to relax the reproductive tract and make the embryo insertion easier. If the embryo successfully attaches to the endometrium, the recipient will become pregnant.

Advantages of in vitro fertilization and embryo transfer

Like artificial insemination, IVF and embryo transfer allow for the mass production of genetically superior progeny by

allowing females to produce more offspring. These technologies have allowed desirable female donors to produce up to 20 offspring each year. In addition, embryo transfer has allowed for genetically inferior females to be utilized for their birthing capabilities, serving as the recipient female. Embryo transfer also allows for the diversification of species within geographical regions, as embryos can be easily shipped across the globe. This is also a much more cost-efficient and bio-secure method compared to transporting live animals (Senger, 2003).

Embryo Flushing

Instead of fertilizing oocytes and culturing the embryos *in vitro* (as in IVF), embryos are often produced *in vivo* and then 'flushed' out of the uterus. In fact, embryo flushing is much more prevalent and cost-efficient than IVF for the production of embryos. Although the first successful embryo flush and transfer was performed in rabbits in 1890, the procedure is primarily done with cattle today. More cattle undergo embryo flushing each year than all other species combined. Embryo flushing is primarily accomplished by artificially inseminating a superovulated female donor with spermatozoa from a genetically superior male. The embryos are collected from the donor after fertilization occurs, typically within 6–8 days. Bovine embryo collection typically employs a Foley catheter, flushing medium, and a collection vessel. The Foley catheter is inserted into the uterus and the flushing medium is passed through the catheter. The catheter typically contains a small balloon that seals off the uterus and prevents the backflow of the flushing medium. The flushing medium is allowed to flow back out of the catheter and is collected in a vessel. Depending on the success of superovulation and fertilization, the flushing medium may contain 1–30 embryos. The typical yield for cattle that undergo superovulation and artificial insemination is 5–7 viable embryos (Senger, 2003). The embryos can be examined by a microscope for viability and transferred to a recipient or cryopreserved using the same methods previously discussed for IVF.

Advantages of in vitro *fertilization embryo production over embryo flushing*

Although embryo flushing is more cost-efficient than IVF, there are a handful of instances when IVF is preferred or necessary. IVF can generate embryos after the death of an animal by surgical extraction of the oocytes. Oocytes can remain viable for 9–12 h after the death of most species. IVF also must be employed when the female is infertile but still has functional ovaries, often the result of infectious diseases. Another cause of infertility in livestock species is the continuous injection of hormones into females. Many female animals may receive hormonal injections throughout their lifetime. This leads to the inability to generate embryos, but oocytes can still be collected.

An in vitro *fertilization technique: Intracytoplasmic sperm injection*

Intracytoplasmic sperm injection (ICSI) is a form of IVF that utilizes only one spermatozoon and one oocyte. Oocytes are first extracted by the transvaginal oocyte recovery procedure. Under high-powered magnification, the oocyte is held by a micropipette while the spermatozoon is injected into it. Once fertilization occurs, the zygote is allowed to mature *in vitro*. Although ICSI has only been around for the past 25 years, many domesticated animals have been reproduced through the procedure, including cattle, pigs, horses, and sheep (Horiuchi and Numabe, 1999). However, the procedure requires more expensive technology and labor than other assisted reproductive techniques, and therefore it is mainly used for research purposes. There are situations where ICSI is used for reproductive purposes, although it is primarily after standard IVF has not been effective. Standard IVF is typically ineffective when the spermatozoa are defective, either because they are nonmotile or cannot complete the acrosome reaction. ICSI remains an inefficient breeding technology and is not as reliable as standard IVF in most domesticated animals even though recent advances have made ICSI more successful. One such advance has been the use of piezo-actuated micromanipulation during ICSI. Piezo-actuated micromanipulation entails rapid and precise insertion of the spermatozoon in response to an externally applied voltage. Piezo-actuated micromanipulation has been shown to improve ICSI fertility in numerous species, including mice and cattle.

Cloning

History of cloning

Although recent advances have opened bountiful opportunities and discussions on animal cloning, cloning experiments have been taking place for more than 100 years. An animal clone is broadly defined as an animal that originates from another animal, and both animals share identical chromosomal DNA. Hans Dreisch created the first animal clones in the late 1800s. He created sea urchin clones by splitting a two-cell embryo and allowing both cells to independently develop into sea urchins. These embryo-splitting experiments continued into the 1900, led by the Nobel Prize winning Hans Spemman's work on salamander embryos. The next major advance came in 1952 when Robert Briggs cloned a frog using a new technique; he used nuclear transfer to transplant the nucleus of a blastomere from a frog embryo into an enucleated egg. Although Briggs showed embryonic nuclear transfer could produce clones, not many believed that adult somatic cells could be used as donors. However, in 1996 the largest breakthrough in animal cloning came in the form of a sheep named Dolly. Dolly became the first animal to be cloned using the nucleus of a differentiated adult cell as a donor. Dolly opened the door to cloning via somatic cell nuclear transfer (SCNT), and many other species have been cloned in the last few decades.

Somatic Cell Nuclear Transfer Procedure

Along Came Dolly

Dolly, the world's most famous sheep, became a sensation in 1996. Dolly was famous because she was the first animal clone that originated from an adult somatic cell. Scientists Ian Wilmut, Keith Campbell, and

their colleagues at the Roslin Institute in Scotland created Dolly from an udder cell of a 6-year-old Finn Dorset white sheep. The udder cell was inserted into an enucleated oocyte of a Scottish Blackface ewe. Once it is was confirmed that the embryo was undergoing normal development at day 6, it was inserted into a different Scottish Blackface ewe. In a sense you could say Dolly had three mothers. On 5 July 1996, 148 days after embryo transfer, Dolly was born as 'a normal vigorous lamb and was standing and sucking unaided within minutes.' When asked how Dolly got her name, Dr. Wilmut responded, 'Dolly is derived from a mammary gland cell and we couldn't think of a more impressive pair of glands than Dolly Parton's.' Out of 277 cell fusions, 29 embryos produced, and 13 surrogate mothers, Dolly was the only live offspring born from Wilmut's experiment. Dolly lived for 6 1/2 years and was euthanized on 14 February 2003. She suffered from an incurable disease known as sheep pulmonary adenomatosis (SPA). SPA is caused by a virus that induces lungs tumors in affected sheep. Dolly's death was not directly caused by her being a clone, as other sheep in Dolly's vicinity died from the same virus. In Dolly's 6 1/2 years she gave birth to 6 offspring, battled arthritis, and was found to have shortened telomeres. Dolly shattered the theory that differentiated cells lose their ability to develop into other cell types. Dolly proved that cell differentiation is not simply a one-way process, and most somatic adult cells are capable of being reprogrammed into any other cell type.

SCNT is now the primary method used in animal cloning. The procedure first begins by extracting oocytes from a female donor and allowing the oocytes to mature *in vitro*. Once an oocyte has matured the nucleus can be removed using a needle aspiration system. The enucleated oocyte is now ready to accept the donor cell. There remains healthy debate concerning whether the donor cell should undergo a serum starvation treatment before being inserted into the oocyte, as well as the significance of the type and age of the cell used. The serum starvation treatment arrests the donor cell in the G0 phase, stopping further division. Once a donor cell is selected it can be inserted under the zona pellucida of the oocyte. The two cells are fused together by a brief electrical stimulus, which is referred to as electrofusion. The developmental and directing factors of the ooplasm reprogram the somatic nucleus to develop into an embryo and eventually a blastocyst, after which it can be transferred into a recipient.

Current State of Animal Cloning

Cloning on the Wild Side

Some scientists are investigating the use of cloning technology as an option to save endangered species and even resurrect extinct ones. Russian and South Korean scientists have been working together to try to clone a woolly mammoth using cells recovered from 10 000 years old frozen remains of a baby woolly mammoth. The scientists plan to clone the mammoth by extracting nuclei from the frozen mammoth cells, transferring them to elephant eggs and stimulating the cells to start dividing. The resulting embryos would be implanted into elephant wombs for gestation.

Brazilian scientists also aim to clone endangered animals. A project designed by scientists from the agricultural research agency Embrapa, together with the Brasília Zoological Garden, will attempt to clone and hybridize jaguars, collared anteaters, maned wolves, and other endangered species. Somatic cells and spermatozoa from eight threatened species have already been collected. The researchers must now receive permission from the government to conduct experiments on the 420 samples already collected. Several environmentalists are concerned about this project because these cloned, hybridized, and captive-bred animals, if mixed with wild populations, could result in potential environmental risks. However, the project was specifically designed to supply zoos rather than replenishing wild populations.

The cloning of endangered species has raised several issues between conservationists and environmentalists, who say that instead of cloning to save these species, more efforts to protect and recover their natural habitats should be made. They believe that conserving the natural habitat where these animals live would have a greater impact on the preservation of these species.

The potential advantages of cloning are innumerable for many industries including agriculture and biomedical research. However, the field is still relatively new and needs extensive research to make animal cloning more efficient. Cloning efficiency is defined as the number of live offspring per embryos transferred. Currently, the efficiency rate for cattle is 6–15% and 6% for pigs. However, for some animals the efficiency is as low as 1–2%, whereas others still have not been successfully cloned (Fiester, 2005). Although cloning efficiency has improved in the past 10 years, these proportions are still substantially lower than other reproductive techniques. In addition, some clones are born with phenotypic abnormalities. The most common abnormality is an unusually increased birth weight, known as large offspring syndrome (LOS). LOS causes difficulties in the birthing process, as well as other health risks for the animal, such as organ defects and diabetes. These abnormal phenotypes are not transmitted to the clone's offspring, which suggest *in vitro* conditions alter the epigenetic patterns of the cloned embryo, as these patterns are reprogrammed during gametogenesis (Prather *et al.*, 2004). These *in vitro* conditions are being studied to help improve efficiency and reduce abnormalities in animal cloning, as a number of biological factors are known to influence the reprogramming of the nucleus.

Production of Transgenic Animals

Inserting human genes into an animal's genome allows animals to produce important human proteins, such as the blood clotting agent factor IX. However, the methods for producing transgenic animals are not very efficient. Incorporation rates of the new gene into their genome are low and occur at random sites which often do not allow the gene to be expressed. Also, the insertion can cause disruption in the expression of another gene. Researchers at the Roslin Institute sought to use cloning as an efficient way to produce transgenic animals. In theory, once a cell line successfully incorporates and expresses a transgene, that cell line can be used as a donor cell for cloning. The clones produced will have the transgene incorporated into their genome and can successfully pass it to their offspring through traditional breeding methods. This could lead to entire herds of transgenic animals expressing important genes for medical and agricultural purposes. Transgenics and cloning also hold enormous potential for

producing organs in animals for human transplants, or xenotransplantation. If animals can be modified to produce viable organs for humans, cloning could drastically increase the human organ supply.

Genome Editing

Precision Editing Opens a World of Possibilities for Transgenics

The precision of nuclease-based genomic editing can lead to custom designed animals with improved traits and modifications to better serve as human disease models. Cow's milk allergy (CMA) is an immunologically mediated allergic reaction to certain proteins in cow's milk. The CMA-inducing protein beta-lactoglubulin causes diarrhea and vomiting in children. It is estimated that the prevalence of CMA varies between 0.25% and 4.9% and is higher in children than in adults. For the last few decades researchers have been trying to create transgenic cows that produce beta-lactoglobulin-free milk, but have been unsuccessful because of a lack of precision associated with gene editing. Recently researchers found a gene encoding microribonucleic acid (miRNA) in mice that targets beta-lactoglubulin mRNA and silences its production. This technology is known as RNA interference (RNAi), and it allows for the elimination of beta-lactoglobulin protein without needing to alter the gene itself. After successfully inserting the miRNA gene into the genome of cow embryos, one calf was born that produced beta-lactoglobulin-free milk.

Although RNAi is effective at silencing genes, it cannot eliminate the protein completely. Transcription activator-like effector nucleases (TALENs) are artificial restriction enzymes created by the fusing of a DNA binding domain with a DNA cleavage molecule. TALENs work by cutting DNA at specific sequences, introducing double-stranded breaks into a gene of interest. When the cells repair the breaks they introduce mutations into the gene that can render the gene nonfunctional. In pigs, TALENs have been used to disrupt genes encoding low-density lipoprotein (LDL) receptors. Pigs lacking these receptors are unable to remove LDL from the bloodstream, causing them to develop atherosclerotic arteries. Such pigs can be used as disease models to aid biomedical research in human atherosclerosis.

Many transgenic technologies are inefficient because they involve nonspecific integration of the transgene into the target genome. In contrast, nuclease-mediated genome editing results in a specific integration. The method relies on the use of artificial proteins made up of customizable, sequence-specific DNA-binding domains fused to a nuclease that cuts DNA in a nonsequence specific way (Joung and Sander, 2013). Zinc-finger nucleases (ZFNs) and recently, TALENS are employed in performing targeted genome editing. ZFNs and TALENS can be described as molecular scissors that cleave double-stranded DNA at a specific site in a predetermined sequence of the genome. The cleavage triggers DNA repair that can be exploited to modify the genome either by targeted introduction of insertions and deletions (gene disruption), base substitution specified by a homologous donor DNA construct (gene correction), or the transfer of entire transgenes into a native genomic locus (Urnov *et al.*, 2010). This new technique has the potential to be used in many applications including therapeutic approaches to treat genetic disease, production of model organisms, and generation of new agriculturally relevant varieties.

Transgenic Technologies for Food and Other Products

Transgenic Animals Can Provide New and Improved Products

Farmers have been using selective breeding to increase desirable traits in agricultural animals since the dawn of domestication. However, the increased production potential possible from traditional selective breeding practices is limited. Advances in molecular biology have made it possible to develop traits in animals quicker and with more precision, allowing farmers an alternative means to increase yields, improve the nutritional value of food products, make animals resistant to diseases, and produce human pharmaceuticals in the milk of transgenic cows, goats, pigs, or rabbits. Some transgenic animals already have been approved by the Food and Drug Administration (FDA) for production of nonfood products, and the AquAdvantage® salmon is close to becoming the first transgenic animal approved by the FDA for human consumption (at the time of publication).

Less smelly pig

From Egg to Plate in Half the Time: Speedy Salmon Promise Profit

AquAdvantage® Salmon are in line to become the first genetically engineered (GE) nonplant food source approved for human consumption by the US FDA. This accomplishment is the culmination of more than 20 years of work, which began during a coffee break. One winter day in the 1980s, when Dr. Choy L. Hew, who studied an antifreeze protein that allows fish to survive subzero temperatures, was chatting with his colleague, Dr. Garth Fletcher. Fletcher was frustrated because he just returned from a fish farm where all the salmon had frozen to death and he challenged Hew to use his molecular biology to do something about this problem. Having limited success enhancing the cold tolerance of the salmon, they altered the plan to increase the growth rate so that they could be harvested before the onset of winter cold. They GE the salmon by attaching the antifreeze protein promoter to the growth hormone gene, causing growth hormone to be produced during the winter months, allowing the salmon to grow year round. They saw the first fast-growing fish in the summer of 1990, and received a patent in 1996. In the same year they met Elliot Entis, who was running his father's wholesale seafood business, at an academic conference. Entis showed a great interest in the fast-growing salmon. He licensed their technology and started A/F Protein. The company, now called AquaBounty Technologies, brought the AquaAdvantge Salmon to a marketable stage. These fish outgrow any wild or farm-raised salmon, and can grow from the egg stage to market weight in 16–18 months, as opposed to 3 years for traditional salmon. The AquAdvantage® salmon are waiting on final approval of the FDA while environmental issues are studied.

One goal of current research is to create transgenic farm animals that are more environmentally friendly. At the University of Guelph in Canada, for example, transgenic pigs have been developed with the issue of manure-related environmental pollution in mind. Referred to as the EnviroPig, this transgenic pig is capable of digesting phosphorus in plants more efficiently than conventional pigs. The EnviroPig contains a bacterial phytase gene controlled by a salivary-gland-specific promoter, which limits the production of phytase to the saliva. Phytase is an enzyme that releases

phosphate from phytate, which accounts for up to 80% of phosphorus content in most feeds. The ability to digest plant phosphorus limits the need for costly feed supplements such as phosphate minerals or commercially produced phytase. In addition, the EnviroPig excretes 30–70% less phosphorus in its waste than conventional pigs. This is environmentally important, as excess phosphate from manure alters the local water environment, causing increased algae growth, production of greenhouse gases, and the death of fish and aquatic animals. The lower levels of phosphorus in pig feces reduce water pollution. The hope for this project was to be able to market the EnviroPig as a more environmentally friendly option with reduced feed costs. The university has applications with Health Canada and the US FDA for the EnviroPig to be approved for human consumption. According to the company website, in 2012, Ontario Pork decided to redirect its research dollars, ending its funding of the EnviroPig program, and the remaining EnviroPigs were euthanized. Ontario Pork's Director of Communications and Consumer Marketing Keith Robbins said of the decision to stop funding of the EnviroPig, "we sort of felt that we weren't getting the kind of return that was originally looked at in concept of that product." The decision ultimately was because of the lack of public demand for genetically modified animals in the food system.

GloFish: GM Pets That Brighten Homes and Hearts

In 2003, Yorktown Technologies created a genetically modified pet. The GloFish®, a fluorescent red zebrafish, has become the first transgenic animal commercially available in the US and a really popular aquarium item. The GloFish is available in five fluorescent colors with the exciting names – Starfire Red®, Electric Green®, Sunburst Orange®, Cosmic Blue®, and Galactic Purple®.

The original zebrafish (*Danio rerio*), from which the GloFish was developed, is native to India and Bangladesh. Because the GloFish was developed from a tropical fish and cannot survive in the colder US waters, it is believed that these GE zebrafish pose no risk to the environment. Because GloFish pose no risk to the environment or entering the food supply, the FDA decided not to regulate these transgenic animals. However, although the GloFish is permitted in the US, the sale of this GM pet is not allowed in the state of California.

The fluorescent zebrafish was primarily developed with the aim to detect pollution by selectively fluorescing when in the presence of environmental toxins. This first fluorescent fish was created in 1999, when Dr. Zhiyuan Gong and his team at the National University of Singapore (NUS) were working with the green fluorescent protein (GFP) gene extracted from jellyfish, which naturally produced bright green fluorescence. This gene was then inserted into a *Danio rerio* embryo and integrated into the zebrafish's genome, allowing the fish to be fluorescent under natural white light and ultraviolet light. Sometime later, these scientists made a deal with Yorktown Technologies to develop the GloFish®.

Although GloFish® pose no risk to the environment, a new variety of the GloFish introduced in February 2012 has raised some concerns. The Electric Green Tetra, a GE black tetra fish, includes genetic material from a fluorescent coral that makes it neon-bright and makes the fish fluorescent when placed under a black light. Some environmentalists and experts are concerned about the new black tetra. If released, this South American fish would be able to survive in the waters of South Florida and Latin America, where they could pose potential environmental risks and have an undesirable influence on natural biodiversity.

More – and better – meat on their bones

The ability to produce transgenic pigs and cattle with enhanced muscle growth is an area of increasing interest. Researchers have been studying the effects of targeting myostatin, the only secreted protein known to negatively affect muscle mass *in vivo*, as well as genes for growth-related hormones and lean muscle mass (Long *et al.*, 2009). Transgenic myostatin knockout cows have been produced in the US; however, there are concerns regarding the increased neonatal morbidity that arises from giving birth to larger calves with increased fetal muscle mass (Tessanne *et al.*, 2012). Currently no myostatin knockout pigs have been developed; however, transgenic pigs for growth-related hormones have been produced. Although they show improvement in growth rate, feed conversion and body fat/muscle ratios, they also showed signs of fatigue, gastric ulcers, and low libido. Transgenic pigs containing insulin-like growth factor-1 and a desaturase gene from spinach have been shown to have increased growth rates and increased levels of polyunsaturated fatty acids, respectively. These new developments come without the negative side effects of previous transgenic pigs. In addition, researchers at the University of Illinois have produced transgenic pigs expressing bovine α-lactalbumin, which leads to an increase in milk production (Wheeler *et al.*, 2001). This increase in milk production was shown to increase the weight gain of piglets suckling from the transgenic gilts compared to control gilts. Gilts are female pigs that have had no more than one litter. When pigs give birth to a second litter, they are referred to as sows. These technologies allow for the decreased use of less effective techniques, such as growth hormones whose residues can be found in the final animal product. Despite these advances, none of these transgenic animals have been approved for human consumption.

Omega-3 fatty acids are found mainly in fish oils and largely considered beneficial to human health. Conventional meat products contain large amounts of omega-6 fatty acids, and low levels of omega-3 fatty acids. Diets with a high omega-6/omega-3 fatty acid ratio are correlated with coronary artery disease, cancer, diabetes, arthritis, and depression. To try and create a healthier balance, researchers have recently developed transgenic pigs and cows containing high levels of omega-3 fatty acids in both their tissue and milk (Lai *et al.*, 2006; Wu *et al.*, 2012). This was done by inserting a gene encoding for an omega-3 fatty acid desaturase into the genome of the pig and cow. Omega-3 fatty acid desaturases are enzymes required for the conversion of omega-6 fatty acids to omega-3 fatty acids. The end result is an increase in omega-3 fatty acids and a decrease in omega-6 fatty acids, thus creating the potential for meat and dairy products with a healthier omega-6/omega-3 ratio.

Not your mother's milk

A team of scientists at AgResearch and the University of Waikato in New Zealand has successfully produced a transgenic cow lacking β-lactoglobulin (BLG) (Jabed *et al.*, 2012). This whey protein is believed to be the main cause of milk allergies in humans, and knocking out this gene could allow for the production of hypoallergenic dairy products. The researchers use miRNA technology to silence the expression of BLG in the milk, making it potentially less allergenic. In addition, high casein levels were reported in the BLG-deficient milk. Casein

makes up 80% of milk protein in conventional cows and is an extremely valuable component of milk because of its nutritional value and processing properties. The increased casein levels associated with this BLG knockout cow could provide increased calcium levels and higher cheese yields. In addition, another group in New Zealand has produced transgenic cows containing additional β- and κ-casein genes (Brophy *et al.*, 2003). These cows have been shown to produce milk with a twofold increase in κ-casein, and up to 20% increase in β-casein levels. The increase in κ-casein has been associated with improved heat stability and cheese-making properties, whereas increased β-casein has been associated with increased milk calcium levels and whey expulsion.

In addition to cows, there is much interest in producing transgenic goats to create healthier milk for human consumption. For instance, changes in the fatty acid composition of milk produced by goats containing a transgene encoding a stearoyl-CoA desaturase (SCD) enzyme has been reported (Reh *et al.*, 2004). SCD works by converting saturated fatty acids into monounsaturated fatty acids. Because one-third of saturated fatty acids in American diets come from dairy products, and saturated fatty acids can lead to increased blood cholesterol levels, leading to increased risk of atherosclerosis and coronary heart disease, the decreased level of saturated fatty acids in milk is an important heath concern. The SCD transgenic goats were shown to have increased levels of monounsaturated fatty acids as well as decreased levels of saturated fatty acids, which could prove to have increased health benefits compared to milk from conventional animals.

Baa baa, transgenic sheep, have you any wool?

Green Pigs Light the Way for Biomedical Research

Dr. Randy Prather is a professor of reproductive biotechnology at the University of Missouri. He has been involved in the push for transgenic pigs in biomedical research, having produced both GFP and yellow fluorescent protein (YFP) transgenic pigs. These pigs contain a GFP gene that comes from a jellyfish, and is commonly used as a molecular marker because it is easily visible under ultraviolet light. Dr. Prather summarizes the importance of this work, saying 'these animals prove that we can make genetic modifications to express desired traits. For xenotransplantation, this is a large step because it means it's possible to change the genetic makeup of the cells to prevent the body's rejection of transplanted organs. However, not everyone is excited about these technological advancements. Kathy Guillermo, a spokeswoman for people for the ethical treatment of animals, believes that transgenic animal experiments like these are unethical and of little use. "On one level, we're just opposed to it period because it's the treatment of animals like objects," Guillermo said. "On another stance, we see it as bad science." Regardless, Dr. Prather and other researchers around the world are hoping transgenic animal models like the GFP and YFP pig will result in advances in the fields of agriculture and biotechnology. "Application of this technology can help feed an ever-growing population, and it can have tremendous potential to alleviate human suffering," Prather said.

In addition to products for human consumption, there are a number of other new, as well as improved products transgenic animals could be utilized for. Increased wool growth in transgenic sheep has been achieved in New Zealand by introducing an insulin-like growth factor-1 gene associated with a keratin promoter (Damak *et al.*, 1996). The keratin promoter allows production of the transgene in the skin and results in an increase in the production of clean fleece weight to conventional sheep. Although no health issues were observed in the transgenic sheep, the staple strength of the wool produced by the male transgenic sheep was lower than that of female transgenic and nontransgenic animals. Further research could result in herds of transgenic sheep capable of higher wool yields than conventional sheep, potentially lowering costs for farmers.

Silk in milk

Transgenic goats are also being produced for dragline silk in their milk. Dragline silk is made by orb spiders and is the strongest known material by weight. Because of its strength as well as its elasticity, there is much interest in large-scale production of dragline silk for use in military uniforms, medical sutures, and tennis racket strings. After failing to produce the material in bacteria and mammalian cell culture, scientists in Canada have successfully inserted the spider silk genes into goat embryos. When the transgenic goats matured, the spider genes were expressed in the mammary glands of females, which began to secrete tiny strands of spider silk in their milk. Once protocols are in place for the purification and spinning, the resulting thread could be used for a number of commercial as well as medical applications.

Biopharming: Transgenic Animal Advances in Medicine and Research

Transgenic animals not only have potential to improve agriculture, but could also lead to significant breakthroughs in biomedical research. For decades proteins such as insulin and human growth hormone have been produced in bacteria and yeast cultures. However, proteins such as blood clotting factors and monoclonal antibodies require complex folding patterns and additional sugar molecules to become biologically active. These sophisticated modifications require the proteins be produced in mammalian cells to be carried out properly, thus showing the limitations of *in vitro* bacterial culture techniques to be able to produce complex proteins. Some examples of transgenic animal systems that are currently being researched include milk, blood, and egg whites.

Complex Protein Production

Transgenic animals in biomedical research can aid in the production and subsequent collection of insulin, growth hormone, blood anticlotting factors, and other biological products in the milk of cows, sheep, and goats. Dairy cows, for example, have a yearly milk output of approximately 10 000 l, making it possible for a single-lactating cow to produce tens of kilograms of therapeutic proteins. Relatively small herds of a few hundred lactating transgenic cows or goats can produce several hundred kilograms of purified protein per year. In fact, it has been estimated that only 60 transgenic pigs would be needed to supply the entire factor IX protein required in the US. This is referred to as biopharming, and is gaining momentum as a potential route for the production of products for medical use.

The first therapeutic protein produced in the milk of transgenic animals to be approved for human use was antithrombin, an anticoagulant protein that can treat patients with a congenital deficiency. GTC Biotherapeutics (Framingham, MA) markets recombinant antithrombin purified from the milk of transgenic goats. In 2006, the European Medicines Agency approved the drug and then in 2009, the US FDA also gave approval. In addition, the production of transgenic pigs whose milk contains human factor VIII and IX, hemoglobin, human protein C, human erythropoietin, human granulocyte-macrophage colony stimulating factor, and Von Willebrand factor are being researched.

In 1997, the first transgenic cow was produced whose milk was enriched with the human protein α-lactalbumin. The transgenic milk, being more similar to human breast milk, is more nutritionally balanced than natural bovine milk and could be given to babies or the elderly with special nutritional or digestive needs. In addition, cows have been produced that secrete human lactoferrin, a glycoprotein involved in innate host defense, in their milk (Van Berkel *et al.*, 2002). Because of lactoferrin's antibacterial, antifungal, antiendotoxin, and antiviral activities, a number of medical uses for this glycoprotein have been considered, such as the treatment of infectious or inflammatory diseases. The ability of these researchers to produce and purify human lactoferrin from the milk of these animals shows the potential of transgenic animals for large-scale production of biopharmaceutical products.

Human Disease Models

An area of biomedical research that has huge potential for transgenic animals is their use as human disease models. Although mice have traditionally been used as the go-to animal model for human diseases, many of the breakthroughs in mice have not translated to humans. Because of their similar size and physiology, there has been increasing interest in using pigs as human disease models. Conventional pigs are already used to study cardiovascular disease, atherosclerosis, cutaneous pharmacology, wound repair, cancer, diabetes, and ophthalmology. Using transgenic technology, pig models are currently being produced for such diseases as Alzheimer's disease, cystic fibrosis, retinitis pigmentosa, spinal muscular atrophy, diabetes, and organ failure (Aigner *et al.*, 2010). Once these animal models have been characterized, new drugs and therapies can be tested before clinical trials.

Xenotransplantation

An estimated 45 000 Americans under age 65 could benefit from a heart transplant each year, but only approximately 2000 human hearts are available. To close this gap, researchers have begun to study xenografts, the transplanting of organs and tissues from animals into humans. Although nonhuman primates such as chimpanzees are genetically closest to humans, reducing the chances of graft rejection, primates are endangered in the wild and their use as a source of replacement organs raises ethical concerns because of their high level of intelligence and the increased risk of disease transmission between such closely related species. As an alternative, some have proposed using pigs as a source of organs because they have large litters, a short gestation time, are anatomically and physiologically similar to humans, are already produced in high volume as a food source, and are currently used to provide some replacement tissues such as heart valves.

Xenotransplantation would have to overcome many technical and ethical obstacles before it can become a reality. One of the first technical issues researchers have focused on are the antigens on the surface of pig cells. These surface antigens are similar to the ABO blood group antigens that trigger severe immune responses called hyperacute rejection. To address this, scientists have inserted human genes into single-cell pig embryos in an attempt to make their cell-surface proteins more similar to human ones so the tissues are no longer antigenic. However, even if this procedure reduces the risk of hyperacute rejection, other immunological barriers to xenotransplantation, such as acute humoral xenograft rejection, thrombotic microangiopathy, and coagulation dysregulation still exist.

In addition, there are concerns of cross-species infections caused by exogenous viruses, such as porcine cytomegalovirus, present in the xenotransplanted organs (Fishman and Patience, 2004). In 1997, Robin A. Weiss, a virologist at University College London, discovered a new class of pig viruses called porcine endogenous retroviruses (PERVs) and determined that they have the ability to infect cultured human cells. The transplantation of a pig organ into a human host would therefore create the opportunity for the transmission of PERVs, potentially enabling such viruses to evolve into human pathogens. Retrospective studies of patients who received heart valves from pigs identified the DNA of PERVs in some recipients. Therefore there is real concern that xenografts from pigs could provide a path for the transmission of novel viruses from animals to humans. Until this issue is resolved definitively, clinical trials of xenotransplantation are unlikely to move forward.

Transgenic Animals with Increased Disease Resistance

The ability to enhance disease resistance in animals holds enormous potential for the continuing field of animal biotechnology. Currently, numerous studies are being performed to induce disease resistance in a variety of animals. Some of the diseases being studied include mad cow disease, foot and mouth disease (FMD), porcine reproductive and respiratory syndrome (PRRS), and avian influenza viruses (AIVs).

Mad Cow Disease

Mad Cow Disease, or more formally bovine spongiform encephalopathy (BSE), is a specific type of a transmissable spongiform encephalopathy (TSE). TSEs are progressive, degenerative diseases of the brain, spinal cord, and central nervous system. They are also characterized by a long period of time between infection and detectable symptoms. The abnormal folding of the prion protein (PrP) is thought to cause TSEs. Abnormally folded PrPs can be transmitted and cause host PrPs to adopt abnormal configurations. Although the first TSE identified in cattle was in 1986 (BSE), TSEs have been documented in a variety of species (Wells *et al.*, 1987). The

human form of the disease is called Creutzfeldt–Jakob Disease (CJD), which was first characterized in 1920. However, scientists linked a new variant of CJD to BSE in 1996. Owing to the seriousness of the disease and the public health concerns, many studies are underway to induce resistance to these prion diseases. The primary method for inducing resistance is to silence the PRNP gene, which encodes for the normal PrP. These knock out studies, performed in cattle and mice, have shown that animals without the PrP are unable to produce and transmit the infectious form of the protein (Büeler *et al.*, 1993; Hirata *et al.*, 2004; Richt *et al.*, 2007).

Foot and Mouth Disease

FMD is a highly contagious disease that infects cloven-hoofed animals (those with divided hoofs). The pathogen responsible for FMD, foot and mouth disease virus (FMDV), is easily transmitted through direct contact, aerosols (air-borne), and ingestion. The virus also replicates rapidly once inside the host, and symptoms typically appear with 2–3 days. There are a variety of symptoms, but lesions on the tongue and feet characterize the virus. The virus is typically only lethal for younger animals. FMD poses enormous economic losses on the global livestock and trade industries. Not only does FMD wipe out herds of animals, many countries refuse to trade livestock with countries that experience FMD epidemics. Currently, vaccines provide the primary method to induce resistance to FMD. Researchers have recently created entirely synthetic vaccines to protect against FMD. However, vaccines remain problematic for eradicating FMD because of the fact there are more than 7 serotypes and more than 60 strains of the virus. This has sparked many studies that explore producing transgenic livestock that are resistant to FMD. Multiple studies have shown that RNAi is a viable antiviral strategy *in vitro* and *in vivo*, either through the use of small interfering RNAs (siRNAs) or short hairpin RNAs (shRNAs) (Haasnoot *et al.*, 2003; Grubman, 2005). Currently, no siRNA or shRNA transgenic livestock have been produced that are resistant to FMD, although many studies are being performed.

Porcine Reproductive and Respiratory Syndrome

PRRS is a viral disease that affects swine. PRRS is the largest economic hurdle the US swine industry faces, as the virus costs the industry approximately US$600 million each year. The two primary symptoms of PRRS are reproductive failure and respiratory complications for younger animals. The porcine reproductive and respiratory syndrome virus (PRRSV) is most often transmitted through direct contact, often appearing in high concentrations in semen, urine, feces, mammary secretions, and nasal secretions. Vaccines have been developed to help control the spread of PRRS, but the efficacy of the vaccines vary. The reason many vaccines are not effective is the virus's ability to generate a high degree of genetic diversity and its remarkable ability to evade host defenses. Owing to the unreliability of vaccines, other methods are being studied to control the disease. Some studies are focused on creating breeding programs that only breed swine with a high resistance to PRRS. Other studies are focused on creating transgenic pigs that are resistant through RNAi.

Avian Influenza Viruses

AIVs are a very diverse group of viruses that infect a wide variety of birds. However, because of their high rate of mutation, AIVs can also infect other species, such as humans. One example is the AIV strand H5N1. This is a fatal strand that can infect humans and many other species. These human health risks have sparked research into creating disease resistant fowls. Transgenic studies are at the forefront of this field. Transgenic chickens that are unable to transmit AIVs to other birds have recently been produced. This is a monumental achievement for genome editing and disease resistance.

Antimicrobials

The immune system of newborn piglets is immature, and thus they are susceptible to many bacterial infections, some of which cause diarrhea. These infections can also significantly reduce newborn survival rate. Although it is common to use antibiotic feed additives for newborns, this has led to a drastic increase in the number of antibiotic-resistant bacterial strains. This has required alternative approaches to prevent bacterial infections in piglets. Transgenic approaches offer great promise. Transgenic goats have been produced that make milk with the same concentration of lysozyme, the natural antimicrobial agent, as human breast milk (Brundige *et al.*, 2008). This milk was fed to piglets and it helped protect against *Escherichia coli* and improved gastrointestinal health. Transgenic cattle have also been produced that make human lysozyme and milk in their milk so that it is nutritionally similar to human breast milk.

Antimicrobial peptides (AMPs) exhibit another crossroad of transgenics and disease resistance. Cecropin B, the AMP that originates from the giant silk moth, has many antimicrobial effects. Many of these antimicrobial effects are against gram-negative bacteria. The gene encoding for cecropin B was transfected into catfish and the Asian medaka fish. Both transgenic fish breeds showed increased bacterial resistance to numerous pathogens.

Biotechnology Enhances and Advances Selective Breeding

Genetic Screening of Breeding Stock

Traditional animal breeding (TAB) exploited variations that existed within breeds and animal populations to bring about genetic improvement in traits of economic importance such as milk yield, growth traits, and egg numbers. TAB has been very successful over the years by utilizing records of the phenotype of an animal and a number of its relatives to estimate the likelihood that an animal will pass on its good traits to its offspring. An obvious example of the success of TAB is the doubling of dairy cow milk yields over the past 40 years (Oltenacu and Broom, 2010). However, for traits that are difficult to measure such as disease resistance, fertility, and feed efficiency, these traditional breeding methods have not been successful.

Genomics on the Dairy Farm: More Accuracy and Less Expense

Older pedigree tests used by the US Department of Agriculture (USDA) Animal Improvement Programs Laboratory were based on rating the genetic fitness of dairy cows by analyzing milk production records and assessing the quantity of certain cells in the cow's udder. Over the past 30 years, farmers and companies have selected for the best dairy cows using these tests. These tests can predict the genetic merit of a cow with 30% accuracy at birth. Breeders used the milk production records of a bull's relatives (mother, aunts, sisters, and daughters) to select good bulls to mate with their best dairy cows. Farmers with good bulls had to pay $50 000 for their bulls to be evaluated by breeding companies, and the breeding companies would create a detailed pedigree showing the bull's ancestry. However, in November 2006 the development of a new test based on genetic markers started. Led by Van Tassel, the USDA has determined approximately 38 000 genetic markers that aid in identifying cows that have the best genes for milk production and pass these genes to their offspring. A small single nucleotide polymorphism (SNP) chip can be used to track these 38 000 genetic markers in cows. This new genetic test can predict the genetic merit of a cow with 70% accuracy, compared to only 30% accuracy using traditional pedigree tests. Furthermore, instead of farmers paying US$50 000 for their bulls to be evaluated by breeding companies, it now costs only US$250.00 to genotype the bulls using this new genetic test.

The idea of using marker-assisted selection (MAS) to overcome the shortfalls of TAB has been around since 1923. MAS is the selection of traits of interest indirectly by selecting genetic markers associated with desired qualities, as opposed to traditional methods of finding desired qualities by observing phenotypic traits. Sax (1923) observed an association between seed color and seed weight and concluded that the gene controlling seed color must be linked to genes that control seed size. Thoday and Boam (1961) attempted to map and characterize polygenes affecting sternopleural chaeta number in *Drosophila melanogaster*. By estimating breeding values based on marker, pedigree and phenotypic information, MAS can bring genetic improvement in traits of animals where TAB alone has failed. In a French MAS program in dairy cattle, estimated breeding values (EBVs) using MAS for all traits considered were more reliable than EBVs estimated from classical selection methods (Guillaume *et al.*, 2008), demonstrating that MAS may lead to increases in genetic improvement as compared with traditional breeding methods.

Beginning in the late 1970's many molecular genetic markers were discovered and developed, including allozymes, restriction fragment length polymorphisms (RFLP), random amplified polymorphic DNA (RAPD), microsatellite DNA and SNPs. The ability to analyze these markers was developed over several decades and has made the mapping of quantitative trait loci (QTL) feasible on a large scale (Brumlop and Finckh, 2010). Out of these genetic markers, SNPs are currently the marker of choice because of their large numbers spaced across the genome. The decreasing cost and rapid progress in next-generation sequencing methods that employ massively parallel approaches in sequencing several hundred thousands to millions of reads simultaneously have led to the identification of many SNPs in livestock species. SNP arrays containing tens of thousands of SNPs distributed throughout the genome are now available for several livestock species (Table 2) and support the interrogation of hundreds of loci at a low cost.

Table 2 Available single nucleotide polymorphism (SNP) chips developed for some animal species

Species	*Identification*	*Provider*	*Number of SNPs*
Cat	Feline	Illumina	62 897
Horse	Equine	Illumina	65 157
Sheep	Ovine	Illumina	5 409
Cattle	BovineHD	Illumina	777 962
Cattle	BovineSNP50v2	Illumina	54 609
Cattle	BOS 1	Affymetrix	648 000
Sheep	OvineSNP50	Illumina	52 241
Cattle	BovineLD	Illumina	6 909
Pig	PorcineSNP60	Illumina	62 163
Dog	CanineHD	Illumina	173 662

Abbreviations: HD, high density; LD, low density.
Source: Reproduced from Eggen, A., 2012. The development and application of genomic selection as a new breeding paradigm. Animal Frontiers 2 (1), 10–15.

A disadvantage in the implementation of livestock MAS is that population-based, genome-wide association studies are unable to detect SNPs associated with a trait if the desired allele has a frequency below 5% or 1% (Brookfield, 2010). Additionally, MAS requires prior knowledge of markers that are associated with traits. Many markers are now known across the genomes of many livestock species, including cows, sheep, and pigs. Genomic selection, as initially proposed by Meuwissen *et al.* (2001), can use all these markers simultaneously to predict the genomic estimated breeding value (GEBV) for traits of animals without needing to know the location of genes in the genome.

Risks and Regulations

As with any foray into a new area of technology, there are several concerns about the use of animal biotechnology in agriculture and biomedical research. There is concern that food products derived from transgenic or cloned animals may pose risks to human health. There are also concerns about potential impacts of animal biotechnology on the environment and on animal welfare, as well as questions about whether the current regulatory structure is adequate to evaluate and control the risks associated with these technologies. Animals pose unique challenges compared to plants, as there is greater concern for the welfare of animals. Animal biotechnology, as well as its regulatory system, has been subjected to increasing attention and discussions among research scientists and the public. (About Bioscience; Animal Biotechnology: Science-Based Concerns, 2002; Cowan, 2010).

Human Health Concerns

Cloned and GE animals can be used as a source of tissues and organs for xenotransplantation and for production of biopharmaceuticals (Animal Biotechnology: Science-Based Concerns, 2002). Although xenotransplantation offers many

benefits, there are some risks including infection and rejection. Recipients of xenotransplantation risk direct exposure to recognized and unrecognized infectious agents such as prions, virus, or bacteria. Additionally, there is potential for future generations to become infected through vertical transmission (transmission of an agent from an individual to its offspring). Secondly, immunologic barriers associated with the use of xenografts are a concern, as in all allograft procedures. Although immune suppression therapies exist, hyperacute rejection is not always blocked (About Bioscience; Animal Biotechnology: Science-Based Concerns, 2002; Medscape).

The use of transgenic animals for the production of biopharmaceuticals for human health purposes has also raised several concerns. First, there is the potential risk of the generation of pathogenic viruses by recombination of vector sequences and related nonpathogenic viruses present in the same animal. The second concern is the possibility that surplus animals or their offspring inadvertently entering the food chain (Animal Biotechnology: Science-Based Concerns, 2002).

Food Safety Concerns

Concerns around all food and food products are based on the concept that they should be free of chemical or biological agents that can affect the safety of the food for the human or animal consumer (Animal Biotechnology: Science-Based Concerns, 2002; Kochhar and Evans, 2007). In 2001, the US producers agreed to keep food products from cloned animals or their offspring out of the food chain until the FDA could evaluate the risks. In 2008, the FDA released their report, which stated that meat and milk from cloned cattle, swine or goats or their offspring are as safe to eat as conventionally bred animals (Cowan, 2010, 2011; Bazer *et al.*, 2010).

Potential food safety concerns about products derived from GE animals, are mainly related to transgene expression. These transgenes could cause proteins to be present in food that could be allergenic, toxic, or have other antinutritional or/and other physiological effects. These concerns are considered a moderate-level concern of food safety and vary according to the gene product, the food product, and the consumer (Animal Biotechnology: Science-Based Concerns, 2002; Kochhar and Evans, 2007).

Animal Health and Welfare Concerns

The impact of genetic manipulation on animal health and welfare are of significant public interest. Ethical discussions are asking if these genetic manipulations can cause unnecessary stress in the animals (Animal Biotechnology: Science-Based Concerns, 2002; Cowan, 2010). For example, biomedical-use animals, specifically for those housed in sterile and isolated environments necessary for production of xenotransplantation tissues may experience stress and develop behavioral abnormalities. Rules are in place to try to alleviate any problems that might be caused by the pigs' environment (Animal Biotechnology: Science-Based Concerns, 2002). Continued evaluation of food safety, environmental safety, and animal welfare issues associated with animal biotechnology will be required as the field evolves.

Environmental Concerns

Several environmental concerns about GE animals are considered of high importance because both early identification and finding solutions to any problem are so difficult. The main concern is the possibility of GE animals entering natural environments (through release or escape) and disrupting ecosystems (Animal Biotechnology: Science-Based Concerns, 2002; Cowan, 2011).

For example, animals with high mobility and that have historic records of causing community damages, such as insects, shellfish, fish, and mice and rats, which can become feral easily and cause a high level of environmental concern. GloFish, a fluorescent red zebrafish, was the first transgenic animal commercially available in the US and a really popular aquarium item. Because this zebrafish is from southern Asia and cannot survive long in the cold US waters, it is believed that these GE zebrafish pose no risk to the environment. However, the AquAdvantage® Salmon (currently being evaluated) grow much faster than any wild salmon and, if released into the wild, could pose significant ecologic and genetic risks to native salmon stocks (Animal Biotechnology: Science-Based Concerns, 2002). This is why the company has proposed to sell only infertile female salmon eggs and which must be grown in inland tanks to reduce any risk of release into the wild. Furthermore, the cloning of extinct species, such as the woolly mammoth, is another focus of recent environmental concerns.

Regulation of Animal Biotechnology

United States

In the US most regulations are generally applied only to the products of biotechnology, not to the processes. It is focused on whether the products are safe for use, or 'generally recognized as safe' (GRAS) (Cowan, 2010, 2011; Bazer *et al.*, 2010). The US FDA and the USDA are primarily responsible for the regulation of animal biotechnology in the US. The FDA is responsible for the regulation of food safety issues for food animals produced by biotechnology, any environmental issues caused by these animals, and the regulation of drug safety. Concurrently, the USDA, with the animal and plant health inspection service (APHIS) and the food safety inspection service, regulates food products produced by animal biotechnology (Cowan, 2010, 2011; Cowan, 2010; Bazer *et al.*, 2010).

In 2009, the FDA released its final guidance statement regarding genetically engineered animals and products regulation. They defined GE animals as "those animals modified by recombinant DNA techniques, including the entire lineage of animals that contain the modification." These modifications are made with the purpose to 'alter the structure or function' of the animals involved. The process of registration and approval for use of new GE animals must follow the FDA's 'new animal drug' procedures. Currently, the FDA is working on the approval of the first GE animal to be used for human consumption. Although AquAdvantage® salmon were declared to pose no risk for human consumers in August 2010 (Cowan, 2010), the process began more than 10 years ago. Final approval will not be given for the salmon until studies of environmental issues are completed, possibly in 2013. However,

the FDA approved the first biopharmaceutical product produced by a transgenic animal (goats) in 2009. This was ATryn®, antithrombin III manufactured by GCC-Biotherapeutics.

When a product from animal biotechnology comes to the market, it is subject to FDA and APHIS labeling requirements. It is considered illegal to introduce food from a GE animal into the food supply without previous approval by FDA. For example, in food biotechnology, those products considered GRAS that are equivalent to food products that are already on the market, such as milk from cows receiving BST do not need to be labeled. However, those foods derived from GE animals that have altered genomes are not considered substantially equivalent and are required to be labeled. Attempts to create state laws for labeling of food produced by biotechnology have failed. Ethical questions regarding such labeling concern the right of the consumers to know the process by which food is produced. FDA is not allowed to consider those ethical questions. Its authority just covers safety issues (Cowan, 2011; Bazer *et al.*, 2010).

European Union and China

Outside the US, the regulation of animal biotechnology can differ a little. The European regulators, in contrast to the American, consider the biotechnology itself as a novel process that requires regulation (Bazer *et al.*, 2010). In the European Union, the European Medicines Agency regulates the approval of pharmaceuticals, whereas the European Food Safety Authority was set up in 2002 to be responsible for scientific risk assessment of food biotechnology. In addition, the European parliament and member states handle the risk management policy. The distribution of genetically modified organisms (GMOs) and GMOs used in food products are regulated by the Directive 2001/18/EC. This Directive requires notification before a product derived from genetic engineering comes to market. Furthermore, it is required that each product containing GMOs be labeled with the sentence: "This product contains genetically modified organisms" (Bazer *et al.*, 2010).

Animal biotechnology in China is regulated by three main agencies: the Ministry of Health, the Ministry of Science and Technology, and the Ministry of Agriculture. Although there is little formal legislation, there have been several statements concerning GMOs, whereas those statements formally apply to animals. Almost all enforcement involves the importation and production of plants instead of animals (CAST, 2010). In China, in contrast to Europe and US, there are no regulations related specifically to animal cloning. Instead, they have regulations regarding human cloning, leaving open all other research. The research in China is more lightly regulated and controlled than clinical and commercial applications. In 2004, an attempt to regulate animal welfare failed. Recently, new attempts have begun, but no regulations have been proposed (Bazer *et al.*, 2010).

Multimedia Annexes

PDF on Artificial Insemination

This PDF gives a basic overview of artificial insemination, beginning with semen collection and ending with the insemination procedure. It includes details such as the optimal thawing temperature for sperm and the accuracy of sperm-sorting procedures. It also details the advantages of disadvantages conferred by artificial insemination.

PDF on *In Vitro* Fertilization

This PDF gives a general overview of the IVF procedure, including the beginning steps of oocyte collection and ending with embryo culture. The PDF was designed for a laboratory course, therefore it includes exact reagents and volumes for the IVF procedure of cattle. It also includes information on embryo culture of other species. ICSI is also discussed.

PDF of the Food and Drug Authorities Final Guidelines on Genetically Engineered Animals

This is the document the FDA released in 2009 (and revised in 2011) that details their current policies on GE animals. These policies include information on introducing transgenic animals into the food supply, environmental concerns, record keeping, and many other topics. The guidelines are very thorough and detailed.

PDF on Molecular Markers

This file has a description of classical technologies involved in the development of molecular markers. Molecular markers discussed include RFLP markers, randomly-RAPD markers, amplified fragment length polymorphism (AFLP®) markers, microsatellite markers, SNP markers, sequence characterized amplified region (SCAR) markers, cleaved amplified polymorphic sequences, intersimple sequence repeat markers, and polymerase chain reaction-based sequence tagged site markers.

See also: Biotechnology: Pharming. Biotechnology: Regulatory Issues. Cloning Animals by Somatic Cell Nuclear Transplantation. Genomics of Food Animals. Stem Cells. Transgenic Methodologies – Plants

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Advances in Pesticide Risk Reduction

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Glossary

Active ingredient Part of pesticide formulation that leads to biological effects of pesticides.
Characterization factors Characterization factors are used to quantitatively model the impact from each emission/consumed resource that comes from the life cycle inventory and are expressed as category indicatory results. The indicator of an impact category can be chosen anywhere along the impact pathway (midpoint or endpoint level). Characterization factors are usually calculated for continental and global scales.
Ecolabeling A voluntary method of environmental performance certification and labeling. An 'ecolabel' identifies the proven environmental preference of a product or service within a specific product or service category.
Endocrine disruptor Chemicals that at certain doses can interfere with the hormone system in mammals.
Hazard Inherent properties of a pesticide, which gives potential for adverse effects to humans or the environment during its production, use, or disposal, depending on the degree of exposure.
LC_{50}-concentration Statistically derived concentration of a pesticide expected to kill 50% of test organisms in a given population under set conditions.
Metabolite Intermediate or product resulting from metabolic processes.
Pesticide effect Result (change in biochemistry, morphology, physiology, growth, development, or lifespan of an organism which results in impairment of functional capacity or impairment of capacity to compensate for additional stress or increase in susceptibility to other environmental influences) from the exposure of humans, flora, and fauna to the (eco)toxicological active ingredients of pesticides.
Pesticide risk Combination of the fate of pesticides in the environment, which controls the potential exposure of humans, flora, and fauna to pesticides, and the (eco) toxicological properties of pesticides, which cause their potential effects on humans, flora, and fauna.
Risk assessment The process of defining the risk associated with a specified use pattern for a pesticide, usually expressed as a numerical probability. Risk quantification has three steps: identification of hazard, establishment of dose–response relationships in target individuals or populations, and exposure assessment.

Introduction

A particular challenge for humans of this century is to secure food for the growing world population accompanied by unprecedented urbanization and rural exodus rates. This challenge is exacerbated by the effects of global warming. As a consequence, risk management in food production systems urgently needs to be improved (Food and Agriculture Organization of the United Nations (FAO) Committee on World Food Security reports). Pesticides play a vital role in maintaining and enhancing agricultural efficiency and productivity, ensuring the quality of produce and availability of perfect produce throughout the year, and minimizing produce losses postharvest. A recent report concluded that without pesticides, crop yields would be halved and food prices would increase by 40% (Rickart, 2010).

The value of global crop protection products at the distributor level totaled US$44 Billion in 2011, which was an increase of 14.9% compared with 2010 (agribusiness consultancy reports). However, data on the global annual total volume of pesticides used are not available. It is suggested that the actual volumes have been declining during recent years in spite of the reported increasing market values (Agrow World Crop Protection News). It is, however, remarkable that the volumes of pesticides applied significantly increased for many years despite the fact that newer pesticides are applied at much lower rates. In Europe, the use of plant protection products is dominated by fungicides followed by herbicides. The volumes of insecticides applied are insignificant (European Commission statistical data). In the US, herbicides dominate the market, which are predominately applied in maize and soybean production systems. In Latin America, the sale of plant protection products has been continuously increasing since the 1990s, which is driven by growing soybean and sugarcane production as forage crops and also for biofuel. The trend for increasing use of pesticides in Asia is driven by the Japanese production systems, in particular the cultivation of rice, which accounted for approximately 40% of the Asian pesticide market value in 2003 (Agrow World Crop Protection News). The intensity of agricultural production is expected to further increase, motivated by the ever-increasing demand for food products from the growing world population and the improved average living standard in many parts of Asia. This will impact pesticide usage. It has to be noted, however, that pesticide volume alone is not a good indicator for risk as explained in the following paragraph.

The potential of pesticides to cause harm has long been recognized. Reports on undesirable environmental consequences of pesticide use are manifold and range from reduced pesticide efficacy due to the development of resistance to pesticides by plants and pests (Waltz, 2010; Palumbi, 2001) to the frequent detection of pesticides in European/US aquifers (Lapworth and Gooddy, 2006; Moncrieff *et al.*, 2008; Denver *et al.*, 2010; Vryzas *et al.*, 2012). Pesticides can potentially cause undesirable adverse side effects on nontarget organisms, humans, and the environment (soils, surface, and groundwater resources) because pesticides are toxic by design and are deliberately released into the environment. Pesticide risk is a combination of the (eco)toxicological properties and the potential exposure of humans, flora, and fauna to the active ingredients – thus, risk depends not only on how toxic a chemical is, but also on how it is actually used, where it is used, how much of it is used, and how often it is used. The fate of pesticides in the environment is crucial for the risks associated with pesticide usage. The (eco)toxicological properties determine the hazard of a pesticide. Effects of hazardous substances are quantified under controlled conditions in laboratory or field experiments by measuring how much of an individual active substance is required to kill or affect test organisms. There is a growing awareness of the environmental risks associated with pesticide use, and an emergent societal pressure to reduce these risks and better manage the impacts of pesticides on the environment.

This article gives a general introduction to the fate of pesticides in the environment, summarizes the risks associated with the production, use, and disposal of pesticides, and provides an overview on current strategies and tools to minimize the risks associated with the use of pesticides. It also points out new directions in the efforts of reducing the risk associated with pesticide use.

Pesticides in the Environment

The International Union of Pure and Applied Chemistry defined pesticide risk as "the probability of any defined hazard occurring from exposure to a pesticide under specific conditions. Risk is a function of the likelihood of exposure and the likelihood to harm biological or other systems" (Holland, 1996). In other words, pesticide risk is a combination of the fate of pesticides in the environment, which controls the potential exposure of humans, flora, and fauna to pesticides, and the (eco)toxicological properties of pesticides, which cause their potential effects on humans, flora, and fauna.

This section provides an overview on both these aspects. The first part of this Section Pesticide Fate is dedicated to the fate of pesticides in the environment, which determines the potential exposure of humans, flora, and fauna to the active substances of pesticides. The second part of the Section Pesticide Effects is dedicated to the potential adverse effects pesticides can have on humans, flora, and fauna. Both the sections conclude with a paragraph in the respective section describing the tools and models that are used to assess pesticide risks.

Pesticide Fate

In this section, the entire life cycle of pesticides is considered, from the manufacturing of the active substances to the formulation of the pesticide product, to the use of the products and the disposal of residual pesticides and containers by the end user.

Pesticide fate during manufacturing and transport

Generally, pesticides are produced in two phases: the chemical synthesis of the active ingredients (manufacturing) is followed by mixing/diluting of the active ingredients with carrier substrates surfactants or other active ingredients into the final pesticide product (formulation). During the manufacturing, formulation, packaging, and distribution of pesticides the potential human exposure to excessive amounts of pesticides is the highest in the entire lifetime of a pesticide. Many studies have analyzed the potential exposure ways and related acute and chronic health risks for workers including neurological, circulatory, and reproductive problems (Sailaja *et al.*, 2006; Bhalli *et al.*, 2006). In the past, not only improper handling of pesticides in manufacturing, formulating, and packaging companies but also pesticide spills during transport have led to accidents worldwide (Cox, 1993). Residents, emergency workers, and the environment are then at the risk of being exposed to toxic emissions often in a cocktail of initially unknown compounds. In 2007, the World Bank Group published a document entitled 'Environmental, health, and safety guidelines for pesticide manufacturing, formulation, and packaging' (World Bank Group, International Finance Corporation Guidelines). These guidelines cover the potential environmental risks, occupational and community health and safety. Performance indicators and monitoring guidelines recommended for air emissions, wastewater, and waste products are provided.

Pesticide fate during and after application

What happens to pesticides following application on the farm has been intensively investigated since the publication of 'Silent Spring' by Rachel Carson (1962). Basically, the fate of pesticides after application is governed by three processes: the partitioning between the different environmental compartments, such as air, soil, water, and plant; the transport in an environmental compartment; and transformation processes. A schematic diagram of the most relevant processes during and after pesticide application is presented in **Figure 1**. Various factors determine the fate and behavior of pesticides including the properties of the active ingredient as well as the other ingredients of the formulated pesticide product, biological, chemical, and physical soil properties; and other environmental factors including climate, weather during application, topography, application techniques, etc. Pesticide properties that are beneficial to the environment may be suboptimal from an economical point of view, for example, a desirable pesticide property from an environmental point of view is a short persistence. However, a longer-lasting pesticide residue might be economically advantageous due to the longer effectiveness of the pesticide as long as the residues are not impacting the crops following in a crop rotation scheme.

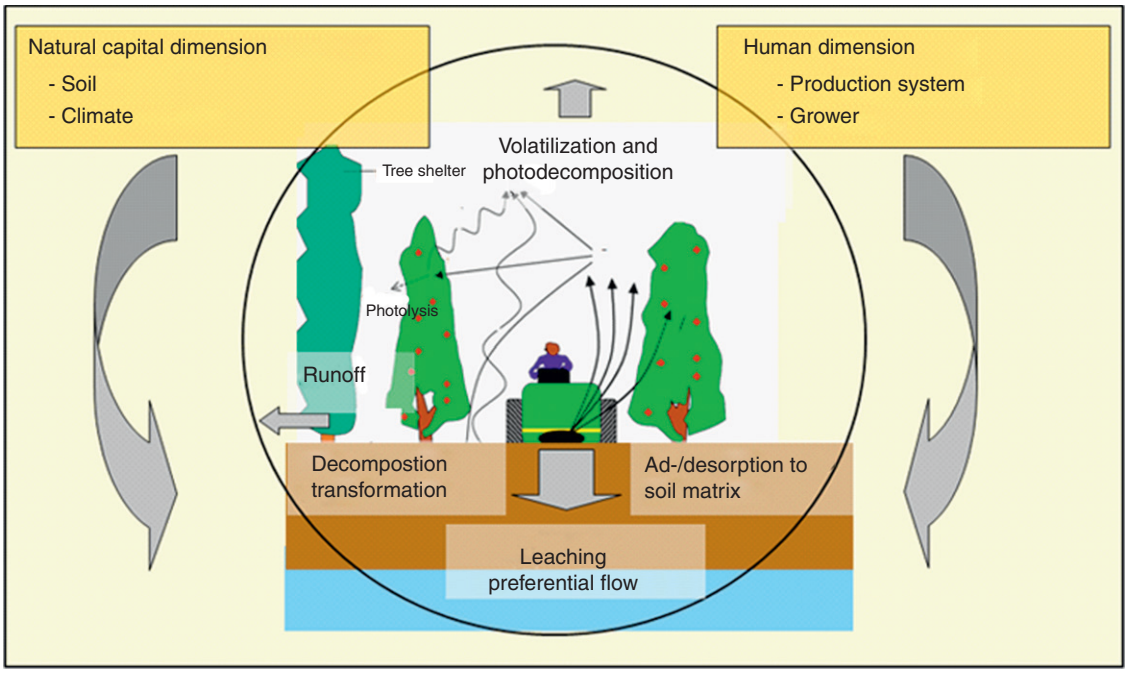


Figure 1 Pesticide fate in the environment after its application.

A thorough understanding of the factors affecting pesticide behavior in the different environmental compartments is necessary to maximize the agricultural benefits and minimize adverse environmental impacts of pesticides. Various review papers have been published on related topics (Gevao *et al.*, 2000; Sarmah *et al.*, 2004; Aislabie and Lloyd-Jones, 1995; Wauchope *et al.*, 2002; Wauchope, 1978; Flury, 1996; Kookana *et al.*, 1998; Beulke *et al.*, 2000; Reichenberger *et al.*, 2007). During the actual application of pesticides, workers and residents can be directly exposed to pesticides through spray drift and volatilization of pesticides, which are influenced by the application techniques, wind speed, humidity, and temperature during application. Exposure of workers is particularly important in greenhouses, because these are relatively closed systems (van Eerdt *et al.*, 2012). Other undesirable losses during and after the application include losses to nontarget areas in the field, such as usually the soil and transport of pesticides into ground and surface water resources. Once the pesticides are in the soil, pesticide–soil–soil water interactions govern their sorption, transformation, degradation, and transport through the soil. Topics that initiated many research activities in this area include the fate of aged residues and metabolites in soils (Ahmad *et al.*, 2004; Gevao *et al.*, 2000; Anhalt *et al.*, 2000) and the impact of pesticide formulation on the behavior of active ingredients (Tsui and Chu, 2003; Contardo-Jara *et al.*, 2009; Evans *et al.*, 1998; Wauchope *et al.*, 1990; Hilz and Vermeer, 2013). A relatively new focus of concern is the environmental fate of nanopesticides, which has been recently reviewed by Kah *et al.* (2013). In the context of pesticides, nanotechnology is used (1) to formulate and deliver active ingredients and (2) to offer new active ingredients, such as nanosilver. Nanoformulations of pesticides are expected to significantly impact the fate of active ingredients; however, the environmental fate of new nanoactive ingredients is poorly understood (Kah *et al.*, 2013).

Among the contamination of air, water, and soil by pesticides, water contamination is still the biggest concern. It originates from two different sources: point and nonpoint sources (Müller *et al.*, 2002). In the literature, this terminology is not used consistently (Leon *et al.*, 2001; Mohaupt *et al.*, 2000; Reichenberger *et al.*, 2007). In accordance with Müller *et al.* (2002), the authors define point pollution as the discharge of a discrete identifiable source like a waste pipe. Therefore, the pesticide load, which is contributed to a stream by a wastewater treatment plant system, is referred to as point source pollution. These loads result from disposal of pesticides, filling and cleaning of spraying equipment on farmyards during dry weather periods, washing off pesticide residues from impervious areas (farmyards, streets, roofs, etc.) during storm events and discharge from greenhouses (EFSA Panel on Plant Protection Products and their Residues (PPR), 2012a). Nonpoint sources or diffuse inputs result from the agricultural application in the field and include processes like soil surface runoff, interflow, preferential flow, drainage, atmospheric deposition, and spray drift (**Figure 2**).

Pesticide fate during disposal

In many countries, no guidelines or structures for pesticide users to dispose of remainders of hazardous products and empty pesticide containers exist. Owing to the lack of proper waste management systems for pesticide containers and residual pesticides, these are often inappropriately discarded, such as in uncontrolled landfills or by uncontrolled burning. These procedures may contaminate soil and water, and expose humans, animals, and plants to pesticide products and their metabolites or toxic emissions. Case studies in Germany reported that the cleaning of the sprayer and tank used for

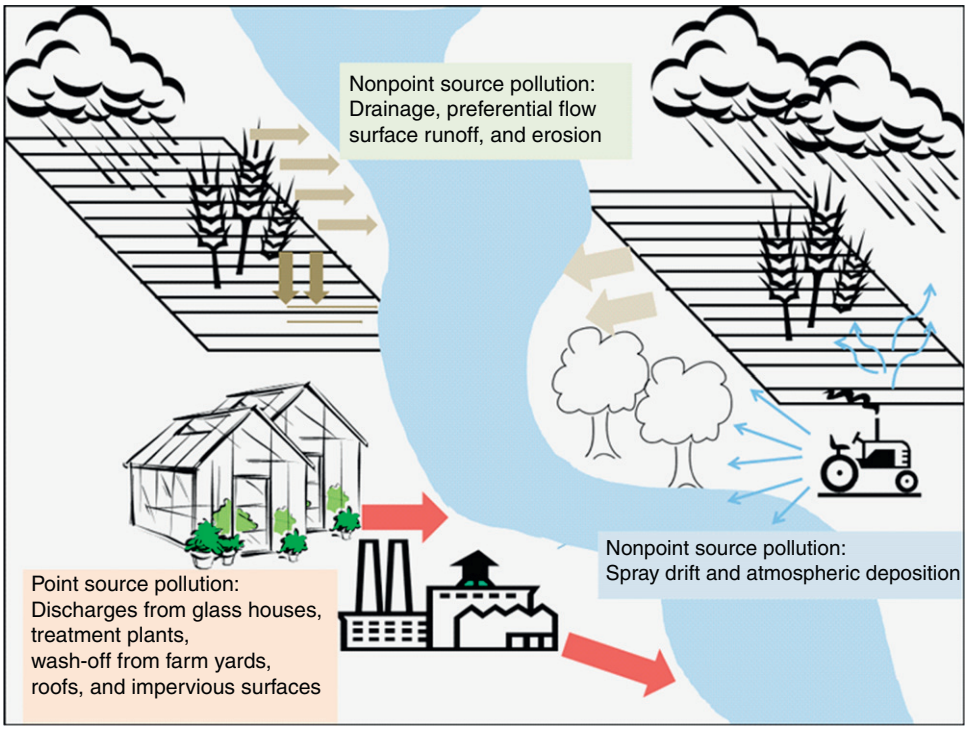


Figure 2 Schematic drawing showing pathways for point and nonpoint source pesticide pollution to surface water resources.

pesticide applications and the inappropriate treatment of pesticide residues left in the tank after application contributed the majority of the pesticide residues detected in surface water resources, which entered the streams through wastewater treatment plant systems (Fischer, 1996; Müller *et al.*, 2002).

On a larger scale, developed countries export unwanted pesticides, for example, pesticides that are no longer permitted, to other, often developing countries. The FAO is dealing with the legacy of problems related to this common practice ('FAO Information'). For example, the FAO currently has a program entitled 'The clean up of obsolete pesticides, pesticides management, and sustainable pest management,' which is part of the European Commission project on 'Capacity Building related to Multilateral Environmental Agreements in African, Caribbean, and Pacific countries' (FAO Information on Multilateral Environmental Agreements).

Pesticide fate models

Pesticide fate models are needed to interpret the observed pesticide distribution in the environment and to improve our understanding of the fundamental processes leading to the contamination of air, water, and soil. Pesticide fate models are also needed to describe human exposure. Human exposure to pesticides can be via dietary, occupational, and environmental exposures. Dietary human exposure to pesticides present in fruits and vegetables is an important aspect of food safety in Europe, the USA, and Australasia. It is the most relevant aspect of human exposure to pesticides. To estimate the dietary human exposure to pesticides different modeling approaches have been developed including point estimates, deterministic, and probabilistic modeling (Suhre, 2000; FAO/WHO, 2001; FAO/WHO, 1997). The scope of this section, however, is limited to the distribution of pesticides in different environmental compartments and environmental pesticide fate models.

A huge number of pesticide fate models has been developed since the 1980s, including PELMO (Klein *et al.*, 2000), CREAMS (Knisel, 1980), Opus (Smith, 1992), MACRO (Jarvis, 1994), HYDRUS-2D (Šimunek *et al.*, 1996), LEACHM (Wagenet and Hutson, 1987), PEARL (Tiktak *et al.*, 1998; Tiktak *et al.*, 2012), RZWQM (Ma *et al.*, 2004), and EuroPEARL (Tiktak *et al.*, 2004). Comprehensive reviews of models for pesticide transport in soils are given, *inter alia*, by Jury and Ghodrati (1989); Cohen *et al.* (1995); Tiktak (2000); Simunek *et al.* (2003); Nolan *et al.* (2005); and Dubus and Surdyk (2006). The majority of these models is deterministic, but some stochastic models have also been proposed (Lindahl *et al.*, 2005; Zacharias *et al.*, 1999; Jury and Roth, 1990; Heuvelink *et al.*, 2010). Deterministic models assume that a given set of initial and boundary conditions leads to a single outcome due to certain processes that can be described mathematically, whereas stochastic models take into consideration the spatial and temporal heterogeneities in soil properties and processes. The outcome of any one realization is considered to be uncertain. A large number of sample realizations lead to the definition of the probability density function for the underlying process.

Regardless of the model complexity, all models simplify reality to a certain degree and the algorithms implemented need to be validated (Arenstein *et al.*, 1993; Armstrong *et al.*, 1996; Clemente *et al.*, 1998; Thorsen *et al.*, 1998). Generally, pesticide fate models need to be calibrated for a site before any attempts of model validation (Dubus *et al.*, 2002; Tiktak, 2000). In spite of extensive efforts in pesticide fate modeling

for approximately 35 years, accurate predictions of pesticide behavior are still a daunting task partly because of the vast spatial variability of environmental parameters affecting pesticide fate (Coquet, 2002; Bundt *et al.*, 2001; Ghafoor *et al.*, 2012; Ghafoor *et al.*, 2011), and also due to existing knowledge gaps and lack of understanding of the process with regard to, *inter alia*, preferential flow, impact of soil structure, and transitional soil properties, such as soil water repellency on fluxes and sorption processes, impact factors controlling transformation and degradation in the subsoil, etc. (Duwig *et al.*, 2008; Prado *et al.*, 2006; Boesten, 2000; Täumer *et al.*, 2006; Jury *et al.*, 2011; Vanclooster *et al.*, 2000).

Most of the pesticide fate models focus on a single environmental compartment, for example, groundwater, and aim to predict environmental concentrations depending on climate, soil, and other boundary conditions. Multimedia fate models as developed by Mackay and Paterson (1991) target mainly persistent pesticides and their transfer between the different environmental compartments on a global scale. There is a need to extend these into models applicable and meaningful for the local scale.

Pesticide Effects

In this section, some examples of pesticide effects resulting from the exposure of humans, flora, and fauna to the (eco) toxicological active ingredients of pesticides are provided. First of all, it has to be noted that chronic and acute effects of pesticides can be distinguished. Chronic toxicity is defined as the "capacity for a pesticide to produce injury following chronic exposure or to produce effects which persist whether or not they occur immediately on exposure or are delayed" (Holland, 1996). In contrast, acute toxicity is the "ability of a substance to cause adverse effects within a short period following dosing or exposure" (Holland, 1996). Furthermore, adverse effects need further specification. In the simplest case, lethal and sublethal effects can be distinguished (Desneux *et al.*, 2007). Duffus (1993) and Nordberg *et al.* (2007) compiled comprehensive overviews on different toxicological terms.

For example, pesticide residues in water resources are discussed as one of the potential factors for fish and amphibian deformations that have been observed globally (Hayes *et al.*, 2010). Negative effect of pesticides on pollinators (Gill *et al.*, 2012) and biodiversity in soils (Bhat, 2012) have been reported. Moreover, pesticide exposure is discussed as a potential trigger for cancer (Alavanja and Bonner, 2012; Ventura *et al.*, 2012; Alexander *et al.*, 2012; Koutros *et al.*, 2013); neuroanomalies among children have been explained by pesticide exposure (Rosas and Eskenazi, 2008), and some pesticides are suspected to act as endocrine disruptors (Mnif *et al.*, 2011). Health issues related to pesticide usage are associated with significant costs. A recent paper estimated that in the US the annual costs linked to pesticide exposures were approximately US$200 million based on the data from emergency department visits, hospitalizations, and for deaths (Langley and Mort, 2012). It has been commonly accepted that pesticide residues in produce are an issue of concern and have led some supermarket chains to devise their own regulations and maximum acceptable threshold values (Lang and Barling, 2007).

Generally, the (eco)toxicological properties of the active ingredients determine the hazard of pesticides. Effects of hazardous substances are quantified under controlled conditions in a laboratory, semifield or field experiments by measuring how much of an individual active substance is required to kill or affect test organisms. The various types of experiments are explained in more detail in the section on registration of pesticides in this article. Problems associated with these tests are that normally the experiments are conducted under controlled conditions, synergy effects of exposure to multiple chemicals are excluded, and effects of metabolites are often not considered. Moreover, the vulnerability of adults and children are very different, and for ecotoxicological tests, the choice of appropriate test organisms is crucial. Pesticide effect models are used to address these problems.

Pesticide effect models

As it is impossible to test all combinations of organism, substance, environmental, and exposure conditions with experiments, models are crucial for the quantification of (eco)toxic effects for the risk assessment of pesticides. Many different pesticide effect models have been developed including, for example, Mastep (Van den Brink *et al.*, 2007), PERPEST (van Nes and van den Brink, 2003), TDM (Ashauer *et al.*, 2007), and General Unified Threshold model for Survival (GUTS) (Jager *et al.*, 2011). The simplest models are statistical (e.g., LC_{50} concentration, lowest observed effect concentration) and physical (e.g., *Daphnia magna*, microcosm) models, which do not incorporate any systematic understanding of the system of interest (EFSA Panel on Plant Protection Products and their Residues (PPR), 2013). In contrast, mechanistic toxicity models make explicit assumptions about the dynamic processes underlying the toxic response. This procedure allows extrapolating results to different exposure and environmental conditions. Mechanistic models have been developed for individuals, populations, and ecosystems (Preuss *et al.*, 2009; Grimm *et al.*, 2009; Jager *et al.*, 2011; Thorbek *et al.*, 2009). Population models aim at extrapolating lethal and sublethal effect from the individual to the population level (Preuss *et al.*, 2010). Ecosystem models allow the risk characterization within ecosystems, integrating biotic interactions (Park *et al.*, 2008; Hommen *et al.*, 1993).

More realistic are the process-based toxicity models, which are dynamic and take into account fluctuating concentrations and pulses of pesticides. They simulate the processes leading to toxicity at the level of organisms over time (Ashauer and Escher, 2010). Usually, this model type predicts survival of individual organisms (Jager *et al.*, 2011) but is now also applied to sublethal endpoints (Ashauer and Brown, 2013). For example, on the level of an individual, this model type simulates sublethal effects over time, based on uptake of the toxicant and damage and repair processes within the organism. This generation of pesticide effect models is labeled toxicokinetic–toxicodynamic (TK–TD) models (Jager *et al.*, 2011). These models provide a conceptual framework to better understand the causes for variability in sensitivity between different species to the same compound as well as causes for

different toxicity of different compounds to the same species. An example of a TK–TD model is the GUTS (Jager *et al.*, 2011). In addition, models taking into account the effect of mixtures of pesticides have been developed and different methodologies have been proposed (de Zwart and Posthuma, 2005).

Strategies to Reduce Pesticide Risks

The most important approaches to reduce pesticide risks include:

- regulate and control pesticide production and use,
- promote safe pesticide use,
- apply pesticide risk assessment tools to optimize pest management,
- apply agricultural management strategies, such as to
  - apply integrated pest management (IPM) practices,
  - convert conventional agricultural production into certified organic production systems, and
  - enhance resilience of agricultural production systems,
- enhance pesticide life cycle stewardship (LCS), such as to
  - conduct life cycle assessment (LCA) of pesticides and
  - promote ecolabeling of products.

Regulation and Control of Pesticides: Registration

Pesticides need to be registered by competent authorities before they can be sold and used. Once registered, its use must be consistent with the approved directions for use on the pesticide's label. As such, pesticide registration is an important mechanism to keep the most toxic substances of the market and inhibit manufacturing of these substances. In the European Union (EU), pesticide regulation (Regulation 1107/2009/EC) offers a framework for the registration of pesticides. According to its preamble, it is required that "pesticides, when properly applied for the purpose intended, are sufficiently effective and have no unacceptable effect on plants or plant products, no unacceptable influence on the environment in general and, in particular, no harmful effect on human or animal health or groundwater."

Pesticide registration is increasingly based on scientifically sound, harmonized, and transparent environmental risk assessment (ERA) procedures. Responsible authorities for developing such methods are – among others – the European Food Safety Authority (EFSA) in the EU and the Environmental Protection Agency (EPA) in the US. For the development of robust and scientifically sound ERA procedures, it is crucial to define clear protection goals. However, protection goals are only broadly defined in EU and US legislation. Therefore, a translation into the so-called 'specific protection goals' is necessary. Specific protection goals define what to protect, where to protect it, and over what time period (EFSA Panel on Plant Protection Products and their Residues (PPR), 2010). This definition is in line with US-EPA's definition of 'generic assessment endpoints.' An assessment endpoint is defined as an explicit expression of the environmental value to be protected, operationally defined as ecological entity and its attributes (US EPA, 2003). The process of developing specific protection goals is part of the problem formulation in the ERA framework (Figure 3). On the basis of these specific protection goals, competent authorities develop guidance to be used by risk assessors. Risk managers finally base the granting of marketing authorizations for individual pesticides on the work done by risk assessors.

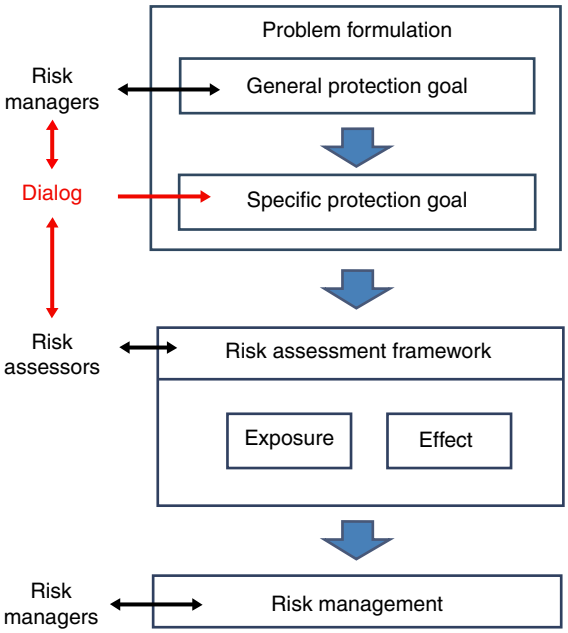


Figure 3 Relation between problem formulation, protection goals, risk assessment framework, and risk management in the process of pesticide authorization (EFSA Panel on Plant Protection Products and their Residues (PPR), 2010).

Tiered approaches are nowadays the basis of environmental risk-assessment schemes that support the registration of pesticides (Brock *et al.*, 2010; EFSA Panel on Plant Protection Products and their Residues (PPR), 2013; EFSA Panel on Plant Protection Products and their Residues (PPR), 2012b; Tiktak *et al.*, 2012; Tiktak *et al.*, 2013). A tier is defined as a complete exposure or effect assessment resulting in an appropriate endpoint (e.g., the concentration in surface water). The concept of tiered approaches is to start with a simple conservative assessment and only to do additional more complex work if necessary (so implying a cost-effective procedure both for industry and regulatory agencies). The general principles of tiered approaches are (Boesten *et al.*, 2007):

1. lower tiers are more conservative than higher tiers,
2. higher tiers are more realistic than lower tiers,
3. lower tiers usually require less effort than higher tiers,
4. in each tier, all available relevant scientific information is used,
5. all tiers aim at the same specific protection goal.

In short, the tiered exposure assessment needs to be internally consistent and cost-effective and needs to address the problem with higher accuracy and precision when going from lower to higher tiers. These principles permit moving directly to higher tiers without performing the assessments for all lower tiers.

An example of a tiered assessment scheme is presented in Figure 4. This example focuses on effects on aquatic organisms

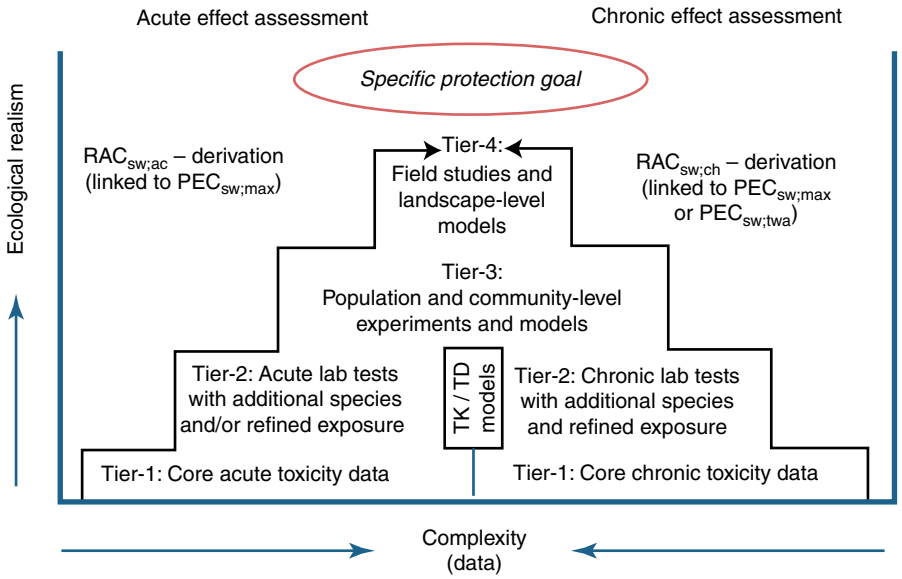


Figure 4 Schematic representation of the tiered approach within the acute (left part) and chronic (right part) effect assessment for pesticides. For each pesticide, both the acute and chronic effects/risks have to be assessed. Each tier results in a regulatory acceptable concentration (RAC) that needs to be compared with a relevant exposure concentration to identify whether a risk is present. PEC, predicted environmental concentration; TX/TD, toxicokinetic/toxicodynamic. Reproduced from EFSA Panel on Plant Protection Products and their Residues (PPR), 2013. Guidance on tiered risk assessment for plant protection products for aquatic organisms in edge-of-field surface waters. European Food Safety Authority Journal 11, 3290–3558. Available at: www.efsa.europa.eu/efsajournal (accessed 06.02.14). doi: 10.2903/j.efsa.2013.3290.

living in the water column of edge-of-field surface waters (EFSA Panel on Plant Protection Products and their Residues (PPR), 2013). The endpoint for each tier is a RAC. The diagram contains two distinct effect assessment schemes, that is, one for acute effects and one for chronic effects. Note, however, that both the schemes aim at the same specific protection goal (which in most cases have only negligible effects at the population level). Tier 1 is a single-species laboratory toxicity test using only core toxicity data. At tier 2, additional single-species tests are added allowing the derivation of more sophisticated and more realistic statistical measures to describe the potential effects. At tier 3, population-level experiments are carried out under semifield conditions (the so-called mesocosms). This allows direct quantification of effects at the population level with realistic pesticide use strategies, which is of course closer to the intended specific protection goal and therefore more realistic. It is, however, also more laborious than single-species experiments. At tier 4, field studies are carried out or population-level models are applied at the landscape level. The latter allows direct quantification of worst-case conditions (e.g., 90th percentiles of effect levels) as is done in the fate part of the risk assessment (Section Regulatory Risk Assessment Models). Although population-level effect models at the landscape level exist (Schmolke *et al.*, 2010), they are currently not operational in the regulatory context.

The RACs obtained in the effect assessment need to be compared with relevant exposure concentrations to identify whether a risk is present. In the acute effect assessment, the RAC is always compared with the concentration directly after exposure (this is usually also the maximum concentration in time). For the chronic effect assessment, some sort of time-weighted average exposure concentration may be used (EFSA Panel on Plant Protection Products and their Residues (PPR), 2013).

So pesticide registration is primarily based on prospective risk assessment. A new element of the EU-Pesticides Regulation is, however, that it provides the possibility to reject pesticides on the basis of intrinsic properties alone (the so-called hazard-based cutoff criteria). This means that pesticides that fail one of the hazard-based cutoff criteria will not be further evaluated even when it is clear that potential exposure is negligible. Cutoff criteria are given for 'persistence, bioaccumulation, and toxicity criteria.' Pesticides can neither be registered if they are mutagenic, carcinogenic, or toxic for reproduction, nor considered to have endocrine-disrupting properties. However, the definitions of some of the cutoff criteria, such as endocrine disruptor, are not yet finalized (Williams, 2011).

Regulatory risk assessment models

Some of the exposure models described under the Section Pesticide fate models are used to support the registration process above. For regulatory purposes, however, the models are used in combination with standardized scenarios and user-friendly software shells. A scenario consists of a combination of soil, climate, and crop parameters to be used in modeling. Standardized scenarios are needed because they increase the uniformity of the regulatory evaluation process by minimizing the influence of the methodology applied and of the person that performs the predicted environmental concentration (PEC) calculation and because they make exposure assessments and their interpretation easier for regulators and industry (Boesten, 2000; Vanclooster *et al.*, 2004; Tiktak *et al.*, 2013). Usually, realistic worst-case scenarios are assumed, and the simulations provide estimates of the exposure

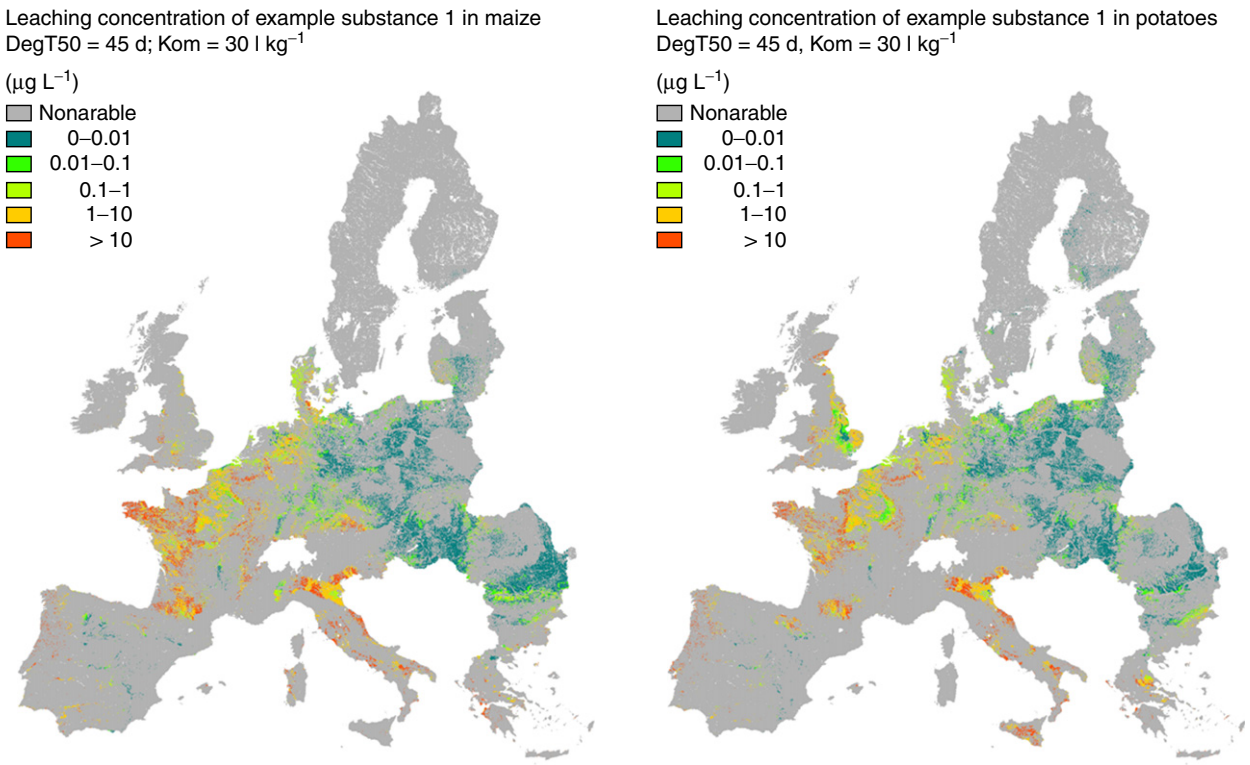


Figure 5 Leaching concentration of an example substance in two different crops, that is, corn (left) and potatoes (right). As the protection goal is the 90th percentile of the leaching concentration in a specific crop, percentiles are only calculated for the area where this crop is present. This implies that the 90th percentile is crop dependent. Calculations are done with a metamodel of EuroPEARL (Tiktak *et al.*, 2006).

concentration that are close to the exposure assessment goal set by risk managers. Examples of regulatory models include MACRO (Larsbo and Jarvis, 2003), PEARL (Leistra *et al.*, 2000), PELMO (Klein, 2011), PRZM (Carsel *et al.*, 1985), TOXSWA (Adriaanse, 1996, 1997), and PERSAM (Tiktak *et al.*, 2013).

In Europe, the development of these models has been coordinated by the forum for the coordination of pesticide fate models and their use (FOCUS). FOCUS has published general guidance documents and reports on the use of pesticide fate and transport models for predicting environmental concentrations in groundwater (FOCUS, 2000; FOCUS, 2009) and surface water (FOCUS, 2001). Recently, this task has been taken over by the EFSA. Their first guidance considered the assessment of exposure of soil organisms (EFSA Panel on Plant Protection Products and their Residues (PPR), 2012b).

As already mentioned, the exposure scenarios must represent the protection goal set by risk managers. In the leaching assessment of pesticides to groundwater, the protection goal was defined to be the 90th percentile of PEC values within the agricultural area of use of the pesticide in each of the nine climatic zones across the EU (FOCUS, 2009). For the exposure assessment of soil organisms, the 90th percentile exposure concentration was used as well, but the number of zones was limited to three (EFSA Panel on Plant Protection Products and their Residues (PPR), 2012b).

EFSA Panel on Plant Protection Products and their Residues (PPR), 2012b developed a statistical approach to find such scenarios. In their approach, scenario development began with the simulation of the concentration distribution in the entire area of use of a pesticide by means of a simple spatially distributed model. In a following step, the scenario was directly selected from the map of the simulated concentration. An alternative to the use of a limited number of worst-case scenarios is to use the spatially distributed model directly. In this approach, maps of the exposure concentration are created for the entire area and the 90th percentile is directly obtained from the frequency distribution of the so-obtained maps (**Figure 5**). Examples of the spatially distributed regulatory models are GeoPEARL (Tiktak *et al.*, 2003) and EuroPEARL (Tiktak *et al.*, 2004).

Enhance Safe and Effective Pesticide Use

Safe pesticide use includes both reducing the health risk for the user and the community and also minimizing the potential environmental aspects of pesticide applications. To enhance safe pesticide use, the general public has to be aware of the risks and problems associated with applying pesticides. Thus, the responsibility for safe pesticide use starts before the user with the registration of products, marketing, and advertising of pesticides. If pesticide products were only available in specialized shops like prescription pharmaceuticals, their distribution and usage would be easier to control. The wearing of personal protective equipment (PPE) during pesticide application as well as the maintenance of PPE should be part of a responsible advertising campaign. The implementation of

Table 1 Selection of potential strategies to enhance the safe and effective use of pesticides

Strategy	*Examples of strategies in use*
Restrict use of certain pesticides to registered users	http://environment.alberta.ca/01598.html http://environment.alberta.ca/01598.html http://www.epa.gov/oppfead1/safety/applicators/applicators.htm
Recordkeeping and information on pesticide use	Walker, 2005[a]
Introduce tax on pesticides	http://files.foes.de/de/downloads/tagungvilm2005/norwaystudy.pdf
Certification for pesticide users and advisers	http://www.extension.umn.edu/pesticides/private.html
Use crop-free or spray-drift buffer strips and vegetated buffer strips around treated areas	http://www.nda.nebraska.gov/pesticide/buffer_strip.html – for a discussion of the usefulness of buffer zones refer to the comprehensive review by Reichenberger *et al.* (2007)[b]
Use of spray-drift reducing technologies	http://www.oecd.org/env/spraydrift/government-laws-policies-and-guidance.htm for news/information on spray-drift reduction technology refer to http://www.sdrt.info/
Inspection of spraying equipment	http://ec.europa.eu/food/plant/pesticides/sustainable_use_pesticides/index_en.htm
Filling and cleaning of spraying equipment in the field	Recommended practice in many European countries
Postmonitoring of registered pesticides that gives a feedback cycle in pesticide registration	http://www.pesticidesatlas.net/
Information and awareness raising – inform the general public and put in place systems to gather information on acute poisoning incidents and chronic poisoning developments	http://ec.europa.eu/food/plant/pesticides/sustainable_use_pesticides/index_en.htm
Prohibit aerial spraying	Europe

[a]Walker, J., 2005. Development of good agricultural practice programs in New Zealand's fruit industries. In: International Seminar on Technology Development for Good Agriculture Practice in Asia and Oceania. Japan: National Agricultural Research Center.
[b]Reichenberger, S., Bach, M., Skitschak, A., Frede, H.-G., 2007. Mitigation strategies to reduce pesticide inputs into ground- and surface water and their effectiveness; A review. Science of the Total Environment 384, 1–35.

administrative controls, such as restricting pesticide usage to registered users and compulsory spray diaries for farmers would improve the safety of pesticide use. Spray diary records from individual pesticide users have been recognized as the best baseline for a comprehensive system for pesticide use recording (Manktelow *et al.*, 2005). In addition, improving the training and education of pesticide users are crucial. Related activities are already in place in many countries with handbooks on safe pesticide use (Marer, 2000), and initiatives like 'safe use' by CropLife International, a federation representing the plant science industry. For example, in New Zealand, a nonprofit trust aims to promote the safe, responsible, and effective use of agrichemicals by offering 'GROWSAFE' training courses that cover the knowledge and practices required for safe, responsible, and effective use of agrichemicals. The situation in developing countries is challenging due to the high level of illiteracy and low education levels, which impede training of pesticide users (Ekström and Ekbom, 2011). Some potential strategies to enhance the safe and effective use of pesticides are summarized in **Table 1**.

Application of Pesticide Risk Assessment Tools to Optimize Pest Management

To evaluate the risks associated with pesticide applications, more than 100 different pesticide risk assessment tools have been developed (Surgan *et al.*, 2010). Many comprehensive reviews, comparisons of different tools, often in the form of case studies, have been published (Labite *et al.*, 2011; Reus *et al.*, 2002; Kookana *et al.*, 2007; Stenrød *et al.*, 2008; Bockstaller and Girardin, 2003; Maud *et al.*, 2001; Dubus and Surdyk, 2006). In general, pesticide risk assessment tools are knowledge-based tools designed to support pesticide users and regulators in their decisions regarding the selection and regulation of the use of pesticides with the aim to minimize associated risks. More specifically, applications of pesticide risk assessment tools include:

- selection of lower risk pesticides,
- selection of pesticides that better match local conditions,
- optimization of pest management strategies as part of IPM systems,
- design pesticide reduction plans at the national and EU level, and
- monitoring the progress of pesticide reduction plans at the national scale.

This broad range of applications is reflected in the wide range of complexity of different pesticide risk assessment tools. All tools have something in common: they combine a range of data into a single or composite index for the comparative evaluation of the risk associated with a specific pesticide. Aggregation of data into an index ranges from simple scoring to fuzzy logic systems (van der Werf and Zimmer, 1998), which integrate both qualitative and quantitative information (Labite *et al.*, 2011). Commonly, the risks assessed are those related to human health, aquatic and terrestrial biota, birds, or the risk to contaminate environmental compartments. As mentioned earlier, the potential for pesticides to result in environmental damage and to adversely affect humans, flora, and fauna is extremely site-specific and is not solely dependent on the (eco) toxicological properties of the pesticide. In addition, application rates and timing are crucial to the fate of pesticides. Thus, more complex tools integrate risks related to pesticide use within a crop protection context at the local scale (Reus

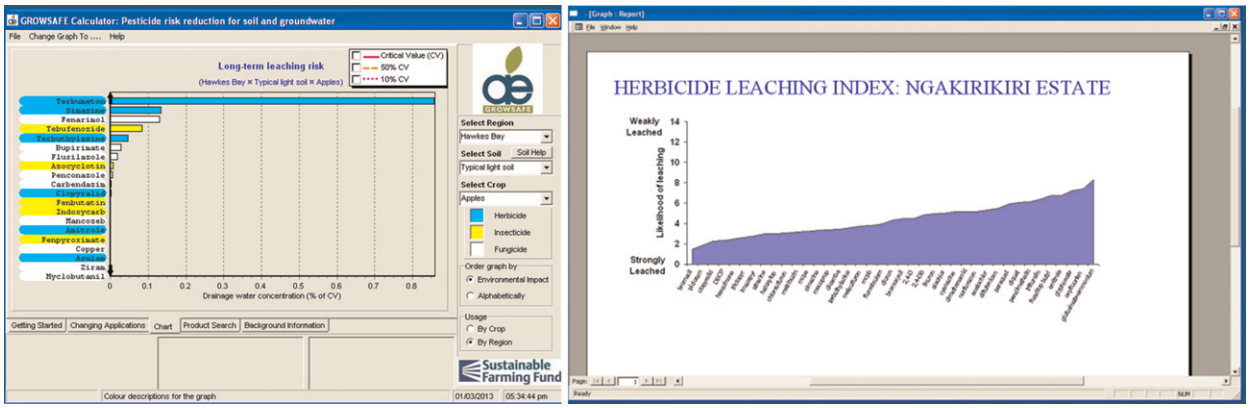


Figure 6 Left: Pesticide risk calculation with the GROWSAFE® Calculator Version 1.0.6.14. Right: Example of the output of the herbicide-leaching likelihood ranking tool PESTPROP. This decision-support tool allows the selection of herbicides with low risk of leaching. PESTPROP uses groundwater ubiquity score (GUS) and the attenuation approach.

et al., 2002), sometimes even at the national or even larger scale (Kruijne *et al.*, 2011).

In principal, pesticide risk assessment tools can be divided into farm-level indicators and complex regional-scale indicators. The latter assist pesticide control advisors and policy makers with the initial screening of pesticides, and regional councils and regulatory authorities to compare different land uses and agricultural management systems with regard to associated environmental pesticide risks (Levitan, 2000; Reus *et al.*, 2002). These indicators consider exposure modeling, which acknowledges the importance of site-specific data on soil characteristics and weather conditions for the fate of pesticides in the environment. Examples are the 1D-deterministic pesticide leaching models SPASMO and PELMO embedded in the pesticide risk indicator GROWSAFE® (Snow *et al.*, 2004) and SYNOPS (Gutsche and Rossberg, 1997), respectively. The Environmental Yardstick for Pesticides uses the PESTLA model to estimate pesticide concentration in groundwater (Reus *et al.*, 2002). Combining pesticide fate models into pesticide risk indicators is desirable. The more comprehensive tools integrate impacts on several environmental compartments and nontarget organisms and take into consideration site-specific data. However, the use of these tools is restricted by the time and effort for gathering the necessary input data, the expertize required to run the models, and the extended calculation time for running the complex models, which in addition requires high-performance computers.

Farm-level indicators assist pesticide users to decide which pesticides to favor in a certain pest control situation. These can be simple scoring tools that focus on the potential contamination of a single environmental compartment by a pesticide. A well-known example is the groundwater ubiquity score (GUS-index), which helps the user to decide which pesticide to select in case the aim is to minimize the potential contamination of aquifers. The assessment is solely based on the persistence and the partitioning coefficient of an active ingredient, that is, the physicochemical properties of the pesticides (Gustafson, 1989). More complex farm-level indicators help pesticide users to better match their pesticide selection with local conditions. Metamodels are elegant solutions that allow pesticide users at the farm level to assess more complex modeling frameworks as described above without the need of expert knowledge, excessive model run-times or data input. An advanced pesticide farm-level risk indicator is a computer-based decision support tool (*p*-EMA) (Brown *et al.*, 2003), which uses the MACRO model to predict pesticide losses to surface and groundwater. MACRO is implemented in *p*-EMA as a metamodel, meaning all the simulations are prerun with the MACRO model and linked to *p*-EMA as a look-up database. FOOT-FS is the successor, a farm-scale tool developed by the FOOTPRINT project (FOOTPRINT, 2010). GROWSAFE® (Snow *et al.*, 2004) is the New Zealand version of a metamodel-based pesticide risk indicator (**Figure 6**). A different promising approach is developing web-based modeling frameworks. For example, the Pesticide Use Risk Evaluation decision support system evaluates site-specific pesticide risks to surface water, groundwater, soil, and air with the ratio between PECs in Californian agricultural systems to the toxicity values of selected endpoint organisms (Zhan and Zhang, 2012).

Apply Agricultural Management Strategies

A range of agricultural management strategies can be employed to minimize the risks associated with pesticide use. Good Agricultural Practice is a key but there are different more specific approaches that are outlined in the next section.

Convert into certified organic agricultural cultivation practices

Converting agricultural production systems into certified organic cultivation conveys the complete ban of all synthetic chemical pesticides. There is an increasing demand for organically grown produce especially in Europe, and the share of land under organic management is rising worldwide. However, the total area of 37.2 million ha of agricultural land under organic management is still small. It represents approximately 1% of the global agricultural land (Willer *et al.*, 2013). Although organic agriculture would immediately eliminate all risks associated with agricultural pesticide usage, it bears other potential problems for growers, society, and the

environment including lower yields and higher demand for agricultural land, more labor-intensive production systems with demand for cheap laborers, food shortages, increased costs of produce, produce not unblemished as desired by the average consumer, lack of research to optimize alternative production strategies, etc. (Gomiero *et al.*, 2011). Environmental benefits are also not always clear. For example, copper preparations and mineral oils are allowed in many countries as fungicides and insecticides in organic agricultural systems, respectively. A recent comprehensive metaanalysis comparing the relative yield performance of organic and conventional agriculture showed that yields from organic agriculture are typically lower than under conventional production systems. In this study, it was also highlighted that under certain conditions organic yields might match conventional yields (Seufert *et al.*, 2012). Seufert *et al.* (2012) concluded that "the factors limiting organic yields need to be more fully understood, alongside assessments of the many social, environmental and economic benefits of organic farming systems."

Apply integrated pest management practices

It is commonly accepted that the use of pesticides will continue to play an important role in modern agricultural production systems. To increase the sustainability of modern agriculture and at the same time ensure high yields and reduce production costs, the use of pesticides has to go hand in hand with IPM practices. The EU is pioneering when it comes to IPM, and have committed to making IPM a reality by requiring European growers to implement the principles of IPM by 2014. Many different descriptions of IPM practices can be found in the literature (Kogan, 1998; Prokopy, 2003). The FAO defined IPM as: "The careful consideration of all available pest control techniques and subsequent integration of appropriate measures that discourage the development of pest populations and keep pesticides and other interventions to levels that are economically justified and reduce or minimize risks to human health and the environment. IPM emphasizes the growth of a healthy crop with the least possible disruption to agro-ecosystems and encourages natural pest control mechanisms." This definition implies that IPM practices should balance economical and environmental and health considerations of pest control. Basic principles of IPM systems include using treatment thresholds to decide when pesticide use is necessary and economically beneficial as opposed to applying pesticides as prophylactic measures. This necessitates that pest and disease levels are monitored accurately in the field. Regional warning systems have been established in many areas. Selecting pesticides with minimum impact on the environment and humans, optimizing application techniques and timing of applications, and applying biological control agents or other alternative pest control strategies (hand weeding and crop rotation) are further basic principles applied in IPM systems (Dent, 2005). The recent EU-project 'Endure' was dedicated to reducing the systematic use of pesticides and promoting IPM. The involved research teams developed an online information center providing information on sustainable crop protection measures tailored to local conditions at country level. Van Eerdt *et al.* (2014) highlighted that quantitative cost–benefit analyses of IPM measures are generally missing, and ascribed this lack to the high regional variability of IPM practices and the difficulty to assess ecological benefits of management changes quantitatively. In addition, their research emphasized the need to understand better the reasons for growers choosing not to adopt IPM measures in order to close the gap between the risk reducing potential of IPM measures and the risk reduction actually achieved by growers in a region. Possible reasons for the lack of adoption may include missing practicability of IPM measures and growers' lack of experience or knowledge to judge potential consequences on yield. Lamine (2011) underscored the role of professional local networks for increasing the rate of growers adopting IPM measures in a region. According to Lamine (2011) such networks provide growers opportunities for exchanging technical experience and learning from each other but also help them to find a different professional identity. The need for extension services and policy advisors to initiate and support respective social dynamics at a local scale was also identified.

Common consequences of implementing IPM practices include the reduction of pesticide volumes used or a change in the use-profile of pesticides. **Figure 7** shows the successful example of introducing IPM measures in New Zealand pipfruit industry. It highlights that both the overall volumes and the potential human, soil, and aquatic ecotoxicity impacts of insecticides used in apple production have substantially decreased (Walker *et al.*, 2009). Between 1995 and 2011, insecticide loading on apples has decreased by 83% with much lower potential (eco)toxicity through implementing sustainability programs. In contrast, van Eerdt *et al.* (2014) found that implementing IPM practices hardly reduced neither the aquatic effects nor the number of pesticide applications. They explained this by the fact that IPM methods usually only target one group of pesticides or a single pest. These authors suggested complementing IPM measures, such as the substitution of high risk pesticides by lower risk pesticides, with other measures including the establishment of wider crop-free buffer strips.

Improve resilience of agricultural production systems

A shift in the focus of agricultural production systems from the sole aim of agricultural production systems to provide food and fiber often culminating in intensive monocultures to agroecological approaches and ecosystem management could improve resilience of agricultural production systems in the future. The development of these concepts is at least partly resulting from the new understanding that our soils, vegetation, biodiversity, aquifers, lakes, streams, and rivers are the natural capital of the Earth and provide ecosystem services to mankind. The Millennium Ecosystem Assessment (MA, 2005) classified ecosystem services into four typologies: the supporting services of soil formation and nutrient cycling, the provisioning service of food, fuel, and fiber production; the regulating services around the buffering and filtering of water, carbon, and gases; and the cultural services of heritage, recreation, and spiritual well-being. Costanza *et al.* (1997) assessed the global flow of ecosystem services from the world's natural capital stocks of materials and energy, and they concluded that the sum value of terrestrial and marine ecosystem services was 1.8 times the value of gross global production. Today, there is a strong pull toward ecosystem management in light of all

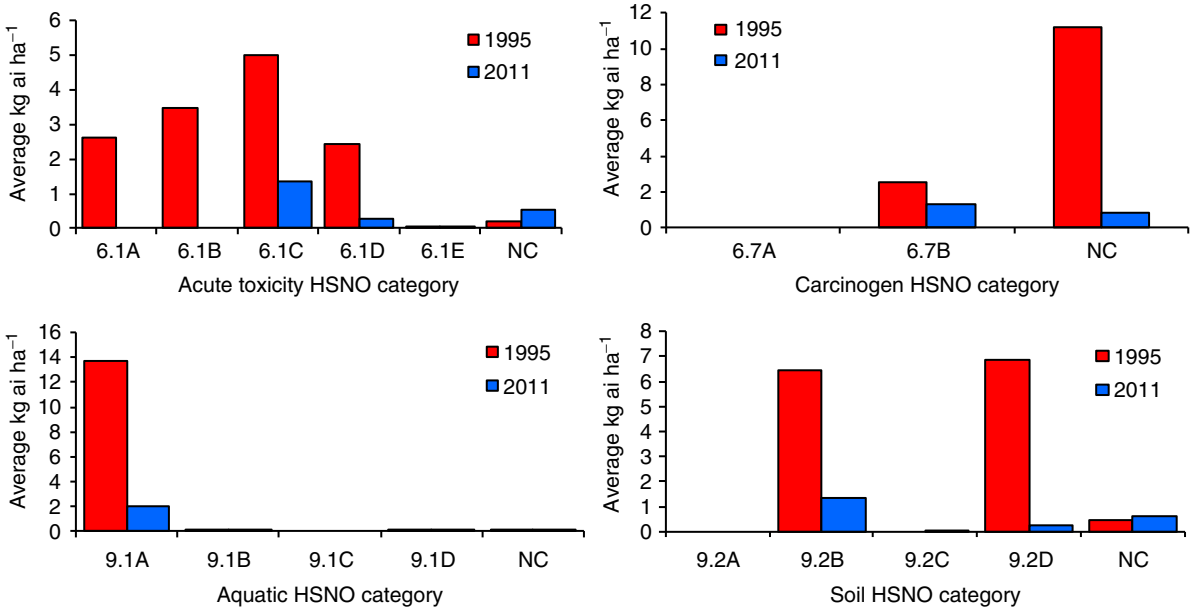


Figure 7 Left: Example of effects of introducing integrated management practices on organophoshate insecticide use on apples in New Zealand (Manktelow *et al.*, 2005). Right: The mean active ingredient use of hazardous substances and new organisms (HSNO) classified 6.1 (human toxicity) and 9.1 (ecotoxic) insecticides applied to apples (Walker *et al.*, 2009).

ecosystem services that the natural capital provides (Winter and Lobley, 2009). In view of this, the European Commission proposes to reward the delivery of environmental public goods, such as permanent grasslands, green cover, crop rotation, and ecological set-aside with the aim to establish refuges and reservoirs for natural antagonists (European Commission, 2010). These measures will result in an increase in the so-called high nature value farmlands, particularly in regions with intensive arable farming (Van Zeijts *et al.*, 2012). High nature value farmlands are characterized by more species diversity. This will – among others – reduce pest attacks and might, therefore, reduce the dependence of chemical pesticides. It will further enhance landscape diversity with the aim to reduce the vulnerability of agricultural production systems and to enhance their resilience (Nicholls and Altierei, 2007).

Enhance Pesticide Life Cycle Stewardship

The conceptual framework of LCS and Extended Product Responsibility could be extended to the stewardship of pesticide products ('Cornell University Information on Research Project'). The framework suggests that all stages of the pesticide life cycle, from product development and manufacture, through distribution and use, to the collection and disposal of unused products and containers should be considered when assessing the risks associated with pesticides. Some practical examples of pesticide stewardship embedded in the European pesticide regulation practices are included in **Table 1**, for example, the postmonitoring of registered pesticides that gives a feedback cycle in pesticide registration. If a given pesticide is frequently detected in groundwater or surface water resources, it will have consequences for the registration of this pesticide in Europe. These consequences include compulsory application of additional risk mitigation measures and withdrawal of the substance from the market. Recently, concepts and tools have been developed that aim at such a holistic environmental assessment of products. These tools include LCAs and product footprinting. The following section is dedicated to explaining the principal ideas of these instruments and provides examples on how these approaches have been applied to the product pesticide.

Conduct life cycle and life cycle impact assessments of pesticides

The first part of this section provides a general introduction to the concept of LCA and the second part describes the current state-of-the-art of applying LCA to pesticides. LCA is a holistic methodology to quantify the potential impacts a good or service has on the environment during its entire life cycle. This definition contains four important terms: life cycle, potential environmental impacts, holistic, and quantification. Life cycle is a fundamental concept in LCA, underlining that a product has a 'cradle' and a 'grave'. A product's use is preceded by design, resource extraction, and production. After use, it is disposed. All these stages may result in environmental impacts that have to be taken into account, as the occurrence of these processes is a direct consequence of the product's existence. The term 'potential environmental impacts' expresses that LCA does not predict the actual environmental effects. Instead the results should be considered as environmental indicators. LCA can be termed holistic to stress the comprehensive scope of the methodology. LCA aims to determine all environmental impacts of all processes related to the life cycle of the studied product, regardless of time or location. Generally, the following impacts are considered: abiotic resource depletion,

greenhouse gas emissions, ozone-depleting emissions, (eco) toxicological impacts, photochemical oxidation, acidification, and eutrophication. These impact categories are far more encompassing than the pesticide effects considered in traditional risk assessments of pesticides. Finally, quantification indicates that LCA is a quantitative methodology, expressing potential environmental impacts in numbers rather than as a qualitative description.

LCA, as defined in the ISO standards 14040 and 14044: 2006, consists of five phases: goal definition, scope definition, inventory analysis (LCI), impact assessment (LCIA), and interpretation. The goal definition describes the motivation for carrying out the study, its purposes, and the target audience. In the scope definition the assessed product is precisely defined. Moreover, a detailed description is given of how the next stages in the LCA will be carried out. In the LCI, all exchanges between the technosphere and the ecosphere, that is, between the product system and the environment, are quantified. For example, in the case of an LCA of a pesticide such exchanges can be emissions of a pesticide to the environment during application, greenhouse gases emitted when producing the pesticide, or the extraction of oil used as a raw material in production. During the LCIA phase the exchanges that were quantified in the LCI are translated into potential environmental impacts. Impact assessment consists of a number of steps that will not be discussed in more detail here. In LCA, the three so-called areas of protection are identified, describing what LCA seeks to protect: natural environment, human health, and resource depletion. Environmental impacts can be modeled at two levels: at endpoint level, which is at the damage inflicted in one of the three areas of protection, or at midpoint level, which means up to any point in the cause-effect chain leading from the environmental exchange to damage. The choice between midpoints and endpoints is one between, among others, uncertainty and ease of communicating results. In the interpretation phase the results from the impact assessment are interpreted. Furthermore, the uncertainty, sensitivity, and consistency of the previous phases are determined. On the basis of this, conclusions are drawn and recommendations are formulated.

There are a number of LCA tools available to assess the environmental impacts of pesticides. Within LCI, inventory analysis, two relevant data sources can be mentioned. The Swiss LCI database Ecoinvent contains inventory data regarding the production of pesticides, on different aggregation levels. This kind of inventory data lists the inputs and outputs to and from the environment required for the production of a given mass of active ingredient. Pesticide-specific data are available for a number of frequently used pesticides and pesticide classes. All data are based on data collected for 78 pesticides used in Europe and the data, therefore, are considered as valid under European circumstances.

Regarding emissions in the use stage of pesticides, when the chemical is applied to the crops, two approaches are currently used in LCA. The first, and dominant, approach is the one applied in crop production processes in the Ecoinvent database. Here, it is assumed that all pesticide used is emitted to the agricultural soil. The second approach is the model PestLCI 2.0 (Birkved and Hauschild, 2006; Dijkman *et al.*, 2012), which calculates emissions from the technosphere to three environmental compartments: air, surface water, and groundwater. An application of the model to leek production is described in de Backer *et al.* (2009). The technosphere in the PestLCI approach is defined as the agricultural field on which the studied crop grows, up to 1 m of depth, as well as the air column above the field, up to 100 m height. Any pesticide leaving this technosphere is considered an emission to the environment. In this approach, the agricultural soil is part of the technosphere. As a consequence there are no pesticide emissions to soil. Emissions to soils outside the technosphere are possible; however, this is considered in LCIA models: in LCI the emissions from the technosphere to the ecosphere are considered, and LCIA models are used to determine the fate of chemicals after they enter the ecosphere. The main reason for excluding the agricultural soil as an emission compartment in PestLCI is that agricultural soil is a highly manipulated soil with reduced biodiversity. Therefore, the soil cannot be considered as a part of the natural environment that LCA seeks to protect.

In the LCIA of pesticides emitted to the environment, a number of tools are available to assess their (eco)toxicity impacts. Most of the recently developed impact assessment methodologies have some way of quantifying these environmental impacts. A frequently applied model is USEtox (Rosenbaum *et al.*, 2008). This model was developed in a consensus process by the developers of a number of toxicity assessment models used in LCA and was found to be the best existing characterization model at midpoint (Hauschild *et al.*, 2013). Besides application in LCIA, USEtox can also be used in comparative risk assessment. USEtox is used to calculate characterization factors for human toxicity and freshwater ecotoxicity impacts of (organic) chemicals. These characterization factors can then be combined with emission data from LCI in order to arrive at the potential environmental impacts. In USEtox, as in other impact assessment models, human toxicity impacts are assessed by means of fate, exposure, and effect factors. These factors, respectively, describe where in the environment a chemical ends up, how much humans are exposed to the chemical, and the damage it does once human beings are exposed. Likewise, freshwater ecotoxicity characterization factors are calculated from fate and exposure factors. Characterization factors are calculated for two geographical scales: continental and global, where the continental scale is nested in the global scale. USEtox users can calculate characterization factors of chemicals not already included in the model by inserting a number of physical and chemical properties of the compound, as well as a limited number of toxicity data.

In current LCA practice, the assessment of environmental impacts is limited to the active ingredient. Although metabolites of the active ingredient sometimes impact the environment, these compounds have so far been ignored in both LCI and LCIA, mainly due to a lack of data.

Promote ecolabeling of food products: Pesticide footprint

As mentioned in the Introduction, increased environmental awareness and changing consumer attitudes are also driving the footprint quantification for products, individuals, activities, businesses, industries, and nations. Of all footprints, the carbon footprint is the most widely used with an internationally

accepted standard, the British PAS2050 (British Standards Institution, 2008). Carbon footprints are measures of the amount of greenhouse gas produced during the life cycle of a product: from its production through processing and storage to its use by the consumer. The labeling of products with carbon footprints allows consumers to choose products according to their global warming potential. The second important incentive for all carbon footprint quantification and analysis is to identify hot spots and to develop mitigation strategies that reduce greenhouse gas emissions. Other footprints are emerging, such as the water footprint, which provide incentives and guidelines for environmentally friendly and economic-sensible production strategies. Ecolabeling is useful for retailers, consumers, and indirectly also for producers (niche products with premium prices). A tool is needed for assessing the environmental impact of pesticides used for producing a specific product. A concept of a pesticide footprint has been proposed that estimates the total loss of pesticides, and the respective impact on humans and ecosystems, per product unit in a life cycle framework. The impact assessment considers how these losses affect humans through the consumption of the product containing residues, and ecosystems through the exposure to residues in the environment (Müller *et al.*, 2010).

Conclusions

Modern agricultural production systems are characterized by innovative management practices and techniques to meet the global food challenge, and the commitment to minimize environmental footprints at the same time and take stewardship of natural capital. There is no doubt that pesticides will continue to play a vital role in these systems. Risks associated with pesticide manufacturing, use, and disposal is inevitable because pesticides are toxic by design. Advances in pesticide risk management are made in partnership of science, industry, government, consumers, and pesticide end-users. Enhanced awareness of consumers, increased product responsibility of pesticide manufacturers and distributors, informed and educated pesticide users, independent expert advisers, and responsible governmental pesticide regulating agencies are enhancing the development of successful pesticide risk reduction strategies. Many different approaches to reduce pesticide impacts on human health and the environment have been developed. In this article, following strategies are introduced: (1) regulate and control pesticide production and use, (2) promote safe pesticide use, (3) apply pesticide risk assessment tools to optimize pest management, (4) apply agricultural management strategies, and (5) enhance pesticide LCS. Regulation of pesticide production and use is indispensable for reducing pesticide risks. It has led to minimizing or banning the use of pesticides in critical areas for environmental and health reasons in the past. Similarly, training, information, and raising awareness to enhance safe pesticide use are necessary but these strategies would not automatically translate into reducing risks. The biggest problem for these strategies to be successful is to establish effective communication channels and to present information in a form accessible to end-users. The development of risk assessment tools goes hand in hand with research. The current knowledge and understanding of pesticide risks is based on experimental research and the modeling of pesticide fate and effects. The application of risk assessment tools is an important part of successful pesticide registration and regulation. To what extent farm-level risk assessment indicators are actually applied on farms and contribute to the reduction of pesticide risks is questionable. Applying agricultural management strategies to reduce pesticide risks has not been widely adopted. The percentage of organic agricultural land has not yet reached 1% of the total agricultural land worldwide. Reasons for the lack of adoption of IPM measures may include missing practicability of IPM measures, growers' lack of experience, and knowledge to judge potential consequences on yield, as well as a general lack of quantitative cost–benefit analyses of IPM measures. Economic constraints may force farmers to concentrate on productivity rather than environmental and ecosystem aspects of their management decisions. Governments and industry foster the idea of pesticide LCS, a concept, which might lead to more tangible benefits in the future if it was embedded in the regulations of pesticide registration.

See also: Computer Modeling: Policy Analysis and Simulation. Edaphic Soil Science, Introduction to. Food Chain: Farm to Market. Natural Capital, Ecological Infrastructure, and Ecosystem Services in Agroecosystems. Organic Agricultural Production: Plants

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Agbiotechnology: Costs and Benefits of Genetically Modified Papaya

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Glossary

Agrobacterium A soil bacterium that infects susceptible plants and genetically transforms the infected plant. Certain species of *Agrobacterium* (e.g., *A. tumifaciens*) is used in the laboratories to genetically transform desired plants for crop improvement.

Coat protein (CP) A viral structural protein that is the only or the major component of the proteinaecious coat of the virus that encapsulates the viral genetic material.

Genetic transformation Transformation of an organism (plant, animal, or a microorganism) for a desired phenotype (trait) using a manipulated DNA fragment (transgene) from another organism (plant, animal, or a microorganism).

Hermaphrodite/hermaphroditic A hermaphrodite is a bisexual organism (plant, animal, or a microorganism) with both male and female characteristics.

Micropropagation Propagation of plants by artificial means from tissues developed from a single plant cell or a tiny piece of plant tissue.

Particle bombardment/biolistics Particle bombardment, or biolistics, is a commonly used method for genetic transformation of plants or other organisms. Transgene DNA-coated metal (gold or tungsten) particles are shot at target cells or tissues using a biolistic device or gene gun. The DNA elutes off the particles that lodge inside the cells, and may be stably incorporated in the chromosomes of target cells or tissues.

PTGS Posttranscriptional gene silencing (PTGS) is the silencing of a gene after its transcription by cleaving or inactivating the transcribed messenger RNA.

RNA silencing Silencing of a gene after its transcription by cleaving or inactivating the transcribed messenger RNA. RNA silencing is also called posttranscriptional gene silencing (PTGS).

Transgene A manipulated DNA fragment from an external source (plant, animal, or a microorganism) used to genetically transform a desired organism (plant, animal, or a microorganism) for a desired phenotype (trait).

Transgenic plant A plant genetically transformed for a desired phenotype (trait).

Papaya Is the Fruit of Angels

Papaya (*Carica papaya* L.) is a short-lived and fast-growing perennial herbaceous plant with a single stem and a crown of large, palmately lobed leaves, producing fleshy delicious fruits, from 8 to 10 months after transplantation in the field. The famous explorer and colonist Christopher Columbus called papaya the "Fruit of Angels." In the seventeenth century, Chinese tribes recognized papaya as a source of traditional medicine and used it for curing certain diseases, including malaria and gastrointestinal infections. Papaya is believed to be indigenous to the tropical regions of Central America. Introduced in Caribbean countries and Southeast Asia during the Spanish exploration in the sixteenth century (Storey, 1969), papaya crop spreads rapidly to the Indian subcontinent and Africa and is distributed widely today throughout tropical and subtropical regions of the world.

Papaya is an important cash crop in the tropics and subtropics and it is economically important because of its edible fruits rich in vitamins A and C (Manshardt, 1992) and latex rich in papain and chymotrypsin with applications in the beverage, food, cosmetic, and pharmaceutical industries (Chan and Tang, 1978). India, Brazil, Indonesia, Nigeria, and Mexico account for more than 70% of the global papaya production (**Table 1**). With a global productivity of 6.85 million metric tons, papaya is one among the 10 most important fruit crops of the world, the others being apple, avocado, banana, grape, mango, pear, pineapple, strawberry, and tomato. However, the relatively fragile and perishable nature of papaya fruit causes it to lag behind several of these major fruits in production, value, and export. Of the global annual quantum of papaya fruit production, only a small fraction of nearly 2% is being exported (Bapat *et al.*, 2010).

Worldwide Threat on Papaya Production by *Papaya Ringspot Virus*

Papaya cultivation is affected by a number of diseases caused by various pathogens. Papaya productivity is limited in many areas of the world due to the ringspot disease caused by the aphid-borne *Papaya ringspot virus* (PRSV), the major obstacle to large-scale commercial production of papaya (Purcifull *et al.*, 1984; Yeh and Gonsalves, 1984). PRSV was first reported in Hawaii in the 1940s (Jensen, 1949a), and subsequently, its prevalence in Florida (Conover, 1964), Caribbean countries (Adsuar, 1946; Jensen, 1949b), South America (Herold and Weibel, 1962), Africa (Lana, 1980), India (Capoor and Varma, 1948; Singh, 1969), the Far East (Wang *et al.*, 1978), and Australia (Thomas and Dodman, 1993) was noticed.

In papaya, PRSV causes symptoms of severe mosaic and distortion of leaves, ringspots on fruits, and water-soaked oily streaks on the upper stems and petioles. It severely affects the growth and development of papaya plants and drastically

Table 1 World papaya production in 2011

Country	Hectare	Metric ton
	(×1000)	(×1000)
India	104.3	4 180.1
Brazil	35.5	1 854.3
Indonesia	11.1	958.3
Nigeria	94.0	705.0
Mexico	14.2	634.4
Ethiopia	17.9	340.2
D. R. Congo	13.2	280.3
Thailand	13.2	271.9
Guatemala	2.2	205.5
China	7.3	181.2
Philippines	8.6	157.9
Colombia	5.0	153.2
Cuba	5.8	135.0
Peru	9.2	125.8
Venezuela	6.6	125.6
Others	73.4	1 503.0
Total	421.5	11 838.7

Source: Data digested from Food and Agriculture Organization (FAO), Statistical Division, 2013 (Available at: http://faostat.fao.org/faostat/).

reduces the number, size, and quality of the fruits and thus causes severe economic loss to growers (**Figure 1(a–c)**). In nature, PRSV is transmitted nonpersistently by aphids (**Figure 1(d)**) (Purcifull *et al.*, 1984) and is mechanically sap-transmissible. Apart from the predominant mosaic strains of PRSV, certain strains of PRSV cause severe wilting and death of the infected plants (Chang, 1979). To date, most of the papaya plantation areas of the world suffer devastation by this virus and lack of an effective control measure completely thwarts the farmers from opting for papaya cultivation. PRSV was reported in 1975 from the southern part of Taiwan, and it destroyed most of the papaya plantations in the country within a few years and caused unprecedented yield loss (Wang *et al.*, 1978).

The aphid-borne PRSV belongs to the genus *Potyvirus* of the family *Potyviridae* (King *et al.*, 2011), one of the largest and economically important plant virus groups. The virion of PRSV is a 780×12 nm flexuous particle (**Figure 1(e)**) with a positive sense single-stranded RNA genome (De La Rosa and Lastra, 1983; Yeh and Gonsalves, 1985). The genomic RNAs of several PRSV strains, including those from Hawaii (Yeh *et al.*, 1992) and Taiwan (Wang and Yeh, 1997), have been sequenced. The PRSV genomic RNA is 10.3 kb in length and it encodes a single polyprotein that is proteolytically processed by three virus-coded proteases into nine final proteins, including the 36 kDa coat protein (CP) for encapsidation of the viral genome (Purcifull and Hiebert, 1979; Gonsalves and Ishii, 1980; Yeh *et al.*, 1992) and the proteins of cylindrical (Purcifull and Edwardson, 1967) and amorphous (Martelli and Russo, 1976) inclusions in the cytoplasm of the infected host cells. The PRSV genomic RNA is uncapped, but it possesses a covalently attached molecule of VPg protein at the 5′ end and a polyA tail at the 3′ end. The first reported PRSV genome contains 10 326 nucleotides with a genetic organization of 5′-leader, P1, HC-Pro, P3, CI, 6K, NIa (processed further into VPg and NIa protease), NIb, CP, and 3′-noncoding region (Yeh *et al.*, 1992). The genetic organization and gene functions of PRSV are presented in **Figure 1(f)**.

No Natural Source for Resistance Breeding and No Effective Control Measures by Agricultural Practices

The species of *C. papaya* lacks effective natural resistance to PRSV and hence conventional breeding of papaya for PRSV resistance is impractical (Cook and Zettler, 1970; Wang *et al.*, 1978). However, PRSV-tolerant lines of papaya have been reported (Cook and Zettler, 1970; Conover, 1976; Conover *et al.*, 1986). Though PRSV-tolerance trait was introduced into several papaya cultivars, the horticultural properties, such as shorter shelf life on markets and more susceptibility to *Phytophothora* fruit- and root-rots, of the resultant papaya lines were not commercially desirable (Mekako and Nakasone, 1975; Conover and Litz, 1978; Yeh and Gonsalves, 1994).

A dominant gene conferring resistance to PRSV P is known to exist in certain wild relatives of papaya such as *C. cauliflora*, *C. stipulata*, and *C. pubescens* (Horovitz and Jimenez, 1967). Certain interspecific reproductive barriers restrict the transfer of the resistance gene of these *Carica* species into *C. papaya* genome (Horovitz and Jimenez, 1967; Manshardt and Wenslaff, 1989). However, fertile interspecific hybrids and F_2 population were obtained from the cross between *C. papaya* and *C. cauliflora* through embryo rescue technique (Khuspe *et al.*, 1980). The success of interspecific hybridization between *C. papaya* and *C. cauliflora* depends on the parental genotypes (Manshardt and Wenslaff, 1989; Azad *et al.*, 2012). To date, no report is available for success in incorporating the resistance from the wild papaya species to the edible papaya.

Other control measures against PRSV, including agricultural practices such as protecting young seedlings with plastic bag after transplanting, spraying pesticides or mineral oil against PRSV-transmitting aphids, eradicating diseased plants in orchards, mulching soil with reflective silver-colored plastic sheet, intercropping of papaya plants with corn as a high-stem barrier, provide only transient and inadequate protection from PRSV infection (Wang *et al.*, 1987; Yeh and Gonsalves, 1994).

Control of *Papaya Ringspot Virus* by Cross-Protection

An earlier infection of a plant by a virus can induce the plant to develop resistance against subsequent infection by the same virus species and closely related species (McKinney, 1929). Hence, mild virus strains that produce attenuated symptoms on crops without adverse effects can be employed to cross-protect crop plants against severe strains of the virus, which otherwise cause high yield loss. In the late 1980s, to find an effective solution to the severe yield loss caused by PRSV, Gonsalves and coworkers at Cornell University and the University of Hawaii initiated attempts involving cross-protection of papaya using a nitrous acid-induced mild strain of PRSV to protect papaya plants from severe infection of PRSV (**Figure 2(a)**).

In this strategy, healthy crop plants of economically important crops are infected with an attenuated strain of a virus to protect the crop against economic damage by severe strains

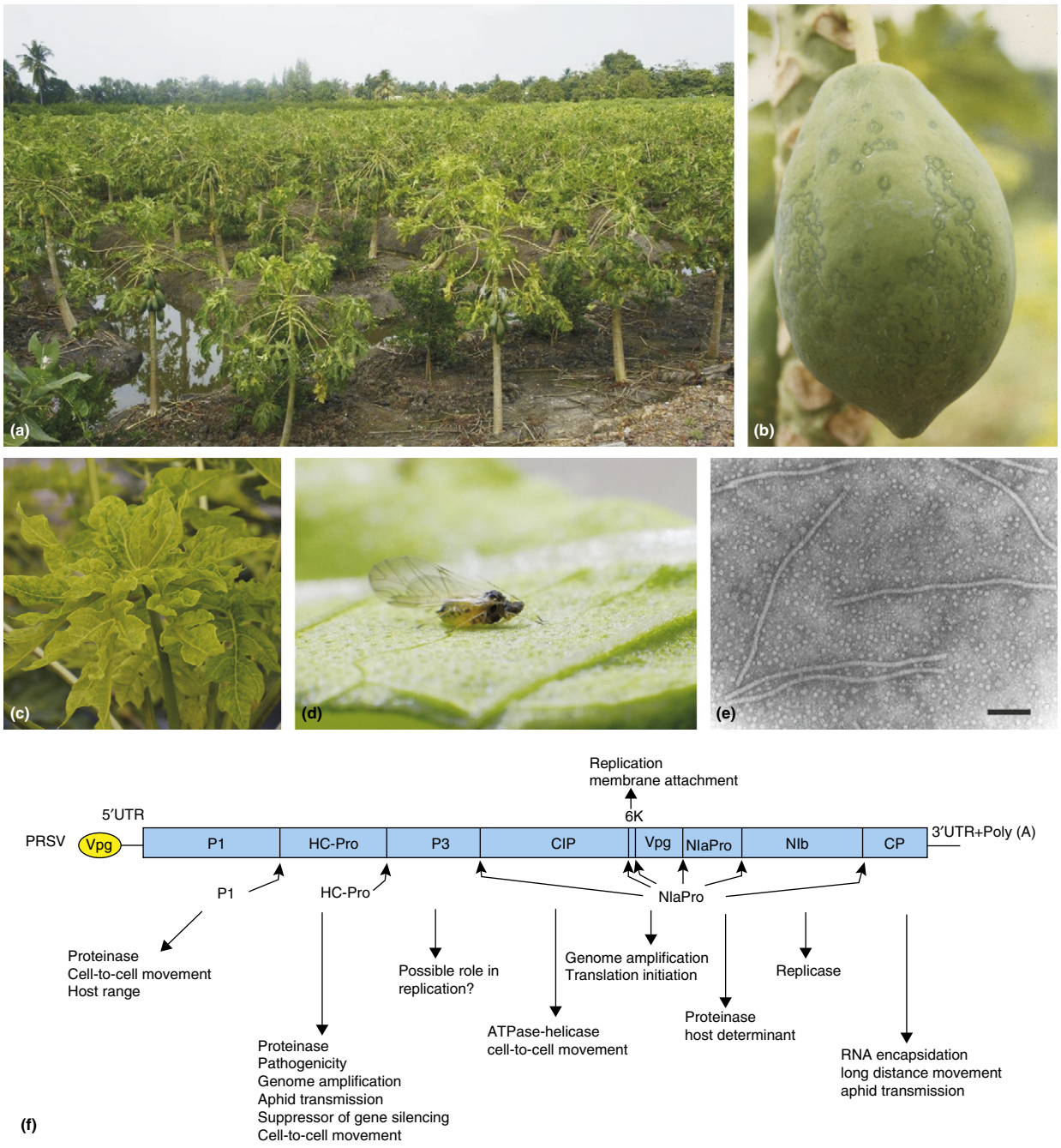


Figure 1 Disease symptoms, aphid vector and particles of *Papaya ringspot virus* (PRSV). (a) A papaya plantation devastated by PRSV. (b) and (c) Symptoms of ringspots on papaya fruit, and mosaic on papaya leaves, respectively. (d) Alate (winged) aphid, the insect vector transmitting PRSV, perching on a papaya leaf. (e) PRSV particles under electron microscope; the scale bar represents 100 nm. (f) Genetic organization and gene functions of PRSV.

of the same virus (Gonsalves and Garnsey, 1989). An attenuated mutant strain of PRSV, designated HA 5-1, was selected following nitrous acid mutagenesis of a severe strain HA originating from Hawaii (Yeh and Gonsalves, 1984). PRSV HA 5-1 was tested extensively in the field and has been used widely in Taiwan and Hawaii since 1985 to permit an economic return from papaya production (Wang *et al.*, 1987; Yeh *et al.*, 1988; Yeh and Gonsalves, 1994). Similar genetically stable, broad-spectrum attenuated strains of major papaya-infecting viruses may be screened from natural sources or engineered in the laboratory for effective cross-protection.

The effectiveness of cross-protection strategy is limited by several technical and practical difficulties, including non-availability of efficient and genetically stable attenuated strains, superinfection by virulent strains, requirement for a large-scale inoculation facility, and insufficient protection



Figure 2 Effective control measures of *Papaya ringspot virus* (PRSV) by cross-protection and netting. (a) Papaya seedlings were mass-inoculated with a mild strain PRSV HA 5-1 by pressure spray (1) and kept in insect-proof nethouse (2). The HA 5-1 cross-protected papaya plant was resistant to severe infection of PRSV HA (3); cross-protected papaya plants loaded with fruits in Taiwan (4); HA 5-1 protected plants loaded with fruits versus unprotected fruitless plants with severe symptoms in a Hawaii field test (5). (b) A papaya orchard protected by netting to avoid PRSV infection (1); Destruction of the protective net by a tropical storm (2). Reproduced with permission from Yeh, S.D., Gonsalves, D., Wang, H.L., Namba, R., Chiu, R.J., 1988. Control of *Papaya ringspot virus* by cross protection. Plant Disease 72, 375–380.

against different strains in different regions (Stubbs, 1964; Gonsalves and Garnsey, 1989; Yeh and Gonsalves, 1994). To reduce the loss from infection by severe strains of viruses, cross-protection strategy may be used along with other control measures, according to the nature of crops and specific situations of geographical regions. However, the success of cross-protection strategy is greatly dependent on efficient large-scale inoculation and complete farmer cooperation during every round of cultivation. In Taiwan, this method was used for control of PRSV during 1984–93, with 200–250 hectors annually applied (Yeh and Gonsalves, 1994). In Hawaii, the cross-protection is working fine against local strains, but the method is not widely extended because of the new control strategy by genetically engineered transgenic resistance. In Thailand, the cross-protection was introduced, but was not widely accepted because HA 5-1 did not provide good protection against Thai PRSV strains (Yeh and Gonsalves, 1994).

Effective Control of *Papaya Ringspot Virus* by Netting

Protecting transplanted seedlings with fine UV-resistant nylon net (32 mesh) by covering the entire orchards provides complete exclusion of aphids that transmit PRSV, and thus guarantees papaya yield (Wang *et al.*, 1987; Yeh and Gonsalves, 1994). After 1994, this method has become the major PRSV control measure in Taiwan, replacing original cross-protection strategy. Currently, a total of 3207 ha papaya orchards are under netting in Taiwan, representing the largest netting cultivation of a perennial fruit crop in the world (**Figure 2(b)**).

The 47 ton ha^{-1} average production of papaya under netting is also the highest production per unit area in the world (COA Agricultural Statistics Yearbook, 2011). However, although such a high production is guaranteed, the flavor and sweetness of the fruits are inferior because the intensity of the sunshine is significantly cut off by the netting. Though this method increases papaya productivity significantly, the accumulating synthetic nylon materials that are difficult to dispose and the hazardous materials produced during burning of those nondegradable polymers are a serious concern, and thus not approved by ecologically conscious people. Also, the high cost for the construction of the netting system, approximately 25 000 US dollars per hectare, is a serious hurdle for small-scale papaya growers. When a tropical storm typhoon hits the island (average 3.5 times a year), most of the papaya growers lose not only the crop, but also the whole netting system. Thus, this is a high cost and risky cultivation method.

Control of *Papaya Ringspot Virus* by RNA Silencing-Based Transgenic Resistance

A disease-susceptible plant can be genetically transformed into disease-resistant plant by incorporation of an appropriate portion of a pathogen's genome into the plant (host) genome. This application is based on the phenomenon of pathogen-derived disease resistance (PDR) (Sanford and Johnston, 1985). For PDR, segments of a pathogen genome can be excised and modified in the laboratory into transgenes and delivered into a plant host by means of particle bombardment (biolistics) or *Agrobacterium*-mediated gene delivery (Chiton, 1983). The genetically transformed plant expresses a pathogen component (a RNA or protein) from the transgene, which sensitizes the plant against the invading pathogen or blocks a crucial phase of pathogen life cycle and thus averts the disease.

Originally, the effectiveness of PDR was critically validated by Beachy and coworkers (Powell-Abel *et al.*, 1986) in the case of the resistance to *Tobacco mosaic virus* (TMV) conferred by the transgenic tobacco lines carrying the CP gene of TMV. The CP gene-mediated transgenic resistance has been proven effective in protecting tobacco, tomato, potato, and other crops from infection by many different RNA viruses (Beachy, 1990; Lomonossoff, 1995; Goldbach *et al.*, 2003). The health and environmental issues can be alleviated or totally avoided by selecting appropriate sequences from pathogens and engineering them into safer transgenes to preempt the possibility of their expression and/or persistent presence of pathogenic proteins or RNA sequences in transgenic hosts. RNA silencing-mediated transgenic resistance is one of the strategies that does not create pathogenic nucleotide sequences or proteins in the host, and hence is totally human-, livestock-, and environment-friendly. In host cells, the long double-stranded RNAs and hairpin-structured RNAs produced by the virus-derived transgene is processed by the host Dicer-like (DCL) protein into a class of small RNAs designated as small interfering RNAs (siRNA). These siRNAs are loaded into RNA-induced silencing complexes (RISCs) containing an ARGONAUTE protein. The siRNAs, which are complementary to the RNA (genome) of the invading virus, is used by the host posttranscriptional gene silencing (PTGS) machinery as a guide RNA to locate the viral genomic RNAs to destroy them (Khvorova *et al.*, 2003; Zamore and Haley, 2005). Excellent reviews (Frizzi and Huang, 2010; Wang *et al.*, 2012) describing the process of PTGS have been published.

The elimination of viral transgenic RNA and viral genomic RNA and prevention of translation of transgenic and viral proteins in the PTGS (RNA silencing)-mediated transgenic plants encouraged many groups to adopt this strategy. Pathogen-derived resistance has been engineered in many economically important crops, and the effective virus resistance of the resultant transgenic lines has been demonstrated (Yeh *et al.*, 2010).

Coat Protein-Transgenic Papaya Resistant to *Papaya Ringspot Virus* Saves Papaya Industry in Hawaii

Papaya is the second largest fruit crop in Hawaii. It is grown commercially for export to the US mainland and Japan. Hawaii exports 25–30% of its produced papaya to Japan. However, the successful present-day Hawaiian papaya industry has a troubled past due to PRSV. In early 1950s, PRSV devastated papaya production on Oahu, forcing the papaya industry to relocate to the Puna district on the Big (Hawaii) Island from the early 1960s. Despite Puna's proximity to the almost abandoned PRSV-infested area, the geographical isolation of Puna and the efforts of the farmers by diligent eradication of diseased plants under the guidance of scientists kept PRSV away from Puna for years. Puna farmers produce 95% of Hawaii's papaya.

First Successful Case of Genetically Modified Fruit Crop for Commercialization

However, the impending danger of PRSV reaching Puna necessitated permanent solution to the PRSV problem. In the late 1980s, to find an effective solution to the severe yield loss caused by PRSV, Gonsalves and coworkers at Cornell University and the University of Hawaii initiated attempts to generate PRSV CP transgenic papaya lines resistant to PRSV. The CP gene of PRSV HA 5-1 was constructed and delivered into payaya genome via particle bombardment (biolistics) of embryogenic tissue derived from premature zygotic embryos of papaya. Tansgenic papaya lines were obtained after regeneration of transformed cells through selection and regeneration steps (Fitch and Manshardt, 1990; Fitch *et al.*, 1992). Under greenhouse and field conditions, the individuals of the PRSV CP transgenic line (55-1) of SunUp papaya cultivar were highly resistant to infection by PRSV isolates originating from Hawaii (Fitch *et al.*, 1992; Lius *et al.*, 1997).

The field trials of the CP transgenic homozygous line of SunUp and CP transgenic hemizygous line of Rainbow indicated their efficacy in managing PRSV in Hawaii (Ferreria *et al.*, 2002). The PRSV resistance of SunUp cultivar is triggered mostly by RNA silencing (Gonsalves, 2002), a process of specific degradation of mRNA responsible for transgenic resistance to plant pathogens (Baulcombe, 1996; Baulcombe, 1999; Hamilton and Baulcombe, 1999). The strong operation of PTGS is likely to be the basis of the estimated 87–99%

reduction in CP levels in the plants of 55-1 line-derived Rainbow and SunUp (Fermín *et al.*, 2011), in comparison to PRSV-infected wild type papaya. Based on the biosafety and economic benefits, these CP transgenic lines of Rainbow and SunUp cultivars of papaya were deregulated in May 1998 by the US Animal and Plant Health Inspection Service and Environmental Protection Agency, and granted approval from the Food and Drug Administration for commercial application (Gonsalves, 2002). This is the first successful case of a transgenic fruit tree being commercialized in the world. Later, PRSV CP transgenic papaya was deregulated in Canada (Suzuki *et al.*, 2007) and Japan (Gottula and Fuchs, 2009).

The Genetically Modified Papaya Cannot Be Applied Outside Hawaii

Owing to the geographical isolation and homogenous PRSV strains in Hawaii, no resistance breakdown has been recorded to date (2013). The Hawaiian papaya industry relies on the PRSV CP transgenic papaya to maintain the production and export of the fruit to US continent, Canada, and Japan. However, the sequence homology-dependent resistance through PTGS on viral CP genes limits the application of these two transgenic cultivars for the management of other PRSV strains in regions out of the geographically secluded Hawaii (Tennant *et al.*, 2001; Gonsalves, 2002). In the case of papaya, a CP transgenic hemizygous line of the cultivar Rainbow, a hybrid derived by crossing a CP transgenic homozygous line of SunUp with nontransgenic cultivar Kapoho, is susceptible to PRSV isolates exotic to Hawaii. However, the CP transgenic homozygous line of the cultivar SunUp is resistant to a wider range of isolates from Jamaica and Brazil, though it is susceptible to isolates from Thailand and Taiwan (Gonsalves, 1998; Tennant *et al.*, 2001; Gonsalves, 2002). The characteristic of sequence homology-dependence of transgenic resistance limits the application of CP transgenic papaya for controlling PRSV in geographical regions other than Hawaii.

Coat Protein-Transgenic Papaya Facing Complicated Situations in Taiwan

In Taiwan, the first PRSV CP transgenic papaya lines resistant or immune to PRSV were generated as early as 1996 (Cheng *et al.*, 1996). Subsequently, PRSV-PLDMV (*Papaya leaf-distortion mosaic virus*) chimeric CP transgenic papaya lines (Kung *et al.*, 2009; for details, see Section Generation of Double Resistance Against *Papaya Ringspot Virus* and *Papaya Leaf-Distortion Mosaic Virus*), PRSV HC-Pro transgenic papaya lines (for details, see Section Threats by *Papaya Ringspot Virus* Super Strains Selected by Coat Protein-Transgenic Resistance and the Solution), and hybrid transgenic papaya lines pyramided with these transgenes (unpublished) have been generated for more effective virus resistance. Though the useful PRSV- and PLDMV-resistant transgenic papaya lines generated in Taiwan have not been deregulated, they have been subjected to long and intensive field evaluations during the period 1996- to date. In parallel, effective genetic transformation and micropropagation methods, which materialize the generation of farmer-preferred all-hermaphrodite population of papaya plants that yield fruits of higher market value, have been developed; the optimized transformation and micropropagation procedures also shorten posttransformational breeding time (also see Sections Current Advances on Papaya Biotechnology, Environmental and Food Safety Assessments of Transgenic Papaya and International Trading, and Concluding Remarks). Overall, the long-term studies from field and laboratory provide useful insights and improve the effectiveness of GM papaya with single-virus, double-virus, or super-virus transgenic resistance. The details are provided in subsequent sections.

The Development of Coat Protein-Transgenic Papaya with Broad-Spectrum Resistance to Different Geographical *Papaya Ringspot Virus* Stains

In Taiwan, the CP gene of a native PRSV strain, designated YK, was used to generate PRSV-resistant transgenic lines of the elite hybrid papaya cultivar Tainung No. 2 by *Agrobacterium*-mediated trasnsformation (Cheng *et al.*, 1996). The transgenic lines showed various levels of resistance, ranging from a few days of delay in PRSV symptom development to complete immunity to the virus (Bau *et al.*, 2003). Several PRSV YK CP transgenic lines, which were highly resistant to the homologous indigenous strain (PRSV YK), also provided wide-spectrum resistance to exotic strains from three different geographical regions, Hawaii, Thailand, and Mexico (Bau *et al.*, 2003) (**Figure 3(a)**). During several field trials from 1996 to 1999, these PRSV YK CP transgenic papaya lines exhibited high degrees of consistent protection against PRSV in Taiwan (Bau *et al.*, 2004).

However, 18 months after plantation in the fourth field trial, unexpected symptoms of severe distortion of fully expanded leaves, stunting of shoot apex, water-soaking on petioles and stem, and yellow ringspots on fruits were noticed on the plants of these lines. The causal agent was distinguished from PRSV by its distinct host reactions and serological properties, and identified as a P type strain PLDMV (Bau *et al.*, 2008), a potyvirus reported from Okinawa, Japan, in 1954 (Maoka *et al.*, 1996). The identified P type Taiwan strain of PLDMV, designated P-TW-WF, was found to be distinct from those from Japan by its inability to infect several cucurbit hosts (Bau *et al.*, 2008), which were reported to be infected by the Japanese strains (Maoka *et al.*, 1996; Maoka and Hataya, 2005). Because all of PRSV CP transgenic papaya lines were susceptible to PLDMV P-TW-WF infection, PLDMV was considered as an emerging threat for the application of the transgenic papaya in Taiwan and other regions (Bau *et al.*, 2008). This situation revealed the urgent necessity for controlling the newly emerging potyvirus PLDMV along with the predominant PRSV in Taiwan and elsewhere (Bau *et al.*, 2008).

Generation of Double Resistance Against *Papaya Ringspot Virus* and *Papaya Leaf-Distortion Mosaic Virus*

Transgenic crops with resistance to multiple viruses can be generated by engineering the plants with CP genes from more than one virus. For generating transgenic papaya lines with resistance to both PRSV and PLDMV, an untranslatable

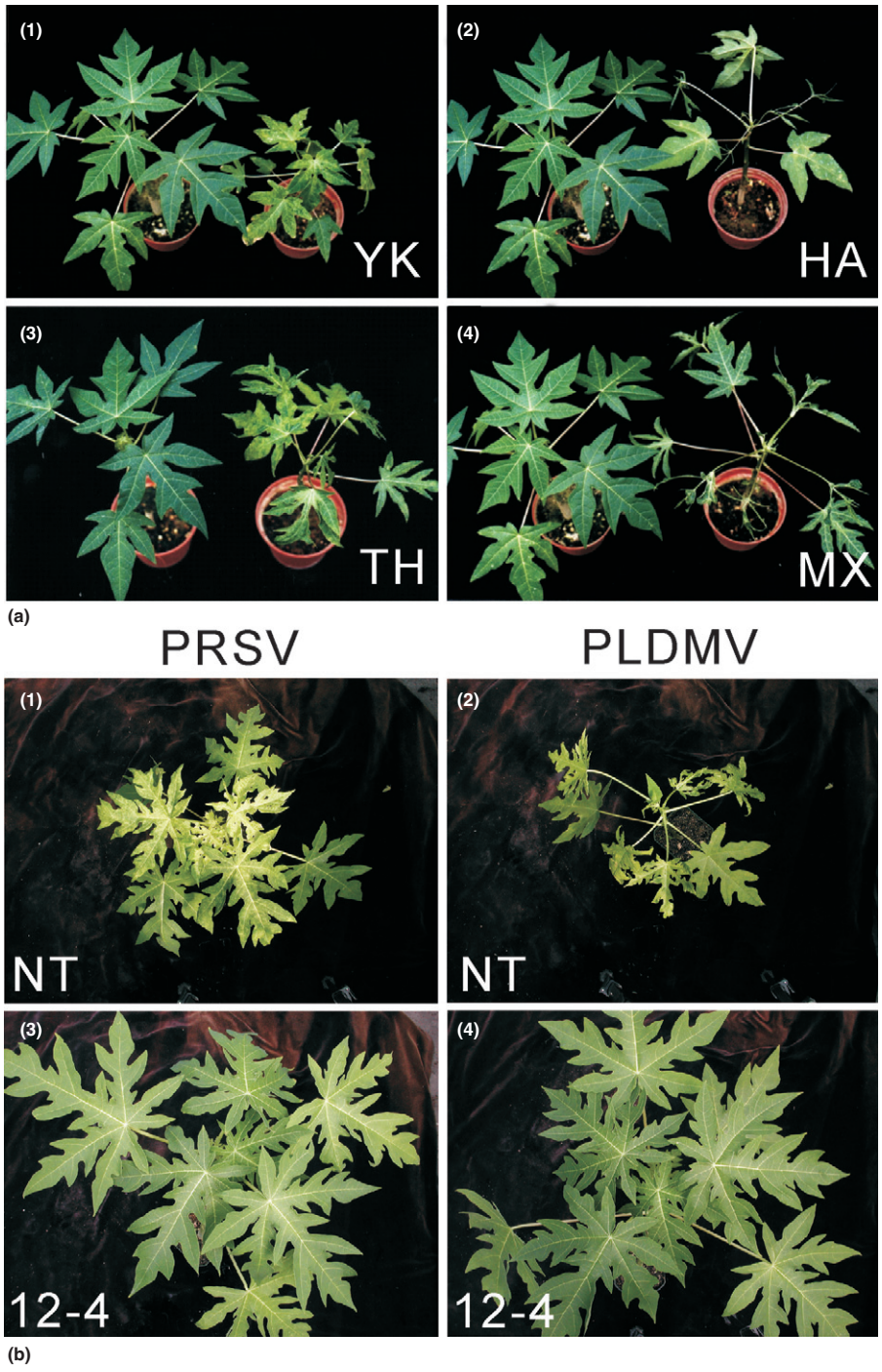


Figure 3 Broad-spectrum resistance of coat protein (CP)-transgenic papaya lines showing single-virus (a) and double-virus resistance (b) to different papaya viral strains. (a) *Papaya ringspot virus* (PRSV) CP transgenic papaya line 19-0-1 showing broad-spectrum resistance to PRSV strain of Taiwan YK (1), Hawaii HA (2), Thailand TH (3), and Mexican MX (e) in contrast to the severely infected nontransgenic papaya plants (1,2,3, and 4 plants at the right). Reproduced with permission from Bau, H.J., Cheng, Y.H., Yu, T.A., Yang, J.S., Yeh, S.D., 2003. Broad spectrum resistance to different geographic strains of *Papaya ringspot virus* in coat protein gene transgenic papaya. Phytopathology 93, 112–120. (b) Double resistance to PRSV and *Papaya leaf-distortion mosaic virus* (PLDMV) conferred by transgenic line 12-4 carrying a PRSV-PLDMV chimeric CP transgene. Nontransgenic papaya plants were susceptible to PRSV (1) and PLDMV (2), whereas the plants of line 12-4 were resistant to PRSV (3) and PLDMV (4). Reproduced with permission from Kung, Y.J., Bau, H.J., Wu, Y.L., *et al.,* 2009. Generation of transgenic papaya with double resistance to *Papaya ringspot virus* and *Papaya leaf-distortion mosaic virus*. Phytopathology 99, 1312–1320.

chimeric construct comprising untranslatable segments of PRSV YK CP and PLDMV P-TW-WF CP genes was constructed and transferred into papaya cv 'Thailand' by *Agrobacterium*-mediated transformation (Kung *et al.*, 2009). The transgenic papaya lines carrying the chimeric CP gene construct were regenerated and micropropagated. Several of the generated PRSV-PLDMV CP transgenic papaya lines exhibited resistance against both PRSV and PLDMV under greenhouse conditions. Molecular analysis of these plants revealed that the transgenic resistance of these plants to PRSV and PLDMV is triggered by the PTGS mechanism. Three lines (10–4, 14–1 and 14–3) showed high degrees of resistance not only to PLDMV P-TW-WF and PRSV YK, which were the transgene donors, but also to the heterologous strains of PRSV MX, TH, and HA, originated respectively from Mexico, Thailand, and Hawaii (Kung *et al.*, 2009) (**Figure 3(b)**). These transgenic papaya plants with PRSV and PLDMV resistance are considered to have a great potential for the control of PRSV and PLDMV in Taiwan and elsewhere (Kung *et al.*, 2009).

Threats by *Papaya Ringspot Virus* Super Strains Selected by Coat Protein-Transgenic Resistance and the Solution

In Taiwan, apart from the PLDMV infection of PRSV CP transgenic papaya lines, they also encountered certain extremely virulent PRSV super strains, including PRSV 5–19. These super strains were able to infect not only the PRSV-resistant transgenic papaya lines (Tripathi *et al.*, 2004), but also the PRSV-PLDMV resistant transgenic papaya lines (You, 2005; Kung *et al.*, 2009). Ironically, the super strain 5–19 was able to breakdown the resistance of the transgenic lines carrying PRSV strain YK CP gene, which shares over 95% nucleotide identity with the CP of 5–19. This level of sequence identity is lesser than those of other PRSV strains that are not virulent enough to overcome the transgenic resistance conferred by YK CP transgene (Tripathi *et al.*, 2004), indicating that the breakdown of the transgenic resistance by 5–19 is not correlated to the sequence divergence between the infecting virus and the transgene.

Subsequent detailed studies on PRSV 5–19, YK, and their recombinants revealed that PRSV 5–19 possesses a stronger gene-silencing suppressor HC-Pro, which can suppress the RNA silencing-mediated transgenic resistance in a transgene sequence homology-independent manner (You, 2005; other unpublished data). Hence, PRSV super strains like 5–19 are regarded as potential threats to the CP gene-mediated single-virus or double-virus resistance of transgenic papaya lines. Such breakdown of transgenic resistance by a strong gene-silencing suppressor of a super strain has strong impacts on the application of transgenic crops for virus control. Moreover, as suggested by the case of PRSV 5–19, the super stains can also wipe out the nontransgenic papaya orchards and cause extreme economic damage.

To disarm the defensive ability of the invading PRSV super strains, new transgenic lines of the papaya cultivar Sunrise carrying the untranslatable full, *N*-, and *C*- terminal region of HC-Pro coding sequences were developed by *Agrobacterium*-mediated transformation of somatic embryos derived from selected hermaphrodite individuals of elite varieties. Several HC-Pro transgenic lines show high levels of resistance to both super strain PRSV 5–19 and other severe strains from Taiwan, Hawaii, Thailand, and Mexico (unpublished data). In the highly resistant lines, low levels of accumulation of mRNA and higher levels of accumulation of siRNA of transgene were observed, suggesting that PTGS was the underlying mechanism for resistance. Such approach is considered more effective than the CP approach, in which HC-Pro can still be processed by autocleavage from the *N*-terminal part of the translated polyprotein to suppress PTGS targeting CP coding sequence that is far down-stream and close to the 3′ terminus of the genome. The results indicated that papaya lines carrying an untranslatable silencing suppressor gene HC-Pro of a PRSV virulent strain can solve the problem resulting from PRSV super strains that create homology-independent transgenic resistance breakdown (unpublished data).

Papaya Production Is Seriously Limited by *Papaya Ringspot Virus* in Southeast Asian Countries

Papaya ringspot disease is the major constraint to papaya production and it causes serious economic loss in Southeast Asian countries, including India, Indonesia, Malaysia, Philippines, Singapore, Thailand, and Vietnam (CABI, 2012; http://www.cabi.org/isc/). The gravity of the PRSV-caused devastation of papaya production and economic loss in these countries can be understood by analyzing the situation in Thailand, which is ironically ranked as the world's ninth most papaya producing country (FAOSTAT, 2013; http://faostat.fao.org/). Angyurekul and Tugsinavisuth (2003), who analyzed the Thai papaya industry during the period 1988–2001, recognized PRSV as the most important threat to Thai papaya industry and emphasized the importance of the development of PRSV-resistant papaya varieties to save the industry. The elite papaya cultivars cultivated in Thailand, Khak Dum and Khak Nuan, which yield red-fleshed elongated fruits, are extremely susceptible to PRSV.

In Thailand, PRSV was first detected at Khon Kaen province, the Northeast region of Thailand in 1975 (Srisomchai, 1975) and spread over the Northeast region in 1981. During 1980s, PRSV rapidly dispersed through the central region of the country, which is the major papaya plantation area, and seriously decreased papaya production nationwide (**Figure 4**). Plantation and production of papaya decreased by more than a half between 1997 and 2006 and the declining trend is continuing to date. Papaya growers decrease the extent of damage of PRSV by shifting cultivation to the new isolated areas, a practice economically unviable. In the Northeast region of Thailand, papaya is cultivated as a backyard crop grown by subsistence farmers.

The magnitude of PRSV devastation of papaya production can be understood by the reported extremely poor papaya productivity in Thailand. More than 98% of papaya produced in Thailand is consumed in the country. In 2010, Thailand produced as low as 211 594 ton of papaya, barely meeting the domestic demand and exporting a paltry 630 ton of papaya (FAOSTAT, 2013; http://faostat.fao.org/). The decrease in yield and insufficient supply of papaya has led to the import of papaya from neighboring countries (Napasintuwong and



Figure 4 Devastation of the disease caused by *Papaya ringspot virus* (PRSV) in Nakhon Pathom, a Province of Central Thailand. (a) Symptoms of ringspots on papaya fruit. (b) Oily streaks on stem. (c) Mosaic and distortion on leaves. (d) A papaya orchard completely destroyed by the ringspot disease. The grower (right front) explaining his pain and sorrow to the experts: Dr. Wichai Kositrana, Kasesart University, Thailand (third from left), Dr. Neal Van Alfen, University of California, Davis (second from left), and Dr. William Lucas, University of California, Davis (first from left).

Traxler, 2009). The quantum of import of papaya, which was started in 2007 in an insignificant quantity, is gradually increasing; in the year 2010, Thailand imported 329 ton of papaya (FAOSTAT, 2013; http://faostat.fao.org/).

Development of Coat Protein-Transgenic Papaya in Thailand

Several strategies to manage PRSV in Thailand include the attempted eradication of infected papaya during 1979–81, in the Northeastern part of Thailand. This program advocated by the Department of Agricultural Extension (DAE), Ministry of Agriculture and Cooperatives (MOAC), was unsuccessful in combating PRSV. The healthy papaya seedlings supplied to the villagers for replacement were infected by PRSV within a short period after planting. Moreover, small-scale papaya growers and subsistence farmers growing papaya as a backyard crop declined to destroy their infected papaya trees, especially during the fruit-bearing stage.

In 1987, collaboration between the Thailand DAE, MOAC, and Cornell University, supported by USAID, was set up to control PRSV by adopting cross-protection and developing PRSV-tolerant papaya cultivars. Cross-protection (also see Section Effective Control of *Papaya Ringspot Virus* by Netting) using nitrous acid-induced attenuated PRSV strain HA5-1 (Yeh and Gonsalves, 1984) and naturally occurring mild strains, including PRV-F1 (Kositratana *et al.*, 1991), was inadequate for sustainable PRSV control in the field trials (Sakuanrungsirikul *et al.*, 2005) and labor-intensive, especially when farmers select hermaphrodite plants after inoculating all seedlings during their early sexually monomorphic stage. In conventional breeding program for tolerant hybrid cultivars (also see Section Control of *Papaya Ringspot Virus* by Cross-Protection), the Thai cultivar Khak Dum was crossed with the tolerant Florida cultivar Cariflora (Conover *et al.*, 1986). However, the resultant three lines, Tha Pra 1, 2, and 3, were insufficiently tolerant to manage PRSV, and they yielded unmarketable fruits (Sakuanrungsirikul *et al.*, 2005).

In Thailand, three independent research groups, (1) Department of Agriculture (DOA), MOAC, in collaboration with Dr. Dennis Gonsalves of Cornell University under the Northeast Rainfed Agricultural Development (NERAD) Project at Northeast Regional Office of Agriculture (NEROA), (2) National Center for Genetic Engineering and Biotechnology (BIOTEC) in collaboration with Kasetsart University, and (3) Institute of Molecular Biology and Genetics (IMBG), Mahidol

University, developed PRSV-resistant transgenic papaya using CP genes of different geographical PRSV strains of Thailand (Warin *et al.*, 2003; Sakuanrungsirikul *et al.*, 2005; Kertbundit and Juricek, 2010).

The Delay in Adopting Transgenic Technology Impedes Papaya Production

Since 1999, evaluation of PRSV resistance and Biosafety assessments of these transgenic papaya lines under greenhouse and field conditions have been conducted (Sakuanrungsirikul *et al.*, 2005; Phironrit *et al.*, 2010; Kongsawat *et al.*, 2011; Chusang *et al.*, 2011), though transgenic papaya has not been deregulated in Thailand. Although the sixth National Social and Economic Development Plan of Thailand (1987–1991) emphasized biotechnology as one of the frontier areas of agricultural development, there are self-limiting constraints and inconsistencies that block the process of deregulation essential for avoiding loss of millions of dollars of economic benefits. In Thailand, the BIOTEC, established in 1983, has played an important role in driving Thailand toward becoming the first ASEAN country to draw the biosafety guidelines in June 1992 (Technical Biosafety Committee, 2010). To ensure safety and to prevent unpredictable risks, Thai government amended the 1964 Plant Quarantine Act to strengthen the regulation of GM crops in 1999. On 17 March 2000, 40 transgenic crops (except corn and soybean) were listed as prohibited and banned from importation and commercialization. On 14 October 2003, an additional 49 GM crops were listed as prohibited, however, allowing import of processed products and materials for research purposes. Flavr Savr tomato was the first transgenic crop introduced into Thailand for field testing in 1994. Following permission for field trial in 1996, Bt cotton was expected to be the first transgenic crop to be deregulated and commercialized in Thailand, following required field assessment. However, in October 1999, certain nongovernmental organizations (NGOs) reported that Bt cotton was spreading from Monsanto's approved site to the fields of local farmers. The political pressure from the assembly of the poor forced the Thailand cabinet to declare a moratorium and to ban all field trials of transgenic plants on 3 April 2001, until the biosafety law is enacted. Only small secluded fields of transgenic papaya at DOA research station, Kasetsart University and Mahidol University were allowed to continue under the IBC regulations. In July 2004, Greenpeace Organization alleged transgenic papaya seed contamination of Khak Dum and Tha Pra cultivar seeds distributed by DOA as an intentional act of DOA and demanded Thai government to immediately destroy all papaya seedlings, trees, fruits, and seeds at the research station to prevent further spread of contamination. Consequently, a series of political, governmental, and legal developments came into force leading to a prime ministerial order to destroy all field trials in the country, a cabinet decision to place a moratorium on all confined field trials in Thailand. Despite the opposition to GM technology by activists, some scientists strongly believe that GM crops have great potential to solve energy and food security problems. As a result, the Thai Cabinet on 25 December 2007 revoked the field trial ban of GM crops, however, with stringent regulatory conditions.

To date (September 2013), no field trials or commercialization of GM crops is allowed in Thailand due to fear of losing export markets, environmental and health concerns, and seed business takeover by multinational seed companies. Little public information is available on the costs and benefits of GM technology to the Thai economy; clear national policies on research and application of GM crops are yet to be made. Economic evaluation of transgenic crops is essential for the development of appropriate future agricultural biotechnology policies. Ex-ante impact assessment based on scientific data and economic environment of GM papaya adoption in Thailand estimated that total economic surplus in the range of US$ 650 million to 1.5 billion would be generated within the first 10 years of adoption. Benefits from GM papaya adoption would accrue primarily to small-scale papaya farmers and also would accrue even with the loss of export markets (Napasintuwong and Traxler, 2009). The delay in adopting transgenic technology in Thailand reflects the lack of comprehensive biosafety laws, public skepticism concerning transgenic plants, the lack of trust in the capability to regulate biosafety, and the effectiveness of the anti GM groups. This situation dissuades Thai researchers from using modern biotechnology to improve the quality and quantity of crop and food productions in Thailand.

Current Advances on Papaya Biotechnology

The government of Taiwan follows the European trend, and has not approved growing any GM crops on the island yet. However, researches for the development of CP transgenic resistance and authorized field tests under isolated conditions have been strongly supported by the government in the past two decades. The GM crop policy deadlock, however, with government's support for the development, analysis, and improvement of transgenic papaya, proves to be a boon in disguise to improve papaya transgenic technology. The basic studies to understand the complexity of potyviruses infecting papaya and the repeated field tests of CP transgenic papaya for more than 10 years helped the advancement of GM technology toward the development of aforementioned single and double resistances to PRSV and PRSV-PLDMV, respectively; and super resistance to PRSV super strains. The findings in concert with the information of integrated genetic map and genome sequence of papaya from the University of Hawaii (Ming *et al.*, 2008; Yu *et al.*, 2009) helped the development of new skills such as marker-assisted molecular breeding for fixation of hermaphrodite sex and fruit quality traits.

In papaya cultivation, because the hermaphrodite fruits are commercially desirable, growers normally plant seedlings in numbers far greater than required, and grow them till early flowering stage to identify and exclude less desired female individuals. To avoid this wasteful and labor-intensive practice, micropropagation by tissue culture techniques to mass produce hermaphroditic papaya plants with uniform fruit size and quality have been developed. New transformation strategy (Kung *et al.*, 2010) using somatic embryos (Lin and Yang, 2001) derived from adventitious root tissues of *in vitro* micropropagated shoots of selected hermaphrodite individuals from different varieties can retain desirable sex and

fruit traits in the regenerated virus-resistant T_0 generation, which can be directly applied for commercialization by the micropropagation method, and thus avoid the lengthy post-transformational breeding process.

The molecular markers developed from the flanking sequences of a particular transgene insert can help identify the homozygotic transgene in the seedlings (Fan *et al.*, 2009). This, coupled with the hermaphrodite sex markers, can promptly identify a hermaphroditic progeny carrying a homozygotic transgene. These molecular markers assisted in pyramiding different transgenes conferring single, double, or super resistance to generate elite papaya hybrids with broad-spectrum resistance against different geographical PRSV and PLDMV strains.

Transgene Integration Event-Specific Markers for Fastening the Process of Molecular Breeding

The issues of concerns have been raised on the safety of food from genetically modified organisms (GMOs) and food production (Singh *et al.*, 2006). Various legislations have been applied in different countries for the GM food approval and labeling. According to European Union (EU) regulation (EC) No. 1830/2003, it is required to trace GMO and products derived from GMOs at every stage from production to the distribution chains (European Parliament and Council of European Union, 2003). The regulation in Taiwan for GM crop field tests and the consequent variety rights also require the information of genomic sequences flanking the transgene for every transgenic line. Therefore, characterization of a particular GM crop to provide specific and reliable information for event-specific detection is crucial to assure regulatory compliance and also important to monitor unauthorized GM crop occurrence in markets and plantations. Several approaches have been developed for characterizing the inserted transgene and plant genomic DNA sequences flanking T-DNA for identification of a transgenic line (Fan *et al.*, 2009 and references therein). Thus, protocols to ascertain integration of T-DNA in transgenic papaya lines have been developed. Screening and confirmation protocols with appropriate oligonucleotide primers designed from the flanking sequences for transgene integration event-specific characterization have been established (Fan *et al.*, 2009). These protocols are important not only for the regulatory requirement and the intellectual protection of the developed transgenic papaya lines, but also for risk assessment, biosafety assay, and molecular breeding of papaya for crop improvement. At present, these transgene integration event-specific markers are being used for monitoring the transgene genotype status of the parental lines and their progenies during the breeding process for pyramiding different transgenes into a super hybrid hermaphroditic papaya line.

Papaya Sex-Linked DNA Markers and Traits Genes for Sex-Determination and Fruit Quality

Carica papaya is a triecious species comprising individuals of male, hermaphrodite, and female sexes; the plants are diploid ($2n=18$). The male plants are solely pollinators and economically unimportant, and, from farmers' perspective, they are a serious liability. Moreover, the female plants, which produce spherical fruits of thinner flesh with more seeds are commercially less desired than the hermaphrodite plants, which produce pyriform fruits of thicker flesh with lesser seeds. Hence, it is important to develop efficient methods for papaya sex-identification at a very early seedling stage at the nurseries to avoid planting individuals of unwanted and less desired sexes in papaya orchards. This necessitates in-depth studies of papaya genetics and subsequent application of outcomes in papaya cultivation.

Earlier studies on the sex of papaya identified a sex-determining gene represented by three alleles, M, M^h, and m; males (Mm) and hermaphrodites (M^hm) are heterozygous and females (mm) are homozygous recessive (Storey, 1938; Hofmeyr, 1938). MM, M^h M^h, and M M^h are embryonic lethal (Hofmeyr, 1938; Storey, 1938). Hence, a hermaphrodite crossing results in a 2:1 segregation of hermaphrodites to females. Cloning and characterization of the papaya sex-determining and sex-related genes have profound applications in papaya production. Papaya possesses recently evolved sex chromosomes. Papaya Y chromosome has a male-specific region, which has undergone severe recombination suppression and DNA sequence degeneration (Liu *et al.*, 2004; Ming *et al.*, 2007). Ming *et al.* (2007) suggested that two sex-determination genes control the sex-determination: a feminizing (stamen-suppressing) gene determines stamen abortion before or at flower inception, and a masculinizing (carpel-suppressing) gene determines carpel abortion at a later flower developmental stage. Recently Ming and coworkers (Gschwend *et al.*, 2011) constructed two bacterial artificial chromosome (BAC) libraries from papaya male and female genomic DNA.

Identification of reliable molecular markers for papaya sex-identification at the seedling stage will facilitate papaya cultivation and breeding by saving time, space, and labor cost. The papaya sex locus has been genetically mapped to a specific linkage group (Sondur *et al.*, 1996). Several random amplified polymorphic DNA (RAPD) and microsatellite markers linked to papaya sex have been reported (Sondur *et al.*, 1996; Parasnis *et al.*, 1999; Urasaki *et al.*, 2002; Deputy *et al.*, 2002). An RAPD papaya sex-determination marker (PSDM) of 450 bp is present in male and hermaphrodite plants, but absent in female plants (Urasaki *et al.*, 2002). Based on such RAPD-based PSDM sequences, fully specific sequence-characterized amplified region (SCAR) markers can be determined for accurate sex-identification. For instance, the SCAR primers, SCAR T12 and SCAR W11, amplify a hermaphrodite- or male-specific SCAR marker. The primer SCAR T12 in combination with SCAR T1, which amplifies a product regardless of sex type, enables prediction of hermaphrodite plants in a seedling population with an overall accuracy of 99.2% (Deputy *et al.*, 2002).

Ma *et al.* (2004) constructed a high-density genetic map of papaya using 1498 AFLP markers mapping into 12 linkage groups spanning a total genetic length of 3294 cM. The genetic map revealed severe recombination around the sex-determination locus with 225 markers cosegregating with sex types. A sequence-tagged high-density microsatellite genetic map of papaya (Chen *et al.*, 2007) and a physical map of the papaya genome with integrated genetic map and genome sequence (Ming *et al.*, 2008; Yu *et al.*, 2009) have been constructed for comparative structural evolutionary genomics of

papaya. In-depth analyses of high-density genetic maps, detailed physical maps, and full genome sequences and molecular/genetic studies are likely to uncover candidate sex-determining genes and other agriculturally important genes of papaya. Skelton *et al.* (2006) cloned and characterized a lycopene β-cyclase (*lcy-β*) gene, which was later renamed as *lcy-β*1 (Devitt *et al.*, 2010), when a second lycopene b-cyclase gene, *lcy-β*2 (along with *lcy-β*1), was cloned and characterized by Devitt *et al.* (2010) from the red papaya cultivar Tainung. Blas *et al.* (2010) cloned and characterized a papaya chromoplast-specific lycopene β-cyclase, CpCYC-b, from SunUp papaya cultivar. The flesh color of papaya fruit, which is determined by lycopene or β-carotenoids accumulating based on the expression pattern of different lycopene β-cyclase genes (Skelton *et al.*, 2006; Devitt *et al.*, 2010; Blas *et al.*, 2010), is an important quality trait that correlates with nutritional value and consumer preference (Blas *et al.*, 2010).

Genetic Transformation Using Somatic Embryos and Micropropagation of Hermaphroditic Plants of Papaya Cultivars

The fruits from hermaphroditic papaya plants are commercially desirable than female plants, for they contain less seeds and thicker flesh (Yeh *et al.*, 2007). However, the sex and other horticultural and fruit traits of transgenic papaya lines can be determined only after flowering and fruit production. Hence, despite the time and effort spent, only a subpopulation of plants is represented by the hermaphrodite plants that are desirable for their fruit quality.

In general, the breeding programs aiming to incorporate the desired sex and other useful traits into commercial hybrid cultivars of papaya are technically complicated, labor-intensive, and time-consuming. In papaya genetic transformation for micropropagation, somatic embryos derived from premature zygotic embryos are the most commonly used starting materials (Fitch and Manshardt, 1990; Cabrera-Ponce *et al.*, 1995, 1996; Cheng *et al.*, 1996; Cai *et al.*, 1999). Such premature zygotic embryo-derived somatic embryos are considered to be the most effective explants for both biolistic delivery and *Agrobacterium*-mediated transformation. However, the immature zygotic embryos are very difficult to obtain and often affected by seasonal factors.

Hermaphrodite plants can be generated as clonal plants using appropriate tissues from selected hermaphroditic individuals through somatic embryogenesis. As shown by Lin and Yang (2001), the adventitious roots developed from *in vitro* shoots of hermaphroditic individuals can be cultured to induce somatic embryos within four months. Using somatic embryos derived from the adventitious roots of *in vitro* shoots of hermaphroditic individuals as explants, Kung *et al.* (2010) transformed the elite hybrid cultivar 'Tainung No. 2' with a chimeric transgene comprising portions of PRSV and PLDMV CP gene sequences. The selected transgenic hermaphrodite lines confer complete resistance to both PRSV and PLDMV. This strategy was also used to produce transgenic plants of the parental lines of Tainung No. 2 hybrid cultivar, including Thailand and Sunrise (Kung *et al.*, 2010).

To ascertain the hermaphroditic criterion of the obtained transgenic lines during early seedling stage, Kung *et al.* (2010) used the hermaphrodite sex-linked RAPD marker amplifiable by the primers SDP1 and SDP2 (Urasaki *et al.*, 2002). The RAPD marker-predicted transgenic seedlings turned up to be a population, exclusively, of hermaphroditic individuals with floral and fruit phenotypes indistinguishable from those of nontransgenic control plants.

Genetic transformation of somatic embryos derived from the adventitious roots of *in vitro* shoots of hermaphroditic individuals of the elite papaya results in hermaphroditic papaya lines of desired horticultural traits for direct large-scale micropropagation without posttransformation breeding. Compared to the recently generated double-virus resistant papaya lines with female sex regenerated from immature zygotic embryos (Kung *et al.*, 2009), which needed several years to generate hermaphroditic papaya with desired properties via breeding, this new approach (Kung *et al.*, 2010) significantly shortens the time-consuming breeding program.

Pyramiding of Single, Double, and Super Transgenic Resistance in a Commercial Hybrid for Global Application

For broad-spectrum resistance to strains of PRSV and PLDMV, a commercial papaya hybrid Tainung No. 2 is currently being developed by pyramiding the transgenes from the parental lines Thailand and Sunrise carrying various transgenes. The breeding procedure involves (1) selection of transgenic lines with high degrees of resistance to PRSV and PLDMV and (2) fixation of the transgene in parental line as homozygote by selfing of double-virus-resistant papaya line of Thailand and super-PRSV resistant papaya line of Sunrise. As demonstrated recently (Fan *et al.*, 2009), appropriate transgenic event-specific primers are used to monitor the transgene-genotypic status of the parental lines or progenies during breeding and to confirm pyramiding of the transgenes in the final hybrid of new Tainung No. 2. In this way, a new Tanung No. 2 hybrid with broad-spectrum resistance to strains of PLDMV and PRSV can be generated within two years. During the process of pyramiding, appropriate sex-linked markers, as suggested by Urasaki *et al.* (2002), are used to confirm the hermaphroditic nature of the hemizygotic or homozygotic status of each papaya line and its progeny. The development of this super transgenic hybrid papaya should have a great potential for global application for controlling different strains of PRSV and PLDMV in different geographical regions.

Environmental and Food Safety Assessments of Transgenic Papaya and International Trading

Environmental organizations, a section of statesmen, and informed public are conscious of the potential risks associated with GM. Scientific and regulatory authorities are also aware of potential environmental and socio-political risks associated with GM crops. Hence, decision making in favor of cultivation of GM crops and commercial release of GM food and other GM products is tough and requires political will. Safety assessment frameworks have been designed to identify potential environmental and food safety risks before commercial release (König *et al.*, 2004).

The analyses of the transgene insertion sites and flanking genomic DNA in CP transgenic papaya did not predict any allergenic or toxic proteins (Suzuki *et al.*, 2008). Moreover, no ecological effects of transgenic papayas on surrounding soil, microflora and insects, and adjacent nontransgenic papaya plants were found (Sakuanrungsirikul *et al.*, 2005). Consumption of GM papaya does not affect human and livestock health, because GM papaya is relatively free from viral components; when compared to the abundance of viral CP in non-GM papaya (which is in general infected with PRSV), the transgenic CP is expressed at very low levels in the transgenic papaya (Fermín *et al.*, 2011). PRSV CP is heat-labile and degraded in simulated gastric and intestinal conditions (Fuchs and Gonsalves, 2007; Roberts *et al.*, 2008; Fermín *et al.*, 2011). Moreover, PRSV CP does not resemble any known allergenic proteins and is not allergenic by property (Fermín *et al.*, 2011). Powell *et al.* (2010) found that long-term exposure to diets formulated with CP transgenic papaya did not result in any significant effects on intestinal morphology, histology, digestive enzyme activities, and intestinal microflora. Lin *et al.* (2013) evaluated the toxicity effects of the fruits of two backcross transgenic papaya lines and their hybrid line and found that the transgenic CP was rapidly hydrolyzed in SGF and the products were undetectable in organs and gastrointestinal contents in rats. Moreover, a repeated feeding of papaya fruits did not evidence biological or toxicological significance between nontransgenic and backcross transgenic papaya fruits in rats. Tripathi *et al.* (2011) showed that the contents of nutrients, benzyl isothiocyanate, and papain of CP transgenic Rainbow papaya are within the range of those of nontransgenic papaya and that the Rainbow cultivar is substantially similar to the nontransgenic cultivar. With regard to the products of the marker transgenes, the safety of NPTII and GUS proteins in transgenic food and feed products has been widely demonstrated in chronic and subchronic investigations (Gilissen *et al.*, 1998; Miki and McHugh, 2004; Ramessar *et al.*, 2007). Moreover, CP transgenic papayas, also harboring *npt*II and *gus*A transgenes, have been on the US and Canadian markets since the late 1990s and mid-2000s, respectively. No evidence of ill effects is linked to their consumption (Fuchs and Gonsalves, 2007).

In the case of the PTGS-mediated transgenic resistance of the CP transgenic papaya, the untranslatable transgenic CP RNA is destined to be degraded and CP is not synthesized; so, most of the above described concern about transgene-derived PRSV CP does not arise.

Concluding Remarks

The transgenic resistance conferred by the viral CP gene has become the most effective method to prevent papaya from infection by the noxious PRSV. In 1998, the Hawaiian PRSV CP gene transgenic papaya cultivars Rainbow and SunUp were deregulated and granted approval for commercialization, representing the first successful application of transgenic fruit tree in the world. Although the transgenic lines are not resistant to most of the PRSV strains from other different geographical areas, the breakdown of the transgenic resistance to PRSV strains indigenous to Hawaii has not been noticed. This probably due to the fact that Hawaii island is isolated by thousand miles of ocean and the virus strains are quite homogenous. Thus, the GM papaya has saved the papaya industry in Hawaii, without any significant adverse effects to environment and human health during the application for more than a decade. After intensive studies to meet the strict biosafety regulations of Japan, the GM papaya of Hawaii was allowed to be sold in Japanese markets since 2011, representing the first case of GM fruit permitted for international trading. If this successful model of production and trading is accepted by most countries, GM papaya will become one of the important fruits for international markets.

In the case of Taiwan, the situation is more complicated. The government follows the European trend, and does not approve the growth of any GM crops on the island yet. However, the research and field tests under isolated conditions have been strongly supported by the government in the past two decades. Our intensive field trials and laboratory investigations of potyviruses infecting papaya triggered advancement of GM technology toward the development of single, double, and super resistances to PRSV, PRSV/PLDMV, and super-PRSV strains, respectively. Also, the micropropagation tissue culture technique, the somatic embryos transformation method, and marker-assistance molecular breeding for fixation of hermaphrodite and transgenes represent the most advanced levels for papaya biotechnological research. However, the national regulations which do not provide the necessary support for the utilization of GM papaya, in fact, hamper the practical application of GM papaya to transform papaya industry. Although the netting system is a very effective way to prevent PSRV infection, the high cost, inferior fruit quality, and environmental hazards make this artificial cultivation system unacceptable for ecologically conscious people.

However, unexpected breakdowns of single-virus resistance of PRSV CP transgenic lines by PLDMV and double-virus resistance of PRSV-PLDMV CP transgenic lines by super strains of PRSV were encountered. The breakdown of the transgenic resistance by the super virulent strain PRSV 5–19 due to its stronger gene-silencing suppression ability of the HC-Pro, which can shut off PTGS and abort the transgenic resistance completely, does not result from the divergence between viral CP gene and the transgene. Thus, the application of CP transgenic resistance based on the mechanism of RNA silencing may select out super strains that contain a stronger silencing suppressor for more virulent infection. These super strains not only threaten the transgenic papaya, but also may wipe out other nontransgenic papaya or other cucurbitaceous crops. Thus, carefully monitoring the dynamic change of virus population after the application of a GM crop is important to prevent the risk of the selection, the emergence, and the spread of such super virulent strains.

In Thailand, although the CP transgenic papaya lines resistant to PRSV have been developed, hope for deregulation of GM papaya is bleak and politically mired. The strong campaign by anti GM crop groups such as Greenpeace Organization strongly influences the policy and regulation for GM field tests and approval. Most of the research on GM papaya is either stalled or inhibited. The production and plantation

areas of papaya are declining, and the sufferings of the growers from PRSV devastation never get eased. This makes a country with excellent potential for surplus production and profitable export of papaya to import the same. In this situation, the benefits of GM papaya are not appreciated and the costs and devastation of PRSV prevail to a worst condition.

To disarm the stronger gene-silencing suppression ability of the invading super strain, new transgenic papaya lines carrying the untranslatable sequences targeting HC-Pro gene have been developed by *Agrobacterium*-mediated transformation of papaya somatic embryos from selected hermaphrodite individuals of elite hybrid cultivars and their parental lines. Several transgenic lines show high degrees of resistance to the super strain PRSV 5–19 and other severe strains originated from different geographical regions. The recent advances in transformation of somatic embryos derived from the adventitious roots of elite papaya cultivars provide a prompt way to generate transgenic papaya lines with desired horticultural properties and hermaphrodite sex, for direct application or to shorten the time-consuming process of breeding. The molecular markers derived from the flanking sequences of the transgene integration significantly fasten the molecular breeding process for pyramiding of single, double, and super transgenic resistance into a commercial hybrid variety. The pyramided transgenic resistance is expected to have a more durable wide-spectrum resistance to different geographical strains of PRSV and PLDMV and can avoid the selection for super virulent virus strains. These will result in a more sustainable application of GM papaya in different regions of the world.

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See also: Agricultural Policy: A Global View. Biotechnology: Regulatory Issues. Cloning: Plants – Micropropagation/Tissue Culture. Plant Virus Control by Post-Transcriptional Gene Silencing. Regulatory Challenges to Commercializing the Products of Ag Biotech. Transgenic Methodologies – Plants

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Agribusiness Organization and Management

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Glossary

Agribusiness The sector of the economy that is the sequence of interrelated activities made up of genetics and seed stock firms; agricultural input suppliers, agricultural producers, agricultural commodity merchandisers, food processors, food retailers, and food consumers.
Capital structure The mix of debt and equity used by a firm to finance its purchase of assets.
DuPont analysis of profitability A financial management tool that decomposes return on equity into its component parts: operating profit margin, asset turnover, and financial leverage.
Entrepreneurship The capacity and capability to identify new business opportunities and to successfully bring that opportunity to market and generate superior financial performance.
Porter's Five Forces analysis A strategic framework useful for assessing industry structure and profitability that includes industry rivalry, power of buyers, power of suppliers, threat of substitutes, and threat of new entrants.
SWOT analysis A strategic assessment at the firm level that includes an analysis of the firm's internal strengths and weaknesses in addition to the firm's external opportunities and threats.

Introduction

The purpose of this article is to discuss contemporary topics in food and agribusiness research with a focus on a definition of agribusiness, a description of the global agribusiness environment, and a discussion of the roles in managing an agribusiness firm.

Concept of Agribusiness

The agribusiness sector is comprised of interrelated subsectors working in concert to provide goods and services to consumers around the world. With the need to accommodate economic, social, and environmental concerns, organizations and managers in the sector share many of the challenges that exist in other business value chains. However, food is an economic good with distinctive cultural, institutional, and political aspects shaping the economic environment of the sector, the organizational structure of its firms, and the choice set available to its managers. Further the fundamental uncertainties emanating from weather and other sources of variability within biology-based production sectors add to the complexity of management in the sector.

Food and Agribusiness Value Chain and Sectors

As depicted in Figure 1, the sector can be thought of as a sequence of interrelated activities made up of:

- Genetics and seed stock firms
- Input suppliers
- Agricultural producers
- Merchandisers or first handlers
- Processors
- Retailers
- Consumers

This, of course, is a general listing and finer distinctions, for example, separately identifying wholesaling and food service, could be done. Supporting these activities are firms that provide services, financing, and research and development to the sector. Also, as indicated in Figure 1, the sector operates in an international context with substantial levels of both imports and exports.

This perspective of the agribusiness sector is not new (Davis and Goldberg, 1957; Sonka and Hudson, 1989). However, there are important differences between this depiction and many that are traditionally offered. First, the depiction in Figure 1 explicitly includes agricultural production, thus eliminating the artificial exclusion of farming enterprises. A second distinction relates to the inclusion of consumers in the diagram. This recognizes the increasing demand by consumers for new products and the resulting impacts on the production, processing, and distribution of food, fiber, biofuel, and other bio-products. Success in the sector requires an understanding of the needs and desires of consumers in both domestic and world markets.

Distinctive Challenges Faced by Food and Agribusiness Firms

There are at least five distinctive characteristics of the sector:

1. Unique cultural, institutional, and political aspects of food, domestically and internationally,
2. 'Uncertainty' arising from the underlying biologic basis of crop and livestock production,
3. Alternative 'forms of political intervention' across subsectors and nations,
4. Institutional arrangements that place significant portions of the 'technology development process' in the public sector, and
5. Differing 'competitive structures' within the stages of the sector.

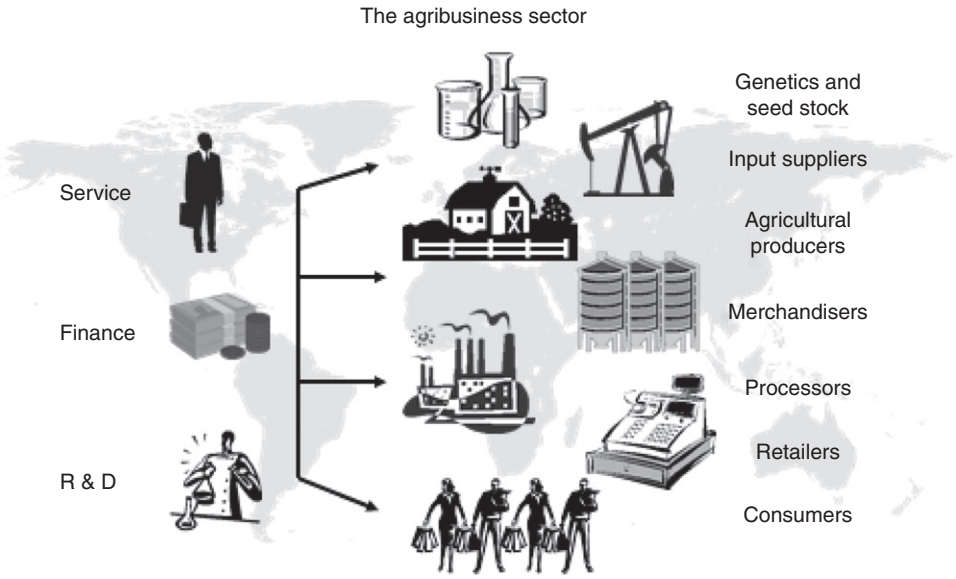


Figure 1 The agribusiness sector. Adapted from Sonka, S.T., Hudson, M.A., 1989. Why agribusiness anyway? Agribusiness 5, 305–314.

These five characteristics suggest the need for targeted managerial skills and knowledge to facilitate effective operation within the sector.

We all understand that food is a necessity for human life. Therefore, assuring adequate amounts of safe, nutritious food (e.g., food security) is a priority for all societies and governments. But food and its consumption are integral parts of the culture of human society. Indeed, anthropologists note that cooking food is one of the actions that uniquely define the human species (Murcott, 1986). Differences across nations and cultures relative to the role of specific foods are critical in understanding the agribusiness sector. For example, although wheat and rice are both food grains, rice in the Japanese culture is far more than just the staple food item that wheat is in the Western nations. The key role of international trade requires that sector managers be aware of these cultural differences.

As evidenced on an increasingly routine basis, the forces of nature (e.g., weather and pests) can overwhelm even the sophisticated technology of modem agriculture. Production, marketing, and financial structures to accommodate normal aspects of 'uncertainty' need to be understood by sector managers. The potential for infrequent but massive deviations also must be appreciated. Plans based on alternative uses of low-priced agricultural commodities, for example, must have contingency options available if the supply of those commodities suddenly is limited. Indeed, strategies for biofuel-based alternatives, developed when commodity prices were low, were severely challenged when food prices sharply increased.

'Political intervention' is a reality of the agribusiness sector. The motivating force for that intervention, however, is not limited to assuring food supplies and maintaining farm income. Issues such as food safety, resource conservation, farm worker safety, and the economic well-being of rural communities are also important. Sometimes seemingly operating at cross-purposes, governmental intervention often is disruptive to operations and markets. Further complications arise because of differing attitudes and forms of intervention internationally.

The potential for major change because of advances in 'technology' seems especially likely within the agribusiness sector. For example, applications of biotechnology both had material market effect and captured media headlines in the past two decades. Application of information technology through precision farming and enormous data sets (known as 'Big Data') may have as pronounced an effect. Globally, major research investigations are pursued in both the private and public sectors. Historically, considerable developmental research has been conducted within public sector institutions and that continues to be the case in developing countries. The management and introduction of new innovations in this sector, therefore, is subject to differing processes than would be the case if developmental research was confined solely to either the private or public sectors.

The agribusiness sector depicted in **Figure 1** is comprised of 'competitive structures' that differ across and within its subsectors. The relatively unique structure of the production sector (large numbers of relatively small units) is widely recognized. At the same time, many agribusiness firms are large and multinational in scope. Organizational structure can have major influences on competition within an industry. Managers within the agribusiness sector must operate within the competitive structure of their subsector while understanding the implications of alternative structures for suppliers and customers.

The five distinctive characteristics just noted do not include several issues normally cited. For example, international trade is not listed because international trade is vitally important in numerous economic sectors. For a manager in the agribusiness sector, however, distinctive features of international trade include cultural attitudes regarding food; the range of political influences; and the potential for sudden supply shocks domestically, among competitors, or within customer nations.

Also noteworthy is that this article proposes that the uniqueness of food in combination with the physical, economic, and social attributes of the agribusiness sector provide important challenges and opportunities for sector managers. This article's focus on food differs from the narrow perspective on farm production with price as the primary measure of performance. Today's agenda does include basic food security for many consumers and nations. However, in other instances that agenda must focus on a consumer who demands a changing variety of food products. Often those products must be attractive to a concerned consumer informed by the media about food safety. Food products must be attractive both in terms of the manner in which they are produced and their long-term effect on human health and the environment.

Global Agribusiness Environment

The agribusiness environment simultaneously is extensively global and intensively local. Trade in agricultural products and the operations of multinational agribusiness suppliers and branded food manufacturers extend around the world. Conversely, even today considerable amounts of agricultural production are originated and consumed in villages and local regions following patterns that have existed for centuries. However, as the world's population increasingly lives in urban settings, the need for effective transportation, processing, and distribution intensifies. National and local government policies and regulations have a strong influence within countries around the world. However, their nature and effect can have markedly differing dimensions. Further the organizational forms and the scale of individual firms often differ markedly between the subsectors that comprise agribusiness. The culmination of these, and other, factors add to the challenge and excitement of managing in the agribusiness sector.

Agribusiness Markets in Developed and Developing Countries

The world economy can be understood as several markets, intercommunicated and linked in different blocks, with totally different dynamics in a much more complex environment.

To simplify, markets can be divided into two major groups: those already developed and mature represented by countries belonging to the European Union, Canada, USA, Japan, and South Korea, for example, and those under development, called emerging economies or countries. Brazil, India, China, Russia, and South Africa (the so-called BRICS) are examples that can be classified in this emerging category as are several other Asian, African, Eastern European, and Latin American economies. These markets differ in important aspects that are summarized in Table 1.

An analysis of this table shows that developed markets are more mature and stable, and have relatively predictable characteristics with very well-established aspects, such as logistics, retail, and institutional environment. This maturity is reflected in the population that tends to search for differentiated products and services, featuring various niches seeking healthy products, environmental and social trends, among others.

Consolidation, Concentration, and Structural Change in Linkages along the Food Value Chain

Changes in the economic environment have incented companies to their activities on core competencies, outsourcing others, and therefore reducing diversification. Concentration

Table 1 Major differences among developed and emerging economies

Developed countries	*Parameter of analysis*	*Emerging countries*
Stable	GDP	Growing
Relatively stable	Population	Growing
Relatively stable	Urbanization of population	Urbanization growing fast and emerging of mega-cities
Mature or declining	Food markets	Sales are booming
Small effect on consumption	Income growth and income distribution	Huge impact on consumption (still a high percentage of income spent on food)
Well educated	Consumer profile	Being educated
More homogenous group	Countries characteristics	Different segments of emerging economies, difficult to aggregate
High quality and sophisticated markets	Quality (food safety) in markets	High level of informal markets and food safety under construction
High percentage of consumption (expenditure) in foodservice	Food service share in food consumption	Smaller participation of expenditure in food service
Quite stable	Retail systems	In transformation
Limited possibility	Expansion of commodity production	High possibility
High sensitivity of population and severe laws, recycling, and consciousness	Environment and preservation issues	Low sensitivity of population and regulation being built
Growing faster	Adoption of biofuels	Low growth
Healthy, veggies, fruits, and organics, among others	Consumption directed to:	Quantity and animal protein
Developed and mature	Logistics and transport systems	Early stage of development, immature
Consolidated, respected, and well known	Institutional environment	Being built with high transaction costs

Source: Adapted from Neves, M.F., 2014. The Future of Food Business, second ed. Singapore: World Scientific, 336 pp.

occurrs in several stages of the food chain participants as suppliers, farmers, food industry, retailers, and foodservice. Concentration and consolidation are rules of the game.

The so-called 'hybrid forms' of supply chain coordination are increasingly replacing open-access markets. As hybrid forms are mostly implemented by contracts, one sees the emergence of collaborative networks based on relationships.

Interorganizational relationships can be formal (based on written contracts) or informal (oral agreements), depending on the institutional environment. Some societies value oral agreements and participants have reputation, and a formal document is not needed to make transactions happen and to guarantee behavior. Other countries need formal documents, and in some countries with weak institutional environments, even these written documents do not have value.

Farms Go beyond Food and Fiber: Energy, Nutraceuticals, and Industrial Products

From a traditional perspective of a farm producing food, recent technology innovations and other advancements are enabling farms to be multiproduct and service suppliers. At least 13 industries increasingly source their raw materials from farms:

1. Food and beverages: to produce human food, including grains, fruits, eggs, vegetables, juices, milk, beef, fibers, and others to an increasing and richer population demanding quantity, quality, procedures, conservation, environment, animal welfare, and others.
2. Feed: food for the animal's growth and development, involving nutrition of larger animals, for pets and others.
3. Fuel: biofuels blending programs, which means fuel coming from the farm using corn, wheat, sugarcane, sugar beet, grasses, residues, and other sources.
4. Pharma-medicine: the growing end-use called 'nutraceuticals,' which means food products together with medicine, it involves producing products that have health benefits, like juice with calcium, lycopene, vitamins, proteins, omegas, and several other merged products.
5. Pharma-cosmetics: products from food/farms that have benefits in terms of beauty, skin, tanning, and other characteristics desired by consumers ('nutricosmetics').
6. Electricity: farm products used as a renewable source of electricity, burning biomass in boilers and generating heat that is transformed into electricity, sold to the power network.
7. Plastics: replacing plastic coming from oil with renewable plastic coming from green and farm materials, like plant-based bottles produced from cane or corn.
8. Environment: farms are being used in the battle against global warming, recovering forests, creek surroundings, rivers, and even benefiting from participation in carbon credit markets.
9. Entertainment/tourism: use of farms and rural lands for tourism, weekend rest for urban families, festivals, educational purposes for kids in schools, hunting, and similar recreational services.
10. Textiles and clothings: natural fibers used to produce textiles and clothes for the fashion industry, like cotton and others.
11. Shoe and leather: leather comes from cattle and other animals.
12. Construction and furniture: wood from planted farms using eucalyptus, compensated woods, and other sources.
13. Paper and packing: materials come from processed farmed wood, producing a pulp that is transformed into paper products.

Uncertainty and Volatility

Uncertainty and volatility could endanger the world's food and agribusiness environment. For example, uncertainty surrounding the outbreaks of foodborne illnesses can have large impacts on the firms that have established a brand reputation for safety. Additional examples of uncertainty are provided in Table 2.

Sustainability and the Triple Bottom Line

Sustainability, broadly defined as 'responsible use of exhaustible energy resources and raw materials' has gained increased awareness around the world. Sustainability has three major dimensions or pillars: the economic dimension (profit), the environmental dimension (planet), and the social dimension (people).

On the economic (profit) front, the major factors to be considered are how companies, networks, and production chains deal with margins, profit, compensation, losses in the chain, communication issues for end-consumers, capital investments and funding for sustainable projects, risk management, technology adoption, and overall strategies to reduce costs and achieve economic sustainability of the business. Without economic sustainability, the other dimensions are difficult to support.

On the environment (planet) front, the major factors to be considered are the impact of the company on the environment, the impact of the company's integrated suppliers, the impact of transport (food miles), packaging (trying always to recycle/reuse/rebuild – using renewable materials and less materials), waste management (less waste; separating and recycling; energy/fertilizers from waste), use of energy, water management (protecting water and adapting best practices), green and environmentally oriented buildings and facilities, carbon emissions/neutralization (carbon footprint), among others.

On the social (people) front, the major factors are working conditions for employees, including the company's suppliers and distributors, health and safety, usage of child labor, working climate, safety equipment, commitment to the local community, facilitate cooperation, smallholder-friendly initiatives, improving local companies' capacity, and promoting product line benefits for consumers, more nutritional and healthy.

Agribusiness Firm Management

Industry-Level Analyses

A firm's strategy can be viewed as how it combines its resources to 'go to market' – to supply products/services to

Table 2 Uncertainties and risks in the business environment

	Examples
Political-legal system	● Risks to democracy in some countries; ● Populist measures of some governments and its impact in social expenditures; ● Terrorists and political attacks using food or other sources; ● Global arming (even atomic) procedures and weapons availability taking to unexpected local or regional wars; ● Riots and other challenging political systems; ● Increase in corruption within political systems; ● Labor laws decreasing work productivity and increasing costs and strikes; ● Growth of illegal crime systems and parallel states (drug cartels, nonlicit trade groups and others); ● Declining support to world's organizations and institutions (e.g., World Bank, ONU, FAO, etc.); and ● Immigration and also migration to urban areas threatening infrastructure.
Economic and natural system	● Fiscal debt crisis in some countries; ● Inflation threats in some economies; ● Not sufficient economic growth mostly in poor and emerging economies pressuring governments; ● Supply chain inefficiencies (poor use of land and other resources); ● Infrastructure collapse; ● Financial systems inefficiencies, failures, and lack of financing capital; ● Controlling diseases spreading among human, animal, or plants; ● Over usage of nonrenewable resources (oil and some fertilizers); ● Water shortages and excess causing droughts and flooding (disasters); ● Temperature changes in some regions, with extreme situations; ● Increasing carbon emissions and its effects over pollution; ● Potable water availability; ● Climate change and other planetary threats; ● Food safety risks due to poor management of food supply chains; ● Natural risks of earthquakes, tsunamis, hurricanes, and other extreme events; and ● The impact of fracking technology and shale gas on production costs and the environment.
Sociocultural system	● Fast changes in consumption behavior; ● Consumer activist movements; ● Environmental movements; ● Nationalistic movements; ● Food security concerns increasing inefficiencies in nonadequate producing areas; ● Food waste concerns; ● Nontolerance in some aggressive religious movements; ● Increase in xenophobic movements; and ● Consumer preferences for credence attributes such as organic, humane, and local production.
Technological system	● Digital systems operation (web-based companies, operational systems, and government systems); ● Data piracy, data frauds, and personal privacy issues; ● Viral communication exposure of individuals, companies, and governments; ● Not controlling new high tech innovations, such as genetically modified, nanotech, and others that may get out of control; and ● Traceability of food products from the farm to the final consumer.

Source: Adapted from Neves, M.F., 2014. The Future of Food Business, second ed. Singapore: World Scientific, 336 pp.

customers. Developing a successful strategy requires thorough assessment of the market forces the firm faces as well as the internal competencies and capabilities of the firm. The market assessment will include evaluation of the overall business/economic conditions, competitor actions and positions, and customer expectations using appropriate analytical framework such as Five Forces models and value chain analysis.

Value chain analysis

Value chain analysis assists in understanding the linkages among activities and processes (and thus stages) from initiation of economic activity to create a product or service to the eventual provision of that product/service to the final consumer/user. Boehlje (1999) identifies six critical dimensions of a value chain reaching from (1) the processes and activities that create the products or services demanded by consumers or end users, (2) the product flow features, (3) the financial flows, (4) the information flows across the chain, (5) the incentive systems to reward performance and share risks, and (6) the governance and coordination systems.

Agribusiness value chain for food could be described as two chains that become one at the consumer end (Figure 2). One value chain follows plants and plant products, and another chain follows animals and animal products. These two chains blend into one chain at the processing and retailing stages of the chain. Value chains can be as simple as five

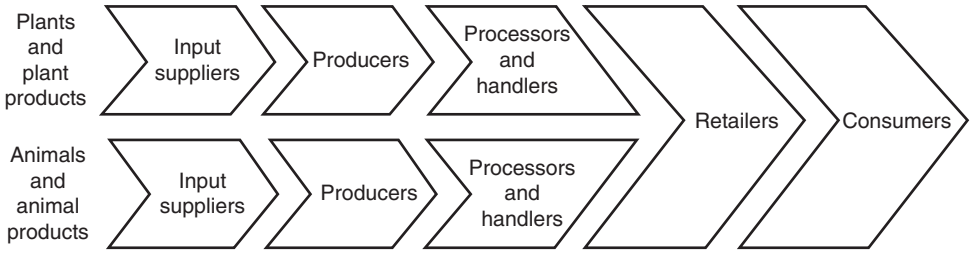


Figure 2 Value chain for plants, animals, and their products.

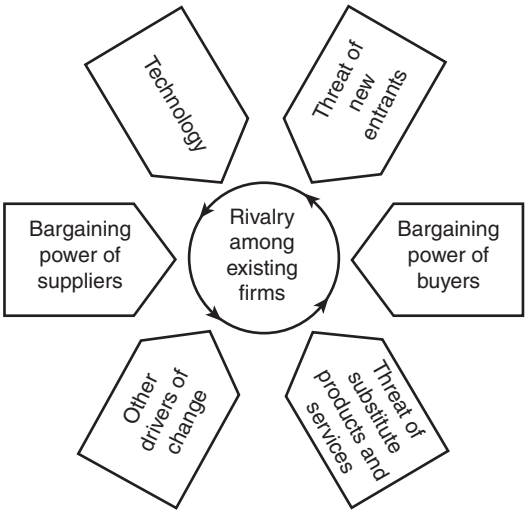


Figure 3 Porter's augmented Five Forces model.

stages: (1) input suppliers; (2) producers; (3) processors and handlers; (4) retailers, and (5) consumers.

Value chain analyses are useful to analyze the structural changes that come along with increased interdependencies of two or more related value chains. For example, due to the application of similar technologies in different sectors (e.g., biotechnology); formerly distinct, value chains are becoming increasingly interlinked and interdependent. Value chain analyses can be used to understand how complexity increases, who will hold the needed competences, how and why vertical integration will occur, and what is needed for successfully managing systemic innovations that affect multiple steps of the supply chain.

Porter's Five Forces

Michael Porter's Five Forces analyses framework is useful to assess industry structure and competitive landscape (Figure 3). Two additional forces affecting competition have been added to Porter's model adding an external dynamic: (1) technology and (2) other drivers of change.

Rivalry among established firms: The level of rivalry within an industry can depend, in large part, on the number of firms, demand conditions, and exit barriers. Owing to the number of firms involved, many agricultural industries are often described as perfectly competitive – as opposed to monopolistic competition, oligopoly, or monopoly. However, government regulation and intervention, as well as the size and dominance of a few firms, can provide different degrees of perfect competition.

Bargaining power of suppliers: Suppliers have power if they are more concentrated than their buyers, do not receive a high percentage of their revenues from one industry, have customers with high switching costs to change suppliers, have a differentiated product, have a product with no substitutes, through either real differences or patent protection, or could integrate forward into additional stages in the value chain.

Bargaining power of buyers: Fewer buyers mean they have greater power. If sellers cannot easily ship their products to other markets, or they do not have price information from other markets, local buyers can have considerable power even though the total number of buyers is large in the wider market. In ways similar to suppliers, buyers have power if they are few in number or a few buy a large percentage of the product in the market, products are undifferentiated commodities, or buyers could integrate backwards in the value chain. Buyers will also bargain harder if the product constitutes a major portion of the buyer's total costs, or if the product has little effect on the quality of the buyer's product or other costs.

Substitute products and services: Substitute products limit the price that producers can seek or ask for without losing customers to those substitutes. Competitive pressure comes from the attempts of the producers of the substitutes to win buyers to their products. The advertising campaigns of the pork, beef, and poultry industries are an obvious example of the competitive pressures due to substitute animal products; each industry feels forced to advertise to keep customers, and cannot charge as much as they would like without pushing their customers into buying other products.

Threat of new entrants: If the costs for new firms entering into an existing industry are sufficiently low, the threat alone may limit the price dominating firms charge to the users. In agribusiness, many subsectors have large initial investments. For example, machinery manufacturing requires large investments in factories to achieve scale economies. The large investments serve as a barrier to entry for new machinery manufacturing companies. Further down the value chain closer to the consumer, established firms invest in branding to create barriers to entry and limit the threat of potential entrants.

Technology: Changes in technology can have a large impact on the production of and demand for a service or product of a firm. The risk from technological change depends on the size and the role of technology in the industry, as well as the speed of technical change. Advances in technology can be disruptive; they can cause leaps that leave users of old technology far

behind. New technology can alter not only the efficiency and cost of the production process, but also the actual products and services offered and demanded by others in the value chain. New chains may be created due to a new technology in communication as well as in products and services.

Other drivers of change: Other drivers of change include changes in government policy and regulations, changes in international trade agreements, demographic changes, and other factors not included in the first six forces. Competitive pressure comes from differing abilities of firms to respond and adapt to these changes. The impact of these forces depends on the scope of the change, the speed at which change is anticipated or actually felt, and the depth and breadth of the responses needed to adapt to these changes.

Market structure and structural change

Useful conceptual frameworks that help understand and explain the structural changes (consolidation, vertical integration, and changes in the vertical and horizontal boundaries of the firms) in agribusiness include: (1) industrial organization and structure, conduct, and performance analysis; (2) transaction cost economies; (3) negotiation/power and trust; (4) strategic management; and (5) risk sharing.

Industrial organization and structure, conduct, performance analyses: One common paradigm used to understand and analyze the competitive characteristics of markets and the firms in those markets is the Structure, Conduct, Performance paradigm. 'Market Structure' refers to the competitive nature of the market. It is characterized at one extreme by many firms of similar size and similar information about market conditions including supply, demand, and prices, which is described as perfect competition; at the other extreme is only one firm with unique information that is a monopoly; or something between these extremes with few firms of different size and information/characteristics, which is described as an oligopoly or monopolistic competition market structure.

As to *conduct*, the prime focus is that of pricing behavior and pricing power. In perfect competition markets, firms have no pricing power. They are price takers with no one firm having the ability to set prices higher than their competitors and continue to sell their product. In a pure monopoly, the firm has no competition and thus it has the power to set high prices without any concern that competitors will take some of the market by charging lower prices. Firms in oligopolistic and monopolistic competition markets have some pricing power depending on the size, information access, and other characteristics of their competitors, and thus have some power to set prices without losing significant market share.

Performance is measured primarily by profits. Perfect competition markets, profits as measured by returns above all costs are zero or minimal because firms will expand output or continue to produce as long as they cover all costs, and no firm has the power to set prices above those costs without losing sales to their competitors. In a monopoly, the firm can generate profits well in excess of costs because of their pricing power, and they do not face the market discipline and competitive pressure to control costs, so monopolies typically have excess profits and may also have higher costs and relatively inefficient operations. Because of the opportunity for a monopoly firm to charge higher prices and extract excess profits from their customers, such behavior is restricted or regulated by antitrust and other laws and regulations. Oligopoly and monopolistic competition industries have modest 'pure profits' (returns above total costs) depending on how competitors respond to each other's pricing or output decisions.

Transaction cost of economics: The concepts of transaction costs and principal-agent theory as conceived by Coase (1937) and expanded by Williamson (1979) and others indicate that structure in terms of the form of vertical linkages or governance in an economic system depends not only on economies of size and scope, but also on costs incurred in completing transactions using various governance structures. Furthermore, these costs and the performance of various governance structures depend in part on the incentives and relationships between the transacting parties in the system: the principal and the agent. Under various conditions, the agent may exhibit shirking behavior (i.e., not performing expected tasks) or moral hazard behavior (i.e., the incentives are so perverse as to encourage behavior by the agent and results that are not consistent with, or valued by, the other party to the transaction, viz. the principal).

Negotiation, power, and trust: More hierarchical governance structures are replacing markets as the coordination mechanism in the agrifood industries. In such systems, negotiation strategy and skill, power, conflict resolution, trust, and performance monitoring and enforcement become central to effective and efficient functioning of the economic system and the sharing of risks and rewards in the system.

Strategic management: strategic management arguments emphasize various approaches that firms must adopt to develop a strategic competitive advantage and to consider in the make or buy decision. In general, the arguments are that competitive advantage is driven by: (a) internal considerations of costs, technology, risks, and financial and managerial resources; and (b) external competitive considerations of synergies, differentiation, and market power and positioning (Harrigan, 1988). The dynamic capabilities approach offers a framework to mitigate changes in the business climate and renew a firm's resources for a sustained competitive advantage in fast changing unstable environments such as those that characterize the agrifood sector (Teece *et al.*, 1997). In fact, given an increasingly turbulent business environment, there are reasons to question the basic concept of a sustainable competitive advantage and replace it with a rather 'temporary' competitive advantage.

Risk sharing: Apgar (2007) argues that value chain partners are critical sources of risk and uncertainty, and they can also provide the potential to mitigate risks and capture opportunities that result from uncertainty. Given the difficulty of establishing sustainable risk/reward sharing arrangements, it is not uncommon for one firm in the chain to become the chain 'captain.' The chain manager or 'captain' may choose to become the residual claimant on profits from the chain as well as assuming a major share of risk, or to share a greater fraction of the profits while shifting more of the risk to the other participants. Failure to find a risk-/reward-sharing arrangement that provides appropriate incentives and is perceived as fair encourages ownership integration of stages by one firm.

Gray and Boehlje (2005) suggests that, in general most tightly aligned supply chains that seek to share risk and

rewards among participants will be increasingly dominated by larger firms at both the buyer and supplier level – leading to more consolidation, particularly at the production end of those industries.

Firm Strategy

Agribusiness firms can employ a number of concepts and tools to craft the best 'fit' between their strengths and the current and future needs of the market. These efforts focus on resources, competencies, and capabilities that create a sustainable competitive advantage, contributing to superior financial performance and mitigating risk from changing market conditions.

SWOT analyses and the value plate

Strategic assessment at the firm level invariably includes analysis of the firm's strengths, weaknesses, opportunities, and threats (SWOT). The opportunities and threats components of the analysis can be directly derived from an effective industry analysis. Although the strength and weakness elements are internally focused, this analysis must consider market and consumer needs and competitor capabilities. In assessing skills and assets, it is critical to candidly evaluate their relevance relative to the following questions (Aaker 1995):

- Why are successful (unsuccessful) firms successful (unsuccessful)?
- What are the key customer motivations?
- What are the large cost components?
- What are the industry mobility barriers?
- Which components of the firm's value chain can create competitive advantage?

Across the sector, assets essential to be successful vary widely. For example, scale and low cost are critical for established grain merchants whereas differentiation and access to specialize skills are critical for high-tech startups. Motivations differ between the farmer and the consumer as customer. Access to safe, affordable food is the need for large segments of the world's population but those characteristics are taken for granted among higher income consumers. Focusing on cost reduction is an important managerial emphasis, especially if the cost component being addressed is substantial. Mobility barriers (both entry and exit) are important because they can indicate the speed at which current and potential competitors can execute strategically.

Assessing capabilities requires detailed examination of the firm and its operations. The internal value chain (or value plate) is a useful tool in this process (Porter). In Figure 4, the firm's primary activities are indicated by the vertical sections within its lower portion. Supporting activities within the firm are represented by the rows across the figure's upper segment. The very right-most section, labeled margin, indicates the goal of profitable operations. It is critically important to recognize that one firm's value plate is linked to its suppliers' value plates and to its customers' value plates.

The importance of each component differs significantly within the sector. Service is critically important in the farm equipment sector whereas inbound logistics is a major success determinant for food processors. Although vastly different in orientation, technology development is a continuous challenge for biotechnology-based input manufacturers and for branded food companies.

The effective use of the skills and assets of agribusiness firms, relative to their competitors, determines the size of the margin component of the value plate. Efforts to increase the margin have traditionally emphasized enhancing efficiency (shrinking the cost components) or increasing revenues (growing the size of the plate). Especially in recent years, outsourcing of support activities has been an important tactic to reduce costs. Aggressive implementation of information technologies has occurred both in the support segment and in the operational components of the primary activities.

Value creation and capture

Value creation, providing goods and services that earn revenues that exceed the cost of doing so, is an elemental reason for a firm to exist. As detailed by Schumpeter (1942), competitive economies rely on market entry and the creative destruction of innovation to shift value to consumers. Value

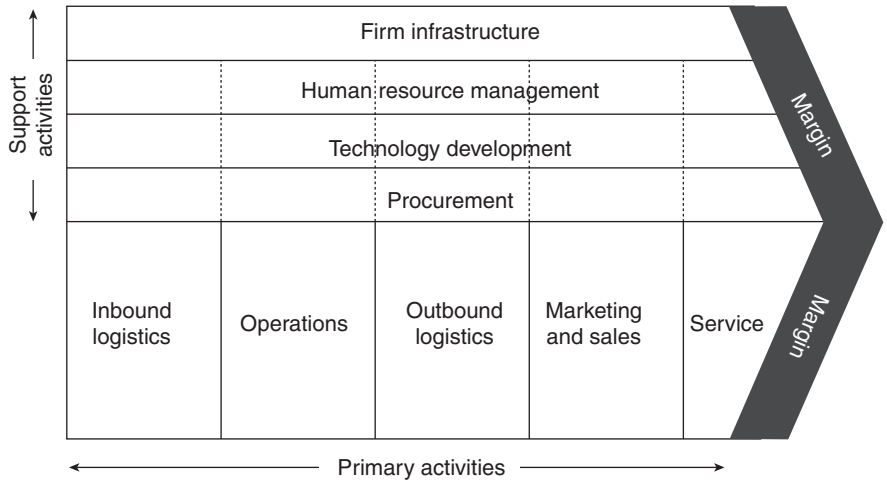


Figure 4 The value plate.

capture emphasizes the extent to which firms, over time, can retain value for their shareholders.

Although value is measurable in financial terms, in today's economy the factors that drive value creation, innovation, people, ideas, and brands, are increasingly intangible in nature. Advances in the capabilities and use of information and communication technologies (ICT) and of science throughout the economy have shifted competitive dynamics, increased the pace of change, and altered the sustaining value of skills and assets. In addition to physical sources of advantage, a long list of categories of intangible assets have advanced in importance, such as technology, innovation, intellectual property, alliances, management capabilities, employee relations, customer relations, community relations, and brand value. As a result, value capture often involves sharing across multiple firms in the value chain.

Agribusiness managers have been adept at integrating science-based innovations as well as ICT-based advances. The future dynamics of the sector are particularly intriguing because successful innovations will need to excel within the 'cyber-physical' context that characterizes operations and markets within agribusiness. Although the advance of cell-phone use has been a recent feature in developing nations, agricultural production (fruits, vegetables, grain, and livestock) still needs to move from rural to urban areas. Unfortunately that process is all too often hampered by inadequate physical infrastructure. Intangible drivers of value creation and capture will be a feature of change within the global agribusiness sector. However, the most substantial gains will accrue to the successful implementation of those drivers in the physical reality of the sector.

Growth

For long-run success, growth is a necessary consideration for the agribusiness manager. Growth introduces vitality into an organization. Further, competitors can be expected to attack the weaker product offerings of the firm. Therefore, growth in some dimension is almost always necessary just to stay even. Although profitable growth is a key managerial focus, sustained profitable growth has proven difficult to achieve – with an estimate that 90% of companies worldwide failed to achieve sustained profitable growth in recent years (Zook, 2010).

Typically, approaches to growth are categorized along the following dimensions:

- Growth in existing product markets
- Product development
- Market development
- Diversification (either in related or unrelated markets)

Bain and Company (Zook, 2010) extends this framework in the context of 'profit from the core,' where successful growth strategies are found to:

- Reach full potential in the core business,
- expand into logical adjacent businesses surrounding the core, and
- preemptively redefine the core business in response to market turbulence.

A recent case study of the Center for Food and Agricultural Business at Purdue University highlights successful firm growth within the sector (Sonka, 2011). JBS United is a diversified mid-sized agribusiness firm, known for its use of R&D to drive innovation that fosters success for its customers. Since its establishment in 1956, it has been headquartered in Sheridan, Indiana. However, its products are employed in animal agriculture throughout the world. In 2010, its sales exceeded US$450 million. As shown in Figure 5, growth has been a constant feature in the firm's history.

In 1956, John Swisher decided to become an entrepreneur and with two colleagues started the firm that has grown into today's JBS United. They chose to initially focus on providing feed for one species, swine, as it would be too difficult to provide high-quality products across species.

Based on the value delivered to its customers, the JBS United firm grew through expansion of market share in its original geography. Over time, friendly acquisitions expanded the market scope for the firm to extend across the Midwest. At the same time, value chain expansion occurred as the firm expanded its farming operations to support applied research and expanded into grain procurement to support its feed milling operations. The acquisition and geography expansion led to entry into dairy nutrition.

Recognizing the dynamic growth opportunities for animal protein globally, JBS United entered the swine nutrition market in the Philippines in the mid-1980s, which was followed

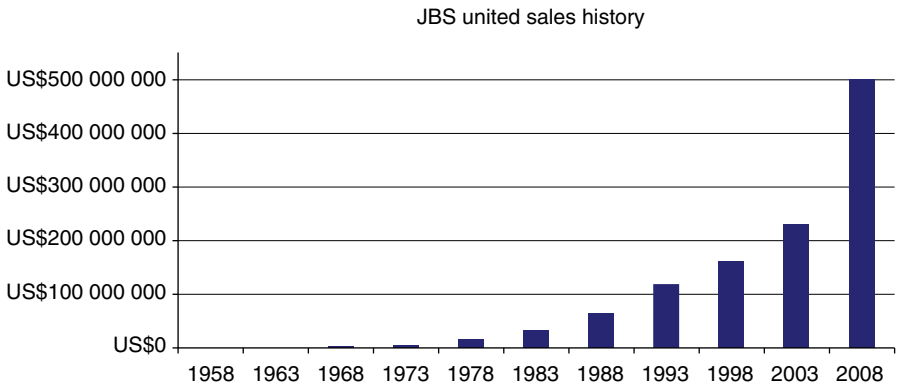


Figure 5 Growth of sales at JBS United, 1956–2008.

by expansion in Southeast Asia and then Central and South America. Since 2000, the firm has participated in successful joint ventures in China, the world's largest pork-producing sector.

Relatively early in the company's evolution, its management team recognized that employing an effective, applied R&D capability would be a key enabler to achieve its market philosophy.

Today, JBS United has an extensive R&D system serving animal agriculture. Research and development capabilities and their value led to establishing the Emerging Technologies Division within JBS United. The division's overriding goal is to advance and develop technologies that will better serve customers and environmental needs worldwide.

Both swine and poultry need phosphorous for bone and muscle development, however, only 20–30% of phosphorus in feed grains is digested. In collaboration with university researchers and by employing its internal capabilities, JBS United brings products to market to dramatically improve the proportion of phosphorous digested. This reduces both costs for the producer and the environmental impact of animal production. Additional products are being developed through joint ventures, which again build on advances in basic science.

The JBS United experience demonstrates the importance of long-term growth for firms in the agribusiness sector. This experience illustrates growth through existing product markets, product and market development, and related diversification. Further it documents that aggressive expansion from the core is possible for small- and medium-sized agribusiness firms.

Marketing

Marketing is one of the most important activities for food and agribusiness companies. Marketing is the relationship development, or the 'contract building' process with possible customers. Successful companies are the ones 'driven by demand,' or companies that pay attention, innovate, and build strong and stable relationships with customers.

Perreault *et al.* (1997) state that if the majority of people, including managers, were forced to define marketing they would say it means 'sales' or 'advertisement.' This answer is not completely true. Sales and advertisement are just two parts of a broader set of marketing strategies. Thus, marketing is defined as "a social and managerial process by which individuals and groups obtain what they need and want through the creation, offer and trade of products and values with others (Kotler, 1997)." Thus, it is a process that aims at satisfying the needs of the customers through trade.

Marketing activities can be divided into two blocks: understanding food and agribusiness customers and performing to meet customers' needs and wants. Understanding the food and agribusiness customers requires firms to assess the needs of the final consumers and intermediaries through a research process. The firms analyze the behavior of consumers to gauge their needs and wants. The firms also scan the macroenvironment (political-legal, economic, natural, sociocultural, and technological) to anticipate changes. The firms also react to competitors' moves in the market. The goal is to identify opportunities to create additional value for customers. The firms will choose among these opportunities based on which consumer market segments the company targets.

Performing is the action the firm takes based on its understanding. Firms offer products that are differentiated from competitors' products. The firms also use the information to generate new and adapt to existing products, brands, and packages to satisfy consumer needs. Firms price the innovative offerings to capture the value created. Firms also implement distribution strategies ensuring products are available to customers at appropriate times and conveniently. Firms communicate the additional value created through advertisements, publicity, and other tools. Now these major marketing performing decisions in food and agribusiness will be addressed.

Performing via product, services, packaging, and brands

Products represent the group of attributes, functions, and benefits that consumers buy. Goods, services, packages, brands, and ideas compose a product, forming a company's offer, trying to meet successfully a consumer need (Perreault *et al.*, 2010; Kotler, 1997). According to Garvin (1987), for an offer to be perceived as 'high quality' by the consumer, the following factors must be considered:

- Performance: refers to the product's capacity of doing well as per expectations;
- Characteristics: concerns the number and complexity of characteristics that differentiate the product;
- Reliability: reflects the possibility of a product failing within a certain time frame;
- Conformity: degree to which the design and operational characteristics of the product comply with preestablished standards;
- Durability: involves the time frame it takes to be replaced;
- Rendered services: development, quickness, and effectiveness of the offered services before, during, and after the purchase;
- Aesthetics: the design, the color, the product's taste, and other more subjective aspects;
- Quality perception: reputation, product, or brand perceived image.

A product, often, comes with a brand. According to the American Marketing Association (AMA) a brand is a name, term, symbol/sign, or a combination of all these, which is associated with different products or services of a specific company. Customers use brands as sources of information, simplifying choices and reducing acquisition risks. They capture beliefs about the attributes and general image of the product among the clients. Manufacturers are more and more interested in selling new products under the protection of well-established brand names, familiar to consumers, increasing their acceptability (Iacobucci, 2001).

Brands allow customers to associate functionalities, images, and experiences. In a competitive market, products become more uniform; therefore, brands evolve to offer differentiated value. The success of the brand depends on associations made only in the customers' minds (**Figure 6**).

Packaging is also an important decision in the product offering. Technological improvements in packaging have made it possible to extend the shelf life of food products. Other



Figure 6 Example logos of food and agribusiness firms.

packaging has enabled consumption on the move, which can alleviate time pressures for the consumer. Innovative packaging has also addressed challenges associated with the negative impact on the environment. Renewable sources of packaging are gaining attention, such as plastics made from cane and corn.

Performing via price

Price can be defined as a relationship that indicates the amount necessary to acquire a given quantity of goods or services (Lambin, 2000). Although other variables of the marketing mix have become important recently, price still remains one of the fundamental elements in setting market share and profitability in companies. Price is also one of the most flexible elements. It can be altered quickly, unlike the other components, such as altering a product or a commitment with a distribution channel.

Even with such an importance, many companies do not set prices well. According to Kotler (1997), the most common errors are: prices overly oriented to costs, prices do not have frequent enough revision to capture market changes, and the price setting does not depend on the rest of the marketing mix and variation not according to different product items, market segments, and purchase occasions. With the information widely available for consumers via the internet, pricing strategies have become much more important and sophisticated.

Food prices are a very sensitive issue, and commodities face huge price variations. For lower income populations, the percent of their income expended on food is higher. Thus, price increases attract substantial media and consumer attention.

Performing via distribution channels (wholesalers, retailers, and logistic operators)

According to Stern *et al.* (1996), distribution channels are a group of interdependent organizations (wholesalers, retailers, and logistic operators) involved in the process of making the company's products or services available for use by customers. The emphasis is on how to plan, organize, and control alliances between institutions, agencies, and internal capabilities in companies. When dealing with channels, it is important to:

- Analyze channels for the company's products and seek new channels, defining distribution objectives, such as: market presence, type and number of points of sale, services offered, market information, product promotion, and incentives.
- Define opportunities and threats of the current distribution system.
- Define the way of entering into markets, if it will be via franchises, joint ventures or other contractual forms, or even via vertical integration; elaborate national or international contracts with distribution channels.
- Determine the annual distribution budget and implement the plan.

In food, due to perishability and the weight/value ratio of all that is being carried, distribution channels and logistics are very sensitive issues.

Performing via integrated communications

Marketing communication consists of efforts made by a company for the transmission of its information to others, seeking to influence attitudes and behaviors. More specifically, communication strives to tell the target customer segments that the right product is available, at the right price, in the right place (Perreault *et al.*, 2010). All modern organizations, private companies, and nonprofit entities, use different forms of marketing communication to promote their offerings. The communication assists firms in achieving financial and nonfinancial objectives. In setting a communication strategy, the following activities should be done:

- Identify the target public that will receive the communication and develop the desired objectives (brand knowledge, brand memory, and persuasion, among others).
- Define the communication mix that will be used: the advertisement plan, public relations and publicity plan, sales promotion plan, as well as direct marketing actions, and web activities, among others.
- Budget and possibly determine the expected return for these investments, measuring well these activities and their impact.

- It is more than just brands in the store and in advertisements, electronic communication is more pervasive and provides more opportunities for communication. For example, firms maintain their own websites and maintain fan pages on social media websites.

In food and agribusiness, communication is an issue that is receiving more media attention. Because of concerns regarding food marketing, human health, and childhood obesity, regulations in food communications are being considered and in some instances implemented.

Performing via sales force and people

The sales force are the people involved in making sales happen. Increasingly, selling is a team activity involving technical, relationship, and commercial skills. The sales force has an immense potential for raising a company's sales; however, it can ruin the whole marketing planning that was made (Zoltners *et al.*, 2001). These decisions are establishing criteria for operation of the sales force in the market, implementation of the sales force, which will be referenced as 'human resources in sales' topics, how to acquire and maintain a well prepared and motivated sales team and, finally, the ways of control in sales. The products and services offered must be attractive to both the end user and the distribution channel.

In marketing, these five blocks of decisions for performance (product, prices, channels, communications, and sales force) is what a company has to beat its competitors in and succeed in the market place. It is very important to have equilibrium in the five elements in order to build stable relationships with customers, and as a manager, keep pressure over the marketing team because markets and customers change and competitors are willing to win over these customers. This understanding is vital for food and agribusiness companies.

In food and agribusiness, the role of the sales force in crop and livestock input suppliers is a fundamental source of knowledge extension to farmers. Several studies have indicated that a company having a strong marketing orientation (that is, a company driven by demand) has better performance in the market place.

Finance

Firms use finance concepts to measure the efficiency of investments and the profitability of operational decisions. Finance is concerned with the sources and uses of cash in the business and the returns to assets (Brigham and Ehrhardt, 2009). Generally speaking, riskier investments should generate higher expected returns to investment. Thus, when agribusiness firms consider investment opportunities, the cost of financial capital is the benchmark return that the investment must return. Once investments are made, managers of agribusinesses use financial statements (income statement, balance sheet, and cash flow statement) to measure, monitor, and correct operational decisions.

Financial statements, financial metrics, and profitability analyses

There are four key financial statements that serve as the basis for tracing the financial performance of the agribusiness firm: the balance sheet, the income statement, the cash flow statement, and the statement of owners' equity. Each of these documents is typically prepared annually, with quarterly updates provided for at least earnings. Corporations are typically required to share an annual report every year with its shareholders. Nearly always these statements are available electronically from the firm's website in the 'Investor Relations' section. Preparation of these documents is completed using the Generally Accepted Accounting Principles or the International Financial Reporting standards, and is typically verified by an independent accounting firm.

Three of the statements report the operations and flow of cash for a period of time: the income statement, cash flow statement, and statement of owners' equity. The balance sheet is prepared for a particular date, and takes stock of the asset, debt, and equity position of a firm on that day. As such the balance sheet can differ substantially depending on the date of preparation in businesses dominated by seasonality, such as they often are in agriculture.

The four financial statements serve as the foundation for the basis of financial performance analysis. These historical documents assist managers in evaluating historical financial performance (trend analysis and benchmarking) and improving future financial performance.

Comprehensive analysis of the financial statements typically focuses on four key dimensions of financial performance: profitability, asset management, liquidity, and solvency. Each manager might tailor particular ratios to his or her firm, but generally aims to improve profitability and asset management while maintaining satisfactory levels of liquidity and solvency.

The most important financial metrics are return on equity (ROE) and return on assets (ROA). As the agribusiness competes for equity investments, it must generate sufficient returns to compensate investors for the level of risk incurred. Return on equity provides a benchmark ratio for which investors compare management's performance with other investment opportunities. Return on equity is impacted by the return on assets of the firm and the financial leverage used (see Section Capital structure), and is often analyzed using DuPont analysis of profitability linkage (**Figure 7**).

ROA measures the operating income generated for the investment in current and noncurrent assets. In the DuPont analysis, ROA is broken down into profit margin (or return on sales) and asset turnover. Profit margin measures the percent of revenue left to compensate financial capital. Asset turnover concerns the ability of management to generate sales (revenue) from the assets employed. Some firms pursue a low margin, high turnover strategy (often employed in retail firms). Other firms pursue high margin, low turnover strategies (often prevalent in manufacturing businesses). The ideal scenario would be to have a high margin, high turnover business.

The capital structure of the firm is concerned with the mix of debt and equity used to purchase the assets (see Section Capital structure). The financial leverage increases when more debt is used, and as a result there is more financial leverage applied to the return on assets of the business. Two broad financial concepts are of importance when considering the use of financial leverage: liquidity and solvency. The earnings leverage refers to the sharing of operating profit margin among lenders and equity holders.

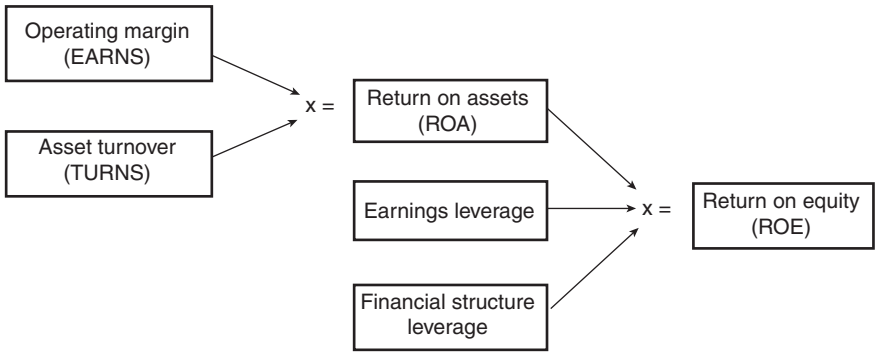


Figure 7 DuPont identity of return on equity.

Liquidity concerns the ability of the agribusiness to generate cash flows to service its debt obligations as they come due in the near term. Working capital, working capital turnover, the current ratio, and the quick ratios are all frequently employed to assess liquidity. Solvency concerns the ability of the agribusiness to meet its long-term debt obligations and is frequently measured by considering some form of the debt-to-asset ratio. Some research has considered the impacts of working capital and accrual changes on the profitability of agribusiness firms (e.g., Trejo-Pech *et al.*, 2009).

Investment analysis and capital budgeting

Agribusiness firms may seek opportunities to acquire assets to grow the business and create additional customer value. The process of evaluating these opportunities is known as investment analysis. Typically, the process involves assessing the likelihood of generating additional revenues into the future and comparing that to benchmarks for returns.

The investment analysis tool that most finance professionals would suggest using is net present value analysis (NPV) or discounted cash flow. The approach requires projection of cash inflows and outflows into the future, the determination of an appropriate discount rate, and typically some level of sensitivity analysis. The projection of cash flows typically begins with the initial outlay to acquire assets and tracks annual cash inflows and outflows related to the project. One must also make an assumption about the time frame of the project and determine a terminal (or salvage) value of the project. The lengths of projections vary, but typically are done for 5–10 or more years of cash flows.

The discount rate must be set to account for the time value of money and the required return needed to compensate the risk involved in the project. Many firms use their weighted average cost of capital (WACC) as the discount rate. This requires the project to generate sufficient returns to compensate financial capital at its current expected returns. Thus, if NPV is positive the firm should accept the project, otherwise reject the project.

Because the process is pro forma in nature, many analyses include testing the sensitivity of the results to important assumptions made in projecting the cash flows. Increased sophistication in spreadsheet programs has allowed sensitivity analysis to become rather detailed.

Firms can also choose to compute and report an internal rate of return for a project. This method uses the same techniques as the NPV analysis, but reports the discount rate that causes the NPV to be zero. This approach is appealing because it reports a rate of return that can be compared to rates of return in other investments or the hurdle rate set by company management. It has drawbacks in that some analyses may have more than one rate that causes NPV to be zero.

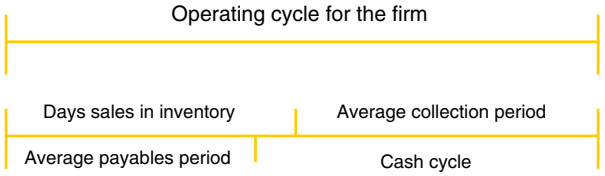


Figure 8 Operating and cash cycles for a firm.

Cash management

Short-run cash management requires agribusiness firms to have the cash necessary to settle accounts as they come due. The firm must have sufficient cash to pay suppliers, employees, management, and other expenses to continue daily operations. Typically, holding large amounts of cash to meet these needs is inefficient because cash held in checking accounts typically generates insufficient return for the firm to compensate the suppliers of cash. Investments in inventories, accounts receivable, and other current assets are additional important uses of cash that are part of operating cash flow. Firm will need to optimize investments in current assets and use of current liabilities to meet the operating needs of the firm. The management of these accounts is related to the cash conversion cycle (Figure 8).

Long-run cash management requires agribusiness firms to have sufficient cash or rapid access to sufficient cash to invest in long-term growth opportunities. Investments in fixed assets, typically termed investing cash flows, can require large amounts of additional capital to acquire the new, long-term assets.

Capital structure

The mix of debt and equity used to finance the purchase of assets is termed as firm's capital structure. The firm must balance the relatively lower cost of debt with the increased financial risk of borrowing. Firms should choose capital structure such that the WACC is minimized, which maximizes the value of the firm. An additional important consideration

in determining optimal capital structure is the tax shield benefits of using debt.

Agribusiness firms may raise financial capital in the form of debt from retail investment banks, the bond markets, and suppliers among others. The firms may also raise financial capital in the form of equity from private investors, the public equity markets, and retained earnings.

Financial risk increases as the debt-to-asset ratio increases. The increased borrowing demands greater cash flows from the business to service the debt. The increasing likelihood of the business being unable to meet the financing demands adds to the financial risk. If the business is unable to meet the demands, the borrowers will move to minimize the losses associated with a bankruptcy, i.e., dissolution of the business.

Operations

The operational activities of the firm are the set of actions taken to transform strategy and plans into deliverable products and services to generate financial and performance results (e.g., customer satisfaction). Operations activities include the full spectrum of work done in a business – running the manufacturing plant, shipping or transporting the product to the customer, sourcing the raw materials to produce the product or service, organizing and implementing the product/service sales activity, etc. Efficient and effective operations require an understanding and assessment of, for example, costs and cost components, product and work force flow scheduling and logistics, inventory management, sales and customer relationship management, selecting and managing the workforce, and capital access and financial management.

Economies of scope and scale

Firms often benefit from being large in terms of their assets and revenues. This happens because short-run fixed costs can be spread out over greater units sold, thus reducing overall average cost per unit. Firms of substantial size may gain cost advantages relative to smaller peers, particularly in industries with large fixed costs. Production of agricultural grain commodities exhibits this feature as land and equipment represent substantial costs. The same can be said for many agribusiness firms, particularly those involved in manufacturing and research and development activities.

Economies of scale refer to the cost advantages accrued to spreading the fixed costs of producing and marketing a singular product. Economies of scope concerns the ability of spreading shared fixed costs over the production and marketing of two or more products. Because many agribusiness sectors have large fixed costs, one often notes that the market has characteristics of a natural monopoly. Rapid consolidation in many sectors has left some with just a few firms operating in an oligopoly. Even in agriculture, the size of farms has grown as the number of farms has declined and acreage farmed has been held steady for about a century (Figure 9).

Logistics

Given the highly perishable nature of many agricultural products, regional production of some widely distributed products and the biological processes that govern agricultural production, excellent logistical management is very important for most agribusiness sectors. Moving products through time and space so that they reach the end consumer is the essence of logistics. Optimizing logistics focuses on reducing waste (shrinkage), minimizing transportation costs, and ensuring timely delivery.

Given that many agricultural products are very perishable, such as raw milk, many sectors are dominated by time specificity. Products must reach the end consumer when they are most desirable and useful, within a relatively limited period of time. Delays can cause enormous losses to the product.

Many agricultural sectors are dominated by complex distribution systems, which further complicate logistics. This interdependent network can delay important customer feedback along the supply chain. For example, many manufacturing sectors, such as farm equipment manufacturers, rely on others to distribute their products to the end users. Farm

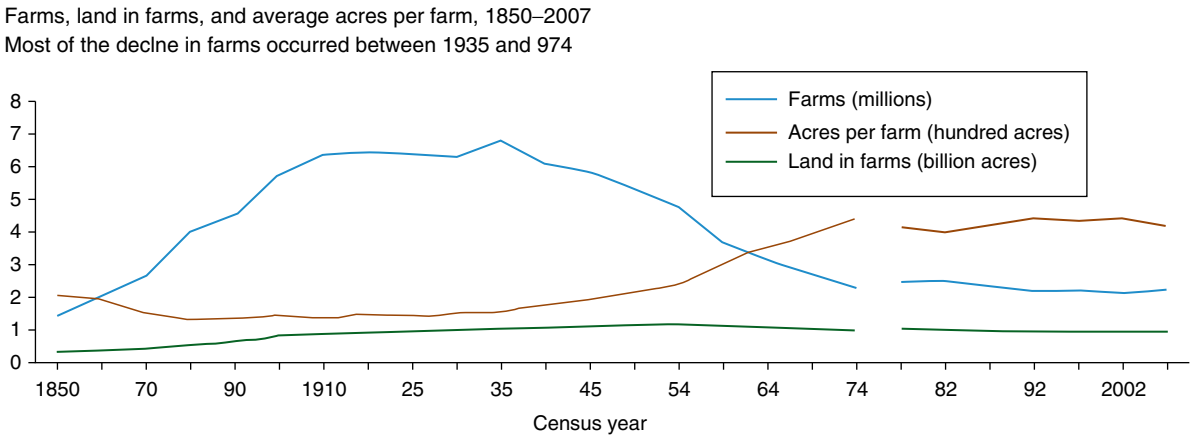


Figure 9 Farms, land in farms, and average acres per the US farm, 1850–2007. The break in the lines after 1974 reflects the introduction of an adjustment to estimates of the farm count and land in farms. Beginning in 1978, the data are adjusted to compensate for undercoverage by the Census of Agriculture. For more information, see Allen (2004). Reproduced with permission from Hoppe, R.A., Banker, D.E., 2010. Structure and Finances of U.S. Farms: Family Farm Report, 2010 Edition, EIB-66, July. U.S. Department of Agriculture, Economic Research Service, compiled from Census of Agriculture data.

equipment retail has been dominated by independent, equipment dealerships that have regional operating territories. To address the lack of communication between end user and manufacturer, increasingly sophisticated technology is being used on tractors to assess performance in the field. Specifically, engine sensors on farm equipment can transmit data for use by the producer, equipment dealership, and equipment manufacturer. This stronger integration of information across the value chain has the potential to greatly enhance the ability of the manufacturer to address user concerns as and when they arise.

Inventory management

Inventory management can play a large role in the success of agribusinesses. Production along the entire chain, particularly in the grain sectors, is dominated by the weather. As a result seasonality has a large impact on inventory management. Agribusiness firms growing seed for future crops must predict several years in advance to have the correct hybrids on hand for agricultural producers.

Inventory management should minimize total inventory costs by considering both carrying costs and opportunity costs. The carrying costs of inventory include the cost of storage facilities and equipment, the interest cost of inventory investment, and shrinkage of inventory. The opportunity costs of inventory are largely composed of missed sales due to insufficient inventory on hand to meet customer demands.

Inventory management can be complicated by the distribution channel. Given that each stage of the supply chain will hold inventories, communication along the chain will be critical in managing inventories of the sector.

Statistical process control and process mapping

Many agribusiness firms use statistical process control to assist with managing quality of products and services (Deming, 1982). Examples of process control include Total Quality Management and Six Sigma initiatives in these firms. The objective is to minimize waste in the production and processing of goods by ensuring that outputs meet certain specifications. One of the distinctive challenges faced by agribusinesses is the uncertainty surrounding the biological processes of production. This makes statistical process control both more challenging and more critical in the success of the value chain. In producing row crops, substantial data is collected and analyzed to help ensure large yields. For example, producers obtain information regarding nutrient health for soil samples. Pests and weeds are closely monitored and addressed as necessary.

Process mapping can also help to ensure the safety and quality of food as it moves through the value chain to the end consumer. In the food processing industries statistical quality control helps to reduce the incidence of foodborne pathogens. For example, food processors use Hazard Analysis and Critical Control Points (HACCP), International Organization for Standardization (ISO) certifications, and Clean in Place (CIP) processes to ensure food safety. The Food and Drug Administration and the US Department of Agriculture (USDA) work together to enforce HACCP systems in the meat and juice systems, whereas many other food industries voluntarily use the systems. The systems require firms to identify, set limits for, and monitor points in the production process at which control can be applied.

Human Capital Management

Human capabilities are essential for agribusinesses to transform assets and raw inputs into products and services that create value for consumers. Successful agribusiness firms have grown beyond the sole proprietorship with just one or two employees to become large, complex organizations that require communication and coordination to execute the firm's operational, financial, marketing, and research and development strategies. Managers throughout the organization need leadership skills to motivate and retain valuable employees. Firms often create a division of human resources to assist with identifying needed competencies and responsibilities of employees and employee competency development.

Organizational structure

As a firm moves beyond an entrepreneurial owner–operator size to a larger, more complex organization, frequently a corporate organizational structure emerges. The organizational structure varies by firm needs, but typically there is a hierarchy of responsibility and authority. At the top of the organizational structure is the President/Chief Executive Officer of the firm, which is hired by a board of directors to lead all functions of the business. Many firms then organize the structure around functional areas. They do so by having a senior manager (often with the title, vice-president) in charge of each functional area, who would report to the CEO. Many of these vice-presidents would have titles such as chief marketing officer, chief financial officer, and chief operating officer, among others. Additional members of the senior leadership team would be added as specific to the firm, such as a vice-president for human resources, vice-president for research and development, or a chief information officer. Firms might also have each of these roles for significant geographical areas or other market segments. One potential drawback to this particular structure is that the functional areas become silos that do not collaborate well with each other.

For the largest organizations the structure might become very complex. Each vice-president might have additional mid-level managers reporting to them that would be responsible for specific divisions within the functional role. These mid-level managers are termed middle management and can serve as a pool of candidates for senior leadership. Additional layers of management may be added between senior management and 'frontline' employees (i.e., factory line workers, sales and service representatives, etc.). The number of layers between the president and frontline employees is an indication of whether the firm has a vertical or flat reporting structure. Vertical structures are very hierarchical with clearly delineated reporting and authority relationships. Flatter structures tend to empower lower-level employees to a greater degree, which might negatively impact firm performance if the employees make poor choices.

Skills and competencies

Employees must come equipped with the requisite skills and competencies needed to maximize the efficiency and

effectiveness of physical assets used by the firm. Employees must be able to execute the implementation plan as it relates to the agribusiness's strategy. To do so, the agribusiness firm will attempt to share knowledge across employees and generations of employees. This can be a challenge though, as some knowledge is explicit whereas other knowledge is tacit. Explicit knowledge can easily be communicated from one person to another by writing it down. Explicit knowledge is often shared in user manuals and company onboarding programs.

Tacit knowledge was first identified by Michael Polanyi. In *Personal Knowledge*, Polanyi (1962) suggests that skills such as riding a bike and hitting a nail with a hammer are difficult to communicate in written form. Rather, the learner must acquire this knowledge by performing the action. Activities in the agribusiness firm that require tacit knowledge can be acquired through training programs that allow the learner to practice the skill in a low risk setting. Strong need exists for experiential learning in agribusiness given the tacit nature of much knowledge in agriculture.

Leadership

As employees move from a frontline role up the organizational structure, they may become managers and acquire direct reports. Direct reports are employees for whose actions the manager is responsible. Becoming a manager requires employees to develop a set of skills that will allow them to motivate their direct reports to maximize productivity for the firm.

Empirical studies by Lombardo and Eichinger at Korn/Ferry International have led to the Lominger Leadership Architect. This leadership development program identifies 67 competencies that are part of eight factors and 21 clusters (**Figure 10**). The eight factors are strategic skills, operating skills, courage, energy and drive, organizational positioning skills, personal and interpersonal skills, trouble with people, and trouble with results. The clusters help to identify skills that are closely related. Many of the competencies identified in the Lominger Leadership Architect are closely related to the development of the managers and executive leaders of food and agribusiness firms.

Currently, little empirical research has been done in the food and agribusiness industries to identify the application of these principles. The opportunities are abound as there has been documented need for additional human capacity to manage and lead the food and agribusiness sectors. Some data indicate, however, that an agribusiness talent gap exists and that the demand for professionals in the sector exceeds the amount of graduates from colleges of agriculture in the United States (USDA National Institute of Food and Agriculture). The USDA issued a report indicating that between 2010 and 2015 an estimated 54 400 jobs would be created annually in agricultural, food, and renewable natural resources. Only approximatey 29 300 students, however, are expected to earn degrees in traditional agriculture and life science-related fields during that same time span.

Human capital development

Firms often invest in the most recent technology for their physical capital. To gain the maximum benefit of this technology, the human capital employed by the firm must be able to implement and exploit this technology. Thus, large firms invest in educational programs for their employees that equip them with additional skills and competencies they may not have had when joining the firm. The ongoing educational, development, and training programs serve to strengthen the organization and its strategic mission.

As agribusiness firms move beyond training for frontline employees, they may begin to invest in educating employees to analyze and address complex problems. Very large agribusiness firms have learning and development departments that create and execute such programs. Some agribusinesses may turn to executive education programs offered by university and consulting firms. For example, the Center for Food and Agricultural Business at Purdue University partners with agribusiness firms to design, develop, and deliver such programs.

In addition to firm investments in human capital, individuals may choose to invest in their own education. One frequently acquired credential is the master of business administration or, specific to agribusiness professionals, a master of agribusiness. For example, Kansas State University offers a Master of Agribusiness degree focused on management education for agribusiness professionals. Other universities offer courses on agribusiness in their more general MBA programs (**Table 3**).

Entrepreneurship, Innovation, and Research and Development

Innovation is essential for meeting changing consumption patterns and improving efficiency along the food chain. Innovation is needed among input suppliers, plant and animal agricultural producers, food distributors, and food retailers to satisfy consumers. Efficiency will come from diffusion and knowledge transfer. When properly produced and used, agricultural inputs help farmers improve yields of high quality products that allow consumers safer, more wholesome, and cheaper food. When considering animal and plant production, agribusinesses need to work in tandem with producers to increase land productivity, shorten plant production cycles, increase efficiency in land operation and management, search for lower environmental impact technologies, have more efficient and conservative soil operations, have localized and adapted solutions and use renewable energy sources for fueling the high energy demanding agricultural activities. Feeling the pressure for more environmental friendly, healthier, and distinguished products, the agro-industry has invested on ecological packing, products with different or enhanced flavor, products that satisfy appetite and work as medicines or cosmetics. The food retail innovation brings us to supermarkets promoting new buying experiences, such as tasting areas, new ways to offer the products, offering complete solutions, increasing benefits for consumers, supermarkets becoming a place of knowledge transfer, where the consumers learn about the products they eat, becoming a place where the industry communicates with its final consumers. Supermarkets are trying to regain some market share that they have been losing to foodservice, such as restaurants, by adding more of the home meal replacement strategies.

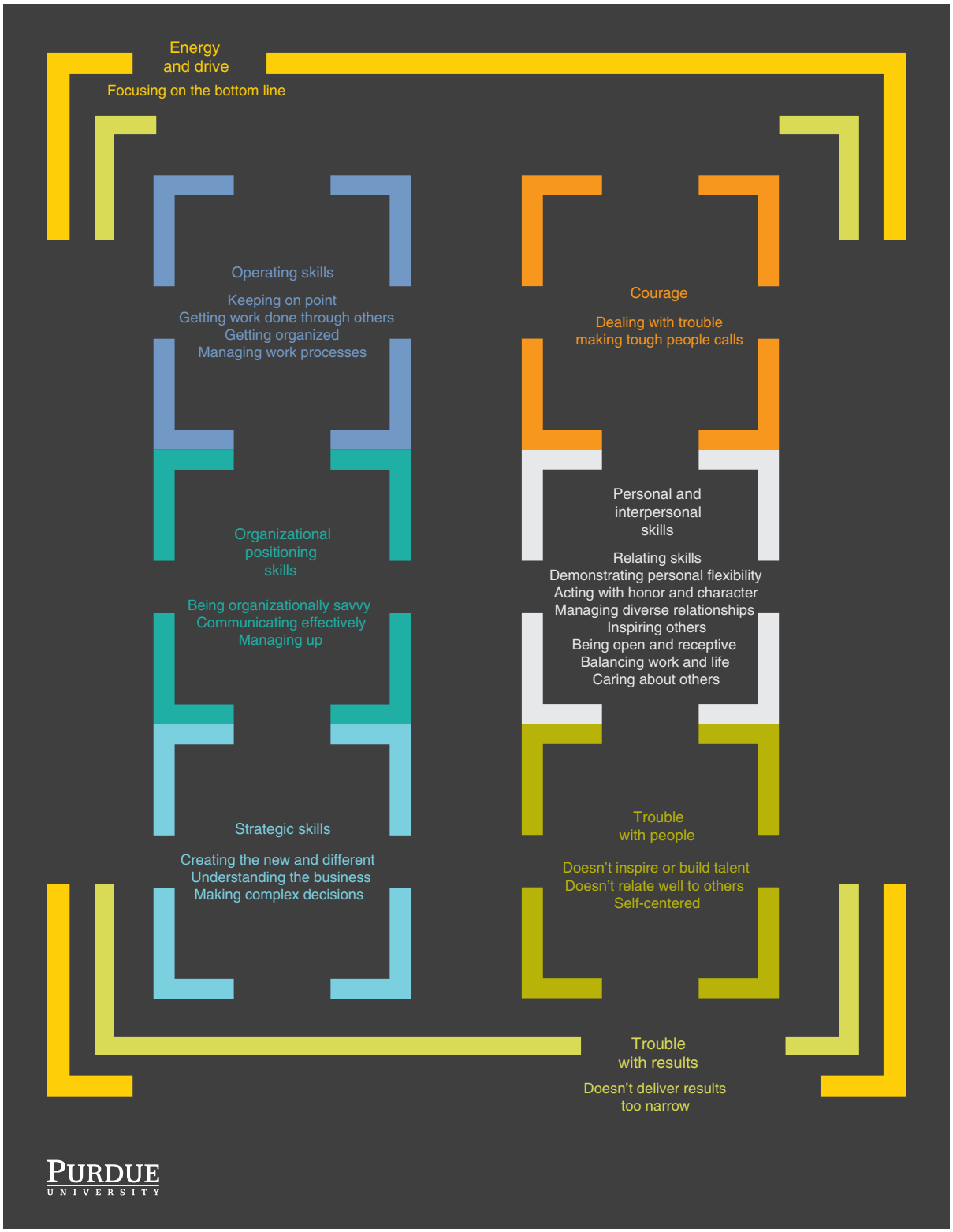


Figure 10 Library structure based on concepts from Lombardo, M., Eichinger, R.W., 1994. FYI: For Your Improvement, A Guide for Development and Coaching, fourth ed. Lominger Ltd Inc.

Entrepreneurship and entrepreneurs

Entrepreneurship is the capacity and capability to identify new business opportunities and to successfully bring that opportunity to market and generate superior (or at least acceptable) financial performance. Entrepreneurs are commonly perceived as risk-takers – they embrace new ideas and are

Table 3 Educational programs in agribusiness management

University	*Country*
Purdue University	USA
Kansas State University	USA
University of Florida	USA
Harvard University	USA
Santa Clara University	USA
Texas A&M University	USA
Wageningen University	The Netherlands
Zamorano	Honduras
INCA	Costa Rica
University of Sao Paulo	Brazil
University of Buenos Aires	Argentina
INSEAD	France and Singapore
MAPP (Denmark Arhus School of Business)	Switzerland
Massey	Australia
University of Pretoria	South Africa
Indian Institute of Management	India
Nanjing Agriculture University	China

willing to encounter financial losses or other exposures to introduce them to the market. In reality entrepreneurs are uniquely skilled at identifying, managing, and mitigating the risks of their new ventures. McGrath and MacMillan (2000) suggest that entrepreneurs have five fundamental characteristics:

1. Passionately seek new opportunities
2. Pursue opportunities with focused discipline
3. Pursue only the very best options – prioritization is critical to success
4. Focus on execution – the entrepreneur doesn't just stop with invention or discovery
5. Engage broad participation in their venture – an inventor may work alone with few collaborators, but a successful entrepreneur is skilled at engaging a large set of participants to bring the new idea to market

McGrath and Macmillan (**Figure 11**) provide more specificity concerning the skills and capabilities critical to successful entrepreneurship.

Innovation and research

Innovation is critical to the long-term success of a firm as well as the economic health of an industry and the overall economy (Gertner, 2008). Brown and Teisberg (2003; p. 1) state that "Innovation is the lifeblood of successful businesses. […] [It] has become every firm's imperative as the pace of change accelerates." Indeed, innovation is a strategy to develop and maintain a sustainable competitive advantage.

Innovation can be a product, a service, a process, a new business model, or a management system that solves a problem and has impact. The food and agribusiness sector is no stranger to innovation. Over the past 150 years, there have been several waves of innovation related to machinery, chemistry, seed, information management, food, restaurants, and services.

In addition, innovation is and will remain essential in the food and agribusiness sector to respond to the critical concerns of society such as new consumer demands, climate change and global warming, food/energy scarcity and security, environmental challenges, and resource use/sustainability. In a recent study by McKinsey on innovation and resource productivity to meet the world's future energy, materials, food, and water needs, four of the top ten opportunities are in the agricultural sector, presenting excellent opportunities for profitability new business ventures: increasing yields on large-scale farms, reducing food waste, increasing yields on smallholder farms, and reducing land degradation.

A key issue in agribusiness R&D and innovation is the length and complexity of the value chain and the challenge is in bringing innovations from the input end of the chain created by the physical and biological sciences of engineering, genetics, nutrition, biotechnology, and nanotechnology to successful market acceptance and adoption at the retail and restaurant (foodservice) consumer end of the value chain. This issue is compounded by the dramatic changes recently in the end uses (bio-fuels, industrial products, etc.) of agricultural raw materials and the development of new value chains in the bio-economy.

The degree of innovativeness – 'new to the world' products compared to incremental 'repositioning' of products – also has a significant impact on structural entry barriers. Disruptive/radical discontinuous innovation by a new entrant can facilitate entry by:

1. Use of new/different resources/inputs, thus challenging the incumbent's control of essential resources;
2. Dramatically lowering the cost of production/distribution; and
3. Introducing superior performing or lower cost products that offset the switching costs of current customers and attract noncustomers.

The long-term implications are for significant challenges to incumbent agricultural production technology firms, as well as product processing firms, as renewable biological-based raw materials become the feedstock not just for food and fiber end-users (the old customers), but for the health/pharmaceutical and industrial products end-users (the new customers) as well.

Managing research and development

Selection of R&D projects: after identifying innovative ideas, a key challenge is to select which ideas will be pursued as part of the R&D portfolio. Most organizations find that they have several good ideas but lack the framework required to select and convert the best ideas into new revenue. With regard to selection criteria, Roucan-Kane (2010) found that food and agribusiness executives prefer (in decreasing order of importance) projects with low risk of technical/regulatory failure, low relative market risk, short-term to market, in-house capability, and high costs already incurred. This work suggests that strategies to manage the risk of technical/regulatory failure and market acceptance merit serious consideration (**Figure 12**).

One way to manage the technical/regulatory and market risk is to select a portfolio of innovation projects with varying degrees of risk as suggested by McGrath and MacMillan (2000). Boehlje *et al.* (2011) illustrate the use of the McGrath

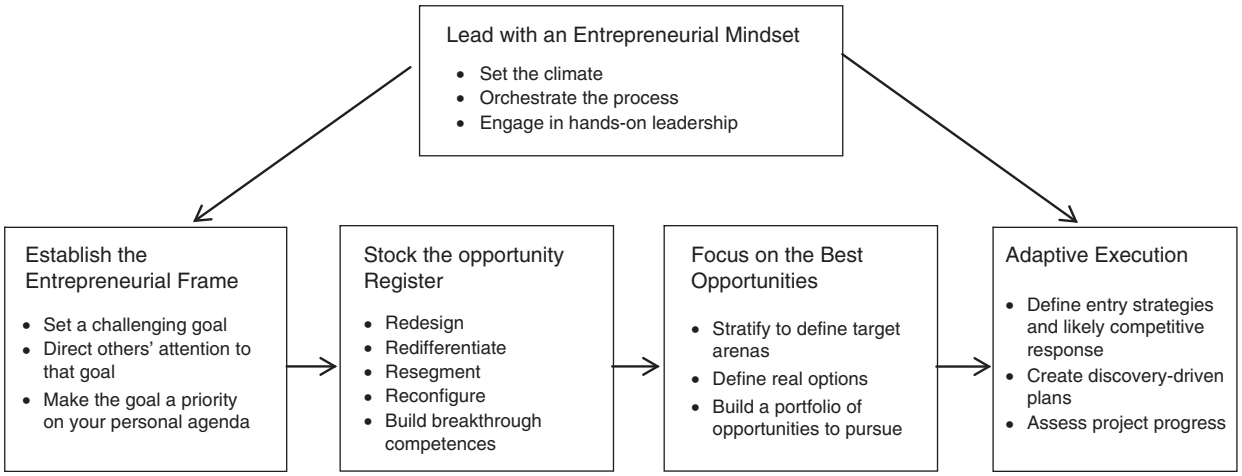


Figure 11 Essentials of entrepreneurial strategy.

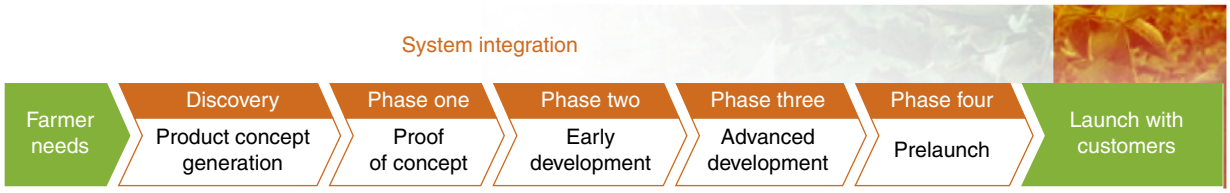


Figure 12 Monsanto's research and development pipeline.

and MacMillan 'portfolio of options' framework to Deere and Company's innovation projects (Figure 13). The framework suggests a diversified portfolio of positioning, stepping stone, and scouting options along with platform and enhancement launches to manage market and technical uncertainties.

Roucan-Kane studied the portfolio of innovation projects for food and agribusiness companies using the same criteria as described earlier. Her survey results indicated that companies tend to diversify their innovation projects in terms of time to market and cost already incurred. They favor projects that are done in-house, and that are not characterized by significant risk of technical/regulatory failure or high relative market risk.

Managing the R&D pipeline: the selection of R&D projects should be regularly reviewed as uncertainty is resolved and new projects enter the pipeline. Cooper's stage-gate process (Cooper, 2001) proposes a structure to continuously analyze the portfolio of innovations and increase the likelihood of success in an uncertain world. His process features five innovation stages: scoping, building a business case, developing, testing and validating, and launching. Each stage (and sometimes within a stage) ends with a gate where the resource allocation and the prioritization of projects is reviewed and changed if needed.

Deere and Company calls its stage gate processes the Enterprise Product Development Process (EPDP) and the Accelerated Innovation Process (AIP). EPDP focuses on incremental innovations, ensuring that these innovations reach the quality standards Deere has set before the product is launched. AIP is targeted toward radical innovations with the use of selection methods such as strategic buckets, structured assessment, and economic models.

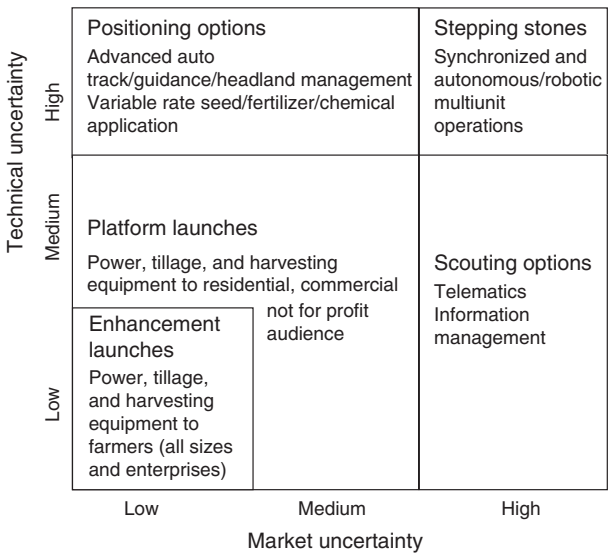


Figure 13 Deere portfolio of innovations. Adapted from Boehlje, M.D., Roucan-Kane, M., Broring, S., 2011. Future agribusiness challenges: Strategic uncertainty, innovation and structural change. International Food and Agribusiness Management Review 14 (5), 53–82.

Conclusions

The purpose of this article is to discuss contemporary topics in food and agribusiness with a focus on definition of agribusiness, description of the global agribusiness environment,

and a discussion on the roles in managing an agribusiness firm. Managers in the agribusiness sector need to be aware of the interrelated subsectors that work together to provide goods and services to global consumers. To be successful in the sector, managers must be able to competently integrate skills and capabilities in the areas of strategy, marketing, finance, operations, human capital, entrepreneurship, and innovation.

See also: Agricultural Cooperatives. Agricultural Finance. Agricultural Labor: Demand for Labor. Agricultural Labor: Supply of Labor. Changing Structure and Organization of US Agriculture. Climate Change, Society, and Agriculture: An Economic and Policy Perspective. Consumer-Oriented New Product Development. Crop Insurance. Farm Management. Food Chain: Farm to Market. Food Marketing. Intellectual Property in Agriculture. International Trade. Markets and Prices

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Agricultural Cooperatives

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Glossary

Equity subscription and redemption Procedures used to determine each member–patron's required annual capital contributions to, and capital withdrawal entitlements from, the cooperative.

Investor-owned firm A firm in which ownership and control are proportionate to equity capital invested, rather than according to use of the firm's services.

Liquidity The ease or cost with which an investor's capital can be converted into cash.

New generation cooperative A marketing cooperative structure stressing closed membership, transferrable and appreciable stock shares, proportionality between equity contribution and patronage, and well-defined marketing contracts requiring as well as guaranteeing member raw product deliveries on stated quantity and quality terms.

Patronage The value of a member's raw product supplied to – or inputs purchased from – a cooperative, which is calculated at estimates of the current market prices of the products supplied or inputs purchased.

Pool The combined net revenue from the whole or a subset of the cooperative's operations, which is allocable to the members who contributed to that subset of operations. Normally, a marketing cooperative's 'pool' refers to revenue less processing cost only, that is, the value of member-delivered raw product is not included in the cost accounting.

Revolving fund The facility in a traditional cooperative for annually retaining equity capital in proportion to a member's patronage that year, holding it without interest, and then redeeming it in cash after a prearranged period or – more typically – when the board chooses to redeem it.

Tax-exempt cooperative A cooperative entitled to exclude from taxable dividends any dividend paid on stock and any nonpatronage income allocated to member and nonmember patrons. Such cooperatives must treat nonmembers the same as members in all respects, including dividend distribution.

Traditional cooperative A marketing, supply, or service cooperative structure stressing open membership, nontransferrable and nonappreciable equity shares, capital subscribed according to patronage but redeemed at the board's discretion, and – in marketing firms – delivery contracts emphasizing member rights rather than obligations.

Unallocated revenue Revenues held on the cooperative's books in unallocated form, that is, not allocated to the account of any particular member.

Introduction

A cooperative is a business owned by the users of its services. In particular, it is a firm whose net revenues are paid to the firm's patrons and on the basis of that patronage. The principal alternative to a cooperative is an investor-owned firm – one owned by those who have invested capital in it, but who do not necessarily patronize its services. An investor-owned firm's net revenues are paid to its equity holders in proportion to the capital they invest rather than, as in a cooperative, according to their patronage. Farmer cooperatives supply farmers with their production inputs, process and market their products, and sometimes provide other services such as price bargaining and trucking. Hence, understanding cooperative organization is essential to understanding the business of agriculture.

Concept of a Cooperative

Cooperative Principles

Cooperative organization of economic activity has a long history, including the collective work efforts of early agricultural societies. The first group of individuals to organize as a modern cooperative was the Society of Equitable Pioneers (1844), a firm established in Rochdale, England to supply its 28 members with weaving materials. Its purpose was to provide inputs to its members at cost and to be controlled on a one-member-one-vote basis. Services to members were to be provided at cost.

In modern cooperatives, democratic member control is still regarded as an essential principle, although voting rights in some firms are distributed according to the member's patronage rather than on a one-person-one-vote basis. The principle of at-cost service also remains. This second principle essentially means that the bulk of the cooperative's net income is distributed (in cash or stock) as a return to patronage, in turn requiring strict limits on the proportion of income distributed as a return to equity. Member–patron control, service at cost, and limited payments to equity capital are, then, the basic elements of a cooperative firm.

Operation at Cost

A brief example will show why paying net margins to members according to their patronage (i.e., to use of the firm's services) is equivalent to providing services to members at cost. Table 1 gives the example of a farm supply cooperative whose business is to supply farmer members with inputs such as fertilizer. The cooperative buys 10 000 units of fertilizer from the manufacturer at a wholesale price of US$0.30 per unit. The cooperative's handling cost is US$0.10 per unit, giving a total raw product and handling cost of US$4000. For simplicity, suppose there are only two members. Member A receives

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Table 1 Net revenue distribution in a hypothetical supply cooperative

Cooperative costs					
Wholesale cost of fertilizers		*Operating costs*		*Total cost*	
Per unit	Total	Per unit	Total	Per unit	Total
$0.30	$3000.00	$0.10	$1000.00	$0.40	$4000.00
Shipments to members					
Member A			*Member B*		
Units	Retail price	Total patronage	Units	Retail price	Patronage
3000	$0.45	$1350.00	7000	$0.45	$3150.00
Net return distribution					
Member A			*Member B*		
Patronage share	Patronage refund	Unit price (cost to member)	Patronage share	Patronage refund	Unit price (cost to member)
3000/10 000 = 30%	$150.00	$0.40	7000/10 000 = 70%	$350.00	$0.40

shipment of 3000 units and member B receives 7000 units from the cooperative. It is assumed that the retail price charged by the cooperative's fertilizer supply competitors is US$0.45 per unit and the cooperative charges this same price to its members on delivery. Member A's total cooperative patronage is 3000 × US$0.45 = US$1350; similarly, member B's patronage is US$3150. Hence, the cooperative's total business volume or revenue is 10 000 × US$0.45 = US$4500.

The cooperative earns a total net return of US$4500 − US $4000 = US$500. The reason for this positive profit is that wholesale price plus per-unit operating cost is less than retail price. To satisfy the at-cost principle, net returns must be distributed to members according to patronage. Inasmuch as member A accounts for 30% of the patronage, he/she is entitled to 30% of net returns or a patronage dividend of US$150 (US$0.05 per unit). Member B accounts for 70% of patronage and so is entitled to 70% of net returns, giving him/her a patronage dividend of US$350 (US$0.05 per unit). Provided the fertilizer is a homogeneous good, the per-unit patronage dividend will be the same for both members as well. Net cost per unit to each member is the retail price originally paid (US $0.45) less the per-unit patronage dividend (US$0.05). That is, members buy fertilizer at cost: a US$0.30 wholesale price plus US$0.10 operating cost. In this particular example, members buy fertilizer US$0.05 per unit cheaper than they would from the cooperative's competitor.

Contrast with Investor-Owned Firms

Although a cooperative distributes net returns or losses primarily to users of the firm's services, an investor-owned firm (IOF) distributes net returns to shareholders, that is, to owners of the firm's capital (Hansmann, 1996). Suppose the fertilizer distribution firm in Table 1 is an IOF rather than a cooperative. Sales quantity, costs, revenues, and total net returns (US $500) are assumed to be the same as in Table 1. If shareholder 1 owns 100 of the 150 shares outstanding, he/she claims two-thirds of the US$500 net return (US$333.33). If shareholder 2 owns the remaining 50 shares, he/she claims one-third of the US$500 net return (US$166.67). The contrast with a cooperative is the clearest if it is imagined that shareholder 1 is the same person as farmer A in Table 1 and shareholder 2 is the same person as farmer B. Farmer A pays US$1350 retail for his/her fertilizer and, as shareholder of the firm, receives US $333.33 in dividends. Farmer B pays US$3150 retail for his/her fertilizer and receives US$166.67 in dividends. Net price to farmer A is US$0.45 − (US$333.33/3000 units) = US$0.34. Net price to farmer B is US$0.45 − (US$166.67/7000 units) = US$0.43. The distribution of the fertilizer cost between the two farmers has shifted considerably from that prevailing in a cooperative.

Modern History and Types of Cooperatives

Modern History

Agricultural marketing cooperatives operated successfully in the United States as early as the 1810s. They included cheese makers, hog processors, and grain elevators. The National Grange, founded in 1867, organized thousands of local associations to purchase farm inputs and sell farm products collectively. Most of them, and successor locals organized by the Farmers' Alliance, had failed by the turn of the century, but the Farmers' Union, founded in 1902, continued the work of establishing county-level supply and marketing coops. The American Farm Bureau Federation also began fostering local cooperatives in the 1920s. Successors of the Farmers' Union and Farm Bureau coops include some of the major cooperative associations of today.

The worldwide cooperative movement received a significant boost through the expansion of the British Empire in the late 1800s. British officials encouraged formation of local cooperatives, linked to national cooperative unions. Most local coops acted as agents for the British-instituted agricultural marketing boards. Agricultural cooperative unions in many low- and medium-income nations remain dependent on

government support; however, such support is waning and they are beginning to stand on their own.

In the US, the Sherman Antitrust Act had in 1890 outlawed "every contract, combination... in restraint of trade." Cooperatives are collective arrangements between farm firms and hence were widely regarded as examples of such illegal combinations. The Clayton Antirust Act (1914) thus specifically authorized "... agricultural or horticultural organizations... not having capital stock..." The more numerous capital stock-based associations then were legalized by the Capper–Volstead Act (1922), widely regarded as the 'magna carta' of farmer cooperatives. Coops legalized by Capper–Volstead must conduct a minority of their business with nonmembers and either be organized on a one-person-one-vote basis or restrict stock dividends to 8% or less. Capper–Volstead assured that a cooperative's mere existence would be insufficient evidence of illegally collusive behavior. Furthermore, Section 2 of the Act allows coops to affect prices as long as they do not do so 'unduly.' Most cooperatives are chartered in a particular state and therefore are subject to state-level incorporation regulations as well.

A Central and 12 regional Banks for Cooperatives were established by the Farm Credit Act of 1933. In 1989, the 11 of the 13 banks merged to form CoBank; the remaining two – in Massachusetts and Minnesota – remained independent. Equity in these banks is held by the cooperatives that borrow from them, and interest rates are determined by the cost of CoBank's capital plus operating costs. In addition to its loans to direct retail borrowers such as coops, the bank provides wholesale loans to affiliated lending associations in the Farm Credit System.

In 2001, when data last became available, approximately 28% of the value of farm products in the US appeared to have been sold through processing/marketing cooperatives and approximately 26% of the value of farm supplies purchased through supply cooperatives. These overall percentages seem to have changed little since the early 1980s. Breakdowns of cooperative market shares in 1996 and 2001, based on rather spotty information, are shown by type of farm product and farm input in **Table 2**. Marketing cooperatives' shares of farm sales range from 0% to 21% in Britain, whereas they range from 20% to 83% in Germany. In recent decades, some US cooperatives have converted into an investor-owned form or have adopted forms combining investor-owned firm with cooperative features (US Department of Agriculture, Rural Development Division, 2010).

Types of Function

Agricultural cooperatives in the US consist of supply, marketing, service, and bargaining cooperatives. Supply coops, illustrated in **Table 1**, provide members with farm inputs such as machinery, fertilizers, pesticides, feed, and fuel. Marketing coops assemble, process or handle, and sell members' farm products. Service coops provide trucking, storage, and other services in which the member retains title to his farm commodity. An important form of service cooperative is the bargaining coop, which acts as farmer–members' agents in negotiating prices and other trade terms with farm product buyers. Some cooperatives provide supply as well as marketing services. Business volume in both supply and marketing cooperatives appears, in constant dollar terms, to have remained approximately flat from 1980 to 2005, and then risen after 2005. Marketing cooperative volume usually has been well over twice that of supply cooperative volume, although since 2005 it has declined to just less than twice (US Department of Agriculture, Rural Development Division, 2010).

Cooperatives are encountered frequently outside agriculture. Examples in the financial sector are mutual insurance companies, mutual savings banks, credit unions, group health plans, stock exchanges, and boards of trade. In the housing sector, they include community associations and condominiums and, in the consumer sector, utility cooperatives, food coops, cooperative nursery schools, and buying clubs of various kinds. Such organizations are true cooperatives if they are run democratically and refund net returns to members in proportion to patronage. Mutual insurance companies, for example, distribute profits in the form of dividends on customers' policies.

Types of Centralization

An agricultural cooperative in the US is considered a local, federated, centralized, or mixed one. Local cooperatives serve farmers in a small area such as one or two counties. A federated cooperative is one whose members are local cooperatives. A federated supply coop might engage in phosphate mining

Table 2 Cooperative share of agricultural business, 1996 and 2001

Products marketed	*Percentage of cash receipts*		*Farm input*	*Percentage of farm production expenditures*	
	1996	*2001*		*1996*	*2001*
Milk and milk products	83	83	Fertilizer	44	45
Cotton	32	43	Petroleum	44	46
Grains and oilseeds[a]	45	38	Crop protectants	32	34
Fruits and vegetables	19	19	Feed	21	15
Livestock	13	13	Seed	10	13
Total[a]	31	28	Total[b]	28	26

[a]Weighted by farm value.
[b]Weighted by wholesale value.
Source: Issues of Farmer Cooperatives and Rural Cooperatives magazines, USDA, 1996–2001 (most-recent figures available).

and fertilizer mixing, transferring the mixed fertilizer to its member locals in order to be distributed to the locals' farmer–members. A federated's net returns are distributed to member–locals in proportion to the local's patronage, and a local's receipts are, in turn, distributed to the local's farmer–members in proportion to members' patronage in the local. Federated coops are sometimes referred to as secondary cooperatives or, in Britain and many other countries, as cooperative unions. Centralized cooperatives operate like locals, that is, admit only individuals as members. The difference between a local and a centralized firm is only in size, the centralized cooperative usually being similar in size to a federated cooperative. Mixed coops are those that admit both individuals and local cooperatives as members.

Like other agricultural firms, US cooperatives are – by merger, acquisition, or dissolution – becoming fewer and larger. The number of marketing cooperatives in the United States fell from approximately 1800 in 2001 to 1218 in 2010. The number of supply cooperatives fell from approximately 1300 to 975. An additional 117 cooperatives were providing services such as trucking, storage, and crop drying in 2010. During that same 2001–2010 period, the number of individual cooperative memberships fell from approximately 5.7 million to approximately 2.2 million. The number of farm memberships, however, remained almost constant. Of the 2310 cooperatives operating in 2010, 2252 were organized on a local or centralized basis, 38 were federated, and 20 were mixed (US Department of Agriculture, Rural Development Division, 2010).

Economic Theory of Cooperatives

The economic theory of cooperatives is a set of related statements about how members, directors, and employees would behave – and what they would achieve – given assumptions about their objectives and resources. Some theorists have considered the cooperative as a single decision-making entity. Others have considered it instead as a loose collection of individual agents, each seeking to promote his/her own special interest. These two schools of thought will be considered in turn, focusing on a single-product marketing cooperative as an example. Application to a supply cooperative is straightforward.

Single Decision Entity

The board of directors may pursue a number of alternative objectives including: (1) maximizing the price paid to members per unit of product delivered (including initial price and per-unit patronage dividend); (2) maximizing members' total – that is farm plus processing – income; and (3) permitting free entry to the cooperative. These competing objectives are best characterized by defining the firm's net margin (NM) function as

$$\mathrm{NM} = Pf(X,R) - WX$$

where P is the price the cooperative receives from selling the good in the final product market (after processing and handling); $f(X,R)$ is the quantity of final good sold, which, in turn, is a function of the resources X used in processing/handling and of the quantity R of the raw good received from members; and WX (the product of vector W of prices and vector X of the resources purchased at those prices) is the cost of resources used in processing and handling. Net margin, NM, excludes the value or cost of member raw product. The cooperative's service-at-cost principle requires that NM be entirely paid to members or patrons, although the practice of holding unallocated revenue violates this principle to some degree.

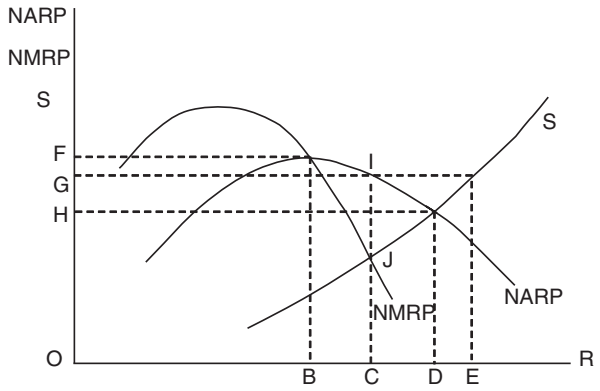


Figure 1 Alternative output rates in a marketing cooperative.

Assuming that the cooperative utilizes its resources X to maximize net margin at any raw product level R, maximized net margin (NM*) can be divided by R to obtain the net average revenue product function (NARP):

$$\mathrm{NARP} = \mathrm{NM}^* R^{-1}$$

Similarly, (NM*) can be differentiated with respect to R in order to obtain the net marginal revenue product function (NMRP):

$$\mathrm{NM}RP = \partial \mathrm{NM}^* / \partial R$$

NARP and NMRP are depicted in Figure 1. As raw product volume rises, NARP first rises as well. The reason is that specialization and learning-by-doing allow per-unit processing costs to fall as volume is boosted. Thereafter, NARP declines as diminishing returns to fixed resources set in or as output price P begins to fall. Where NARP reaches its highest point, NARP and NMRP always equal one another (Royer and Smith, 2007).

Also included in Figure 1 is the cooperative members' supply curve S. This curve represents the horizontal summation of all members' marginal costs of farm-producing the commodity in question. In other words, S represents, at a given raw product production level R, the cost of producing one more unit of the commodity.

Inasmuch as *NARP* is the full per-unit price the cooperative pays each member for product delivered (including initial price and per-unit patronage dividend), operating at raw-product volume B in Figure 1 would achieve objective (1), namely creating (at F) the greatest value per unit of raw product. Objective (2) would be achieved by operating at raw-product volume C instead, where member supply function S intersects the *NMRP* function. This is the full-income-maximizing point

because it equates the marginal cost of farm production with the marginal net revenue from its sale on the final-product market. Finally, objective (3) is achieved by operating at raw-product volume D because, at any lower volume, the full raw-product price paid by the cooperative (height of the NARP function) exceeds the minimum price a potential member would accept (height of supply function *S*) (Clark, 1952; Helmberger and Hoos, 1962; LeVay, 1983).

Solution (2) is socially optimal in the short run because it equates the marginal cost with the marginal benefit of member raw product. However, it is a complicated solution to enforce. If CJ is paid to members as their initial price, JI would be the per-unit patronage dividend. Full price would be CI. But this price would induce members to produce and deliver quantity OE rather than OC. A way must be found to limit supply to OC or to allocate the cooperative's net margin on a nonpatronage basis. In contrast, free-entry Solution (3) would reduce members' net incomes to zero in the long run. The reason is that free entry to the cooperative would shift raw-product supply curve *S* to the right until the cooperative payment per unit of raw product is reduced to the member's per-unit cost of production, as opposed to marginal cost of production represented by raw-product supply curve S (Sexton, 1986). Actual cooperative pricing practice varies widely (Sexton *et al.*, 1989; Soboh *et al.*, 2009; Yoo *et al.*, 2013).

Multiple Decision Entities

A distinction should be made between (1) whether members would initially agree to any given raw-product pricing policy and (2) whether that policy would remain feasible in the sense of providing an incentive for every member to remain in the cooperative once the policy is enforced. The former question, a collective choice one, can be addressed by first specifying the cooperative's voting process, then determining whether the price policy would be selected by majority vote, given the characteristics of the individual members. The latter question, one of membership stability, has been addressed through the use of 'cooperative games,' in which the analyst specifies the minimum incomes which various subgroups of the membership would earn if they formed their own cooperative or traded instead with an IOF. Cooperative games – which may be applied to many situations other than to cooperative business firms – are useful if members differ from one another in farm size, efficiency, or other factors.

Consider, for example, the case in which the cooperative's per-unit operating cost is substantially lower at the present volume than at the smaller volume that would result if some members quit. Under a number of reasonable assumptions about the cooperative's cost structure, it is easy to show that larger volume members could credibly threaten to quit unless they were granted concessionary pricing terms. Furthermore, it would often be in the interests of smaller members to grant such concessions to forestall the cooperative's breakup. In the absence of concessions (which would involve departing from the simple patronage-based dividend allocation shown in Tables 1 and 4), a breakup would occur unless the larger members were motivated by altruism or other extra-economic objectives. For this reason, it has been observed that solution (i), point B in Figure 1, may be the long-run equilibrium volume of a cooperative, because a subgroup of members can increase its incomes by breaking off to operate at this more efficient point.

Cooperative Management

Pricing and Pooling

The cooperative's elected board of directors establishes policy and oversees the activities and performance of hired management. Board members usually are chosen on a rotating basis at the annual meeting or by mail ballot. Issues about which the board must decide include types of offered services, pricing and pooling, financial structure, credit, and member and employee relations. The authors will consider pricing and pooling in the next two paragraphs. The context used is again that of a marketing cooperative.

A few marketing cooperatives credit a member with the full market value of raw product on its delivery to the coop for processing or handling. This market value is then debited, along with other costs, from the cooperative's revenue to determine the net margins that will be allocated back to the member on a patronage basis. Coops that operate this way may be termed 'buy/sell' coops. 'Pooling' cooperatives are those which do not credit members with the market value of their raw products on delivery and which, therefore, do not debit raw product value from the returns eventually allocated back to members on a patronage basis. In either event, part of the member's allocation usually is paid in cash, part in equity certificates. If raw products are homogeneous across members, the decision whether to credit a member on delivery with the market value of his/her product does not affect the sum of payments he/she will receive from the cooperative.

A complicating factor is that most cooperatives deal in heterogeneous products, either in the sense of various grades of the same commodity or of various commodities. Such grades and commodities can, for payment purposes, be grouped in any way the cooperative chooses. Let P_j be the per-unit valuation (often the raw-product market price) of the *j*th raw product, Q_j the quantity of *j* supplied by members, and R_j its per-unit resale revenue in the final product market less the cooperative's per-unit operating cost (including any member credits at delivery time). Assume the firm operates a number of separate pools and let J_k represent the subset of the firm's products included in the *k*th pool. The cooperative's per-unit payment to members for the *j*th raw product shipped to the *k*th pool is (Buccola, 1991):

$$\text{Unit payment} = \left[P_j\left(\sum_{J_k} P_j Q_j\right)^{-1}\right]\sum_{J_k} R_j Q_j$$

The member producer of product *j* participates in the net earnings of all products involved in the pool in which *j* belongs. Products often are pooled in this way to reduce member risk through diversification or to simplify accounting or because the raw products are commingled during processing. Raw-product valuations, P_j, are in many cases difficult

to establish and create significant conflict on the board of directors.

Equity Subscription and Redemption

As indicated above, part of a member's patronage refund (which may in a marketing cooperative include some or all of the 'market value' of the raw product) normally is paid in the form of a certificate, the corresponding cash withheld to provide the firm's equity capital base. Besides withheld patronage dividends, coops have two other ways to subscribe equity capital: outright purchase (often when a member joins) and reunit retains. The latter are used primarily in marketing firms and consist of a fixed capital obligation for each physical or value unit of commodity that a member delivers to the cooperative.

Equity subscribed by withheld patronage dividends, outright purchase, or per-unit retains can be accounted for in either stock or nonstock form. The principal nonstock device is the certificate of equity, variously known as a revolving-fund, patronage-refund, or revolving-capital certificate. The equity portion of the cooperative's balance sheet indicates each member's equity share of the firm as determined by the value of his/her equity certificates and book credits. In the conventional cooperative structure, most certificates and credits carry no vote, are nonnegotiable (cannot be traded), and bear no interest.

Approximately three-quarters of the US cooperatives are organized on a stock basis, that is, account for a part of a member's equity through stock certificates. Some issue a limited amount of preferred stock, which in most states is limited to a dividend rate of 8% or less. Common stock, found more frequently, usually does not pay dividends and is nonnegotiable. Except as specified in the cooperative's equity retirement plan (see next paragraph), it cannot be cashed in for more than its par value, which generally is quite low. Preferred and common stock typically account for the minority of the firm's equity capital. A portion of a coop's equity normally is also held in unallocated form – not allocated, that is, to the account of any particular member (Barton and Schmidt, 1988; US Department of Agriculture, Rural Development Division, 2011).

A member's allocated capital, whether in stock or nonstock form, can be revolved or redeemed (paid in cash) to the member in a number of ways. Table 3 lists the alternatives and the percentages of cooperatives employing them in supply and (as an example) in grain- and oilseed-marketing cooperatives. Most financial analysts favor one of the bottom three methods in Table 3. Age-of-Patron and Estate-Settlement methods allow the quickest growth in cooperative operations but, especially in view of their noninterest-bearing nature, create illiquidity by depriving members of their equity contributions for long periods. Rotation cycles in a coop's Revolving Fund plan tend to vary at the board's discretion, so member payouts are often rather unpredictable. Under reasonable parameter assumptions, the Percentage of Pool plans yield members the highest present value of redemption cash flow. Base Capital plans best ensure that a member's proportionate share of capital investment remain close to his patronage share of the firm's business. Until recently, however, they have been rarely used (see Section New Generation Cooperatives). In recent decades, cooperatives have tended to move away from the Estate Settlement method to Revolving Fund approaches (US Department of Agriculture, Rural Development Division, 2011).

A key objective of the cooperative's equity plan should be proportionality between capital investment and patronage because, in its absence, the owners of the cooperative are not exactly its users. The nature of the equity redemption scheme is, in fact, more important in a cooperative than in an IOF. In the latter, returns are obtained partly when dividends are paid on the stock and partly when it is sold. Because, in a cooperative, stock and nonstock certificates are almost always nonnegotiable, members usually depend on the Board's equity redemption policy for reclaiming their investment.

Taxation

The Revenue Act of 1913, which established income taxation in the US, exempted 'agricultural and horticultural associations' from income tax. The argument was that such associations allocate most of their net earnings to individual members and hence do not earn a profit as corporate entities.

Table 3 Cooperative equity redemption plans

Plan name	*Description*	*Percent of the US supply cooperatives using (2008)*[a]	*Percent of the US grain/oilseed-marketing cooperatives using (2008)*[a]
Age of patron	Redeem all capital when member reaches a specified age (e.g., 65 or 70)	38	30
Estate settlement	Redeem all capital at member's death	50	58
Revolving fund	Redeem all capital held at specified number of (e.g., 10) years	43	45
Percentage pool (% of all equities)	Annually redeem a constant specified percent of member's allocated equity	17	13
Base capital	Redeem or subscribe capital to maintain fixed proportion to member's recent average patronage	2	1

[a]Because cooperatives often simultaneously use more than one equity redemption method, percentages do not sum to 100.

Source: Reproduced from US Department of Agriculture, Rural Development Division, 2010. Cooperative equity redemption. Rural Business Cooperative Programs, Research Report 220. Washington, DC: US Department of Agriculture.

Table 4 Taxation of a hypothetical supply cooperative

Recent value of sales	US$26 000 000.00
Operating cost	23 500 000.00
Net margin	2 500 000.00
Pretax unallocated revenue	250 000.00
Tax on unallocated revenue (@ 35%)	87 500.00
After-tax unallocated revenue	162 500.00
Allocatable member income	2 250 000.00
Total value of goods sold to members	26 000 000.00
Predollar dividend (all members)	0.086538
Dollar value sold to member X	3640.00
Total paid to member X	315.00
Paid in cash (@ 25%)	78.75
Paid in certificates	236.25

Qualifications to this exemption were included in subsequent Revenue Acts, although federal tax policy on cooperatives has remained fairly constant since 1962. For income tax purposes, federal law permits any firm to deduct from its revenues all operating expenses and any rebates to patrons for which there was a preexisting legal obligation at the time of transaction. Such rebates include per-unit retains or patronage dividends the cooperative had agreed to pay members (or any other patron) for their earlier purchases or sales through the cooperative. That is, net returns on member and nonmember patrons' business the cooperative was obligated to allocate to individual members and other patrons are not taxable to the cooperative. Coops which deduct from reported revenues any per-unit retains or dividends on patronage business are called 'nontax-exempt' cooperatives.

In addition to deducting per-unit retains and returns on patron business, certain cooperatives may deduct stock dividends paid in the current year and any nonpatronage income allocated back to member and nonmember patrons. (Nonpatronage income is an income that is unrelated to the firm's farm supply or product-marking business, for example rental income on the firm's property.) Agricultural cooperatives falling into this 'section 521' or 'tax-exempt' category must, among other restrictions, treat nonmember patrons the same as member patrons in pricing and in equity subscription and retirement plans. Supply cooperatives cannot do more than 15% of their business with nonmember nonfarmers. 'Tax-exempt' status does not ordinarily result in significantly lower income tax than that paid by 'nontax-exempt' cooperatives.

Table 4 shows the tax treatment of a hypothetical multiproduct agricultural supply cooperative that conducts business with members only and has no nonpatronage income. The distinction between tax-exempt and nontax-exempt status makes no difference in the Table 4 example. Tax is paid on unallocated revenue only; income allocated to individual members is not taxed. To determine members' rates of return per unit of patronage, the patronage dividend is first computed as a percent of total member business. That rate of return is then multiplied by each member's total patronage to give the member's total dividend. In the example shown in Table 4, 25% of the dividend is paid to the member in cash and the remainder is held as equity capital, to be redeemed in cash at a later date.

Cooperatives and Economic Performance

Cooperatives have long been regarded as a way in which producers or consumers can substitute for inadequate market services by providing the services themselves. Thus, farmers persuaded that IOF processors pay less than full value for farm products, or charge more than full cost of farm inputs, can form a cooperative to provide the product-handling or input-supply service themselves. Because, broadly speaking, service inadequacy implies and is implied by a departure from competition, such a cooperative becomes a competitive yardstick – a means of both judging how inadequate the IOF performance has been and providing a remedy for that inadequacy. Expressed differently, cooperatives arise and thrive best when markets are missing, namely when the investment climate that would bring forth adequate market services is missing. The competitive yardstick cooperative is, in a stylized way, the traditional open-membership coop because free member entry and exit would eliminate any monopoly elements in the cooperative's own service provisions.

By the same token as profit opportunities grow, allowing markets to become more diversified or competitive, cooperatives begin to compete less successfully with investor-owned firms. This explains why cooperatives tend to play a more prominent economic role in poorer than in wealthier economies and in more socialized than in more capitalist ones. Declining trade barriers during the past four decades, and consequent rising incomes and market globalization, have thus put great pressure on the cooperative business form. Important cooperatives in the US and Europe have become bankrupt or have converted to IOF or semi-IOF form in recent years (Cross *et al.*, 2009). And country-wide cooperative unions in poor- and middle-income nations that once served as agents of government development programs are losing their subsidized status. A prominent example is the National Agricultural Cooperative Federation (NACF) of Korea, which recently ceased subsidizing its farm supply and marketing division with income from its banking division.

Problems with the Cooperative Form

The traditional cooperative's disadvantage in the face of a competitive IOF economy can be traced to four interrelated problems. The first, known as the horizon or liquidity problem, is that – as discussed in the Section Equity Subscription and Redemption – the portion of the member's annual dividend retained as capital stock (withheld patronage dividend) usually is held by the cooperative without interest until the board decides otherwise. The investment often is not revolved back until the member's death. The prospect of this illiquidity discourages membership and hence investment. The second, free-rider problem, is that each member receives the same access to the cooperative's input-supply, -processing, and -marketing services per dollar of his/her patronage, despite that some members have invested more in the cooperative than others have. Newer and smaller volume members typically free ride on the older and larger volume ones, who account for most of the capital trapped in the revolving fund.

Free riding is encountered most likely when coop membership is heterogeneous or the firm operates away from the maximum point on its net average revenue product (NARP) curve. At cooperative volume OC in **Figure 1**, the additional cooperative net margin created by one more unit of raw product is vertical distance OJ (height of the NMRP function above C). If net margins are distributed in proportion to patronage, the same extra unit instead will be paid the greater amount CI (height of the corresponding NARP function). Hence, other members subsidize that last unit by amount JI. Any side payments to nullify such subsidies tend to be divisive. For this reason, a cooperative's success depends partly on the degree of cooperative spirit among the members, including certain individuals' willingness to bear an excess share of the total burden (Cechin *et al.*, 2013).

The third or agency problem is that, on account of the traditional cooperative's one-person-one-vote rule, those with little capital in the cooperative have, besides equal per-dollar benefit of the firm's services, equal control of the policy decisions. This disproportionality between investment and voting power discourages large-volume patrons from participating because the interests of smaller patrons typically differ from those of larger ones (Pozzobon and Zylbersztajn, 2013). Finally, an information or oversight problem is created by the absence of cooperative stock from public exchanges. Public stock prices encapsulate outsiders' judgments about a firm's financial health, which can be used, for example, to determine executive salaries. If such a piece of information is absent, cooperative members must rely on their own direct evidence, such as operating statements and balance sheets, to assess management performance. Perusals of that sort are usually impractical – they involve high monitoring costs.

All four of the above problems arise because member property rights in a cooperative are poorly defined. In particular, the member has an inadequately defined: (1) claim to the cooperative's net income and (2) control over the cooperative's assets – over its investments, contracts, and business policies (Chaddad and Cook, 2004). The control problem is connected, as already seen, to the disproportionality between a member's investment and voting rights (Chaddad and Iliopoulos, 2013).

Analysis of the net-income issue is more complicated. Four aspects of a member's net-income claim (cooperative stock share) can be distinguished: whether the claim is: (1) restricted to member patrons, (2) redeemable from the cooperative, (3) transferrable to other individuals, or (4) appreciable in value. In traditional cooperatives, income claims are restricted to member patrons, redeemable only with board approval, and nontransferable. They also are nonappreciable, that is, their value cannot change with the firm's profitability. The member's property rights are, in short, weak and unclear, severing members' interests from the firm's interests. In most cooperatives, as already seen, a member's net return share is not even held proportionate to his/her share of the firm's capital, although some capital contribution plans do ensure such proportionality.

New Generation Cooperatives

The net result of these difficulties is to discourage investment, undermining the cooperative's ability to grow and compete with other firms. Mathematical models of a farmer's choice between marketing his product through a traditional cooperative and an investor-owned marketing firm underscore this phenomenon. The models show that, as final-product markets become more competitive and the IOF loses its ability to influence prices, the cooperative's competitive yardstick effectiveness in escaping IOF market power declines. Because the cooperative's horizon, free-rider, control, and oversight problems remain, it is motivated to restructure itself into an IOF or move toward bankruptcy (Cross and Buccola, 2004).

As an alternative to such bankruptcy or outright IOF conversion, new cooperative forms have arisen in recent years. Some cooperatives now sell transferrable, appreciable shares to nonmembers and nonpatrons – to business firms in particular – most often through a subsidiary or joint venture. The New Generation cooperative (NGC), found especially in the US and usually engaged in processing and marketing, is particularly important (Cook and Chaddad, 2004; Fulton and Sanderson, 2003; Fulton, 2001; Coltrain *et al.*, 2000). In an NGC, each member's raw product deliveries to the cooperative are determined by a tonnage- and quality-defined contract, expressed as the member's obligation as well as right and combined with his/her obligation to purchase a particular number of capital shares. Such shares can be sold to, or purchased from, other members or nonmembers.

Thus, the membership in the new generation cooperative is closed, as distinguished from the open membership in most traditional cooperatives. Identity of each member's raw product typically is preserved in the course of processing and sale, so patronage dividends paid to each member are specific to his/her own delivery lots. Consistent with cooperative principles, ownership is thus linked to patronage but, as with larger investor-owned firms, rights to such ownership can freely be bought or sold. And consistent with the worldwide trend toward identity-preserved niche marketing, emphasis is placed on quality- and time-specific delivery contracts between member and cooperative.

In contrast to the traditional cooperative's open-membership policy, successful raw-product value enhancement in an NGC involves restricting membership. Closed membership is essential for maintaining a volume low enough to capture the extra-competitive profit afforded by the firm's quality, reputation, and marketing niche. These gains accrue to the cooperative's farmer members in the form of extra-competitive returns to the members' fixed farm and cooperative assets. In a social welfare sense, the supernormal returns can be justified by the special quality, service, or innovation in the NGC's product, which a perfectly competitive commodity market could not offer. Under open membership, those gains instead would attract new members, whose additional supply would drive final product prices downward. But the New Generation cooperative form has drawbacks as well. The goal of maximizing the return to equity is often inconsistent with the goal of maximizing the return to patronage. Improving equity returns may, for example, require buying raw product on the open market at the expense of processing the cooperative members' own farm goods. Because the NGC seeks to enhance the return to member equity as well as to member patronage, a tension is created between these two goals (Kalogeras *et al.*, 2013).

Solution of the control problem in cooperatives is also often difficult. In the US, incorporation laws in most states require cooperatives to guarantee one vote to each member in Board elections, preventing any proportionality between control and capital investment. As a partial solution to this problem, and to provide the external oversight available to publicly traded firms, some cooperatives – especially in Northern Europe – employ a Board of Commissioners in addition to a Board of Director's (Hendrikse, 2004). Commissioners, selected from outside the cooperative, have some influence over Director's decisions. Regardless of board's decision structure, members lose control over their cooperative as it grows because growth requires delegating power to management. From a control perspective, indeed, very large cooperatives closely resemble very large investor-owned firms.

Cooperative as Social Transformation

An alternative to providing members more well-defined property rights is to shift away from rather than toward such rights. In particular, some analysts view the cooperative form not as one element of a competitive market (the competitive yardstick school) but as an alternative to capitalism. They argue that, in the absence of a fully cooperative economy, IOFs will pay farmers below-competitive prices and charge consumers above-competitive ones. Cooperative organization of production and distribution would bring a more just society, in which communities are united and beyond selfishness. This thinking was an important element of the 'cooperative commonwealth' movement of the early twentieth century, associated with organizer and theorist Aaron Sapiro.

Among its modern heirs is the United Nations, which, in its declaration of 2012 as the International Year of Cooperatives, said cooperatives will "not only [promote] better business but advance sustainable development … and promote equality and social integration." The UN and its partners promote and raise awareness of cooperatives by holding public forums and advocating government policies conducive to cooperative growth. They see cooperatives as a move toward 'social, economic, and environmental sustainability,' and call for a 'paradigm shift for economy and social inclusion.' The International Cooperative Alliance, a consortium of member nations' country-wide cooperative unions, is a prominent example of this movement. Like the Sapiro cooperatives of the early twentieth century, its emphasis is on training, promotion, and political action rather than on strengthened property rights, and on more expansive cooperative goals rather than the more specialized ones in a New Generation cooperative.

Universal cooperative organization is unnecessary for, and likely would prevent, the maintenance of competitive prices. Models suggest that even the threat, let alone presence, of a cooperative's entry into an imperfectly competitive IOF market is especially effective in moving consumer prices toward the competitive norm (Sexton, 1990). An IOF considering entry into an agricultural processing market recognizes its new presence may boost raw product prices and reduce final-product prices, both of them impairing its likely profit. The cooperative entrant worries only about its potentially depressing influence on final-product prices because any raw-product price change would be passed on to farmer members in the form of higher farm revenue. Thus, the threat of a cooperative's entry is more credible than of an IOF's entry, implying that the freedom to form a cooperative is an especially potent force toward market efficiency.

Summary

The cooperative or user-owned way of organizing an agricultural services firm is fundamentally different from the investor-owned way. In the former, net returns are paid to the farm products supplied to or inputs purchased from the firm. In the latter, net returns are paid to the capital. Efforts to keep cooperative members' capital investments proportionate to the values of their product supplies or input purchases are difficult to implement. And their implementation moves the organization in the direction of an investor-owned model.

Because a farmer's products and input uses are far less mobile than his/her capital potentially is, user-based control of a services firm is much less flexible than capital-based control. Farmer capital can quickly be moved from Brazilian sugar refining to Canadian phosphate mining. The farm's own sugarcane production and phosphate use cannot. This difference lies at the heart of the allocative inefficiencies to which cooperatives are prone, and explains why cooperatives tend to fail when investment markets are widespread and liquid.

Such a competitive ideal can, however, never be fully realized in given situations. Regulation often pushes prices above the competitive norm or below what attracts enough supply. The scale of investor-owned marketing or input services often is inadequate, especially in low-population areas or, especially, when the services are new, innovative, or specialized. Cooperatives then arise to protect members from these government and capital failures.

Yet the cooperative itself is an element of the market system, as one can see from the coop's enhancement of competition even in the face of being injured by it. The rise of vertical integration – a contract-specific relationship between two firms that bypasses the more anonymous marketplace – is a case in point. Being supplier- or buyer-owned, a cooperative is itself an instance of vertical integration and therefore a natural part of market development. Governments' declining use of cooperative federations as agents of farm subsidies more likely underscores this essentially market nature of cooperative organization.

See also: Agribusiness Organization and Management. Agricultural Finance

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Agricultural Ethics and Social Justice

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Glossary

Analytical agricultural ethics The review and investigation of concepts, arguments, and implicit norms as they are deployed in developing an understanding of agricultural practice.

Burdens of proof The criteria that must be met for a particular ethical judgment to be made or reversed.

Communitarianism A philosophical approach that emphasizes the importance of tradition, the fundamental role that a society plays in forming political and moral reasoning, and the slow change of culture.

Consequentialism A philosophical approach that stipulates that all human actions be justified solely in terms of their consequences or effects on others' welfare.

Ethical reductionism A philosophical approach where ethical concepts are reduced to statements about individual and subjective experiences; it promotes a strong division between fact and value.

Ethics The systemization and defense of values, standards, and conceptions that are used to make ethical judgments regarding human conduct.

Food deserts Urban areas with limited access to nutritious foods that are often disproportionately made up of poor socioeconomic classes and minority communities.

Food security The establishment of market-based mechanisms meant to ship food to other areas experiencing scarcity.

Food sovereignty A broader conception of food that moves away from market-based systems where human rights concerns are bound up within the food systems themselves.

Informed consent Occurs when parties (that must bear risks) voluntarily agree to do so under conditions of full disclosure; when informed consent is lacking, even low-level beneficial risks may be rejected.

Justice The terms 'ethics' and 'justice' are often used interchangeably, as there is no standard method to distinguish between the two. However, justice is commonly defined in two ways within philosophical traditions. First, traditional philosophers, such as Plato, used the word 'justice' to indicate a personal or individual virtue. Second, philosophers such as John Rawls and Ronald Dworkin argued that the locus or the appropriate place of justice is the social institution or structure of society. This second definition of justice is most widely held today.

Liberalism Although there are many forms of liberalism, in general liberals hold the view that liberty is the attribute of primary political value. In addition, current forms of liberalism largely accept the view that the locus or the appropriate place of justice is the social institution or structure of society.

Metaethics A branch of ethics that attempts to understand the epistemological, psychological, and semantic presuppositions of ethical properties, attitudes, and judgments.

Neoliberalism A form of liberalism that promotes the use of a largely unregulated market system to distribute goods.

Practical ethics The application of values, standards, and conceptions used to make ethical judgments to real life situations. This also includes the abstraction of ethical principles from specific contexts.

Reductionism The reduction of a complex system or set of phenomena to a formal set of interrelated rules.

Rights The justified or enforceable claims that may be made on behalf of right-holding parties; it is typically thought to provide absolute protection of individual interests against social benefits.

Scientific reductionism The reduction of a system or complex set of phenomena to a set of rules solely based on scientific principles; for example, one could reduce the functioning of the human organism to chemical principles and completely disregard psychological principles.

Substantive agricultural ethics Prescribes specific action plans, practices, and policies for persons and organizations involved in agricultural issues; its aim is to present arguments for or against a proposed course of action that applies those concepts, rules, and standards with clarity, rigor, and logical coherence.

Utilitarianism A nineteenth century approach to ethics that has greatly influenced the twentieth century public policy, particularly in the arena of cost–benefit and risk–benefit management; the term was first used by Jeremy Bentham and then by John Stuart Mill. The Utilitarian maxim states that the correct action is the one that produces the greatest amount of good for the greatest number of people.

Introduction

The word ethics is often used interchangeably with the word morality to indicate goals, norms, and values that are taken to guide human action. A common, but far from universal, distinction is to define ethics as the systematic study of moral codes, particularly with regard to criticism, justification, and acceptability of social norms. As critical evaluation of moral norms itself implies the application of norms; scholarly work on ethics has perennially been accused of circularity, dogma, relativism, and begging precisely the question it attempts to answer. Scholarly study of morality has, nevertheless, made it

possible to provide considerably more explicit, locally coherent, and rigorous arguments on goals, norms, and values than are typically found in ordinary life.

Agricultural ethics is the criticism, analysis, and justification of systematic moral codes and the acceptability of social norms that exist or are applied to practices of food and fiber production, distribution, and consumption. Given this definition, agricultural ethics can be understood as an interdisciplinary research and education area. Research and teaching on ethics take place to some degree in all disciplines of the social sciences and humanities, although some practitioners of these disciplines have disavowed work on ethics. The most typical disciplinary home for work in ethics has been philosophy, although departments of theology, religious studies, and political science also typically have specialists in ethics. Recent work in agricultural ethics emphasizes (1) unintended health, safety, and environmental impacts of agricultural technology; (2) the structure of agriculture, including distribution of benefits from agricultural production; and (3) questions of conduct, character, and professional ethics. In addition, special attention has been given to the moral standing of agricultural animals and to ethics as it relates to agricultural biotechnology. Depending on the ethical framework utilized by specific theorists working in this field, the above topics can also be framed as justice issues. As is illustrated below, the ethics of agriculture and justice are tightly linked.

Agricultural Ethics

Broadly speaking, ethics (also known as moral philosophy) is the systemization and defense of values, standards, and conceptions that are used to make ethical judgments regarding human conduct. Ethicists study how people should act and ethical norms are understood to be implicitly found within cultural practices, grounded in psychology, and able to be discovered through reason. Here ethical norms are understood to be an accessible part of the world. This branch of philosophy can, roughly, be divided into three major areas: metaethics, normative ethics, and practical ethics. Metaethics attempts to understand the presuppositions and logical structure of ethical properties, attitudes, and judgments (Sayre-McCord, 2012). This branch can be understood as a broader (or meta) analysis of ethics. In contrast, normative ethics is the development of general principles or standards that make particular actions 'right' or 'wrong' and the creation of theories that explain why some choices are better than others. This branch of ethics maps on well to the general definition given above and is often what is meant when the word 'ethics' is used without qualification. Engaged or practical ethics also focuses on determining right action but specifically with respect to real life situations. Sometimes engaged ethics not only involves the application of ethical theories to particular cases, but it also includes the derivation of ethical norms from specific contexts and integration with factual matters that can significantly influence the content and meaning of a normative claim or judgment.

Although metaethics is an important subfield, normative ethics and engaged ethics are of particular importance for those attempting to better understand agricultural science, technology, and farming methods. The following two methodological approaches are common in agricultural ethics. Analytic agricultural ethics undertake review and investigation of concepts, arguments, and implicit norms as they are employed in developing an understanding of agricultural practice, its goals, and the secondary social and environmental consequences of food and fiber networks. Analytic ethics aim to improve understanding of concepts, rules, and standards that are commonly used to frame and defend moral judgments and prescriptions for action. Substantive agricultural ethics prescribe specific action plans, practices, and policies for people and organizations involved in agricultural issues. The aim of substantive ethics is to present arguments for or against a proposed course of action that applies those concepts, rules, and standards with clarity, rigor, and local coherence.

Agricultural Ethics and Justice

It is important to note here that the terms 'ethics' and 'justice' are often used interchangeably, as there is no standard method to distinguish between the two. For example, sometimes 'ethics' and 'justice' are used to mark a distinction between personal conduct (ethics and morality) and the norms or standards that should govern the structure of the societies and the political life (justice or social ethics). There is also a broad distinction between justice as administered by courts of law and social justice, or just, fair, and morally defensible social arrangements. Traditional philosophers, such as Plato, might have used the word 'justice' to indicate a personal or individual virtue, but the broad philosophical interest in liberty (usually referred to as 'liberalism') that swept Europe during the eighteenth, nineteenth, and the twentieth centuries now dominates most discussions of social justice, even for those who wish to contest or critique the liberal approach.

In contrast to individual conduct, philosophers such as Rawls (2001) and Dworkin (1996) argued that the locus or the appropriate place of justice is the social institution or structure of society. Roughly, liberal philosophers identify liberty as the attribute of primary sociopolitical value (Cranston, 1967) and thus consider institutions (or rules) that protect it 'normatively basic' (Gaus, 1996). For liberalism, the product of a properly set up political structure is a just society. The central question then involves deciding whether or not laws are justified in limiting the personal liberty of citizens. Examples of fundamental rights commonly supported by liberalism include free trade, freedom of religion, and private property, as these universal rights are believed to promote personal liberty (Gaus and Courtland, 2010). The question of whether an agricultural practice (such as a specific pesticide) is to be banned qualifies as a case in point, because the ban will limit a given farmer's liberty by constraining the choice of technologies that can be used. Thus, as there is no standardly recognized method of drawing a distinction between ethics and justice, many ethical issues in agriculture can also be understood as justice issues.

History of Agricultural Ethics

Normative or ethical implications of agriculture were a common topic for scholars of philosophy, society, and biology for

most of the 3000-year history of Western thought. Aristotle discussed the configuration of agriculture he thought necessary for fulfilling human promise. More recently, Thomas Jefferson was both a scientifically informed practitioner of agriculture at his Monticello plantation and a philosopher of agriculture who contributed enduring analysis of how farm structure is related to problems of governance in a democracy.

Ethical reflection on agriculture carried over into the twentieth century through the efforts of scientists and agricultural leaders, such as Liberty Hyde Bailey and Henry Wallace, but the systematic discussion of agriculture was virtually absent in the writings of the late nineteenth and twentieth century philosophers and moralists. The last generation of philosophers to discuss agriculture as a philosophical topic is the one that included John Stuart Mill, Ralph Waldo Emerson, and Karl Marx. Each of these three authors wrote extensively on agriculture, but no one recognized as a leading contributor to philosophical or religious ethics since them has done so.

After World War II, agricultural scientists and leaders gave little systematic attention to ethical issues. Agricultural ethics was not included in the curriculum of agricultural colleges. Ethics became increasingly marginalized though in the 1950s and 1960s, with only a handful of social scientists undertaking normative evaluation of agriculture. Even in these studies, the role of ethics was largely implicit in that the norms or values on which evaluations had been based were seldom stated and almost never defended on philosophical grounds. Significant exceptions to this rule can be found in the work of agricultural economists John Brewster, Harold Breimyer, and Glenn Johnson. These works were almost totally ignored by professionals in liberal arts disciplines, such as philosophy, religious studies, and political science. Indeed, the decline of attention to ethics in agriculture reflects a general decline in attention to ethics throughout all departments of universities in the decades following World War II.

In 1962, Rachel Carson published Silent Spring. Although it was not in itself a philosophical book, Carson's critique of agricultural chemicals was arguably the first in a series of criticism of the agricultural practices that had emerged following World War II. Frances Moore Lappe's Diet for a Small Planet; Jim Hightower's Hard Tomatoes, Hard Times; Wendell Berry's The Unsettling of America; and the republication of Walter Goldschmidt's 1947 study As You Sow were among the most influential and most enduring of critical works published before 1980. Books by critics of agriculture have since proliferated, with at least a dozen published every year in the decade between 1982 and 1992. Although these books seldom present rigorous empirical or philosophical arguments for their conclusions, they typically make an explicit statement of the goals, values, and norms on which their evaluations of agriculture depend. They have in this way provided the source material for a resurgence of interest in careful scholarly attention to the philosophical foundations of agricultural practice.

As public criticism and mistrust of agricultural practices grew under the influence of these critics, agricultural institutions showed a renewed interest in the study of agricultural ethics. Courses were offered in some agricultural colleges, and a limited amount of research by philosophers and social scientists had been undertaken. Ethics and values issues have also become topics for symposia at disciplinary meetings of agricultural scientists and at consensus conferences intended to establish priorities for research and for policy change. Attempts to extend work on ethics to producer groups have thus far been limited. Although agricultural ethics remain somewhat marginal in the agricultural disciplines, the role of ethics in curriculum, research, and public policy has been increasingly accepted. Today both analytic agricultural ethics and substantive agriculture ethics are blooming with many agricultural ethicists making use of historical ethical frameworks, such as (1) rights-based ethics, (2) consequentialism, (3) communitarianism, and (4) environmental ethics.

Rights-Based Ethics and Agriculture

Rights-based ethics enter into issues surrounding agriculture and food systems when the implementation of new technologies or new policies is thought to violate the basic rights of individuals. In many cases, economic or governmental power is marshaled to deny particular groups civil rights, such as insuring a group's physical or mental integrity, life, and safety. There is little doubt that the historical industrialization and consolidation of agriculture and food production systems (such as the initial implementation of animal slaughtering technology and confined feeding operations) were accompanied by violations of civil liberties. For example, in the 1906 novel The Jungle, Sinclair (2012) graphically portrayed the lives of immigrants working in the early Chicago meatpacking industry, illuminating the poor working conditions, exploitation, and unnecessary hazards experienced by the workers. Such conditions would clearly be labeled unethical from a rights-based approach. Today similar arguments have been made regarding the conditions faced by workers in current meatpacking operations and migrant and seasonal farmworkers.

In addition to ethical issues surrounding the civil rights of workers, Schrader-Frechette (1999) argued that the violation of the basic rights of individuals can also occur where risks are not voluntarily chosen but involuntarily imposed. Examples of this could include food safety policy, if the consumer is not involved in the process of forming this policy, as each time a person consumes a food product there is a slight risk that they will get a foodborne illness. In addition, if specific groups or subgroups of the population, such as minority communities or those of low socioeconomic classes, suffer from a lack of access to quality food, then this could also be considered a violation of their rights, as they are not equally benefiting from the food system and, in some cases (such as when these groups make up the majority of the workforce employed in agriculture and food processing), are forced to take on a disproportionate share of the risks associated with the production of food.

The framing of food access as a justice issue and violation of rights is gaining steam in both society at large and some academic circles. For example, as Schanbacer (2010) argued, some development scholars focused on combating hunger are moving away from a call for food security – or the establishment of market-based mechanisms meant to ship food to other areas experiencing scarcity – and instead advocating food sovereignty or a broader conception of food where human rights concerns

are bound up within the food systems themselves. Here 'food security' should be understood as a policy with an aim of ensuring food availability for purchase, whereas food sovereignty connotes an entitlement (or positive right). In addition, local food justice movements, made up of active citizens, are working to combat 'food deserts' or urban areas with limited access to nutritious foods that are often disproportionately made up of poor socioeconomic classes and minority communities. These areas often lack grocery stores, farmer's markets, and other distribution points for nutritious foods.

Consequentialism and Agriculture

The primary philosophical opposition to rights-based ethics comes from those who espouse an ethical approach referred to as 'consequentialism.' Consequentialism stipulates that all human actions need to be justified solely in terms of their consequences or effects on others' welfare. The most popular form of this ethic is commonly labeled 'utilitarianism,' after the works of Jeremy Bentham and John Stuart Mill gained prominence during the eighteenth and nineteenth centuries. According to utilitarianism, the evaluation of these consequences include the following mandates: (1) it must be comprehensive or include all parties affected and all effects, (2) it must be additive or its benefits and harms need to be able to be summed up, (3) it must be comparative or include the comparison of possible consequences from alternative actions, and (4) it must be optimizing, or the appropriate action must produce 'the greatest good for the greatest number' (Sen, 1987). Utilitarian ethical approaches closely correspond to common quantitative tools of analysis developed by welfare economists, such as probabilistic risk analysis and cost–benefit analysis. Such tools have been used by the United States during the process of siting hazardous waste facilities. However, it is important to note that these tools are not, in themselves, prescriptive.

The work of the Nobel laureate in economics Amartya Kumar Sen has had enormous influence on utilitarian approaches in domains of crucial importance for agriculture, economic development, and natural resource management. Sen (2000) began by pointing out frequently overlooked inconsistencies in utilitarian interpretations of social welfare but moved on to develop his 'capabilities' approach that combines some of the ethical insights and strengths of rights theory with a social choice framework that allows utilization of the analytic tools that had been developed by economists working with utilitarian ethical assumptions. Succinctly, the capabilities approach uses economic tools to analyze policy alternatives, but instead of optimizing wealth or social utility, it recommends a focus on people's capabilities or, as Sen had said, 'freedoms' (Sen, 2000). Thus, the capabilities approach brings economics-based policy analysis broadly into conformity with conceptions of justice advocated by John Rawls (Sen, 2009).

Communitarianism and Agriculture

Another ethical approach, specifically communitarianism, is increasingly entering into issues surrounding agriculture and food systems. In sharp contrast to liberalism, communitarians emphasize the importance of tradition, the fundamental role that society plays in forming political and moral reasoning, and the slow change of culture (Bell, 2012). Modern versions of this ethical theory largely began as critiques of John Rawls' political philosophy, which emphasizes the role of an individual in society and includes the assumption that the purpose of the state is to secure liberty and fairly distribute resources. Both of these attributes have been contested by communitarian philosophers, such as MacIntyre (1984) and Sandel (1981). For example, Alasdair MacIntryre argued that a morally right action should be understood in terms of virtues that are grounded in the community's conception of right conduct. For communitarians, principles of justice must be found in the traditions of specific societies and thus are not universally applicable. However, it should be noted that a communitarian may object to the use of liberal terms here, as they argue that these may promote selfish behavior.

In addition, communitarian philosophers, such as Sandel (1981) and Taylor (1989), argued that a person is largely constituted through community attachments, such as family ties, localities, and religious traditions. This conception of the self is in sharp contrast to the overly individualistic liberal conception of the person; a person who attempts to push for solely selfish interests. Communitarian ethics are relevant to food and agriculture because many traditional agricultural societies have articulated both cultural identity and moral responsibilities through norms that emerge out of longstanding farming practices and attachments to the land. Smith (2003) argued that Wendell Berry, a well-known critic of industrial farming practice, had a fully developed political ethic based jointly on a communitarian ethic and a deep suspicion of the impact that industrial technologies had on farm households and rural communities.

Some contemporary food-oriented social movements appear to be motivated by communitarian ethics. Individuals and groups combating food deserts not only conceive the lack of access to fresh fruits and vegetables as a justice issue but also often have deep commitments to their specific community. Many of these groups argue that common strategies used to fight food deserts, such as creating neighborhood gardens, not only address problems surrounding food access but also serve as a way to empower individual communities through the development of small scale, embedded economies, and combat implicit racism in the food system. Another strategy or goal of these organizations is to reconnect fellow community members to their food traditions. Similarly, local food scholars, such as DeLind (2011), argued that the local food movement (which is similar but distinct from food justice movements) is as much about place making and community building as it is about securing food access. She writes that local food is both a "part of a regenerative agrifood system... [and] also about restoring 'a public culture of democracy' and engaging in the continual creation, negotiation, and re-creation of identity, memory, and meaning" (p. 279). Thus, both food justice movements and local food movements appear to be deeply grounded in communitarian principles, such as a commitment to and cultivation of community, the importance of culture and tradition, and the conception of the self as embedded within a specific context.

Environmental Ethics and Agriculture

Similar to the communitarian view that principles of justice must be distilled from the traditions of specific societies, those involved in local food movements often conceive of food systems as dynamic (or connected to politics, history, and ecology) and place based (Dahlberg, 1993; DeLind, 2011). Although this ethical approach is similar to communitarianism, it is distinct due to the fact that the understanding of who or what is an 'ethical patient' has been broadened to include the surrounding ecosystem, biotic communities, and nonhuman animals. Ethics such as these are often generally labeled as 'environmental ethics' or 'ecological ethics.' Food or agricultural ethics can be understood as one subfield in environmental ethics, as these ethics often take the ecosystem into account due to the fact that food production is inexorably tied to the environment. In addition, environmental ethics come in many forms, as they often include aspects of classical positions, such as rights-based ethics and consequentialism, and more radical conceptions of what it means to be an ethical or just human being.

For example, according to Warren (2000), environmental ethics can be roughly divided into four categories: house positions, reformist positions, 'mixed reform and radical' positions, and radical positions (p. 77). House positions are ethics that use mainstream or classical arguments, such as consequentialism, but apply them to the environment. These arguments are 'housed within' the larger ethical traditions that they draw from. Reformist positions reevaluate key assumptions built within classical ethical arguments and reform or revise them so that the environment becomes morally considerable. Regan's (2003) work on animal ethics is a prime example of a reformist environmental ethic. 'Mixed reform and radical' ethics are those that not only utilize aspects of reformist ethics but also incorporate new or radical ideas into the ethic (p. 82). According to Karen Warren, this includes the work of Leopold (1966) and Thoreau (2004). Finally, radical positions are environmental ethics that introduce new considerations into the ethical dialog. This category includes such ethics as bioregionalism, social ecology, ecological feminism, and deep ecology.

Several of these environmental ethics are increasingly entering into issues surrounding agriculture and food production. For example, environmental impacts of industrial farming practices and confined feeding operations (CAFOS) that affect surrounding populations are often critiqued using various environmental ethics, such as house ethics based on utilitarianism or rights-based approaches and more radical forms, such as deep ecology and ecological feminism. In addition, the specific treatment of animals within agriculture is another area where such ethics have been used to defend changing husbandry practices, such as arguments for the inclusion of enrichment activities in CAFOS and the requirement that chickens be stunned before slaughter. In addition to arguments based on efficiency and cost–benefit analyses, environmental ethical arguments are increasingly prevalent during food and agriculture policy formation, especially when boards decide on or edit standards meant to ensure the ethical or just use of nonhuman others, the environment, or what levels of environmental impacts are morally acceptable.

In addition, many of these ethics and competing conceptions of justice are being blended and incorporated as citizen movements apply them on the ground. For example, as partially illustrated above, the local food movement utilizes communitarian, rights-based, and radical conceptions of justice. It utilizes communitarianism due to the fact that, within this movement, people are understood to be deeply imbedded in local contexts and just actions, be that to others or to the land, can be distilled from the traditions of specific societies or traditions. It utilizes an expanded liberal conception of justice, as it includes a mandate for the just distribution of resources. Finally, it also incorporates radical conceptions of justice, as it expands the sphere of moral patients to include the surrounding environment, and conceptualizes food systems as 'regenerative' or guided by principles of ethics, equity, and ecology. Thus, ethics and understandings of justice are not static but are social constructs and are thus constantly in the process of transformation and change.

Although an understanding of agricultural ethics can be gained through the analysis of the ethical frameworks utilized by the field, it is important to recognize themes emphasized by recent work. Such themes include (1) unintended health, safety, and environmental impacts of agricultural technology; (2) the structure of agriculture, including distribution of benefits from agricultural production; and (3) questions of conduct, character, and professional ethics. These themes form the topics of the following sections.

Unintended Consequences

Many criticisms of modern agriculture have noted unwanted and unintended consequences of agricultural chemicals. Pesticides have had documented effects on wildlife populations, and some are known carcinogens. Nitrogen fertilizers can pollute groundwater and surface water. Many agricultural chemicals have long been known to have toxic effects when improperly handled, stored, or applied. It is clear that neither manufacturers nor producers intended or wanted these consequences, and both groups have made efforts to mitigate and control unintended consequences. Nevertheless, unintended consequence of agricultural chemicals pose ethical problems in that it is impossible to eliminate the risk of an unwanted event entirely. Furthermore, there is often disagreement about the degree of risk associated with agricultural chemicals. Some individuals express far greater concern about exposure to pesticides than others. Producers, scientists, and chemical manufacturers thus face the problem of managing concern for unwanted effects, even when the empirical evidence for such effects is scant, controversial, and even nonexistent. Whether real or imagined, unwanted consequences of chemical have significantly affected the reception of many agricultural technologies, including mechanization and biotechnology, among producers and food consumers since 1962.

An analysis of ethical issues associated with unintended consequences surveys the assumptions and implicit norms that have guided action contributing to the unintended outcomes. Public claims expressing a rationale or justification of such action are scrutinized, and the pattern of reasoning is exposed. In many cases, disagreement over agricultural

practices can be traced to incommensurable assumptions in the way that antagonists view the world and the relation of moral norms to human action. This is a disagreement that is both more subtle and more long lasting than simple disagreement over values. Alternative approaches to the problem of unintended consequences provide an example. Many people, especially those associated with the agricultural sciences, exhibit behavior and speech that is most consistent with the utilitarian approach to ethics outlined above. Environmentalist, agrarian, and consumer critics have rejected this basic approach, sometimes assuming a pattern of thought more consistent with rights.

The utilitarian strategy adopts an ethical norm that requires decision makers to anticipate the consequences of their actions and policies to the fullest extent possible and to weigh the costs associated with unintended consequences against the acknowledged benefits of technology accruing in the form of increased food availability, increased profitability of farming, and decreased consumer food cost. This strategy presents a series of methodological and philosophical problems, in that unwanted costs are often difficult to quantify, and in that there are philosophical disagreements over when to accept trade-offs. A severe distributive inequality, for example, might provide a reason to reject technologies that clearly produce more aggregate benefits than harms.

A rights-based strategy assumes that individuals may be accountable for predictable, although unintended, consequences of their action. Rights provide criteria for accountability because acts that do not interfere with others' rights are judged ethically permissible. When individuals and organizations act within their rights, their actions are ethically acceptable without regard to whether they optimize the trade-offs of cost and benefit. However, virtually all of the unintended consequences associated with agriculture constitute interference in some form. A strict application of rights constraints implies that all such actions should be prohibited. A more adequate determination of accountability requires one to see that many individuals have acted in ways that collectively produce the unintended consequence. Hence, the accountability of individuals and groups depends on how their activity is related to the activity of others who may share or wholly assume responsibility for consequences.

In application, the rights approach to agricultural ethics often establishes burdens of proof that must be satisfied before an action is undertaken, rather than absolute constraints. A burden of proof is a criterion that establishes which party can be held accountable for consequences. A key burden of proof in evaluating unintended consequences is informed consent. Individuals who use an agricultural technology or product under conditions of informed consent can be understood to have accepted responsibility for the consequences of use. Scientists, extension agents, and private sector firms that introduce technology under conditions that secure the informed consent of affected parties satisfy ethical norms and may not be held accountable for unintended consequences. The criterion of consent transfers accountability to the affected parties. Consent criteria present a series of philosophical problems not unlike utilitarian approaches, in that the conditions for expression of consent are complex. Consent implies that people have meaningful options, that there are commonly recognized practices that imply consent, and that those giving consent have full knowledge of the unintended consequences that might ensue. As such criteria are seldom fulfilled completely, burdens of proof are often satisfied in the same idealized fashion that utilitarians perform optimizing calculations.

Although both strategies are idealizations, each establishes a general conceptual approach to problems in agricultural ethics at cross purposes with the other. The utilitarian strategy begins with an assessment of the likely consequences associated with an agricultural technology or practice. In the case of a chemical pesticide, the consequences would include risks to the health of farm labor and to food consumers as well as benefits to producers in the form of increased profitability. If a proposed activity has a significant impact on consumer food prices, it will be important to anticipate indirect effects on the availability of food for the poor. When all the relevant consequences have been assessed, the proposed activity can be compared with one or more alternatives. As a minimum, alternatives include simply using and not using the proposed pesticide, but the array of possible strategies for use is always complex, include licensing for restricted versus general use, notification, rules that may or may not be included, etc. The comparison allows one to make a fairly sophisticated judgment about the trade-offs between two choices.

Trade-offs themselves can be complex. A simple-minded decision rule for utilitarian ethics is to allow an action whenever benefits outweigh costs, but there may be alternatives that produce a more attractive ratio of benefit to cost. One may also face a choice between one option that has a high benefit to cost ratio, yet returns few fatal benefits, and another with a less attractive ratio of benefit to cost that produces more benefits (at higher costs). Distributive issues also make trade-offs difficult to compare. For example, one chemical may pose a low-level risk of cancer to many food consumers, whereas another may pose little or no risk to consumers but may be far more dangerous to handle in the field. One may thus be comparing a low-level risk to all food consumers against a high-level risk to a small group of agricultural labors. A question of fairness arises, particularly if the laborers are comparatively less well-off as a group than food consumers. Here costs (in the form of risk) are not comparably distributed by each option.

The alternative strategy for dealing with unintended consequences would approach the decision to use an agricultural chemical by examining a series of burdens of proof. Here the beginning assumption is that agents are responsible for unintended consequences of their action. However, a manufacturer of a chemical may shift responsibility to the actual users of the chemical, provided that criteria for informed consent have been met. Similarly, a producer may shift responsibility for unintended consequences to employees or consumers when these groups are informed of the potential consequences and when they have meaningful opportunities to make alternative choices. On this view, the residue of agricultural chemicals poses no ethical problem as long as consumers have both a reasonable opportunity to get information about unintended consequences and an alternative choice in the form of organic foods. If these conditions are met, then there may be chemical residues, and consumers have

to bear the responsibility for any consequences for their choice of foods.

The burdens of proof that must be met in developing and promoting an agricultural technology may seem heavy when described abstractly. In practice, they are consistent with the general structure of a free market economy, provided that two conditions are met. Sellers must provide full information, and sellers' economic power must not become so concentrated that buyers are effectively denied a meaningful opportunity to choose alternatives. It is important to note that consent criteria do not necessarily produce a socially optimal outcome from a utilitarian perspective. One reason it may not is that buyers may have faulty preferences. They may, for example, choose foods that are unhealthy, or they may place too much emphasis on immediate gratification. Many economists assume that consumers' actual preference constitute the norm for determining a social optimum. If immediate gratification and consumption of unhealthy food are defined as a benefit in virtue of the fact that such activities satisfy consumer preferences, there will be less divergence between utilitarian and consent criteria than would be the case when costs and benefits are defined according to criteria that are independent from existing preferences.

The economic concept of market failure is also an instance where consent and utilitarian criteria diverge. Resource economics identifies a number of situations in which buyers and sellers making voluntary exchanges will reach outcomes that all would regard as suboptimal. The American dust bowl has frequently been analyzed as an instance of market failure. Under utilitarian criteria, market failure provides a justification for regulation, the coercive application of state power to ensure that individuals and organizations do not engage in practices that produce the unwanted outcome. Such state actions can come into direct conflict with ethical criteria associated with property rights. The result is a philosophically based political conflict between those who advocate such action on the part of government as a violation of consent criteria implied by common notions of property rights.

Structure of Agriculture

Ethical issues associated with the structure of agriculture overlap with those of unintended consequences to the extent that changes in the size distribution or number of farms can be understood as an unwanted consequence of technological change. The general relationship between means of agricultural production and norms for land entitlement and property rights has, however, been an enduring philosophical question. As noted above, Aristotle thought that achievement of moral virtue among the elite of society depended on a release from labor of agricultural production that could only be provided through a system of agricultural production based on human slavery. In the eighteenth century, John Locke defended the enclosure movement that removed English lands from common pastoral use and converted them into privately controlled croplands on the grounds that enclosure returned far more benefits in the form of increased food availability. At about the same time, Jean Jacques Rousseau argued that the primary impact of privatization of agricultural lands was to create scarcity, by creating a privileged class of land-holding aristocrats.

This pattern of divergent philosophical views has continued. Some, such as economist Luther Tweeten, evaluate changes in the distribution of farms by size and by type of ownership in terms of criteria that stress efficiency and aggregate benefits of farm production. Others, such as sociologist Jack Kloppenburg, stress how changes in agricultural practice have favored the interests of a few influential individuals generally working behind the scenes.

The dispute is particularly relevant for planning and evaluating agricultural development. Agricultural development programs, such as the Green Revolution, have been based on the view that carefully managed increases in agricultural productivity are a necessary condition for improved conditions in the developing world. On the opposing view, dependency theorists have argued that underdevelopment has been caused by exploitative encouragement of sugar, tobacco, coffee, tea, and other stimulant production in developing countries as well as production of 'luxury' crops, such as fruits, oilseeds, and spices. This group sees little hope for development until the developing world's cycle of dependency on developed countries (first for production technology and expertise, then for export markets) is broken.

One way to analyze the contrast between the two philosophies is to return to the distinction between utilitarian and rights-based ethics. On a utilitarian view, changes in farm structure create costs in the form of financial and emotional consequences for those who exit farming. There may also be more abstract costs in the form of esthetic and historical values associated that like a given farm structure or broader patterns of culture. The key question is whether production efficiencies achieved through new technology and the resulting farm structure produce benefits that outweigh these costs. For a rights theorist, the comparison of cost and benefits is largely irrelevant. The key question is whether affected parties were adequately involved in the events that cause a change in structure. Dependency theory, for example, may be interpreted as resting on the claim that affected parties in the developing world have been denied any meaningful opportunity to reject the offer of Green Revolution technology. Hence, the resulting changes in farm structure do not satisfy burdens of proof that relate to participation, representation, and consent of affected parties.

It is most likely that those who defend the record of change in farm structure would be willing to accept a utilitarian characterization of their ethical rationale. Luther Tweeten has done so explicitly. Some critics would base their objections on rights claims, whereas others diagnose a more fundamental problem. Like utilitarians, critics such as Kloppenburg or Wendell Berry (discussed below) would concentrate on the consequences of farm structural change. They would, however, argue that the relevant consequences are far more comprehensive and systematic than utilitarian defenders have recognized. This form of criticism has emphasized the reductionism implicit in the defense of the status quo, a tendency to evaluate action in terms of criteria that fail to account for holistic or systematic effects.

Reductionism is seldom defined precisely in critics' writings. Two themes that recur are scientific reductionism and

ethical reductionism. Scientific reductionism is the belief that obtaining knowledge is an additive process. The building blocks of this process are specific facts or observations that are localized in time and space. Scientific theories consist in generalizations of laws that aggregate data. Critics argue that this approach to knowledge can never capture the systematic interrelationships of natural and social phenomena and hence will tend to overlook important environmental and social consequences. Spokesmen for the status quo often attempt to meet these criticisms by arguing that the critics' claims are not adequately supported by data. A vicious circle of claim and counterclaim ensues. Scientific reduction is also associated with the philosophical view that science is value free. The claim is asserted in two distinct senses. One is that the process of conducting research and establishing facts through experiment is not influenced by values. The second is that data and theoretical generalizations produced scientifically do not, in themselves, entail value judgments. In application, the alleged value-free nature of science functions very much like an ethical norm, instructing scientists to avoid overt expressions of value judgments in their scientific practice. It is in such applications that scientific reductionism has tended to stifle research, teaching, and public discussion of agricultural ethics.

Ethical reductionism (sometimes called methodological individualism) is the belief that all ethical significance derives from impact on or action of individuals. Costs, benefits, and rights violations alike are, for the reductionist, significant only when they affect individuals, rather than groups or, more abstractly, culture as a whole. Critics argue that changes in farm structure can produce broad cultural patterns that transform the values and world view of future generations. These changing world views may lead future individuals to evaluate farm structure very differently. The ethical individualist does not find the change significant, precisely because individuals living in the future culture are unlikely to perceive themselves as victims. From the reductionist perspective, if no one complains, nothing is wrong. Ethical reductionism is influential because many rural social scientists assume that value is a function of individual preferences. One of the most effective criticisms (unrelated to agriculture) is Aldous Huxley's novel Brave New World, in which citizens of the future are totally content with lives in which they have been genetically, chemically, and behaviorally conditioned to take pleasure in circumstances that present generations would find totally devoid of meaning and morally intolerable.

Scientific reductionism is relevant to ethical analysis of changes in farm structure because some critics believe that changes in farm structure that produce broad-scale environmental, social, and cultural changes are not amenable to analysis and identification by the methods of reductionist science. If choices or policies cannot be justified scientifically, the reductionist concludes that they cannot be justified at all. Ethical reductionism is relevant because, to the extent that these changes affect culture and the transmission of values from one generation to another, it may be difficult to identify harms or rights violations that apply to specific individuals. This theme in the criticism of farm structure overlaps with the next area – conduct and professional ethics.

Conduct and Professional Ethics

The third area of concentration in agricultural ethics has to do with conduct. Agricultural producers and those employed in agribusiness should adhere to standards of professional conduct, and the standards of conduct for agricultural research form a related category. Critics and representatives of the agricultural establishment alike have raised concern over the conduct of those involved in pesticide sales and in certifying the safety and efficacy of input chemicals and agricultural products. Professional conduct is, perhaps, the most obvious area of relevance for agricultural ethics and one where violations of legal and ethical norms can stir significant public attention. Philosophical questions arise in determining the precise role responsibilities of agricultural professionals, but in general, these ethical issues are far less contentious than those that arise in the first two categories. Although the enforcement of norms for good professional conduct can be a difficult practical problem, there is often a broad consensus of opinion even among practitioners on what the norms are.

The writings of Wendell Berry and his followers provide one exception to the generally noncontroversial nature of issues involving ethical conduct. Berry has argued that changes in farming practice and rural communities have produced a situation in which all persons are less able to engage in virtuous conduct. Specialization in food production and distribution has, in Berry's view, fractured the integrity of family-based production and consumption and has made it difficult to perceive social responsibilities to family members and to others in the community. Similarly, this specialization has made it difficult to perceive human dependency on nature and on natural cycles for restoring the environment and replenishing the resource base. Berry thus argues that industrialized agriculture necessitates unethical conduct, not only on part of agricultural producers but also on the part of society at large. Berry's concerns with personal conduct thus overlap with criticism of reductionism discussed above.

Berry's sweeping claims aside, the most serious problems arise in constructing procedures for enforcing what would commonly be regarded as acceptable norms for professional conduct. Farmers may have incentives to abuse chemicals, to adulterate products (spraying water into a grain truck to increase weight is a well-known abuse), or to cheat on Federal programs. Similarly, agribusiness firms producing inputs may have incentives to misrepresent the safety and effectiveness of their products, and food-processing firms may have incentives to pass contaminated or adulterated products on to consumers. Finally, public officials, including research scientists, may have incentives to favor special interests, including industry and producers, over the public good. Philosophical questions arise in how government should regulate such activities and when penalties should be applied for noncompliance. This area of agricultural ethics becomes closely involved in agricultural law.

Research Ethics in Agricultural Science

The conduct and professional ethics of agricultural scientists deserve special attention. Whether basic or engaged, science is

an activity dedicated to the production of knowledge. Scientists have long recognized that the success of this enterprise depends on strict adherence to the norms of honesty in reporting results and openness in being willing to consider alternative hypotheses. First-order issues in research ethics stress the importance of these norms to the research enterprise and decry the occurrence of fraud, deceit, and coercion in science. These norms can be described as an element of professional ethics for the scientist. The doctrine of academic freedom was advanced in the nineteenth century to protect the openness of scientific inquiry and to protect scientists from reprisal when they reported unpopular results. Historically, scientific organizations have relied on the process of socialization to enforce norms of honesty. During recent years, however, it has become clear that scientists can advance their careers, as well as commercial products, through fraud and deceit, and new concerns have been raised about the integrity of the scientific community.

Recent work in the philosophy of science by Steve Fuller and in the sociology of science by Bruno Latour has established the basis for understanding second-order issues in research ethics. These authors have shown how scientists are taught to believe that science is founded on value-free objective procedures, whereas ethical norms are based on emotion or mere opinion. Belief in the value-free nature of science is often expressed as scientific and ethical reductionism, as discussed above. Belief in the value-free nature (e.g., objectivity) of science does not strictly entail that ethical questions about the choice of a scientific research project, or about the unintended consequences of a scientific finding, are inimical to the methods and practice of science. Nevertheless, practices in many agricultural research organizations discourage deliberation of ethical issues as unscientific. Although these beliefs represent value judgments themselves, they have allowed scientists to project a public image of being neutral parties, committed only to the facts, and unmotivated by value judgments or norms.

When the belief that science should always produce more knowledge is combined with a belief that applying ethical standards to research choice is inimical to science, scientists and scientific organizations may become committed to a goal of always increasing knowledge but at the same time rejecting the legitimacy of other interests that may oppose the creation of new knowledge (or may feel that resources are better invested in other goals). Scientists who adopt this posture pursue funding and freedom to conduct research but refuse to participate in debate over the goals or value of research on the grounds that doing so will comprise objectivity. In this situation, scientists are an interest group whose interests depend on being thought to have no interests. The situation creates incentives for duplicity and self-deception within the scientific enterprise and may ultimately erode scientists' commitment to the norms of honesty and openness. The alternative is to reject either the norm of advancing knowledge or the belief that science is value free. Either way, scientists have a responsibility to review the value of their research programs and to at least consider the significance of unintended consequences. The conclusion is that the second-order ethical deliberation should be accepted as an intrinsic element of scientific practice.

Animal Well-Being

The legal and ethical protection of animals has a long standing in the United States. Anticruelty statutes were enacted in some colonies before the Revolutionary War. More recently, animal protectionists have noted concern for the well-being of farm animals in confinement settings, especially since the publication of Ruth Harrison's Animal Machines in 1966. However, the principal focus of the recent animal rights movement has been to oppose the use of animals in product testing and biomedical research. The biomedical debate has become quite acrimonious, with some parties on both sides taking extreme positions. Few in ethics would deny that caregivers have ethical responsibilities to assure well-being of farm and food animals.

Farmers and ranchers have traditionally been thought to be especially respectful of the well-being of food and farm animals. They have been thought to possess personal moral concern for animals. Also, animal health and well-being have been thought to correspond closely to a producer's interest in efficiency and marketability of animal products. The correlation between producer and animal interests fails to obtain when any one of three conditions obtains. First, some products, such as *foie gras* or pale veal, may require production methods contrary to animal well-being. Second, some elements of animal well-being may be realizable only under ideal conditions seldom realized in either wild or domesticated settings. Third, with large operations or high stocking rates, the management costs of attending to the needs of a few individual animals will not always be matched by returns based on average or aggregated sales of animal products. Animal protection organizations have criticized agricultural producers on each of these three points. The political rhetoric of the animal experimentation debate influences criticisms of agriculture, and ambiguous terminology presents a barrier to any clear presentation of ethical issues. Multiple uses for the terms animal welfare and animal rights are especially confusing. For some, the term 'animal rights' implies an extreme reformist position, whereas 'animal welfare' is taken to imply an attitude favoring moderate or no reform in animal agriculture. Popular use suggests that those who express support for animal rights merely feel that individual animals' interests deserve consideration and do not propose radical change in animal agriculture. More formal uses of these terms have been introduced into the literature by two influential philosophers, Peter Singer and Tom Regan.

Peter Singer advocates an animal welfare philosophy in a series of articles and in his book Animal Liberation. Singer is a utilitarian philosopher who believes that the morality of an action is to be evaluated by assessing its consequences. The key to the animal welfare philosophy is the belief that comparable interests deserve equal consideration without regard to species. This means that comparable experience of physical pain, for example, would be given equal consideration without regard to whether the pain is experienced by a pig, monkey, or a human being. Singer explicitly notes that many interests do not admit of meaningful cross-species comparisons and that the complex cognitive interests of human beings establish bases for evaluating consequences to humans in a manner that is unparalleled for other species. Hence, Singer's view admits of many opportunities in principle where human interests are

favored over animals' and even where animal pain or suffering may be justified by compensating benefits to humans. However, Singer is also of the opinion that animals in confinement settings suffer to a degree that makes it impossible to justify human consumption of food animals. Hence, he is commonly associated with the so-called animal rights group advocating radical change.

Tom Regan has made numerous public appearances on behalf of animal interests, especially since the publication of his book The Case for Animal Rights in 1983. Regan advocates an animal rights philosophy that is opposed to the animal welfare philosophy of Singer. In summary, Regan's view states that Singer's utilitarian position does not provide adequate reason for protecting the interests of individual animals. Aggregation of costs and benefits to human and nonhuman animals leaves open the possibility that significant harms to a few individual animals can be compensated by relatively insignificant benefits to a large number of human beings. This argument has been especially relevant to the cases of product testing and scientific research. According to Regan, animals are 'subjects of a life.' Accordingly, humans must respect their interests. Although Regan's view would allow priority to comparable human interests (e.g., one might sacrifice animal lives to save human lives), his animal rights philosophy prohibits the aggregation of relatively low-level interests (such as gustatory pleasure) to compensate for harms of an ethically fundamental sort.

Although the writings of Singer and Regan represent the philosophical distinction between animal welfare and animal rights, both have advocated vegetarianism. For Singer, vegetarianism is a specific response to the use of confinement systems and high stocking rates. For Regan, vegetarianism is a general moral responsibility that would apply at all times and places. As both Singer and Regan are sharply critical of animal agriculture, the more moderate views of Bernard Rollin have had more influence within animal science and veterinary medicine. Rollin has written several influential works, such as his 1987 book The Unheeded Cry, but a paper entitled 'Animal welfare, animal rights and agriculture' provides a particularly concise statement of his views. For Rollin, the idea of animal rights represents the consensus judgment of society that the interests of individual animals matter and that producers may be required to sacrifice financial gains in order to assure that vital interests are met. Rollin thinks that this idea is generally consistent with traditional notions of animal husbandry, but the emphasis on narrow scientific or economic measures of productivity and animal health have caused erosion of moral concern for food animals. Rollin urges animal rights as a philosophy that is, in effect, a return to more humane and responsive practices of traditional husbandry.

Agricultural Biotechnology

The rapid growth of recombinant deoxyribonucleic acid (DNA) transfer techniques and their application to agricultural science have created a situation in which agricultural biotechnologies present excellent case studies for many of the ethical issues discussed above. Unintended consequences of agricultural biotechnology have stimulated the most acrimonious debate. In the early 1980s, Jeremy Rifkin's Foundation for Economic Trends filed lawsuits designed to ensure that those undertaking research and development of agriculture biotechnology assume responsibility for all social and environmental consequences. The first round of debate focused on ice-nucleating bacteria that could provide crop protection against freezing temperatures as low as 30 F (-1 °C). Rifkin delayed experiments with these bacteria by raising questions about whether scientists had undertaken adequate review of potential environmental consequences.

The second round of debate had focused on recombinant bovine somatotropin (BST), a genetically engineered version of the hormone that can be used to stimulate milk production in dairy cows. The unintended consequences that raised concern with BST stressed social impact on the structure of the US dairy industry. Economic analysis predicted that the technology would accelerate a shift from small to large dairies and from the northeast to the south and southwest as principal production regions. Concern over the impact on the health of dairy cows has been raised, largely associated with mastitis problems associated with the increased volume of milk production. Finally, consumer groups expressed reluctance to accept milk produced using recombinant BST, despite scientific evidence documenting safety and quality.

In addition to these problems associated with unwanted consequences, recombinant techniques have been associated with ethical questions about property rights and about the religious and metaphysical implications of biotechnology. Property rights issues concern the question of whether newly discovered or assembled segments of genetic code qualify as patentable material or material that can be owned. The issues have been most hotly debated for animal patents. On the side of animal patents is the incentive effect of property rights for potential producers of recombinant technologies. Against animal patents are the claims that genetic sequences are 'nature's handiwork' and that biotechnologies should be regarded as scientific discoveries (which are traditionally not patentable) rather than as inventions. Religious and metaphysical considerations enter the discussion of property rights when people express the view that life forms should not be owned or, perhaps, manipulated. In this regard, the emergence of biotechnology has apparently brought longstanding practices of genetic manipulation and breeding into the public consciousness for the first time.

Biotechnology is religiously significant because for some people, at least, the ability to move genetic material from one animal to another raises questions about the ethical significance of species boundaries. These questions are of two sorts. First, theologies that propose a difference in kind between human and nonhuman animals are challenged by the new molecular biology. Second, some religious views interpret the existing distribution of species as God's handiwork and interpret genetic modification as a violation of absolute constraints on human action. Religiously based concerns often enter debates indirectly, being expressed along with secular ethical concerns about property rights or unwanted consequences. The US tradition of separating church and state may make religiously based arguments seem less legitimate in the public policy context.

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Agricultural Finance

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Glossary

Agribusiness Refers to farm input supply firms, food processing firms, fiber manufacturing firms, and other firms in the nation's food and fiber system other than crop and livestock producers.
Credit scoring Approach used by lenders to quantitatively evaluate the credit worthiness of a borrower.
Farm Credit System System of federally chartered, privately owned banks, and associations that lend primarily to agricultural producers and their cooperatives.
Farm Service Agency Governmental agency involved in direct lending and loan guarantees to creditworthy borrowers that may have a difficult time obtaining financing from commercial sources.
Financial intermediaries Entities that obtain loanable funds from savers in the economy and then lend these funds to borrowers.
Food and fiber industry Network of input supply firms, crop and livestock producers, food processing firms, fiber manufacturing firms, and related distribution firms associated with the supply of food and fiber products to final demand.
Macroeconomic policy Typically refers to the monetary actions taken by the Federal Reserve System, the government spending authorized by the US Congress, and the taxation policies approved by the US Congress and implemented by the Internal Revenue Service.
Net present value Discounted sum of projected net cash flows for a potential investment.
Risk efficient frontier Set of asset that offers the maximum possible expected returns for a given level of risk.
Risk premium Difference between a decision maker's expected risky return and value the decision maker would accept if all risks were removed.
Vertical integration Coordination and integration of successive stages in production, processing, and distribution.

Introduction

The field of agricultural finance encompasses a broad range of interest ranging from 'micro' issues associated with firm-level investment and financing decisions made by crop and livestock producers as well as agribusiness firms to 'macro' issues associated with the effects that macroeconomic policy, farm commodity policy, resource policy, and international trade policy have on the financial structure and performance of the nation's food and fiber system.

Microagricultural Finance

Topics in microagricultural finance include concepts of investment and financing decisions under both certainty and uncertainty, including the methods used to evaluate investment projects and alternative approaches to acquiring these resources.

Overview of Financial Management

The concepts of financial management in agriculture involve the acquisition and utilization of financial resources by crop and livestock producers and by agriculturally related businesses. Emphasis in this section is placed on the introductory concepts of theory of investment and financing decisions, the evaluation of new investments, resource acquisition in agriculture, financial analysis in agriculture, and the financial intermediaries involved in delivering debt capital to agriculture. Major microissues related to agricultural finance are also presented. These issues and concepts are linked throughout the entire food and fiber system: from input supply firms and financial intermediaries to crop and livestock producers, and onto food and fiber manufacturers and distributors.

Theory of Investment and Financing Decisions

The fundamental concepts of finance theory apply similarly to farms and ranches as well as other firms in the economy. Crop and livestock producers typically have relatively little market power, often being price takers in both input and product markets. Agribusinesses like input manufacturers have more market power and often participate in thinner, less-liquid markets.

Concepts of investment and financing decisions under certainty

The major components of financial theory include a decision maker's utility function, productive investment alternatives, and financial markets. A simple model with no taxes, no transaction costs, and no uncertainty of investment decisions is used to outline the theoretical framework. Decisions are made in a one-period context. The decision maker is endowed with income at the beginning of the period and at the end of the period. At the beginning of the period the individual determines how much to consume (C_0) and how much to invest to provide for end-of-period consumption (C_1). All individuals prefer more consumption to less (marginal utility of

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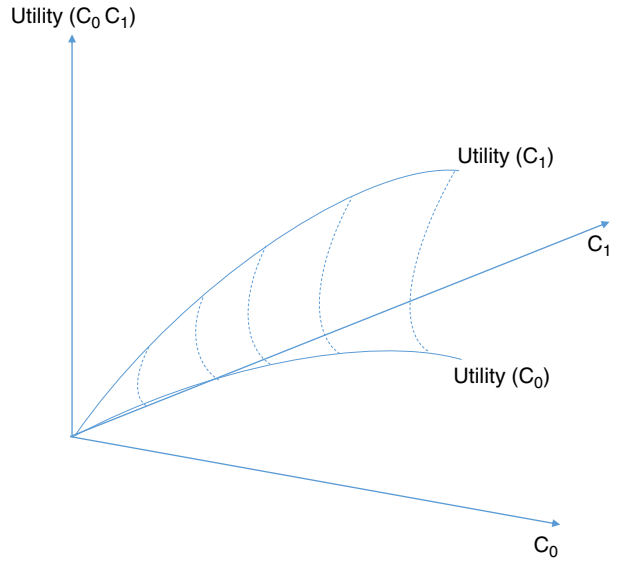


Figure 1 Utility functions and indifference curves. C_0 is beginning of period consumption, C_1 is end of period consumption, the dashed contour lines represent the indifference between beginning and end of year consumption.

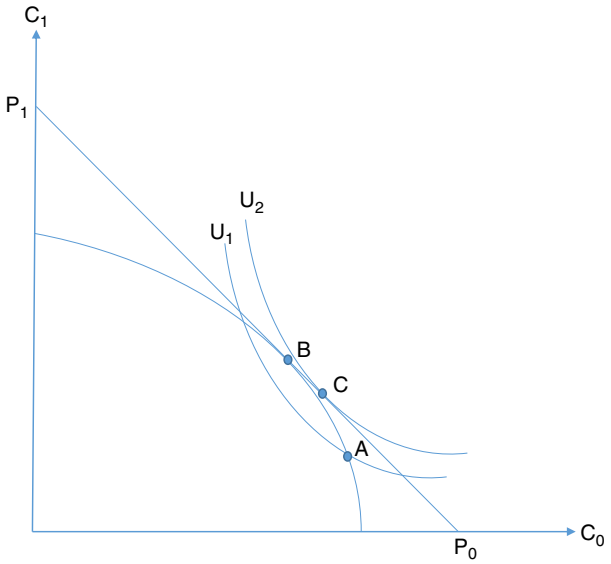


Figure 2 Optimal investment and financing decisions. The production possibility set is represented by P_0P_1 and the set of indifference curves by U_1 and U_2.

consumption is always positive) and hence the marginal utility of consumption is decreasing. Utility curves for beginning-of-period and end-of-period consumption are shown in Figure 1. Each individual may have different utility curves. The dashed contour lines indicate trade-offs between beginning-of-period consumption and end-of-period consumption. Utility is equal at points along these contour lines, and the lines thus are referred to as indifference curves. The slope of a line tangent to an indifference curve measures the rate of trade-off between C_0 and C_1 and is referred to as the marginal rate of substitution between beginning-of-period consumption and end-of-period consumption. The slope of this line can be represented as $-(1+r)$, where r is the individual's subjective rate of time preference.

Assume individual decision makers have opportunities to invest in productive assets that allow units not consumed at the beginning of the period to be augmented to more than one unit of future consumption. In the absence of financial markets, an individual decision maker will invest in all productive opportunities that have rates of return higher than the decision maker's subjective rate of time preference (r).

To complete the model, assume that financial markets exist and thus there is an opportunity to lend and borrow unlimited amounts at a market-determined rate of interest (i). These borrowing and lending activities allow the individual decision maker to reallocate consumption between the beginning and end of the period to attain higher levels of utility and thus improve economic well-being. The presence of financial markets allows the individual decision maker to invest in all productive assets that have rates of return that equal or exceed the market rate of interest (i) instead of the subjective rate of time preference.

These concepts are illustrated in Figure 2. The production possibility set is represented by P_0P_1 and the set of indifference curves by U_1 and U_2. Given that interest rates are positive, all funds lent at the beginning of the period will receive interest plus principal at the end of the period. The future value of one unit lent at the beginning of the period is increased by a factor of 1 plus the market-determined rate of interest (i). Thus, the slope of the capital market line is $-(1+i)$.

Suppose the initial endowment is point A. The individual decision maker may move along the capital market line or production possibilities set to achieve the highest possible utility. In this example, the higher return is achieved by moving up the production possibilities set to point B where the rate of return on investments is equal to the market rate of interest, a tangency with the subjective rate of time preference (U_2) is achieved at point C. This tangency is at a higher level of utility than that achieved without financing opportunities.

Thus, the process can be depicted as a two-stage process. First, the individual decision maker invests in all production opportunities that have returns, which equal or exceed the market rate of interest. Second, the individual decision maker borrows or lends in the financial market until the market rate of interest is equal to the decision maker's subjective rate of time preference. The first step does not use the decision maker's utility function and thus, under certainty conditions, the investment condition (stage 1) is considered separate from the financing condition (stage 2). This condition is known as the Fisher Separation theorem.

Concepts of investment and financing decisions under uncertainty

Crop and livestock producers are inherently faced with risk. Commodity price fluctuations, weather variability, spoilage, disease, and changes in government policies interject considerable risk into their decision-making process.

The three theoretical concepts essential to understand financial models under uncertainty include concave utility functions, certainty equivalents, and risk premiums. The marginal

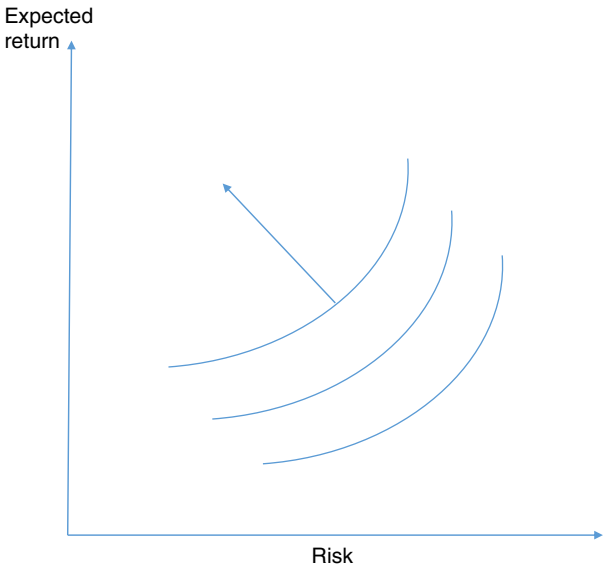


Figure 3 Indifference curves and attitudes toward risk. Indifference curves between risk and return for risk adverse investors. Preference is upwards and to the left.

utility of profit declines for concave utility functions. Crop and livestock producers with concave utility functions are considered risk averse. Risk-averse decision makers prefer a certain investment to one with an equal but uncertain return. A risk-averse decision maker is willing to pay a price for a certain investment that yields the same utility as the expected utility of the risky investment. The completely certain price is considered the certainty equivalent. The difference between the expected value and the certainty equivalent value is the risk premium. The risk premium is the decision maker's required compensation for accepting risky investments.

A risk-averse decision maker's preference structure between risk and return can be represented by indifference curve analysis. Figure 3 shows indifference curves for risk-averse decision makers. The direction of preference is represented by an arrow (up and to the left). The slope of the indifference curves indicates the marginal rate of substitution between risk and return. In this case, the marginal rate of substitution is the amount of expected return the decision maker requires for an additional unit of risk. Different decision makers will have different degrees of risk aversion and thus will have different marginal rates of substitution.

Investment decision techniques under certainty

In the previous sections a simple one-period model is discussed. These models are extended to incorporate multiperiod investment decisions and refined to evaluate alternative projects. The methods are referred to as capital budgeting techniques. These techniques are used to aid investment decisions for all types of agribusiness firms. Refinancing of debt and buy versus lease decisions are also analyzed using these techniques. The techniques can be used to select among independent projects or rank mutually exclusive projects based on specific budget constraints. In general, there are five capital budgeting techniques used to evaluate investment decisions. These include the following: (1) the payback method, (2) the accounting rate of return method, (3) the net present value method, (4) the internal rate of return method, and (5) the modified internal rate of return method.

The payback and accounting rate of return methods do not account for time value of money and thus limit their overall usefulness. The payback period is calculated as the number of years it takes to recover the initial cash outlay. The accounting rate of return is the average after-tax profits divided by the initial outlay.

The three other methods each account for the time value of money. The net present value of a project is calculated as the sum of all discounted cash flows of the project. Each cash flow is discounted by factors that convert each cash flow into a net present value. The factors are based on the decision maker's opportunity cost of capital. The internal rate of return of a project is the rate that equates the present value of all inflows and outflows. However, the method assumes that all cash flows can be reinvested at the internal rate of return. The modified internal rate of return is calculated by first finding the net present values of all cash outflows using the decision maker's opportunity cost of capital. Second, the future value of all cash inflows are estimated also using the decision maker's opportunity cost of capital. The modified internal rate of return is the discount rate that equates the present value of the cash outflows with the future values of cash inflows.

The net present value and modified internal rate of return are the preferred methods. Mutually exclusive projects of similar size are ranked the same with each method. However, when size differences among the projects occur, the net present value method provides a more consistent indicator of how an individual project will affect the overall value of a firm.

Adjustment for risk in decision making

Each of the five methods discussed in the previous section assumes certainty of future cash flows. However, considerable uncertainty is present among agribusiness firms. Four general methods have been used to account for risk in the investment decision framework. These include the following: (1) the maximin decision criterion, (2) the coefficient of variation criterion, (3) the expected present value criterion with adjusted discount rates, and (4) the certainty equivalent criterion. Each of the methods have drawbacks with the choice of method depending on the frequency the decision maker is confronted by similar investment decisions, the magnitude of the risk involved, and the decision maker's aversion to risk.

The maximin decision criterion uses the maximum (or the largest) of the minimum (or the smallest) outcomes associated with a decision alternative. This criterion simply selects the decision alternative with the best of the worst outcomes. The method does not account for the probability of any of the outcomes. The coefficient of variation is the ratio of the standard deviation of possible outcomes divided by the expected present value. For the coefficient of variation criterion, the decision maker chooses the decision alternative that has the lowest, nonnegative coefficient of variation. This method does not account for differing degrees of risk aversion.

Another commonly used method is to adjust the discount rate for decision alternatives with different levels of risk. A problem with this method is the data required to estimate the

adjusted discount rate. The certainty equivalent criterion involves selecting the decision alternative with the highest certainty equivalent. This criterion incorporates the risk aversion of the decision maker. However, the values that are used to estimate a decision maker's utility function and certainty equivalent are subject and difficult to estimate quantitatively.

Resource Acquisition in Agriculture

The financial barriers to enter production agriculture have increased. Inflation, technological change, and increases in farm size have been the primary causes of the increased capital requirements. The combination of increasing capital requirements and low profit margins restricts crop and livestock producers in their capacity to acquire control of the land, machinery, livestock, and other resources necessary to compete. The increased capital requirements also limit growth. Crop and livestock producers are evaluating and using alternative methods of resource control and management.

Sources of funds used to acquire control of resources can be broadly classified as debt and equity capital. The degree to which that debt capital is used by a producer is a key issue. Tax deductibility and cost usually favor the use of debt capital over equity capital, whereas administrative and bankruptcy costs increase as the proportion of debt capital increases. Thus, theoretically each decision made may have an optimal equilibrium combination of debt and equity.

Equity capital

The primary source of equity capital in production agriculture is through retained earnings or surplus profits kept in the business. Other common sources of equity capital have resulted from gift and inheritances from previous generations and pooling of equity capital through partnerships or corporations.

There are two types of partnerships common in agriculture: general partnerships and limited partnerships. With general partnerships, each partner is explicitly involved in both ownership and management. Furthermore, each partner has unlimited liability for obligations incurred by the business and the liabilities incurred by other partners. Limited partnerships are comprised of limited and general partners. The liability of the limited partners is restricted to the investment in the business.

The corporation is a legal entity held as share or claims on the net worth and profit stream of the business. Although partnerships and sole proprietors dissolve on death, corporations permit continuity over generations. Two types of corporations are important in agriculture: Subchapter S and Subchapter C. A Subchapter S corporation is limited to 35 stockholders and taxed as a partnership. With the Subchapter S corporation, all profits are allocated to the stockholders for income tax purposes. A Subchapter C corporate stockholder must pay taxes only on the cash dividends received and thus this entity may offer some income tax incentives for high-tax-bracket stockholders.

Many corporations and partnerships are created for the purpose of pooling family equity capital. However, public and private placements of equity shares in production agriculture are becoming more common in agriculture. An example is life insurance companies that are becoming more active in acquiring equity shares in agricultural operations as well as direct investment in agricultural assets as methods to diversify pension funds.

Leasing

An arrangement commonly used in agriculture is the farm lease. The lease basically transfers capital from the lessor to the lessee for an agreed period of time. Leasing is a common method for producers to control farmland. Share leases and cash leases are common with real estate leases. With crop share and livestock share leases, the lessor and lessee share in the costs and production, whereas the cash lease is simply an agreed cash price paid for the rental of the land.

Machinery and equipment leasing is also common in agriculture. In agriculture, operating and capital leases are used to acquire control of machinery and equipment. Operating leases are short-term contracts ranging from a few hours to a year. Custom hiring is a common operating lease arrangement. Custom hiring involves the owner furnishing the machine, operating expenses, and labor. Capital leases are a longer term arrangement. The financial obligations of capital leases are quite similar to debt arrangements.

Contract production

Agriculture has witnessed strong trends toward increasing specialization and coordination at the various stages of the production cycle. The coordination may be with successive stages in production and distribution (vertical) or between two or more units of production within the same economic stage (horizontal). Vertical integration of input suppliers, processors, and distributors is becoming more common in agriculture. An increasing proportion of assets used in the farming sector is being supplied or financed by input suppliers, processors, and distributors. Vertical integration of vegetable and fruit industries has been in existence for a long time. Livestock industries, such as poultry and hogs, are also becoming more vertically coordinated. A producer may be able to shift price and yield uncertainties to the contracting firm with vertical coordination. However, future contractual arrangements create additional uncertainties.

Debt capital

Debt capital are funds acquired from financial intermediaries. Costs include interest costs, fees, and closing costs. Interest costs are fully tax deductible and thus typically carry a lower cost than equity capital. Debt capital is typically distinguished between operating debt and term debt. Operating debt is used to finance the purchase of operating inputs, whereas term debt is often used to finance depreciable assets and farm real estate. Operating debt is typically repaid during the production cycle, whereas term debt is paid over several years.

Financial Analysis of Agricultural Producers

The accounting practices followed by many crop and livestock producers have traditionally been both informal and simplistic. However, the increasing use of debt capital and the

formation of more complex organizational structures have increased the need of standardization of financial records for crop and livestock producers.

Accounting practices

In conjunction with the 1987 Agricultural Credit Act, a presidentially appointed commission on agricultural finance emphasized the need for greater standardization of financial reports and analysis of the farm industry. As a result, the Agricultural Division of the American Bankers Association formed a task force of representatives from lending institutions, academic institutions, regulatory agencies, computer software firms, the farm management consulting industry, and the accounting industry. The Farm Financial Standards Task Force, renamed to Farm Financial Standards Council (FFSC), provided guidelines regarding the reporting of financial information for farm and ranch businesses.

The four financial statements recommended by the FFSC include the following: (1) the balance sheet, (2) the income statement, (3) the statement of cash flows, and (4) the statement of owner equity. These four statements are linked to provide a business (assets) and the levels of debt and equity used to acquire the assets. The income statement is a summary of the revenue and expenditures of the business over a specified period of time. The statement of cash flows is a detailed summary of the cash inflows and outflows over a specified period of time. The cash inflows and outflows are separated according to operating, financing, and investment activities of the firm. The statement of owner equity reconciles the change of equity from one period to the next.

Each of these statements may be prepared on a historical basis or a pro forma (projected) basis. These financial statements organized the data needed to analyze the risk and performance of the business. The primary areas of analysis include solvency, profitability, liquidity, repayment capacity, and financial efficiency. Solvency measures the level of debt relative to the equity capital or the overall capital of a business. Profitability is the ability of the firm to generate earnings, whereas liquidity relates to the firm's capacity to generate cash to meet financial commitments without loss of value. Repayment capacity measures related cash generated by the operation to cash obligations of the firm. Financial efficiency measures refer to the utilization of assets within the business. Other financial efficiency measures relate operating and financing expenses to total production.

Credit scoring and risk rating systems

Financial statements and financial ratios measure the degree of financial risk faced by a crop or livestock producer. Crop and livestock producers use the measures to monitor financial strength and future growth capabilities, whereas financial intermediaries use the measures to determine credit worthiness of an operation.

More formal risk rating systems of credit evaluation are currently being implemented by agricultural lenders. The risk rating systems are designed to measure (1) the borrower's potential default on a loan or probability of default and (2) the magnitude of potential loss, given that a default has occurred or loss given default. The goal of the ratings is to array borrowers and loans from the highest credit default risk to the lowest.

Risk rating models have been developed through lender's experiences as well as statistical methods. The lender experience models are formulated by lenders based on historical observations of variables that are related to overall loan performance. Statistical development of risk rating models involves the mathematical representation of a group of subjective and objective independent variables into an equation that determines the credit worthiness of a business. The objective variables often include collateral value, financial ratios, production efficiency measures, and trend values of financial measures. Management ability is a common subjective measure included in risk rating models. The applications of risk rating models include determination of credit acceptance, loan pricing based on riskiness of the loan, establishment of loan loss provisions, and loan portfolio monitoring. The dependence on the model results varies among lenders. In some cases, model results are used as the sole determinant in the decision process, whereas other lenders use the results in conjunction with other criteria.

The statistical approaches used to determine the variables and their respective coefficients include linear regression, discriminant analysis, and logistic regression. The independent variables include various financial, economic, and subjective variables, whereas the dependent variable is a measure of historical loan performance. In general, results indicate that the independent variables selected and their respective coefficients differ substantially across studies and are very sensitive to the data sample.

Providers of Debt Capital

The major sources of debt capital to agriculture include: (1) commercial banks, (2) the Farm Credit System, (3) life insurance companies, (4) Farm Service Agency (FSA), (5) farm-related trade and agribusinesses, (6) individuals, and (7) Farmer Mac. Each of these sources play a vital role in providing debt capital to agriculture. However, sources of funds, regulatory constraints, and individual risks faced by each are different.

The forecasted amount of farm debt outstanding at the end of 2013 is US$308.3 billion. On 31 December 2012, commercial banks held 39.6% of all farm loans with the Farm Credit System holding 40.7%. This is a significant shift in market shares from 1982 when commercial banks held 22.2% and the Farm Credit System held 34.0%. A large reason for the shift in market shares has been the increased emphasis of commercial banks on farm real estate lending. The market share of farm real estate debt by commercial banks has increased from 7% in 1982 to 34% by year-end 2012. The market share for the Farm Credit System increased from 43% to 46.1% over the same time period.

Currently, issues involving providers of debt capital to agriculture include the following: (1) the role and performance of the Farm Credit System, (2) consolidation activities of commercial banks, (3) the increased competitive position of nontraditional lenders, (4) increased regulatory environment resulting from the financial crisis, and (5) government lending.

Role and performance of the farm credit system

Institutions in the Farm Credit System are federally chartered and privately owned. One objective of the charter is to improve the income and well-being of crop and livestock producers by furnishing competitively priced credit and related services to creditworthy borrowers through all economic conditions.

The primary sources of funds for the Farm Credit System district banks are obtained through the sale of system-wide securities in the national financial markets. The Federal Farm Credit Bank Funding Corporation is responsible for selling the securities. The securities are treated as Governmental Agency Securities and trade at 20–50 basis points above US Treasury securities. Equity capital of the various cooperatively controlled banks and associations is obtained by sale of stock to borrowers and through retained earnings. The banks are regulated by the Farm Credit Administration.

During the early 1980s, the Farm Credit System experienced severe financial problems. The system's capital and surplus declined to more than US$6.1 billion in 1985 and 1986. The problem involved loan losses resulting from producers' financial problems as well as lowering net interest margins. The Farm Credit System held a large volume of long-term securities at high interest rates whereas current market rates on loans were low. As a result, in December of 1987, the US Congress passed the Agricultural Credit Act of 1987. The major provisions included restructuring options of the Farm Credit System, federal financial assistance, greater flexibility in capitalizing the system, and creation of an insurance fund.

Currently, the Farm Credit System institutions have restored the soundness of their operations: restructuring of the System's banks and lending associations is continuing as these institutions seek great efficiency and risk-bearing capacity in their lending operations. On 1 January 1988, there were 12 districts with a total of 377 associations. On 1 July 2013, there were 4 districts and 82 associations. The impact the corporate restructuring of the Farm Credit System has on the delivery of debt capital to farm and ranch borrowers has also received considerable interest among policy makers, academicians, credit institutions, and borrowers themselves.

Consolidation activities of commercial banks

Considerable consolidation has occurred within the commercial banking industry. There were 14 507 commercial banks in 1984. By year-end 2012, there were 6112. Most of the reductions were a result of unassisted mergers. The bank merger and acquisition activity was higher than any other industry over this time period. As a result of changes in federal and state legislation, interstate acquisitions by bank-holding companies have been a large part of this acquisition activity. Since states liberalized geographical expansion regulations, interstate banking has increased.

The growth of mergers and acquisitions in the banking industry has been accompanied by a multitude of theories and philosophies debating the rationality and public benefits of this expansion activity. Opponents of bank combinations suggest that undue concentration may inhibit competitive forces and thus increase monopoly elements in the economy. In addition, opponents in rural areas argue that acquisitions often result in locally disinterested intermediation activities and decisions. Some of the activities suggested by adversaries of bank expansion include siphoning deposits out of rural areas, warehousing out-of-market loans at the subsidiaries, and allocating nonproportional operating expenses to subsidiaries. These adverse activities could result in higher credit costs to borrowers or reduced credit availability to agriculture and other small businesses in local communities. Advocates of bank expansion suggest that combinations will benefit society by reducing inefficiencies in the banking system through resource reallocation. The potential for geographical and produce diversification also exists. In addition, local community services may be enhanced by additional services available through larger institutions.

The consequences of the heightened consolidation of the banking industry are essential components in the agricultural economy as well as the national economy. Commercial banks held over US$118 billion of agricultural debt outstanding as of end of year 2012. As a result, estimations of inefficiencies within the banking industry and the evaluation of the changes in competitive forces due to structural shifts within the banking industry are research areas receiving considerable attention among researchers in agricultural finance.

Increased competitive position of nontraditional lenders

Another current issue in agricultural finance related to the emergence of other nontraditional lenders is the increased competitive position of nontraditional lenders. Vertical integration is becoming more prevalent in some areas of production agriculture, especially in the livestock sector. The vertically integrated firms are typically much larger and more complex than the traditional family operated businesses. Furthermore, credit demands for these firms are also different. In many cases, the small-community bank and the Farm Credit System have been unable to meet the credit demands of these firms. Therefore, these firms have accessed nontraditional sources of capital through large commercial banks or investment banking firms.

Other nontraditional lending sources are also becoming more competitive. These nontraditional lenders include input supply firms and farm implement dealers. Loans from these firms are typically derived from the purchase of a farm input or product. However, these firms are also expanding into operating lines of credit. The facilitation of sales, convenience to borrowers, and profitability are primary motivations for these firms to offer credit. Compared with the highly regulated banking industry and Farm Credit System, these nontraditional firms face few regulatory hurdles. Opponents of these firms often argue that an unfair playing field exists. The evaluation of the competitiveness and viability of these firms to deliver debt capital to crop and livestock producers is an emerging concern in agricultural finance.

Increased regulatory environment resulting from the financial crisis

Most institutions lending to the US agriculture weathered the financial tsunami and the economic recession resulting from the 2007 global financial crisis. Many of the agricultural-related institutions did not participate aggressively in the high-risk housing or commercial real estate markets. As a result, institutions lending to agriculture did not sustain the substantial

liquidity and capital problems faced by many global financial institutions. In general, credit remained available for farmers and ranchers throughout the financial crisis. The profitability of production agriculture through the crisis certainly played a critical role in credit quality and quantity at institutions providing capital to agriculture.

Regulatory costs, including the Dodd–Frank Wall Street Reform and Consumer Protection Act, present challenges for many institutions lending to agriculture and rural America. As a share of total operating costs, these regulatory costs are greater for smaller institutions. Regulators are also placing higher regulatory emphasis on banks with significant concentrations in industry sectors, such as agriculture. The implementation of the Basel III capital requirements also place additional costs on institutions lending to agriculture. The spillover impacts of the Dodd-Frank regulations to the agricultural sector will most likely reduce profit margins at institutions.

Government lending

As an agency of the US Department of Agriculture, the FSA serves as a source of debt capital for rural Americans. The FSA originates loans and guarantees loans to qualified applicants who have experience in farming and ranching, who are the owners or operators of a farm or ranch at the time of borrowing the loan, and whose livelihoods depend on farming or ranching.

Concerns have surfaced regarding government subsidies that have focused increased interest on reducing FSA direct lending and increasing its emphasis on loan guarantees. Loan guarantees transfer the funding and loan administration to private lenders and provide greater flexibility in loan pricing.

Macroagricultural Finance

The second major area of emphasis in agricultural finance reflects an aggregate or 'macro' view of the economic performance and financial structure of the nation's farms and ranches and their relationship to other sectors in the general economy. Information on macroagricultural finance developments is of interest to macroeconomic policy makers, farm commodity policy makers, financial institutions and their regulators, agribusinesses, and rural development specialists.

Sector Economic Accounts

An important foundation to macroagricultural finance has been the development of a system of economic accounts for agriculture. Most economists are familiar with the national income and product accounts maintained by the US Department of Commerce and the flow of funds accounts and national balance sheet maintained by the Federal Reserve System. Many, however, are more likely aware of the role the US Department of Agriculture plays in supplying the sectoral information for agriculture incorporated into these national accounts or the applications agricultural economists make of these sectoral data. The set of economic accounts for agriculture, developed and largely maintained by the US Department of Agriculture, not only provides input to the economy-wide set of accounts but also represents a major source of data to descriptive and quantitative behavioral research in agricultural finance.

Sector income account

The US Department of Agriculture's sector income account dates back to the early 1900s (U.S. Department of Agriculture, 2013). This account has been expanded over the years to provide detailed information on cash receipts from farm marketing of crops and livestock, government payments, and other sources of farm-related income. This account also provides detailed information on farm production expenses, capital consumption, and capital expenditures for durable production inputs like tractors and other farm machinery and equipment, trucks, and farm structures.

Figure 4 shows the historical trends in nominal and real net farm income reported in the sector income account. Nominal net farm income has increased sharply since the turn of the century, whereas the purchasing power of net farm income has increased at a much more modest pace. Along with the rise in net farm income, considerably more year-to-year variability is seen, particularly since the commercialization of the ethanol industry.

If one looks below the sector level, one will find that the growth in biofuels has increased the demand for feed gains used in producing ethanol, which while driving up feed grain prices received by crop producers has driven up feed costs for livestock producers, narrowing/eliminating their profit margins in recent years.

Higher net farm incomes in general, however, have allowed many producers to pare back their leverage positions. The combination of reduced indebtedness and historic low interest rates resulting from extraordinary monetary policy measures employed by Federal Reserve to combat the 2007–09 recession has led to a marked decline in interest expenses relative to farm sector revenue as shown in Figure 5. This trend peaked in 1983 when the combination of high interest rates and low revenue levels led to a serious financial crisis in agriculture. The quantitative easing policies adopted by the Federal Reserve beginning in 2008 have lowered interest rates to historically low levels, which, in turn, have led to a substantial reduction in farm interest expenses relative to farm revenue. Another factor involved here is the weakening of the US dollar as interest rates decline, which has increased revenue from exports of agricultural production.

Another story line revealed in the sector income accounts is the declining role played by government payments to agriculture as farm incomes have achieved record levels. Figure 6 shows that government payments to producers principally in the form of deficiency payments when crop prices were low leading to the ethanol boom played a substantial role in bolstering net farm income. Beginning in the mid-2000s, however, this role has been substantially reduced to fixed direct payments, which are more likely to be eliminated in new farm legislation as a greater role is envisioned for crop insurance.

Sector balance sheet account

The US Department of Agriculture began to publish a balance sheet for agriculture in the 1940s. This account presents a

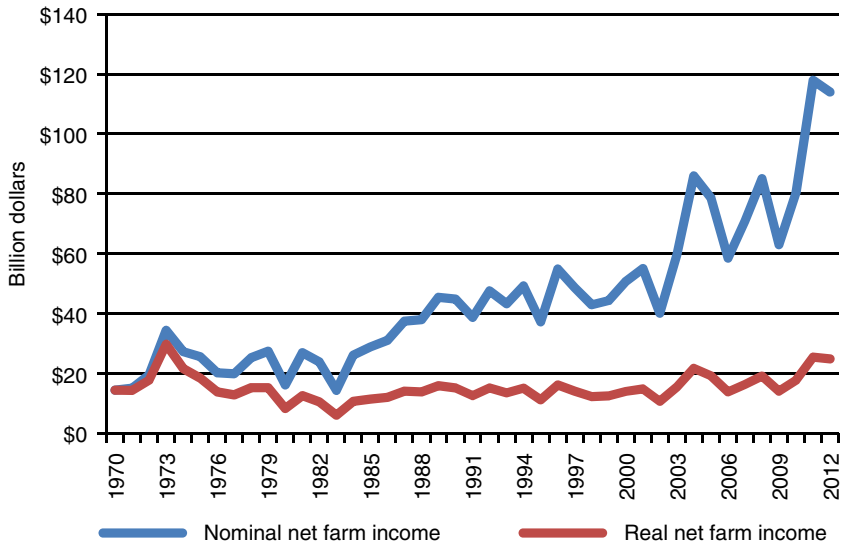


Figure 4 United States' net farm income.

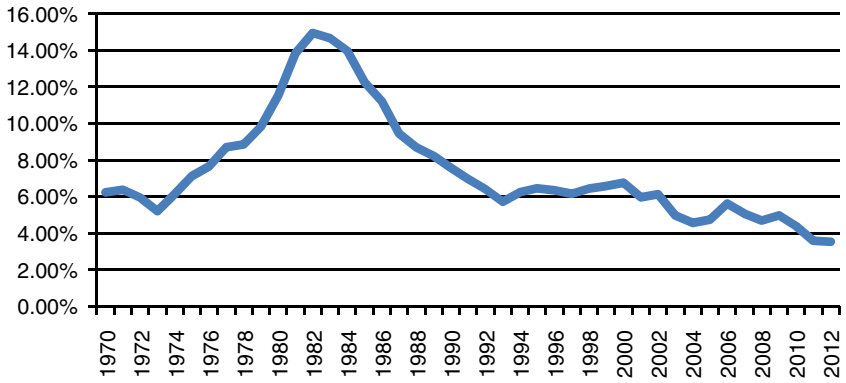


Figure 5 Interest expenses decline.

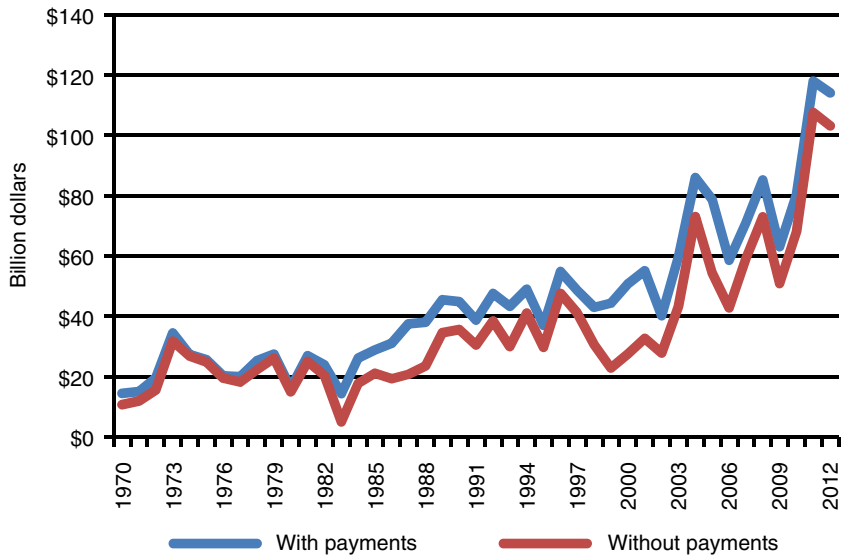


Figure 6 Importance of government payments.

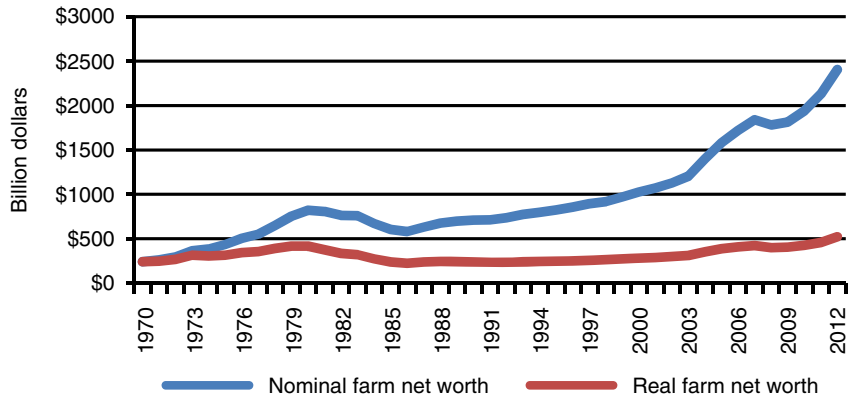


Figure 7 Nominal and real farm net worth.

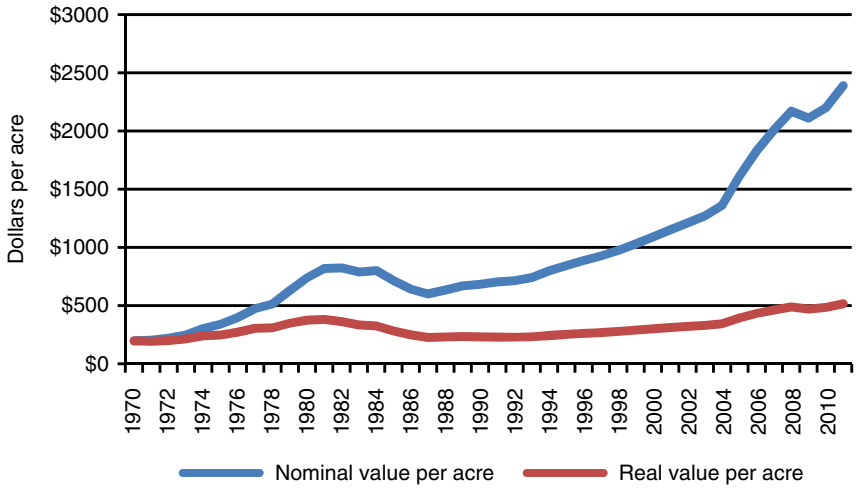


Figure 8 US value of farmland per acre.

measure of liquidity, solvency, and wealth of farm businesses as of 31st of December each year. The asset coverage in this account includes the current market value of farmland, farm buildings, livestock on farms, crop inventories, farm machinery, and other production inputs. This coverage also includes financial assets held for farm business purposes. The liability side of this balance sheet provides information on year-end farm real estate and nonreal estate debt outstanding. The debt ratio published with this account represented the major aggregative financial indicator used by analysts for many years. A maturing farm sector, where many family-owned farms have little or no farm debt outstanding, has reduced the interpretive value as a financial indicator at the sector level.

Figure 7 illustrates the growth trend in nominal and real farm net worth over the past five decades. This figure shows that although real net worth thus far in the 2010s is not appreciably different from what it was before the farm financial crisis in the early 1980s, the nominal value has increased substantially. This has further helped to reduce the debt ratio, particularly since the mid-2000s when the ethanol boom began in earnest. Thus, the real wealth position of farm asset owners at year-end in 2012 is slightly higher than what it was before the farm financial crisis in the early 1980s.

Much of the growth in farm net worth can be attributed to rising farmland values, particularly in feed grain-producing regions of the country. Figure 8 shows the trend in nominal and real farmland values per acre over the past five decades. Many mid-western states have realized double-digit increases in nominal farmland values since the mid-2000s; thanks to the growing demand for ethanol feed stock as well as a growing demand for agricultural products in emerging economies, like China.

In addition to these sector accounts published at the national level, the US Department of Agriculture periodically published the income and balance sheet accounts on a state basis for those desiring to conduct regional or state-level analyses. Other related data important to macroagricultural finance researchers contained in publications or websites maintained by the US Department of Agriculture include measures of productivity and efficiency, costs of production for crop and livestock operations, and trends in agricultural resource use.

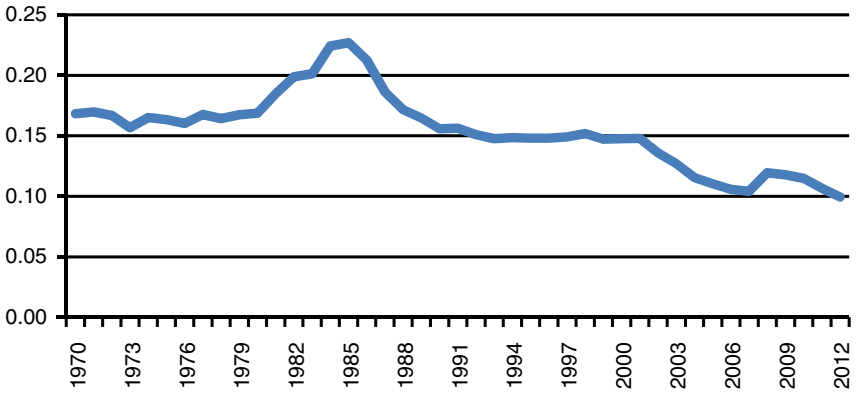


Figure 9 Sector debt-to-asset ratio.

Other sector financial information

The income statement and balance sheet accounts provide the basis for other assessments of macroagricultural finance. An example is the development of a sector-level annual sources and uses of funds statement. This would capture sources of funds from farm revenue and net borrowings as well as uses of funds attributable to cash farm operating expenses as well as capital expenditures for machinery and structures. The difference between these sources and uses of funds would explain the net increase in financial assets.

The income statement and balance sheet accounts, along with other available data, can also serve as the basis for calculating an aggregative set of financial indicators for the sector. This includes measures of liquidity, solvency, profitability, efficiency, and debt repayment capacity. Figure 9, for example, illustrates the trend in the farm debt ratio, which has declined sharply from the levels seen during the farm financial crisis in the mid-1980s. The US Department of Agriculture publishes a national-level time series indicating the used borrowing capacity at the sector level. One can construct similar series at the state or regional level using available state publications.

Other analyses possible using data from the US Department of Agriculture include a comparison of market value farmland values versus their capitalized values using published time series data on rents and the 10-year constant maturity government bond rate.

Research applications

The information contained in the US Department of Agriculture's sector economic accounts and related data sets is not only useful in current situation analysis but also represents a major source of data for research designed to project the effects that a broad range of macroeconomic, farm commodity, and international trade policies can have on the economic growth and financial performance of agriculture. Researchers dating back to the early 1950s have been developing statistical-based models of agricultural activity using, to varying degrees, information contained in these and related time series published by the US Department of Agriculture.

Although the sector provides a rich database to support positive and normative analysis of its structure and performances, the potential for aggregation bias is significant. Drawing implications from national data and models can lead to misleading conclusions regarding the financial health of the sector. Greater disaggregation of the accounts by major types of farming operations on a regional basis can help to avoid these issues. For example, assessments based solely on a national farm debt ratio, debt coverage ratio, or measures of unused borrowing capacity are examples of indicators that can contribute to misleading conditions facing farm financial institutions.

Modeling Aggregate Financial Performance

A second dimension to macroagricultural finance research has to do with understanding and projecting aggregate investment expenditures, farmland values, and the financial structure of the farm sector. Considerable resources have been committed to modeling these aggregate time series over the post-World War II period in both public and private sectors.

Modeling farm sector investments and asset values

Early studies of aggregate investment expenditures in agriculture focused principally on farm tractors. Many of these studies made overly simplifying assumptions with respect to the cost of capital and measurement of capital stocks and flows. These studies were followed by more rigorous efforts to expand the cost of capital to include monetary and fiscal policy-related variables as well as an accounting of the physical deterioration of an input's productive capacity, or capacity depreciation, across different vintages and types of machinery. This allows researchers to capture the direct and indirect effects of changes in macroeconomic policy on the investment expenditures that impact the productive capacity in agriculture. Modeling the demand for fixed assets should also reflect portfolio balance considerations with desired financial asset holdings.

There have been many studies focusing on explaining the determinants of farmland market values using a wide variety of quantitative approaches. Some researchers have focused on the capitalized value of farmland per acre as opposed to the market value, noting the disparity between these two time series in the early 1980s to mid-1980s when market values were slow to adjust to changing economic conditions affecting rents and interest rates. The ability to project the effects that

changing economic conditions brought about by policy and other factors enables lenders and others visualize how these events might alter the demand for debt capital in agriculture and the financial strength of crop and livestock producers.

Modeling farm sector financing

Attempts to model and project the annual borrowing and repayment of loans to agriculture have been largely unsuccessful due in part to a lack of data. For example, the annual flow of loan funds to financing farm operating expenses is unknown. The sector balance sheet account allows a measure of annual changes in real estate and nonreal estate debt outstanding from one year to the next. But this omits that portion of loan funds borrowed annually by producers that is used and repaid within the year. Data on interest expenses on real estate and nonreal estate loans potentially omit the interest expenses on short-term borrowing as well as the use of credit cards and lines of credit used and paid down during the year. The growing dichotomy between the size of farming operations and ownership structure makes it difficult to model aggregate farm financing behavior.

Key Linkages to Rest of the Economy

Previous mention was made of the effects that macroeconomic policies (domestic and global) have on the financial strength and performance of US agriculture. Researchers focusing on modeling the potential impact of these policies have to decide to what degree they want to endogenize the interface between agriculture and rest of the economy.

This issue can be viewed from several perspectives, including the interface between the domestic and global economy and whether to treat this interface as entirely exogenous, recursive, or simultaneous. The latter two choices require considerable time and resources. Input–output models and CGE models by definition endogenize the linkage between agriculture and the general economy. Econometric models, either structural or time series in design, also capture links to the domestic economy in various ways. Few, if any in recent years, capture these linkages in a fully simultaneous manner.

Domestic linkages

The interface between agriculture and the domestic economy occurs where producers acquire inputs (including loan funds) as well as in the markets where they sell their production. (The large integrated firms in the broiler, turkey, egg, and hog businesses frequently endogenize many of these relationships with the firm, thereby increasing the efficiency of their operations.) Furthermore, policy actions and other economic shocks occurring outside agriculture can be transmitted to crop and livestock producers in these markets. For example, research has shown that monetary policy directly affects the current operations and growth of agriculture through the cost and availability of loan funds. This represents a direct linkage between the policy action and the farm borrower. This same monetary policy, however, has an impact on other sectors of the economy as well and thus can alter the equilibrium levels of prices in all markets.

There are four major linkages between agriculture and the domestic economy. These variables are (Penson *et al.*, 2014):

- Interest rates – Producers generally borrow significant amounts of operating capital to finance current operations. Those modernizing their machinery or expanding the size of their operations also borrow a significant amount of debt capital to finance asset acquisitions. Thus, a one percentage point rise in interest rates will affect interest expenses and hence net farm income.
- Rate of inflation – Producers are generally price takers in the markets in which they buy variable and fixed production inputs. Sellers in these markets typically have the market power that enables them to pass along increases in their costs to producers.
- Unemployment rate – Many producers either work themselves or have a spouse and family members who work off the farm or ranch. Off-farm income represents a significant source of internal funds, particularly for small- or mid-sized farms that have a seasonal farming operation. An increase in the unemployment rate reflecting tighter employment opportunities and layoffs can affect this source of funds, and
- GDP growth rate – The economic growth of the economy can affect consumer disposable income and hence their demand for goods and services. Agriculture is less directly affected by economic growth in the domestic economy than the demand for durable goods and services. This is evidenced more by the low-income elasticity of demand for agricultural products (less than one) than by that for nonfood products.

The record levels of net farm income in the 2010s thus far have been helped by historically low interest rates and inflation rates. Studies focusing on demand systems for food products have provided estimates of elasticity for a wide range of commodities. Results suggest an inelastic demand and low-income elasticity for agricultural products. This has implications for price variability as supply shifts and muted effect of changes in disposable personal income as conditions change in the economy. Agriculture fared relatively well during the 2007–09 recession when most sectors exhibited weakened performance.

International linkages

Another factor contributing to record net farm income levels in the 2010s is the net export demand for agricultural products. This has been aided by a weak US dollar versus currencies of exporting nations. Considerable attention has been given in the literature to modeling international agricultural trade flows, including the effects that changes in foreign currency exchange rates can have on net exports for specific agricultural commodities like wheat and corn. The implication for finance is that low exchange rates can induce exports of agricultural products and vice versa. The record levels of net farm income in the 2010s thus far have also been helped by historically low value of the dollar.

The global financial crisis following the 2007–09 US recession has had an impact on all nations to varying degrees. The European Union and euro zone nations, for example, were

seriously affected by this crisis, with many nations continuing to deal with recessions long after the US economy began to expand. Although this has affected net exports to that market, many emerging nations, like China and India, with populations experiencing rising per capita income levels, continued to represent a strong export market for the US agricultural products.

Role of Policy

An important dimension to macroagricultural finance is the impact that macroeconomic, farm commodity, international trade, and other policies have on agriculture and the rest of the food and fiber industry. In discussing each of these areas, it is important to distinguish between the general impacts of these policies, in addition to their financial implications.

Macroeconomic policy impacts

Macroeconomic policy makers want to know the likely effects of their actions not only in the general economy but also specific sectors in the economy like agriculture. Not all sectors are affected the same when a policy change or economic shock occurs in the economy. Perhaps no other sector exhibits the unique direct and indirect effects from a macroeconomic shock like agriculture. Of interest here is the fact that a large share of the 'cause and effect' is financial in nature. Table 1 summarizes the likely short run effects specific combinations of monetary and fiscal policy have on agriculture.

The 2007–09 recession in the US economy, referred to by some as the Great recession because of its duration, occurred at a time when interest rates were already low. Hence, the traditional tools employed by the Federal Reserve to stimulate the economy were off the table. With an effective federal funds rate near zero, the Federal Reserve turned to extraordinary tools to provide liquidity to the economy and keep long-term interest rates low. A series of three quantitative easing (QE) initiatives began in 2008 involving purchasing agency securities and mortgage-backed securities. These purchases reached US$85 billion a month in 2013. The levels of these purchases were tied to targets for the civilian unemployment rate and PCE-based inflation rate. This approach was augmented by 'operation twist' beginning in late 2011 that involved the Federal Reserve buying long-term securities while selling short-term securities in an effort to keep long-term interest rates low.

Agriculture is typically a beneficiary of expansionary macroeconomic policies. Although the unemployment rate has remained sticky above the Federal Reserve's target, interest rates, inflation, and the foreign exchange rate – three important macrovariables for agriculture – fell to historic lows. This helped to lower interest expenses (Figure 5), to avoid inflationary pressures pushing up input costs, and helped to make US agricultural products more affordable to emerging economy nations, like China.

Several fiscal policy actions during the 2007–09 recession, including stimulus checks and bailouts of General Motors, Chrysler, and AIG, helped the economy by minimizing the depth of the 2007–09 recession. However, fiscal policy makers did little to alleviate the uncertainty about future taxation and spending programs following the recession. This uncertainty created an environment where businesses in general and financial markets remain conservative regarding future expansion. This environment has had a much greater impact on other sectors of the economy like housing than it had on agriculture.

Farm commodity policy impacts

The federal government has a long history of supporting prices and incomes in agriculture when the need arose. Low commodity prices for major crops, like corn and wheat, have traditionally meant higher deficiency payments paid to producers participating in these farm programs (Figure 6). These policies affect the level of sales activity in backwardly linked farm input sectors as well as forwardly linked food processing sectors. These payments have also helped to stabilize farm financial markets by aiding producers' debt repayment capacity. Such support programs, to the extent they are expected to continue, are capitalized into the valuation of long-term assets, like farmland.

With the farm program legislation up for renewal, the Senate and House appear to support a greater role for federally subsidized crop insurance programs designed to offer varying degrees of yield and revenue support tied to premium rates paid by participating producers. Limited revenue insurance programs to date have been available to livestock producers. Agricultural lenders typically require borrowers to verify that

Table 1 Impacts of macroeconomic policy on agriculture

Policy effects on	*Expansionary monetary policy*	*Expansionary fiscal policy*	*Contractionary monetary policy*	*Contractionary fiscal policy*
Crop price				
Domestic demand	Raise	Raise	Lower	Lower
Export demand	Raise	Lower	Lower	Raise
Net impact	Raise	Lower	Lower	Raise
Livestock prices	Lower	Raise	Raise	Lower
Farm input prices	Raise	Raise	Lower	Lower
Farm interest rates	Lower	Raise	Raise	Lower
Net farm income	Raise	Lower	Lower	Raise
Farmland prices	Raise	Lower	Lower	Raise

Note: Direction of change is not unambiguous, but rather conditional on the relative market share for export demand and relative price elasticity of export demand. A relatively high market share or relatively high price elasticity of export demand is assumed in this table. It is assumed the impact on crop prices and interest payments offsets the impacts on livestock prices when calculating net farm income and farmland prices for both crop and livestock producers.

they are a participant in federal support programs, like crop insurance.

Resource policy impacts

Agriculture is a dominant user of the United States' natural resources, such as water, timber, and land. Numerous government agencies, such as the Environmental Protection Agency, the US Department of Agriculture, and the US Department of the Interior, have supervisory jurisdiction over the use of these resources and associated use of manufactured resources like agricultural chemicals. In recent years, many have become concerned with pollutants in water supplies and carcinogens in food supply caused by agricultural production practices.

Resource policy concerns have led to bans on the use of specific agricultural chemicals in the production of food grains and other crops. Reductions in yields and hence net farm incomes could vary regionally depending on the level of input use required to achieve a desired yield. The economic performance and financial position of farm borrowers would vary accordingly, with crop producers in northern regions faring better than crop producers in the more temperate southern regions, and with crop producers in general being less affected financially than livestock producers.

Trade policy impacts

Crop agriculture has become export dependent. Typically, more than one-fourth of all agricultural production is exported, accounting for roughly one-third of farm income. Wheat, cotton, and rice are major crops depending on export markets as a major source of demand. Horticultural products and meats are less export dependent than row crops, although their market shares are increasing. A strong export demand has indirect ramifications in backwardly linked input supply sectors and forwardly linked processing and trade sectors in the US food and fiber industry.

Distortions to agricultural trade in the form of tariffs and quotas have prompted major trading nations to participate in the General Agreement on Tariffs and Trade. These negations typically liberalize trade in agricultural products. Exchange rates, influenced by monetary policies of trading nations, have become one of the most important economic variables affecting US agricultural trade in cases where exports account for a large share of production. For the most part, preferential trade agreements entered into by the United States have taken the form of free trade areas. The North American Free Trade Agreement is an example. Other forms of free trade zones include economic unions like the European Union.

Disclaimer

In this article, Sections Microagricultural Finance and Macroagricultural Finance were written by the authors Paul N. Ellinger and John B. Penson, Jr. respectively.

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Agricultural Labor: Demand for Labor

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Glossary

Capital Services of a machine, equipment, or building.
Isoquant A graph showing all combinations of inputs (labor, capital, and materials) needed to produce a particular amount of output with given technology.
Labor Services of a worker or laborer.
Labor demand Derived from the demand for the output, given the prices of output and inputs and technology.
Materials Intermediate inputs, for example, fertilizer, pesticides, seeds, fuel, and electricity.
Production function The relationship of output (volume of produce, goods, or services) to inputs (labor, capital, and materials) and technology.
Technology The result of specific application of information or knowledge which results in a particular algebraic relationship among output and inputs, or technical efficiency of production.

Introduction

Agriculture has historically been a sector characterized by much hard physical labor performed sometimes under adverse weather and environmental conditions. However, farming in the US has advanced through oxen, horses and mules, steam tractors, and then tractors with internal combustion engines to provide power on farms. Tractors started to be a competitive source of power in the early twentieth century, as progress moved from steam to internal combustion engines and steel to air-inflated rubber tires. Early reapers and binders were forerunners of stationary threshing machines, and mobile combines or mechanical harvesters for grain, beans, and cotton became available over 1930–1960s. However, hand harvesting of fruits and vegetables continued into the late 1960s. The invention and later adoption of the self-propelled mechanical processed tomato harvester in the mid-1960s was a major labor-saving factor in fruit and vegetable harvesting. However, with later related inventions, further saving in labor and improvement in product quality were the result. Mechanical harvesters were developed for some other processing fruits. Although fresh fruit and vegetable harvesting continues largely by hand, mechanical aids have made harvesting faster and with less stress on workers' backs.

US agriculture competes with other sectors of the economy for inputs of labor, chemicals, building materials, and land. Since 1980s, an increase in international competition in grains, oilseeds, fruits and vegetables, and livestock and livestock products has occurred with, for example, Mexico and Chile, as low cost suppliers of fresh fruits and vegetables (Calvin and Martin, 2010). However, for an extended period, US growers have drawn on illegal and legal workers from Mexico as sources of planting and harvesting labor in these crops. In particular, mechanization and modification of production practices and improved management practices have been central to reducing labor requirements for the growing and harvesting of all kinds of crops. Calvin and Martin (2010) report that mechanical harvesting is most prevalent in horticultural crop harvesting, being 75% of vegetables and melons and 55% of fruits. In 2009, the largest (harvested) volume of US fruit and vegetable crops (in millions of tons) are: tomatoes (15.6), oranges (9.2), grapes (7.3), apples (5.0), potatoes (4.1), melons and cantaloupes (3.2), head lettuce (2.5), sweet corn (1.5), strawberries (1.4), and carrots (1.1) (USDA, NASS, 2011a,b,c).

This article provides a long-term perspective on the demand for farm labor in the US. It does this by taking up the following topics: (1) the economics of labor demand (the conceptual economic model of production and supply of output and demand for inputs); (2) mechanization of agriculture in the nineteenth and twentieth centuries (also see Huffman, 2012); (3) substitution of biological advances and chemicals for farm labor and other agricultural materials; (4) more on mechanization of fruit and vegetable harvesting; (5) structure of farms; (6) estimates of the wage elasticity of demand for farm labor (from aggregate data); and (7) conclusions.

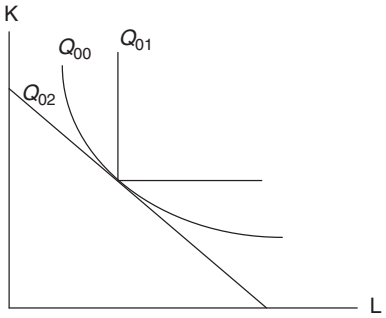
In the long history of agriculture, mechanization has generally required a transformation of a farming system, for example, new machinery, larger field sizes, new crop varieties, new field configurations, and new harvesting and storage/packing equipment, storage facilities and processes. In addition, a significant capital outlay is frequently required. A better picture of all of this unfolds in the following pages.

The Economics of Labor Demand

To set the stage for a deeper understanding of the economics of labor demand, the author develops some terminology associated with a farm output production function, farm profit maximization and input demand. Consider a production function for a single output (Q) that uses inputs of labor services (L), capital services (K), and materials (X):

$$Q = F(L, K, X, \tau) \quad [1]$$

In agriculture, farm labor includes the farm operator, unpaid family labor and other labor hired by the farm operator or manager, but contract farm labor, fertilizer, and pesticide application and custom harvesting are part of the materials.



Note:

$Q = F(L, K; \tau)$

$\Delta Q = MP_L \Delta L + MP_K \Delta K = 0$

$MP_K \Delta K = -MP_L \Delta L$

$\therefore MRS_{KL} = \dfrac{\Delta K}{\Delta L} = -\dfrac{MP_L}{MP_K}$

Q_{00}: *K* and *L* with generally variable input ratios or combinations (curved isoquant)

Q_{01}: *K* and *L* used in fixed proportions (right angle isoquant)

Q_{02}: *K* and *L* are perfect substitute 1-to-1 (straight line isoquant)

Figure 1 Isoquant showing combinations of capital (*K*) and labor (*L*) to product Q: variable input proportions, fixed proportions and perfect substitutes.

Generally, materials include farm feed, pharmaceuticals, fuel, seeds, farm purchased fertilizers and pesticides, and utilities.

In eqn [1], τ is an efficiency parameter that summarizes how effectively labor, capital, and materials are converted into output Q, either neutrally or in a biased way. We will proceed for now assuming that it is fixed. For eqn [1], the marginal product (MP) of labor (marginal change in Q because of a marginal increase of L) is denoted as $\partial Q/\partial L = MP_L(L, K, X, \tau)$. Likewise the MP of capital (K) and materials (X) are $\partial Q/\partial K = MP_K(L, K, X, \tau)$ and $\partial Q/\partial X = MP_X(X; L, K, \tau)$, respectively.

An isoquant is the graph used by economists to display the combinations of L, K, and X required to produce a given amount of output, Q_0. Mathematically, they are simply level curves of a multivariable function, which in this case is a production function. Figure 1 shows three different types of technical relationships between inputs of labor and capital for producing a given quantity, Q_0 With the isoquant labeled Q_{00}, there are general-variable factor proportions or a wide range of ratios of K to L that will produce the given quantity of output. With Q_{01}, the inputs must be used in fixed proportions, say one unit of capital and one unit of labor to produce one unit of output. Additional labor (capital) without additional capital (labor) does not produce any additional output. For example, roughly fixed proportions exist between tractor drivers and tractors, but of course the size of tractor and skill of the operator can differ and in this way effectively change the proportions. Also, by having multiple drivers, the tractor can be operated nearly 24 h per day. With Q_{02} the inputs are perfect substitutes, for example, one unit of capital and one unit of labor are interchangeable in the way that they impact Q_0. In the case of perfect substitutes, a better example is using male labor with blue and brown eyes. They are interchangeable with no impact on production.

Hayami and Ruttan (1985) have assembled some data on labor (workers) and capital (measured in horsepower) to produce wheat in 44 countries. Orazem (1998) has converted this information into a unit isoquant, which graphs combinations of capital and labor required to produce a single bushel of wheat. See Figure 2, which has the usual 'convex to the origin' shape revealing general substitution possibilities between capital and labor for wheat across countries that have very different wage to capital rental rates.

The most notable production function is the (general) Cobb–Douglas (C–D), which relates output Q to a special power function in input quantities (Douglas, 1976).

$$Q = AL^{\alpha}K^{\beta}X^{\gamma}, A = A(\tau), \quad 0 < \alpha, \beta, \gamma < 1 \qquad [2]$$

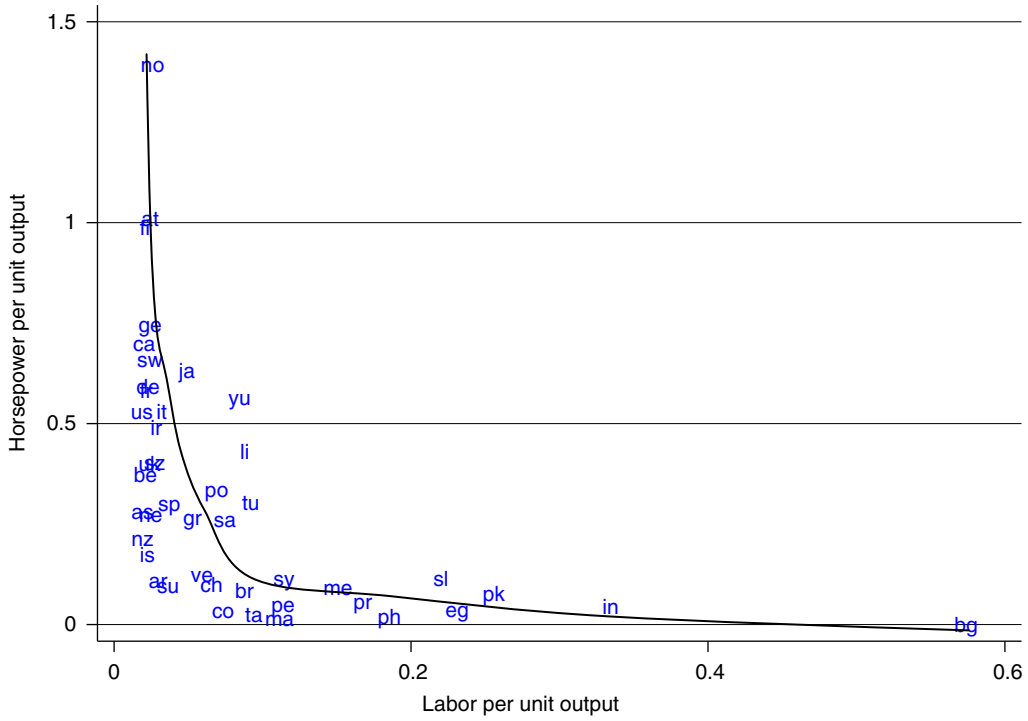
Its MPs are proportional to the average products (APs) in a special form; for labor, $MP_L(L, K, X, \tau) = \alpha AL^{\alpha-1}K^{\beta}X^{\gamma} = \alpha Q/L = \alpha AP_L(L, K, X, \tau)$. Likewise, for capital, $MP_K(L, K, X, \tau) = \beta AL^{\alpha}K^{\beta-1}X^{\gamma} = \beta Q/K = \beta AP_K(L, K, X, \tau)$, and for materials, $MP_X(L, K, X, \tau) = \gamma AL^{\alpha}K^{\beta}X^{\gamma-1} = \beta Q/X = \gamma AP_X(L, K, X, \tau)$. Under an assumption of the C–D production function, Figure 3 displays the marginal product of labor against the labor per unit of output (bushel of wheat) for 44 wheat-producing countries (Orazem, 1998). For small amounts of labor it shows rapidly diminishing marginal product of labor, and then the rate of decline slows and the marginal product remains relatively unchanged for large amounts of labor per unit of wheat.

Returning to eqn [2], if there is constant returns to scale in using L, K, and X to produce Q, then a doubling in each of these inputs results in a doubling of the output (Q), or $\phi = \alpha + \beta + \gamma = 1$, but, generally, one expects there to be decreasing returns to scale – a doubling of inputs results in less than a doubling of output.

For farms or the farm sector, a standard assumption made by economists is that farmers accept the price asked for by suppliers of inputs and take the price offered to them by buyers of their output – roughly competitive markets for output and inputs reign. In the short run, it may be plausible to assume that capital (K) and material (X) are fixed, and labor (L) is variable. Under these conditions, what is the optimal amount of labor to use? Note that short-run profit is defined as

$$\pi_S(P_Q, W_L, \bar{K}, \bar{X}, C_0, \tau) = P_Q F(L, \bar{K}, \bar{X}, \tau) - W_L L - C_0 \qquad [3]$$

where W_L is the wage rate or opportunity cost of one unit of labor and C_0 are fixed costs, possibly associated with fixed



$$Elasticitiy - of - substitution = \sigma_{KL} = \%\Delta\left(\frac{K}{L}\right) / \%\Delta\ \left(\frac{W_L}{W_K}\right) \geq 0$$

Figure 2 Labor and capital (as horsepower) use per unit of agricultural (wheat) output. Data across 44 countries. Figure was constructed from data reported in Hayami, Y., Ruttan, V.W., 1985. Agricultural Development: An International Perspective. Baltimore, MD: Johns Hopkins University Press.

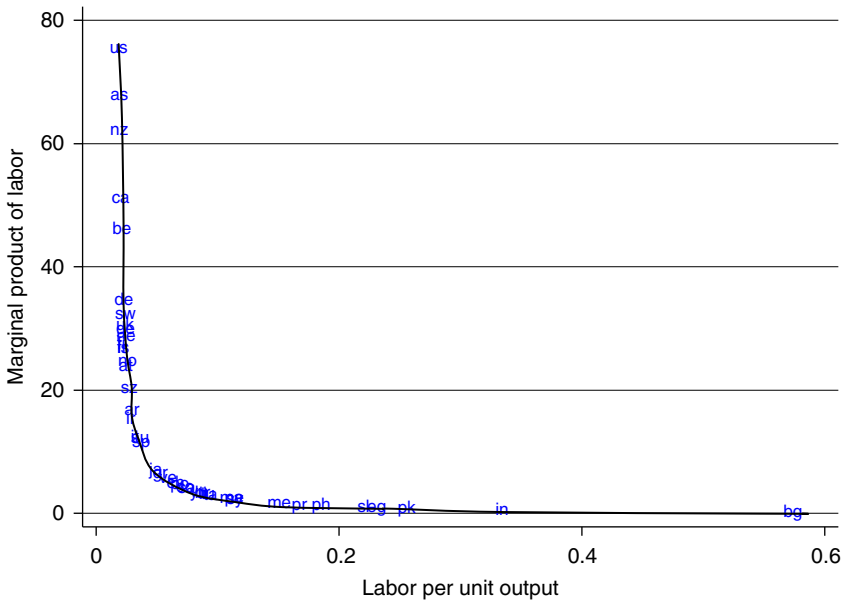


Figure 3 Marginal product of labor as a function of the quantity of labor. Data on wheat equivalent production across 44 countries. Figure was constructed from data reported in Hayami, Y., Ruttan, V.W., 1985. Agricultural Development: An International Perspective. Baltimore, MD: Johns Hopkins University Press.

K and X. The optimal usage of labor occurs when $\partial\pi/\partial L = P_Q \partial Q/\partial L - W_L = P_Q MP_L(L,\bar{K},\bar{X},\tau) - W_L = 0$, provided profit at an optimum is positive, or the value of the marginal production of labor is equal to the wage rate. In the C–D case, this condition reduces to $P_Q \alpha Q/L = W_L$, or the optimal short-run amount of labor demanded is

$$L_S^* = d_S(P_Q, W_L, \bar{K}, \bar{X}, C_0, \tau) \quad [4]$$

Figure 4 displays the short-run demand curve for labor with its characteristic negative slope – as the wage rate increases, the quantity demanded of labor declines, other things equal. For example, continuing with the example of wheat production, Figure 5 plots an approximation to the empirical demand for labor in wheat production across 44 countries, and also includes a graph fitted roughly through the frontier associated with these points. Under the assumption that farmers are using roughly the optimal short-run amount of labor, it shows that the value of the marginal product of labor is decreasing as more labor is used in wheat production. Moreover, Figure 6 plots the optimal capital-labor ratio as the real wage rate rises in wheat production across 44 countries.

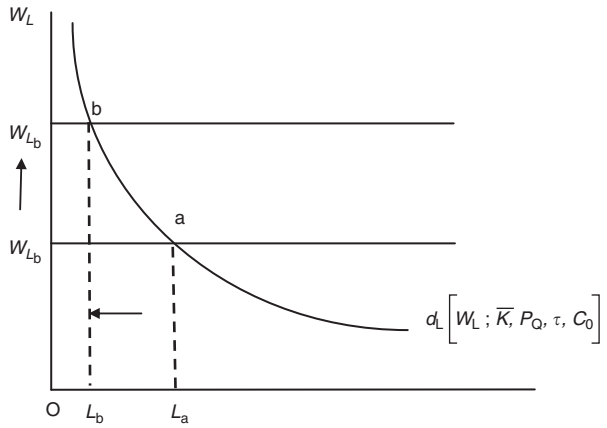


Figure 4 The short-run labor demand curve. W, wage.

Moreover, if eqn [4] is substituted into $Q = F(L,\bar{K},\bar{X},\tau)$, one obtains the short-run supply function for Q or

$$Q_S^* = S_L(P_Q, W_L, \bar{K}, \bar{X}, C_0, \tau) \quad [5]$$

Hence, the quantity supplied of Q varies with the output price, P_Q, which represents a movement along the short-run output supply curve; and with the wage rate, W_L. Moreover, when the wage rate increases, this increases the cost of production, other things equal, and the quantity supplied of output will be reduced or the supply curve for output will shift to the left (provided the firm does not shut down because profits are negative). The short-run supply curve has a positive slope – quantity supplied is positively related to the price as shown in Figure 7. At output price P_Q^0 the optimal output is Q_1 When the wage rate increases to W_{L_2}, the supply curve for Q shifts left and the new optimal output is Q_2.

In the long-run, labor (L), capital (K), and materials (X) are all variable, and all three of these inputs must be used optimally at the same time to maximize the long-run profit function:

$$\pi(P_Q, W_L, W_K, W_X, C_0, \tau) = P_Q F(L,K,X,\tau) - W_L L - W_K K - W_X X - C_0 \quad [6]$$

which, assuming positive labor, capital, and materials inputs, requires that the following conditions simultaneously hold

$$\partial\pi/\partial L = P_Q MP_L(L,K,X,\tau) - W_L = 0 \quad [7]$$

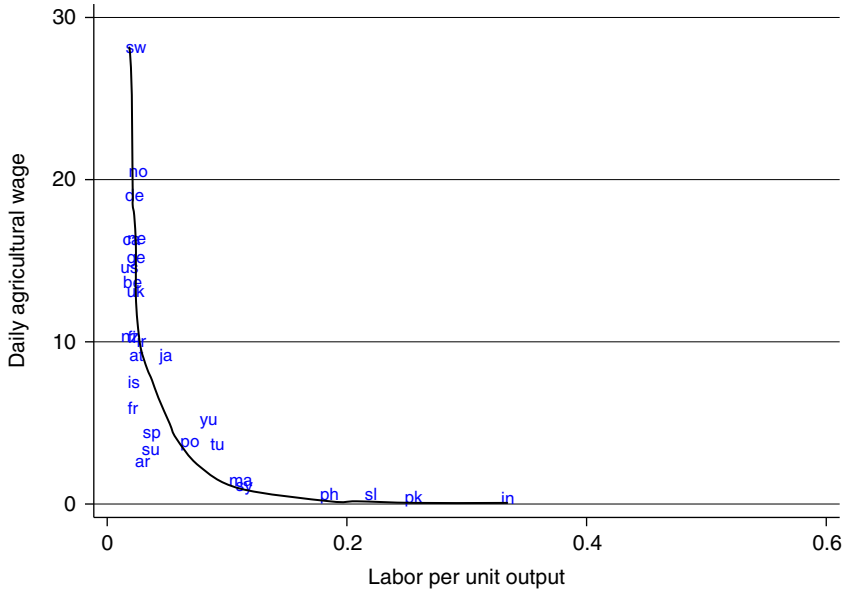


Figure 5 Short-run labor demand: labor use in wheat production across 44 countries. Figure was constructed from data reported in Hayami, Y., Ruttan, V.W., 1985. Agricultural Development: An International Perspective. Baltimore, MD: Johns Hopkins University Press.

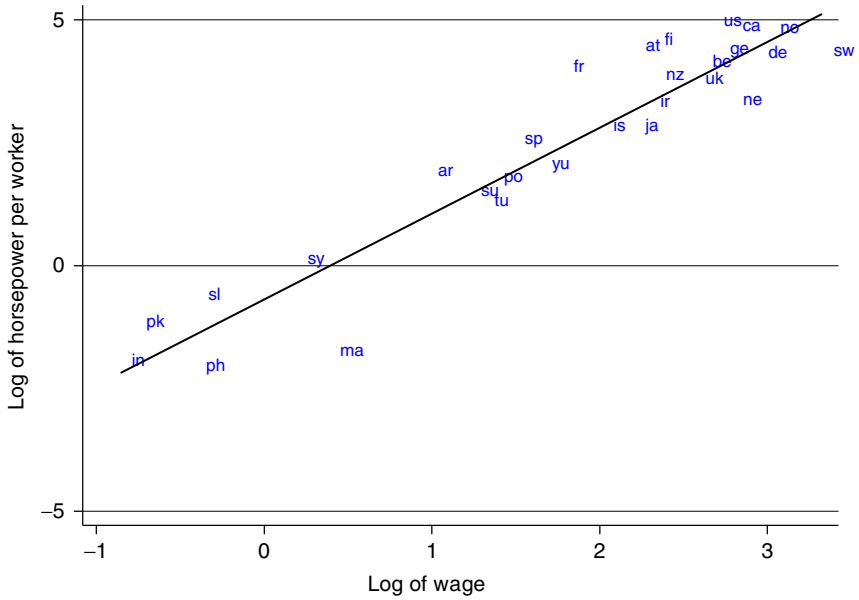


Figure 6 Capital per unit of labor as wage to labor rises: labor use in wheat production across 44 countries. Figure was constructed from data reported in Hayami, Y., Ruttan, V.W., 1985. Agricultural Development: An International Perspective. Baltimore, MD: Johns Hopkins University Press.

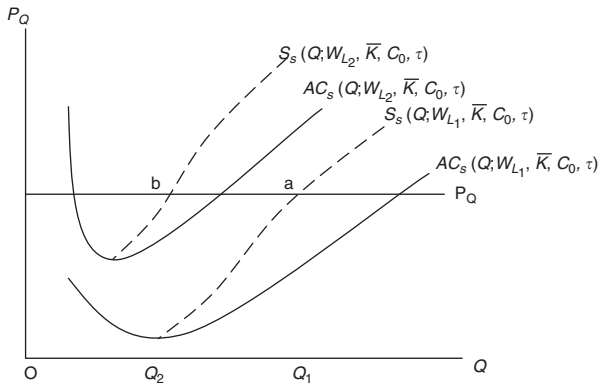


Figure 7 The short-run supply curve for output (Q). *P*, price.

$$\partial\pi/\partial K = P_{\mathrm{Q}} MP_{\mathrm{K}}(L,K,X,\tau) - W_K = 0 \qquad [8]$$

$$\partial\pi/\partial X = P_{\mathrm{Q}} MP_{\mathrm{X}}(L,K,X,\tau) - W_X = 0 \qquad [9]$$

$$\pi^*(P_{\mathrm{Q}}, W_{\mathrm{L}}, W_{\mathrm{K}}, W_{\mathrm{X}}, C_0, \tau) \geq 0 \qquad [10]$$

Equation [10] is the condition for the firm to operate at positive output, long-run profit at optimal input use must be positive, or zero. Moreover, when eqns [7]–[10] hold and the production function is strictly concave, one can solve these equations for the profit maximizing or long-run input demand functions.

$$L^* = d_{\mathrm{L}}(P_{\mathrm{Q}}, W_{\mathrm{L}}, W_{\mathrm{K}}, W_{\mathrm{X}}, C_0, \tau) \qquad [11]$$

$$K^* = d_{\mathrm{K}}(P_{\mathrm{Q}}, W_{\mathrm{L}}, W_{\mathrm{K}}, W_{\mathrm{X}}, C_0, \tau) \qquad [12]$$

$$X^* = d_{\mathrm{X}}(P_{\mathrm{Q}}, W_{\mathrm{L}}, W_{\mathrm{K}}, W_{\mathrm{X}}, C_0, \tau) \qquad [13]$$

What eqn [11] indicates is that in the long-run profit maximizing situation, the optimal amount of labor is determined by the price of labor, price of capital, price of materials, and by the fixed cost C_0, which will generally be different than in the short-run situation and might be smaller, as well as the technology parameter τ. Moreover as the wage rate for labor increases, the quantity demanded of labor decreases. The impact of an increase in the rental on capital W_{K} (price of materials W_{X}) could be to increase, reduce, or leave unchanged the demand for labor.

Maintaining the assumption of C–D production, one finds that the long-run demand for labor function is

$$\begin{aligned} L^* &= [\alpha^{(\beta+\alpha-1)}\beta^{-\beta}\gamma^{-\gamma}A^{-1}\cdot P_{\mathrm{Q}}^{-1} W_{\mathrm{L}}^{(1-\beta-\gamma)} W_{\mathrm{K}}^{\beta} W_{\mathrm{X}}^{\gamma}]^{1/(\alpha+\beta+\gamma-1)} \\ &= [A^* P_{\mathrm{Q}}^{-1} W_{\mathrm{L}}^{(1-\beta-\gamma)} W_{\mathrm{K}}^{\beta} W_{\mathrm{X}}^{\gamma}]^{1/(\alpha+\beta+\gamma-1)} \end{aligned} \qquad [14]$$

This has the unique attribute of being a power function in the output and input prices because of a duality (similarity) in the functional form of the production function and profit function (Beattie and Taylor, 1993). The long-run demand equations for capital and materials have a similar symmetric expression. From eqn [14], the wage (capital rental, materials price, output price) elasticities of labor demand, respectively, are

$$\eta_{L^* W_{\mathrm{L}}} = (1-\beta-\gamma)/(\alpha+\beta+\gamma-1) < 0 \qquad [15]$$

$$\begin{aligned} \eta_{L^* W_{\mathrm{K}}} &= \beta/(\alpha+\beta+\gamma-1) < 0, \\ \eta_{L^* W_{\mathrm{X}}} &= \gamma/(\alpha+\beta+\gamma-1) < 0 \end{aligned} \qquad [16]$$

$$\eta_{L^* P_{\mathrm{Q}}} = 1/(\alpha+\beta+\gamma-1) > 0 \qquad [17]$$

Note that increasing the size of α (which is proportional to labor's cost share) and holding $\alpha+\beta+\gamma$ constant increases the own-price elasticity of demand for labor. Also, as the size of $\alpha+\beta+\gamma$ (<1) increases, the positive output price elasticity of demand for labor increases.

On substituting the profit maximizing long-run input demand functions for L, K, and X from eqns [11]–[13] and rearranging, we obtain the long-run supply function for Q

$$Q^* = S(P_Q, W_L, W_K, W_X, C_0, \tau) \qquad [18]$$

which relates the quantity of Q supplied on to the output price, the three input prices, the technology parameter, and C_0. When the production function is C–D, as in eqn [2], and the input demand functions are of the form of eqn [14], and $\pi_L^* > 0$, the C–D supply function is

$$Q^* = P_Q^{(\alpha+\beta+\gamma)/(1-\alpha-\beta-\gamma)}[A(\alpha/W_L)^{\alpha}(\beta/W_K)^{\beta}(\gamma/W_X)^{\gamma}]^{1/(1-\alpha-\beta-\gamma)} \qquad [19]$$

From eqn [19], the elasticity of supply of Q with respect to the wage rate is

$$\eta_{Q^* W_L} = -1/(1-\alpha-\beta-\gamma) < 0 \qquad [20]$$

and the elasticity of supply of Q with respect to its own price is

$$\eta_{Q^* P_Q} = (\alpha+\beta+\gamma)/(1-\alpha-\beta-\gamma) > 0 \qquad [21]$$

It is important to note that the own-price elasticity of supply of Q changes at each point along the supply curve, holding the prices of the inputs, the technology parameter, and C_0 constant. However, an increase in the wage rate (rental on capital, or price of materials) causes the supply curve for Q to shift to the left, or reduces the optimal amount of output to supply.

In eqn [1], there is a technology parameter τ. We have proceeded under the assumption that whatever this technology is, it is fixed or unchanging. We now want to release this assumption because this permits a generalization of the production framework that we have developed above. It can also be interpreted as changing the effective number of units that we bring to the production process, or increasing the amount of available labor, capital, and materials. We focus on two general types of technical change: truly neutral and biased. To be truly neutral, when τ increases, it increases the marginal products of all three inputs by the same proportion or percentage (%). For example, for a given quantity of labor, capital, and materials, a 10% increase in the marginal products of all inputs will result in the possibility of producing 10% additional output at the same total cost, and the marginal cost of producing Q will decline by 10% and profit will rise by 10%. This seems highly beneficial for firm owners and input suppliers, but it would be misleading to believe that technical change is 'free:' to be sure, there are associated costs, privately or collectively (Huffman and Evenson, 2006).

To consider biased technical change, we shall limit our inputs to labor and capital, and then there are two types of bias: (1) labor saving (or capital using) and (2) capital saving (or labor using) at a given set of relative input prices producing an unchanged amount of output Q. Because much of the technical change in US agriculture can be viewed as labor saving (or capital using), we will consider this type further. Holding expenditures and input prices constant, we start at point a on iso-cost line C_0C_0', where the isoquant Q_{01} is tangent to it in Figure 8. After labor-saving technical change, we produce the same amount of output, but now the isoquant has rotated counterclockwise and becomes tangent to C_0C_0' at b, which is to the left of a. Hence, to produce the same amount of output and at the same resource costs in both situations, the optimal amount of capital to use increases from K_a to K_b, but the optimal amount of labor declines from L_a to L_b. This can only occur if, at the intersection of the two isoquants, the marginal product of labor has risen relative to the marginal product of capital. One might ask how this could occur. The new technology must increase the marginal product of labor relative to the marginal product of capital for all input combinations, that is, make labor more productive. Regarding input demand at given input and output prices, this labor-saving technical change will increase the demand for capital and reduce the demand for labor. Moreover, this type of change is necessary for economic growth, which simultaneously requires food production to increase so as to release labor so that it can migrate out of agriculture and obtain nonfarm employment. Although some of these adjustments will be taken up in the next section, Huffman and Orazem (2007) have a more extensive discussion of the structural adjustments that must accompany modern economic growth and development.

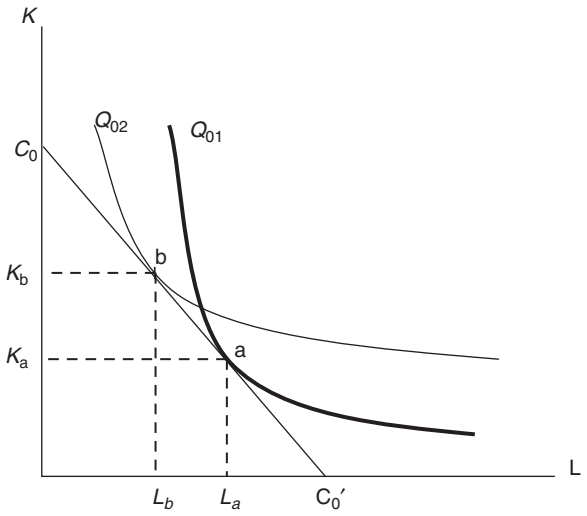


Figure 8 Labor saving (or capital using technical change). *C*, cost.

This section provides the theoretical and empirical foundations of labor demand. It shows that the demand for labor depends on input prices, technology, and the price of the output produced. A change in any one of these factors will change the quantity of labor demanded. When the price of durable goods declines, as when new equipment becomes available to farmers, this may cause labor-saving technical change as well as a substitution away from labor toward machine services. Cheap immigrant farm labor has kept wage rates low for fresh fruit and vegetable harvesting, and this has caused the quantity of labor demanded to be larger than it might otherwise have been. However, progress has been made

in developing mechanical harvesters for agricultural products that undergo further and generally off-farm processing. The invention of pesticides has also been labor saving and materials input using. Farm size has been somewhat conditioned by the amount of work that 1.5 full-time equivalent person years can undertake, but with a long sequence of labor-saving technical changes, farm size has increased dramatically in terms of the volume of output(s) that can be produced, whereas keeping the amount of farm labor used relatively unchanged. Finally, the theoretical framework provides a basis for econometric models that can be used to estimate coefficients needed to derive own-price and cross-price elasticity of demand for labor in agriculture. These topics are taken up in the following sections.

Mechanization of US Agriculture in the Nineteenth and Twentieth Centuries

The abundance of free land ended in the US at about 1890, at which time the application of science to the development of new agricultural technologies started (Huffman and Evenson, 1993). In particular, the Hatch Act of 1887 was passed to endow each state with support for establishing and maintaining state agricultural experiments at land grant universities. Rapid growth in the US population ended in 1920 with the imposition of a new immigration policy that imposed strict quotas by national origin.

Farm mechanization in the US took the form of substituting tractors for human and animal power. Olmstead and Rhode (2008) call the period 1840–1910 the 'great period' of US farm mechanization; certainly, this is the first great mechanization period. The adoption of new farm technologies was closely tied to the adoption of horses and mules, as opposed to oxen or human labor for power on US farms. They suggest that a common definition of farm mechanization is the adoption of a machine that allows farmers to substitute animal (horse)power for human labor, thereby enabling a farm worker to cultivate more area (or harvest more grain, cotton, or hay) per day or week. They report that in a sample of 628 Illinois farmers in 1860, mechanical reaper owners possessed 5.9 horses and mules and 0.43 working oxen – twice the ratio of equine to bovines found in the sample area of Illinois in the general population of farmers. The new reapers were associated with the use of a faster draft mode and complementary biological advances (improved crop varieties). They also document that from 1850–1910, farm acres per worker increased as horsepower per worker increased.

The invention and improvement of gasoline farm tractors was central to long-term mechanization. The early farm tractors were behemoths, patterned after the giant steam tractors that proceeded them – some weighing 10 ton but yielding relatively little drawbar or towing horsepower (10–30). They were, however, somewhat more efficient in developing belt-power or stationary power. These tractors were used for plowing, harrowing, and belt work but not for cultivating fields of row crops or for powering farm equipment in tow. Innovative advances between 1910 and 1940 dramatically reduced the size and weight of these tractors and increased their versatility, so that they were now useful for a much wider range of farm tasks. Importantly, these new tractors weighed less than 1 ton.

Olmstead and Rhode (2008) report that The Bull (first available in 1913) was the first small and agile tractor, Henry Ford's popular Fordson (first available in 1917) was the first mass-produced entry, and the McCormick-Deering Farmall (first available in 1924) was the first general-purpose tractor capable of cultivating row crops, such as corn and cotton. The Farmall was the first gasoline-powered tractor to incorporate a power takeoff, which enabled it to transfer power directly to implements under tow. Allied innovations such as improved air and oil filters, stronger implements, pneumonic rubber tires rather than steel wheels, and the Ferguson hydraulic three-point hitch system greatly increased the tractors' lifespan and reduced the work of farmers and animal power. The reduction in weight and increase in versatility of tractors was primarily a consequence of the change from steel wheels to rubber tires, and this also extended machine life because of reduced vibrations, increased the usefulness of tractors for hauling wagon loads of materials on roads and increased drawbar pulling efficiency by a large magnitude. Farmers could also move much faster and more easily travel to widely dispersed fields for field work.

In 1910 there were negligible number of tractors on US farms and approximately 23 million draft animals. Because tractors were making slow progress to the late 1910s and the number of draft animals on farms was somewhat increasing, draft animals were growing in number relative to tractors until about 1917. After that, the number of farm tractors on farms steadily and measurably increased, and as this occurred, the number of draft animals declined. By c. 1943 there were equal numbers of draft animals and tractors on US farms, approximately 13 million, but the trends accelerated after the end of World War II, when new farm machinery became readily available again. By 1960, the source of power on US farms had totally reversed – largely tractors and only a few draft animals (Olmstead and Rhode, 2008, p. 374).

With the advance of tractors came inventions and innovation in mechanical combines and corn and cotton pickers. These were immensely labor-saving technologies. When harvesting of corn was by hand, as it was in the US Midwest to the late 1940s, a good husker could pick only approximately 100 bushels per day. Horse-drawn corn huskers and pickers first became available in the 1920s, but they were not very effective, especially in wet field conditions. Power driven mechanical corn pickers (of the corn ear) were not possible until tractors were developed with live power takeoffs (Bogue, 1983). Moreover, low pressure pneumatic rubber tires on farm tractors increased field speed, reduced fuel use, reduced soil compaction, and even allowed machines to be driven on hard surfaced roads. Invention of hydraulic lifts to raise and lower heavy two-row mounted corn pickers also was a major saver of human effort (Colbert, 2000).

By 1940, there were approximately 100 000 mechanical corn pickers operating in the US, with approximately 20% in Iowa, where approximately 50% of the corn was mechanically harvested. By 1948, US farmers owned approximately 300 000 mechanical corn pickers, with one-quarter of them in Iowa. By 1952, Iowa farmers owned approximately 110 000 mechanical corn pickers, and over 95% of their corn was harvested

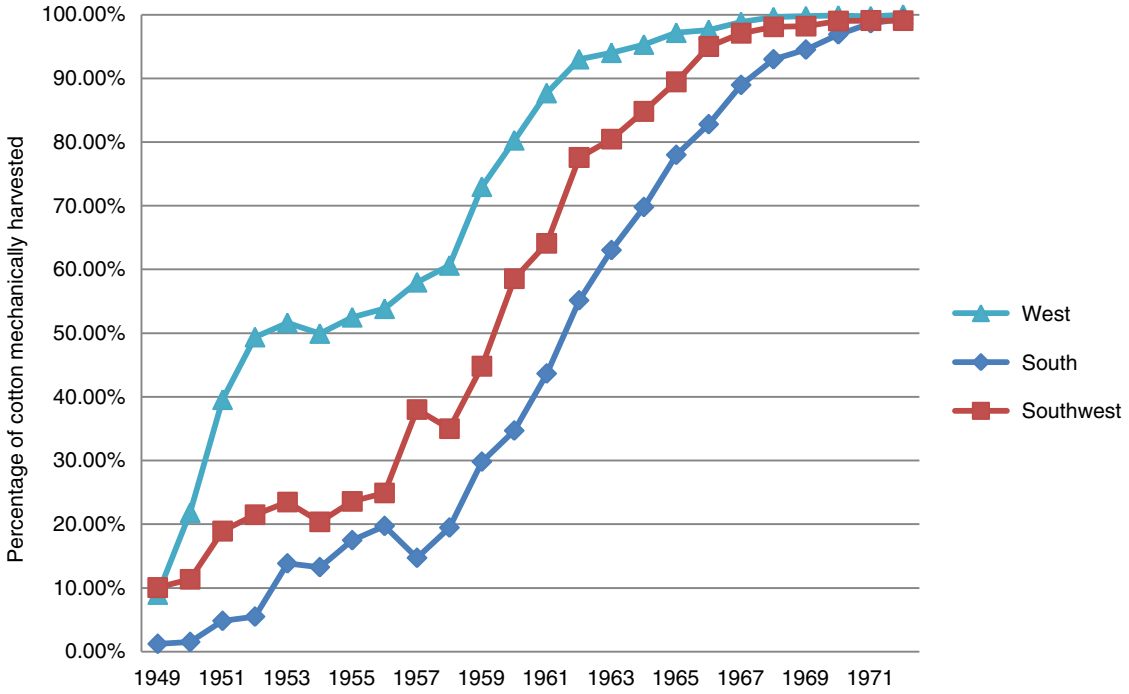


Figure 9 Percentage of cotton mechanically harvested by region, South, Southwest, and West, 1949–72. South includes Alabama, Arkansas, Georgia, Louisiana, Mississippi, Missouri, North Carolina, South Carolina, and Tennessee. Southwest includes Oklahoma and Texas. West includes Arizona, California, and New Mexico. US Department of Agriculture, Statistics on Cotton and Related Data, 1920–1972 (1974).

mechanically by that date (Colbert, 2000). Although the adoption of tractor-drawn or tractor-mounted corn pickers occurred over roughly 1940–60, many technical advances and improvements have occurred in mechanical corn pickers and combines since then. Today, almost all corn is harvested with a field combine that separates the corn kernels from the stalk, husks, and chaff. However, with a two-row mechanical corn picker of the early 1950s, a Midwestern farmer could harvest over 100 bushels of corn per hour.

Even larger changes came with the shift from hand to mechanical harvested cotton in the US South, which occurred starting in 1949 and largely ending by 1970 (Street, 1957; Meier, 1969; Heinicke and Grove, 2005). Two different technologies for cotton production had evolved in the US: (1) labor intensive Southern plantation production with its origins in black slavery; and (2) Southwestern irrigated desert production using day-haul labor, linked to migrants such as the braceros, which were Mexican contract labor employed under the Mexican Farm Labor Program of 1942–64. Because irrigated cotton faced many fewer weed problems, a permanent supply of labor was not needed on cotton farms in the West, but was needed in the South. When slavery ended in the South in 1865, many slaves became small tenant sharecroppers and continued to produce and harvest cotton until the harvesting of cotton was mechanized. Cotton production in the Southern Plains States of Texas and Oklahoma faced conditions somewhat intermediate between the South and West.

Given many factors, including differences in the supply of harvest labor, mechanical cotton harvesters were adopted more rapidly in the Southwest than in the South. For example, in the West, the percentage of cotton that was machine harvested increased from 10% to 50% in 4 years. In Texas and Oklahoma the increase was from 10% to 23% in the same time period. However, in the South, it took 7 years for mechanical harvesting to increase from 1% to 20%. More rapid adoption in the South did not occur until the 1957–64 period, when the percentage of machine harvested cotton rose from 10 to 65% (in the Southwest the increase was from 35% to 85%). Over this same time period in the West, the percentage of machine harvested cotton rose from 60% to 96% (Heinicke and Grove, 2005; see **Figure 9**).

In the production of processed tomatoes in California, all were hand harvested before 1965 – a hard, hot summer job. Research and invention to mechanize harvesting of processing tomatoes in California (CA) was spurred by the anticipated end of the Bracero Program in 1964. In the 1950s, 5.3 h of harvesting labor were required per ton of processed tomatoes. In 1950, Hanna from the department of Vegetable Crops, and Lorenzen, from the department of Agricultural Engineering, both at University of California-Davis (UC Davis), started to develop a system for mechanically harvesting processing tomatoes. Hanna started breeding a tomato that could withstand the stress of mechanical handling, would ripen uniformly and would detach from the plant during machine harvesting. Lorenzen worked on a machine that cut the plant at soil level and lifted it to a shaking mechanism. In the late 1950s, another UC Davis agricultural engineer developed a fruit-vine separator for Lorenzen's machine. By 1960, the University of California had obtained a patent for the new

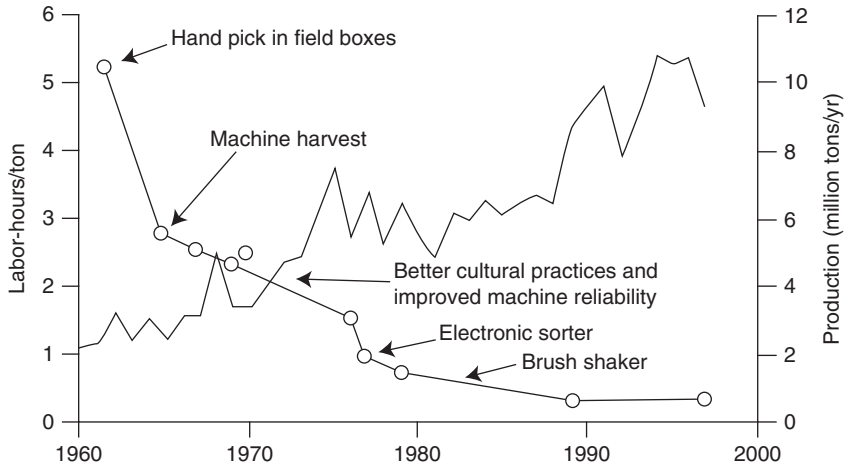


Figure 10 Typical harvest labor use and annual production of processing tomatoes: California, 1960–97. Reproduced from Thompson, J.F., Blank, S.C., 2000. Harvest mechanization helps agriculture remain competitive. California Agriculture 54 (3), 51–55.

tomato variety, and the Blackwelder Manufacturing Company undertook manufacturing and selling the first mechanical tomato harvesters.

This early mechanical tomato harvester cut the tomato plants at soil level and lifted them up into a shaking mechanism or separator that separated the fruit from the vines. Twelve workers rode on the early machines to sort the fruit, remove green or blemished tomatoes and clods of dirt, requiring 2.9 h of harvesting labor per ton of fruit, or a 60% reduction from hand harvesting. The tomatoes were conveyed directly into pallet bins that were transported on a trailer pulled beside the harvester (Thompson and Blank, 2000).

In 1964, 75 harvesters were sold in California, and in 1965, 250 were sold, yielding a combined capacity to harvest roughly 25% of the tomato crop. By 1969, 95% of the CA processing tomato crop was harvested by machine, at major social gain (Schmitz and Seckler, 1970). In the mid-1970s, a further major technical advance occurred with the invention of high-speed electronic color sorters, which identified and used blasts of air to separate ripe fruit from green and rotten fruit and clumps of dirt. With improved leveling and ridging of tomato fields, new tomato varieties and a new brush shaker innovation, labor requirements were reduced from 12 to 2–4 hand sorters per machine or to 0.4 h per ton (**Figure 10**). See **Figure 11** for a working Johnson mechanical tomato harvester. Over 35 years, this dominant CA technology has reduced labor requirements per ton of CA processing tomatoes by 92%, but this was not without major migrant farm labor issues (Schmitz and Seckler, 1970).

Current models of the Johnson self-propelled tomato harvester sold by the CA Tomato Machinery Company are equipped with two, 32-channel high-speed color and dirt sorters, use 2–4 hand sorters, and cost roughly US$450 000 (in 2010 dollars), with a life of 15–20 years under intensive postharvest maintenance. They have a maximum capacity of 70 ton h^{-1} and are regularly operated in two, 10 h shifts. Total harvesting costs are approximately US$28 per ton in 2010 prices. Under this new technology for California processing tomatoes, yield per acre and total production have increased



Figure 11 Self-propelled Johnson Mechanical Tomato Harvester (ca. 2010). Courtesy of California Tomato Machinery.

from 3 million tons (69% of total US tonnage) in 1965 to approximately 12 million tons in 2010 (96% of total US tonnage). (In the 1960s, US production of processed tomatoes was divided among three areas: California, the Eastern states of New Jersey, Delaware, Maryland, Pennsylvania, Virginia and New York; and the Midwestern states of Indiana, Illinois, Ohio and Minnesota. Now only 4% of production is outside of California.)

Substitution of Biological Advances and Chemicals for Farm Labor and Other Agricultural Materials

Field crop improvement has been the result of organized public research and innovative genetic improvement by private seedsmen and seed companies, and farmers' improvements in cultural and management practices. One of the great success stories of US agricultural research and development is the contribution of enhanced genetic potential to grain yields in major field crops. The rapid gains for corn started in 1930, for soybeans in 1940, and for wheat after 1954. The research work that underlies these genetic advances was largely undertaken in the public sector during the first half of the twentieth century. The scientific discovery of hybrid corn varieties for the

Corn Belt was the result of cooperative research undertaken between agricultural experiment stations and the USDA. Reproduction and sale of these early hybrids, which became available to farmers in the late 1920s (Griliches, 1960), were left to the private sector. For example, Pioneer raised its first commercial hybrid seed corn in 1925 and sold its first in 1926.

After the initial round of hybrid corn adoption, the same principles were applied to develop a sequence of new hybrids, with each new generation of hybrids producing some superior characteristics and replacing existing lines. Moreover, in the 1960s, corn breeders moved to single-cross hybrids to obtain higher yielding corn varieties. Over 1925–75, private seed corn companies used mostly public sector (state agricultural experiment stations of the Midwest and USDA) developed inbred lines in their double-cross corn varieties sold commercially. This, however, began to change c. 1970, and by 1984, the private sector was largely developing its own inbred lines used in commercially successful hybrid corn varieties for Midwestern farmers (Huffman and Evenson, 1993, pp. 155–162).

Soybeans became an important oilseed and meal source in the 1950s. Although early genetic improvement came from genes of imported varieties, a successful public soybean improvement program emerged in the US by the late 1960s (Huffman and Evenson, 1993, pp. 162–167). In these early years, farmers purchased seed beans from other farmers or from private seed companies and planted them. They frequently saved their own seed and planted it, but as genetic resistance to pests eroded, farmers sought out new bean seed. The USDA and later the state agricultural experiment stations were involved in the early development of soybean varieties that were adapted to the Midwest.

The soybean is self-pollinated and extremely photoperiod sensitive. In self-pollinated crops, it is difficult to create hybrids and easy for farmers to save and plant their own seed, and photoperiod sensitivity means that each soybean variety will perform well in only a small geo-climatic area.

In the 1960s and 1970s, farmers were using crop rotation, mechanical cultivation, and hand weeding to control weeds, which can dwarf soybeans.

Starting in the mid-1960s private sector soybean breeding emerged, and the relative importance of private sector developed soybean varieties grew after the passage of the 1970 Plant Variety Protection Act, and the 1985 *ex parte* Hibberd court decision. With this act, the private sector had stronger property rights to their new varieties (Huffman and Evenson, 1993, pp. 162–167). By 1990, the private sector had become the dominant source of new soybean varieties for Midwestern farmers.

Early successful wheat varieties were imports, largely from Europe. By 1949, public sector research activity had become a source of successful wheat varieties for farmers in the Great Plains and Midwest. Wheat is also a self-pollinated crop, and farmers can successfully save part of their harvest for next years' seed. Historically, yield improvement has been slow (Huffman, 2009). Hence, even with the 1970 Plant Variety Protection Act, the private sector did not find wheat varietal development to be a long-term profitable activity. This left new varietal development largely to the public sector. For the Corn Belt States, soft red winter varieties are most frequently planted by farmers, and for Minnesota, hard red spring and durum wheat varieties are most frequently planted (Huffman and Evenson, 1993, pp. 167–177).

Private sector development and the sale of commercial pesticides to farmers, starting in the 1940s and accelerating in the 1970s, provided a less labor and machinery intensive method for controlling plant pests. In 1999, US expenditures on insecticides were $3 billion or 33% of the world market. Forty-five percent of the insecticides applied were devoted to the agricultural sector. Although insecticides were initially hailed as a miraculous method to eliminate pest problems, the widespread use of any particular insecticide results in the development of tolerance by the target pests (Zilberman, 2004), high rates of insecticide application, and low effectiveness of these chemicals. In addition, high rates of application of insecticides have frequently caused environmental and human damage (Fernandez-Cornejo, 2008; NRC (National Research Council, Committee on the Impact of Biotechnology on Farm-Level Economics and Sustainability), 2010).

In the US, the use of herbicides or weedkillers in agriculture increased dramatically after the 1950s; herbicide use is now greater than the combined use of insecticides and fungicides. Plants exhibit varying levels of tolerance to herbicides. Some plants are highly sensitive and can be damaged or killed by very low doses of certain herbicides, whereas plants that have a high tolerance can be unaffected by herbicides that kill other plants. Hence, farmers have used private sector developed herbicides to selectively control weeds in field crops for more than 40 years.

The discovery of DNA in 1953 and a gene splicing technique in 1973 set the stage for genetic engineering of new field crop varieties for herbicide tolerance (HT) and insect resistance (IR) in the 1990s.

One major pest experienced by Midwestern farmers is the European corn borer, which damages stocks and makes the corn plant subject to lodging. *Bacillus thuringiensis* is a bacteria that occurs naturally in the soil. Several advantages exist for *B. thuringiensis* corn varieties. (*B. thuringiensis* produces spores that form the crystal protein insecticide δ-endotoxins. The protein toxin is active against species of the order Lepidoptera, Diptera, Coleoptera, Hymenoptra, and nematodes. When these insects ingest toxin laden crystals, chemicals in their digestive track activate the toxin. It inserts into the insect's gut cell-membrane, and dissolves, and eventually causes death of the insect.) First, the level of toxin expressed can be very high, thus delivering a lethal dosage to target insects. Second, the corn plant produces the toxin throughout its life and the toxin is expressed relatively uniformly throughout all plant parts. Hence, *B. thuringiensis* provides season-long protection against target insects, but has no significant effect on other insects. Third, the toxin expression can be modulated by using tissue-specific promoters, and fourth, GM resistance replaces the use of synthetic pesticides in an attempt to kill target insects. Fourth, the *B. thuringiensis* toxin expressed in the corn plants is not toxic to humans or animals. Although the early *B. thuringiensis* corn varieties were resistant to the European corn borer, they were also somewhat protective against the corn earworm, the southwestern corn borer, and to a lesser extent, the cornstalk borer (Fernandez-Cornejo and McBride, 2002). Later, *B. thuringiensis*-corn varieties also carried resistance to

corn rootworms, which are a pest that reduces and weakens the root structure of corn plants. New evidence shows that farmers planting nonGM corn hybrids are major beneficiaries from other farmers planting *B. thuringiensis*-corn hybrids because area-wide moth counts have been steadily declining as the *B. thuringiensis*-corn adoption rate in an area increases (Hutchinson *et al.*, 2010). However, some evidence of resistance to GM rootworm control is surfacing (NRC (National Research Council, Committee on the Impact of Biotechnology on Farm-Level Economics and Sustainability), 2010).

Some farm crops have also been engineered for HT. For example, one crop variety is resistant to a particular commercial herbicide – largely Monsanto's Roundup, which contains the active ingredient glyphosate. HT has been introduced into US commercial soybean, corn, cotton, and canola varieties. With Roundup Ready soybean varieties, farmers plant the HT variety and roughly one month after emergence of the crop and accompanying weeds they apply Roundup, which kills all of the plants in the field except for the Roundup Ready Soybean plants. This then leaves the treated soybean fields largely free of weeds. Moreover, the effectiveness of applying the herbicide Roundup to Roundup Ready soybean plants is not sensitive to modest deviations in the application date, which is a major advantage to farmers that have off-farm jobs, other competing uses for their time, or who face uncertain (rainy) weather conditions. However, localized problems with weed tolerance to glyphosate have occurred (Fernandez-Cornejo, 2008; NRC (National Research Council, Committee on the Impact of Biotechnology on Farm-Level Economics and Sustainability), 2010).

Although there have been periodic claims that GM wheat varieties will soon be available to US farmers, this has not occurred. GM wheat varieties with HT have been tested, and GM resistance to the fungus Fusarium, which degrades grain quality, could also benefit growers (Wilson *et al.*, 2003). However, a large share of US wheat is exported, and the current opposition of Europe, Japan, Korea, and some other Asian countries to GM products continues. With this political resistance, general US introduction of GM wheat could significantly reduce export demand for US wheat (Taylor *et al.*, 2003). Although a two-tiered handing, storage, and marketing system where GM and nonGM wheat are separated might be acceptable to importers of US wheat, this system would be costly to operate, and there remains major concern about adventitious comingling of GM and nonGM wheat crops (Wilson *et al.*, 2003). Hence, the successful development of a GM wheat market is still in progress. One broad implication is that low investment in general genetic improvement of wheat and a lack of GM wheat varieties tolerant to herbicides have undoubtedly been a factor behind wheat losing its competitiveness with corn and soybeans in Midwestern states.

A recent National Research Council (NRC) report (NRC (National Research Council, Committee on the Impact of Biotechnology on Farm-Level Economics and Sustainability), 2010) summarizes the generally favorable environmental effects of these GM crop varieties. However, when US farmers purchase GM soybeans, they must sign an agreement with the seed company waving their right to save GM seed for their own use or for sale. Ht corn has many of the same advantages, although corn is naturally more weed resistant than soybeans. The herbicide Atrazine can be used on nonGM corn to control broadleaf weeds. However, Atrazine use has contaminated ground water in the Midwest, and consumption of this polluted water is alleged to be associated with birth defects, some forms of cancer and other health problems that the Environmental Protection Agency is continuing to review.

In 1995, no significant acreage of US crops was planted to biotech crop varieties, and in 1996, the rate of adoption was low, being higher for *B. thuringiensis* cotton and Ht soybeans than for Ht corn and cotton or *B. thuringiensis* corn (**Figure 12**). *Bacillus thuringiensis* cotton has been adopted in some areas of the South, but not in other areas where insect problems, including tolerance to chemical insecticides, were less severe. The HT cotton adoption rate surpassed *B. thuringiensis* cotton adoption by 1998, reflecting the fact that weeds are a persistent problem in cotton relative to insect pests, and Ht cotton has experienced higher adoption rates than *B. thuringiensis* cotton through 2010.

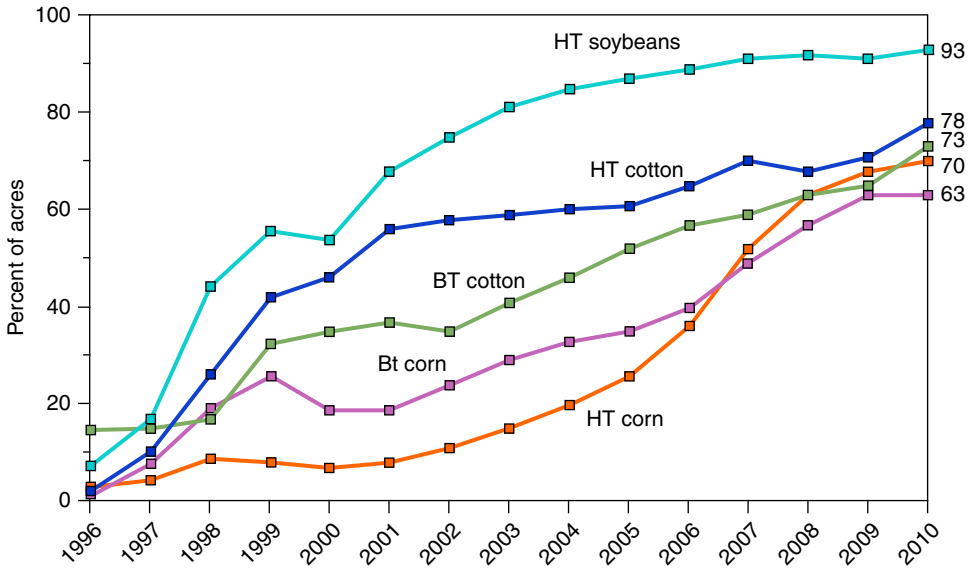
In sum, these new biological controls of crop pests provide important and effective substitutes for farm labor, machinery, and insecticides.

More on Mechanization of Fruit and Vegetable Harvesting

Although the most storied success in mechanical fruit and vegetable harvesters is the self-propelled tomato harvester in California, mechanical harvesters are being used by growers to harvest tomatoes in the Eastern Corn Belt, and other fruits and vegetables for processing in California, Florida, Arizona, the Upper Midwest, and New England. In the Midwest and Eastern processed tomatoes, the Pik Rite Company is a leader for inventing and manufacturing tractor-drawn harvesters for small-scale fruit and vegetable harvesting. Pik Rite's first mechanical tomato harvester was built in 1983, and sales began in 1986 after 3 years of improving and testing.

The Model 190 is a low capacity, 30–40 ton h^{-1}, harvesting machine with a lateral rotating single-brush-shaker system (**Figure 13**). (The model HC 290 is a high capacity, 70–80 ton h^{-1}, harvesting machine with a dual lateral brush-shaker system.) This machine has high-speed optical color sorters with blasts of air that aid separating ripe tomatoes, unripe tomatoes, and chunks of dirt. The cost of this machine is US$150 000–US$160 000 in 2010 prices, and has a work life of 12–15 years, but harvesting costs in the Midwest are substantially higher than in California, roughly US$48 per ton (in 2010 prices). The Pik Rite tomato harvester is in use in Indiana, Michigan, Ohio, and Pennsylvania.

In Midwest- and Eastern-grown cucumber, carrot, and pepper production, Pik Rite also develops and markets tractor-drawn mechanical harvesters for processing cucumbers, carrots, and peppers. The cucumber harvester has a special dirt removal system that uses blasts of air along with a 'scrubber' belt to remove trash (see **Figure 14**). It also has nonpinch conveyor chains, spaced so that small- and medium-sized cucumbers are saved and elevated to a storage bin, but oversized fruit exit with the vines into the field for better harvesting efficiency. This separation process is aided by blasts of air



Data for each crop category include varieties with both HT and Bt (stacked) traits.
Sources: 1996–1999 data are from Fernandez–Cornejo and McBride (2002). Data for 2000–10 are available in the ERS data product, Adoption of genetically engineered crops in the U.S., tables 1–3

Figure 12 Rapid growth in adoption of genetically engineered crops continues in the US.



Figure 13 Pik Rite 190 Tractor-drawn mechanical tomato harvester (ca. 2010). Courtesy of Pikrite.



Figure 14 Pik Rite Tractor-drawn mechanical cucumber harvester (ca. 2010). Courtesy of Pikrite.

blowing the vines, and chaff upward and out of the rear of the machine. This machine can unload 125 bushels in 20 s.

In Florida orange and orange juice production, historically the trees were hand-picked by workers on ladders with a bag, and when the bags were filled, the worker transferred the fruit to a large metal box on the ground. Several companies, for example, Coe-Collier, OXBO, and Korvan, manufacture and sell tree fruit harvesters to Florida orange growers. These machines are basically of two types. One type is a shake-and-catch system consisting of a two-part self-propelled unit, with the main power unit grasping the trunk of the tree. The second part of the harvester moves along the opposite side of the tree with a system to collect, store, and convey the fruit into a truck to be transported to a semitrailer at the edge of the grove. The two units lock together around the trunk (or limb), and both have a slopping to the middle catchment rail system, for example, see the Coe-Collier trunk shaker and receiver in Figure 15.

The power unit shakes the trunk (or limb) of the tree, and this hopefully dislodges the fruit so that it falls on the catchment rails, rolls to the middle, and is conveyed into a truck. The stems of citrus fruit are tightly attached to the tree limbs, and this type of citrus harvesting machine shakes the trunk vigorously to generate enough force to dislodge fruit. The severity of this shaking can seriously damage the bark on the orange trees, and orange growers in Florida are not currently using the shake-and-catch harvester. However, a very similar harvester is used for California processing plums, where the ripe fruit detach more easily.



Figure 15 Coe-Collier self-propelled trunk shaker and receiver for mechanical harvesting Florida processing oranges (ca. 2010). Reproduced from Futch, S.H., Roka, F.M., 2004. Trunk shaker mechanical harvesting system. Citrus Industry 85 (7), 20–21, with permission from University of Florida, IFAS Extension.

The second type of mechanical harvester for processing oranges is the bat-shaker system. With this system, a tractor-drawn machine containing rotating bats is pulled alongside a row of trees containing ripe fruit. The rotating bats then dislodge the fruit, and they fall to the ground. The fruit is then picked up by hand labor or rakes, and windrow machines gather and collect them. OXBO also makes a tree canopy-shaker with a catching table. Only the self-propelled shake-and-catch system is being used by Florida orange growers (Calvin and Martin, 2010).

Because oranges remain firmly attached to the tree, even when ripe, they are difficult to dislodge. This has hindered the development of mechanical harvesters. The University of Florida (U FL) has experimented with fruit-loosening agents, such as abscission. When applied, this chemical loosens the stems so the ripe fruit is more easily dislodged, which reduces damage from mechanical harvesting. However, mechanical harvesting of Valencia oranges poses an additional problem in that there are two seasons of fruit at harvest time: (1) mature fruit ready for harvest, and (2) young crop of oranges intended for the next year's harvest. A successful abscission chemical is applied to selectively loosen the mature fruit, leaving the young crop unaffected. Overall, because of potential tree damage, tightly clinging fruit, and two-crops on one tree at the same time, mechanical harvesting of FL oranges for processing has a low adoption rate (6–12%) (Roka, personal communication, 2010).

Mechanical harvesters have also replaced hand harvesters in the production of tart cherries in Michigan. These machines are of a shake-and-catch type, similar to the Coe-Collier FL orange harvesting machine though much lighter (see Figure 16). This machine is a two-part self-propelled unit where the catching table continuously moves harvested fruit to bins. Ripe tart cherries bruise some in this harvesting system, but because the cherries are going immediately for processing, the damage has not been viewed as significant. A large share of Michigan sour cherries are now harvested using this technology.



Figure 16 Self-propelled mechanical sour cherry harvester: shake, catch, and convey method (ca. 2010).



Figure 17 Korvan Co. self-propelled mechanical (wine) grape harvester (ca. 2010). Courtesy of Oxbo.

At one time, all California wine grapes were hand harvested, but growing international competition in the wine market has induced major cost savings, except in high-end wines. Currently, a large share of CA wine grapes is mechanically harvested. These machines are relatively tall, self-propelled units that straddle the trellised grapevine rows. The harvester has rotating arms that dislodge the fruit, which is then caught on a table and conveyed into a wagon. See the Korvan machine (Figure 17).

All strawberries continue to be hand harvested because, they are quite delicate and mainly harvested for the fresh market. Although other berries were traditionally hand harvested, the Korvan Company manufactures and sells a mechanical berry picker for processing berries (largely for raspberries and blueberries). This machine is self-propelled and surrounds the row of berry bushes similar to the wine grape harvester (Figure 18). This machine does some damage to the fruit, but because it is going immediately for processing, this is not generally viewed a serious problem.

A little experimentation has been done with robotic harvesters that use GPS to scout fruit locations and then pick the fruit. However, electronic assessment of tree fruit is



Figure 18 Korvan Co. self-propelled mechanical bush-berry picker: raspberries, blackberries, and blueberries (ca. 2010). Courtesy of Oxbo.



Figure 19 Self-propelled straight-through mechanical potato harvester (ca. 2010). (http://www.potatoharvesterusa.com/html/straight_thru_harvester.html; www.advancedFarmEquipment@Lenco-harvesters.com).



Figure 20 Washington State University and the USDA-ARS self-propelled mechanical fresh market apple (sweet cherry) harvester.

complicated by the fact that tree limbs and unripe fruit may block the view of the electronic 'eye' sensors.

As suggested above, advances in mechanical harvesting of fresh fruits and vegetables for the fresh market have progressed more slowly than for processed produce. However, the share of potatoes harvested for the fresh market has been and remains substantial, and the first mechanical harvesters were invented almost 100 years ago. Incremental innovations have transformed these machines into modern, self-propelled mechanical potato harvesters. Although simple mechanical potato diggers existed in the early 1900s, the first complete harvester-separator machines did not exist until the 1950s. Today, large-scale harvesting is done by a self-propelled machine that scoops up the potato plant and the soil beneath it. This material is elevated by a rotating apron-chain consisting of steel links several feet wide, which allows loose dirt to fall away, while retaining ripe potatoes. The chain deposits this mixture into an area where further separation occurs. Potatoes are then continuously elevated into a trailing wagon or truck. The most complex designs use vine choppers and shakers, electronic sorters and a blower system to separate good potatoes from rotten potatoes, stones, dirt, and vines (Figure 19). These are used for harvesting potatoes for the fresh and processing markets.

Other mechanical harvesters for fresh fruits and vegetables are largely experimental. Fresh market CA iceberg and organic lettuce, melons, strawberries, and tomatoes have substantial harvesting costs, and harvester-aids have reduced the workload. For example, the heads of iceberg lettuce are cut by hand and trimmed, then laid on a table that coveys them to the center, where workers on the field wrap them in plastic and place 32-heads per box, which are then stacked on the wagon. This process has significantly reduced the cost of harvesting and packing iceberg lettuce. A similar process is applied to melons and cantaloupes, with the slight distinction that they are packed directly into boxes without plastic wrap. Although the hand-harvesting cost of fresh market CA strawberries is very high, approximately US$615 per ton (in 2010 prices), this high-value delicate crop, which grows close to the ground and does not ripen uniformly, is currently impossible to mechanically harvest.

Washington State University and the US Department of Agriculture's Agricultural Research Service (USDA-ARS) scientists have developed a mechanical harvester for fresh market sweet cherries and apples (Peterson, 2005). A chemical fruit-loosening agent (abscission) is first applied to the trees a few days before harvesting. The mechanical harvester is a two-part, self-propelled machine, with each part going on opposite sides of the trees. Cushioned catcher pans on each unit are used to seal around the trunk and connect the two units. The harvester has a high density rubber arm on each unit that bumps the tree branches, and this energy dislodges the ripe fruit (see Figure 20). Both harvesting units have inclined catchment tables, but the mechanical conveyors are covered with a soft,



Figure 21 BEI International, Black Ice self-propelled harvester for delicate berries using air jests and padded walls and catchment areas (ca. 2010). Courtesy of BEI International.

spongy material that reduces impact, and the padded conveyers move the fruit gently to the outer top side of each of the machine catching tables. As the fruit rolls over the table, a fan blows away leaves and trash, and the fruit passes to two slowly rotating modest sized storage bins or boxes.

A benefit to growers and consumers is that mechanically harvested cherries have less bruising or damage than hand-harvested fruit and reduced exposure to bacteria-laden human hands. However, sweet cherry consumers are accustomed to their cherries having stems, but the mechanical harvested cherries are stemless. For mechanically harvested sweet cherries and apples, a special tree architecture is needed – short with a 'Y' shape, as opposed to the 20–25 feet tall conventional trees (see **Figure 20**). The mechanical sweet cherry harvester has excellent long-term potential for harvesting high-quality sweet cherries for the fresh market, at an 80–90% reduction in harvest labor costs, with less damage than hand-harvested cherries (Whiting, 2006).

The new BEI Black Ice Harvester works with delicate bush berries – raspberries, blackberries, and blueberries. The Black Ice Harvester uses jets of air to create a turbulent local environment within the machine and around the berries, which then gently dislodge those that are ripe. Between padded walls, the berries fall onto a bed or table (the Centipede Scale catching frame), and then are gently conveyed to one pound or smaller containers that are carried on the machine (**Figure 21**). A major advantage of this machine is that berries and bushes are not touched by a picking or rotating-arm mechanism. This helps minimize damage to ripe berries and scarring of the bushes. Given the minimal plant damage from the harvester, the machine can be used to make multiple passes over the same bushes as the berries ripen at different dates. With this machine, quality meets or exceeds that of hand-harvested fruit, and because no human handling of the fruit is required in the harvesting and packing, there are reduced food safety concerns. The machine is currently being farm tested, and its estimated cost is US$150 000 (in 2010 prices) for the smaller rear-loading model and US$200 000 for a larger top-loading model.

Structure of Farms

The structure of US farming has changed steadily over time, particularly after the available free land from the Homestead Act ended in the 1890s. Advances in size have been primarily driven by long-term mechanization, later automation, and long-term rising real wage rates in nonfarm sector (Huffman, 1996). Other factors include the use of improved of crops and livestock, which have dramatically raised the productivity of land and labor.

Aggregate US farm output was 5.5 times larger in 1990 than in 1890, but the number of farms has declined from 4.5 million (after peaking at 6.4 million in 1910) to 1.9 million in 1990. Currently, there are approximately 1 million farms in the US. With the number of farms declining and aggregate farm output growing rapidly, average output per farm (in constant output prices), one plausible measure of farm size, grew rapidly. Using this measure, average farm size was 1.6 times larger in 1940 than in 1890, but was 8.8 times larger in 1990 than in 1940 (or 14 times larger than in 1890). Since 1960 US farms have become more specialized in their products, and the average number of products per farm has declined everywhere except perhaps in California, where there is an incredible array of crops produced – roughly 250 currently. Somewhat surprising is the fact that USDA data show that aggregate real inputs under the control of US farmers have hardly changed since 1900, but real output has been growing exponentially at 1.6% yearly. This is only possible when there are large increases in multifactor productivity (Huffman and Evenson, 2006).

Long-term trends in labor, land, buildings, farm machinery, and farm chemicals are less well-known (see **Figure 22** and data for 1910–95). These data show a sizeable decrease in the demand for farm labor, especially after 1950, and the changes are generally parallel to the reduction in the number of farms. At the same time, machinery and chemical (fertilizers and pesticides) input use increased, whereas land and buildings inputs remain largely unchanged over time. Thus, land and buildings inputs per farm have risen at approximately the same annual rate that farm numbers have declined. The positive trend in machinery input shows a major reversal in 1980, and declined through 1994 (see Huffman and Evenson, 2001).

Estimates of the Wage Elasticity of Demand for US Farm Labor

The economics of labor demand is more complex than its underlying simplistic theory, but it provides a conceptual framework on which empirical estimates of the wage elasticity of demand for labor can be obtained. Huffman and Evenson (1989) and Schuring *et al.* (2013) have extended this conceptual model to include multiple outputs (up to four) and multiple inputs (up to five). (These articles use a normalized quadratic profit function from which the multiple-output supply and

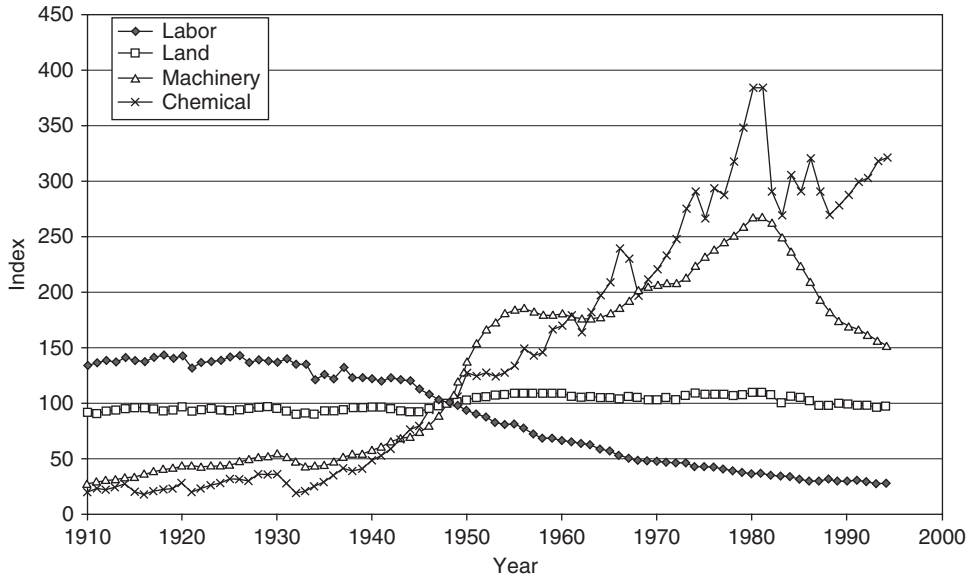


Figure 22 US aggregate usage of farm labor, land, machinery, and chemicals, 1910–94 (1948 = 100). Adapted from Huffman, W.E., Evenson, R., 1989. Supply and demand functions for multiproduct U.S. cash grain farms: Biases caused by research and other policies. American Journal of Agricultural Economics 71, 761–773.

Table 1 Output supply and input demand price elasticities: US cash grain farms, 42 states, data at 5-year intervals (1949–74)

Quantity	*Price elasticity with respect to normalized price of*						
	Fertilizer	*Fuel*	*Machinery*	*Labor*	*Wheat output*	*Soybean output*	*Feed grain output*
Inputs:							
Fertilizer	−1.203	0.237	0.334	0.278	−0.283	1.000	−0.364
Fuel	0.342	−0.717	0.690	−0.362	−0.370	0.370	0.278
Machinery	0.199	0.285	−0.606	0.464	−0.203	0.008	−0.147
Labor	0.130	−0.117	0.363	−0.508	−0.416	0.033	0.516
Outputs:							
Wheat	0.116	0.105	0.140	0.367	0.968	−1.051	−0.646
Soybeans	−0.852	−0.082	−0.011	−0.059	−2.178	1.313	1.871
Feed Grain	0.094	−0.050	0.064	−0.285	−0.404	0.565	0.016

Note: The elasticities in the last row and column are derived residually, others are estimates; all evaluated at the sample mean of the data.
Source: Reproduced from Huffman, W.E., Evenson, R., 1989. Supply and demand functions for multiproduct U.S. cash grain farms: Biases caused by research and other policies. American Journal of Agricultural Economics 71, 761–773.

input demand functions are derived. The C–D production function does not generalize to multiple-output technology in any meaningful way.) The first econometric study uses data on outputs, inputs, and prices of cash grain farms in 42 US states over 1949–74. Because the output and input quantity data were derived from the Census of Agriculture, observations are at 5-year intervals over this 25-year period.

Table 1 reports own-price elasticities of demand for inputs and supply for outputs by farms, which are evaluated at the sample mean of the data. They are the numbers on the diagonal in the table, for example, −1.203 in the first row and column represents the own-price elasticity of demand for fertilizer, or a 1% increase in its price causes a 1.2% decline in the quantity of fertilizer demanded by cash grain farmers over the sample period. Also, note that farm labor has the lowest own-price elasticity (i.e., smallest negative) of demand. The own-price elasticities of supply of outputs are positive, as expected, and large for soybean and wheat, but quite small for feed grains, which may be because of a restrictive government farm program on feed grain acreage during this era.

The off-diagonal elements are cross-price elasticities, for example, 0.237 at the top of the second column represents the 0.24% change in the quantity demanded of fertilizer, because of a 1% change in the price of fuel. The own-price elasticity of demand for farm labor is shown to be −0.51, or a 1% increase in the real wage reduces the demand for farm labor by 0.51%. A 1% increase in the price of machinery (fertilizer) increases the demand for labor by 0.36% (0.13%), but an increase in the price of fuel by 1% reduces the demand for fuel by 0.12%. These are largely as expected.

Table 2 Output supply and input demand elasticities: eight Midwestern states, annual data (1965–2004)[a]

Quantity	*Elasticity with respect to price of*								
	Soybean	*Corn*	*Wheat*	*Livestock*	*Farm capital*	*Farm labor*	*Farm energy*	*Farm chemical*	*Other farm materials*
Outputs:									
Soybean	0.110	−0.233	0.007	0.134	−0.093	−0.052	−0.008	0.078	0.056
Corn	−0.149	0.315	−0.052	0.208	−0.086	−0.041	−0.028	−0.110	−0.058
Wheat	0.055	−0.594	0.927	−0.706	0.047	0.274	−0.224	−0.277	0.040
Livestock	0.045	0.109	−0.032	−0.032	0.060	0.018	−0.002	−0.014	−0.152
Inputs:									
Farm capital[b]	0.073	0.106	−0.005	−0.140	−0.016	0.008	0.031	0.010	−0.067
Farm labor	0.022	0.028	−0.016	−0.023	0.004	−0.045	0.005	−0.009	0.035
Farm energy	0.028	0.152	0.108	0.022	0.137	0.038	−0.409	0.078	−0.154
Farm chemical	−0.122	0.269	0.059	0.067	0.021	−0.033	0.035	−0.667	0.370
Other materials	−0.019	0.030	0.002	0.153	−0.029	0.027	−0.015	0.080	−0.229

[a]The elasticities in the last row and column are derived residually, others are estimates; all evaluated at the sample mean.
[b]Farm machinery and breeding stock, but not farm land.
Source: Adapted from Schuring, J., Huffman, W.E., Fan, X., 2013. Aggregate Supply and Demand Functions for Midwestern U.S. Farms Under Rapid Technical Change. Ames, IA: Department of Economics, Iowa State University.

A change in the real wage also reduces the quantity of soybeans and feed grains supplied, but increases the quantity of wheat supplied, most likely because the latter is less labor intensive. Also, an increase in the real price of soybeans and feed grains increases the demand for farm labor, but an increase in the real price of wheat reduces the demand for farm labor. A number of other price elasticities may be of interest to some readers.

Schuring *et al.* (2013) use annual data on all farms of eight Midwestern states, 1965–2004, and in a similar study, **Table 2** reports estimates of the own- and cross-price elasticities of supply and demand, evaluated at the sample mean of the data. It shows that the own-price elasticity of demand for farm labor is −0.045, which is approximately one-tenth the size of the US cash-grain farm study. An increase in the wage for farm labor also reduces the demand for farm capital and chemicals, but increases the demand for farm capital (machinery and breeding stock) services, farm energy, and other materials. An increase in the real price of corn and soybeans increases the demand for farm labor, but an increase in the real price of wheat and livestock reduces it. A general interpretation of the other elasticities is similar.

These results show that one can obtain empirical estimates of the wage elasticity of demand for farm labor from aggregate data. However, the empirical results suggest that for cash grain farms and Midwestern farms, the wage elasticity of demand for labor is relatively small, or labor demand is wage inelastic. It is expected that the wage elasticity of demand for labor in the production of fruits and vegetables is somewhat larger because labor's cost share is much larger there than for wheat, feed grains, and Midwestern livestock.

Conclusions

With continued innovation in farm machinery, genetic improvement of crops and farm animals, and a return to rising real wage rates, we can safely predict that the quantity of labor used in US agriculture will continue to decline slowly and the number of farm workers will decline and farm size will continue to increase. Future mechanization of fruit and vegetable crops will be driven largely by benefit-cost considerations, including the likely future international competitiveness of the US industry. Relatively efficient machines exist for mechanically harvesting vegetables and fruits for the processing market. The most exciting finding is that there are new and effective harvesters that are in the final stages of testing for fresh market berries, apples, and sweet cherries. These technologies would move forward rapidly if there is a sudden increase in the cost of harvesting labor, or uncertainty of labor availability. Furthermore, these machines have potential for other crops. However, a short-term hurdle is that some crops are declining in planted acreage because of changing demand and international competition, and older tree and vine architectures are not compatible with newer harvesting systems. As it becomes more profitable for farmers to adopt this next generation of harvesting technology, orchards may increasingly be replaced with shorter and trellised trees and vines. Uniform ripening of fruit and berries is also critical to the success of these new harvesting systems (Huffman, 2012).

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See also: Agricultural Labor: Labor Market Operation. Agricultural Labor: Supply of Labor. Agricultural Mechanization. Biotechnology: Herbicide-Resistant Crops. Production Economics

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Agricultural Labor: Gender Issues

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Glossary

Encomienda Grants of land that included rights to the labor of all residents on that land.
GlobalGAP International standard for good agricultural practices.
Guest workers Individuals invited (by receiving a limited visa) to work in a specific country for a specified time period.
Hacendado Owner of large land areas.
Hacienda A large land area.
Inelastic demand Demand that does not respond to changes in price.
Petrodollars Money generated by the sale of oil and natural gas.
Piece rate Work that is paid per unit produced or for specific task completed.
Reproduction of costs of labor What it takes to bear and raise a child, educate and train her, and provide for her health and well-being until she enters the labor force.
Undocumented Without legal status in the country where the individual resides. This status occurs when one overstays one's visa or enters without official endorsement.

Introduction

Women and girls have worked in agriculture since plants and animals were domesticated (Flora, 1985). Agricultural labor can be unpaid (such as on-farm family labor), paid-in-kind (such as barter or labor exchange), self-employed (such as marketing of one's own produce), or wage labor (World Bank, 2009). As a few accumulated land from the many, women work as comanagers, unpaid household labor, field hands, or in packing sheds. With the industrialization of family farms, women shifted from producers of agricultural goods to consumers (Barlett, 1993; Akyeampong and Fofack, 2012). Global production, distribution, and marketing systems are increasingly flexible and feminized (Bain, 2010, p. 343). This has increased the vulnerability of women farm workers, and at the same time it has increased the profitability of labor-intensive agricultural production. Women farm workers, who represent 20–30% of the approximately 450 million people employed worldwide as waged agricultural workers (the proportion is higher, at approximately 40%, in Latin America and in the Caribbean and parts of Africa), face specific difficulties (DeSchutter, 2012; Fontana *et al.*, 2010). Moreover, when all agricultural workers, paid and unpaid, are considered, women make up the majority of those workers.

History of Women as Agricultural Labor

Traditional communities were based on subsistence production with very little for sale. As these communities were penetrated by world markets, the division of labor in agriculture changed dramatically. In much of the colonized world, particularly Africa and Latin America, the first impact on traditional farming systems was the removal of male labor to work in seasonal plantation agriculture. Men were needed for the sugar and banana harvest. A few women followed to provide the necessary domestic functions of food and laundry. However, generally, women remained at home in charge of the subsistence production plots and animal production activities. Disruption of traditional farming systems intensified as harvests of export crops such as coffee and cotton utilized the entire families as laborers (Flora, 1988).

Integration into a world economic system changed land use – from subsistence crops and those destined for domestic markets to export crops. In much of Latin America, for example, large areas of very good land was given out as Spanish or Portuguese land grants and were farmed extensively with livestock, predominately cattle. Indigenous peoples and *mestizos* had use rights to land, on which they raised subsistence crops in exchange for the labor they provided to the *hacendado* (owner of extensive land holdings). These labor relations allowed the large landowners to access labor of the entire family at no monetary costs.

Hacienda agriculture involved appropriation of the and by the colonial power, who then deeded it to those who had provided the crown with enough wealth or conquest to justify their new landed status. The indigenous people on the land were part of the package in the *encomienda* system that paralleled the land granted by the crown. The peasants, now bound to the land by complex systems of legal and debt peonage, provided labor and received the use of a parcel of land for their own subsistence production, following the feudal land and labor relationships in Europe in the sixteenth century. *Hacienda* agriculture was much more self-contained than plantation agriculture, with little market orientation. Both male and female labor were often extremely cruelly used (Carrion, 1983).

Colonization in Africa and Asia followed similar patterns as the newly arrived Europeans established plantations of monoculture export crops, which needed seasonal labor. The institution of the 'hut tax' required cash payments and forced many farm households to sell their labor to the colonists on plantations or in the mines in order to escape imprisonment by the colonial power for nonpayment of taxes.

In attempts to rationalize and intensify production, particularly for export, colonial powers and nation states worked

hard to first privatize and then alienate land. In traditional agricultural communities, much land was controlled in common with village leaders assigning land use on a year-by-year basis. In this system, women had access to land through traditional land use rights. As land became titled and later sold, it was almost always titled in the name of the man in the household rather than the man and woman. The new private plots in the reformed areas and in new colonization and transmigration areas favored men's crops. There was seldom land left for the women's gardens, which were often vital for household nutrition and even survival (Lado, 1992). Women's collective production efforts were eliminated entirely. Often the animals that women would pasture, such as small ruminants, also were not allocated land for grazing. Women, thus 'freed' from production agriculture on their own land, were available for seasonal farm work on large estates and plantations.

The advent of capital-intensive export agriculture created a rural labor force totally dependent on sale of its labor. Many peasants lost their land use right, as a strategy of landowners to make sure peasants had no claim on the land. A relatively large rural labor force was thus available, forcing wages down, except for peak harvest periods. Women and men increasingly sold their labor for the same tasks, including the harvesting of coffee (a traditional source of temporary rural employment for women in peasant families) and cotton and for weeding and other cultivation tasks in row crops. Women again did the same agricultural work as men, this time for a wage as piece work, and were responsible for their household tasks.

Piece-rate pay is based on how much a task is completed, generally based on the number of baskets filled or the weight of the amount harvested. This is generally advantageous to the employer, as work becomes self-enforcing and requires much less supervision. Though the most efficient women may do well with this system of remuneration, it is often unfavorable to women in heavier tasks, where pay is calculated based on male productivity standards. Piece-rate pay encourages workers, especially women, to have their children in the field with them as helpers to perform the task faster (DeSchutter, 2012).

The year 1973 was a landmark for the developing countries, as events were set in motion that greatly affected the structure of agriculture around the world and the role of women within that structure (Flora, 1990). It was the year of the world oil crisis, with drastically increasing oil prices that dramatically shifted the terms of trade for most developing countries. In oil-purchasing countries with import substitution industries highly dependent on petroleum imports to run their factories, even more pressure was put on the export sector. More land went into export crops, even as prices dropped due to overproduction and inelastic demand. For the oil-producing countries, it meant increased indebtedness, with much of the borrowed money used to import food, as the subsistence agriculture sector, already relegated to women and virtually ignored, became even less viable. Suddenly there were lots of petrodollars recycle, and international banks competed to lend money (Flora, 1990). As inequality increased, more women entered the agricultural labor force. Deere and Leon de Leal (1982) show how in Latin America the sexual division of labor in agriculture declined, and yet wage differentials increased. In countries such as Ecuador, women were rarely employed as agricultural workers compared with men, and when they were employed received half the pay. They were most often employed as nonpaid family agricultural workers (Pontón and Pontón, 2008).

Women as Flexible Agricultural Labor: The Current Situation

While in the past plantations sometimes had a captive labor force which housed the entire families all year round and utilized all family members at times of peak labor demand, the emergence of factories in the field depended on a mobile labor market that appeared when labor was required. Those workers in fields and packing houses are hired on a temporary, part-time or contract basis and their wages and benefits are typically low (Allen and Sachs, 2007). With contracts, the grower has no legal responsibility to the workers, often resulting in lack of enforcement of the few labor laws that exist to protect agricultural workers (Standing, 1999).

As Pearson (2007) makes clear, labor markets are gendered institutions that reflect the socially constructed divisions of labor. In agricultural work, as in other sectors, women are in jobs that are temporary, part-time, and are considered low skilled. The majority of agricultural wage laborers in many countries, particularly women, either are working on land owned by spouses, families, or neighbors or are hired in informal markets. Most women working in agriculture thus typically do not have contracts that provide them direct control over the returns to their labor or that legally oblige employers to provide benefits or adhere to existing labor laws (World Bank, 2009).

Women are disproportionately represented in the 'periphery' part of the workforce that coexists with the 'core' segment of permanently employed farmworkers (FAO, 1998). The periphery segment of the farm labor market is generally paid on a piece-rate basis. This 'periphery' segment of the workforce is made of unskilled workers, often without a formal contract of employment, and their work is often seasonal or temporary (or classified as such even when it is in fact continuous). The main reason, according to DeSchutter (2011), that women are disproportionately represented in this segment is because they have fewer alternative options and are thus easier to exploit.

According to the World Bank (2009), women represent a larger proportion of laborers than men in the agricultural sectors of Asia, sub-Saharan Africa, and the Middle East and North Africa. Women also dominate in some Caribbean and Central American countries, especially in economies with low per capita income and increasing dependence on labor-intensive export agriculture.

Migrant Women Farmworkers

Migrant labor in agriculture is increasing, even as the agricultural labor force as a whole shrinks. Growth in agricultural employment has come in areas such as horticulture, floriculture, aquaculture, pigs, and poultry, in which factory-style operations are possible and economical. Economies of scale

apply, so the bulk of the work is carried out by paid employees (ODI, 2007). Women figure prominently in these sectors, such as shrimp-processing plants in Argentina, Bangladesh, India, and the Pacific Islands and poultry processing in Brazil. An increasing number of these industries employ labor under temporary conditions or through third parties.

Maintaining women in casual, informal employment and paying them less (or paying them through their male partners) are often justified through their roles in social reproduction (Raynolds, 2001).

Around the world, the globalization of fruits and vegetables has shifted agricultural work from men to men and women, with women seen as cheaper and more flexible workers for highly seasonal work (compared with plantations for bananas, palms, and other tropical crops) (Doss and SOFA Team, 2011). In many countries in Africa, Asia, and Latin America, women, who had not traditionally worked in agriculture on a salaried basis, are hired to harvest and pack the nontraditional export crops. They work long hours, often on a piece-rate basis and are not enrolled in social security or other benefits programs. They often do not have access to basic sanitary services. Usually hired as contractors, rather than direct hires, they have very little support in organizing collectively, even in countries such as Argentina with relatively strong labor laws.

Although fruits and vegetables in international value chains need contingent flexible labor that women tend to provide, the move from integrated peasant systems to plantations creates another type of women farmworkers. In Indonesia's palm-oil production, shifting land tenure from the community to the state, coupled with the family head (male) system of smallholder rights registration, has resulted in women as a type of plantation worker (White and White, 2012). Corporate land deals that basically expropriate communal land were granted in the 2004 Plantation Act through long-term land use concessions for 35 years and extendable for another 25 years. These concessions abolish customary rights (Raworth, 2004). Some plantations combine a nucleus estate with small holder production. However, often new smallholders are recruited from even poorer areas, displacing traditional farm families, or plots are allocated far from the farm household residence, creating conflict with the families who live there.

In many cases, the families do not receive the promised plots, and family members become plantation workers: contract workers (mainly male), casual workers for specific tasks (both male and female), and unpaid family members who assist the hired workers without pay or labor rights. These workers are primarily females and children. Spraying and fertilizing has become women's work, with substantial unprotected exposure to highly toxic chemical substances. Both hot weather and the fact that they must individually purchase safety equipment means that few women wear protective gear. At the same time, dependence on cash has increased, as monoculture had made both gathered foods and chicken raising impossible. Plantation work is typically piece rate, enhanced by more hands picking and packing. Women, especially, tend to be accompanied by children, male and female, in the fields (DeSchutter, 2011). Plantations depend on low-paid or unpaid family labor during seasonal peaks in labor demand. Women and girls, who still have their daily and often onerous household tasks, are an important part of this labor force.

The International Migration of Farmworkers

In richer countries, such as those in the European Union (EU), the US, Canada, Australia, New Zealand, Norway, Israel, the Russian Federation, South Korea, and the United Arab Emirates, where incomes have risen, the poor have become urbanized, and the rural poor are often aged or infirm, international migrants from poor areas in developing countries provide the bulk of the agricultural labor, both seasonal and year round. Although there have been some attempts to regularize such workers, many do not have legal documentation, which makes them particularly vulnerable to exploitation by employers, contractors, and smugglers and employers vulnerable to periodic raids and decimation of the productive workers through arrests and deportation. Thus many employers of agricultural workers are demanding immigration reform, either, as in the US, through comprehensive immigration reform (such as the National Milk Producers Association) or improved guest worker programs (Agricultural Workforce Coalition).

Guest Worker Programs

One way to get agricultural labor at minimum costs of the country in which the work is performed is through seasonal migrant labor, This allows the sending country and sending households to pay the reproductive costs of labor, whereas the employer only has to pay the labor costs, which, by recruiting many such workers, can be kept low. Countries such as the UK and Australia have instituted 'working holiday' programs to offset labor shortages in horticulture. Women often take advantage of such opportunities to be in the countries without sponsorship.

Some countries have institutionalized legal mechanism to recruit seasonable farmworkers. Women are increasingly part of this group in many countries. All low-skilled visa programs, which is how farm work is classified, must balance several potentially conflicting goals.

- Guarding against the exploitation of foreign workers.
- Maintaining appropriate wage and working conditions for domestic and foreign workers.
- Make the legal employment-based immigration system sufficiently attractive to employers to discourage illegal employment.

Many of the visa programs, such as that in Norway, require unskilled (agricultural) workers to be outside the country for at least 6 months before reentry. There are often quotas for agricultural workers. To receive the visa, the workers must already have an employer. These programs do not allow for family members to accompany the workers.

Some temporary visas for seasonal agricultural workers are based on government to government agreements, as in Canada, the Russian Federation, and South Korea. This can

provide more protection for agricultural workers, and uses sending country institutions for labor recruitment.

In the EU, guest worker programs have been facilitated by the entry of second tier countries into the common market, which means workers can cross borders without visas or specific labor contracts. Immigration is a shared competence between the EU and its 27 Member States. The EU has enacted legislation in the areas of visas, residence permits, family reunification, and illegal immigration, among others, but the EU Member States have the right to determine the number of admissions of third-country nationals in their territory for employment purposes, including temporary workers. The European Commission has adopted a proposal that would establish a fast-track procedure and a single residence/work permit for seasonal workers, including a multiseasonal permit. The EU has an agreement with Turkey regarding immigrants of Turkish origin (Library of Congress, 2013).

Guest workers programs have generally recruited males, but that is changing in such countries as Canada. The Seasonal Agricultural Worker Program (SWAP) in Canada is highly regulated to be sure that the migrants return home and presumably receive their labor rights.

There is little research done on migrant women entering male-dominated occupations, such as farm labor, and how that occupational migration flow is gendered. As women enter these highly masculinized programs, they face a number of problems that do not confront women working in the feminized part of the agricultural labor force (Preibisch and Encalada Grez, 2010). The women who qualify for the Canadian guest worker program (temporary visas) must come from rural areas and have experience as farmworkers. Yet they face disapprobation from their employers and their home communities for transgressing gender norms to migrate where their race, class and citizenship makes them exceedingly vulnerable. It is difficult for them to claim their rights under Canadian law.

In the US, immigrants were 4% of the farmers and farm labor force in 1970. By 2000, they were 22% of the farmers and farm labor force – primarily farmworkers. Mexican women were half as likely as Mexican men to be employed as agricultural workers, but they make up a substantial minority of the migrant agricultural labor force (Lowell *et al.*, 2006; Roenblum and Brick, 2011). Only 3% of unauthorized women work in agriculture, compared with 13% of unauthorized men (Capps *et al.*, 2013). The temporary agricultural worker program visa in place in 2013 – H-2A – is generally felt by farmers and farmworkers to be inadequate. The farmer must prove there are no green card or citizen workers available in the area, a procedure that can prove onerous. Then the farmer can recruit foreign workers, which is why many rely on labor contractors to get workers to the job as quickly as possible. Workers with H-2A visas are not eligible for permanent residency whereas they are in the US. Permanent visas for ongoing, nontemporary positions are heavily oversubscribed, and must be reapplied for each year to stay in-line.

Guest worker programs are a concern because they are costly and bureaucratic, consistently circumscribe workers' rights, and provide the wrong incentives to both workers and employers, resulting in the continued use of undocumented labor. Guest worker programs will not work for smaller farms, which are widely dispersed and have many different types of labor needs.

The undocumented network migration system has worked well both for agriculture as for other manually intensive industries in the United States. It is self-recruiting, self-transporting, and self-housing. It is the low-cost, market-based option, and the rational approach to eliminating undocumented labor would be to legalize this undocumented system itself, and allow the labor market, not the government, to allocate immigrant workers (Runsten *et al.*, 2013).

Key Gender Issues

Women worldwide combine their domestic responsibilities with their wage-earning activities. Lack of access to fuel and water in some rural areas, and lack of child care in other areas encourages women to take short-term agricultural work in order to continue their strenuous household obligations. Employers often refuse to hire pregnant workers, so women disguise their pregnancies in order to maintain their access to income.

Occupational segregation by gender within agriculture tends to justify paying women less than men. Bello Barros (1993) found strict gender divisions of labor in the apple industries of both Chile and Virginia, but that work that was male in one country was female in the other. In Chile, men pack the apples, whereas in Virginia women pack the apples. The high-value agricultural export industry is highly segmented and gender segregated (World Bank, 2009; Barrientos and Perrons, 1999). Dolan and Sorby (2003) cite vineyards in Northeast Brazil, fruit in Chile, flowers in Colombia and Mexico, horticulture in Kenya, vegetables in Sinaloa, Mexico, deciduous fruit in South Africa, and flowers in Uganda as employing more than 50% women in sex-segregated tasks.

Some tasks are 'feminized,' such as weeding on the farm, or poultry processing and flower packing in the factory, despite evidence of the ability of men to perform these tasks equally well in other companies or countries. The reverse also holds, and generally men run equipment and handle tools, jobs that usually require training, not a high level of strength, and elicit higher wages. Occupational gender segregation is particularly strong in some countries in South Asia, Southeast Asia, and Latin America (World Bank, 2009).

Stereotyping of gender roles is ubiquitous. For example, a manager in a cut-flower-processing plant in Kenya said that "women are more dexterous, which is good for flowers" (Collinson, 2001). This is mirrored in the cut-flower industry in Colombia and Ecuador (Korovkin, 2003; Lara, 1995; Medrano, 1996; Silva, 1996). Confining women to a limited number of occupations has high equity and efficiency costs, and it contributes to misallocation of labor and suboptimal investments in women's education because girls' potential is usually gauged through current market opportunities (Tzannatos, 1999).

Violence, Health, and Safety

The high prevalence of women in casual, low-paid employment with limited security leads to other abuses. Young

women from very poor areas become an increasing part of that migrant stream. Underage Khmer, Lao, and Myanmar girls migrate to work in agriculture in Thailand, where some are held captive working under poor conditions (Pearson *et al.*, 2006).

Violence and sexual harassment in the workplace are more frequent under these conditions. Men supervisors control decisions concerning work performance and hence remuneration for the 'task.' Studies have shown that women must trade sex for job security, markets, and other employment benefits that should be part of the labor contract. In studies of the cut-flower industry in Kenya, women reported that supervisors required sexual favors for job security, and refusal could lead to dismissal (Dolan *et al.*, 2002). This harassment occurs in spite of company codes of conduct that prohibit such behavior.

In India, despite the rise in agricultural workers wages that accompanied the Green Revolution from 1966 to 1988, women continued to receive substantially lower wages. Indeed the differential was greater in the Indian states with the highest increase in yields (Singh, 1996). Among the US farm workers, women are more vulnerable to exploitation than men, and they are paid even lower wages and given fewer benefits than their male family members (Kearney and Nagengast, 1989). The continuing vulnerability of female agricultural workers is demonstrated in a 2013 documentary aired on both PBS and Univision.

Women face health hazards in the cultivation of many crops reporting back pain and pelvic problems in rice cultivation and weeding. Agricultural work can be arduous for both sexes, but to the extent that women are concentrated in specific activities, they will experience greater exposure to some risks. Occupational safety risks can be high in factories and agro-processing plants, including equipment accidents, exposure to unsafe conditions, and contact with chemicals and toxic substances. Women who work in fish- and shrimp-processing experience arthritis and other negative health effects of standing or sitting in wet, cold environments for 10–12 h a day (USAID/GATE Project, 2006). In a recent study of the fish and shrimp industry in Argentina, the majority of the women interviewed held temporary jobs and therefore had no medical or social coverage. More than two-thirds of the women interviewed work more than 5 days a week, and 63% work more than 8 h a day (Josupeit, 2004).

The high value fruits and vegetables grown in monocultures require high rates of pesticide application. Although GlobalGAP's Labor Standards for Health and Safety offer some protection for full-time workers, particularly pesticide applicators, workers hired by contractors or part-time temporary workers are not necessarily included (Bain, 2010). These positions are generally held by women. They are subject to indirect exposure through pesticide drift at work and in their nearby homes (Harrison, 2011). Besides the dangers of pesticide drift, women pickers risk pesticide poisoning through residues on fruit and leaves as they are seldom provided with protective clothing and gear, particularly in developing countries. Pressures by retailers for cosmetic quality and low costs encourages hiring women as low cost, flexible, temporary subcontracted employees, for whom pesticide training and protective gear would be an extra cost in a tight-margin market. As employees of the contractor, the growers and their corporations have no direct responsibility for health and safety. Besides, in many countries, such workers are either undocumented or with employer-validated visas; there are huge penalties in terms of job loss and deportation for those who complain.

Health risks in the growing horticulture industry include exposure to toxic products through inadequate training and protective clothing, poor hygienic conditions, and physical demands and long hours. Every year at least 1 70 000 agricultural workers are killed as a result of workplace accidents, and some 40 000 of these are from exposure to pesticides (ILO, 2003). To the extent that women predominate in some of these activities, they have greater exposure.

Under conditions of temporary, seasonal, or limited contracts, no health insurance is provided. Where there are no on-site medical facilities, these women, in greater proportion than men, bear the cost of medical services. In factories or on plantations, such as in fruit-producing areas in South Africa, medical facilities may be few or lacking, and workers may even be dependent on employers for transport to medical facilities.

Potential for Improvements

The World Bank suggests that trade agreements include a gender analysis, examining the relative prices of factors that change demand for labor as sectors expand and contract; and extending legal rights frameworks for women agricultural laborers, including labor law and its implementation and enforcement. Unfortunately, those countries where women agricultural workers are most disadvantaged also tend to have the weakest labor rights enforcement mechanisms.

Even in countries where labor laws are seldom enforced, programs that help women agricultural workers become aware of their rights can strengthen the demand for labor law enforcement and reforms. Such education can strengthen local organizations of agricultural workers and help them be more inclusive of women as they negotiate with governments and with growers.

The disproportionate number of women in casual and seasonal jobs and the attendant risks for women and children increases the necessity to increase social protection for them (ILO, 2002). Social protection can focus on reducing risks or on maintaining assets. In the context of agricultural labor, social protection refers mainly to medical and unemployment benefits and pension provision. The extension of public social protection programs to temporary, casual, and seasonal laborers will address some of the issues of gender inequity in agricultural labor.

Unemployment insurance, health insurance, and pension programs are all inaccessible to temporary and casual workers in most developing countries and in some developed countries (FAO Legal Office, 2002). The private sector is unwilling to bear the full cost of these programs, so there must be an evaluation of the balance between private and social costs and benefits needs.

Labor contracts, particularly enforcing those of subcontracted workers, are particularly important. However without legal status in the country where they work, female

workers are unable to enforce contracts, even if they have them. A number of groups, such as Oxfam International, are working directly with major brands to ensure the enactment and enforcement of standards that take women and farm workers into account.

Improving Health, Security, and Safety

Providing a healthy workplace and maintaining the health of workers should be good business, but managers of companies may have to be convinced of the economic benefits of, or be forced into, applying basic standards. Health concerns for women include violence and sexual harassment in the workplace, exposure to human immunodeficiency virus (HIV) and acquired immunodeficiency syndrome (AIDS), as well as occupational safety issues surrounding, for example, accidents and exposure to unsafe conditions, chemicals, and substances. Overtime and night shifts can also create safety concerns for women, although these can also be used to restrict women from employment categories.

Improved information and data provided by laborers and labor organizations concerning a perceived problem can help lead to its resolution. Dissemination of policies is important, and the implementation of training programs is necessary. Worker organizations, supported by Non-Governmental Organizations (NGOs) are the most effective mechanism for such dissemination and education with the cooperation of employers. This is made more difficult when workers are subcontracted, as is increasingly the case.

The workplace is an extremely effective center for HIV and AIDS awareness campaigns. Plantations in Uganda were experiencing extremely high rates of mortality, but as government campaigns were complemented by company information and condom distribution, the mortality rate has fallen significantly. Human rights work in some regions has been expanded to domestic violence and its social and economic repercussions. Some companies have recognized the cost of violence and facilitated support for abused women (World Bank, 2009).

The ILO (2012) suggests that countries guarantee the equal treatment of part-time workers for social benefits, as is being done in many Organisation for Economic Co-operation and Development (OECD) countries. They also urge legal reforms to ensure formal equality, antidiscrimination laws and procedures, and equal tax treatment. However, such legislation to challenge gender stereotypes and confront discrimination are difficult to apply in the case of women agricultural workers, even in OECD countries.

Monitoring and Evaluation

Currently, there are few data on women agricultural workers, particularly those in flexible positions. Furthermore, that data are quite suspect, as often those who must cooperate to give data or access to the workers for sampling feel that such data might disadvantage them. In the US funding for the Survey of Agricultural Workers, conducted through the USDA is constantly under threat. Fiscal austerity gives cover for not knowing what is happening with the agricultural labor force. Data from 2012 state that only 18% of the 6 76 000 farm laborers and supervisors are female. Other key information has not been analyzed by gender. Almost three-quarters of hired crop farmworkers are not migrants, but are considered settled, meaning they work at a single location within 75 miles of their home. This number is up from 42% in 1996–98. Such proximity increases the possibilities of women becoming flexible farmworkers.

In other countries, the data are equally difficult to access, and probably equally threatening. Like in the US legal status of the worker or members of the worker household make it imperative that trust exists between the entity collecting the data and the employer, contractor, or worker. Less obtrusive data can be gathered from program records (numbers of farm operators trained in occupational health and safety issues), administrative records (incidence of occupational health and safety incidents and measures taken to prevent future incidents; number of women and men from district employed in agricultural enterprises annually), union records (percentage of women and men in activist or leadership positions), training records (number of women and men receiving training on labor standards and employment rights per quarter), government social security records (access of women and men to social security and unemployment insurance), legal authority records (change in number of cases of women and men accessing legal advice regarding legal rights), among others.

Subcontracting makes this all more difficult, as it is often unclear who the employer is and what obligations and responsibilities fall to which entity. In many countries, labor contractors remain unregulated and continue to operate with questionable legality. It is, however, a vicious circle for female agricultural workers, for without the number of workers it is difficult for auditors to verify the adequacy of standards that must be determined by the numbers, such as provision of toilets and adequate living quarters (Bain, 2010).

Conclusion

Although mechanization has decreased the number of farmworkers worldwide, women make up an increasing proportion of those who do farm work. They are more likely than men to be employed as flexible farm labor in intensive agricultural production, particularly horticulture, including the flower industry. The increasing use of contract labor and the lack of clear legal protections, particularly for immigrant farm workers, make women vulnerable to sexual and wage exploitation. Family responsibilities drive them into flexible farm labor increase their work load as they perform both domestic and paid labor.

Availability of affordable child care and transportation services to farmworkers increases the well-being of both mothers and children, as they must no longer choose between children in the field or left in a compound alone.

Around the world, women's groups are educating women agricultural workers about the legal rights as workers and encouraging them to demand them. These groups also provide support as women join together to demand their rights from labor contractors, employers, and the state. Increasing the ability of women agricultural workers to bargain collectively,

supported through effective policies and laws, would increase their ability to demand and receive equality of opportunity policies, equal pay for work of equal value, maternity leave and benefits, child care and reproductive health services. Preparing women for leadership roles in the male-dominated unions and following gender-equity guidelines increase union sensitivity to the gender implications apparently neutral issues for collective bargaining, including how wages are determined, leave, overtime, or bonus systems as these often in reality impact women and men differently (DeSchutter, 2012).

The ILO's mandate on gender equality is to promote equality between all women and men in the world of work. This mandate is grounded in International Labor Conventions of particular relevance to gender equality – especially the four key equality Conventions. These are the Discrimination (Employment and Occupation) Convention, 1958; Equal Remuneration Convention, 1951; Workers with Family Responsibilities Convention, 1981; and the Maternity Protection Convention, 2000. The mandate is also informed by Resolutions of the International Labor Conference – the highest level policymaking organ of the ILO – in 1975, 1985, 1991, and the June 2004 Resolution on Gender Equality, Pay Equity, and Maternity Protection.

Regularizing the access of agricultural workers, male and female, through a graduated visa program as proposed by Runsten *et al.* (2013) would go a long way to increasing the well-being of all women agricultural workers, as a legally divided workforce disadvantages both employers and workers and give women collectively an opportunity to address their shared issues around agricultural work.

See also: Agricultural Ethics and Social Justice. Agricultural Labor: Demand for Labor. Agricultural Labor: Labor Market Operation. Agricultural Labor: Supply of Labor. Agricultural Law. Agricultural Mechanization. Changing Structure and Organization of US Agriculture. Farm Management. Global Food Supply Chains. Organic Agricultural Production: Plants. Rural Sociology. Tree Fruits and Nuts

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Agricultural Labor: Labor Market Operation

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Introduction

Agriculture is full of paradoxes. Farmers are often praised as the independent yeomen who provide living links to the nation's founding fathers, yet agriculture receives more federal subsidies than many other US industries. There were too many farmers during the 1950s, when a million Americans a year moved to cities, whereas alleged shortages of farm workers were the rationale for importing almost 500 000 Mexican Braceros a year to work in the fields.

Thomas Jefferson, the third US President, believed that family farmers were the backbone of American democracy. Jefferson's phrase, engraved on the wall of a reading room in the Library of Congress, proclaims that "Those who labor in the earth are the chosen people of God." Jefferson believed that rural life was superior to urban life and a nation of self-sufficient family farmers who owned the land they farmed would guarantee respect for private property and preserve American democracy.

Family farms were the ideal as well as a widespread reality in 1790, when the first Census of Population found that 90% of the four million US residents lived in rural areas. The model farm included farmer, a large family, and perhaps a hired hand, usually a young man who lived with the farmer's family temporarily before becoming a farmer in his own right. Everyone on family farms worked to meet peak seasonal labor needs, explaining why school schedules were adjusted so that children were available when needed on the farm.

The fact that crops needed more workers during some seasons than others encouraged diversification to spread out the work and to make farm families self-sufficient. Most family farms in the early nineteenth century raised crops and tended livestock, and most did not generate a surplus to sell because there were few large US cities and European farmers produced similar crops. As technology increased the productivity of farmers, family farms got larger, producing a surplus to sell to urban residents in expanding US cities and abroad.

There were two other US farming systems that dealt very differently with the need for seasonal farm workers. In the southeastern states, plantations produced cotton and tobacco that were exported to northern Europe and other areas that could not grow these long-season crops. Slaves were bound to their plantations, ensuring that seasonal workers were available when needed. Slaves were eventually replaced by sharecroppers who lived and worked on small plots of what had been plantation land, and in the twentieth century, mechanization reduced the need for seasonal workers on cotton farms, although tobacco farms continued to rely on foreign-born farm workers.

The western US states had large landholdings often assembled by entrepreneurs who grazed cattle or raised wheat in the mid-nineteenth century. The transcontinental railroad, irrigation, and other changes made it profitable to switch to labor-intensive commodities in the 1870s. Large landowners expected to sell small plots of land to the family farmers who arrived by train, because it was assumed that large farm families were necessary to provide seasonal workers needed for fruit farming. However, a seasonal workforce was available with the Chinese workers who were imported to build the railroad and driven out of cities by discrimination. Farmers hired the Chinese to fill seasonal jobs, and waves of migrants with few alternatives to seasonal farm work followed, including the Japanese, Filipinos, Mexicans, and Dust Bowl Okies and Arkies in the 1930s.

This article summarizes the operation of the farm labor market, focusing on the unique ways in which agriculture handles the 3-R functions of all labor markets – recruitment, remuneration, and retention. It also reviews the Bracero and H-2A programs that provide farmers with legal guest workers and the efforts of unions to organize farm workers and bargain for wage and labor market changes. The farm labor market has always been different from other labor markets, and farm–nonfarm labor market differences still persist in the twenty-first century.

Farm Labor Market

All labor markets perform three essential functions that can be summarized in words that begin with R: recruitment, remuneration, and retention. Recruitment deals with matching workers and jobs, remuneration with motivating workers to perform by offering them wages, and retention with keeping the best workers and ensuring that sufficient workers will be available to fill seasonal jobs.

Agriculture deals with each of these R-functions in unique ways. For example, farm workers are often recruited in crews of 20–40 via intermediaries such as farm labor contractors, whereas nonfarm employers are more likely to recruit individual workers and screen them with written applications and interviews. Most US jobs pay hourly or monthly wages, whereas a significant share of farm jobs, especially seasonal jobs harvesting fruits and vegetables, pay piece-rate wages such as US$20 to pick a 1000 pound bin of apples, that is, worker earnings reflect productivity at the employer-set piece rate. Few farm employers have formal systems to identify the best workers or job-related benefit systems that aim to retain them. Instead, farm employers have more often worked together to ensure that sufficient seasonal workers will be available for all farmers when such workers are needed.

Recruitment and Contractors

Recruitment matches workers with jobs. In agriculture, where large numbers of workers are required to fill seasonal jobs, the most efficient recruitment mechanism is a central clearinghouse that allows farmers to list their job vacancies and workers to seek seasonal jobs that maximize their earnings and

minimize their unemployment and commuting time. Such clearinghouses can be operated by (groups of) employers, unions via hiring halls, or the public Employment Service, whose offices are now known as One Stops (www.careeronestop.org).

The logic of a central clearinghouse to minimize uncertainty for growers and unemployment for workers is clear, but there are few examples of their successful operation. Between the 1930s and 1960s, the US Department of Labor (DOL) operated a Farm Placement Service (FPS), which involved government agents taking job orders from farmers and helping migrant and seasonal workers to find jobs (Goldfarb, 1981). Some farm employers formed associations that acted as clearinghouses for seasonal jobs and workers, and some of these employer associations became labor contractors that moved workers from one member's farm to another.

Farm worker groups sued the US DOL in the 1960s, alleging that the FPS discriminated against farm workers by sending farm workers only to farm jobs, rather than providing them access to the full range of farm and nonfarm jobs at the Employment Service, including training services. In a 1973 settlement of the NAACP versus Brennan suit known as the Richey Court Order, DOL agreed to provide farm workers the same services that it provided to other workers, and the FPS was dismantled (Goldfarb, 1981). The public Employment Service today makes very few worker–job matches in US agriculture.

The employer associations that served as clearinghouses for workers and jobs also curtailed their activities, especially in California, as unions spread in the 1970s. The Coastal Growers Association (CGA), organized as a labor contractor in 1961 to pick lemons in Ventura County, CA, USA, provides an example. CGA's professional managers were able to reduce the number of pickers from more than 8500 to 1300 within a decade, demonstrating the inefficiencies that had crept into the farm labor system when the availability of Braceros held down wages (Mamer and Rosedale, 1980). The average earnings of these fewer workers rose to twice the minimum wage, and CGA provided job-related benefits such as health insurance, paid vacations, and subsidized housing that were rare for seasonal farm workers.

The win–win benefits of applying modern human resource policies to seasonal farm workers spread in California, Florida, and other major producers of fruits and vegetables during the 1970s, so that most agribusinesses had a personnel manager and employee handbook by the early 1980s. However, workers at CGA and many of the other associations voted for union representation, in part because personnel managers coming to agriculture from nonfarm firms were familiar with unions and did not oppose them as strongly as growers who hired workers directly. When the United Farm Workers (UFW) union went on strike in support of demands for significant wage increases at the associations in the early 1980s, the farmer members of the associations, aware that peso devaluations were increasing the availability of unauthorized Mexican workers, used labor contractors who hired newly arrived Mexicans to get their crops picked. Many of the contractors remained in business after the strikes ended and won enough business from growers leaving associations so that the associations went into a death spiral, unable to cover their fixed costs with ever smaller workloads. The CGA went out of business in 1986 and most of the other associations also disappeared (Lloyd *et al.*, 1988).

The UFW tried to fill the void left by the demise of the FPS and employer associations with union-run hiring halls, but they proved inefficient. Under UFW contracts, farm employers were supposed to call the UFW when they needed seasonal workers. The UFW ranked workers by their seniority with the union rather than their seniority on their farms requesting workers, making farmers unhappy, and the UFW sometimes split up families that wanted to work together, frustrating workers. The UFW abandoned hiring halls in the 1980s.

Job–worker matching in agriculture today is generally decentralized and often involves contractors. Contractors and other intermediaries match most seasonal workers and jobs in a system that can lead to simultaneous labor shortages and surpluses because of conflicting incentives. Farmers, who do not pay workers while they wait for work to begin, have an incentive to request 'too many workers too soon,' while contractors seeking jobs for their crews have an incentive to promise 'more workers sooner' to win jobs on farms. There is far more publicity of subsequent farmer complaints of labor shortages than of worker complaints of unemployment.

Farm labor contractors (FLCs) charge a fee to match farm workers with jobs. Intermediaries such as FLCs are common in labor markets where workers are hired in crews for short-duration jobs and employers may not speak the language of the workers they hire. Contractors were once a bilingual member of the crew, as with the Chinese crews in the 1870s that included a bilingual 'head boy' who arranged seasonal farm jobs for his 20–30 compatriots and worked alongside them (Martin, 2003, Chapter 2). During the 1920s, contracting became an independent business, with contractors profiting from the difference between what the farmer paid to have a job done and what the contractor paid the workers. Some of the first farm labor strikes in California involved workers protesting against farmers who hired seasonal workers only via contractors (Fisher, 1953).

The federal government began to regulate contractors in the 1960s by requiring them to register and identify themselves. Contractors today are registered by federal (www.dol.gov/whd/forms/fts_wh530.htm) and state agencies (www.dir.ca.gov/databases/dlselr/farmlic.html) that require background checks, tests of labor and pesticide laws, and bonds from which workers can collect unpaid wages. The intent of ever-stricter regulation of contractors has been to drive out of business the 'bad apples,' but enforcement data suggest that labor law violations remain common. Inspections usually find that the majority of contractors are violating at least some labor, immigration, and/or tax law; a sampling of charges is at Rural Migration News (2012).

Most contractors evade effective enforcement of labor laws for a simple reason: enforcement depends on complaints, and the employees of contractors rarely complain. The US Industrial Commission explained early in the twentieth century that contractors can 'drive the hardest kinds of bargain' with the immigrant workers they employ because they "know the circumstances from which workers come." (quoted in Fisher, 1952, p. 43). It is hard to get immigrant farm workers, who may be from the same village as the contractor and dependent on the contractor for a job as well as housing and rides to

work, to complain of violations of labor and other laws of which workers may be unaware. When there is enforcement against contractors, it is often hard to prove violations, because written contracts are rare and it is costly to obtain evidence from often illiterate and non-English speaking workers.

Throughout the US, most farm workers are hired directly by farmers, usually by bilingual foremen or supervisors who become the 'boss' in the eyes of workers. Some farm operators learn Spanish so that they can interact directly with their employees, but most rely on bilingual supervisors or turn to labor contractors to obtain seasonal workers.

Remuneration and Wages

Work is the exchange of effort for reward, and the second function of labor markets is to remunerate or motivate workers. There are two major remuneration or wage systems in agriculture: hourly and piece rate. Salaries are sometimes paid to supervisors and to some workers employed in year-round jobs in dairies.

DOL's National Agricultural Worker Survey (NAWS) in recent years found that 75% of farm jobs paid hourly wages and 25% paid piece-rate wages or a combination of hourly and piece-rate wages. Piece rates were most common in fruit-harvesting jobs, whereas nursery workers were usually paid hourly wages.

A far higher share of farm jobs paid piece-rate or incentive wages in the past, because piece rates make the cost of getting work done predictable without screening workers. For example, it costs an employer US$100 to have 1000 pounds of table grapes picked if the piece rate is 10 cents a pound regardless of whether one fast picker or three slow pickers do the work. However, worker earnings are different if one worker rather than three workers performs the work.

Before minimum wage laws applied to the farm labor market, farm employers could hire everyone who showed up to work and paid them for the work they accomplished, so that children typically earned the least and young men the most. Today, labor laws require all workers to receive at least the minimum wage. If employers pay piece-rate wages, they must record the units of work accomplished and hours worked of each worker. If a piece-rate worker does not earn at least the minimum wage, the employer must 'make up' his or her pay so the worker gets at least the minimum wage, although most employers terminate workers who do not earn at least the minimum wage.

With the minimum wage higher than the federal US $7.25 h^{-1} level in most major farm labor states, including US $8 h^{-1} in California and US$9.19 h^{-1} in Washington in 2013, many farm employers have switched to hourly wages to reduce record keeping. There are two other reasons for the rising share of farm jobs that pay hourly wages. First, farm workers have become more homogeneous, so their productivity does not vary as much as in the past when the farm workforce included children, women, and older workers rather than today's mostly young Mexican-born men. Second, new technologies allow farm employers to control the pace of work in the fields, as when a crop such as broccoli is picked and packed by workers who walk behind a machine whose speed is controlled by the driver, who can be told by the employer how fast to drive. If employers can control the pace of work, there is no need to pay piece-rate wages to induce faster work.

Piece-rate wage systems are most common when it is hard for employers to monitor the pace of work. For example, many growers of apples and oranges pay piece-rate wages of US$15–20 per 1000 pound bin to workers who climb trees and are thus often out of sight. A worker's earnings are the higher of the minimum hourly wage or his or her piece-rate earnings, and employers usually set piece rates so that the average worker earns more than the minimum wage so that the workers have an incentive to work fast even if their work cannot easily be monitored.

Piece-rate wage systems create a so-called iron triangle between the government-set minimum hourly wage, the employer-set piece rate per unit of work, and the productivity standard, the units of work per hour or day expected of a worker. In a series of suits that spanned two decades, worker advocates challenged Florida sugarcane mills that told workers that they would be satisfactory workers if they cut at least a ton of cane an hour, but, in fact, required cane cutters to cut 1.5 tons of cane an hour (Martin, 2009, Chapter 4). The minimum wage was US$5.30 h^{-1}, and the sugar mills assigned workers to cut rows of cane and 'checked out' or terminated those who were too slow. Some of the cane cutters who were checked out cut more than a ton of cane an hour, but not the 1.5 tons an hour expected by the mills, prompting the suits that alleged that workers were owed additional wages because they should have been paid US$5.30 a ton rather than the US$3.75 a ton, which they were paid (Brenner, 2001). Some of the mills settled, but the mills that contested the suits won, in part because of the difficulty of defining a piece rate in cane cutting.

Most farm employers pay farm workers the minimum wage, although some pay US$0.50 or US$1 h^{-1} more in order to attract the best workers. Most farm labor data sources report average hourly earnings, which reflect what workers actually earn under a variety of wage systems – hourly, piece rate, and hybrid. The ratio of average farm to average nonfarm average hourly earnings has been 50–60% over the past two decades, that is, farm workers earn approximately half as much as nonfarm workers. However, farm workers typically receive fewer employer-paid benefits than received by nonfarm workers, making their total compensation less than half of the average of nonfarm workers.

The cost of employing workers includes hourly wages plus mandatory and voluntary fringe benefits. Mandatory benefits are those that the employer must provide to workers, including social security, unemployment and disability insurance, and workers' compensation for work-related injuries. Voluntary fringe benefits include health insurance, paid vacations and holidays, and extra pension benefits. Hired farm workers are less likely to receive voluntary fringe benefits, or to receive lower levels of such benefits, than nonfarm workers.

The Bureau of Labor Statistics reported that the average cost of employing private sector workers in March 2012 was US $29 h^{-1}, including 70% for wages and salaries of US$20.30 and 30% for fringe benefits that cost employers US$8.70 h^{-1} (www.bls.gov/news.release/ecec.nr0.htm). Legally required benefits cost employers an average US$2.35 h^{-1} or 8% of employee compensation, whereas voluntary benefits cost employers an average 22% of employee compensation. The most

expensive voluntary benefit was life, health, and disability insurance, which cost US$2.35 or 8% of employee compensation, whereas paid vacation, holidays, and other leaves cost US$2 h^{-1} or 7%. Employer contributions for retirement benefits and employee savings cost US$1 or 4% and supplemental pay for overtime, shift differentials, and bonuses averaged US$0.85 or 3%.

Fringe benefits can be expensive to provide to farm workers because of their low earnings. Benefits such as health insurance for workers and their families that cover off-the-job injuries and illnesses require monthly payments that are independent of earnings. Under some UFW contracts, farm employers contributed US$2.70 h^{-1} for health insurance in 2012 for workers earning US$10 h^{-1}, making the employer's cost of health insurance 27% of hourly wages and far more than the average for private sector workers. Most nonunion farm employers restrict fringe benefits to year-round workers, and some report that many of their employees who are offered fringe benefits that require employee copays do not participate.

Instead of health, pension, and other benefits, farmers sometimes provide housing to attract and retain good workers. However, exposes of poor housing conditions led to higher federal and state standards for farm worker housing. As farmers are not required to provide housing, many responded to tougher housing standards by closing their housing, which pushed farm workers into cities and towns in agricultural areas where they competed with other tenants for housing.

The cost of living in cities in agricultural areas is usually more than what farmers charged for on-farm housing. Workers living in cities often pay US$50–100 a week for housing and must usually pay for rides to work, which can be US$25–40 a week. Federal and state governments make grants and loans to provide subsidized housing for farm workers, but government housing usually favors families with children, requires proof of legal status, and has long waiting lists.

As most farm workers do not live on the farms where they are employed, there are special issues associated with transportation between farm worker's homes and jobs in areas without public transportation. Most farm workers drive themselves to the field or orchard to which they are asked to report, and many carpool because they lack a vehicle or want to save fuel costs. Workers who transport nonfamily members often accept 'gas money,' raising questions about when a car pool driver becomes a commercial transport operator. Some farm operators, especially in border areas where workers walk across the Mexico–US border daily, as near Yuma, Arizona and Calexico, California, have buses to take workers to fields.

Persons who use vans to transport farm workers to fields for a fee are known as 'raiteros,' and there have been tragedies involving raitero vans. Processing tomato harvest normally runs 24 h a day during the 8-week harvest, and 13 tomato sorters who had worked all night were killed in Fresno County on 9 August 1999 when the van in which they were riding collided with a tractor-trailer truck that was making a U-turn during the early morning hours on a remote farming road. The farm-labor contractor operating the van was fined US$21 500 for allowing them to be transported in an illegally operated vehicle (Rural Migration News, 2000).

Many farm labor vans, including the one involved in the Fresno accident, have their regular seats removed and wooden benches installed along the sides of the van in order to accommodate more workers. The California Legislature responded to the tomato workers' accident with a law in 2000 that requires all vans that charge farm workers fees to have regular seats with seat belts.

Retention, Training, and Productivity

The third key labor market function is retention, which involves identifying and developing incentives to keep the best year-round workers employed on the farm and encouraging the best seasonal workers to return to the farm the following year. Most US employers have formal systems that involve supervisors to evaluate workers periodically, and these evaluations are used to determine promotions and wage increases.

Few farm employers have formal personnel systems. Instead, the two major methods of recruitment and worker evaluation illustrate agricultural extremes in personnel practices. Some farmers, especially those who work closely with one or a few year-round workers in dairies and similar operations, ask current employees to refer friends and relatives to fill vacant jobs. Current workers tend to refer only friends and relatives who can perform the work, and they usually orient and train the workers they recommend. In this way, network recruitment simplifies the task of finding and training workers (Martin and Perloff, 1997).

The other personnel extreme involves growers who hire crews of seasonal workers via contractors or foremen. These operators often rely on intermediaries such as contractors to bring crews of interchangeable workers to the farm to perform a particular task such as weeding or harvesting. Contractors and foremen also rely on network hiring, having some of their 'regular' workers recruit friends and relatives, but the farmer rarely knows who is in the crew or the exact worker turnover rate.

Crew-based hiring explains why recruitment and retention are often part of the same labor market function. An analogy to obtaining irrigation water may be helpful to understand agricultural recruitment and retention options. One way to irrigate crops is to flood fields with water so that some trickles to each tree or vine; the other extreme involves laying plastic pipes on or under the ground and dripping water and nutrients to each tree or vine. If water is cheap, farmers flood fields with water; if water is expensive, farmers may invest in drip irrigation systems.

The analogy to farm worker recruitment and retention is clear. Do farmers collectively flood the labor market with workers, usually by getting border gates opened or left ajar, so that there are enough workers to fill all seasonal jobs, or do they recruit and retain the best farm workers for their operation? The best way to ensure that there is plenty of irrigation water is to invest in more dams and canals; the best way to flood the labor market is to invest in politicians willing to provide easy access to foreign workers.

Guest Workers: Braceros and H-2A Workers

Foreign-born workers have long been a large share of the hired farm workforce in the western states. Most stayed in seasonal

farm work a generation or less, until they could find nonfarm jobs that offered higher wages and year-round employment. The children of seasonal farm workers educated in the US rarely followed their parents into the fields, so farmers constantly worried about who would replace the farm workers who left for nonfarm jobs.

During the late nineteenth century, most seasonal farm workers on large farms in the western states were Chinese and Japanese, but the source of new farm workers changed in the twentieth century to Mexico. Mexicans were admitted as guest workers under two Bracero (strong arm) programs, one between 1917 and 1921 and the other between 1942 and 1964 (Martin, 2003, Chapter 2). Today, Mexican guest workers are admitted under the H-2A program, a guest worker program that many farm employers consider too bureaucratic and expensive. With half or more of farm workers unauthorized (NAWS), farmers want Congress to modify the H-2A guest worker program or create a new guest worker program for agriculture.

Mexican Braceros

The first Mexico–US Bracero program began on 23 May 1917, as farm employers complained of labor shortages during World War I. The US DOL, which included the Bureau of Immigration at the time, allowed the admission of Mexicans primarily for 'employment in the sugar beet fields of California, Colorado, Utah, and Idaho and the cotton fields of Texas, Arizona, and California' (Scruggs, 1960, p. 322). By the early 1920s, Mexicans were 'the principle workforce in many southwestern farming areas' (Scruggs, 1960, p. 319).

The American-workers-first principle of subsequent guest worker programs was laid out in this first Bracero program. US farm employers had to recruit US workers and to make written offers of 'wages, housing conditions, and duration of employment.' If they could not find US workers, they could hire Mexican Braceros, who were to receive the 'prevailing wage,' which was the wage paid "for similar labor in the community in which the admitted aliens are to be employed." (CRS, 1980, p. 10). Farm employers had to provide housing for Braceros, and this housing had to satisfy state laws or standards set by DOL if there were no state laws governing farm worker housing.

There were several features of the first and subsequent guest worker programs that proved troublesome. For example, some of the wages earned by Braceros were withheld by the US farm employers, deposited with the US Postal Savings Bank, and then transferred to Mexico, where Braceros who returned were supposed to receive these forced savings. However, many returned Braceros never received these withheld wages. A second issue involved the debt accumulated by Braceros in the farm labor camps where they lived. Some Braceros wound up owing more than the wages they earned to the US farm where they worked because of purchases of food and alcohol in the camps. The Mexican government complained about these issues, and the two governments allowed the Bracero program to end in 1921. Some ex-Braceros migrated illegally to the US during the 1920s because there was no US Border Patrol until 1924.

During the 1930s, Dust Bowl migration brought 1.3 million people known as Okies and Arkies to California, swelling the state's population by 25%. Some sought to be farm workers, and they soon learned that California's commercial farms hired crews of seasonal workers when needed, not year-round hired hands who lived and ate with the farmer's family. Some Dust Bowl migrants wound up in tent camps known as Hoovervilles, where unions and 'agitators' highlighted the inequities of large landowners who benefited from government irrigation projects and farm programs but paid seasonal workers low wages only when they were needed. Dust Bowl migrants were US citizens who could vote, and there was concern that Hoovervilles could become a fertile breeding ground for Communists and others who wanted to make major changes in the US socioeconomic system.

Two congressional committees examined farm labor conditions in California and other western states during the late 1930s. They agreed that there were serious problems but disagreed on the appropriate federal response (Martin, 2003, Chapter 2). The House Committee on Un-American Activities warned that dissatisfaction in the Hoovervilles opened the door for Communists and urged vigilance and enforcement against 'Communist agitators.' Many cities and counties in agricultural areas responded with ordinances, later declared unconstitutional, that prohibited 'labor agitation,' rallies, and picketing.

The Senate Education and Labor Committee, however, concluded that the solution to farm labor discontent was to extend collective bargaining rights to farm workers. The National Labor Relations Act of 1935 gave private sector nonfarm workers the right to form unions and to bargain collectively with their employers, in part to reverse the wage cuts that were thought to be prolonging the Depression. However, farm workers were excluded from the NLRA under the theory that most were hired hands with the same interests as farmers, that is, farm workers wanted government programs to raise farm prices, not legal protection to form unions.

Congressional disagreements about how to respond to farm worker's discontent and the outbreak of World War II shifted government's attention elsewhere. The tenor of the farm labor debate changed, from what to do about surpluses of farm workers during the 1930s, to complaints of labor shortages in the early 1940s. California farmers requested Mexican Braceros in 1941, but their request was rejected by the DOL at the behest of the California governor (Rasmussen, 1951, p. 200). However, a federal interagency committee concluded that Mexican workers would be needed to harvest US crops in the fall of 1942, and Mexico and the US signed a new Bracero agreement on 23 July 1942.

The Bracero program was small during World War II, admitting a peak of 62 000 Mexican workers in 1944. However, the program expanded in the 1950s, admitting a peak of almost 450 000 Braceros in 1956. The availability of Bracero guest workers held down farm wages, enabling labor-intensive agriculture to expand in California and other western states at a time when the interstate highway system was reducing the cost of transporting fresh fruits and vegetables for long distances. Rural Mexicans gained familiarity with US farm jobs, and some migrated illegally to the US after the Bracero program ended in 1964. Many Mexican-Americans, who had to compete with Braceros in the fields, moved from the agricultural areas of California to cities such as Los Angeles and San Jose, where there were no Braceros.

Numerous commissions and reports criticized farmers for mistreating and underpaying Braceros and US farm workers, but the CBS documentary, Harvest of Shame, that aired on Thanksgiving Day in November 1960 prompted action. Newly elected President, John Kennedy, ordered the US DOL to enforce minimum wage and other regulations that aimed to protect US and Bracero workers, which raised labor costs and prompted labor-saving mechanization in some field crops including cotton harvesting and sugar beet thinning. The Kennedy Administration announced that the Bracero program would end in 1961, but in response to farm employer pressure, the program continued until 31 December 1964.

H-2A Workers

After the Bracero program ended, many California farmers expected to employ Mexican workers under the H-2 guest worker program, which was established in the 1952 Immigration and Nationality Act and was used to import Caribbean workers who primarily hand cut sugarcane in Florida and harvested apples along the eastern seaboard. Unlike the Bracero program based on a Mexican–US Memorandum of Understanding, the H-2 program was part of the US immigration law.

However, the H-2 program included requirements that drew protests from California farmers, such as a requirement to pay H-2 guest workers the highest of three wages: the federal or state minimum wage, the prevailing wage for similar work in the area, or the DOL-calculated Adverse Effect Wage Rate (AEWR), which was typically the highest of the three. The DOL also limited H-2 guest workers to 120 days in the US, which was not a problem in the eastern states that had shorter growing seasons, but California farmers wanted to employ Mexican workers for 11 months a year.

The DOL Secretary, Wirtz, asserted that the purpose of these H-2 regulations was to reduce admissions of foreign workers in order to reduce unemployment among US farm workers. Farmers were unhappy, and Senators from California and Florida in 1965 introduced legislation to transfer responsibility for certifying farm employer's requests for foreign workers from the DOL to the USDA. Their effort failed on a 46:45 vote because Vice President Hubert Humphrey cast a vote to break the previous tie and keep the administration of the H-2 program within the DOL (Congressional Research Service, 1980, p. 42).

Most H-2 guest workers between the mid-1960s and -1980s were Jamaicans who cut sugarcane in Florida and picked apples from Maine to Virginia. There were ongoing disputes between worker advocates who believed that the DOL was failing to protect US workers and farm employers who believed that the DOL was putting unnecessary hurdles between them and the H-2 guest workers on whom they relied. For example, apple growers sued the DOL when it ordered them to hire inexperienced Louisiana workers who responded to their required recruitment advertisements rather than experienced Jamaican apple pickers. However federal courts ruled that US employers must hire US workers who can do the job even if the foreign workers are more productive.

The H-2 program was changed into the H-2A program by the Immigration Reform and Control Act of 1986, which changed the DOL regulations and incorporated them into law, making them harder to change. Under current regulations, US farmers anticipating shortages of workers to fill temporary or seasonal jobs can request certification from the DOL to employ H-2A guest workers. The DOL certifies farm employer's requests for H-2A guest workers and if it finds that US workers who are 'abled, willing, and qualified' are not and will not be available to fill the job vacancy for which the employer is requesting guest workers and that the employment of the H-2A workers will not adversely affect similar workers, the DOL certifies the farm employer's need for guest workers.

Approximately 7000 farm employers request certification to fill more than 90 000 farm jobs a year with H-2A workers, and the DOL approves more than 90% of their requests. To be certified by the DOL to hire H-2A guest workers, farm employers must offer the highest of the minimum, prevailing, or AEWR wage and free and approved housing, meals, or cooking facilities. They must promise to reimburse workers for their inbound travel costs after 50% of the employer-specified contract is completed and provide work or pay wages for at least three-fourth of the contract period. The employer must submit job offers that include these promises to local Employment Service offices and interview any US workers who respond to their recruitment. Employers attach the DOL's certification to a request to the DHS, which transmits its approval to a US Department of State consulate abroad where foreign workers are given H-2A visas. Most farm employers use an agent or belong to an association that handles the paperwork and visa issuance.

Approximately 10% of H-2A certifications each year are in North Carolina, where the North Carolina Growers Association charges its member growers who primarily produce vegetables and tobacco US$1000 for each H-2A worker. The next leading H-2A states are Georgia and Virginia, where, as in North Carolina, ex-DOL or state officials who used to administer the H-2A program established agencies to help farm employers navigate the certification process. The H-2A program is expanding fastest in Washington, where some apple growers who were required to terminate unauthorized workers, after government audits of their employment records, built the housing required by the H-2A program and were certified to employ H-2A workers (Rural Migration News, 2010).

Proposed Reforms

Farm employers would like three major changes to the H-2A program that could change the farm labor market by increasing the share of guest workers among US crop workers. First, farm employers would like to 'attest' or promise in documents filed with the DOL that they need guest workers and are paying prevailing wages, ending the current processes that involves the DOL supervising their efforts to recruit US workers. Attestation would effectively shift control of the border gate from the US DOL to employers.

Second, rather than provide free housing to H-2A workers, farm employers would like to pay a housing allowance of US $\$1–2\ h^{-1}$, depending on local costs to rent two-bedroom units that are assumed to house four workers, if state governors certified that there was sufficient rental housing for the guest

workers in the area where they would be employed. Substituting a housing allowance for providing housing would make it much easier for farm employers in California and other states where most labor-intensive agriculture is in urban or metro counties with strict zoning regulations to hire guest workers.

Third, farmers would like the AEWR, the special minimum wage that must be paid to guest workers, to be rolled back and studied. The AEWR for California in 2012 was US$10.24 h^{-1}, whereas the state's minimum wage was US$8, so reducing the AEWR to US$9 h^{-1} or less would help to offset the cost of the housing allowance.

These three employer-favored reforms to the H-2A program are included in the Agricultural Jobs, Opportunity, Benefits, and Security Act (AgJOBS), a proposal negotiated between farm worker and farm employer advocates in the fall of 2000 (Martin, 2005). Many farm worker union and farm employer groups support AgJOBS, but not the American Farm Bureau Federation, which in the fall of 2012 unveiled its own proposed new guest worker program that was embraced by many other farm groups that joined the Agriculture Workforce Coalition (www.agworkforcecoalition.org).

Under the AFBF proposal, farm employers would have two options to employ guest workers. The first would give an unlimited number 11-month visa to foreign workers who could move between different US farm employers who were registered with the USDA. These free-agent guest workers would have to leave the US for a month a year but could return year after year. The second option would allow farm employers to offer renewable 12-month visas to foreign workers who would be tied to their farms. These contract workers would have to leave the US at least 30 days every 3 years.

Unions

Unions are organizations of workers whose purpose is to raise wages and improve conditions for members who pay the dues that support the union. Unions put pressure on employers in four major ways – with strikes that reduce the supply of a good or commodity; activities that reduce the supply of labor or preserve jobs, such as limits on immigration or clauses in collective bargaining agreements that limit mechanization; political activities to obtain favorable laws and their interpretation; and consumer boycotts to reduce the demand for particular commodities. Employers counter these union weapons by replacing workers who strike, engage in political activities to win laws favorable to management rights, and by advocating more immigration and other policies that increase the supply of labor.

US union membership has been in a long-term decline, so that only 11% of the 128 million wage and salary workers were union members in 2012, down sharply from 20% in 1983 (www.bls.gov/news.release/union2.nr0.htm). There were 14.3 million union members in 2012, including seven million private sector workers and 7.3 million public employees. Local government workers had the highest unionization rate, 42%, whereas agriculture had the lowest, 1.4%. By occupation, education workers had the highest unionization rate, 35.4%, and farming had the lowest rate, 3.4%.

Farm workers are an attractive target for unions because there are millions of farm workers, their wages are relatively low, and farm workers have been receptive to promises of higher wages and better working conditions. But organized farmers had the upper hand over unorganized farm workers throughout most of the twentieth century, largely because most farm workers found it easier to exit the farm labor market for upward mobility rather than join or form a farm labor union to voice collective demands for higher wages and benefits. As a result, there have been few persisting union–management agreements in agriculture. The longest collective bargaining relationship in California agriculture is between the Teamsters and Bud Antle (now Dole Food Company), which began in 1961. US unions such as the United Auto Workers and the United Steel Workers, by contrast, have had continuous relationships with major auto and steel makers since the mid-1930s.

The scarcity of union–management agreements in agriculture, and the fact that few have persisted, reflects several factors including the tendency of the most able farm worker union leaders to move on to nonfarm jobs and the fact that many farm worker organizers in the past were radicals seeking to transform the economy. During the twentieth century, farm employers often unified rural residents and local law enforcement agencies against 'outside agitators,' and federal and state governments were slow to extend labor relations rights to farm workers, making it hard to develop sustainable farm worker unions.

Pre-UFW Unions

The American Federation of Labor (AFL) began as a national organization of craft unions in 1886. The AFL's member unions, such as carpenters or bricklayers, organized workers into unions that reflected worker crafts or occupations. In 1903, several AFL unions announced plans to organize farm workers, but their union drive soon sputtered, in part because the AFL unions feared that organizing farm workers would upset farmers, who could use their power in Congress and state legislatures to restrict all union activities.

The Industrial Workers of the World (IWW) or 'Wobblies' was a revolutionary union founded in 1905 by Eugene Debs and other radical labor leaders who felt betrayed by the AFL unions. Their goal was to replace what the IWW called a 'wage slave system' of employers and employees with worker-run cooperatives. The IWW wanted to organize all workers into 'one big union' that included skilled as well as unskilled workers and minorities such as Chinese and Japanese farm workers, who were excluded from most AFL unions.

The IWW successfully organized many of the wheat harvesters in the Midwestern states early in the twentieth century. A peak of 250 000 mostly white workers migrated from Texas to Canada, harvesting wheat and other grains from south to north. Most traveled by riding freight trains without paying, and migrants without an IWW 'red card' were sometimes prevented from riding the rails. A typical IWW 'plan of action' at a particular farm involved an IWW organizer or 'job delegate' getting a job and helping the workers to organize a strike.

Some employers tried to harvest crops with strikebreakers, which often led to violence and the arrest of 'outside agitators.'

In California, IWW organizers targeted migrants who harvested wheat, the so-called 'harvest or bindle stiffs' (Steven Street, 1998). IWW organizers mingled with farm workers during the winter months when they 'holed up' in cities, explaining from soapboxes why workers needed to support radical change in the US economic system to improve their wages and living conditions. Local authorities often used unconstitutional means to restrict the activities of IWW organizers, which gave its message more publicity. For example, Fresno in 1910 denied IWW organizers the right to make speeches and distribute literature, but publicity about this unconstitutional interference with free speech helped to raise awareness of and membership in the IWW. The IWW claimed 10 000–12 000 members in northern California in 1912 (Jamieson, 1945, p. 60).

The Wheatland hops riots of 1913 illustrate the clash of extremes in farm fields that led to violence and ultimately the demise of the IWW (Jamieson, 1945, 60–63; Daniel, 1981, 89–91). Wheatland is a small community 30 miles northeast of Sacramento in Yuba County, and harvesting the hops used to make beer was labor intensive. Many harvesters were white men who responded to handbills distributed by farmers such as Durst, who advertised for 2700 workers to harvest hops in August 1913 and at a higher-than-usual piece-rate wage of US$1 per 100 pounds.

When 2800 workers traveled to Wheatland, Durst cut the piece rate to US$0.90, because he had housing only for 1700 workers. The workers protested, and IWW organizers helped them to form a protest committee and demand that Durst pay the US$1 advertised wage. Durst called the local sheriff on 3 August 1913, saying that the IWW was trying to take over his ranch. When the sheriff tried to arrest strike leaders, a district attorney, deputy sheriff, and two workers were killed. Most of the workers on the Durst ranch left before the National Guard arrived to restore order, and no contract was signed between Durst and the IWW.

IWW leaders were convicted of inciting a riot and were sentenced to prison. Governor Hiram Johnson appointed a Commission on Immigration and Housing in 1913 to examine what became known as 'the first California labor cause célèbre.' Economist Carleton Parker concluded that the Wheatland riot "embodied the state's great migratory labor problem," the broken wage promises of employers (Daniel, 1981, p. 91). Parker and the Commission urged growers, despite the 'general superabundance' of farm workers, to honor the wage promises they made in handbills and urged the state to enact and enforce housing and sanitation standards in farm labor camps.

The peak year for farm worker strikes was 1933, and the reason was that the prices received by farmers rose but farm worker wages did not. Farmers' prices fell between 1929 and 1932, the US unemployment rate reached 24%, and the farm workforce swelled with urban workers who lost their jobs returning to the fields. California farmers cut wages from 35–50 cents an hour in 1929–30 to 15–6 cents in 1933. The Communist-dominated Cannery and Agricultural Workers Industrial Union (CAWIU) followed the IWW pattern of taking over the leadership of spontaneous worker protests and strikes and helping workers to present demands to employers. CAWIU-led strikes were often violent, in part because growers and their foremen were often deputized to help local law enforcement.

There were 37 strikes involving 48 000 farm workers in 14 crops in California in 1933, culminating in an October cotton harvesters strike. Harvest-time strikes during the spring and summer usually resulted in wage increases, so that by fall, workers were prepared to strike again to get a wage increase for picking cotton, the crop that employed most of the workers. Cotton farmers met in September to set a piece-rate wage of pay 60 cents per 100 pounds of cotton picked, up from 40 cents in 1932 but less than the US$1.50 of 1929. Cotton harvesters were expecting wages to rise to at least US$1, and the CAWIU called a strike on 4 October 1933 to support its demand for a US$1 per 100 pound piece rate. Growers evicted 10 000–20 000 strikers and their families from on-farm labor camps, and most moved into CAWIU-run tent camps.

The strike was condemned by farmers but were supported by local leaders. A Tulare newspaper editorialized that "the strike would vanish into thin air overnight if the outside agitators were rounded up and escorted out of the county, as they should be" (Jamieson, 1945, p. 103). Farmers tried to break up striker rallies, and two workers were killed in Pixley, CA, USA. State officials urged local authorities to disarm the growers, who instead issued more gun permits, prompting the reporters who arrived to cover the strike to turn against growers for refusing mediation.

The strike threatened the cotton crop. The Governor appointed a UC fact finding missions that recommended a 75-cent piece rate. Banks persuaded farmers to pay 75 cents by threatening to withhold financing for the 1934 cotton crop, and the Governor announced that workers who did not go to work by 16 October 1933 would be denied state relief in the winter months. The 75-cent wage appeared to be at least a partial victory for the CAWIU, and it prompted farmers to form a new organization, the Associated Farmers of California, which persuaded most rural counties to enact antipicketing ordinances that were used to prosecute CAWIU organizers.

The Associated Farmers, financed largely by nonfarm banks, railroads, canneries, public utilities, and the Industrial Association of San Francisco, provided funds to local law enforcement to monitor CAWIU leaders. It succeeded, and 14 CAWIU leaders were convicted of instigating violence and were sent to prison in July 1934. The CAWIU showed that farm workers could be organized to strike in support of higher wages, but the CAWIU's policy of not signing contracts, and its communist orientation, persuaded growers to organize themselves into effective antiunion associations.

United Farm Workers

Cesar Estrada Chavez (1927–93) is the best-known US Mexican-American: more US schools, streets, and libraries are named after Chavez than any other Hispanic. Chavez was born in Arizona, and his family lost its farm and became migrant farm workers in the 1930s.

Chavez left a job registering voters in the Sal Si Puedes (Get out if you can) barrio of San Jose, California, in 1962 to help

farm workers in the Tulare county city of Delano. With the help of school teacher Dolores Huerta, Chavez launched the Farm Workers Association (FWA) to help farm workers with government paperwork in exchange for US$3.50 monthly dues. In 1964, the FWA was renamed the National FWA (NFWA), and in 1965 the NFWA conducted a successful rent strike against the public housing authority in Tulare County.

In the spring of 1965, when Coachella Valley table grape growers offered workers US$1.25 h^{-1}, the Filipino-dominated Agricultural Workers Organizing Committee called a strike against to demand the same US$1.40 h^{-1} that had been paid to Mexican Braceros in 1964. Growers raised to US$1.40 did not recognize the AWOC as the representative of table grape pickers. When the harvest moved north to Delano, growers again announced a US$1.25 h^{-1} wage, prompting the AWOC to strike on 8 September 1965 for US$1.40 h^{-1}. Chavez's NFWA joined the AWOC, and growers harvested their grapes with FLC-supplied workers and did not recognize the AWOC–NFWA as a union for their workers. The AWOC–NFWA merged into the UFW union in 1967 (www.ufw.org).

Chavez quickly assumed leadership of the strike and urged a consumer boycott and nonviolent resistance to turn the struggle over wages into a case of powerless farm workers against powerful agribusiness. His major innovation was to apply pressure to growers when there were no crops to be harvested, and to enlist unions, churches, students, and politicians to picket liquor stores before Christmas 1965, urging Americans not to buy the liquor products of Schenley, a conglomerate with 3350 acres of vineyards near Delano.

The Schenley boycott was successful: liquor sales fell, and Chavez kept the boycott in the news with a succession of high-profile visitors to Delano. For example, the US Senate Subcommittee on Migratory Labor held a hearing in Delano in March 1996 that featured a televised argument between Senator Robert Kennedy (D-MA) and the Kern County sheriff over constitutional rights. The sheriff said that he arrested UFW supporters because he knew they were about to break the law, prompting Kennedy to counter that Chavez and the farm workers had the right not be arrested until they broke laws. The NFWA began to march from Delano to Sacramento on 17 March 1966, and as the marchers neared Sacramento for an Easter Sunday rally, Schenley agreed to raise wages by 40%, from US$1.25 to US$1.75 an hour, approximately twice the minimum wage.

The UFW collected signatures from farm workers that authorized the UFW to represent them at other farms. It then sent letters to farmers asserting that the UFW represented their workers and asked the farmer to sign the union's standard contract or begin negotiations. If the farmer refused, the UFW threatened a consumer boycott, and its boycott threats led to contracts with wineries including Almaden, Christian Brothers, and Paul Masson.

The UFW in January 1968 sent we-represent-your-workers letters to the state's table grape growers. The growers did not respond, and the UFW launched a nationwide boycott of grapes, La Causa, that made Cesar Chavez a household name. The grape boycott is considered one of the most successful consumer boycotts in the US history. According to a September 1975 Harris poll, 12% of Americans avoided grapes in the late 1960s and early 1970s, and per capita grape consumption fell from 3.4 pounds per person in 1968 to 2.2 pounds per person in 1970–71. Chavez, hailed as the Latino Martin Luther King, was featured on the cover of Time magazine on 4 July 1969 under the headline, The Grapes of Wrath.

Grape grower Lionel Steinberg signed a contract with the UFW on 10 April 1970, ending La Causa. Other grape growers followed, signing contracts that offered harvesters US $1.75 h^{-1}, and the UFW soon had 150 contracts covering 20 000 workers. The contracts included clauses restricting mechanization and pesticide usage, and the UFW announced plans to follow in the footsteps of construction and longshoremen unions by being the organizing institution in what had been a casual labor market, with UFW hiring halls allocating work according to each worker's seniority with the UFW.

The UFW had a rival, the Teamsters union that represented truck drivers as well as many of the workers employed in canneries and processing sheds. When the UFW sent its 'we-represent-your-workers' letters to lettuce growers in 1970, most responded that their field workers were already represented by the Teamsters. The UFW attacked the Teamsters and the growers, emphasizing that many workers did not know the Teamsters represented them and that 'secret contracts' were signed to avoid the UFW.

The UFW was an early supporter of the Democratic candidate for governor in 1974, Jerry Brown. After he won the November 1974 election, Brown made the enactment of a farm labor relations law his top priority. The Agricultural Labor Relations Act (ALRA) was signed into law on 5 June 1975 so that the first elections could be held during the peak harvest period, and 15 artichoke workers employed by Molera Agricultural Group near Castroville made history by casting votes in the first Agricultural Labor Relations Board (ALRB)-supervised election in September 1975. The UFW and the Teamsters competed vigorously in these first ALRA elections. There were elections on five or more farms every day in the fall of 1975, a total of 418 in the first 5 months the ALRA was in effect. The UFW won 198 or 55% of the 361 elections in which a winner was certified, and the Teamsters 115% or 32%.

Unionization was expected to transform to farm labor market, double farm wages in California and the rest of the US, and close the farm–nonfarm wage gap. However, experienced observers were more skeptical about unionization. Fuller and Mason (Fuller and Mason, 1977 p. 80) concluded that farm worker unionization will "continue to be more exceptional than dominant" (1977, p. 79), but added that farm worker unions representing a small share of farm workers could nonetheless 'become politically influential with respect to laws and programs affecting all farm workers.'

Rising farm wages and the introduction of fringe benefits for unionized farm workers raised labor costs and spurred efforts to develop labor-saving machines including some developed by the University of California researchers. The UFW and the California Rural Legal Assistance organization sued the UC in 1978, charging that researchers were using tax monies to develop machines that displaced farm workers and small farmers. Stopping mechanization research became the UFW's 'No. 1 legislative priority' (Business Week, 30 January 1978) and was largely achieved as rising unauthorized migration weakened the UFW and reduced wage increases (Martin and Olmstead, 1985).

In 1979, the UFW won a Pyrrhic victory from which it never recovered. In the Imperial Valley next to the Mexican border, the UFW had expiring contracts with 26 vegetable growers. Most were negotiated in 1975–76 and raised wages from US$3.11 h^{-1} to US$3.70 h^{-1} by 1978; the federal minimum wage rose from US$2.10 in 1975 to US$2.65 in 1978. The UFW demanded a 42% wage increase for entry-level workers, which would have raised them from US$3.70 h^{-1} to US$5.25 h^{-1} and, according to farm employers, more than doubled labor costs. Growers countered with an offer of a wage increase of 21% over 3 years, prompting the UFW to call strikes in mid-January 1979. The UFW and employers placed advertisements in Mexicali newspapers (most workers lived in Mexico and commuted daily to US farm jobs), explaining the demands and offers.

The strike involved some 4300 workers and affected some of the largest vegetable growers, including Bruce Church and Sun Harvest, a subsidiary of United Brands (Chiquita bananas). The UFW complained that growers encouraged unauthorized migration to get strike breaking workers from Mexico, battles on the picket lines resulted in the death of a UFW member. The strike and disease reduced the supply of winter lettuce by one-third. However, the demand for lettuce is relatively inelastic, meaning that the quantity sold does not vary much with its price, so lettuce prices tripled and grower revenues doubled (Carter *et al.*, 1981). Many sympathetic observers questioned the UFW's strategy. One article noted, "Although Chavez claims the union is striking to win wage parity with industrial workers, most observers say he purposely brought on the strike in an attempt to rally the union." (Business Week, 5 March 1979).

The UFW strike was losing momentum in the summer of 1979, when Meyer Tomato in the Salinas Valley agreed to raise wages by 43% over 3 years to US$5.29 h^{-1} by 1982. The wage leader, Sun-Harvest, agreed to a US$5.25 minimum wage and newspapers hailed the 'record contracts' won by the UFW. The UFW charged that the lettuce growers who did not sign contracts offering US$5.25 h^{-1} violated the ALRA by failing to bargain in good faith when they broke off negotiations, raised wages, and began to hire replacement workers. The ALRB agreed with the UFW and ordered the Imperial Valley growers to pay tens of millions of dollars of makewhole wages and benefits to farm workers including those who went on strike. This ALRB decision was eventually overturned by appeals court rulings that the growers were engaged in hard rather than unlawful bargaining, and many of the firms that signed contracts with the UFW went out of business or did not renegotiate with them.

The UFW lost contracts and influence in the 1980s and was only a shadow of its former self when Chavez died in 1993. President Clinton awarded Chavez a posthumous Medal of Freedom in 1994, and Chavez was widely hailed as the Latino Martin Luther King who used a union of farm workers to call attention to the issues of Hispanic farm workers. Chavez said he wanted to be remembered for "attack[ing] that historical source of shame and infamy that our people in this country lived with: the humiliation brought upon generations of dark-skinned farmworkers by corporate agribusiness."

Arturo Rodriguez, Chavez's son-in-law, became the new UFW president in 1994 and settled many long-running labor disputes by dropping charges that particular employers violated the ALRA in exchange for contracts. For example, the UFW settled a long-running dispute with lettuce grower Bruce Church Inc (BCI) in May 1996 by signing a 5-year collective bargaining agreement, but BCI soon stopped growing lettuce. The UFW won a mandatory mediation amendment to the ALRA in 2002 that allows either employers or unions to request mediation to negotiate a first contract. If the mediator fails to help the parties reach agreement, he can recommend a contract that the ALRB can impose on the parties (Martin and Mason, 2003).

Unions play a relatively small role in the farm labor market of California and most other major farming states. Four major explanations have been advanced for the relative paucity of unions in agriculture: union leadership failures, politics, farm employer changes, and immigration. The union leadership failure is the most common explanation, with most analyses asserting that Cesar Chavez was a charismatic leader able to articulate the hopes of farm workers, but Chavez and the UFW were unable to negotiate and administer union contracts to the satisfaction of employers and experienced farm workers. As workers left for nonfarm jobs, the UFW was unable to organize newcomer farm workers (Pawel, 2009; Ganz, 2009).

The second explanation involves the politics surrounding the ALRB, the state agency that administers the ALRA. Democratic governors made key appointments to the ALRB between 1975 and 1982, Republicans between 1983 and 1998, Democrats between 1999 and 2004, Republicans between 2005 and 2011, and Democrats since then. This 'it's-all-politics' theory holds that the effectiveness of a self-help labor relations law depends on which party makes appointments to the ALRB, the agency that enforces the law (Majika and Majika, 1982).

The third explanation emphasizes that union successes of the 1960s and 1970s were mostly with employers who hired farm workers directly and had brand names that made them vulnerable to union-led boycotts of their farm and nonfarm products. Boycott-vulnerable corporations such as Seven-Up, Shell Oil, and United Brands sold their California farming operations in the 1980s, and the UFW found it harder to deal with the independent growers who replaced them. There was also an increase in the use of intermediaries such as contractors, and the combination of independent growers and intermediaries such as FLCs reduced union power.

The fourth explanation is immigration. The UFW had its maximum impacts on farm wages between the mid-1960s and the early 1980s, when legal and unauthorized immigration was low. (Illegal) migration began rising in the 1980s, rose more in the 1990s, and peaked during 2002–07, when an estimated 500 000 unauthorized foreigners a year, including 300 000 Mexicans, settled in the US. These migrants increased the supply of farm workers and made it hard for unions to win wage and benefit increases via collective bargaining (Martin, 2009).

Farm Labor Organizing Committee (FLOC), Coalition of Immokalee Workers (CIW), and Other Unions

States with large numbers of farm workers include California, Florida, North Carolina, Texas, and Washington. There is a

significant farm worker union activity in North Carolina and Florida.

The Ohio-based FLOC, founded in 1967 by Baldemar Velasquez, became a union in 1979 and refined the UFW's boycott strategy (www.floc.com). FLOC threatened consumer boycotts of the pickle and tomato products processed and sold by food companies such as Campbell's and Heinz unless they persuaded the farmers who grew pickles and tomatoes, and hired workers to pick them, to recognize FLOC as the farm workers' bargaining representative.

In 1985, after a march from Ohio to Campbell headquarters near Philadelphia, FLOC reached three-way agreements with Campbell's Vlasic subsidiary and its tomato and pickle growers in Ohio and Michigan. Farmers who wanted to grow tomatoes and cucumbers for Vlasic recognized FLOC as the union for approximately 800 farm workers, and Vlasic raised the prices it paid to farmers to cover the higher wage and benefit costs of the contracts. Because farm workers are not covered by labor relation laws, there was no need for elections to determine worker preferences, and there were none. FLOC has offices in Florida, where many of the cucumber pickers live when they are not in Ohio, and in North Carolina, where FLOC represents pickle harvesters employed by growers who deliver cucumbers to Mount Olive.

FLOC is pressuring tobacco firms to establish labor standards for the farms from which they buy tobacco, extending its strategy of using pressure on buyer of farm commodities to improve wages and working conditions for farm workers. Reynolds American in 2012 agreed to meet with FLOC and discuss the conditions of workers on the North Carolina farms from which it buys tobacco. FLOC says that 30 000 workers are employed in North Carolina tobacco fields and it represents 27 000 farm workers in Ohio and North Carolina.

The CIW in Florida tried to persuade tomato growers to raise piece-rate wages for a decade before turning to a boycott of fast-food chains that bought mature-green tomatoes (www.ciw-online.org), those that are picked green and ripened with ethylene to turn them red. Beginning with Taco Bell in 2005, most major fast-food chains signed agreements with the CIW, agreeing to pay an additional 1.5 cents a pound for the Florida tomatoes they buy, with one cent going to pickers, doubling the usual US$0.35 for picking a 35-pound bucket of tomatoes to US$0.70.

The CIW's Fair Food Program (FPP) includes mandatory training on worker rights and a grievance procedure. Tomato growers found to be in violation of FPP standards risk lose the right to sell to fast-food chains. The Fair Food Standards Council (http://fairfoodstandards.org), which monitors and audits the FPP, reported that US$6 million in extra payments were made to tomato pickers in 2010–11 and 2011–12.

Collective bargaining aims to enable farm workers to help themselves to increase wages and working conditions. During the twentieth century, farm worker union activities have been 'much ado about nothing' because diverse farm workers often share only one goal: finding a better nonfarm job as soon as possible.

Farmers have been well-organized to resist farm worker unions, and the federal government has not extended labor relations rights to farm workers.

At the dawn of the twenty-first century, there is more agreement on trends affecting farm workers and the farm labor market than on what these trends mean for unions and collective bargaining. The major trends likely to influence the relative strength of unions and farm employers include: the rapid growth of the Hispanic population, presumed to be sympathetic to farm worker unions and thus to increase support for boycotts; continued immigration that may make it hard for unions to use traditional weapons such as strikes to push up wages; and changes in the food sector, such as the consolidation of grocery stores that tends to put downward pressure on farm prices. Farm worker unions believe that an amnesty for currently unauthorized farm workers would embolden them to join unions and press for wage increases. Farm employers prefer guest workers who may be harder to organize.

The realization by farm worker unions and farm employers that their struggles are being played out on a larger stage has broadened the interest of unions in pesticides, water, and other issues. The UFW, for example, remains a major player in Democratic Party politics in California and influences especially Latino lawmakers on issues such as allowing farmers to sell their water to cities, benefiting the farmers but reducing jobs for farm workers, using state funds to promote farm commodities, and developing tighter regulations on pesticides.

Conclusions

Agriculture is a peculiar industry with a unique labor market. The three R-functions of all labor markets are dealt with differently in agriculture. Farmers often rely on intermediaries such as contractors to assemble crews of workers and move them from farm to farm, many farm operators use piece-rate wage systems to give workers an incentive to work fast without close supervision, and farm employers have more often cooperated to ensure that they collectively have enough seasonal workers to fill farm jobs rather than individually developing mechanisms to identify and retain the best workers on their particular farm.

Approximately three-fourths of US hired farm workers were born abroad, usually in Mexico, and half of all farm workers are not authorized to work in the US. Farm employers believe that US workers shun especially seasonal farm jobs and want the government to make it easier for them to hire foreigners as legal guest workers. Twice in the past, between 1917 and 1921 and again between 1942 and 1964, the US government allowed farmers to recruit Mexican Braceros to fill seasonal farm jobs. A separate guest worker program, H-2 between 1952 and 1986 and H-2A since 1987, is used mostly by farm employers in the eastern states to recruit foreign workers to fill seasonal jobs. US farmers have been asking Congress to relax regulations governing the H-2A program for the past two decades, especially rules that require them to try to recruit US workers, to provide guest workers with free housing, and to pay them a super minimum wage known as the AEWR.

Guest workers change the farm labor market by altering recruitment, remuneration, and retention, with agents handling recruitment in worker countries of origin, guest workers who are aware that termination means losing the right to be in

the US having extra motivation to perform work to the satisfaction of the employer, and retention not an issue because guest workers must leave the US when their jobs end or visas expire. Farm worker unions change the farm labor market in opposite ways. Unions often want a voice in recruitment, and some have tried to operate hiring halls to which employers turn when they need workers. Unions generally favor wage-leveling pay systems and often establish higher-than-minimum wages for the workers covered by the contract. Finally, union contracts usually include seniority and benefit provisions that make it worthwhile for a worker to remain with one farm.

The farm labor market today is at a crossroads. Farm employers and farm worker advocates agree that government policies, especially immigration policies, are likely to shape recruitment, remuneration, and retention. Employers would like more farm workers to be legal guest workers, whereas worker advocates favor legalizing currently unauthorized workers and encouraging farmers to raise wages and take other steps to retain them.

See also: Agricultural Labor: Demand for Labor. Agricultural Labor: Gender Issues. Agricultural Labor: Supply of Labor

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Relevant Website

www.doleta.gov/agworker/naws.cfm
NAWS. National Agricultural Worker Survey.

Agricultural Labor: Supply of Labor

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Introduction

Food and fiber is produced on farms in a land-intensive and biological production process by three major types of workers: farm operators, unpaid family workers, and hired workers. Around the world, 59% of the estimated 1.1 billon people employed on farms in 2000 were farm operators and members of their families, and 450 million or 41% are hired or wage workers (Pigot, 2003, p. 38).

The employment of all three types of workers on farms falls with economic development, but the employment of farmers and unpaid family members tends to fall fastest. In the US, hired workers were approximately 60% of average employment on farms in 2010, and farmers and unpaid family members approximately 40%. The consolidation of farms into fewer and larger units that specialize in the production of one or a few crop or livestock commodities promises to further increase the farm worker share of average employment on US farms.

Consolidation of farm production on fewer and larger farms, with hired workers doing an ever rising share of farm work, is occurring around the world. Hired workers do most of the farm work in the production of labor-intensive horticultural crops in Western European countries, and many are migrants from poorer countries, as with Poles employed on German farms, Ukrainians employed on British farms, and Romanians employed on Italian farms. In Japan and Korea, migrants from the Philippines and Vietnam often work on farms that produce labor-intensive crops, as the wives of farmers, as trainees, and as guest workers. In many developing countries, workers from lower wage neighboring countries do much of the work on larger farms and plantations, from Malaysia and Thailand in southeast Asia to South Africa to Costa Rica. This article focuses on the US, which has some of the world's largest labor-intensive farms that hire workers, but the trend toward producing labor-intensive crops on so-called factories in the fields and employing workers who migrate from lower wage areas within their country or another country is universal.

In the US, agriculture is defined for employment purposes in Section 3(f) of the Fair Labor Standards Act (www.dol.gov/whd/regs/statutes/FairLaborStandAct.pdf) as "farming in all its branches…including the cultivation and tillage of the soil, dairying, the production, cultivation, growing, and harvesting of any agricultural or horticultural commodities…the raising of livestock, bees, fur-bearing animals, or poultry, and any practices (including any forestry or lumbering operations) performed by a farmer or on a farm as an incident to or in conjunction with such farming operations, including preparation for market, delivery to storage or to market or to carriers for transportation to market." One practical consequence of this definition is that workers who pack produce on the farm where they work are considered farm workers if the farmer packs only his own fruit. By contrast, farmers who pack their own and other farmers' fruit employ nonfarm workers in what are considered nonfarm operations.

Farm workers (45–2092.02) are defined in the US occupational system ONET as persons who "manually plant, cultivate, and harvest" crops with hand tools that range from hoes to knives. Their job titles include harvester, orchard worker, picker, farm worker, irrigator, and weeder (http://www.onetonline.org/link/summary/45–2092.02). The list of farm worker-related occupations (http://www.onetonline.org/find/quicks=farm+worker) includes agricultural equipment operator (45–2091.00), farm equipment mechanic (49–3041.00), and farm workers who attend to live farm, ranch, or aquacultural animals (45–2093.00).

Hired workers are not spread evenly throughout the US agricultural sector. Almost 500 000 US farms, a quarter, reporting expenses for hired workers in the 2007 Census of Agriculture (COA), but half of these US$26 billion in farm labor expenses, were paid by less than 75 000 producers of labor-intensive fruits, berries and nuts, vegetables, potatoes and melons, and horticultural specialties such as greenhouse and nursery crops (Fruit, Vegetable, and Horticultural speciality (FVH) commodities). Most farm labor expenses were paid by large farm employers in California, Florida, Texas, and Washington, demonstrating that hired farm worker employment is concentrated in three interrelated ways, by commodity, size of farm, and geography.

Hired farm workers, especially those employed on farms producing FVH commodities, are mostly immigrants from Mexico. Before the Immigration Reform and Control Act (IRCA) of 1986, the best evidence suggested that up to a quarter of hired farm workers in southwestern states such as California were unauthorized (Martin *et al.*, 1985). Before IRCA, farmers did not face fines for hiring unauthorized workers, and their distribution in agriculture reflected the risk of losing their workers if immigration authorities drove into fields and checked the legal status of workers. For example, the highest share of unauthorized workers was found in less perishable crops such as citrus. There were fewer unauthorized workers in more perishable leafy green vegetables where producers could lose revenue if their workers were apprehended.

Since the mid-1990s, over half of hired farm workers employed on US crop farms have been unauthorized (Martin, 2009). In contrast to the distribution of unauthorized workers before immigration reform, unauthorized workers today are found throughout the US agricultural sector, including on dairy and other livestock farms that offer year-round jobs. The share of unauthorized workers, approximately 50%, is similar from Vermont dairies and North Carolina vegetable fields to California fruit and vegetable farms.

This article summarizes the characteristics of hired workers employed on US farms. Data are drawn primarily from the US Department of Labor's National Agricultural Workers Survey (NAWS), which has been interviewing 2000–3000 farm

workers a year since 1989 (www.doleta.gov/agworker/naws.cfm). The NAWS was launched to determine if immigration reforms enacted in 1986 contributed to farm labor shortages, and has continued to generate a wealth of information on hired farm workers and their families. The NAWS does not interview workers employed on livestock farms and excludes H-2A guest workers on crop farms.

Farm Employment

In the US and many other industrial countries, hired workers dominate average agricultural employment. During the 1990s, when USDA's National Agricultural Statistics Service (NASS) collected data on farmers, unpaid family workers, and hired farm workers, there were an average 2 million farmers and unpaid family workers and 1.3 million hired workers employed on US farms, meaning that farmers and unpaid family members accounted for 60% of average farm employment.

The employment of all three types of workers on farms have trended downward, but the employment of farmers and unpaid family members fell fastest, so that hired workers were approximately 60% of average employment on farms in 2010. The labor force projections in **Table 1** suggest that the number of farm operators and unpaid family members will continue declining, whereas the number of hired workers stabilizes, so that the share of average employment contributed by hired workers rises to 62% by 2020.

The most detailed source of data on farm employment is from the COA that the US and most other countries conduct periodically (www.agcensus.usda.gov/index.php). In the US, all places that normally sell at least US$1000 worth of farm commodities are surveyed in the years ending in two and seven. Some 482 000 US farms reported almost US$22 billion in labor expenses for workers hired directly by the farm operator in the 2007 COA, and another US$4.5 billion for contract labor, which involves workers brought to farms by labor contractors and other intermediaries. Total labor expenses of US$26 billion were a seventh of farm production expenses.

Farmers reported hiring 2.6 million workers in the 2007 COA, including 35% or 910 000 workers who were hired for 150 days or more on their farms. This 2.6 million jobs-on-farms number must be interpreted carefully because it does not include workers brought to farms by contractors and other intermediaries, and it double counts individuals who are reported by two farmers.

There are several ways to convert the total number of farm jobs into average employment or year-round equivalent jobs in order to compare farm and nonfarm employment. For example, average employment is approximately 1.5 million in US food manufacturing (North American Industry Classification System (NAICS) 311), which means that adding up the employment of wage and salary workers each month in industries ranging from meatpacking to fruit and vegetable freezing and canning and dividing by 12 months generates an average 1.5 million employees. Hired farm workers are not included in the Current Employment Statistics program (www.bls.gov/ces), so their average employment must be estimated.

Average employment of hired workers on farms can be estimated by dividing the farmers' expenditures on hired workers by average hourly earnings to calculate the number of year-round or 2000 h-jobs on farms. The NASS surveys farm employers quarterly to obtain employment and earnings data on hired workers (http://usda.mannlib.cornell.edu/MannUsda/viewDocumentInfo.do?documentID=1063). In 2007, NASS reported that farmers paid hired workers an average US $10.21 an hour, the same year that farmers reported US$26.4 billion in labor expenses. Dividing labor expenses by average hourly earnings, as in **Table 2**, suggests 1.2 million full-time equivalent (FTE) or 2000 h a year jobs on US farms in 2007, about the same as average employment in 2002 using that year's labor expenses and average hourly earnings.

The Quarterly Census of Employment and Wages (www.bls.gov/cew) collects data on the employment and earnings of workers in establishments covered by Unemployment Insurance (UI). The QCEW has several advantages over the COA, including detailed data by commodity and geographic area, but its coverage of farm workers is not complete. All farm workers in

Table 2 US: Hired worker hours, 2002 and 2007

	2002	*2007*
Farm sales (US$billion)	200	297
Labor expenditure (US$billion)	22	26
Sales to expendure ratio	9.1	11.4
Average earns (US$/h)	8.80	10.21
Hours worked (mils)	2 500	2 547
FTE jobs (2080 h)	1 201 923	1 224 290

Source: Reproduced from Census of Agriculture and NASS Farm Labor.

Table 1 US: Total and hired worker employment (thousands): 2000, 2010, and 2020

Sector and labor type	*2000*	*2010*	*2020*	*Change (%)*	
				2000–10	*2010–20*
Agriculture	2 396	2 135	2 005	–11	–6
Wage and salary	1 354	1 282	1 236	–5	–4
Operator and family	1 042	853	769	–18	–10
US total	143 236	143 068	163 536	0	14

Source: Reproduced from Sommers, D., Franklin, J., 2012. Overview of projections to 2020. Monthly Labor Review 135 (1), 3–20. Available at: http://www.bls.gov/opub/mlr/2012/01/ (accessed 04.02.13) and Henderson, R., 2012. Industry employment and output projections to 2020. Monthly Labor Review 135 (1), 65–83. Available at: www.bls.gov/opub/mlr/2012/01/ (accessed 04.02.13).

major farming states such as California and Washington are covered, but workers employed by smaller farm employers in about half the states do not have to participate in UI. The QCEW estimated that 1.2 million of the average 1.4 million hired farm workers in 2011, almost 86%, were covered, reinforcing the estimate that the average employment of hired workers on US farms is 1.2–1.4 million (www.bls.gov/cew/cewbultn11.htm).

There are more farm workers than the average employment of hired workers on US farms because of seasonality and turnover, that is, more than 1.2 million individuals work on farms during a typical year in order to fill peak employment requirements and to account for the fact that many workers are employed less than a full year. During the 1980s, the number of unique individuals employed sometime during the year for wages on farms was 2.5 million, according to supplemental questions attached to the December Current Population Survey (CPS) that generates the unemployment rate each month (Oliveira, 1989).

The CPS farm worker supplement was discontinued, but a count of unique individuals reported by agricultural establishments to UI authorities in California, a state that requires all employers paying US$100 or more in quarterly wages to provide UI coverage to workers, found over two individuals for each year-round farm job in the state (Khan *et al.*, 2004). A two-to-one ratio between farm workers and year-round farm jobs suggests 2.4 million hired farm workers across the US, including 800 000 in California.

Farm Workers: US and Foreign Born

The supply of US farm labor, including the human capital embodied in workers, depends on the decisions of US workers about where to work (approximately 30% of hired crop workers are US born, but almost all new entrants to the farm workforce were born abroad), immigration patterns and the decisions of immigrant workers, and training (two-thirds of US-born crop workers, but only an eighth of the foreign born, completed high school). Hired farm workers are mostly immigrants from Mexico with little education, and most are unauthorized.

The US Department of Labor's NAWS finds a mostly young, Mexican-born, and male crop workforce (www.doleta.gov/agworker/naws.cfm). In recent years, 70% of crop workers were born in Mexico, three-fourths were male, and half were unauthorized. Half of crop workers were under 35 years, two-thirds had less than 10 years schooling, and two-thirds spoke little or no English.

Almost three-fourths of foreign-born workers interviewed by the NAWS are unauthorized, which makes over half of all farm workers illegal, undocumented, or unauthorized. Some 1.1 million unauthorized farm workers were legalized in 1987–88 under the special agricultural workers (SAW) program, and there were four SAWs for each unauthorized worker in the first NAWS survey in 1989.

However, many of the newly legalized SAWs began to leave the farm workforce, so that by 1991 the declining share of SAWs matched the rising share of unauthorized workers. Since the mid-1990s, there have been almost four unauthorized workers for each legalized SAW worker. Unauthorized workers are half of crop workers, but the share of SAWs has declined to less than 10%. The SAW experience suggests that, if there were another legalization of unauthorized farm workers, most would leave farm work within 5 years unless they were required to continue performing farm work (**Figure 1**).

Between 2007 and 2009, almost 30% of crop workers were born in the US and 70% were born abroad, almost always in

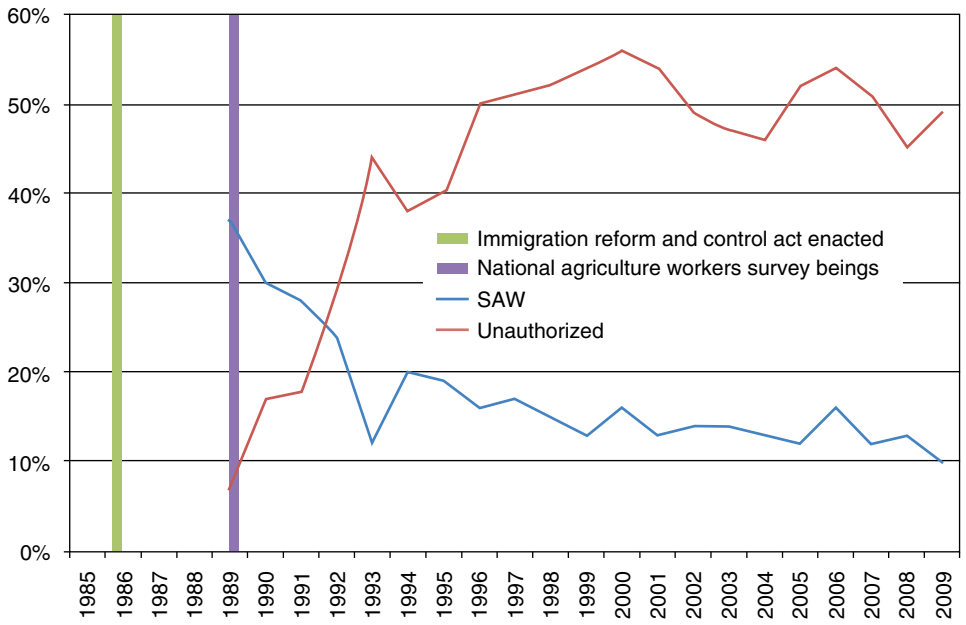


Figure 1 Special agricultural workers (SAWs) and unauthorized crop workers, 1989–2009. Reproduced from NAWS (http://www.doleta.gov/agworker/naws.cfm).

Mexico. Table 2 shows that foreign-born and US-born farm workers were similar in many respects. Their average age was 36–37 years and 77–78% was male. About the same share of foreign-born and US-born workers had incomes below the poverty line, a third of foreign-born families received some means-tested welfare benefit versus a quarter of US-born families, and very few workers were follow-the-crop migrants.

Foreign-born workers differ significantly from the US-born crop workers in legal status, education, and English. For example, 55% of the foreign born are unauthorized, only 13% completed high school, and just 3% spoke English well. Foreign-born crop workers are also more likely than US-born crop workers to be married (Table 3).

The NAWS found that most foreign- and US-born crop workers got their first farm jobs at the age of 22–23 years and had done an average 13 years of US farm work when interviewed. However, foreign-born workers were more likely to be hired by contractors and other intermediaries than US-born workers, 17% versus 2%, more likely to be working in FVH crops, and more likely to be filling harvest jobs, 52% versus 27%. Almost 40% of US-born workers are employed in field crops such as corn and grains, and more than 35% in nurseries.

US-born workers had average hourly earnings of US$9.74 in 2007–09, almost a US$1 an hour more than the average US $8.89 of foreign-born workers. Foreign-born workers had more days of farm work in the past 12 months, 200 versus 180, and were less likely to have health insurance provided by their current farm employer. A seventh of foreign-born workers, versus a quarter of US-born workers, had employer-provided health insurance in their current job.

More than three-fourths of foreign-born workers, and two-thirds of US-born workers, plan to continue working in agriculture for at least five more years. A third of the foreign-born, versus two-thirds of the US-born, say they could find a nonfarm job within a month.

Table 4 examines two groups of farm workers whose share of crop workers changed over time. SAW-legalized farm workers, including a few workers legalized under the general legalization program in 1987–88 and Central American programs in the 1990s, fell from 32% of all crop workers to 15% between 1989–91 and 1998–2000; the share of SAWs has since stabilized at just more than 10%. Foreign-born newcomers, who are workers in the US less than a year before they were interviewed, rose sharply during the 1990s to almost a quarter of all crop workers in 1998–2000. Since then, the share of newcomers has fallen to less than 10% between 2007 and 2009.

As would be expected, SAW-legalized workers are much older than newcomers, as they had to do farm work as unauthorized foreigners in 1985–86 to qualify for legalization. The average age of SAW-legalized workers was 49 in 2007–09, versus 25 for newcomers. Three-fourths of the SAW-legalized workers did not move, but a quarter returned to Mexico in the past year, usually over the Christmas holidays. More than 90% of the newcomers to the US farm workforce moved from Mexico to the US in the year before they were interviewed.

SAW-legalized workers are older and have less education than foreign-born newcomers, on average 5 versus 6 years (7% of both groups had graduated from high school in 2007–09), but are much more likely to speak some English and to have incomes above the poverty line. By contrast, approximately 95% of foreign-born newcomers had below-poverty level incomes. A third of foreign-born newcomers were employed by labor contractors, versus less than a fourth of SAW-legalized workers, including only an eighth in 2007–09. Foreign-born newcomers had fewer days of farm work than SAW-legalized workers, in part because not all were in the US for the full year before being interviewed.

Approximately 90% of both SAW-legalized and foreign-born newcomer workers are employed in FVH commodities, a pattern that has not changed over the past two decades. The share of both SAW-legalized and foreign-born newcomer workers filling harvest and postharvest jobs has been falling, and was half or less in 2007–09.

SAW-legalized workers earned an average 1.5 times the federal minimum wage in 1989–91, but their average premium over the minimum wage fell in the subsequent periods. Foreign-born newcomers earned a 30% premium over the federal minimum wage in 1989–91, and they averaged only 10% above the federal minimum wage in 2007–09. A third of SAW-legalized workers, but only an eighth of newcomers, believe they could get a nonfarm job in a month.

In a hired farm workforce that involves 2.5 million individuals working for wages on US farms sometime during a typical year, making the hired farm workforce equivalent to the average employment of janitors and cleaners, farm worker averages can obscure important changes. For example, almost all foreign-born farm workers were born in Mexico, but

Table 3 All, US-born and foreign-born crop workers, 2007–09

All, US-Born and Foreign-Born Crop Workers, 2007–09
US-born were 29% of all workers between 2007 and 2009

Demographics	*All*	*US-born*	*Foreign-born*
Authorized (%)	52	100	45
Male (%)	78	77	78
Average age (years)	36	37	36
HS and more education (%)	28	68	13
Speak English well (%)	30	97	3
Married (%)	59	44	65
Families <poverty income (%)	23	23	23
Families with welfare (%)	30	23	32
Follow-the-crop migrant (%)	6	1	7
Farm work			
Age at first farm job (years)	23	22	23
Average years of farm work	13	14	12
Directly hired (%)	88	98	83
>10 years current employer (%)	17	20	15
>4 farm employers past year (%)	1	0	1
FVH crops (%)	78	56	88
Harvest and postharvest jobs (%)	45	27	52
Wages, benefits, and plans			
Average hourly earnings (US$)	9.13	9.74	8.89
Farm days worked, past year	194	180	200
Health insurance, current job (%)	18	26	14
Continue farm work> 5 years (%)	73	66	78
Find nonfarm job<1 month?	44	76	31

Abbreviations: FVH, fruit, vegetable, and horticultural speciality; HS, high school.
Source: Reproduced from NAWS interviews 2007–09.

Table 4 Foreign-born farm workers, 1989–2009

	SAW-legalized			*Foreign-born newcomers*		
	1989–91	*1998–2000*	*2007–09*	*1989–91*	*1998–2000*	*2007–09*
Share of workers (%)	32	15	12	4	23	9
Demographics						
Authorized (%)	100	100	100	13	1	1
Male (%)	86	88	84	74	88	88
Average age (years)	32	40	49	23	25	25
HS and more education (%)	2	1	2	7	1	1
Speak English well (%)	3	4	2	7	1	1
Married (%)	63	77	87	41	36	34
Families < poverty income (%)		36	12		94	94
Families with welfare (%)	13	31	37	2	2	3
Follow-the-crop migrant (%)	25	13	3	16	14	7
Farm work						
Average years of farm work	8	17	26	1	1	1
Directly hired (%)	76	76	88	58	60	70
FVH crops (%)	86	87	87	93	77	93
Harvest and postharvest jobs (%)	59	39	45	72	44	51
Wages, benefits, and plans						
Average hourly earnings (US$)	5.51	6.93	9.82	4.91	5.98	7.87
Federal minimum wage (US$)	3.80	5.15	7.25	3.80	5.15	7.25
Farm days worked, past year	191	193	226	77	76	90
Health insurance, current job (%)		11	26		1	4
Find nonfarm job < 1 month?	45	40	37	20	13	12

Abbreviations: FVH, fruit, vegetable, and horticultural speciality; HS, high school; SAW, special agricultural worker.
Source: Reproduced from NAWS interviews 1989–2009.

increasingly in southern rather than west-central Mexico where Braceros were recruited between 1942 and 1964 (Martin, 2009). Some Spanish-speaking west-central Mexicans have become supervisors of newly arrived indigenous workers from southern Mexico who may not speak Spanish well, reflecting the growing complexity of the hired farm workforce (Mines, 2010).

Immigration Reform and Farm Workers

The NAWS has found a more stable hired farm workforce in recent years. In recent years, the average age of workers has increased, workers are obtaining more days of farm work, and more say they plan to remain farm workers longer than the usual 10 years. The share of more-than-10-year workers rose from 30% in 1999–2000 to 45% in recent years, which may reflect more difficulties finding nonfarm jobs as a result of the 2008–09 recession and fewer new newcomers due to stepped up border controls that encourage farm employers to raise wages and make more efforts to retain current workers.

The NAWS found rising average hourly earnings, as reported by workers, from approximately US$6.70 in 1999–2000 to US$9.40 in 2009–10, up 40% (nominal) and 16% in real terms. Annual farm worker earnings rose as well. The NAWS collects farm worker income in categories, and approximately 40% of farm workers reported US$5000 to US $15 000 in farm earnings in 1999–2000, compared with 35% in 2009–10. Meanwhile, the share of workers earning more than US$20 000 rose from less than 5% to approximately 25% over the past decade.

However, half of crop and nursery workers remain unauthorized, helping to explain the keen interest of farm employers in immigration reforms that could lead them to fire experienced but unauthorized workers to avoid fines unless their currently unauthorized workers were legalized. The prospect of new requirements that employers use the Internet-based E-Verify system to check the legal status of newly hired workers has encouraged most farmers to demand easier access to legal guest workers to fill farm jobs. However, there is not yet any agreement on a package of new measures to keep unauthorized workers from getting US jobs and allowing farm employers to more easily hire guest workers.

Dealing with Illegal Immigration

The US is a nation of immigrants. The US Presidents frequently use the phrase "e pluribus unum" to remind Americans that they share the experience of themselves or their forebears leaving another country to begin anew in the US. Immigration is widely believed to serve the US national interest, as immigrants better themselves while enriching the US (Martin and Midgley, 2006).

The major immigration issue for the past quarter century has been what to do about illegal immigration. The US had 40 million foreign-born residents in 2010, including 11 million, approximately 30%, who were illegally present (Martin and Midgley, 2006). Public opinion polls find widespread dissatisfaction with illegal immigration, showing that most Americans believe that the federal government should do

more to reduce illegal immigration. For example, a CNN/ORC poll in November 2011 found 55% of respondents supported deporting unauthorized foreigners in the US, whereas 42% would offer them a path to legal residence (www.pollingreport.com/immigration.htm).

Disagreement over what to do about illegal migration has stymied immigration reform for the past two decades. After the mid-1990s farmers acknowledged that half of their workers were unauthorized and tried to persuade Congress to make it easier for them to employ legal guest workers, but President Clinton in June 1995 made a statement that blocked their efforts, saying: "I oppose efforts in the Congress to institute a new guest worker or 'bracero' program that seeks to bring thousands of foreign workers into the US to provide temporary farm labor." (Martin, 1998).

Neither farm employers nor worker advocates knew what would happen in the 2000 elections. However, the election of President Vicente Fox in Mexico, who made a Mexico–US guest-worker program his top foreign policy priority, prompted them to negotiate the Agricultural Jobs, Opportunity, Benefits and Security Act (AgJOBS) in Fall 2000 (Martin, 2005). AgJOBS would repeat of the 1986 approach to unauthorized farm workers, viz, legalize currently unauthorized farm workers and make it easier for farm employers to hire legal guest workers.

Farm employers and worker advocates joined a coalition of groups advocating comprehensive immigration reforms with three prongs, more enforcement to deter unauthorized migration, legalization for unauthorized foreigners in the US, and new guest worker programs. The Mexican government pressed President George W. Bush to endorse comprehensive immigration reform and Mexico's then Foreign Minister Jorge Castaneda laid out a four-pronged reform agenda in June 2001 that included legalization, a new guest-worker program, reducing border violence and exempting Mexico from visa quotas, and concluded: "It's the whole enchilada or nothing." Fox was visiting Bush in Washington DC and pressing for this 'whole enchilada' immigration reform just before the 11 September 2001 terrorist attacks.

The terrorist attacks pushed immigration reform into the background, but after the unemployment rate dropped below 6% in 2003 and some employers complained of labor shortages, the stage was set for a debate. Congress tackled immigration in 2005, 2006, and 2007, at the height of the housing boom. The Republican-controlled House moved first, approving an enforcement-only bill in December 2005 that would have required all employers to participate in a federal program now called E-Verify that allows employers to check the legal status of new hires against government databases. The House bill also called for hiring more Border Patrol agents and building a fence along a third of the 2000 mile Mexico–US border and would also have defined 'illegal presence' in the US a felony, making it harder for unauthorized workers to become legal guest workers and immigrants in the future.

Reaction against this so-called 'Sensenbrenner bill' culminated in a 'Day Without Immigrants' 1 May 2006 that saw some meatpacking plants, home builders, and restaurants close for the day as more than a million protestors took to the street and called for a path to legalization for unauthorized foreigners in the US. These demonstrations were cited as the Democratic-controlled Senate approved the Comprehensive Immigration Reform Act (CIRA) in May 2006. Like the Sensenbrenner bill, CIRA would have required employers to submit data on all new hires to a government database and added fences and Border Patrol agents. However, instead of defining unauthorized foreigners as felons, CIRA would have allowed them to earn a legal immigrant status by paying fees and taxes and learning English (Martin, 2006). CIRA, whose supporters included Senators Edward Kennedy (D-MA) and John McCain (R-AZ), would have created a new guest worker program that adjusted admissions to employer requests for guest workers.

When the Senate tackled immigration reform again in 2007, it was unable to approve a revised version of CIRA despite the active support of President Bush. Republicans who opposed 'amnesty' and Democrats who feared that more guest workers would hurt US workers combined to defeat CIRA (Migration News, 2007a). In response, the Bush administration stepped up raids of workplaces with unauthorized workers, such as the one at Agriprocessors in Postville, Iowa, that resulted in the arrest of approximately 400 workers in May 2008. The Department of Homeland Security worked with the Social Security Administration to include with the no-match letters that SSA sends to employers who submit data on 10 or more workers whose name and number do not match SSA records a notice to inform employers they would be considered to have knowingly hired unauthorized workers if they continued to employ workers for whom SSA had identified discrepancies (Migration News, 2007b). Farm employers feared that they would have to risk fines for knowingly hiring unauthorized workers in order to get their crops picked.

There was little willingness to tackle immigration reform during the recession that began late in 2007 and the presidential elections of 2008. President Obama supported comprehensive immigration reform during the campaign, but stepped up enforcement at the border and inside the US to prove to skeptics that the federal government could reduce illegal migration. During Obama's first 4 years, the Mexico–US fence was extended to a third of the 2000 mile Mexico–US border and the number of Border Patrol agents increased to more than 20 000. These enforcement efforts and the US recession combined to reduce apprehensions of foreigners just inside the US border to 340 000 in FY11, the lowest number since the early 1970s (Migration News, 2012b).

Obama's interior enforcement strategy has been more controversial. DHS stopped workplace raids in 2009 and launched I-9 audits that involve checking the forms completed by newly hired workers and their employers. These so-called silent raids have DHS agents telling employers which of their employees appear to be unauthorized and asking employers are to notify these employees and ask them to clean up the discrepancies in their records or terminate them. For example, Gebbers Farms in Brewster, Washington, a 5000-acre apple and cherry operation north of Wenatchee, wound up terminating 550 workers in 2010, almost half of its workers, after an I-9 audit (Rural Migration News, 2010b).

The recession and heath care dominated domestic policymaking in recent years, and legislative action to deal with unauthorized migration shifted to the states. Beginning with Arizona, more states have been enacting laws that require

employers to use the federal government's E-Verify system to check the legal status of new hires and to have state and local police check the legal status of persons they encounter during traffic stops and other interactions (Martin, 2012). The US Supreme Court, which upheld Arizona's Legal Arizona Workers Act in May 2011 requiring employers to participate in E-Verify, is expected to rule soon on the Support Our Law Enforcement and Safe Neighborhoods Act (SB 1070) enacted in 2010.

Other states followed Arizona, enacting laws to reduce illegal immigration by requiring employers to participate in E-Verify and to have the police to check the legal status of persons they encounter. In 2011, Alabama, Georgia, Indiana, South Carolina, and Utah enacted such laws, prompting the US Department of Justice to sue to block these laws from going into effect by arguing that these state laws were an unconstitutional infringement on the federal government's authority to establish immigration policy. Federal judges blocked implementation of most sections of the immigration control laws of Arizona, Georgia, and South Carolina, but not those of Alabama. The US Supreme Court in June 2012 maintained many of these injunctions that prevented state immigration control laws from going into effect, but allowed provisions that require state and local police to determine the status of persons they 'reasonably suspect' are not lawfully in the US to be implemented. Some farmers allege that state immigration control laws discourage farm workers from coming to or staying in their states.

Immigration Reforms and Farm Workers

Farm employers and worker advocates have been active participants in the immigration reform debate. During the first attempt to deal with illegal migration in the IRCA of 1986, farm employers and worker advocates eventually agreed on a compromise that legalized unauthorized farm workers who had done at least 90 days of farm work in 1985–86 and made employer-friendly changes to the then agricultural guest worker program, whose name was changed from H-2 to H-2A (Martin, 1994).

Farm labor costs were expected to rise after enactment of IRCA as farmers raised wages to retain legalized workers or built housing to employ H-2A guest workers. Instead, illegal immigration continued and unauthorized workers used false documents to get hired. As the employers do not have to determine the authenticity of the documents presented by newly hired workers, they were not liable if the workers were later found to be unauthorized. Immigration reform thus contributed to the spread of unauthorized workers throughout the US agriculture sector (Martin *et al.*, 1995).

There were few complaints of farm labor shortages in the 1990s. Farm employers aware that a rising share of their workers were unauthorized, pushed for employer-friendly changes to the H-2A program, and new guest worker programs, but President Clinton threatened to veto any new guest worker program, and none was enacted. For example, Rep Richard Pombo's (R-CA) bill to grant temporary work visas to 250 000 foreign farm workers who could 'float' from farm to farm was defeated by the House in March 1996 (Rural Migration News, 1996).

In Fall 2000, worker advocates and farm employers negotiated AgJOBS to repeat the IRCA approach to unauthorized migration and agriculture, viz, legalize the current unauthorized farm wrokers and make it easier for farm employers to hire legal guest workers in the future. AgJOBS included several important changes. Like the SAW legalization program, AgJOBS would allow currently unauthorized farm workers to legalize their status immediately. However, to 'earn' a regular immigrant status for themselves and their families, foreigners legalized under AgJOBS would have to continue to do farm work, a provision aimed at preventing an immediate exodus of newly legalized farm workers to nonfarm jobs (Martin, 2009).

There have been several iterations of AgJOBS. The most recent version, S 1038 and HR 2414 introduced in May 2009, would have allowed up to 1.35 million unauthorized farm workers who did at least 150 days or 863 h of farm work in the 24-month period ending 31 December 2008 to apply for Blue Card probationary status (Rural Migration News, 2009a). Blue Card holders could work and travel freely within the US and enter and leave the US, and could earn an immigrant status for themselves and their families by continuing to do farm work over the next 3–5 years. AgJOBS has three continued farm work options: (1) performing at least 150 days (a day is at least 5.75 h) of farm work a year during each of the first 3 years after enactment; (2) doing at least 100 days of farm work a year during the first 5 years; or (3) working at least 150 days in any 3 years, plus 100 days in the fourth year (for workers who do not do 150 days in the first 3 years).

For 6 years, farm employers of Blue Card holders would have to provide their employees with written records of their farm work and submit a copy to DHS or face fines of up to US $1000. DHS would check documentation of the farm work of Blue Card holders and, after they paid fees and fines, Blue Card holders and their family members could become immigrants.

AgJOBS would change the H-2A program in three major ways to make it easier for farmers to recruit and employ legal guest workers (Rural Migration News, 2009a). First, farm employers could attest that they need guest workers and are paying prevailing wages rather than have Department of Labor (DOL) supervise their efforts to recruit US workers, a process called certification. Attestation would effectively shift control of the border gate from the US Department of Labor to employers.

Second, rather than provide free housing to H-2A and out-of-area US workers as is required currently, AgJOBS would allow farm employers to pay a housing allowance of US$1–2 an hour, depending on the local costs to rent two-bedroom units that are assumed to house four workers, if state governors certified that there is sufficient rental housing for the guest workers in the area where they will be employed. Third, the Adverse Effect Wage Rate (AEWR), the minimum wage that must be paid to legal guest workers, would be frozen at last year's levels and studied, effectively reducing the AEWR by US $1–2 an hour and offsetting the cost of the housing allowance.

Despite bipartisan support, AgJOBS has not been enacted. Meanwhile, farmers aware that (1) half of their workers are unauthorized, (2) federal I-9 audits of their employment records can remove a large share of their workers, and (3) more states are enacting laws requiring employers to use E-Verify

express worries about obtaining new and replacement workers, worry that they could lose a large share of their workers suddenly to federal or state enforcement. Farmers are especially fearful of requirements to participate in the E-Verify program, which involves submitting data on newly hired workers to a federal database and learning instantly if the worker is authorized to be employed in the US.

The House Judiciary Committee in September 2011 approved the Legal Workforce Act (HR 2164) to phase in E-Verify for all US employers over 4 years. Farmers oppose a federal requirement to check the legal status of newly hired workers unless it is accompanied by employer-friendly changes to the H-2A guest worker program or a new program. A requirement that all farm employers participate in E-Verify without a new guest worker program, farmers argue, means labor shortages and crop losses, as allegedly occurred in Alabama and Georgia after state immigration control laws went in effect in 2011. Several House Republican proponents of mandatory E-Verify introduced proposals for new guest worker programs in Fall (2011), but they were not acted upon (Rural Migration News, 2011).

Recent years have generated record net farm income and rising land prices. Despite fears of more enforcement, farmers have not yet changed crops to avoid the need to hire workers. If there is market demand, farmers are planting more despite fears of labor shortages, as with strawberries, where acreage doubled between 1990 and 2010 (Calvin and Martin, 2010). However, fears of labor shortages and disruptions make farm employers well aware of the three major immigration options that could affect the future availability of farm workers, viz, *status quo*, enforcement and guest workers, and comprehensive reform.

A continuation of the status quo would mean that about half of farm workers remain unauthorized, that federal I-9 audits and state laws disrupt employment and hiring unevenly, and that farm employment shifts toward the extremes, to intermediaries willing to absorb the risk of enforcement and toward investment in housing in order to employ H-2A guest workers. New entrants to the farm workforce would continue to grow up outside the US, and enter the US illegally to do farm work or enter legally as guest workers. Unauthorized workers fired after I-9 audits or not hired because their employer participates E-Verify typically remain in the US and move on to another employer, so the status quo is likely to promote worker circulation that limits employer training of workers and worker advancement on particular farms.

The second option is stepped-up enforcement and new or revised guest worker programs. More federal enforcement and state immigration control laws could be coupled with new guest worker programs or revisions to the current H-2A program that include the revisions in AgJOBS, viz, no DOL-supervised recruitment of US workers, no requirement to provide housing for guest workers, and a lower minimum wage for guest workers. Several of the proposals made by and on behalf of farm employers would shift the administration of new or revised guest worker programs from the US Department of Labor to the US Department of Agriculture. Farm worker advocates oppose these so-called E-Z guest worker proposals.

The third option is comprehensive immigration reform that deals with all unauthorized foreigners in the US, the 1 million employed in agriculture and the 7 million employed in nonfarm jobs, as well as their 3 million dependents. Comprehensive immigration reform has three major components: enforcement, legalization, and guest workers, but the details of each component, and an assessment of how they could interact, makes enactment difficult. For example, how should employer participation in E-Verify be phased in, and should farm employers be exempt from having to recheck the legal status of returning seasonal workers? Should there be a separate legalization for unauthorized farm workers, and should it require farm workers to want to earn and immigrant status to continue to do farm work, or would any US work suffice to earn an immigrant status? Finally, what new guest worker program can balance the interest of farmers in having sufficient seasonal workers while protecting farm workers?

Farmers and Farm Workers

Most US farm operators are older US-born white men, whereas most hired farm workers are younger immigrant Hispanic men. The median age of all US workers is 41 years; the median age of farm operators is late 50s, and the median age of hired farm workers is less than 30 years. Farming is a multigenerational career for many farm operators but a less-than-a-decade job for most hired workers.

The US has what has been called an 'apartheid farm work force' of mostly older, white, and US citizen farm employers and mostly young, Hispanic, and foreign-born hired workers. If current trends continue, new hired workers will continue to be born outside the US, whereas future farmers will be born in the US.

Hired Hands versus Hired Workers

Thomas Jefferson, an agrarian fundamentalist who believed that family farming would preserve democracy and respect private property as they farm the land they owned averred that: "those who labor in the earth are the chosen people of God." In a country offering free land, Jefferson did not believe that the US would have a permanent class of hired farm workers. Instead, he considered farm workers to be youthful 'hired hands' who lived and worked temporarily alongside the farmer before climbing the agricultural ladder from farm worker to farm operator (Martin, 2003, Chapter 2).

This worker-to-farmer mindset helps to explain why hired workers were initially excluded from federal labor laws during the 1930s. During Congressional debates on the federal minimum wage and other labor laws, it was frequently asserted that farmers and farm workers had the same interests in higher crop and livestock prices, making employer–employee relationships in agriculture different from those in the factories affected by labor laws and unions (Martin, 2003, Chapter 3). There was always more myth than reality to the agricultural job ladder, especially in California, and it became clearer during the 1930s, when Dust Bowl migrants who migrated to California found large and specialized farms that hired crews of seasonal workers when needed. Dust Bowl migrants, English-speaking US citizens, and their presence prompted

many studies of farm workers while inspiring John Steinbeck's epic novel, 'The Grapes of Wrath.'

Farm labor reformers during the 1930s were divided about how government should respond to the system of large and specialized farms that relied on armies of low-skilled seasonal farm workers that had evolved in the western states. Economist Paul Taylor wanted to break up large farms into smaller family-sized operations, fulfilling Jefferson's dream, while lawyer Carey McWilliams believed that California agriculture would continue to be dominated by 'factories in the fields' and wanted to extend factory labor laws to large farms (Martin, 2003, Chapter 2). The fact that most US farms were operated by families, the divisions between farm labor reformers on appropriate policies, and the outbreak of World War II that enabled many Dust Bowl migrants to find nonfarm jobs combined to reduce the urgency of dealing with farm labor issues. Instead, Mexican Bracero farm workers were admitted to the US beginning in 1942, and their presence influenced wages until the Bracero program ended in 1964 (Martin, 2003, Chapter 2).

Farm workers, who were initially exempt from social security, UI, and minimum wage laws, are now protected under most federal labor laws, although sometimes at different levels, as with overtime pay, which is applicable to farm workers only after 10 h a day and 60 h a week in California, versus 8 h and 40 h for nonfarm workers. Farm workers continue to be excluded from the National Labor Relations Act (NLRA), which governs the union organizing and bargaining in the private sector, although farm workers in California have more rights under the state's Agricultural LRA than they would have under the federal NLRA.

Most of the largest farm employers around the US are covered by most federal labor laws, and the majority of farm workers are in states such as California and Washington that have eliminated most labor law exemptions for agriculture. California has been a leader in enacting special laws to protect farm workers, including from heat stress. Since 2005, farm employers must make available at least a quart of water per worker per hour, provide access upon request to shade for at least 5 min to workers suffering from heat illness, and ensure that shade is available for up to a fourth of the workers when the temperature exceeds 85 °C. Employers must train their workers and supervisors about heat illness, monitor new hires, and have a written plan to deal with workers suffering from heat illness (Rural Migration News, 2008).

Many farm–nonfarm differences in labor laws have been eliminated, but agriculture remains what has been called an 'American apartheid' industry. There may be no other US industry in which most employers are older white US citizens and most hired workers are young Hispanic immigrants. Many of the Hispanic immigrants are from rural Mexico, and many would like to move up the agricultural job ladder in the US from farm worker to farmer. However, the job pyramid in agriculture is steep, offering relatively few opportunities for those who begin as seasonal workers to move up to year-round jobs in agriculture and eventually to farm operators.

The inability of most farm workers to climb the agricultural ladder to farm operator means that the best way to assist most seasonal farm workers is to help them to find nonfarm jobs. The best way to help the children of farm workers to achieve higher incomes than their parents is to provide education so that they can find nonfarm jobs. The federal government's Migrant and Seasonal Farm Worker (MSFW) assistance programs, launched during the 1960s when farm worker wages were rising rapidly after the end of the Bracero program, aimed to help MSFWs and their children 'escape' from (mostly seasonal) farm jobs (Martin and Martin, 1993).

Most farm workers seeking upward mobility find it easier to move out of agriculture rather than move up the job ladder in agriculture, and their children educated in the US rarely follow their parents into seasonal farm work. There are many reasons why most hired farm workers find it hard to move up in agriculture, including limited access to capital in the capital-intensive FVH sectors of agriculture where most farm workers are employed, low educational and language attainment, and a lack of agriculture-specific expertise, for example, in cooling and marketing perishable commodities.

Climbing the Agricultural Job Ladder

The commodities with the most common movement from worker to operator include strawberries, where most of those making the transition bring only their own labor to newly established farming operations. Many smaller strawberry growers lease land and plants from a cooler and marketer, whose field man tells them when to irrigate and fertilize. Small strawberry growers are contractually required to harvest and deliver their berries to the cooler, who deducts the cost of any loans and selling costs from revenue before sending the balance to the grower.

By some estimates, two-thirds of California strawberry growers are Latinos, many of whom used to be pickers. Most Latino berry growers have only a few acres, so they farm much less than two-thirds of the approximately 40 000 acres of California strawberries. The high share of Latino growers may help to explain the low earnings of berry pickers, which are the lowest of any commodity in California, an average US$10 an hour in 2010 when the average for California agriculture was US$11.62. Indeed, average earnings in strawberries were less than the US$10.50 an hour paid to employees of labor contractors.

Strawberries farming is very labor-intensive, requiring an average 1.5–2 workers per acre (Rural Migration News, 2009b). However, they also generate high revenues of US $40 000–US$60 000 an acre, so that even a 5-acre operation can have up to 10 employees and up to US$300 000 in annual revenue. Small farmers often have difficulty managing cash flow when workers must be paid weekly but marketers pay farmers every few weeks, prompting some researchers to conclude that small Hispanic strawberry growers are essentially sharecroppers for the marketers (Wells, 1996). A few worker-to-strawberry-farmers have been successful, but many struggle and some revert from farm operator to hired worker.

It may be easier for immigrant workers in year-round jobs in smaller dairies and nurseries to climb the agricultural ladder from worker to farmer, as year-round workers often live on dairy farms and work alongside their employers every day. Some of the farmers who get to know and trust year-round workers may finance their transition from worker to operator; however, there are few examples of such farmer-financed

transfers of operations to hired workers. Alternatively, there may be an evolution toward fewer and larger farms that rely both on hired managers and hired workers. If pension and insurance funds continue to buy land and rely on farm management firms to farm it, there may be more rather than fewer layers between seasonal farm workers and the beneficiaries of their work.

A system of large farms with hired managers and hired workers may embrace the adage that 'agriculture is different' and requires a foreign-born workforce to fill especially seasonal jobs. If the government were to embrace the notion that the hired farm workers of tomorrow are growing up today somewhere outside of the US, the focus of policy debates might shift from whether immigrant farm workers are necessary for US agriculture to how they should be admitted and managed.

The 'agriculture is different' mantra is repeated frequently in debates over immigration reform and agriculture. Senator Charles Schumer's (D-NY) asserted that "even if [farm employers] offer Americans twice or sometimes three times the minimum wage and provide benefits, American workers simply won't stay in these [farm] jobs for more than a few days." (Rural Migration News, 2011) Senator Dianne Feinstein (D-CA) said: "I think a country that's strong really should be able to produce its own food, but you can't do it with domestic labor, and that's just a fact." (Rural Migration News, 2010a).

The US government has been unwilling to make an explicit agriculture-requires-foreign-workers statement. Instead, the government has continued past policies of allowing farmers who anticipate labor shortages to request permission to employ H-2A guest workers. There will be an ongoing debate over how many hurdles employers must surmount before they can employ the foreign workers they prefer that is fueled on the one hand by reports of labor shortages that lead to crop losses and on the other by reports of abused workers.

Farm Wages and Food Costs

What does the debate over farm workers, farm structure, and immigration reform mean for consumers? The answer is surprisingly little, as US consumers spend relatively little on food eaten at home, farmers get less than a third of retail food spending, and farm workers get less than a third of farm revenue.

The US Bureau of Labor Statistic's Consumer Expenditure Survey reported that there were 122 million 'consumer units' in 2011 with an average of 2.5 persons, 1.3 earners, and 1.9 vehicles. Average consumer unit income before taxes was US $63 700 and average annual expenditures US$49 700 (www.bls.gov/cex).

These consumer unit or household expenditures included US$6460 for food, approximately 13% of average spending. Food spending was divided between food consumed at home, US$3800 or 58% of food spending (US$73 a week), and food bought eaten from home, US$2600 or 42% of food spending (US$50 a week). The cost of food away from home largely reflects convenience, service, atmosphere, and other factors not related to food costs. For example, a rule of thumb is that food costs are approximately 35% of the price of food in cafeteria-style restaurants, 30% of the consumer price in fast food, and 25% in fine dining.

To put food spending in perspective, consumer units or households spent far more on other items. For example, spending on housing, US$16 800, was almost three times more than spending on food, and spending on transportation, US$8300, exceeded spending on food. Consumer unit or household spending on health care, US$3300, and entertainment, US$2600, almost matched spending on food.

Most analyses of farm worker wages and food costs are limited to spending for food consumed at home. The largest food-at-home expenditures were for items in which farm worker wages are a small share of retail prices, including meat and poultry, for which consumer units or households spent an average US$832 or US$16 a week. Expenditures on cereal and bakery products, US$531, exceeded the US$407 spent on dairy products.

Farm worker wages loom largest in the prices of fresh fruits and vegetables, but consumers spend relatively little on them. Average consumer unit or household spending on fresh fruits were US$247 in 2011, and on fresh vegetables US$224, for a total of US$471, or US$9 a week, plus an additional US$116 spent on processed fruits and US$128 spent on processed vegetables. The average consumer unit spent almost as much on alcoholic beverages, US$456 in 2011, as on fresh fruits and vegetables, US$471. Farmers get a small share of the retail food dollar, more for meat and dairy products and less for wheat and grains. Farmers received an average 28% of the retail price of fresh fruits in 2009, and 25% of the retail price of fresh vegetables, so consumer expenditures of US$471 on these items meant US$125 to the farmer (www.ers.usda.gov/Briefing/FoodMarketingSystem/pricespreads.htm).

Farm labor costs are typically less than a third of farm revenue for fresh fruits and vegetables, meaning that farm worker wages and benefits for fresh fruits and vegetables cost the average consumer unit US$41 a year. Consumers who pay US$2 for a pint of strawberries are giving 56 cents to the farmer and less than 20 cents to the farm worker; those spending US$2 for a head of lettuce are giving 50 cents to the farmer and 15 cents to the farm worker.

If farm wages rose, what would happen to consumer expenditures on fresh fruits and vegetables? In 1966, the United Farm Workers union won a 40% wage increase for some table grape harvesters, in part because the Bracero program that brought Mexican workers into the US ended in 1964. The average earnings of field workers were US$10.33 an hour in 2011, so a 40% wage increase would raise average hourly earnings to US$14.46 an hour. If this wage increase were fully passed on to consumers, the 15–20-cent farm labor cost of a pint of strawberries or head of lettuce would rise to 20 to 28 cents, and the retail price would rise from US$2 to US$2.08.

What would a sharp increase in farm wages mean for a typical household? A 40% increase in farm labor costs translates into a 3.6% increase in retail prices. This relatively small jump in retail prices is due to two major factors: the small farm share of retail prices and the small share of farm worker wages in farm revenues. If farm wages rose 40%, and the wage increase were passed fully to consumers, average spending on fresh fruits and vegetables would rise by approximately US$17

a year. However, the average earnings of seasonal farm workers, now approximately US$10 000 a year, would rise to more than US$14 000 a year, or from below the 2011 poverty line of US$10 890 for an individual to above the line.

Food Processing and Meatpacking

Food manufacturing (NAICS 311) employed an average 1.4 million workers in 28 500 establishments in 2010. Average weekly wages were US$780, or 70% of the average US$1100 a week in manufacturing. Average weekly earnings tend to fall as employment rises in food manufacturing, so that workers in small sectors, such the 59 000 employed in grain and oil seed milling (NAICS 3112) earned an average US$1000 a week, whereas workers in larger sectors such as fruit and vegetable preserving (NAICS 3114) earned an average US$810 a week.

The largest food manufacturing subsector is animal slaughtering and processing (NAICS 3116), which employed 486 000 workers in 2010, a third of food manufacturing employment, to turn cattle, hogs, sheep, and poultry into meat and other products. Meatpacking wages averaged US$630 a week, approximately 77% of the average in food manufacturing and 57% of the average earnings of all manufacturing workers. Approximately 60% of meatpacking workers are in rural areas, making animal slaughtering and processing the largest manufacturing employer in rural America.

Meatpacking has changed over the past three decades from a mostly urban to a mostly rural industry in response to a search for cost savings and innovations such as preparing retail cuts of meat in meatpacking facilities. Average hourly meatpacking earnings, which were similar to wages in durable manufacturing sectors such as autos in the 1970s, are today about half the average manufacturing wage of US$24 an hour. Large plants in small towns can change their demography quickly, which has sometimes led to tensions as residents complain of non-English speaking residents. On the contrary, some local residents benefit by renting housing or selling food to newcomers in towns that were often losing population.

Meat processing is a nonfarm industry critical to US agriculture. Livestock and products account for half of annual farm sales, and cattle, hogs, and broilers account for two-thirds of livestock sales. Red meat production has been rising, from 46 billion pounds in 2000 to 49 billion pounds in 2010, whereas poultry meat production rose from 36 billion pounds to 43 billion pounds in the same period. Exports of beef, pork, and poultry rose from 9 billion pounds in 2000 to 14 billion pounds in 2010, whereas imports fell from 4 billion pounds to 3.4 billion pounds. The US has a significant trade surplus in meat.

From Urban to Rural

Meat processing has changed in scale and location, so that today there are fewer and larger farms, feedlots, and meat processors, reflecting a general consolidation in US agriculture and manufacturing. Meat production in the 1960s and 1970s shifted from urban areas near the consumers of meat products to rural areas nearer cattle and poultry producers, as from Chicago to Garden City, Kansas (MacDonald and Ollinger, 2000).

The share of meat processing employees in nonmetro areas rose from less than half in 1980 to 60% by 2000, and many of the new plants in rural areas are larger than the older urban plants they replaced. More than 85% of US beef, pork, and chicken are from large plants that process at least 500 000 cattle, a million hogs, and several million chickens a year, and most have more than 400 employees. Meat products are usually transported from the plants to supermarkets and other outlets in refrigerated trucks.

The shift of meatpacking from urban to rural areas was prompted by several factors, including lower land and labor costs in rural areas, less stringent environmental restrictions, and easier access to animals. Lower labor costs in rural areas encouraged urban supermarkets paying high wages to butchers to request preparation of meat products that were ready for sale to consumers at the processing plant, so that boxed, vacuum-packed, and cut-up and sometimes cooked and seasoned meat products are now prepared in processing plants. Retail packages of meat rather than carcasses have become the primary output of the plants. One summary concluded that meatpacking work is "hard and dangerous, and wages are low by manufacturing standards, although often high compared with alternative employment in the rural communities in which plants are concentrated." (Craypo, 1994, p. 85).

The meat processing industry has four major segments, animal slaughtering (NAICS 311611), meat processed from carcasses (311612), rendering and meat byproduct processing (311613), and poultry processing (311615). Poultry processing has about as many employees as meat processing, but meat wages are typically higher than poultry wages because more of the meat plants are in higher-wage midwestern states, whereas poultry processing is mostly in lower-wage southern states.

The poultry processing developed later than meatpacking, but became the first vertically integrated meat industry, meaning that poultry processors supply chicks and feed to farmers who own the buildings and supply the labor to raise the chickens. Almost all US broilers are raised under contracts with processors. The cattle industry is least vertically integrated, in part because it has two distinct segments. Mostly small feeder cattle operations raise calves and sell them to generally larger feedlots that 'finish' the cattle. The more concentrated poultry industry has been associated with falling costs and rising consumption of poultry products.

Meatpacking is one of the most dangerous manufacturing jobs in the US, with injuries that include muscular trauma, repetitive motion disease, cuts, and strains. The Bureau of Labor Statistics (www.bls.gov/iif) conducts an annual survey of workplace injuries and reports an incidence rate, the number of injuries and illnesses reported per 100 full-time equivalent workers. In 2010, some 3.1 million nonfatal workplace injuries and illnesses were reported by private industry employers, an incidence rate of 3.5 reportable injuries per 100 equivalent full-time workers. The rate was 4.4 for manufacturing, 5.8 for food manufacturing, and more than 10 in animal slaughtering and processing.

Historically, most meatpacking workers outside the southern states were represented by unions that had master agreements with the largest packers. Union strength peaked in

1968, when more than 90% of meat production workers belonged to unions and the average meatpacking wage of US $3.45 an hour was 15% above the average manufacturing wage of US$3 an hour (Craypo, 1994, p. 71). During the 1980s, many of the unionized plants in urban areas closed amidst a wave of strikes to protest requests for wage concessions. By 1986, average meatpacking wages of US$8.24 an hour were 18% below the average manufacturing wage of US $9.75. Meatpacking wages continued to fall, and by 1990 the US$8.73 an hour wage was 24% below the US$10.85 average manufacturing wage (Craypo, 1994, p. 71).

Meatpacking Workers

Meatpacking has long attracted workers with relatively little education and sometimes little English, but meatpacking wages were comparable to those of other manufacturing industries when meat processors were in urban areas. Few meatpacking workers followed plants from urban to rural areas, so when the industry moved, it had to find a new workforce.

Meat processing facilities in rural areas generally do not have to compete with other factories for workers, and often recruit workers from out of the area, especially to staff second or night shifts. Refugee resettlement in the 1970s and 1980s brought Asians to the Midwest, and the 1986 IRCA facilitated the geographical and occupational mobility of newly legalized Mexicans. Many saw moving from seasonal farm to year-round meat processing jobs as a step up the US job ladder.

There is little systematic data on employer preferences for particular types of workers. Poultry plant managers in the late 1980s told interviewers that Asians and Hispanics had a 'better work ethic' than local Blacks and Whites. Griffith also noted that economic growth offered local workers other job opportunities, encouraging many to quit meatpacking jobs. Many immigrant workers moved to meatpacking jobs on their own, but some plants offered cash bonuses of several hundred dollars to current workers and others who referred persons who stayed on the job 60 or 90 days. Networks evolved to bring US-born as well as Mexican-born Hispanic workers from South Texas and other areas with high unemployment rates to midwestern meatpacking plants.

Once a core group of Asians or Hispanics is employed in a plant, network hiring can take over recruitment, with current workers bringing friends and relatives to fill vacant jobs (Griffith, 1988, p. 35). Network hiring shifts most recruitment and training costs to currently employed workers, who bring only those who can do the work and often act as the mentors of newly hired workers. The Los Angeles Times on 10–12 November 1996 profiled one network that moved workers along the so-called 'chicken trail' from South Texas to Missouri (Katz, 1996). Hudson Foods, based just outside Noel, Missouri, paid South Texas recruiter B. Chapman US$175 for each worker who was referred and hired in its chicken processing plant. The reporter was selected by Chapman, traveled to Noel, and lived with 135 other migrant poultry workers in a converted motel, paying US$45 per week in rent.

Hudson employed 200 workers to process 1.3 million chickens a week. Worker turnover was very high; Hudson reportedly hired 50 new workers a month. Approximately 45% of the unionized labor force was Latino, and Hudson offered the current employees who referred the new workers a bonus of US$300. Hudson's Human Resources Director said: "there's a large number of jobs that very few citizens in the US want to do, but they're there and they need to be done...One of the social goods the poultry industry provides is employing people who would otherwise have a great deal of trouble getting employed."

The arrival of immigrant workers at Hudson and other meat processing plants rarely displaces local workers and sometimes increases productivity. New plants in rural areas tend to have more labor-saving and worker-friendly technologies, providing a cleaner and safer work environment than was available to workers in older urban plants. If the availability of immigrant workers allows a second work shift, employers may invest in more expensive air- and electric-powered knives that make work easier for all workers, potentially reducing the injuries and illnesses in meatpacking.

Enforcement

Meatpacking drew the attention of immigration enforcement agencies during the late 1990s, when an estimated 25% of meatpacking workers were unauthorized. Operation Vanguard subpoenaed employment records from meatpacking plants, compared information provided by newly hired workers on I-9 forms with government databases, and instructed employers to ask employees who appeared to be unauthorized to clear up discrepancies in their records before INS agents came to the plant to interview them. When employees were informed of INS suspicions that they were unauthorized, most of the workers quit.

Vanguard was attacked by meatpackers, farmers, unions, and Hispanic groups, prompting INS headquarters to order its suspension in 2000. The subsequent lack of enforcement contributed to the jump in the Hispanic share of employment in meatpacking between 2000 and 2005. However, beginning in 2006, meatpacking plants were often targeted in raids seeking unauthorized workers. The Immigration and Customs Enforcement agency used 1000 agents to inspect workers at six plants owned by Swift on 12 December 2006, arresting almost 1300 of the 7000 workers employed on the day shift in these plants. Crider Inc., a poultry processor in Stillmore, Georgia, lost three-fourths of its 900-strong workforce when ICE agents mounted a raid on Labor Day weekend in 2006. In the aftermath of the raids, many meatpackers enrolled in E-Verify, the Internet-based database that allows employers to check the legal status of newly hired workers.

The result was a reversal of the growing share of Hispanics in meatpacking between 2005 and 2010. EEOC data, which report the sex, race, and ethnicity of employees (www.eeoc.gov/eeoc/statistics/employment/jobpat-eeo1/index.cfm) in most US establishments, show that the share of Hispanic workers in food manufacturing and meat packing rose rapidly between 2000 and 2005 but fell between 2005 and 2010. In 2000, Hispanics were 38% of all employees in animal slaughtering and 48% of animal slaughtering laborers. The Hispanic share of animal slaughtering workers rose by approximately 10%

points between 2000 and 2005, and then fell to 2000 levels or below by 2010.

Reasons for the rising share of Hispanics among laborers in meatpacking include network hiring and recruitment during periods of low unemployment. Reasons for the falling share of Hispanics since 2005 include well publicized workplace raids in 2006–07 and I-9 audits since the 2008–09 recession that increased unemployment and made year-round meatpacking jobs that often pay US$12 an hour more attractive, and more employers enrolling in E-Verify, which may discourage unauthorized workers from applying for jobs.

Community Impacts

The arrival of Hispanic workers can quickly change the face of rural areas that sometimes have not experienced significant immigration for a century. The new residents have been welcomed in most areas, especially those losing people and jobs. Hispanic immigrant meatpacking workers buy and rent homes and shop at local stores, helping to stabilize local economies.

There are also new tensions with demographic change. Many local residents complain about the side effects of the changing labor force, including more students with limited English proficiency in local schools and more uninsured patients seeking health care at local clinics and emergency rooms. Many meat processing plants provide health insurance and other benefits after 60 or 120 days of employment but, with high turnover, a significant share of the workers in a particular plant may not have employer-provided health insurance.

Two extremes mark the reactions of meat processors to these externalities from hiring migrant workers. Some recognize that they are hiring workers from outside the area with little English and formal schooling, and some have formed partnerships with local community colleges and high schools to offer classes in English, finance, and other life skills to their workers. For example, Tyson Foods has an education assistance plan that reimburses 75% of the cost of tuition, books, and fees (up to US$3500 a year) for coursework that helps to meet the company's business needs. In Grand Island, Nebraska, Swift & Co. built a two-classroom school near its plant in 2002 so that workers could attend high school classes before and after their work shifts; the local school district provided a teacher and a teacher's aide.

The other end of the spectrum is marked by processors who say that their major economic contribution is the facility they provide for local farmers and the payroll they provide to local workers. Meatpackers who do not make impact payments, sponsor sports events, and inform community leaders of their plans may contribute to the backlash against immigration in some communities. Some cities and counties have voted against zoning or other changes needed to open or reopen meat processing facilities.

Many rural counties in the Midwest are losing people, forcing residents to choose between depopulation and diversity. Over the past 50 years, census-defined rural counties without a city of at least 2500 people lost more than a third of residents in 11 Great Plains states, with farm-based counties away from interstate highways losing the most residents. Of the 99 US counties with the highest percentage of residents older than 85 years, all but two are in the Great Plains.

The General Accounting Office (1998) concluded that there were mixed effects of immigrants. On the one hand, the arrival of immigrants helped to stabilize populations that were shrinking, and counties with meatpacking plants had faster increases in per capita income and retail sales than non-meatpacking countries. On the other hand, the increased number of poor and limited-English proficient children in schools and very high turnover among workers prompted teachers to complain that it was very hard to educate children who may be in their classrooms for only a short period. The housing market tightened with the influx of workers, especially for inexpensive rental housing such as mobile homes.

Conclusions

Farm operators, unpaid family workers, and hired workers are the three major types of workers employed on US farms. Over the past quarter century, the share of average employment contributed by hired workers has been rising, so that hired workers are now about 60% of average employment on US farms. These hired workers are concentrated in three interrelated ways, by commodity, size of farm, and geography, so that most hired workers are employed on large farms in California and a few other states that produce labor-intensive fruit and vegetable commodities. Dairies and nurseries are also important employers of farm workers.

Over half of the hired workers on US farms have been unauthorized since the mid-1990s, and almost all new entrants to the farm workforce are unauthorized. Farm work is more often a less-than-10-year job than a career, and older hired workers who find nonfarm jobs are typically replaced by youthful newcomers from rural Mexico, giving especially seasonal agriculture something of a revolving-door labor market.

This revolving door is threatened by immigration reforms that may make it more difficult for newcomers to enter from abroad. Farm employers want new and modified guest worker programs to make it easier to hire the foreign workers who are over two-thirds of US farm workers, whereas worker advocates argue that there must be strong recruitment, housing, and wage requirements to protect foreign and US workers. Farm employers and worker advocates reached a compromise in 2000 known as AgJOBS to legalize currently unauthorized farm workers and make it easier for farm employers to hire guest workers in the future, but they have been unable to persuade Congress to enact AgJOBS.

Instead, the federal government has gradually tightened border and interior enforcement, and some states have implemented immigration control laws, in ways that have generated farm labor shortage complaints. Most complaints of labor shortage reflect special circumstances, such as particularly light or late harvests in remote areas that do not attract workers, but farmers fear that they could face labor shortages that would result in sharply higher wages. For this reason, farm employers have a keen interest in immigration reform proposals.

Given immigration policy uncertainties, many farmers are hedging their bets. Most oppose federal laws requiring employers to use E-Verify to check new hires and the enactment

of state laws penalizing employers and unauthorized workers unless these enforcement efforts are accompanied by employer-friendly guest worker program. Some employers are investing in housing so that they can employ H-2A guest workers, and some are investing in mechanical aids to enlarge the pool of available workers and labor-saving mechanization to adjust to fewer and more expensive workers. History is unlikely to repeat itself and flood the farm labor market with new workers, as in the late 1980s, but it is not clear whether and how fas farm labor costs under *status quo* and immigration reform scenarios will change.

See also: Agricultural Ethics and Social Justice. Agricultural Labor: Demand for Labor. Agricultural Labor: Gender Issues. Agricultural Labor: Labor Market Operation. Farm Management

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Agricultural Law

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Glossary

Ad valorem taxation A tax based on the fair market value of the real estate. The value is calculated on the property's potential for its highest and best use.

Appropriation doctrine State legislative delineation of rights and priorities to water resources.

Conservation easement An easement that sets forth conservation objectives such as preserving wildlife habitats, riparian lands, forests, or farmland.

Point-source pollution Water pollution from a single point such as a pipe or concentrated animal feeding operation.

Preferential assessment The modification of ad valorem taxation under which qualifying land is assessed according to its current use value rather than fair market value.

Production contract Agreement by which a producer agrees to feed and care for livestock or poultry owned by a contractor for payment.

Right-to-farm law Legislative antinuisance provisions which say qualifying activities are not nuisances so that farmers have the right to continue farming even though their activities are objectionable to neighbors.

Riparian doctrine Common law doctrine delineating rights to water resources.

Security agreement A contractual arrangement in which the borrower assigns collateral as security for the repayment of a debt to the lender.

Transferable development rights A form of development control under which landowners are provided financial incentives to conserve agricultural land uses.

Introduction

The hard economic times of the 1930s contributed to ideas that farmers and farm communities needed legal expertise. In 1933, V. O. Braun, a lawyer from Owosso, Michigan, published a book titled, *Agricultural and Business Law for the Farmer*. Twenty years later, faculty from land grant universities in the north-central region recognized the changing structure of agriculture and published proceedings from a seminar titled, 'Legal Aspects of the Family Farm Corporation.' The communications and ideas of this faculty led to discussions of having more structured venues for communicating information dealing with agricultural law.

Meanwhile, other legal experts developed materials and published information on agricultural law. In 1979, the *Agricultural Law Journal* (discontinued) was initiated to provide scholarly articles about agricultural legal issues. Articles in law reviews and other publications provided a foundation for agricultural law in the 1980s. A multivolume treatise, *Harl, Agricultural Law*, provided in-depth coverage of agricultural law topics. The authors and their literature shaped the issues, legislation, and jurisprudence forming agricultural law.

Agricultural law includes numerous legal topics and agricultural law practices have changed over the years. The early issues centered on property and business arrangements. In the 1970s, many agricultural lawyers spent considerable amounts of time on property taxation and estate planning. Farm financial issues in the 1980s drew attention to financial matters including bankruptcy. The industrialization of agriculture and concerns about environmental quality in the 1990s meant that agricultural law expanded to encompass issues such as water pollution from concentrated animal feeding operations (CAFOs). Issues on genetically modified organisms, animal welfare, agricultural labor, and food safety have also become important. The potential breadth of an agricultural attorney is unlimited. Agricultural law can be described as the application of legal principles to agricultural, rural, environmental, business, and food issues.

A discussion of the topics of agricultural law would not be complete without a foundation of the institutions that have been developed to support agricultural lawyers. Although any law school graduate may become an agricultural lawyer, specialized agricultural law organizations and publications have become prominent in assisting lawyers in serving agricultural clients. These clients include farmers and ranchers producing food and fiber products, input suppliers, processing facilities, retailers, distributers, and customers and consumers of agricultural products. Thus, the discussion of agricultural law is very broad and no single term includes the entire clientele. For simplicity, the clientele will be referred to as 'producers' despite the fact that it includes marketers and others.

For a summary of agricultural law topics, the article will look at the US and what agricultural law means to agricultural producers and their counsel. Part II describes some of the resources that are available to persons wanting more information about agricultural law. The discussion of topics commences in Part III with transactions in real property. Part IV covers leases and granting access to property, whereas Part V looks at agricultural nuisances. Part VI addresses business arrangements, whereas Part VII looks at governmental regulations and programs that provide rules that are important in maintaining a viable agricultural sector. Governmental regulations dealing with water resources and environmental quality are examined in Parts VIII and IX. Finally, a collection of other agricultural law topics is covered in Part X.

Institutions Supporting Agricultural Law

At the suggestion of the Farm Foundation, a group of American lawyers dealing with agriculture converged in 1980 and

established the American Agricultural Law Association (AALA), a national organization of professionals with interests in agricultural law. This organization is a nonprofit organization that serves as the preeminent organization for agricultural law in the US. Membership consists of a broad range of agricultural law practitioners, academics, government workers, and lawyers working for agricultural interest groups (Uchtmann, 2007). The AALA has yearly annual continuing legal education conferences that address a multitude of agricultural law topics. The AALA also has a LISTSERV so that members can make inquiries and share information.

In Europe, national agricultural law associations exist in many countries. In 1957, lawyers founded the Comité Européen de Droit Rural (CEDR), also referred to as the European Council for Agricultural Law. The CEDR is the only pan-European organization representing lawyers and professionals interested in rural law and has consultative status with the Council of Europe. The CEDR holds a European Congress on Rural Law in odd-numbered years and invites representatives from the AALA and other countries to participate.

Several American law schools offer agricultural law courses in which students learn subject matter that is important for rural law practices. In 1981, the University of Arkansas launched an advanced master of law degree in Agricultural Law, which has evolved into the LL.M. in agricultural and food law. Students with a law degree return to law school for more specialized training. This program remains the only American advanced degree in agricultural law and attracts students from all over the world. Law schools at Drake University, Penn State University, and in Canada, the University of Saskatchewan, have centers specializing in agricultural law that organize programs and publish information to assist others with agricultural law issues.

Several American land grant universities offer undergraduate courses in agricultural law and related legal subjects, and a few have agricultural law centers. Undergraduate students receive training in law topics that will help them in their careers and many secure jobs with agricultural business firms. Courses may include agricultural law, agribusiness law, environmental law, tax law, and food law. Some universities have minors in agricultural or agribusiness law.

Nearly 20 universities have joined an interactive distance education alliance of universities headquartered at Kansas State University known as Great Plains IDEA. In 2012, AG*IDEA, an affiliate of Great Plains IDEA, offered the first undergraduate agricultural and environmental law courses through distance learning technology. Students are able to complete a minor in agricultural or environmental law through the AG*IDEA program.

Land grant universities may also have an agricultural law expert who provides training sessions and assistance through the Cooperative Extension Service. This faculty develop and deliver programs in their state to assist agricultural producers and others by providing information concerning legal issues. The programs by extension faculty involve educational training rather than giving legal advice.

Other specialized groups provide training, support, and services for persons needing legal assistance in rural communities. The American Bar Association (ABA) has various subcommittees that address agricultural law. Many state bar associations have agricultural law committees that assist rural practitioners through contacts and programs.

The National Agricultural Law Center at the University of Arkansas is an agricultural law research and information facility that is independent and national in scope. In conjunction with the AALA, it maintains an agricultural law blog (http://www.agandfoodlaw.com/2009/01/about-this-blog.html) as a resource for securing information on many agricultural law topics. The Farmers' Legal Action Group, Inc. of St. Paul, Minnesota, offers legal services to family farmers and their rural communities to help keep family farmers on the land.

Specialized literature on agricultural law is also prominent and assists practicing attorneys in becoming aware of contemporary legal developments that may impact their clients. Four American law schools have law journals specifically dealing with agricultural and food law. The oldest is Drake University's *Drake Journal of Agricultural Law*. The University of Arkansas Law School publishes the *Journal of Food Law and Policy*, the University of Kentucky the *Kentucky Journal of Equine, Agriculture, and Natural Resources Law*, and the San Joaquin Law School the *San Joaquin Agricultural Law Review*. Other journals on agricultural law include the *Jahrbuch des Agrarrechts* (University of Göttingen, Germany), *Agrarisch Recht* (Institute for Agricultural Law, Wageningen, The Netherlands), and the *European Food and Feed Law Review* (Lexxion Verlagsgesellschaft mbH, Berlin).

Transactions in Real Property

One of the most conspicuous subject areas of agricultural law deals with real property. Deeds, ad valorem taxation, preferential agricultural assessment, farmland preservation, and corporate farm laws are issues that have been important components of the practices of agricultural lawyers.

Real property is often an agricultural producer's major asset and agricultural lawyers assist in the preparation of documents used with the purchase and sale of real estate. Documents may include deeds, lien releases, easements, mortgages, loans, and guarantees of title. Counselors also assist clients by checking for liens and encumbrances against the property. Other advice may address alternatives regarding the ownership of property, as a producer may want to use a business entity such as a partnership, limited liability company, or corporation.

Because producers use vast acreages for the production of crops and animals, ad valorem taxation on real estate is an important issue. Under ad valorem taxation, land is assessed at fair market value. Whenever nearby properties are used for nonagricultural purposes with higher market values, assessors can base the farmland's value on its potential to be developed for nonagricultural purposes. This means that farmland next to residential and commercial properties can have higher property taxes than comparable agricultural land in the more distant countryside.

In the 1950s, subdivisions and nonagricultural land uses were moving into agricultural areas near populated areas causing the property taxes of agricultural landowners to increase to an extent that taxes became a financial impediment to viable production. To assist in preserving farmland, farm groups and agricultural lawyers advanced a new taxation model

known as preferential assessment. Preferential assessment involves the assessment of qualifying land at its use value rather than fair market value. Generally, the adoption of preferential assessment requires an amendment to the state constitution and the adoption of legislation delineating use value qualifications. Under preferential assessment, landowners may be required to sign contractual agreements to keep their lands in agricultural production for a number of years. Legal counselors provide property owners advice about the advantages and potential problems of entering such agreements.

Agricultural lawyers are also involved with efforts to preserve farmland. They work with landowner clients to determine whether to participate in state programs involving preferential assessment, farmland preservation, conservation easements, and transferrable development rights. Agricultural lawyers may also be involved in helping communities develop zoning ordinances and agricultural districts that are supportive of continued agricultural production.

In cases where owners want to protect agricultural land, legal counsel may draft a conservation easement to preclude the future development of the property. A conservation easement sets forth conservation objectives to preserve wildlife habitats, riparian lands, forests, or farmland. An easement may delineate purposes for which the property may not be used and its restrictions are perpetual. Under the applicable state law, an organization holds the conservation easement and is granted the power to constrain the rights of the landowner.

By voluntarily placing a conservation easement on property to preserve farmland, landowners qualify for tax benefits. Because the property cannot be developed, its real estate taxes may be lower than comparable properties without an easement. The value of a donation of a conservation easement is deductible from the donor's income under federal income tax law. The value of property subject to a conservation easement may also be taken into account for estate tax purposes.

Another institution used to preserve farmland involves a state or local program for transferable development rights (TDRs). Under a TDR program, a rural landowner sells development rights to private developers and the farmland is limited in its future uses. By purchasing development rights, developers are granted rights to develop properties at higher densities in nonrural areas. Under this arrangement, agricultural producers receive compensation without having to sell or develop their lands.

Legal counselors may be called on to assist clients in forming farm corporations that comply with their state's legislation against corporate farms. Several states in the upper Midwest have delineated prohibitions on the corporate ownership of farmland with exceptions for family farms and active agricultural producers. Justifications for limiting corporations from owning farmland include a dislike for industrialized agribusiness and absentee ownership as well as concerns about environmental damages and rural depopulation.

Leases of Real Estate Interests and Granting Access to Property

Because farmland is expensive and heirs are often hesitant to sell family farm properties, many producers rent considerable acreage for agricultural production. Lawyers are needed to help with contractual provisions that set forth agreed terms between landlords and tenants. With new emphasis on domestic energy sources, producers are entering leases to allow others to develop wind energy resources or engage in oil, gas, and mineral extraction. Rural property owners also may require legal assistance for arrangements involving others coming onto their properties for recreational, hunting, and agritourism purposes.

Two types of traditional farm leases covering the rental of land to grow crops are used: crop share leases and cash rent leases. Crop share leases generally involve a division of supplying farm inputs and sharing the value of the harvested crop. These arrangements facilitate the extension of credit by the landlord and sharing the risks of a poor crop between the landlord and tenant. Although the landlord supplies the land, typically the tenant pays for the variable inputs including fertilizer, seed, pesticides, irrigation, and cultivation.

Cash rent leases entail the landlord receiving a cash payment in exchange for the tenant's use of the land. Under cash rent leases, landlords do not share with expenses or income from the production of the crop. This means the tenant assumes all of the risks of crop production. Tenants often seek multiyear leases so that they can apply fertilizer nutrients to enhance production and receive the benefits of nutrients that remain in the soil for a subsequent year's crop. Leases also may need to address credit arrangements, liens on the crop, options to purchase, and insolvency.

Many rural landowners have opportunities to consider leasing their properties for activities including hunting, recreation, wind energy, and oil, gas, and mineral extraction. Before entering these leases, landowners need to consider a range of potential consequences that may accompany giving others access to their properties. One major issue is whether the property owner might be held liable for an accident to another person who is on the leased property. Because an accident might result in large medical expenses and personal injury costs, provisions might assign responsibilities or require insurance coverage.

Landowners entering leases for the extraction of oil and gas need to be concerned about environmental damages. A majority of these leases are written by the drilling companies and fail to adequately address responsibilities regarding land contamination and degradation. Without legal advice, landowners may sign leases that fail to hold drilling companies responsible for damages associated with faulty equipment and negligent activities. Roads and pads for drilling activities may adversely affect existing property uses. Hazardous fracturing chemicals may be released from leaking casings, blowouts, spills, and flowback that contaminate the land, surface water, or even groundwater. After a well is drilled, the drilling company may leave sump holes, mud pits, and obsolete equipment on the site, and contaminants on the property may mean it has diminished in value. These potential problems suggest that competent legal advice should be secured before signing a lease.

Over the past half century, farm interest groups have advanced several legislative ideas to limit liability for accidents by persons invited on rural properties. State recreational use statutes were adopted to provide incentives for property owners to allow others to use their property gratuitously by

altering the duties property owners owe recreational users. By redefining the duty of care, a state's recreational use statute makes it less likely that a property owner will be liable for damages to an injured recreational user. Counsel can help property owners determine whether they qualify under a statute for protection against liability.

Complex equine liability statutes have been enacted by more than 40 states to help protect owners and others from liability for equestrian accidents. Most equine liability statutes declare that equine owners and others are not liable for injuries resulting from the inherent risks of equine activities. In addition, equine liability statutes may specify duties of care for providers and have requirements for warning signs and liability releases. Legal counsel can help property owners meet conditions necessary to qualify for protection against liability for some accidents.

Agricultural lawyers also assist clients who want to provide activities for tourists. Agritourism has become an important source of income for some producers, with activities including petting zoos, hay rides, corn mazes, pick-your-own operations, theme parties, picnics, and winery tours. However, producers need to be concerned about financial liability for persons injured on their properties, and several states have adopted agritourism statutes to limit liability. The most common legislative term says that participants should assume inherent risks while participating in agritourism activities.

Agricultural Nuisances

With the expansion of residential areas into the countryside in the 1950s, conflicts between agricultural practices and nonfarm residential property users became a problem. Persons living in suburbia did not like the noises, dust, and smells that accompany aspects of agricultural production. Many of the objections centered on practices involving animal manure. Agricultural lawyers were called on to defend producers against lawsuits based on nuisance. If a jury found that an agricultural practice was a nuisance, the producer could be enjoined from continuing the practice. This resulted in producers not being able to profitably continue with their farming operations. Moreover, producers were hesitant to make investments in their operations because of uncertainties about future complaints from neighbors.

To counter injunctive relief available in nuisance lawsuits, state legislatures adopted antinuisance laws. These laws became known as 'right-to-farm' laws because by precluding injunctive relief under nuisance law, they enable producers to continue farming despite the objectionable activities. A majority of the right-to-farm laws adopted a 'coming-to-the-nuisance' exception under which a person who moved next to an established farm could not claim the farm's activities were a nuisance. In this manner, right-to-farm laws enabled producers to continue with activities despite the fact that the neighbors felt the activities were a nuisance. Right-to-farm laws in some states also offer antinuisance protection to qualifying agricultural businesses.

Because right-to-farm laws delineate a state's antinuisance rules, they preempt attempts by local governments to regulate agricultural nuisances. However, local governments may continue to regulate agricultural activities under zoning or local health laws unless state legislation says otherwise. Although right-to-farm laws operate to protect producers against some nuisance lawsuits, legal counsel may be required to evaluate whether the law applies to the facts of a given situation. Each state's right-to-farm law contains specialized provisions delineating qualifications before the protection applies. Moreover, amendments to state right-to-farm laws have resulted in very different provisions for each state.

Another issue under right-to-farm laws is whether the provisions of a state law constitute an unconstitutional taking. In 1998, an Iowa right-to-farm law was found to create an easement that constituted an unconstitutional taking of private property (Centner, 2000). The court felt that the Iowa legislature went too far in attempting to preserve farmland, and in a subsequent lawsuit, this was related to the protection of property rights provided by the Iowa Constitution. Safeguards and regulatory provisions incorporated in right-to-farm laws of other states should thwart similar constitutional challenges.

Business Arrangements

Another prominent area of agricultural law deals with business arrangements used by producers and related firms in the production and marketing of agricultural products. Legal counselors give advice on contractual agreements, help clients form business entities, oversee documents used in securing financing, assist indebted operators with bankruptcy, and provide advice on estate planning.

Producers generally seek assistance from legal counsel whenever entering a major contractual obligation to ascertain that the agreement accomplishes its intended purpose without creating any unnecessary complications. Important contracts include agreements for forming businesses, purchasing businesses, buying and selling property, mortgages, leases, loans, easements, lien releases, and security agreements that pledge collateral as security for borrowing money. Counsel can explain the meaning of legal terms, add provisions to offer protection against potential problems, suggest the removal of onerous or unnecessary provisions, and offer advice on alternatives.

Agricultural producers raising large numbers of animals, especially hogs and poultry, often sign production or marketing contracts with business firms known as integrators. The contracts are written by the integrators with detailed provisions affecting production activities. Under a production contract, the producer feeds and cares for the animals and is paid pursuant to a contractual pricing formula determined by the performance of the animals. Under a marketing contract, the producer agrees to sell or deliver animals to an integrator according to pricing terms set in the contract. Agricultural lawyers may be needed to offer advice on the terms of these contracts, although producers may have few options for alternative marketing outlets for their animals (Looney and Poole, 1999).

Agricultural law practitioners help clients make decisions about whether to operate as a sole proprietorship or to form a

business entity. Producers may find it advantageous to form a business entity to raise funds, have family members or friends as partial owners, limit liability for losses and accidents, and transfer assets on death. Each state has separate legislation governing business entities that include corporations, Subchapter S corporations, cooperatives, partnerships, limited partnerships, and limited liability companies.

A disadvantage of some business entities is income taxation at the firm level. Legal counsel can explain how each business entity might fit the needs of a client's farming situation. Favorable state legislation regarding limited liability companies suggests that this form of business is well suited for many small businesses. A limited liability company allows income to pass through to owners so that there is only a single level of income tax and liability is limited to the assets of the company.

A major reason for forming a business entity is liability for accidents. Farming is a dangerous occupation given the chemicals and equipment used in producing food and animals. Any farm or business that employs nonfamily workers or has people coming onto the property should be concerned about being held liable for damages from an accident. For example, a worker may suffer severe injuries from operating a piece of farm equipment. This suggests that the operator may want to consider forming some type of business entity that would own the land and equipment and employ the worker. The producer could own other assets outside the business entity, such as a house, bank accounts, stocks, and bonds. By structuring the business entity as owner of machinery and property and the employer of workers, a producer may successfully shield assets outside the entity from liability related to a major accident.

Over the years, agricultural lawyers have been involved with helping producers form agricultural cooperatives, and assisting clients in their dealings with their cooperatives. Distinct legal provisions for this form of business and controversies on paying out dividends to members have meant that specialized legal counselors are needed to assist producers as well as cooperatives.

Counselors help agricultural producers and agribusiness firms grapple with problems connected with credit and security interests (Meyer, 2010). Producers often seek counsel to assist with documents involved in securing financing for the purchase of seeds, fertilizer, equipment, and other production inputs. Agricultural producers depend on the advice of agricultural lawyers before signing these contractual arrangements to ascertain that terms are reasonable and do not delineate any adverse provision that may interfere with future business arrangements.

When borrowing money to purchase personal property, borrowers sign a security agreement listing collateral as security for the repayment of the loan. Security agreements have significant ramifications concerning ownership and rights in property. Legal advice is important when delineating terms of a security agreement because of the options available for listing collateral. Collateral may include accounts, goods, stock, livestock, equipment, inventory, and farm products. Special rules apply to farm products as opposed to other types of collateral so different financial arrangements may be needed to safeguard the interests of a client.

Lenders often want to list several categories of collateral to guarantee assets for the repayment of debts. Borrowers want to limit the collateral listed in a security agreement so that they have unencumbered collateral to use in securing additional financing. Counselors can advise clients on which collateral to list and advise them on their rights in collateral listed in more than one security agreement. Because multiple parties may have a security interest in the same property, a major objective is to help clients structure business transactions so that no money is lost because of the insolvency of another. Lawyers also advise clients on how they might secure priority on collateral in the possession of someone else.

Owing to the cyclical nature of commodity prices and other problems, agricultural producers may become so indebted that they need to consider bankruptcy. Poor economic decisions in the 1970s led many producers to experience financial difficulties and secure the assistance of agricultural lawyers for advice about bankruptcy. Competent legal counsel is important because bankruptcy does not need to result in the liquidation of property. Rather, separate chapters of the federal Bankruptcy Code offer different bankruptcy options for financially distressed producers.

In 1986, Article 12 of the federal Bankruptcy Code was adopted to provide advantageous provisions for qualifying financially challenged family farmers (Geyer, 1997). The article allows farmers to demand concessions from secured creditors and write down secured debt. Under the article's provisions, farmers can be rehabilitated and continue with their farming operations. Legal counselors help farmers use bankruptcy provisions to reorganize their businesses with less debt and continue farming.

The imposition of federal gift and estate taxes means that estate planning is an important part of many agricultural law practices. Owing to the value of farm buildings, equipment, and farmland, agricultural producers often have sizable estates. With the death of a farm owner, the payment of estate taxes may interfere with the transfer of a farm to heirs. Because federal estate tax provisions change, legal counselors help clients structure estate plans to minimize taxes while achieving the transfer of assets to desired beneficiaries. For example, a producer may want to structure assets to take advantage of the special use valuation of farmland for estate taxation purposes under Section 2032 A of the Internal Revenue Code. Because a decedent must meet requirements concerning the ownership of qualified real and personal property, as well as the use of the property for 10 years after death, planning is needed to qualify for this valuation provision.

Governmental Regulations and Programs

The uniqueness of agriculture has led legislative bodies to adopt special programs and exceptions that are important to the profitability of many producers. Agricultural lawyers are called on to assist producers in structuring their businesses to take advantage of benefits provided by federal farm programs and to comply with applicable regulations. Legislative and regulatory provisions dealing with income taxation, federal farm programs, disaster and insurance programs, marketing

issues, and product labeling are important to many farm businesses.

Federal income taxation continues to be a major issue for many agricultural producers because of changes to the Internal Revenue Code. Legal counselors provide suggestions for structuring business activities to take advantage of deductions and credits to reduce federal and state income taxes. Many state Cooperative Extension Services offer yearly income tax training for legal practitioners and accountants that provides updates on tax provisions and ideas for assisting clients in reducing taxable income.

Agricultural producers have a variety of property that may qualify for income tax deductions, credits, and favorable depreciation schedules. Tax law provisions on capital gains rates, domestic production activities deductions, depreciation, weather-related event taxation, like-kind exchanges, government payments, income averaging, and self-employment taxes have meant that legal counsel specializing in tax law can offer suggestions to help producers reduce income tax bills. In some situations, counsel may advise producers to generate expenses such as investing in new equipment to provide offsets and deductions to lower tax bills. Other advice may involve like-kind exchanges that avoid recognizing gains from the sale of equipment and requesting selected types of payments from governmental farm programs to defer income.

Owing to the pervasive regulation of agricultural activities by the federal government, many agricultural lawyers have developed expertise in administrative issues accompanying agency decisions. This requires familiarity with federal administrative law, the rights of producers under a given governmental program, and dealing with the agency when there is an issue about qualifying for a program or program benefits. Issues between agricultural producers and the government under federal farm programs have provided agricultural attorneys opportunities to help producers secure earned benefits.

Over the years, financial incentives offered through federal farm programs have been important to producers. Historic federal farm programs have provided price supports, income supports, recourse loans, marketing orders, and various assistance programs to support continued agricultural production. As new programs are introduced, legal counselors can assist agricultural producers in determining ramifications of participation. Other advice may center on maintaining flexibility for adjusting to potential changes in federal programs and helping producers restructure so they can participate.

Agricultural lawyers are also needed when a disaster strikes and a producer seeks advice on how to qualify for assistance. Under the Federal Crop Insurance Act, agricultural producers can secure insurance to manage risk and have protection against substantial losses that occur because of drought, flood, or other national disasters. Legal counsel may be sought by a producer with a crop insurance or disaster claim that was disallowed for failure to follow 'good farming practices.' Counsel can help secure an expert's opinion to develop a record that supports qualification for a claim. The overturning of a decision by an insurer or governmental agency requires considerable proof and needs to be handled correctly to succeed.

Other federal disaster assistance programs are also important to agricultural producers who experience a major natural disaster. Lawyers can assist clients in determining whether they qualify for payments under the Emergency Loan Program, Disaster Set-Aside Program, Noninsured Crop Disaster Assistance Program, Supplemental Revenue Assistance Payments, Tree Assistance Program, Livestock Forage Disaster Program, Haying and Grazing of the Conservation Reserve Program, Conservation Stewardship Program, Livestock Indemnity Program, and the Emergency Conservation Program.

Because producers of livestock often confront a market with few buyers for their animals, Congress enacted the Packers and Stockyards Act. The act was intended to help producers by preventing processors from creating monopolies. Given the market concentration of major firms as well as the contractual arrangements of many processors, individual producers may have little choice in marketing outlets. Counsel can help producers determine whether a processor's practices have an adverse effect on competition contrary to the provisions of the Packers and Stockyards Act.

Producers and buyers of fruits and vegetables have special needs accompanying marketing transactions for fresh produce. Provisions of the federal Perishable Agricultural Commodities Act govern various aspects of the marketing arrangements to give assurance that growers are paid. Under the act, a trust is formed for receivables and proceeds from the sale of produce. Agricultural lawyers work with growers and dealers to meet the financial obligations covered by federal law.

Consumer demand for specialized food products and more information on food labels has created opportunities for differentiating products to garner higher prices. Food product marketers depend on product labels to position their products in the marketplace. Yet the labels must conform to labeling requirements set forth by federal and state laws. If information on a label is false or misleading, it is misbranded. Moreover, the absence of information relevant to the issue may cause labeling to be misleading. Legal counsel may be needed to ascertain that a client's labeling information complies with misbranding legislation. Other advice might be needed to determine the legality of voluntary labeling involving negative characteristics such as rBST and genetically modified organisms.

The US Department of Agriculture (USDA) regulates labels on some food products. Its organic seal may be used on products that were grown or produced in compliance with National Organic Program regulations. Under the USDA's organic program, detailed requirements on production practices must be followed before a product can be labeled as 'organic.' Certifying agents accredited by USDA are used to provide third-party certification of producers' organic plans. Organic food production has become an important segment of agricultural production.

Legal counsel remains important in organic production because of unresolved issues and controversies about qualifications. Producers continue to need assistance in comprehending the rules overseeing organic certification. Legal counsel may be necessary to seek redress for spray drift damages from neighboring property owners. Organic labels containing value judgments may be found to be misleading under the Food, Drug, and Cosmetic Act. Insufficient testing and minimal oversight of certifiers may lead to controversies about products labeled as organic. Legal counsel may be needed to represent producers or consumers in these disputes.

The USDA also oversees country-of-origin labeling and labels containing process information such as notations on irradiation and antibiotics. Given the complexities of misbranding law, legal counsel will undoubtedly be asked to examine a proposed label with such information to ascertain compliance with the law. Legal advice may also be needed on conforming to packaging requirements established by the Federal Trade Commission.

Related to food labeling are new legal requirements for menu-labeling at restaurants adopted by the Food and Drug Administration. The Patient Protection and Affordable Care Act of 2010 was enacted by Congress to govern restaurant menu-labeling. Under the law, caloric information to help people control obesity must be provided by restaurants, similar retail food establishments, and vending machine operators that are part of a chain with 20 or more locations or 20 or more vending machines. The act also preempts local and state regulations, and allows restaurant and vending machine operators to voluntarily elect to be subject to the federal regulations and thereby avoid having to comply with state and local regulations. Legal counsel can provide advice on voluntary and required information on labeling to help clients maintain compliance with the applicable regulations.

Water Resources

The production of food and fiber products is dependent on the availability of water resources. Both water quantity and quality affect the viability of crop and animal production. In more and more situations, agricultural producers need legal advice on how to comply with legal requirements dealing with water resources. Additional legal advice may examine the future availability of sufficient water and how to address issues of water quality.

Owing to the provisions of the US Constitution, the federal government is involved in water issues that affect agricultural producers. Provisions regarding treaties with Indian tribes, compacts between and among states, and the Commerce Clause have justified Congressional action in enacting regulations governing water allocations, flood control, irrigation projects, and pollution. Simultaneously, each state has its own water law. Legal counsel may be called on to assist producers in determining rights to water and the legality of using water from a water body.

State water law may incorporate principles of the riparian doctrine, delineate an appropriation doctrine governing water rights, or use a combination of both. The riparian doctrine was adopted by most states in the eastern part of the US. Water usage is part of land ownership and applies to landowners adjacent to surface waters. There is a division between natural use and artificial uses of water. A landowner may use unlimited quantities of water for natural uses but only reasonable quantities for artificial water uses such as impoundments and irrigation.

Conflicts involving insufficient quantities of water in states following the riparian doctrine have led state legislatures to adopt water-permitting systems. This means that water usage for irrigating crops is governed by the riparian doctrine amended by state appropriation provisions. Counsel may be needed to advise agricultural producers on their rights under the permitting system and how to qualify for future rights to water resources.

In situations of water scarcity, the riparian doctrine does not provide a reasonable reconciliation of competing uses for water resources. This has led state legislatures in the western part of the US to adopt appropriation doctrines to delineate their state's rules for water usage. Each state has adopted rules delineating priority rights in the use of water resources. The first person to use and file for the use of water from a water source is known as the senior appropriator. This person may continue to use the full allocation of water in subsequent years, although rights may be lost for not using an allocation. Subsequent users are junior appropriators. In years when there is insufficient water, junior appropriators may not receive their full allocations.

The appropriation doctrine is accompanied by issues demanding legal assistance. Allocations that cross state borders may be governed by federal treaties and court rulings. Cities may purchase water rights from landowners in the countryside leaving subsequent landowners without water. In some states, public sentiment may favor the reallocation of water from agricultural uses to other public needs. Another issue is retaining sufficient surface waters for recreational and scenic purposes. States continue to grapple with ideas to amend water usage rules to maximize the beneficial use of scarce water resources. Issues involving transfers of water rights may require careful legal analysis of competing interests and legislative pronouncements.

Environmental Issues

Producers have a responsibility in disposing of their byproducts and wastes responsibly so that they do not adversely affect others. Given damages that may be caused by pollutants, numerous environmental laws have been enacted and many apply to agricultural production (Centner, 2004). In pursing their activities, agricultural producers must desist from practices that release pollutants in violation of federal, state, and local environmental laws and regulations.

Turning to water quality, agriculture is listed by the US Environmental Protection Agency (EPA) as the major polluter of streams and lakes in the country. Under the US Clean Water Act, EPA has adopted numerous regulations that address the impairment of water quality by agricultural activities. Federal law distinguishes point sources of pollutants from nonpoint sources. Any point-source discharge of pollutants into federal waters needs a permit. Nonpoint-source pollution is regulated by the states.

A major issue involves pollutants from CAFOs. CAFOs are listed as point sources of pollution so that any CAFO with a discharge of pollutants into federal waters needs a National Pollution Discharge Elimination System permit. As a result of litigation commencing in 1989, EPA agreed to develop rules for CAFO discharges that would comply with the Clean Water Act. In 2003, 2008, and 2012, EPA adopted revised regulatory provisions for CAFOs. Agricultural lawyers continue to advise CAFO operators on the requirements delineated by the regulatory and judicial changes to the federal provisions.

Producers being charged with an environmental violation often employ legal counsel. Governments may assess considerable penalties for noncompliance. For example, an operator of a CAFO making a false statement in applying for a National Pollution Discharge Elimination System permit may be fined up to $10 000. An operator making an unauthorized discharge may be fined up to $37 500 per day (Centner and Newton, 2011).

Unacceptable air quality is also an issue that some agricultural lawyers may be called to address. Many CAFOs release significant quantities of air pollutants. Some states have decided that potential health problems associated with hydrogen sulfide, ammonia, and particulate matter releases from CAFOs merit regulation (Endres and Grossman, 2004). Agricultural lawyers can help clients meet requisite air quality controls and respond to enforcement actions.

Another air quality concern involves too much particulate matter in rural areas. Owing to vehicles on dirt roads and farm machinery in fields, considerable dust pollutes the air. Agricultural interest groups are seeking new legislation to relax air quality standards in rural areas. In 2011, bills were advanced in Congress to enact a 'Farm Dust Regulation Prevention Act' to enable state and municipal governments to exempt qualifying particulate matter from federal air quality controls. Under the provisions of the bills, mining, petroleum exploration and extraction, smelting, power generation, hydraulic fracturing, and other commercial and industrial activities would be able to release greater quantities of carcinogenic heavy metals in rural areas. The adoption of one of these bills might be expected to generate considerable work for attorneys in developing local regulations and responding to alleged violations.

Most agricultural producers take efforts to conserve their soil resources and seek guidance when the federal government introduces a new conservation program. The enactment of the Food Security Act of 1985 ushered in voluntary stewardship practices for private lands. Agricultural lawyers were called on to help clients discern the meaning of the swampbuster and sodbuster provisions of the Food Security Act in relation to the client's eligibility for benefits under other federal programs. Producers also considered whether to participate in the Conservation Reserve Program under which acreage is set aside from production in exchange for annual rental payments from the government.

Legal counselors may work with producers in analyzing the merits of participating in a number of federal environmental programs. These include the Environmental Quality Incentives Program, the Conservation Stewardship Program, and the Wetlands Reserve Program. However, despite many years of conservation efforts, agriculture remains a significant source of pollution of our nation's rivers and streams. The voluntary approaches for the adoption of stewardship practices have not provided lasting environmental protection. Future proposals to reduce pollution may be expected and legal counsel may assist producers in making decisions that will enable them to comply with new restrictions.

Agricultural producers may need the services of an agricultural lawyer to respond to allegations of damages accompanying the use of pesticides. Spray drift, the physical movement of pesticide droplets or particles through the air to any nontarget site, may cause problems when different crops are grown in close proximity. Agricultural attorneys may be called on to address allegations of drift damages in lawsuits based on trespass, nuisance, and negligence. Remedies under state law vary considerably given antinuisance protection and distinctions under trespass law for intangible drift.

Producers may also file a lawsuit against pesticide manufacturers for damages because of pesticides not performing as intended. Although the Federal Insecticide, Fungicide, and Rodenticide Act offers considerable protection for manufacturers of registered pesticides, producers are able to claim violation of state law labeling requirements if they are equivalent to federal misbranding provisions. Producers may also seek damages for crop losses under allegations of defective design, defective manufacture, negligent testing, and breach of express warranty. Lawsuits require considerable legal and scientific expertise to establish or disprove liability.

Agricultural lawyers may become involved with issues involving climate change. Although temperature and rainfall changes affecting crop production receive considerable attention, regulatory efforts to reduce greenhouse gas emissions affect agriculture. Producers may need to change practices to contribute to international efforts to address climate change (Hamilton, 2011b).

Other Issues

Agricultural lawyers have become involved with and provide advice on numerous other issues affecting agriculture. These efforts are important in helping agricultural producers develop and maintain viable business operations, respond to social expectations, and adjust their operations to changes in technology and the marketplace. Issues include food safety, genetically modified seeds, organic production, controlling diseases, migrant labor, animal welfare, energy, and local food production.

Food safety has become an important concern for many people, and numerous federal, state, and local regulations have been enacted to help guarantee safe food supplies. Some laws prescribe requirements that help guard against unwholesome foods and others provide for the inspection of food items and businesses processing food products. Federal agencies with food safety oversight include the Food and Drug Administration (part of the US Department of Health and Human Services) and the Food Safety and Inspection Service (part of the US Department of Agriculture). Many states have their own food safety provisions and inspection programs.

Outbreaks of food-caused illnesses show the need for food safety regulations. Although governments are in charge of prosecuting persons and firms that violate laws in placing unwholesome foods in the marketplace, legal counselors may be called to offer advice to persons injured by unwholesome food items. Counselors also help clients meet the regulatory requirements. This may include determining if a regulation applies to a client's activities, helping farm businesses comply with applicable regulations, or responding to allegations of a failure to comply with safety requirements.

A special food safety issue involves the sale of raw (unpasteurized) milk. To safeguard public health, federal law

precludes the sale of raw milk across state borders. However, a number of state legislatures have passed laws to allow the intrastate sale of unpasteurized milk. Legal counsel can help producers recognize the liability risks of selling raw milk and help them comply with the legal proscriptions.

Biotechnology and genetically modified seeds have revolutionized agriculture. Owing to seed patents, plant variety protection certificates, trade secrets, and licensing agreements, firms that develop seeds have property rights that may preclude others from adopting these innovations. Every genetically engineered organism needs a permit before it is introduced into the environment, with the Animal and Plant Health Inspection Service overseeing the permits. Agricultural lawyers may be called to offer advice to producers on the meaning of the intellectual property rights held by companies selling seeds. They may also become involved in lawsuits against agricultural producers over the infringement of patent rights.

Under US law, seed companies can sell patented seeds conditioned by a technology licensing agreement under which the seller expressly retains ownership of the genes and gene technologies (Endres, 2004). The agreement can preclude the buyer from saving any seed for planting the following season or from supplying seed containing protected genes to others. Agricultural producers who save seed for planting a subsequent crop despite their agreement to the contrary can be sued and held liable for the infringement of the seed company's rights.

A more disturbing problem is whether a farmer should be liable for infringing a seed developer's rights when pollen from genetically engineered plants is carried to conventional plants and protected genetic markers are found in the genes of the conventional plants. Under a Canadian lawsuit, a farmer was liable for patent infringement because patented genetic sequences were present in the farmer's crops because of pollen drift. Agricultural producers may face a patent-infringement lawsuit because of pollen from another producer's genetically engineered crops being detected in their crops. Aggressive enforcement of patent rights by seed developers means producers must respect established property rights.

Governmental efforts to control the introduction of foreign pests and disease outbreaks are important to agricultural production. To control the dissemination of a new disease, governments can destroy property exposed to the disease without compensation and quarantine animals. Given recent occurrences of citrus canker, citrus greening, mad cow disease (bovine spongiform encephalopathy), avian influenza, and H1N1 (swine) flu, governments have sometimes taken strong actions to eradicate a disease. Questions arise about who should pay for property that is destroyed or damaged by governmental actions (Centner and Ferreira, 2012).

Agricultural lawyers advise governments and producers on their rights concerning the destruction of diseased property. Under American jurisprudence, property owners have implied obligations not to use property in a manner injurious to the community. Simultaneously, however, federal and state constitutions require governments to pay for property taken for public use. Methods and programs to control disease may involve incentives for producers to invest in disease-prevention measures so that diseases do not become established. Disease eradication is important because it can reduce the need for pesticides and can lower costs of production.

Sources of manual labor continue to be important for agricultural production and producers are challenged by legal prescriptions governing laborers. Producers may need counsel to advise them on practices necessary for compliance with the law, particularly with respect to workers from foreign countries. Owing to exceptions under the Fair Labor Standards Act, agricultural workers may be exempt from minimum wages and overtime. Under the Migrant and Seasonal Agricultural Workers Protection Act, workers are entitled to prompt and full payment for their labor and safe, healthy housing. Aggrieved workers are able to bring lawsuits for damages or injunctive relief. However, an exception for small enterprises means that many workers are not protected. Controversy also exists about whether employers are responsible for workers' preemployment expenses including transportation, visa, and recruitment costs.

Producers who cannot find sufficient domestic workers may be able to bring nonimmigrant foreign workers to the US under a guest worker program. Program requirements vary and may require a showing that there are not sufficient workers willing and qualified to perform the seasonable labor needs. Another requirement may include documentation that the foreign workers do not adversely affect the wages and working conditions of similarly employed US workers. Programs often have requirements concerning housing, cooking facilities, and sufficient hours during the contract period. Workers may be granted a visa for a limited amount of time and may be precluded from seeking alternative jobs.

Producers are also often confronted with undocumented aliens seeking work. With an absence of proper documentation, it is illegal to employ these persons. The Immigration and Nationality Act requires employers to verify eligibility of individuals to be hired. Owing to dissatisfaction with rules for nonimmigrant foreign workers and undocumented aliens, Congress will debate this issue and may pass new legislation so that producers will need to make adjustments to their employment arrangements.

Concerns about illegal immigration and the lack of jobs for Americans have led some state legislatures to take actions to prohibit undocumented aliens from working within their borders. States have enacted laws with penalties for employers who fail to verify employment eligibility and for harboring undocumented aliens. Furthermore, an alien's failure to carry a registration document may be a state offense. Agricultural attorneys can help producers and workers in meeting the requisite legal requirements.

During the decade of the 2000, animal welfare issues became important to production practices in the US and Western Europe. Concerns about the ethical treatment of animals led animal rights groups to advocate legislation requiring more space for animals confined in cages and crates. The legislation affects producers of sows, chickens, and veal calves. Furthermore, because consumers want animals to be humanely treated, large food marketers and restaurant chains began adopting requirements under which producers must adopt space requirements. More and more companies are including animal health provisions in contracts with agricultural producers, employing veterinarians to provide care to animals at

producers' farms, conducting audits of producers' premises to check on such things as animal access to food and water, and monitoring worker training.

In 2011, the United Egg Producers and the Humane Society of the US agreed to work together to push for federal legislation regarding space requirements for hens producing table eggs. Proposed legislation would establish required floor space per hen. Individual states would be precluded from adopting space requirements in addition to or different from those set forth in federal law.

Public sentiment also raises questions about whether producers of animals for food should use husbandry practices that cause excessive pain to their animals. Husbandry practices involving tail docking, castration without an anesthetic agent, and beak trimming of poultry are controversial because of the public perception that they cause excessive suffering to the animals. California has banned tail docking of cattle. Individual US state legislatures are considering legislation to limit husbandry practices associated with pain.

Another development involves state legislative initiatives by agricultural interest groups against undercover operations by animal activists who fraudulently gain entry to facilities and subsequently distribute unauthorized information or images. Legislative proposals labeled as 'Ag Gag' laws are being introduced to limit these fraudulent activities. Although abuses have occurred with the dissemination of false information about agricultural producers, concern also exists that 'Ag Gag' laws stifle the exposure of inhumane and illegal practices. Provisions of some laws may also interfere with the freedom of speech.

The agricultural industry is concerned about energy and the production of biofuels as a source of energy. Congress has altered the face of rural America by deciding that the country needed to encourage the use of renewable energy sources, including the use of agricultural crops for ethanol and biodiesel production (Grossman, 2010). In 2012, approximately 40% of the nation's corn crop was used for ethanol production. Agricultural lawyers offer advice to Congress, producers, and others concerning the impact of various energy policies that affect the use of farmland.

The decade of the 2010 is one in which many Americans are asking what can be done to improve access to healthy food and help local communities. Local food production and direct farm marketing have been proposed as ways to improve access to healthy food and help rural communities (Hamilton, 2011a). Some people view the local production of food as a public service to their community and are motivated to participate despite the unprofitability of the enterprise. Others advance the idea that eating local fresh produce may help address obesity.

A locavore movement involves consumers buying locally produced food to garner freshness, support their local economy, and develop social connections to local food producers. By encouraging local agriculture, food consumers see themselves as helping to preserve nearby farmland for agricultural and recreational use, wildlife habitat, and wetlands. Food hubs are being organized to coordinate production and marketing of local foods to meet consumer demands.

Another justification for supporting the local food movement is based on a premise that less greenhouse gas will be produced if food products do not have to be shipped long distances. However, the transport of food to market may constitute $< 5\%$ of the food's life-cycle greenhouse gas emissions. Owing to the small scale of many local producers, the production of local foods may release as many greenhouse gas emissions as imported foods produced at larger, more efficient farms.

To assist entrepreneurs who desire to commence or expand local food production, agricultural lawyers can help with the establishment of business firms and contractual arrangements. Lawyers can also suggest practices to enhance the financial viability of local food efforts. One idea is to assist clients in devising a common-interest community that includes a governance mechanism for decision-making and a revenue device for spreading costs and income (Schutz, 2011). Consumer support for local foods suggests that the locavore movement will be important for many communities.

Conclusory Comments

Although this article has focused on legal issues in the US, several topics may be expected to be important internationally (Cardwell, 2004; Rogers, 2008). Agricultural lawyers in most countries assist producers with legal documents concerning land, contracts, and financing arrangements. They also may assist in restructuring operations to take advantage of support programs and marketing opportunities. In other cases, counselors are involved in land reform.

Agricultural lawyers might be involved in three policy issues that continue to affect world food supplies and the provision of food to the hungry. Food safety, food security, and trade impediments are matters that governments can address to facilitate better living conditions.

People all over the world are concerned about food safety. The agricultural law community can help governments develop appropriate regulatory provisions to reduce risks of contamination during the production and marketing of food products. Moreover, persons involved in marketing unwholesome food products need to be held accountable for damages.

Food security continues to be a problem not only in the developing world, but also for many people in the developed world. The availability of sufficient food supplies may be exacerbated by climate change. The legal community needs to foster programs and ideas to help get food to persons who are hungry.

Legal counselors may also need to become involved in opposing regulations that constitute barriers to international trade. Countries are able to adopt phytosanitary measures relating to food safety and animal health with respect to imported pests and diseases. However, protectionist interest groups sometimes convince governments to adopt regulations such as domestic subsidies for agricultural products, import quotas, and standards that differentially impact foreign suppliers. A major source of disagreement involves import restrictions on food items produced from genetically modified organisms. Are the restrictions a justifiable precautionary approach to a risky technology or an unjustifiable barrier to trade? Another potential barrier may be an environmental

measure to promote a domestic environmental norm at the expense of foreign producers. Potential barriers involving animal welfare may also interfere with trade.

Agricultural lawyers are instrumental in helping clients and governments with activities involved in with supplying safe food products. Although lawyers' activities vary in different countries, the topics addressed by American agricultural lawyers offer ideas for augmenting food production and food safety. Specialized agricultural lawyers can become involved in marketing arrangements and a regulatory framework that fosters reasonable food prices and minimizes risks of unwholesome food products.

See also: Agricultural Cooperatives. Agricultural Ethics and Social Justice. Air: Confined Animal Facilities and Air Quality Issues. Animal Welfare: Stress, Global Issues, and Perspectives. Biotechnology: Regulatory Issues. Climate Change, Society, and Agriculture: An Economic and Policy Perspective. Dust Pollution from Agriculture. Food Labeling. Food Law. Intellectual Property in Agriculture. Market-Based Incentives for the Conservation of Ecosystem Services in Agricultural Landscapes: Examples from Coffee Cultivation in Latin America. Organic Agricultural Production: Plants. Quarantine and Biosecurity. World Water Supply and Use: Challenges for the Future

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Agricultural Mechanization

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Glossary

Biological innovation Improvements in seed, fertilizer, and cultural practices directed to adapting plants to new environments, combating pest threats, and increasing yields and labor productivity; also improvements in breeding stock, feeding practices, and health directed to increasing livestock productivity.

Combine A mobile harvesting machine that combined the cutting and threshing operations into one device. The early combines were mammoth machines often powered by about 40 equines.

Cotton gin A machine perfected by Eli Whitney in 1793 to separate the seed and fiber in Upland cotton.

Cradle A scythe with a small wooden frame attached at the rear of the cutting blade used to harvest small grains. The frame caught cut grain and stalks helping to prevent the grain from shattering. In North America this device replaced the sickle and scythe in the late eighteenth century. It in turn was replaced by the mechanical horse-drawn reaper beginning in the late 1830s.

General purpose tractor This machine which first appeared in 1924 spaced the wheels so that the tractor could work among growing crops. This was one of many innovations that significantly increased tractor versatility and which contributed to its diffusion.

Lister (also called a middlebuster) A lister is a plow that throws the soil on both sides of the furrow.

Mechanization Mechanization involved the replacement of simple hand tools and human power by more complicated machinery powered by animals, fossil fuels, and electricity.

Sea Island cotton Very long staple, high quality, cotton introduced into North America in the latter decades of the nineteenth century. It was primarily grown in a limited range along the coasts of Georgia and South Carolina. It commanded a premium price.

Upland cotton Short and medium staple length cotton grown in more varied conditions than Sea Island. American breeders significantly improved Upland cotton varieties in the nineteenth century. The seeds of most upland cotton varieties cling to the fiber making it difficult to remove the seeds without an improved gin.

This article highlights one of the epic stories in world history. In the nineteenth and twentieth centuries, powerful forces continuously reshaped world agriculture. In the US, the nineteenth century witnessed the addition of hundreds of millions of acres of farmland, and millions of farms and farmers. With this expansion, the farm population grew. It approached its zenith around 1910, but the relative size of the farm population was shrinking. In 1790, roughly 90% of the US population lived in rural areas and most of these people were farmers; in 1910 approximately 35% of the US population resided on farms. By 2010, only 1.5% of the labor force worked on farms. In the twentieth century, the amount of farmland changed little, but the growing gap between farm and nonfarm incomes and opportunities contributed to a massive exodus from America's farms. In the 1950s alone, more people moved off farms than resided on farms in 2000.

Throughout most of human history, and in large parts of the world today, the dominant concern has been how to produce enough food and fiber to feed and clothe the population. Over the course of the past 200 years in the US, the creation and diffusion of new technologies fundamentally changed agricultural constraints and dramatically reduced the real price of most farm products. The innovations can be grouped into two distinct groups: mechanical technologies and biological technologies (meaning improved fertilizers, seeds, irrigation, and the like). In this article the authors focus on some of the landmark mechanical developments of the last two centuries. Mechanization involved the replacement of hand tools and human power by machinery and draft power (first from animals and later from fossil fuels and electricity). These changes typically increased the amount of land one worker could cultivate and harvest, and they often also increased land yields by allowing more timely and more thorough work. These changes dramatically increased farm productivity and changed the nature of farm work. At the millennium, the typical American farm worker produced over 15 times as much output as a worker in 1900 and 30 times as much as in 1800 (Weiss, 1991, p. 6).

Grain Harvesting and Threshing Machines

The mechanical revolution in American agriculture is symbolically identified with the introduction and diffusion of the threshing machine and the mechanical reaper (along with its close cousin the mechanical mower). These machines were marvels in their day, and people would travel for hours just to be able to watch early prototypes in exhibitions. As an indication of their significance, Cyrus McCormick, the principal inventor of the reaper, was acclaimed as the 'man who made bread cheap.' Dramatically lowering the cost of grain in an age when bread was a dietary staple and many people spent over one-half of their income on basic foodstuffs was indeed a significant achievement.

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The threshing machine, which separated small grains (wheat, oats, barley, and rye) from the stalks and husks, represented the first great step in grain mechanization. This advance dated back to the work of Scottish engineer Andrew Meikle in the 1780s. Before the diffusion of the thresher, farmers had to beat the grain with a flail. In some areas, farmers laid the cut grain and stalk on hard ground and then trampled it with draft animals to dislodge the grain. This task often extended for months following the harvest. In 1791, both Thomas Jefferson and George Washington viewed a threshing demonstration, and Jefferson was so impressed that he ordered one of Meikle's models from London. By 1796, Jefferson operated three threshers at his Monticello estate. The spread of threshers in England in the 1820s contributed to widespread rural uprisings, commonly known as the 'Captain Swing' riots. Farm workers, threatened by the loss of employment, resorted to smashing machines and threating farmers. One usually thinks of innovations being more likely to gain a foothold if they address a peak load constraint, such as exists during the grain harvest. But the thresher replaced labor during the off season when wages were relatively low, and when the rioting wage-workers in England had few alternative employment prospects. In the North American grain belt, where owner-occupiers and family members performed much of the farm work, the adoption of the labor-saving threshing machine was generally welcomed, not resisted.

As with other machines, widespread diffusion came after many improvements, both large and small. One major innovation came in the mid-1830s with the addition of a winnowing mechanism. Before this, farmers had to winnow the threshed grain by throwing it into the air in a natural breeze or use a fan to create airflow. The heavier grain would fall separately from the chaff. Another avenue of innovation was to improve the treadmill powering the machine. In 1830, John and Hiram Pitts, originally from Maine, patented a device with a 'railway' tread power. In 1834, they added an apron carrier, and by 1837, the twin Pitts brothers had created what is often considered the first commercially successful American-made thresher. Many other companies manufactured threshers in North America, including J. I. Case, the Wood brothers, and Aultman. Machines came in many sizes. In some communities, neighboring farmers organized local threshing bees, in which the machine was owned by one farmer and others contributed labor and draft stock in exchange for the services. In other places, threshing was done by itinerant private contractors who rented machine services to farmers who provided much of the labor and some of the horses to power the operation. On the giant grain ranches in California in the 1870s, a typical threshing crew might have consisted of 18 men, including one engineer, two feeders, one sack sewer, and 14 laborers. Over the next decade several labor-saving inventions, such as the derrick table to convey the grain from the stack to the thresher and a self-feeder, reduced the labor requirement by almost a third. The use of threshers allowed farmers to process their cut grain sooner after the harvest, thereby reducing exposure to damage from insects and adverse weather. By reducing the need for labor over the fall and winter months, the thresher actually increased the relative peak load labor demand during the harvest season. This problem of the seasonality of labor demand was addressed in part by the mechanical reaper.

For millennia, small grains had been harvested with sickles. Men and women had to stoop over, grab a clump of stalks with one hand and then cut it with the sickle. The grain was then gently laid on the ground so that seeds did not shatter. Scythes (a tool with a long handle and a curved blade approximately 3 feet long) were used to mow grass and harvest grains. A harvester using a scythe could stand erect and work much faster, but grain was more apt to shatter. In the late colonial era, American farmers began adding a wooden frame to the rear of the blade to catch the cut grain. This tool was called a cradle. With the turn of the arm, the cradler could lay the cut grain to the ground thereby reducing shattering. One cradler could do the work of several workers with sickles. With the advent of the cradle, harvesting changed from a task performed by both men and women to what was principally a man's job. There was still plenty of work for women and children: the grain (still attached to the stalk) needed to be gathered into small bundles and stacked in a shock to dry. Before the mechanical thresher, the grain would then be threshed and winnowed by hand (Rogin, 1933).

Reapers in the US date to the patents of Obed Hussey (1833) and Cyrus McCormick (1834). Their machines represented the first steps in a process which would revolutionize the harvesting of small grains. The reaper was refined throughout the next several decades, and its key features were embodied in the harvesters, headers, and combines that succeeded it into the fields. The essential elements of early reapers as they emerged in the 1850s included a cutting bar with reciprocating knives. The bars ranged from 4 to 6 feet in length and extended out one side of the machine. The grain fell onto a platform from which it was manually raked to the ground – at first by a worker who trotted next to the machine. A reel rotated in front of the cutting bar to push the grain into the knives. In addition to a driver and a raker, a crew of approximately six workers was needed to bind and shock the cut grain. Most early reapers required four horses. As machine draft declined with improved design and construction, two-horse machines became the rule. The basic machine of the 1850s probably did the work of five to seven men working with cradles. In addition, the reaper technology was adapted to developing specialized mowers to cut grass for livestock. This greatly reduced the labor required to maintain milk cows and led to an increase in dairy production (Hutchinson, 1930, pp. 250–275, 366; Olmstead, 1976).

Reaper and mower manufacturers developed some of America's first large integrated factories, and they eventually catered to a national and even a world market. McCormick, the most important of the early producers, moved his operation from Virginia to Chicago in 1847–48 to be closer to the growing Midwestern market; in 1858 he made over 4500 machines. Many other producers entered the market, with several surpassing McCormick. In the 1850s and 1860s, total output soared. Improved production processes and fierce competition drove down real machine prices and output reached 80 000 machines by 1865. At the same time, machine quality continued to improve.

By early 1860s, many reapers were equipped with automatic rakes that neatly deposited bundles of wheat on the

Table 1 Acres of small grains harvested per worker day

Method	*Acres/day*
Scythe	1/3–1/2
Cradle (late eighteenth century)	1
Reaper (1833)	1.5–2
Self-raker (1854)	2–2.5
Self-binder (1881)	10–12

Source: Compiled from Hayami, Y., Ruttan, V., 1985. Agricultural Development: An International Perspective, revised ed. Baltimore: Johns Hopkins University Press, p. 81.

ground to be gathered and shocked. This saved the labor of an additional worker. In the 1870s, an ingenious twine binder was attached to new reapers. This tightly bound the bundles, making them easier to shock. Table 1 charts the increase in acreage harvest per day of work associated with the adoption of more advanced grain-harvesting techniques.

As is common with many paths of innovations, the rate of advance in productivity during the improvement phrase (from reaper to self-binder) was greater than during the initial invention phrase (cradle to reaper). But taking this first step was necessary to create the platform for the subsequent improvements. In the East and Midwest, twine self-binders remained the dominant harvesting technology well into the twentieth century.

But in California innovation took a different path, which would eventually change harvesting around the world. Several features of California agriculture – high wages, large-scale farms, and a distinct climate – help explain the different course of harvesting innovation. In addition, Californians learned how to manage large teams of eight or more animals – a skill alien to most farmers in other regions. For these reasons, California farmers increasingly adopted 'headers' in the 1860s. A header had a high cutting bar so that it only cut the top of the plant. The cut grain was then transported on a continuous apron to a wagon or header box. Headers had longer cutting bars than reapers and, hence, greater capacity, but the most significant advantage was that headers eliminated the need for binding. This feature saved the labor of about five binders. The initial cost of the header was approximately 50–100% more than the reaper, but its real drawback was that it required the grain to be fully ripe and dry at harvest-time. This involved enormous risks in the humid Midwest, but not in California.

Once a farmer had a header, it was natural to run a thresher next to it – the two machines worked in tandem. Many inventors in the East and Midwest had attempted to perfect a machine that both reaped and threshed. One of the most successful was Hiram Moore's combine (built in 1835). Moore operated his machines on his own and neighboring farms in Kalamazoo, Michigan for about five seasons, yet it did not gain lasting acceptance in the Midwest. Combining suffered from the same problems with moisture that plagued heading in humid areas. In 1853, Moore's invention was given new life when his son operated a model on a farm near San Jose, California even though it was destroyed by fire after harvesting only 600 acres. From this inauspicious start, the combined harvester business gradually took root in California. By the mid-1880s, Stockton, California became the center of production and home to firms such as the Holt Company and the Stockton Combined Harvester and Agricultural Works (Olmstead and Rhode, 1988).

The California combines were much larger than any equipment common in the Midwest during the nineteenth century. Ca. 1900, the most popular self-binding reapers had 6-feet cutting bars, with a capacity of 10–12 acres per day using 2–3 horses. By this time, the standard California combine had a cutting bar of 16–22 feet, a daily capacity of 22–30 acres, and required a team of 25–35 horses. The largest combines adopted in the Midwest in the 1920s and 1930s were smaller than the standard California machine of the 1880s. As a rule, farmers east of the Rockies seldom teamed more than eight horses and did not use large-scale equipment in the field until after the introduction of the gasoline tractor.

The enormous teams in the West posed a threat if the animals bolted – runaway teams destroyed many combines. The search for a solution led George Berry of Visalia to develop the first steam traction combine in 1886. This combine had a massive 40 feet long cutting bar and supplied itself with fuel, burning the cut straw. Many manufacturers followed Berry's example, and throughout the 1890s both Daniel Best and Benjamin Holt improved their steam tractors to pull ever larger combines. These machines never gained wide acceptance, in part because of the fire danger. But a lasting spin off of the steam traction engine era was the development of the gasoline powered tracklaying tractor.

The evolution of the combine involved making the machines smaller and more versatile, and perfecting its components for use in harvesting corn, beans, peas, and other crops. This process started during WWI, when gasoline tractors began to replace steam tractors and horses for propulsion, and when internal combustion engines were added to drive the cutting and threshing equipment. By the late 1920s, models with 8 and 10 feet cutting bars with the machinery driven by the tractor's power take-off were widely available. This allowed the combine to be profitably employed in the grain-growing regions east of the Rockies. In Kansas, combines were an infrequent sight before 1918. They harvested approximately 30% of the state's wheat by 1926 and 82% by 1938. By this date, combines harvested about one-half of US wheat acreage. The next big advance was the arrival of the self-propelled combine. With the tractor built into the machine, one worker could operate both the combine and tractor. In the 1940s, as specialized custom harvesting became more widespread, there was a reversal in the trend toward smaller machines. The share of all US wheat acreage harvested by combines rose to more than 75% by 1945 and nearly 95% by 1950 (Brodell, 1952, pp. 2–5; Quick and Buchele, 1978).

The combine also adapted to harvest other crops. By 1950, combines harvested almost two-thirds of the nation's oat acreage and almost all soybean acreage. The advent of improved corn head attachments in the early 1950s allowed combines to become the dominant maize-harvesting technology by the mid-1960s. With the vast reduction in the need for seasonal harvest labor, many farm families, perhaps aided by a few hired workers or a custom operator, could now manage the harvest. Farm life was changed dramatically. Perhaps the most appreciative were the farm wives, who no longer had to cook for the armies of migrants who followed the harvest.

Tractors

As one has seen, the quest to apply mechanical power to the farm long predated the gasoline tractor. Farm steam engines probably first made their appearance in cotton gins, and mobile engines were adapted to power threshing machines in the late 1840s. A number of early inventors constructed massive steam plows. In 1858, Joseph Fawkes exhibited a steam plow at the Illinois State Fair. In the decade following the Civil War, many manufactures ventured into constructing prototypes. Philander H. Standish of Martinez, California was an important pioneer. On May 10, 1868, Standish patented a steam engine plow, and according to contemporary accounts actually plowed 100 acres with it. In 1868, a Standish steam traction engine named 'The Mayflower' drew huge crowds at the California State Fair. But for all the interest, the monster machine never was a mechanical or financial success.

An alternative was offered by the English cable system of plowing. The cable system consisted of two stationary steam engines located at opposite sides of a field. Steel cables attached to the engines pulled the plow across the field with the engines alternating the pulling. This method required five to eight men: a foreman, two engineers, one or two teamsters, and two plowmen. The cable plows were expensive, and the steel cables, which needed replacement roughly every year, cost between $600 and $900 each. The expense limited the market to a few experimenters with very large estates. A significant problem with the early steam traction engines was their reliance on the models built for steam threshing that made them unsuitable for plowing. The traction gears were not strong enough to pull the drawbar, the drive wheels were not large enough, the machines were difficult to operate, and the plows too often snagged in uneven terrain.

The 1870s and early 1880s were a period of experimentation, with no individual or model dominating. Gradually, through trial and error, various technological changes were made to increase the practicality of mobile steam plows. Two industry leaders emerged, both of which were located in Stockton, California and both of which were active in the early combine harvester industry. Daniel Best and the Holt Brothers both produced models with horizontal boilers. These weighed over 10 tons, could plow approximately 40 acres a day, and ca. 1890 sold for approximately $4500. Because they were so large and so expensive, their primary market was the large California wheat ranches. By 1890, eastern and Midwestern producers such as J. I. Case of Racine, Wisconsin were manufacturing steam traction engine plows. The Case machine was suitable for plowing, harrowing, hauling, running threshing machines and sawmills, rolling streets, and pulling combines as well as plows (Wik, 1953).

Steam traction engines could be built to run off of virtually any type of fuel. In the East, farmers often used coal and wood, but in the West the price of these fuels was generally so high that manufacturers constructed straw-burning engines. By the turn of the century, steam traction plows were established as an alternative to horse-drawn plowing in the West. In the East, steam plowing did not become popular until the early years of the twentieth century, with the advent of stronger and lighter weight engines. Everywhere, improved designs increased steam pressure and enhanced reliability.

The steam plows needed several men to attend them. A skeleton crew included the engineer, the fireman, and a man with horses to haul fuel and water. The engineer steered the plow and was usually in charge of the plowing operation. Probably the most crucial job was that of the fireman. Great skill was needed to keep the fire burning steadily so that the steam pressure was kept constant all day long and the boiler was not allowed to run dry. It was also the most uncomfortable job. In warm weather, the fireman was warmer still, standing only a few feet from the firebox heated to nearly 2000 °F. In addition, the water in the boiler, at 325 °F, radiated still more heat, 'drenching the fireman in his own sweat, and perhaps reminding him of Hades itself.' The 'water-boy' or hauler position also required a measure of responsibility. With a boiler requiring 2000 gallons per day and fuel of a ton of coal or its straw equivalent, the hauler was kept busy. The boiler had to be kept full of water or risk the danger of explosion. Water quality was a problem, especially in the arid West. The relatively scarce surface water supply forced western operators to rely on artesian well water, leading to the problem of 'hard' or alkali water. The calcium, sodium, and magnesium in the water disagreed with the digestive system of the steam engine. These minerals coated the insides of the boiler and flues, often ruining the machine within 2 years. Another major drawback of the steam traction engine was the tendency to emit sparks from their smokestacks, particularly when using straw for fuel. This created an obvious fire hazard.

By the early 1900s, steam traction plowing reached its zenith, but even in the West, where they were most common, steam plows were never replaced draft animals as the primary source of farm power. The diffusion of steam plows represented an important step in moving American agriculture out of the horse age by paving the way for the acceptance of the gasoline tractor and other types of farm machinery. The giant traction plows created excitement and an interest in mechanization, and many farmers developed skill in operating and repairing the machines which would prove handy for operating the next round of inventions. Moreover, many steam traction plow companies would become innovators in the application of gasoline engines to agriculture.

The internal combustion engine was about to forever transform rural America. This took several forms. The automobile and motor truck helped integrate the farm into the broader world. On the farm itself, tractors increased the horsepower available to farmers and increased farmer productivity, drastically reduced the need for seasonal labor, and changed social relationships. The integration of the tractor as an essential part of other types of equipment, such as the self-powered combined harvester and the mechanical cotton picker, magnified the tractor's impacts.

Patterned after the giant steam plows, the early gasoline tractors were behemoths. They were suitable for plowing, harrowing, and belt work; but they were not useful for cultivating in fields of growing crops or for powering equipment in tow. The gasoline engine offered numerous advantages over the steam engine. It was less prone to explosion and, therefore, much safer to operate, it did not require constant supervision, it provided high power at a much lighter weight, it required only one person to operate, thereby saving greatly in labor costs, it eliminated the problem of poor water and lack of

water, and it was not an ever-present fire danger; in short, it was more economical and a great deal safer. Between 1910 and 1940, innovations vastly improved the machine's versatility and reduced its size, making it suited to a far wider range of farms and tasks. At the same time, largely as a result of progress in the new mass production industries, the tractor's operating quality greatly increased, and its price fell.

Several key advances marked the otherwise gradual improvement in tractor design. The Bull (1913) was the first truly small and agile tractor, Henry Ford's popular Fordson (1917) was the first mass-produced entry, and the revolutionary McCormick-Deering Farmall (1924) was the first general purpose tractor capable of cultivating amongst growing row crops. The Farmall was also one of the first machines to provide a power-takeoff, which transferred power directly to implements under tow. A succession of secondary innovations such as stronger implements, pneumatic tires, improved air and oil filters, and the Ferguson three-point hitch and hydraulic system vastly increased the tractor's life span and utility. These changes yielded enormous returns. As an example, rubber tires increased drawbar efficiency in some applications by as much as 50%, reduced vibrations thereby extending machine life, and enhanced the tractor's usefulness in hauling (a task previously done by horses).With greater mobility, farmers could more easily use a tractor on widely separated fields (Gray, 1954; Williams, 1987).

Again, a separate innovative path developed in California. The heavy steam tractors and early wheeled gasoline designs were not suitable for the enormous ranches in the newly reclaimed lands in the vast Sacramento-San Joaquin Delta. Even horses had difficulty working on these highly productive but soft peat soils. The solution was a tracklaying or crawling tractor – what would become known as a Caterpillar design. The principle of the tracklayer was to widen the area of contact to spread the weight of the machine and increase its traction. In the culmination of several years of effort, Benjamin Holt successfully tested a 40 hp crawler on a delta island near Stockton in 1904. Although the crawlers were first designed to solve an essentially local problem, this innovation was of global significance. The Caterpillar Tractor Company (formed by the merger of the Holt and Best enterprises) would build larger more powerful equipment that rapidly spread throughout the world (Olmstead and Rhode, 1988).

Knowledgeable observers argued that these improvements in tractor design greatly increased performance and durability. As an example, Roy Bainer, one of the deans of the agricultural engineering profession, was an early tractor adopter as a young man. He noted that without improved air filters his machines lost power and needed a valve job within a year of entering service. He also maintained that the Ferguson hitch revolutionized the tractor's capabilities. The rapid diffusion of some of the changes is consistent with Bainer's informed view. The standard-wheeled models fell from approximately 92% of all tractors sold for domestic use in 1925 to approximately 4% in 1940. Conversely, general-purpose tractors, which were first introduced in 1924, composed 38% of sales in 1935 and 85% by 1940. In a similar fashion, within 6 years after the introduction of pneumatic tires in 1932, 95% of the new tractors produced in the US were 'on rubber.' By 1945, over 70% of all wheeled tractors on farms had rubber tires (McKibben and Griffen, 1938, p. 13; US Bureau of the Census, 1947, p. 13; Olmstead and Rhode, 2001).

Developments since WWII have mostly refined existing designs by increasing tractor size and adding driver amenities, such as power steering and air-conditioned cabs. Farmers have come a long way from the time when they walked the fields behind horse-drawn plows. After remaining roughly constant from 1920 to 1940, the average horsepower of new tractors quadrupled between 1947 and 1977, reflecting a shift in farmers' preferences toward larger machines.

Figure 1 offers a view of the transition from equines to tractors in the US between 1910 and 1960. The number of farm horses and mules peaked at 26.7 million head in 1918, and the number of working animals (aged 3 and over) peaked in 1923 at 20.7 million head. After 1925, draft animal numbers steadily declined, falling below 3 million by 1960.

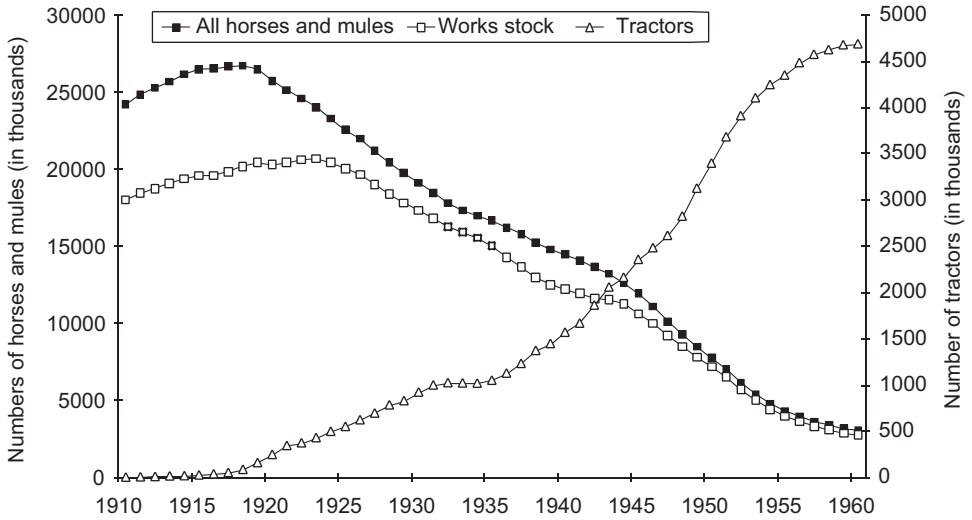


Figure 1 Number of draft animals and tractors in the US (1910–60). Reproduced from Olmstead, A.L., Rhode, P.W., 2001. Reshaping the landscape: The impact and diffusion of the tractor in American agriculture, 1910–60. Journal of Economic History 61 (3), 670.

The stock of tractors began to expand rapidly during WWI, rising to a plateau of approximately 1 million machines in 1929. A second burst of growth began in the late 1930s, leading the tractor stock to climb above 4.5 million units by 1960. The percentage of US farms reporting tractors rose from 47% in 1940 to 83% in 1954. The diffusion of the tractor exhibited significant regional variation, with the most rapid adoption in the West North Central and Pacific regions. The arrival of general-purpose tractors in the mid-1920s sped the pace of diffusion in the East North Central region. All regions experienced a slowing of diffusion during the Great Depression followed by an acceleration during and immediately after WWII. By 1950, the tractor had largely replaced the horse throughout the North, and was rapidly becoming a fixture in the South.

The simple measures of diffusion miss the tractor's impact on the total horsepower capacity available to farmers. The extra power gave farmers more versatility, especially in peak-load periods. Between 1910 and 1960, national farm draft power soared over four-and-one-half times, whereas cropland harvested remained roughly constant. Tractors accounted for approximately 11% of national stock of farm horsepower capacity in 1920, 64% in 1940, and 97% in 1960. Thus, compared with the percentage of farms reporting tractors, the measure of diffusion using power capacity started higher, and grew faster and more smoothly (Olmstead and Rhode, 2001). But as a share of new horsepower capacity, the movement to tractors was even faster. By 1930, tractors provided approximately 80% of the new horsepower adopted by farmers; and by 1940, the figure had risen to approximately 90%. Essentially farmers had a stock of the old form of power which remained available, but new investment went to machines not animals. The result was that the average price of draft animals fell. This price movement helped keep the animal mode of production competitive long after breeders dramatically reduced producing new equine capital.

The tractor's impact on labor and land use altered the course of American development. The decline in the farm population after 1940 represents one of the great structural shifts in American history. By 1960, tractors had reduced annual labor needs in agriculture by roughly 1.7 million workers; this represented over 25% of the total decline in farm employment since 1910. This makes the tractor one of the greatest labor-saving agricultural inventions of any age. The tractor also stimulated the growth in the average size of farms.

In recent years, policies have subsidized farmers to grow corn and other crops to produce ethanol. The idea is to substitute crops for oil. These policies would have to be expanded significantly to approach the land use patterns of the pretractor age. In fact, the tractor was one of the greatest land-saving innovations in the history of agriculture, allowing American farmers to convert approximately 80 million acres of cropland and another 80 million acres of pastureland from supporting draft animals into providing products for human consumption. To provide perspective, the cropland diverted represented approximately 25% of the US total. It was roughly equivalent to adding acreage equal to two-thirds of the cropland harvested in the entire territory of the Louisiana Purchase to the nation's effective land base. Much of the land previously used to feed draft animals went to feed dairy cows and beef cattle. But there is more: by allowing farmers to work better, the tractor had a direct impact on yields. Thus, one of the seminal mechanical inventions of all time was both a major labor-saving and land-saving innovation (Olmstead and Rhode, 2001). Overall, the tractor's impact on land use and productivity added significantly to America's agricultural surpluses, and surely depressed crop and livestock prices. This contributed to the great upheavals of the interwar years, and to pressure for government farm programs. By the 1930s, the acreage no longer needed to feed draft animals roughly equaled the acreage removed from production by the USDA's wheat, cotton, and corn programs (Olmstead and Rhode, 1994).

Tools for Tillage

The authors touched on tillage equipment in their discussion of tractors, but the developments in this broad category of implements deserves its own account. The objectives of tillage operations ca. 1930 included opening the soil so that rain could absorbed; limiting erosion; pulverizing the soil; integrating stubble, straw, and fertilizer; aerating the soil; tamping the soil; and destroying weeds and injurious insects. These various tasks led to the development of a wide variety of specialized tillage implements, namely moldboard plows, disk plows, listers, and several types of harrows (Davidson, 1931, p. 80).

The six decades before the Civil War witnessed vast improvements in cast iron and steel moldboards. Many farmers entered the nineteenth century with a one-handled ox-drawn plow which was made completely of wood, except perhaps for a small iron tip. This device lacked a moldboard to turn the furrow; it scratched the surface rather than plowed the soils. By contrast, the standard plow of the mid-nineteenth century was a balanced horse-drawn two-handled model, with a variety of interchangeable cast-iron shares and moldboards for different conditions. A notable step in this change was the 1837 invention by John Deere, a blacksmith from Grand Detour, Illinois, of a self-polishing cast steel plow. After moving to Moline, Illinois in the late 1840s, Deere began marketing his perfected steel plow in the Midwest. In that region, damp soils would cling to – rather that scour off – the moldboards of most previous types of plows. The smoothed surfaces of Deere's plows solved the problem of sticky soils. A related advance was the development and commercialization of chilled cast-iron plowshares by James Oliver of South Bend, Indiana in late 1850s and 1860s. In the late nineteenth century, wheeled models became common. Wheeled plows may be further distinguished along two lines: the number of bottoms and whether the driver rides or walks. Plows with more than one bottom are called gang plows; those with a seat for the driver, sulkies.

Over time there was a general movement toward larger implements, first for big teams of horses and the rare steam traction engines, and later for the revolutionary gas tractors. Tractors offered more power and speed than horses, thus requiring larger and stronger equipment to take advantage of the larger capacity and to withstand the increased stress. With the introduction of the general-purpose tractor and the three-point

lift system, the use of mounted tools, from plows to cultivators, soared. Since 1900, the manufacture of tillage equipment has followed a trend common to many industries. Seven or eight full-line companies, that is, producers of tractors as well as implements, have captured most of the market. These companies were, in order of importance (ca. 1935), International Harvester, Deere, Case, Oliver, Allis-Chambers, Minneapolis-Moline, Massey-Harris, and Avery. In 1937, these eight firms produced approximately 95% of the tractor plows sold in the US, nearly 80% of the disk and spring-tooth harrows, about three-fourths of the spike-tooth harrows, around two-thirds of the sulky plow and two-horse walking plows, and somewhat less than half of the one-horse walking plows.

As smaller tractors became popular after 1915, two- and three-bottom gang plows rose in significance. At first, horse-type plows often were adapted to two- and three-plow tractors, but the hitching arrangements and their ability to withstand the increased stress left much to be desired. For example, the first tractor plows were attached only with chains and were impossible to back up. More rigid hitches remedied this failing. Other improvements, such as heat-treated parts and stronger frames, made the plows more durable. Although the changes in design were relatively minor, the quality improvements were dramatic. A study by leading agricultural engineers judged the tractor plow of 1932 was about twice as good as that of 1910–14. With the advent of power lifts on tractors around 1930, plows mounted directly onto the tractor were adapted. The carriage or wheeled frame could be discarded, and lifting and adjustment performed mechanically. The introduction of impediments for the Ferguson three-point linkage system and hydraulic lift further increased efficiency (Bainer *et al.*, 1953, ch. 6). Tractor manufacturers saw the need to better match their machines and the equipment they towed, and many leading firms began to offer specially designed tillage equipment as early as the 1920s. This led to the integration of many equipment makers and tractor companies into full-line firms.

Besides improved plows, several other pieces of primary tillage equipment came into vogue in the late nineteenth century. One was the lister or middlebuster, which was essentially two moldboard plows set back-to-back to throw soil to both sides. Much like plows, listers were available in walking, riding, and tractor-mounted models. Disk plows also appeared by at the end of the nineteenth century. The disks were set at an angle both to the ground and the direction of motion. For tractor gangs, four to six disks were the most common. Replacing the share, moldboard, colter, and jointer of the moldboard plow with a rotating disk was first conceived as a means of reducing draft. But disks lacked the suction of the moldboard plow and needed greater mass to maintain penetration. The heavier frames and added weights increased the disk's draft. Disk plows do not turn the soil as thoroughly as moldboards. The choice of whether to use a disk or a plow often depended on the type of soil.

Three types of harrows were employed on American farms: the spike-tooth, the spring-tooth, and the disk harrow. The oldest of these is the spike-tooth harrow, which traces its ancestry back as far as the plow. The first spike-tooth harrows were purportedly of a triangular or 'A' configuration, reminiscent of the ancient Roman harrows. The triangular models continued to be popular for orchard and vineyard work, but for most applications these were replaced by rectangular harrows. Though less widely used, spring-tooth harrows also were adopted after their perfection in the 1870s. By 1896, John Deere was offering spring-tooth harrows that were similar to those used today. These harrows replaced the peg of the spike-tooth harrow with flat coiled steel teeth. Unlike the spike-tooth model that levels the soil, the spring-tooth variant is sufficiently aggressive to destroy weeds and to substitute for repeated plowing in many instances. It is principally used to prepare the seedbeds for row and truck crops.

The disk harrow has been uniquely adapted for cultivating, turning under cover crops, and incorporating fertilizer among trees and vines. Disk harrows and disk plows were different machines. The harrow is comprised of several gangs of 14–24 inch, relatively shallow concave disks that turn together. By contrast, the disk plow has a smaller number of larger, deeply dished disks which are independently mounted at an angle on a wheeled frame. (The vertical or one-way disk plow is something of a combination of the two with large disks turning as a unit mounted in a wheeled frame.) There were many harrow types, including a single disk, tandem or double disk, and offset disk. These had different disk arrangements, which turned the soil in different directions. In the 1890s, John Deere offered a reversible disk. In its closed form, the gangs were set as in a 'V' frame. But the gangs could also be extended outward and, though separated by several feet at the center, used to cultivate in orchards beneath the branches. The single gang of the 1890s with a large number of small closely spaced disks remained essentially unchanged for the next two decades. With the advent of the tractors, a second set of disks was added. These tandem disks harrowed more thoroughly and eliminated the need to make a second pass (Davidson, 1931).

Other implements evolved to plant, thin, cultivate, and distribute chemicals. These include broadcast seeders and drills for field crops, planters, and thinners for row crops, cultivators, fertilizing equipment, and sprayers for orchards and fields. There are two broad categories of seeders: those used in field crops such as the small grains – that is, principally broadcasters and drills – and those used in row crops such as corn, cotton, beans, and truck crops – that is, planters and, later, precision planters.

For early producers of field crops, the first group was, by far, the most important. Yet, the advantages of the drill were soon recognized. Drills look much like boxseeders except that they have furrow openers, seed tubes to deposit the seeds below the surface of the soil, and coverers. Both drills and the later boxseeders had force-feed mechanisms to regulate the flow of seeds from the hopper. Drills assured more uniform distribution and reduced the amount of seed needed by almost half. By the mid-1890s, single- and double-disk openers, which reduced draft requirements, came into vogue.

For row crops, both planters and cultivators reached a high state of development. Among the most versatile and widely used machines was the corn or cotton planter. It typically had two distributing units, each with seed hopper, meter, tube, and shoe-type furrow opener (to maintain a straight row), and a concave steel presswheel, mounted on a three-wheel sulky frame. At the side, a marker, usually a disk on an extended rod,

assisted by indicating the center of the next set of rows. With changes in the seed metering device, the planters could be adapted to most row crops. A more ingenious variant, the checkrow planter, seeded with such accuracy that the cross-rows were straight. As this planter traveled down the rows, a check reel on the planted side gathered in a wire anchored at the row's end and a reel on the unplanted side dispensed wire for the next pass. Uniformly-spaced buttons on the wire caused the seed valve in each dispensing mechanism to trip, planting hills of seeds at even intervals. This method was commonly used in the Corn Belt, as cotton and other row crops were usually drilled with little regard for the spacing between the seeds until the late 1940s. Cross-cultivating was the principal advantage of a checkrow planting. Farmers hoping to reduce spring thinning had to wait for the development of precision planters. These machines, introduced in the post-WWII era, placed single seeds at uniform intervals to form a stand that could be thinned entirely by machine or with only a minimum of hand hoeing. The planters relied on two new elements. The first was a highly accurate seed-metering device, added to the traditional row crop drill. The second, and far more important, was seed processed to be uniform in size and shape, which would germinate at a high rate.

Cultivators include implements used to loosen and pulverize the soil but without inverting it as in plowing. Jethro Tull, the eighteenth-century English pioneer of agricultural technology, is credited with first attempting to replace hand hoeing in these tasks with horsepower. The primary purpose was to destroy weeds. Besides promoting plant growth through killing weeds, cultivation (or tillage performed after the crop is planted) also may aid in the application of irrigation water, incorporate chemical fertilizers, and facilitate the harvest.

The slave South plantation owners were slower to adopt mechanical technologies in cotton production, but even here one sees labor-saving advances that reduced the need for hoeing. Examples include the use of equipment for shallow cultivation, such as scrapers, skimmers, and sweeps. By some accounts, the scraper, which could shave the bed close to the cotton, cut the labor needed to clean and thin an acre in half. Many planters also adopted mechanical seeders, which saved labor at seeding time. The trend was to plant less seed more carefully to cut the time needed to thin and cultivate the crop (Gray, 1941, pp. 700–702).

Cotton Mechanization: Gins and Harvesters

The two big breakthroughs in the mechanization of cotton production were separated by roughly 150 years. In 1790, cotton was a relatively minor crop in the fledgling US; long-staple Sea Island cotton had only recently been brought to the US; the low quality short-staple Upland varieties of the day were mostly grown for home consumption. By 1850, cotton was the nation's leading export crop, and the US dominated the world cotton market. Cotton became by far the South's leading crop and the most important use of slave labor. The usual story explaining this transition combines the increased world demand stemming from the Industrial Revolution in Britain and the genius of Eli Whitney, who, in 1793, invented the saw-toothed cotton gin (which removed the seeds from the lint). Soon after that, models allowed one laborer to do the work of a 100 workers plucking the seeds by hand. Improved versions were much more productive. Table 2 traces the number pounds of cotton cleaned per day using various techniques. Whitney's gin broke a technological bottleneck allowing southern planters to vastly expand cotton production. The cotton gin represents an example par excellence of a labor-saving innovation.

Table 2 Cotton ginned per day

Method	*Quantity (£)*
Hand (1788)	2
Whitney (1793 Saw Gin)	80
Whitney (1800 Model)	350
Improved (1866 Gin)	3000

Source: Compiled from Lebergott, S., 1984. The Americans. New York: W.W. Norton, p. 170.

The story usually ends here, but much more needs telling. First, recent research suggests that adapting more primitive roller gins, which had long been available, might have at least partially solved the ginning problem. Such gins were capable of separating 25 pounds per work-day of Sea Island cotton. In additions, inventors besides Whitney were developing saw gins for upland cotton. So Whitney's invention was important, but perhaps not absolutely necessary. Secondly, and paradoxically, over the long run the gin led the South to require more not less labor: the labor-saving gin made growing labor-using cotton profitable. Before its invention, the high labor requirement made cotton uncompetitive with grain in labor-scarce America. After the Whitney's invention cut the ginning requirements, cotton crossed the threshold of profitability and was cultivated on an extensive scale. Finally, although the gin was important, another truly critical factor propelling the growth of the South's cotton industry in the pre-Civil War era was the work of plant breeders who produced higher quality varieties that were also far easier to pick, more productive, and more disease resistant. Largely because of better varieties, the quantity of cotton a slave could pick in a day increased about four times between 1810 and 1860. So, the final assessment is that invention, refinement, and spread of Whitney's gin represented a key mechanical innovation in the development of agriculture, but there was a lot else going on (Olmstead and Rhode, 2008b; Lakwete, 2003, pp. 22–23).

A number of mechanical innovations increased productivity in cotton production, but the next truly revolutionary advance did not begin to diffuse until after WWII. In 1928, J. D. Rust perfected a primitive spindle machine, but the depression era labor glut limited demand for this innovation and discouraged investors. When labor became scarce during and after WWII, the machine still needed to be perfected to be suitable for wide adoption. In addition, cotton breeders needed to create a less woody plant that ripened uniformly to make machine picking more feasible. In an earlier age, breeders had worked to make 'high' cotton that ripened in stages to make hand pickers more productive; now they

changed course to meet the needs of the new machines. Both private and government breeders undertook this challenge.

At this juncture, California once again took center stage in the history of the cotton picker much as it did in the development of the combined harvester. Cotton did not emerge as a significant crop in California until WWI. In fact, despite many attempts to introduce cotton dating back to the Mission era, continuous production on even a small scale did not begin until 1906. In terms of bales produced California ranked tenth among all states in 1929. By 1959, it ranked second. Many of the same economic and geographical conditions (high wages, large farms, dry weather during the harvest, etc.) that made California farmers eager adopter of combined harvesters also applied to cotton harvesters. Picker manufactures understood this and focused their early experiments and first commercial ventures in the San Joaquin Valley. In 1943, International Harvester evidently had five one-row pickers operating commercially in the valley. These were experimental machines which would need improvement. In addition, Mack Rust (J. D.'s brother) moved to California to test and perfect his machine. Gradually the mechanical defects were worked out and the Rust machine became commercially viable in the late 1940s. Allis Chalmers and Ben Pearson, Inc. both began making the Rust machines under license in 1949. The number of machines thought to be working in California increased from 20 in 1945 to 3700 in 1951 – this represented 50% of the machines in the US. In 1955, machines harvested approximately 65% of California's cotton compared to approximately 25% for the nation as a whole. By 1970, virtually the entire US cotton crop was mechanically harvested. The mechanization of the cotton harvest, coupled with the decline in cotton acreage, were among several factors that contributed to the contraction of the southern labor market as the number of sharecroppers fell from 776 000 in 1930 to 121 000 in 1959 (Street, 1957; Musoke and Olmstead, 1982).

Dairy Innovations: From Churns to Milking Machines

There is an old saying that "farming ain't what it used to be." Few farming sectors have changed as much as dairying. New technologies changed the gender division of labor, increased productivity, changed the physical location of many activities from farms to creameries, led to significantly lower consumer prices, and vastly increased food safety. Dairy farming was historically a highly labor intensive activity. The rise of commercial dairying in the early nineteenth century created economic opportunities, particularly for women, who provided almost all of the labor for milking cows and making butter and cheese. Dairying ranked with nascent textile manufacturing sector as a source of employment for northern women in the mid-nineteenth century. As milk output increased and cow lactation periods lengthened because of better breeds and feeding methods, dairying provided more year-round employment. Making butter was arduous. After milking the cows, women carried the milk to the milkhouse, poured it into skimming pans, skimmed the cream, churned it into butter, drained out the buttermilk and kneaded in salt, packed the butter into molds to form bricks, and then packed the bricks into pails or boxes (Jensen, 1986, pp. 92–113).

There was a stream of labor-saving mechanical innovations in butter production, many aimed at producing a better churn. From 1802 to 1849, the Office of Patents issued nearly 250 patents on butter making machinery, 86% of them for churns. The new technologies had an enormous impact. During the colonial period women often churned butter using a bowl and spoon. Dasher churns were common in some areas by the 1770s. With this device a women could make one or two pounds of butter at a time; this achievement required working the churn for approximately 3 h. Although still laborious, this was a significant improvement over using a spoon and bowl. By 1850, improved churns produced approximately 125 lb of butter in as little as 90 min. The larger churns were powered by dogs, sheep, or calves walking on a treadmill. The advent of the creamery moved butter and cheese production off the farm and changed the gender division of labor by bringing more men into the activity (Jensen, 1988, p. 820; 1986, pp. 104–105).

The movement of cheese and butter making to the factory allowed for more economies of scale, and creameries adopted a number of biological and mechanical innovations. The continuous centrifugal cream separator invented by Carl Gustav Patrik De Laval of Sweden in 1878 was particularly significant. American inventors were also at work – between 1872 and 1909, the US Patent Office issued 127 patents for milking machines. The early De Laval machines could process approximately 300 lb of milk a day. This was an enormous advance over letting gravity separate the cream in shallow pans for 2–3 days (during which milk often soured). Danish immigrants brought the first separator to the US in 1882 (Christensen, 1939, p. 338; Edwards, 1949; Jensen, 1986, pp. 98–9; Fussell, 1966, pp. 160–202).

By the twentieth century, many of the mechanized activities had moved off the farm. The functions the remained on farms ensured that dairying remained a highly labor-intensive activity. Ca. 1910, a dairy farmer had to work 10 times as many hours as a modern farmer to produce one gallon of milk. Ca. 1940, dairying (including the caring for dairy animals) required almost 4 billion hours of labor per year in the US; this was one-and-a-half times more than that devoted to producing cotton. One of the most important mechanical developments was the milking machine employing the intermittent suction principle. First marketed approximately 1905, these machines saved approximately 30 h per cow, or about one-fifth of the annual labor requirement. The machines spread slowly at first, owing to the structure of dairy farming, the lack of electricity, improper sanitary practices, and 'hard times' on the farm. In 1910, approximately 12 000 farms possessed milking machines; this was less than one of every 400 farms that reported dairy cows. By 1940, the number of farms possessing milking machines had climbed to 190 000. But at even at this date, about only one in ten dairy cows was milked by machine. Thereafter, diffusion was rapid, with one-half of cows milked mechanically by 1950. By 1965, approximately 500 000 farms, including virtually all commercial dairies, reported using milking machines. The spread of milking machines was part of a larger mechanical revolution on dairy farms; other changes included refrigeration, electric lights, and improved hay harvesting and manure handling machinery, and transportation equipment. Bulk cooling and

handling techniques made the traditional milk can obsolete (Forste and Frick, 1979).

Perspectives

To this juncture, our story has emphasized the role of mechanization in reshaping the productivity and structure of American agriculture. Other forces arising from better and more intensive applications of chemistry, biology, and genetics to agriculture have also played a major role. Social scientists long argued that in the US relatively cheap land and expensive labor led farmers, inventors, firms, and governments to concentrate on mechanization rather than other forms of technical change (which for simplicity the authors have called 'biological innovations'). By this reasoning, biological innovations such as hybrid corn only became prominent after the 1930s – well after the closing of the frontier and when, according to the standard account, an increasing scarcity of land and a rapid decline in commercial fertilizer prices made such innovations profitable. Proponents of this view explicitly argued that mechanical technologies were almost exclusively labor saving – they increased the output per worker. Biological technologies were primarily land saving – they increased output per acre (Cochrane, 1979, pp. 201–202). This stylization seemed to fit the long sweep of American development, because until the 1930s output per worker had risen considerably, but output per acre for major crops had changed little. Although still repeated, this general view has recently been discredited.

For many reasons, trends in output per acre understate the contributions of biological innovations. Agricultural production is an inherently biological process that uses organisms to transform sunlight and soil nutrients into food and fiber. Evolving pests and diseases constantly threaten the efficiency of this transformation process. Machines may become obsolete, and they can wear out; but a new machine of the outdated design will work more or less like the equipment it replaced. This is not true for biological technologies. Farmers and scientists have long understood the Red Queen effect: one has to run fast just to stay in one spot. A once productive plant variety can become worthless as pathogens evolve to penetrate its defenses. Moreover, the introduction of invasive species from foreign lands can dramatically cut yields. In addition, yields often suffered as agriculture moved westward. Introducing production to new environments required biological learning that involved adapting plants to meet new, often hostile, conditions.

The once strict association of machines with only saving labor and of biological advances with only saving land is very questionable. As noted above, the tractor 'saved' over 160 million acres of crop and pastureland by the 1940s, and better cotton varieties increased slave picking productivity by four times in the half century before the Civil War. These are not isolated examples. What sense does it make to say that better tillage equipment are machines so they save labor, but if a farmer replaces some of this equipment with improved herbicides, this saves land? Once one abandons the old paradigm and reexamines American agricultural development, a record of biological innovation emerges that went hand in hand with the better documented record of mechanization. New wheat varieties allowed for movement of production onto colder, hotter, and more arid lands. New varieties also were constantly introduced and developed to combat rusts and other diseases. New corn varieties merged the old northern flints with southern dents to produce the prolific varieties that would define the American Corn Belt. Researchers then set their sights on pushing production into colder climates. Soybeans, alfalfa, and Bahia oranges, and numerous other plants were introduced and acclimated for varied growing conditions. Breeders redesigned the structure of all major species of livestock, vastly increasing their productivity. Often, biological and mechanical innovations depended on one another, as with the breeding cotton and tomato varieties more suitable for machine picking. In 1920, the vast majority of the plows, reapers, and combines operating in American wheat fields worked land that had not been in agricultural production in 1850; and, given the wheat varieties known in America at that earlier date, land which could not have sustained commercial wheat production. The key point is that America's long history of agricultural mechanization was a part of a much more dynamic set of events (Olmstead and Rhode, 2008a). Together, mechanical and biological innovations fundamentally restructured rural America, and vastly increased the supplies of food and fiber for a demanding world.

See also: Agricultural Labor: Demand for Labor. Biosecurity and Equine Infectious Diseases. Breeding: Animals. Changing Structure and Organization of US Agriculture. Forage Crops. Land Use, Land Cover, and Food-Energy-Environment Trade-Off: Key Issues and Insights for Millennium Development Goals

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Agricultural Policy: A Global View

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Glossary

Common agricultural policy instruments That alter international competitiveness include both border and domestic measures. Border measures include import and export taxes and subsidies, as well as quantitative restrictions such as import or export quotas or bans. All of these measures drive a wedge between the prices observed in domestic and international markets. This wedge has the same magnitude for producers and consumers at least at the border, in contrast to price-distorting domestic consumer and producer taxes or subsidies or quantitative restrictions on consumption or production, which affect just one of those two sides of the market for internationally tradable goods. Domestic subsidies or taxes on or border measures affecting inputs into farming also will alter producer incentives and, in the process, distort the demand for and prices of inputs. These contrast with government-provided or government-subsidized investments in agricultural R&D, rural infrastructure, or rural education and health, which can increase returns to producers without directly distorting product or input prices.

The nominal rate of assistance (NRA) Measures market distortions imposed by governments that create a gap between the current domestic price of a product and the price that would exist under free markets. Under the 'small-country' assumption, this rate is computed as the percentage by which government policies have raised gross returns to farmers above what they would have been had the government not intervened (or the percentage by which government policies have lowered gross returns, if NRA <0). It therefore includes the effect of not only output-price-distorting policy instruments but also measures that alter the cost of farm inputs.

The relative rate of assistance (RRA) Is defined in percentage terms as:

$$\mathrm{RRA} = 100 * [(100 + \mathrm{NRAag}^{t})/(100 + \mathrm{NRAnonag}^{t}) - 1]$$

where NRAag^{t} and $\mathrm{NRAnonag}^{t}$ are the percentage NRAs for the tradable parts of the agricultural and nonagricultural sectors, respectively. If both of these sectors are equally assisted, the RRA is zero. This measure is useful in providing an internationally comparable indication of the extent to which a country's sectoral policy regime has an anti (or pro-) agricultural bias. The RRA recognizes that farmers are affected not just by prices of their own products and inputs but also by the incentives faced by nonagricultural producers bidding for the same mobile resources.

The trade reduction index (TRI) Measures the extent to which import protection or export taxation reduces the volume of trade. The TRI is defined as the percentage uniform trade tax that, if applied equally to all agricultural tradables, would generate the same reduction in trade volume as the actual intrasectoral structure of distortions to domestic prices of such tradable goods.

The welfare reduction index (WRI) Is the percentage uniform trade tax that, if applied equally to all agricultural tradables, would generate the same reduction in national economic welfare as the actual intrasectoral structure of distortions to domestic prices of these tradable goods. The WRI recognizes that the welfare cost of a price distortion imposed by a government is related to the square of the price wedge and thus is positive, regardless of whether the government's policy favors or hurts producers in a particular sector.

Introduction

Throughout history the agricultural and food sector has been subjected to perhaps more heavy-handed governmental interventions than any other sector. Agricultural trade-related policies account for an estimated 70% of the global welfare cost of all merchandise trade distortions, even though the agricultural sector contributes only 6% of global trade and 3% of global income (Anderson *et al.*, 2010, Table 2.3).

For advanced economies, the most commonly articulated reason to restrict food trade has been to protect domestic producers from import competition as they come under competitive pressure to shed labor. Such measures harm not only domestic consumers and exporters of other products but also foreign producers and traders of food products. For decades, agricultural protection and subsidies in high-income (and some middle-income) countries have depressed international prices of farm products, lowering the earnings of farmers and associated rural businesses in developing countries.

Meanwhile, developing countries' policies have further depressed the price incentives for their farmers, thus exacerbating the deleterious effects of the richer countries' farm policies. Governments of many developing countries have taxed their farmers more heavily than producers in other sectors. In addition, many developing countries chose to overvalue their currency and to pursue an import-substituting industrialization strategy by restricting imports of manufactures. Together, these measures have indirectly taxed producers of other tradable products in developing economies, most of whom have been farmers.

The resulting disarray in world agriculture has manifested itself in overproduction of agricultural products in high-income countries and underproduction in low-income countries. This disarray also means that there has been less international trade in such products than would have been the case under free trade. The end result is thinner and thus more volatile markets for these weather-dependent products.

Agricultural policies became newsworthy during 2008–12 because international food prices spiked upwards three times in that period. Biofuel policies have partly caused these price spikes, and in turn, the effects of biofuel policies have been exacerbated by the trade-policy responses of numerous countries at a time of low global grain stocks. Responses by food-surplus developing countries have typically involved restrictions on exports, while those by food-deficit developing countries have involved a lowering of import barriers. The ostensible motivation of policymakers has been to prevent a decline in national food security: each country has aimed to protect its domestic consumers (and indirectly, to protect the current government from losing power). Together, however, these measures have amplified international price spikes so that each country's measures have harmed other countries' consumers (Carter *et al.*, 2011; Martin and Anderson, 2012).

Changes in food prices create winners and losers, especially among the poor. It has been argued for decades that such distortions have added to global inequality and poverty, because three-quarters of the world's poorest people depend, directly or indirectly, on agriculture as their major source of income (World Bank, 2007). Protectionist policies of high-income countries have been partly responsible for international income inequality and poverty in developing countries, but so too has the antiagricultural bias of many developing countries' policies, according to a recent set of economy-wide empirical studies (Anderson *et al.*, 2010).

The agricultural policies of rich countries have not been motivated by their effects on global poverty but rather by domestic political concerns. Agricultural policy remains important in rich countries despite the relatively small and still-declining share of agriculture in GDP and employment. For example, the common agricultural policy (CAP) in the European Union (EU) continues to absorb 40% of the entire EU budget. That importance is reflected in the priority these countries' trade negotiations place on farm policies in the current round of World Trade Organization (WTO) negotiations – on which the future growth of global income and the trade of all goods and services depend.

Some agricultural- and trade-policy developments of the past half-century have happened quite suddenly and been transformational. Such events include decolonization in Africa and elsewhere around 1960; the creation of the CAP in Europe in 1962; the introduction of flexible exchange rates from the 1970s; liberalization, deregulation, privatization, and democratization in many countries from the mid-1980s; the opening of markets in China in 1979, in Vietnam in 1986, and in Eastern Europe (following the fall of the Berlin Wall) in 1989; and the demise of the Soviet Union in 1991. However, less well known are the influences of policies that change gradually in the course of economic development, as incomes grow and comparative advantages evolve. Even these patterns are subject to disruption though: since the 1980s many countries have begun to reform their agricultural and trade policies. These trends and turning points are revealed in a global five-decade database of evidence recently compiled by the World Bank, exposing the extent to which recent agricultural policy reforms have succeeded in reversing the prior era's policy distortions – and throwing up signs of an emergence of agricultural protection in middle-income countries (see Section Policy Impacts on Agricultural Prices). Recent improvements in political-economic conceptual lenses, combined with this global database, allow the empirical testing of a rich menu of hypotheses about patterns of market intervention across countries, commodities, and policy instruments (see Section Why Governments Distort Agricultural Markets the Way They Do?). This in turn provides insights into the sustainability of these reforms (see Section Prospects for Further Policy Reforms).

Policy Impacts on Agricultural Prices

Empirical indicators of agricultural price distortions have been provided annually since the late 1980s by the Secretariat of the Organisation for Economic Co-operation and Development (OECD) (2012) for its 30-member countries. They have become known as producer and consumer support estimates, or PSEs and CSEs. The Organization for Economic Co-operation and Development (OECD) (2009) has also released PSEs and CSEs for Brazil, China, South Africa, and former Eastern bloc countries, which are being updated bi-annually. However, the OECD provides no comprehensive time-series rates of assistance to producers of nonagricultural goods to compare with the PSEs, or of what took place in those advanced economies during earlier decades. Data for these earlier decades from today's developed economies are needed in order to assess how various countries' policies evolved during stages of development similar to those of today's middle-income countries. As for developing countries, almost no comparable time-series estimates were generated in the two decades following the seminal work of Krueger *et al.* (1988, 1991), which covered between 15 and 25 years before 1985, until the release in 2008 of a new database of agricultural distortions by the World Bank (Anderson and Valenzuela, 2008, updated and extended by Anderson and Nelgen, 2013). This new data set complements and extends the OECD's PSE/CSEs and the Krueger, Schiff, and Valdés studies. It provides similar estimates for significant developing economies, and it estimates new and more comprehensive policy indicators.

The new World Bank database covers 82 countries that together account for between 90% and 96% of the world's population, farmers, agricultural GDP, and total GDP. The sample countries also account for more than 85% of agricultural production and employment in each of Africa, Asia, Latin America, and the transition-economies region of Europe and Central Asia, as well as for all of agricultural production and farm employment in OECD countries. Not all countries had annual data for the entire 1955–2010 period, but the average number of years covered is 45 per country. Policy indicators are computed for 75 different farm products, with an average of almost 11 per country. This product coverage represents approximately 70% of the gross value of agricultural

production in each of the focus countries and just under two-thirds of global agricultural production, valued at undistorted prices over the period covered. Of the world's 30 most valuable agricultural products, the indicators cover 77% of global output (ranging from two-thirds for livestock to three-quarters for oilseeds and tropical crops and five-sixths for grains and tubers). These products represent 85% of global agricultural exports. Such comprehensive coverage of countries, products, and years offers a reliable picture of long-term trends and fluctuations in policy indicators for individual countries and commodities, as well as for country-groups, regions, and the world as a whole. This data set reveals distinct patterns of price distortions across countries and over time, as well as policy turning points. After defining the indicators, these patterns are summarized here under four headings: sectoral distortion variation across countries; intrasectoral variation across farm products; year-to-year variations in rates of distortion; and policy-instrument choices.

Measures of Price Distortions

Typically, agricultural and nonagricultural trade measures (border taxes and protectionist nontariff barriers (NTBs)), together with multiple exchange rates, have distorted product prices more commonly than have trade subsidies, direct domestic producer or consumer subsidies, or domestic taxes or quotas that alter product or input prices. However, in high-income countries, export subsidies grew in importance in the 1970s and 1980s and, since the 1980s, domestic support measures that (to varying extents) are decoupled from production decisions have begun to play a larger role. Furthermore, since the inception of the WTO in 1995, most NTBs have been converted to tariffs. In many countries, however, those tariffs have been legally bound at well above applied rates, and are specific to the quantity imported rather than a percentage of the import price, so that such countries have been able to continue to vary the extent of their border restrictions as international prices or domestic supplies fluctuate from year to year.

To capture the extent of government intervention on farmer incentives, a nominal rate of assistance (NRA) is estimated. The NRA measures distortions imposed by governments that create a gap between current domestic price and the price that would exist under free markets. Under the 'small-country' assumption, this rate has been computed for each product as the percentage by which government policies have raised gross returns to farmers above what they would have been had the government not intervened (or the percentage by which government policies have lowered gross returns, if NRA < 0). The rate includes the output-price-altering equivalent of any product-specific input subsidies or taxes. (The NRA differs from the OECD's PSE in that the PSE is expressed as a percentage of the distorted rather than the undistorted price, and hence is typically smaller than the NRA and cannot exceed 100%.)

A weighted-average NRA for all available products is derived using the value of production at undistorted prices as product weight. To this NRA for available (covered) products is added a 'guesstimate' of the NRA for noncovered products (on average, approximately 30% of the total in value terms), along with an estimate of the NRA from nonproduct-specific forms of assistance to (or taxation of) farmers.

Since the 1980s, some high-income governments have also provided decoupled assistance to farmers. Because this support, in principle, does not distort resource allocation, its NRA has been computed separately and is not included for comparison with the NRAs for other sectors or for agriculture in developing countries. Each year, each covered commodity's industry is classified as either import-competing, as producing an exportable, or as producing a nontradable. The aggregate noncovered industry group is also subdivided into these three categories. This classification allows the generation each year of the weighted-average NRAs for exporting versus import-competing producers to capture changes in the antitrade bias that typically prevails.

Also reported is a production-weighted average NRA for nonagricultural tradables, so that this rate may be compared to the rate for agricultural tradables via the calculation of a relative rate of assistance (RRA). The RRA recognizes that farmers are affected not just by prices of their own products but also by the incentives faced by nonagricultural producers bidding for the same mobile resources. That is, it is relative prices, and hence relative rates of government assistance, that affect incentives to producers. The RRA is defined in percentage terms as:

$$\mathrm{RRA} = 100 * [(100 + \mathrm{NRAag}^{t})/(100 + \mathrm{NRAnonag}^{t}) - 1]$$

where NRAag^{t} and $\mathrm{NRAnonag}^{t}$ are the percentage NRAs for the tradable parts of the agricultural (including noncovered) and nonagricultural sectors, respectively (Anderson *et al.*, 2008). Note that if both of these sectors are equally assisted, the RRA is zero. This measure is useful because, if it is below (or above) zero, it provides an internationally comparable indication of the extent to which a country's sectoral policy regime has an anti- (or pro-) agricultural bias.

The cost of government policy distortions in terms of resource misallocation tends to be greater as the degree of substitution in production increases. In the case of agriculture, which involves the use of land that is sector-specific but transferrable among farm activities, the greater the dispersion of NRAs across industries within the sector, the higher will be the welfare cost of those market interventions. For this reason it is also useful to draw on indicators developed by Anderson and Neary (2005) and adapted for agriculture by Lloyd *et al.* (2010). These are a welfare reduction index (WRI) and a trade reduction index (TRI). The former measure recognizes that the welfare cost of a price distortion imposed by a government is related to the square of the price wedge and is thus positive, regardless of whether the government's policy favors or hurts producers in a particular sector. The TRI measures the extent to which import protection or export taxation reduces the volume of trade. It is the percentage uniform trade tax that, if applied equally to all agricultural tradables, would generate the same reduction in trade volume as the actual intrasectoral structure of distortions to domestic prices of such tradable goods. Similarly, the WRI is the percentage uniform trade tax that, if applied equally to all agricultural tradables, would generate the same reduction in national economic welfare as

the actual intrasectoral structure of distortions to domestic prices of these tradable goods.

Variations in Sectoral Distortions

Historically, the higher a country's per capita income, the higher have tended to be its nominal – and especially relative – rates of assistance to agriculture (NRAs and RRAs). More generally, policy regimes, on average, have had a pro-agricultural bias in high-income countries and an anti-agricultural bias in developing countries. However, since the 1980s, both the antiagricultural policy bias in developing countries and the pro-agricultural bias in high-income countries have diminished, and the two groups' average RRAs have converged toward zero (Figures 1 and 2).

In the case of developing countries, it is clear from Figure 2(a) that the rise in their average RRA is due as much to a decline in assistance to nonfarm sectors (especially cuts to manufacturing protection) as to declines in agricultural disincentives (especially cuts to export taxes). However, the extent and speed of convergence vary across regions. Among developing countries, convergence has been greatest for Asia and least for Africa; among high-income countries, it has been greatest for the EU and almost nonexistent for other Western European countries. The sole exception is the dip for most countries in 2005–10, when international food prices rose steeply. For EU members, the RRA declined from an average of 77% in the 1980s to 11% in 2005–10. Consequently, the trade- and welfare-reduction indexes of the two main country-groups have traced an inverted-U shape, rising in the mid-1980s before more than halving since then (Figure 3).

The averages reported in Figures 1–3 hide the fact that both the level and rate of change in distortion indicators still vary considerably across countries. National RRA estimates for 2005–09 varied from approximately 40% for several African countries to approximately 100% for a few high-income countries (Figure 4). Clearly, much could be gained from further reforms to remove these cross-country differences, which would lead to international relocations of production and consumption.

The extent to which RRAs vary at any level of per capita income or comparative advantage is substantial. Based on regression analysis over the full time series from 1955 to 2007, per capita income and comparative advantage account for 59% of the variation in RRAs globally. Note that the average RRA for developing countries, which converged toward zero from the 1980s, did not stop at zero but 'overshot.' For Korea and Taiwan, this evolution to a positive RRA occurred in the early 1970s, for the Philippines it happened in the latter 1980s, and for China, India, Indonesia, and Malaysia it happened in the first decade of the current century. By just focusing on agricultural NRAs, and bearing in mind the sharp rise in international prices of farm products in 2008, it is clear from Figure 5 that agricultural protection is growing in Asia's three most populous countries.

Intrasectoral Distortion Variations

Within a country's agricultural sector, whether the country is developed or developing, product NRAs vary widely (Figure 6). Some commodity product NRAs are positive and high in almost all countries (sugar, rice, and milk). Others are

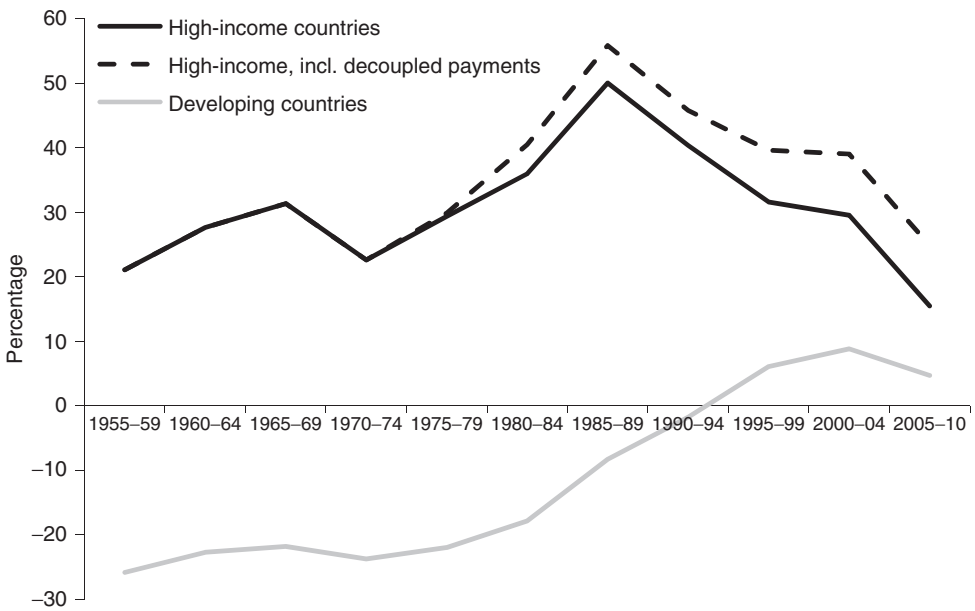


Figure 1 Nominal rates of assistance to agriculture in high-income and developing countries, 1955–2010 (%). Five-year weighted averages, with decoupled payments included in the dashed line. Reproduced from Anderson, K. (Ed.), 2009. Distortions to Agricultural Incentives: A Global Perspective, 1955–2007. London: Palgrave Macmillan and Washington, DC: World Bank (Chapter 1), updated from estimates in Anderson, K., Nelgen, S., 2013. Updated National and Global Estimates of Distortions to Agricultural Incentives, 1955 to 2011. Available at: www.worldbank.org/agdistortions (accessed 29.04.14).

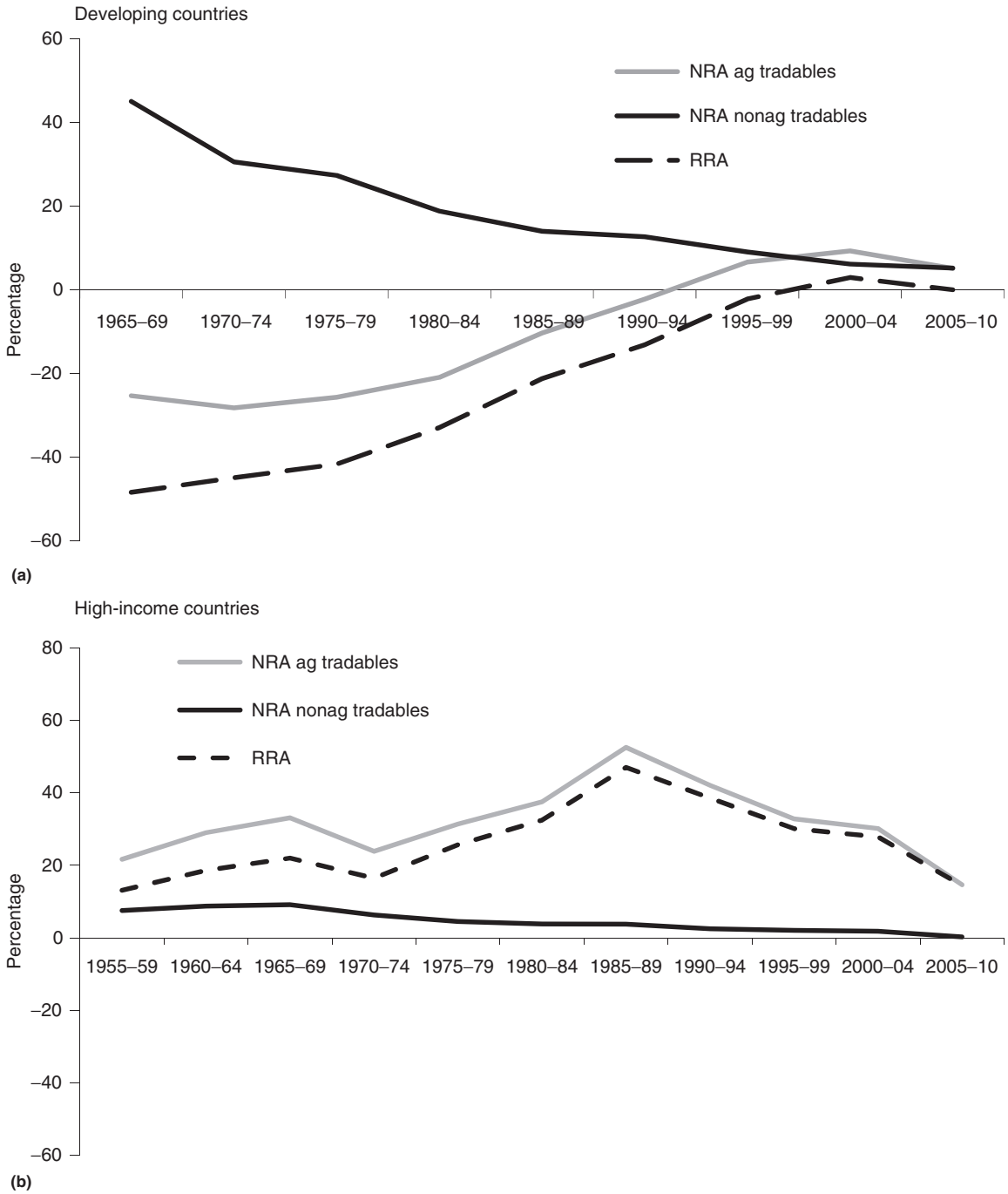


Figure 2 Developing and high-income countries' nominal rates of assistance (NRAs) to agricultural and nonagricultural tradable sectors, and relative rates of assistance (RRAs), 1955–2010 (%). Calculations use farm production-weighted averages across countries. RRA is defined as $RRA = 100 * [(100 + NRAag^t)/(100 + NRAnonag^t) - 1]$, where $NRAag^t$ and $NRAnonag^t$, respectively, are the percentage NRAs for the tradable segments of the agricultural and nonagricultural sectors. Reproduced from Anderson, K. (Ed.), 2009. Distortions to Agricultural Incentives: A Global Perspective, 1955–2007. London: Palgrave Macmillan and Washington, DC: World Bank (Chapter 1), updated from estimates in Anderson, K., Nelgen, S., 2013. Updated National and Global Estimates of Distortions to Agricultural Incentives, 1955 to 2011. Available at: www.worldbank.org/agdistortions (accessed 29.04.14).

positive and high in developed economies but have been highly negative in numerous developing countries (most noticeably, cotton). Still other product NRAs are relatively low in all countries (feed grains and soybeans as inputs into intensive livestock; pork and poultry as standard-technology industrial activities).

The failure of global variability across commodities to decrease significantly suggests that the movement of the

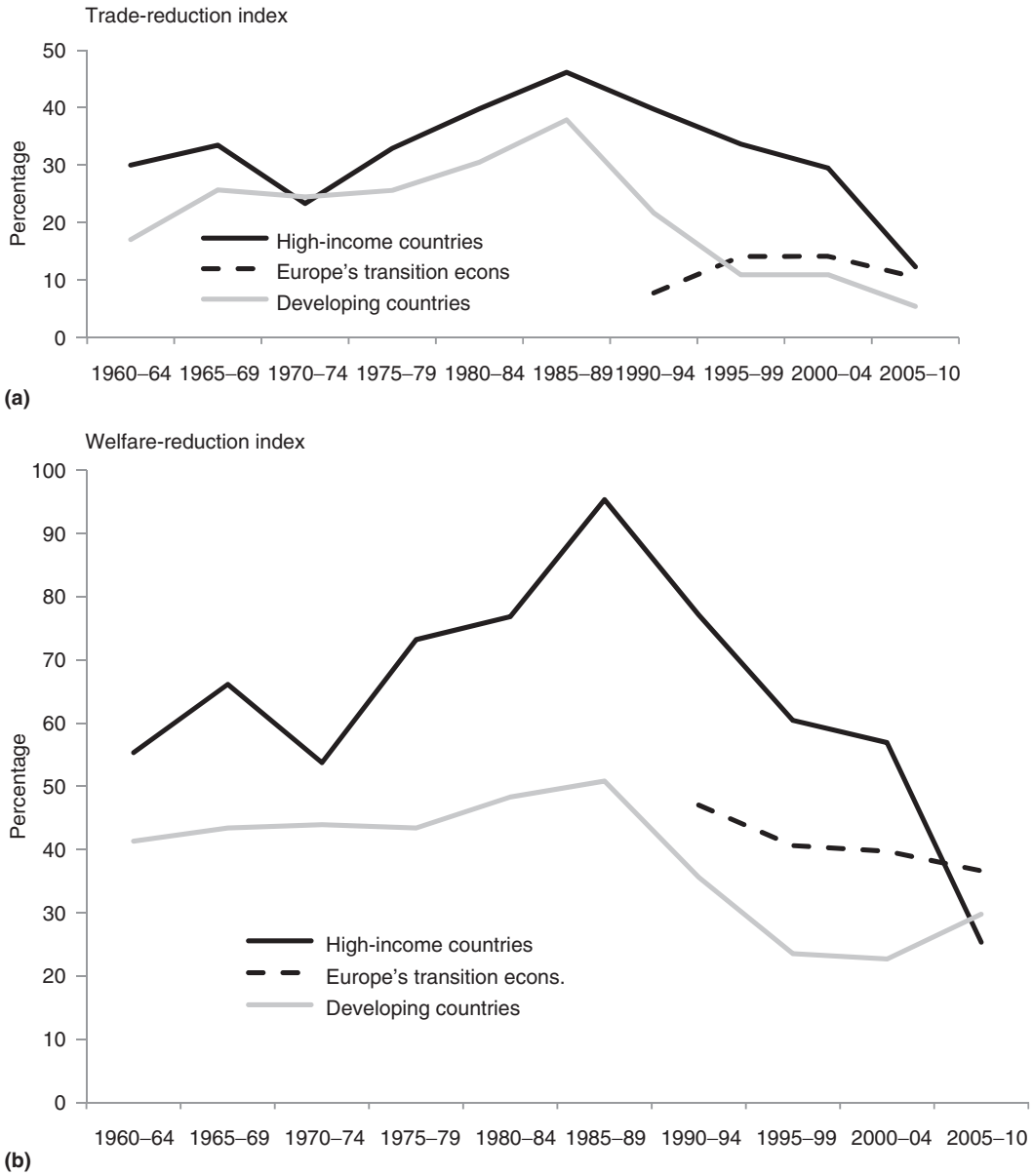


Figure 3 (a) Trade-reduction indexes (TRIs) and (b) Welfare-reduction indexes (WRIs) among high-income, transition, and developing countries for tradable farm products, 1960–2010 (%). Reproduced from Lloyd, P.J., Croser, J.L., Anderson, K., 2010. Global distortions to agricultural markets: New indicators of trade and welfare impacts, 1960 to 2007. Review of Development Economics 14 (2), 141–160, based on time-series estimates in Anderson, K., Croser, J.L., 2009. National and Global Agricultural Trade and Welfare Reduction Indexes, 1955 to 2007. Available at: www.worldbank.org/agdistortions (accessed 29.04.14), and updated using Anderson, K., Nelgen, S., 2013. Updated National and Global Estimates of Distortions to Agricultural Incentives, 1955 to 2011. Available at: www.worldbank.org/agdistortions (accessed 29.04.14).

mean-NRA toward zero has not been accompanied by a fall in the variance across commodities within the sector. This pattern explains why the WRI in Figure 3(b) is still well above zero, because the welfare cost of a sector's policy regime is greater the more dispersed are commodity NRAs within that sector. As is the case for variations in sectoral distortion across countries, much could be gained from intra-country resource reallocation within the agricultural sector and from the altered consumption patterns that would emerge from removing cross-product differences in NRAs.

A crucial component of the NRAs' product dispersion is that the agricultural policy regimes across countries tend to have an antitrade bias. This bias has declined over time for the developing-country group, mainly owing to declines in agricultural-export taxation, and despite growing agricultural-import protection. For the high-income group, the anti-agricultural trade bias has shown less of a downward trend over time, because agricultural-export subsidies rose and then declined, as did import protection (Figure 7). These factors explain the smaller decline in the TRI for high-income versus developing countries (Figure 3(a)).

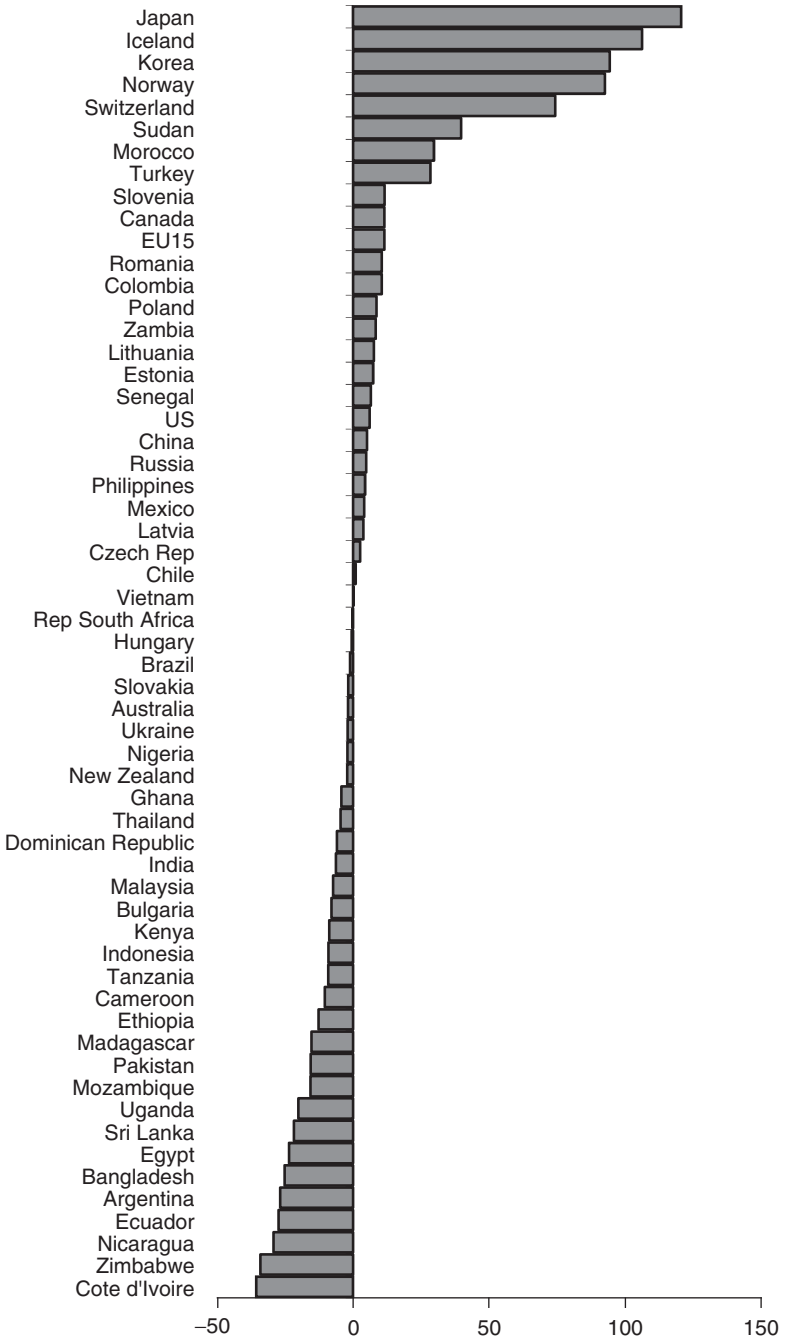


Figure 4 Relative rates of assistance by country, 2005–10. Reproduced from Anderson, K. (Ed.), 2009. Distortions to Agricultural Incentives: A Global Perspective, 1955–2007. London: Palgrave Macmillan and Washington, DC: World Bank (Chapter 1), using Anderson, K., Nelgen, S., 2013. Updated National and Global Estimates of Distortions to Agricultural Incentives, 1955 to 2011. Available at: www.worldbank.org/agdistortions (accessed 29.04.14).

Year-to-Year Variation

Around the long-run trend for each country, much fluctuation is seen from year to year in individual product NRAs. This tendency has not diminished since the mid-1980s for developing countries, and it has even increased for high-income countries. The negative correlation of a commodity's NRA with movements in its international price is largely responsible for this pattern. On average, barely half of the change in an international price is transmitted to domestic markets within the first year. As noted in the Section Introduction, governments are keen to prevent domestic prices from being affected by spikes in international prices. In both agricultural-exporting and agricultural-importing countries, and in high-income as well as developing countries, large changes in NRAs occur during periods of international price spikes – whether up, as in 1974 and 2008, or down, as in 1986 (Anderson and Nelgen, 2012).

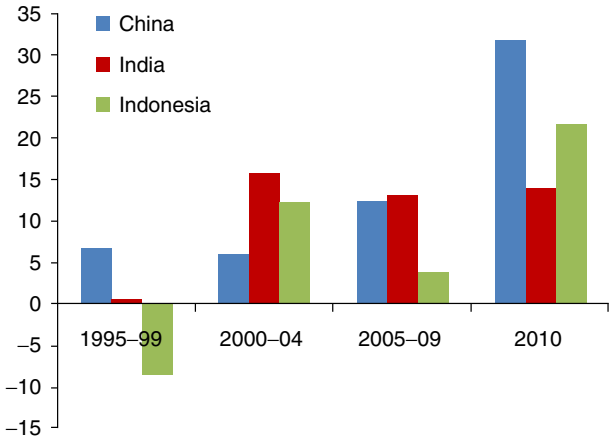


Figure 5 Agricultural nominal rates of assistance in China, India, and Indonesia, 1995–2010 (%). Compiled from estimates in Anderson, K., Nelgen, S., 2013. Updated National and Global Estimates of Distortions to Agricultural Incentives, 1955 to 2011. Available at: www.worldbank.org/agdistortions (accessed 29.04.14).

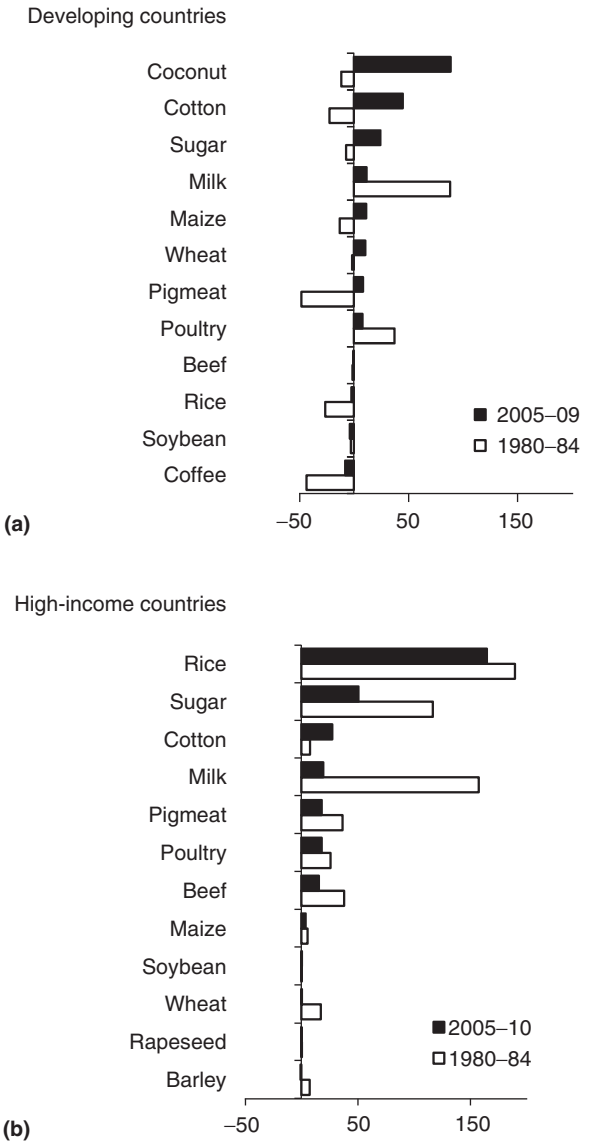


Figure 6 Comparison of earlier (1980–84) and more recent (2005–10) nominal rates of assistance in (a) developing and (b) high-income countries, by product (%). Reproduced from Anderson, K., Cockburn, J., Martin, W. (Eds.), 2010. Agricultural Price Distortions, Inequality, and Poverty. Washington, DC: World Bank, Figure 2.6, updated using Anderson, K., Nelgen, S., 2013. Updated National and Global Estimates of Distortions to Agricultural Incentives, 1955 to 2011. Available at: www.worldbank.org/agdistortions (accessed 29.04.14).

Relative Contributions of Policy Instruments

Across countries and time periods, governments have used a broad array of policy instruments. These include distortions to input markets (largely subsidies, plus controls on land use), production quotas, marketing quotas, target prices, price subsidies or taxes in output markets, and, especially, border measures that directly tax, subsidize, or quantitatively restrict international trade. Meanwhile, public agricultural-research investments amount to less than 2% of the gross value of agricultural output at undistorted prices in high-income countries. In developing countries, an even smaller percentage (1%) has been devoted to research and development (Anderson, 2009, Table 1.11).

Country expenditures on public-good research investments pale in comparison to losses resulting from commodity price distortions. The major vehicles responsible for these losses are trade-policy instruments such as export and import taxes and subsidies or quantitative restrictions, along with (in the past) multiple exchange rates. These trade-policy instruments account for no less than three-fifths of agricultural NRAs globally. As a result, they are responsible for an even larger share of the global welfare cost and agricultural WRIs, because trade measures also tax consumers, and welfare costs are proportional to the square of a trade tax. In contrast, internal domestic agricultural policies that directly subsidize or tax outputs and inputs have contributed only minimally to NRAs in the past.

Among trade-distorting policy instruments, it is clear from Figure 8 the extent to which export taxes have been phased out by developing countries. In sharp contrast, as assistance to import-competing agricultural subsectors of developing countries has grown (Figure 7(a)), the relative importance (from a national welfare perspective) of import taxes has increased dramatically (Figure 8). In Western Europe, the growth of decoupled, more direct income-support measures, along with the virtual abolition of all support measures in Australia and New Zealand, reveals a far different pattern than in high-income countries in East Asia, where border-measure supports continue to dominate (Figure 9).

Input subsidies are a relatively minor component of most countries' assistance to farmers. But they lingered on in Australia and New Zealand when most other forms of assistance were being phased out, and such subsidies have also remained approximately one-fifth of the total NRA in the US (Anderson, 2009, Chapters 4 and 5). With two notable exceptions, input subsidies are even less common in developing countries, where funds for such direct subsidies are scarcer. The important exceptions are India and Indonesia. In India, input

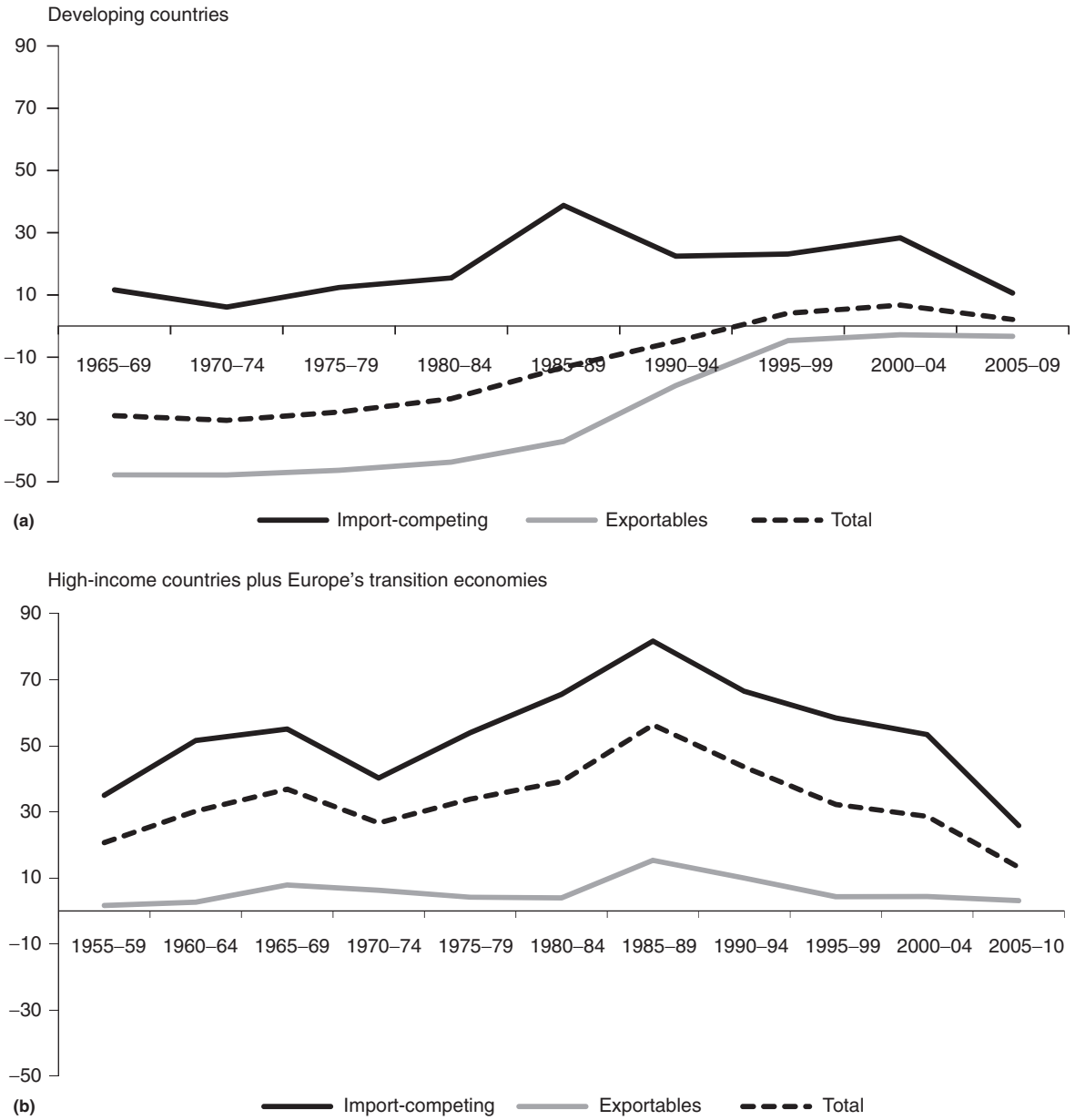


Figure 7 Nominal rates of assistance (NRAs) to exportable, import-competing, and all covered agricultural products in (a) developing and (b) high-income and European transition economies, 1955–2010 (%). Five-year weighted averages for covered products only. The total also includes nontradables. The straight line in the upper segment of each graph represents an ordinary-least-squares regression based on annual NRA estimates. Reproduced from Anderson, K. (Ed.), 2009. Distortions to Agricultural Incentives: A Global Perspective, 1955–2007. London: Palgrave Macmillan and Washington, DC: World Bank (Chapter 1), updated using Anderson, K., Nelgen, S., 2013. Updated National and Global Estimates of Distortions to Agricultural Incentives, 1955 to 2011. Available at: www.worldbank.org/agdistortions (accessed 29.04.14).

subsidies contributed 7–9% points to the agricultural NRA in the 1990s and 10 points in 2000–04. In Indonesia, such subsidies have contributed 2–4% points to the agricultural NRA since 1990. They also contributed from 5 to 9 points in the 1970s and 1980s, even at times when the overall agricultural sector of these countries had a negative NRA.

Up to the 1980s – and in some cases the early 1990s – it was quite common for developing-country governments to intervene in the market for foreign exchange. Such interventions added to the antitrade biases that were targeted at tradable sectors, including agriculture. However, these interventions largely disappeared by the mid-1990s, as initiatives took hold to reform overall macroeconomic policy. In China, for example, trade taxation associated with the country's dual- exchange rate system accounted for almost one-fifth of the (negative) RRA in the 1980s. However, since the mid-1990s, that system has been abolished (Huang *et al.*, 2009).

As governments seek to prevent domestic prices from being affected by periodic spikes in international prices, large

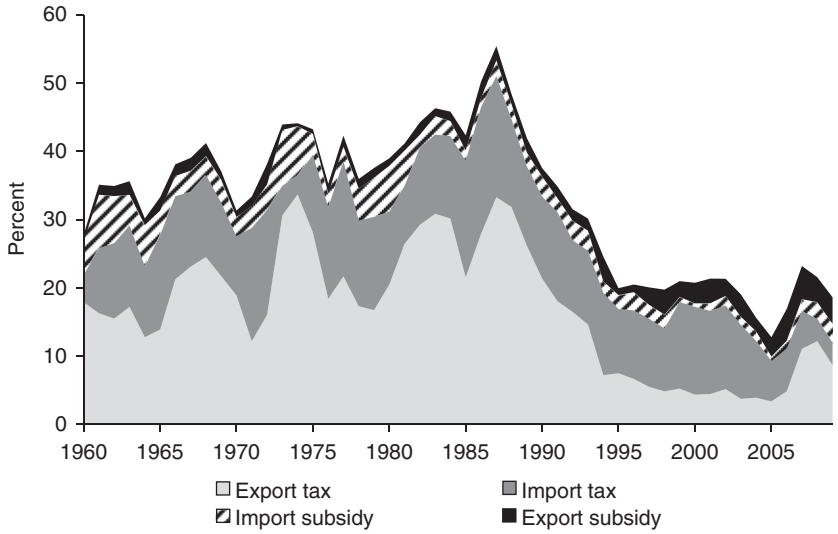


Figure 8 Contributions of various instruments to the border component of the welfare reduction index (WRI) for developing countries, 1960–2010 (%). Derived from estimates reported in Croser, J.L., Anderson, K., 2011. Changing contributions of different agricultural policy instruments to global reductions in trade and welfare. World Trade Review 10 (3), 297–323, updated using Anderson, K., Nelgen, S., 2013. Updated National and Global Estimates of Distortions to Agricultural Incentives, 1955 to 2011. Available at: www.worldbank.org/agdistortions (accessed 29.04.14).

changes in the relative importance of different policy instruments occur. This is evident from the estimated contributions to total agricultural WRIs of various policy instruments during the upward price spikes around 1974 and 2008 and the downward spike around 1986 (Figure 8). In some cases, trade taxes even temporarily disappeared; in other cases, trade subsidies emerged or expanded. Even when aggregated overall developing countries, the contribution of export taxes and import subsidies to the overall WRI rises and falls with international prices, whereas the opposite is true of import taxes and export subsidies.

Why Governments Distort Agricultural Markets the Way They Do?

Much of the variations in policy interventions over time and across sectors, individual commodities, and alternative policy instruments revealed above can be explained using the lens of political economy. Various schools of thought in political economy have provided insights into the conflicts between the public interest and special interests that naturally emerge in the design and implementation of public policies, including those that affect agricultural and food markets. These are used to explain several of the stylized facts presented in the section Policy Impacts on Agricultural Prices.

Income Redistribution

Distortions in agricultural and food markets result from policies designed to alter the distribution of income from what would otherwise emerge under unfettered market outcomes. Income distribution may change for structural or cyclical reasons. For example, overall economic development is typically associated with some sectors growing and some declining faster than others. In addition, agricultural markets and food prices fluctuate around longer term trends, causing important short-term changes in income and welfare distribution. Historically, this has induced governments to intervene in order to (partially) offset these market developments. This tendency involves increasing import tariffs or export subsidies when market prices decline and suspending import tariffs or export subsidies (or increasing export taxes or import subsidies) when market prices rise.

Changes in incomes in different sectors (or between different groups in society) create political incentives – both on the demand (farmers' and consumers') side and the supply (politicians') side – to exchange government transfers for political support. When farm incomes from agricultural markets decline relative to producers' incomes in other sectors, farmers are more likely to seek nonmarket sources of income such as government support. They do so either because the return on investment is greater from lobbying activities than from market activities (because the willingness to vote for and support politicians grows as the political rents that are generated increase) or because aversion to loss determines political reactions (Tovar, 2009; Swinnen, 1994; Baldwin and Robert-Nicoud, 2007).

Reduction of Agricultural Disincentives in Developing Countries

The observed correlation between RRAs and economic development can be explained largely by fundamental economic forces, including growth, structural adjustments, information costs, and changes in governance structures.

Economic growth, restructuring, and political incentives

Economic structural factors other than income distribution affect political incentives. In a poor economy, most workers are agricultural, and laborers (especially nonfarm laborers)

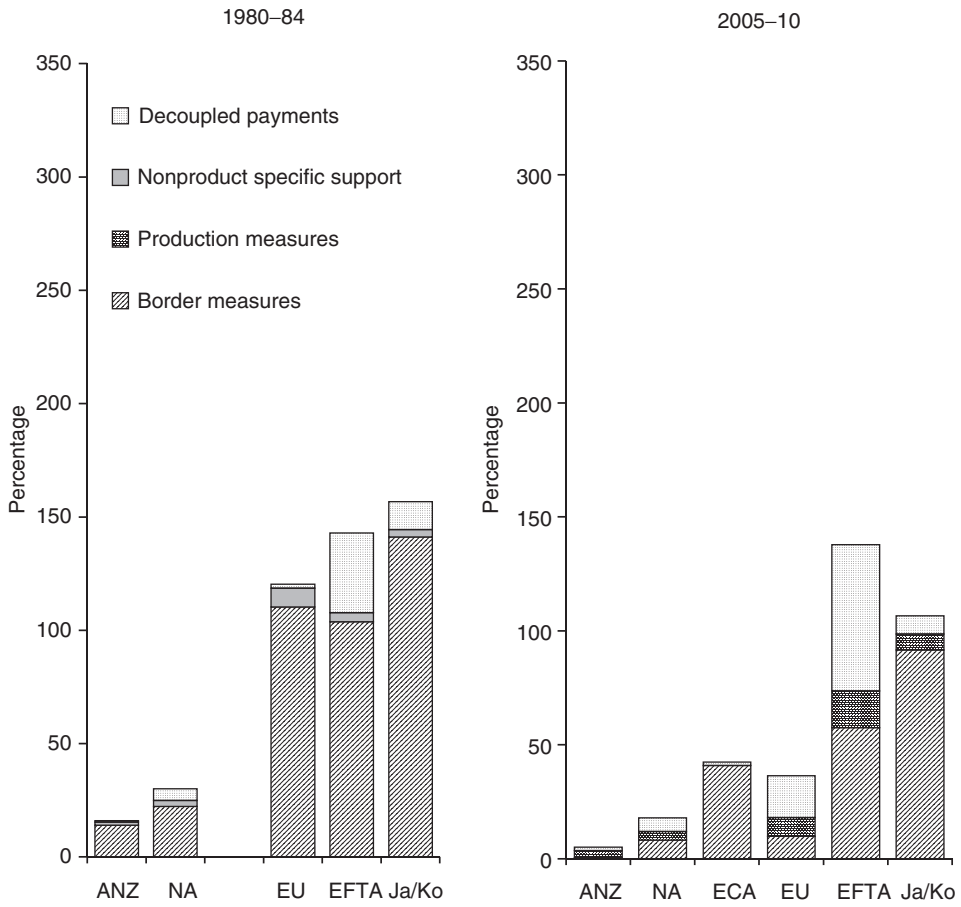


Figure 9 Comparison of earlier (1980–84) and more recent (2005–10) contributions of various policy instruments to the producer component of the welfare reduction index (WRI) for selected high-income and transition countries (%). ANZ, Australia and New Zealand; EFTA, European Free Trade Area; EU, European Union of 27 member countries; Ja/Ko, Japan and (South) Korea; and NA, North America. ECA is a term used by the World Bank to denote the transitional economies of Central and Eastern Europe and Central Asia. Reproduced from Croser, J.L., Anderson, K., 2011. Changing contributions of different agricultural policy instruments to global reductions in trade and welfare. World Trade Review 10 (3), 297–323, updated using Anderson, K., Nelgen, S., 2013. Updated National and Global Estimates of Distortions to Agricultural Incentives, 1955 to 2011. Available at: www.worldbank.org/agdistortions (accessed 29.04.14).

spend a large share of their income on food. Accordingly, the benefit to industrialists of a border tax – regardless of whether it targets manufacturing imports or food exports – is proportionately far greater than the loss it imposes on farm income. By contrast, in an advanced industrial economy, in which a lower percentage of workers labor on farms and in which workers generally spend a small share of their income on farm products, a rise in the relative price of farm products benefits farm households proportionately far more than it harms nonfarm households and industrialists (Anderson, 1995, 2010; Anderson *et al.*, 1986). The per-unit political cost of increasing farm incomes by raising the RRA thus decreases as the economy becomes less agrarian. In other words, even though the share of farmers in the voting population declines, less opposition to protecting farmers arises when there are fewer of them (Swinnen, 1994).

Democratization

Many developing countries have experienced democratization over recent decades. The implications for agricultural policies are not straightforward. The very factors that make it difficult for farmers to organize politically (such as their large number and geographic dispersion) render them potentially powerful in electoral settings (Bates and Block, 2010; Varshney, 1995). Because greater insulation of decision-makers implies that they can follow their personal preferences to a greater extent in selecting policies, their ideologies or other types of preferences are a key variable. This has little predictive power in the absence of specific information about those preferences. One implication, however, is that if dictatorial leaders are less constrained in setting policies, all else constant, there should be more variation in observed policy choices under dictatorial regimes than under democracy.

Swinnen *et al.* (2001) show that changes in electoral rules that have disproportionately benefitted agriculture (e.g., extending voting rights to small farmers and tenants in the early twentieth century) have induced an increase in protectionism. In contrast, other electoral changes have not affected agricultural protection because they increased the voting rights of both those in favor and those against farm protection.

Olper *et al.* (forthcoming) exploit the time-series and cross-sectional variation in the World Bank's database to show that democratization reduced agricultural taxation and increased agricultural subsidization because most political transitions occurred in poor countries with many farmers.

Lobby organization of farmers, agribusinesses, and consumers

Improvements in rural infrastructure have affected agricultural interests' ability to organize for political action. Regardless of governance structures, in order to influence political choices effectively, interest-group members must act in unison. For their collective action to yield meaningful results, organizational structures must be established that can mobilize resources and direct individual action. The greater the number of politically active members in an organization whose interests are aligned, and the more resources at the organization's disposal, the greater will be its political power base.

Olson's (1965) collective-action theory predicts that in poor countries, food consumers (net buyers of food) will wield more political power than farmers (and even more than the subset of net sellers of food). Consumers are often concentrated in cities, where political coordination and enforcement costs are more favorable than is the case in rural areas where farmers reside. However, as the economy develops – and especially as the share of agriculture in employment declines and rural infrastructure improves – the cost of political organization for farmers decreases. This cost reduction is likely to increase the effectiveness of farmers' representation of their interests and, as a consequence, of their lobbying activities.

Researchers debate whether changes in relative collective-action costs can explain major changes in agricultural policies. Although rural infrastructure and information have improved significantly as countries have developed, even in developed countries, the number of farmers remaining is still very large.

The growth and concentration of agribusinesses and food-processing companies, which are sometimes aligned with farm interests in lobbying for agricultural policies, serve to strengthen pro-farm interests (Anderson, 1995; Rausser *et al.*, 2011). Because farm lobbies and agribusiness interests can coalesce and are increasingly well capitalized and concentrated, they have been an important force in orchestrating public policies that benefit their interests (Gawande and Hoekman, 2006; López, 2008). In Europe, the growth of agricultural protection has been associated with the growth of cooperative agribusiness and food-processing (and even transport and storage) companies (Swinnen, 2008).

Rural communication and mass media

Information plays a crucial role in political markets, organization, and policy design. Downs's (1957) 'rationally ignorant voter' principle means that it is rational for voters to be ignorant about certain policy issues if the costs of information are higher than the (potential) benefit of being informed. This argument immediately implies that policies will be introduced that create concentrated benefits and dispersed costs, because the information costs are relatively large for those who carry the burden of financing transfers and relatively small for those who receive the benefits (Rausser, 1992). As a result, forces that change information costs may cause changes in public policies, including agricultural protection. One example is enhanced rural communication infrastructure, which occurs either through public investments (as in many high-income countries earlier in the twentieth century) or through technological innovations and commercial distributions (as in the recent dramatic increase in mobile-phone use in rural areas of developing countries).

Another influencing factor is the spread of commercial mass media (McCluskey and Swinnen, 2010). While television and radio were always commercial in countries such as the US, this was not the case in many other countries where, until relatively recently, radio and television were mostly publicly owned (and many newspapers were linked to political parties). Access to mass media empowers people politically, and a more informed and politically active electorate increases the incentives for a government to be responsive (Besley and Burgess, 2001; Strömberg, 2004).

Mass media can alter the landscape of political competition. Group size (e.g., the number of farmers vs. the number of food consumers in the economy) helps determine lobbying effectiveness. Mass media alter these mechanisms by providing more information to larger groups (Kuzyk and McCluskey, 2006; Oberholzer-Gee and Waldfogel, 2005). Strömberg (2001, 2004) shows that mass media bias their information toward groups that are more attractive to advertisers.

Olper and Swinnen (2013) argue that mass media will increasingly weaken the political power of small groups (in rich countries, farmers; in poor countries, consumers) and reinforce that of large groups and groups attractive to advertisers (in rich countries, consumers and urban interests; in poor countries, farmers). Thus, mass media favor rural interests (thus leading to higher RRAs) in poor countries but urban interests (thus leading to lower RRAs) in rich countries.

Structural-adjustment programs and policy conditionality

Another key issue is the impact of international financial institutions (such as the World Bank and the International Monetary Fund) and the policy conditions they impose on developing countries as part of their lending. The structural-adjustment programs in Africa and Latin America in the 1980s and the programs in the transition countries in Europe and Asia in the 1990s often required the borrowing governments to liberalize their policies and reduce distortions. Some policy reforms were reversed after the loans were in place, but many appear to have stuck (Akiyama *et al.*, 2001; Kherallah *et al.*, 2002).

In the transition countries of Europe and Central Asia, this shift has caused a significant reduction of subsidies to agriculture (Anderson and Swinnen, 2010). In Sub-Saharan Africa, the structural-adjustment programs are partially responsible for a significant reduction of taxes on farmers (an estimated average increase in RRAs of approximately 20% points, according to Swinnen *et al.*, 2011).

Summary

The reduction of antiagricultural policies in developing countries during the past decade has been caused by economic growth, by the shift in the political–economic equilibria induced by such growth, and by changes in governance and

media structures. As rural infrastructure improves and communications costs fall, farmers become more aligned and politically more effective. This development again contributes to a shift in the power balance in favor of rural interests. Moreover, as economies develop, the role of agribusiness and food companies – often with cooperative roots – expands. These more concentrated and better capitalized organizations often form powerful lobby coalitions with farmers' interest groups. Reduced taxation of agriculture in many developing countries that experienced income growth during recent decades is consistent with the identified forces sourced with a political-economic lens. The reduction of antiagricultural policies over the past two decades has been reinforced by political reforms (democratization) and by the growth of commercial media.

Reduction of Agricultural Subsidies in High-Income Countries

RRAs increased as incomes grew from the 1950s to the mid-1980s. But since then, there has been a change in trend. The latter shift has been particularly pronounced in the EU. Several factors seem to have played a role in this recent reversal in higher income countries, including the WTO, information and mass media, and EU-specific effects.

Agricultural policies were integrated in the WTO as part of the Uruguay round agreement on agriculture (URAA) in 1994. The impact of the URAA differs strongly between countries that participated in the negotiations and those that joined later. For the countries that participated in the Uruguay round, the URAA may have constrained the growth of agricultural protection afterwards (Anania *et al.*, 2004; Swinnen *et al.*, 2012). However, the WTO's impact on agricultural policy in, for example, the US over the past two decades has been very limited (Orden *et al.*, 2010).

The URAA's effects were different for countries that joined after the WTO's creation or went through institutional changes that affected their WTO constraints. For example, the WTO conditions imposed on China and Russia during their WTO accession processes have been much more stringent than was the case for some of the older WTO members (Drabek and Bacchetta, 2004; Evenett and Primo Braga, 2006).

In the EU, new countries' accession has required reforms of the EU's agricultural policy in order to avoid conflicts with the WTO. Although probably the most important aspect of the reforms has been a shift to less trade-distorting instruments, a substantial decline in the EU's RRAs has also occurred. The RRA declined from approximately 70% in the 1980s to less than 40% at the turn of the century, and, for the core 15 countries, to 11% in 2005–10 (**Figure 7**).

Since the 1980s, mostly poorer countries have joined the EU (e.g., Spain, Portugal, and Greece in the 1980s, and ten East European countries in the 2000s), apart from the three rich but small ones that joined in 1995. This has reduced the pressure to increase RRAs. In addition, several of these countries were not part of the GATT, and their integration in the EU caused GATT constraints for the Union as a whole in the 2000s. These constraints generated pressure to reduce total agricultural support. In high-income countries generally, the growth of commercial mass media may have played a role in reducing RRAs. Whereas the effect of mass media in developing countries is to reduce agricultural taxation, in rich countries, mass media typically help reduce agricultural support. Olper's and Swinnen's (2013) findings imply that by increasing government accountability, competition in the mass-media market often reduces distortions to agricultural and food prices.

A Shift to (More) Decoupled Subsidies in High-Income Countries

Reinstrumentation of assistance has occurred in some but not other high-income countries, involving a movement away from market-price support toward domestic decoupled measures (**Figure 9**).

The selection of policy instruments is influenced by several factors. First, different instruments imply different deadweight costs in redistribution. When exports are large, countries are more likely to use nondistortionary or less distortionary instruments than border measures (Swinnen *et al.*, 2012).

Policy instruments also differ in implementation costs. Trade taxes (either import tariffs or export taxes) are easiest and least costly to implement (Dixit, 1996; Rodrik, 1995). In many developing countries, the system for administering and enforcing income taxes or subsidies in the past may have been too costly to implement. Governments will choose trade (and market) interventions less often as their administrative capacity to tax and subsidize incomes improves.

Accessions to the GATT and WTO may have influenced the nature of the policy-instrument interventions more than the total level of policy transfers. Because a key purpose of the WTO is to reduce trade distortions, accession to the WTO should cause a shift toward less trade-distorting policies.

Because the decline in the EU's RRAs plays an important role in the overall RRA decline of high-income countries (**Figure 7**), the URAA (and later WTO Doha Round) negotiations have triggered an important change in agricultural policy-instrument choice in the EU over the past decades: a shift in the 1990s from price support to direct payments and to decoupled payments in the 2003 Reform of the CAP. These consecutive reforms strongly reduced the trade distortions.

The URAA has had less impact on US agricultural policies. Nonetheless, the US administration has attempted reforms to insure that many US agricultural subsidies are classified as 'green box' (i.e., nontrade distorting) under the WTO agreement (Orden *et al.*, 2010). In this sense, the motivation for its policy reforms appears to be similar to the EU's. These common outcomes for both the EU and the US suggest that WTO constraints could play an increasingly important role in reducing distortions if a substantive agreement could be reached in the current Doha Round. Such WTO constraints also induce emerging countries (such as China) to choose nondistorting (or less distorting) policy instruments as they attempt to support the incomes of agricultural households.

Finally, the revenue motive for governments will also affect the choice of policy instruments. If the tax infrastructure is less developed, governments have greater incentives to use tariffs

instead of direct income support to assist farmers. Rich countries have used value-added taxes more efficiently, and new information technologies have lowered the cost of providing decoupled payments to targeted groups (Alatas *et al.*, 2012).

Differences in Assistance between Commodities

Why is intrasectoral dispersion of NRAs so large in so many countries? Why are some commodities (rice, dairy, and sugar) assisted in virtually all countries (**Figure 6**)? There are several reasons to expect differences in NRAs not only among countries but also among specific agricultural commodities within a country. One explanation is that, for reasons similar to those that underlie countercyclical support, governments are more likely to support (sub-)sectors with a comparative disadvantage (imports) than (sub-)sectors with a comparative advantage (exports). Differential effects on government revenues also help explain why taxation is higher for specific commodities that are net exported: tariff revenues and export taxes increase government revenues, and, in the case of larger economies, improve their terms of trade, whereas trade subsidies do the opposite. Moreover, in poor countries in which tax-collection institutions are weakly developed, trade taxes (either import tariffs or export taxes) are often an important – or the only substantive – source of tax revenue.

Demand and supply characteristics matter as well. Raising tariffs on commodities that are more important for consumers, such as staple foods, will be opposed more often than will raising tariffs on commodities that are less important as a consumption item, and vice versa for producers. Demand and supply elasticities also affect the distortions and costs of policies (Gardner, 1983, 1987; Rausser and de Gorter, 1989; de Gorter *et al.*, 1992). The distortions (deadweight costs) and budgetary costs of policy intervention typically increase with higher supply elasticities and with the commodity's trade balance (that is, when its net exports increase). Because of the inherent changes in the distribution of costs and benefits of policies and the associated political incentives, political-economy theories predict that sectors with higher supply elasticities will be subsidized less often (or taxed more often) and that commodity support is negatively related to supply elasticities. Again, these factors are likely to affect also the choice of policy instruments, as, for example, when governments restrain supply responses through such additional regulations as marketing quotas and/or land controls (Rausser, 1992; Rausser *et al.*, 1984).

Another explanation is that the costs of implementing (and enforcing) certain policies can be quite different because of differences in the way commodities are marketed. For example, commodities that are perishable and require processing, such as sugar and dairy products, are typically marketed through processing companies – a point at which governments can intervene at relatively low cost. In contrast, it can be more costly to intervene in the case of products that are easily storable and which farmers can market directly to consumers (or to other farmers).

Finally, governments have treated perennial crops differently than annual crops (McMillan, 2001). Once farmers have incurred the costs of establishing a perennial plantation, they will continue to produce the exportable crop as long as the price they receive covers incremental or harvesting costs (Gawande and Hoekman, 2010).

Prospects for Further Policy Reforms

From our assessment, it is clear that much progress has occurred in the past decade or so in improving our understanding of why governments distort incentives facing agriculture. Certainly, more empirical testing of hypotheses suggested by theorists could be carried out, but considerable light has already been shed on most of the stylized facts raised by the World Bank's documentation of the evolution of global price distortions since the 1950s. That understanding suggests that there is room for cautious optimism about the prospects for future agricultural policy reform. Admittedly, it is troubling that some developing countries have moved from negative to positive RRAs and that agricultural protection and market distortion have recently increased in three of the most important developing countries, namely China, India, and Indonesia. In high-income countries, too, although the World Bank data reveal declining trends for NRAs, these trends do not necessarily reflect actual changes in their distorting policy instruments. Instead, higher world food prices largely explain the reductions in measured NRAs in the past 5 years. But many other countries' RRAs do appear to have converged toward zero (that is, where their assistance to agricultural and nonagricultural tradables is approximately equal), and other high-income countries have been lowering their RRAs nontrivially since the late 1980s.

Global and regional institutions appear to have played an important role in contributing to these reforms. Of particular importance to the decline in the RRA for the EU has been the institution of the General Agreement on Tariffs and Trade (and now the WTO). However, the recent shift in agricultural policies focusing on renewable energy (particularly in the USA, the EU, and Brazil) has major implications for world food prices and security. Ongoing research should make as transparent as possible the continued pursuit of protectionist measures by various countries in the form of biofuels policies, which tend to raise world food prices, in contrast to traditional agricultural policies, which historically have depressed these prices.

Prospects for policy reform will be influenced by the changing landscape of organized economic interests. Interactions between farmers and landowners, agribusiness, food and retail companies, environmentalists and other groups clearly influence agricultural policy negotiations and debates in all countries. The vertical relationships between farmers and agribusinesses are often critical in sustaining policy reforms. Capturing opportunities to form new coalitions among the interests of farmers, downstream agribusiness, food consumers, and environmental groups will largely dictate sustainable policy reforms that promote the provision of local public goods, agricultural productivity, and markets for environmental services. Certainly the many complex factors that contribute to distortion of agricultural and food markets can impede as well as promote progress, but hopefully continued

reform of entrenched policies and practices, along with heightened scrutiny of new developments, will promote greater transparency and cooperation.

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See also: Food Security: Development Strategies. Food Security, Market Processes, and the Role of Government Policy. Government Agricultural Policy, United States. International Trade. Markets and Prices

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Agroforestry: Complex Multistrata Agriculture

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Glossary

Agroforest Complex agroforestry system with a forest-like structure; synonymous to complex multistrata agroforestry system.

Complex multistrata agroforestry system (CMSAF) Tree-dominated land use system with two or more strata of trees or shrubs and a substantial degree of structural complexity within at least one of the strata.

Homegarden Intimate, multistorey combination of various trees and crops, sometimes in association with domestic animals, around homesteads.

Remnant vegetation Plants remaining from previous forest when the vegetation was cleared for planting. They can make a significant contribution to the composition, especially of CMSAF with understorey tree crops.

Shade trees, shade canopy Upperstorey in a system with understorey tree crops; usually fulfills various functions such as production of timber and nontimber tree products besides shading.

Traditional knowledge and practice Knowledge and practice which have been used for time periods ranging from decades to millennia by local people.

Introduction and Definition

Complex multistrata agroforestry systems (CMSAF) are tree-dominated land use systems with two or more strata of trees or shrubs and a substantial degree of structural complexity within at least one of the strata. This structural complexity is usually the result of a mix of species and age classes. Simple two-strata systems consisting of a monospecific understorey of tree crops and an equally monospecific overstorey of planted shade trees or other tree crops (say, cocoa under coconuts or coffee shaded by one legume tree species) are not included here in CMSAF, although the limits are not well defined. The economically dominant species in CMSAF are mostly planted, and this distinguishes these systems from managed natural forests. However, CMSAF can contain a significant number of spontaneous trees, shrubs, vines, epiphytes, and other plants that are remnants of the vegetation that was cleared to make place for the agroforestry system or its regeneration. Other species were brought in through natural seed dispersal or regenerated from the planted trees under the canopy or in clearings. The survival and growth of these species, many of which may also have commercial or subsistence uses, depends on their shade tolerance and management of the system.

In many parts of the humid and subhumid tropics and some savannah areas, CMSAF are a traditional way of growing tree crops. Four basic types of CMSAF are classified here:

1. CMSAF based on shade-tolerant understorey crops such as cocoa (*Theobroma cacao*), coffee (*Coffea* spp.), tea (*Camellia sinensis*), or cardamom (*Elettaria cardamomum*) grown under a complex and often species-rich canopy of native and/or planted trees.
2. CMSAF based on overstorey crops such as rubber (*Hevea brasiliensis*), damar (*Shorea javanica*), or durian (*Durio zibethinus*) grown under extensive management that allows the development of a substantial amount of native vegetation that forms most of the understorey and also mixes with the main tree crop in the overstorey.
3. Mixed systems of understorey and overstorey tree (and other) crops such as homegardens where the complexity of the vegetation is the result of high diversity of planted species that are often intensively managed.
4. Disturbed natural forests that are locally enriched with planted tree crops, but where the native vegetation predominates.

The complex structure of CMSAF can thus result either from extensive management and tolerance of natural vegetation where it does not interfere too much with the main commercial species and harvest operations (types 1, 2, and 4) or from intensive management, as is the case in homegardens (type 3). In the latter, a range of under- and overstorey species are intentionally planted and managed together in a complex spatial and temporal arrangement.

CMSAF with a large percentage of natural vegetation have also been termed 'agroforests' by Michon and de Foresta (1999) and Schroth *et al.* (2004c) in reflection of their forest-like characteristics. Some types of CMSAF are almost indistinguishable from natural forest to the untrained eye, especially if seen from a distance or from above (**Figure 1**). There are, however, also clear differences between even the most complex CMSAF and natural forest, as discussed in the Section on Types, Composition, Distribution, and Temporal Dynamics of CMSAF.

CMSAF are remarkable among agroforestry systems for their high diversity, which is either of cultivated species and varieties ('planned biodiversity') or of native species of plants and fauna ('unplanned biodiversity'), or sometimes both. They are also among the land use systems that are most likely to hold carbon stocks and perform hydrological functions relatively close to those of natural forests. The provision of these environmental services by these traditional agroforestry systems has attracted some attention with regard to how and to what degree the management of these systems can be intensified to increase their production and hence the living standards of their owners, but at the same time conserving their environmental service roles. This can be thought of as



Figure 1 Shaded cocoa agroforest (cabruca) in southern Bahia, Brazil. Reproduced from (with kind permission from Springer Science and Business Media) Schroth, G., Faria, D., Araujo, M., *et al.*, 2011b. Conservation in tropical landscape mosaics: the case of the cacao landscape of southern Bahia, Brazil. Biodiversity and Conservation 20, 1635–1654.

'ecological intensification.' These questions will be briefly reviewed in the Section on Production and Intensification.

Types, Composition, Distribution, and Temporal Dynamics of CMSAF

CMSAF Based on Understorey Crops

Moderately, shade-tolerant tree crop species such as cocoa, coffee, and tea are grown in a wide variety of land use systems. These range from unshaded and sometimes irrigated monocultures at one extreme of a gradient of increasing complexity through simply structured shaded systems consisting of a monospecific understorey of the tree crop and an often equally monospecific overstorey of planted shade trees to CMSAF and even natural forest where these species are native, at the other extreme (Figure 2). The use of shade is a traditional practice in many regions where these crops are grown. It has a number of benefits in terms of microclimatic protection, maintenance of nutrient cycles, and biological processes such as pollination and pest control, especially where no agrochemicals are used (Schroth *et al.*, 2001; Tscharntke *et al.*, 2011). For example, early attempts to grow cocoa in West Africa with little or no shade failed because of the intensity of insect attack that required the use of synthetic pesticides (Schroth *et al.*, 2000). Even intensively managed tree crop systems often use some shade, typically leguminous tree species such as *Erythrina* spp., *Inga* spp., *Gliricidia sepium*, or *Leucaena leucocephala*. These species are nitrogen fixing, are easy to establish, and can be conveniently lopped for shade adjustment and increased nutrient recycling. Where hurricanes are frequent, as in the Caribbean, they can grow back even after severe damage. They are also often present as a middle stratum in CMSAF. Unfortunately, some tree species, including *L. leucocephala*, have become invasive in regions where they were introduced as shade trees (Richardson *et al.*, 2004).

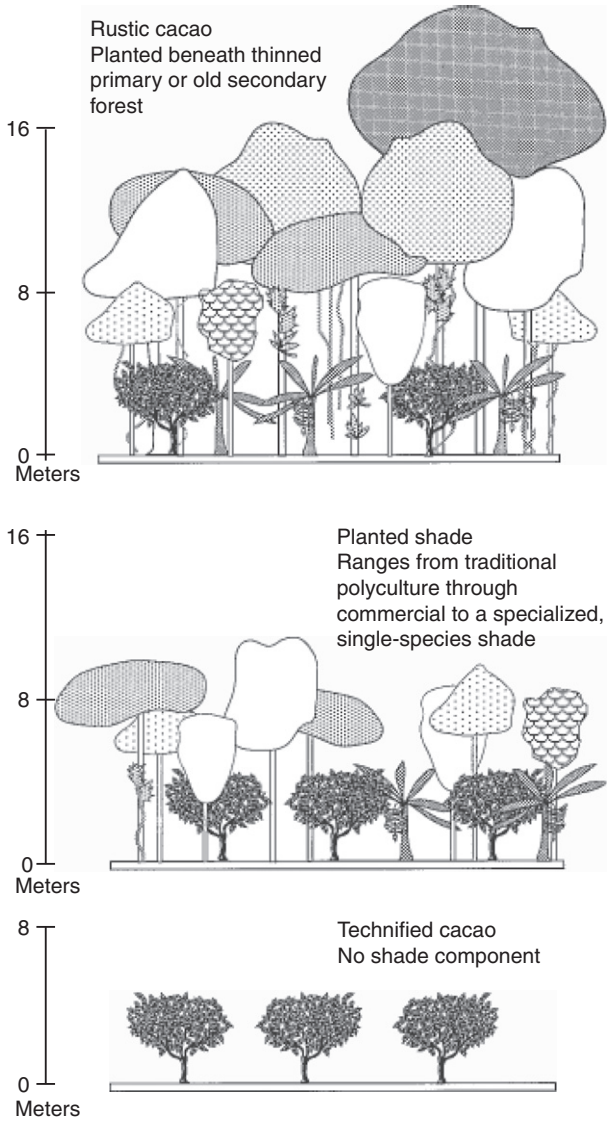


Figure 2 Gradient of cocoa production systems with varying degrees of complexity. Reproduced from (with kind permission from the Royal Swedish Academy of Sciences) Rice, R.A., Greenberg, R., 2000. Cacao cultivation and the conservation of biological diversity. Ambio 29, 167–173.

The canopy of CMSAF with understorey tree crops is often composed in part of remnant primary or secondary forest trees, or the natural regeneration from them, that were retained when tree crops were first planted. The remnant trees may have been retained either because they were considered useful (e.g., for food, medicine, or timber) or because they were difficult and laborious to fell (de Rouw, 1987). In addition, interplanted fruit trees are often present. Such systems also allow for periodic abandonment of the crops at times of low prices. For example, in Bahia, Brazil, the practice of cocoa planting into thinned forest ('cabruca') evolved as a labor-saving practice that was maintained even when extension services recommended clearfelling of the forest and planting of exotic leguminous shade trees (Johns, 1999). In these cabrucas, cocoa grows under a mix of native trees, planted leguminous

shade trees, and fruit trees, such as the exotic jackfruit (*Artocarpus heterophyllus*) and cajá (*Spondias mombin*), the latter introduced from the Amazon. These fruit trees are particularly prominent because they are preferred by farm workers and can regenerate spontaneously, especially during phases of extensive management or temporary abandonment (Sambuichi *et al.*, 2012). Bananas (*Musa* spp.) are also often present. There is also a recent trend of enriching the cabrucas with other commercial tree species, such as rubber trees (Schroth *et al.*, 2011b).

There is a wide variety of cocoa production systems in West and Central Africa, with a clear east–west gradient of decreasing shade use. According to Gockowski and Sonwa (2008), medium to heavy shade (i.e., CMSAF) is used by more than 50% and 60% of cocoa farms in Nigeria and Cameroon, respectively, but less than 30% of cocoa farms in Ghana and Côte d'Ivoire. Within Ghana, Ruf (2011) reported a trend of decreasing shade use on cocoa farms from the older, eastern cocoa regions to the newer, western cocoa regions. This changing attitude toward shade is apparently related to the adoption of cocoa varieties that are less shade tolerant as well as related to forest laws that restrict the farmers' rights to selling farm timber. The use of shade has also been in decline in Côte d'Ivoire, in part related to the dominant role of migrant farmers from nonforest areas during the expansion of the cocoa sector in the second half of the twentieth century (Ruf and Schroth, 2004). Differences in the attitude toward, and knowledge about, forest trees as cocoa shade between local and migrant cocoa farmers have also been shown in Cameroon (Laird *et al.*, 2007). In southern Cameroon, where CMSAF are the dominant practice in cocoa farms, trees of other species contributed 25% to total farm revenues (Gockowski *et al.*, 2010). A trend of increasing replacement of forest trees with fruit trees with increasing proximity to the capital Yaoundé has been observed. This suggests that farmers intensify and diversify their cocoa systems as they gain market access for a wider range of products (Sonwa *et al.*, 2007).

Coffee and tea are also sometimes grown in CMSAF, although the most complex types are perhaps less frequent than those with cocoa. In the case of coffee, systems with a large percentage of native forest trees in the canopy are also called 'rustic systems' or 'traditional polycultures,' whereas systems with a dominance of planted and managed fruit and timber trees (including bananas and plantains) in the canopy are referred to as 'commercial polycultures' (Moguel and Toledo, 1999). CMSAF with coffee can be found in several parts of Mesoamerica, including the Sierra Madre de Chiapas in southern Mexico, where Arabica coffee is often interspersed with forest and fruit trees and sometimes with ornamental palms (**Figure 3**). This forms a landscape mosaic made up of coffee agroforests, natural forest, and cattle pasture (Schroth *et al.*, 2011a). In El Salvador, most of the 'forest' cover consists of coffee agroforests (Somarriba *et al.*, 2004). A common practice in Costa Rica and other parts of Central America is the association of coffee with commercial timber trees, especially laurel (*Cordia alliodora*) as well as fruit and leguminous shade trees. In India's main coffee region, Kodagu in the Western Ghats mountains, coffee is often grown under a highly diverse canopy of native forest trees that were retained when coffee was planted into partially cleared forest, as well as fruit trees



Figure 3 Mixed agroforest of coffee (*Coffea arabica*) and ornamental palms (*Chamedorea* sp.) in the Sierra Madre de Chiapas, Mexico. Reproduced from (with kind permission from Springer Science and Business Media) Matocha, J., Schroth, G., Hills, T., Hole, D., 2012. Integrating climate change adaptation and mitigation through agroforestry and ecosystem conservation. In: Nair, P.K.R., Garrity, D.P. (Eds.), Agroforestry – the Future of Global Land Use. Dordrecht: Springer, pp. 105–126.

such as jackfruit, areca nut (*Areca catechu*), coconut (*Cocos nucifera*), and bananas. In this region, the coffee area has doubled in the past 35 years, often at the expense of private forests (Garcia *et al.*, 2010). Coffee is a component of some traditional multistrata agroforests in East Africa, such as the Chagga homegardens on Mount Kilimanjaro that are now suffering from increasing population pressure leading to land fragmentation and species loss (Kumar and Nair, 2004). In Guinea in West Africa, coffee agroforests form bands around villages where they were planted either in forest fallows or by reforesting savannah land. They are composed of an understorey of Robusta coffee (*Coffea canephora*), a middle stratum of fruit trees such as cola (*Cola nitida*), avocado (*Persea americana*), plantains (*Musa* spp.), etc. and an overstorey of timber trees and oil palm (*Elaeis guineensis*) (Correia *et al.*, 2010).

Miang tea, for chewing, is grown in traditional CMSAF in mountain villages of northwestern Thailand as well as in parts of China. In Thailand, the secondary forest is enriched with tea bushes, associated with other crops and sometimes cattle, forming a belt on mid-slope between the homegardens around the villages in the valleys and the mountain forest. When these systems are abandoned because of labor shortage, they gradually revert to forest (Schroth *et al.*, 2004c).

CMSAF can also involve herbaceous understorey crops as their principal commercial species. For example, in various parts of Asia and East Africa, cardamom (*E. cardamomum*) is grown in the understorey of thinned forest after removing the native understorey vegetation (**Figure 4**). The management of such systems can be relatively intensive, involving weeding and fertilizing the cardamom. Canopy opening and understorey clearing increase the germination and growth of pioneer species, including exotic species, so that the tree species composition of such agroforests can differ substantially from that of natural forest (Dhakal *et al.*, 2012; Hall *et al.*, 2011).



Figure 4 Cardamom (*E. cardamomum*) agroforest in Sri Lanka. (Photo: Glatzel, G., unpublished, with kind permission)

Depending on the size of the planting and the intensity of the disturbance and management, these systems can form a transition between CMSAF based on understorey crops and forest-enrichment systems that are discussed in the Section on Forest-Enrichment Systems.

CMSAF Based on Overstorey Crops

Tree crops which form the upperstorey canopy when they are productive are also grown in a wide range of systems and management intensities. For instance, although rubber latex is frequently produced by trees grown in monoculture plantations, it is also still extracted from native forest trees in parts of the Amazon. It is also produced in CMSAF land use systems of intermediate intensity, such as the rubber agroforests which have been independently developed by small farmers both in Indonesia and the Amazon by integrating these trees into their slash-and-burn rotational systems with food crops. In the Tapajós valley of the Brazilian Amazon, this type of rubber agroforestry was probably developed during the rubber boom late in the nineteenth or very early in the twentieth century (Schroth *et al.*, 2003). Rubber seeds are initially planted with cassava (*Manihot esculenta*) or sometimes other food crops. When annual cropping stops after approximately 2 years, the rubber seedlings are occasionally weeded until they can compete with the fallow regrowth. Tapping begins after approximately 8 years (sometimes earlier) and requires the clearance of paths between the rubber trees, whereas elsewhere the secondary forest is allowed to develop (**Figure 5**). This system is still being practiced, although many of these agroforests are now inactive. Interruption of the tapping during the dry season and during times of low rubber prices in combination with the extensive management practices results in the formation of secondary forests enriched with rubber trees. These cover large parts of the river banks of the Tapajós and neighboring rivers to the present day (Schroth *et al.*, 2003).

In Indonesia, rubber agroforests have evolved on the islands of Borneo and Sumatra soon after the introduction of the rubber tree from Brazil in 1910. Rubber seedlings are planted into slash-and-burn plots with dryland rice (*Oryza sativa*), otherwise the management is very similar to that in the Brazilian rubber agroforests (Gouyon *et al.*, 1993; Michon, 2005). However, in contrast to Brazil, smallholder rubber agroforests soon took over from large estates to become the dominant form of rubber cultivation in Indonesia (de Jong, 2001), covering 2.5–3 million hectare, supplying more than 70% of the rubber produced in the country and providing income to some 5 million people. In these Indonesian agroforests, the density of rubber trees is initially approximately 500–600 trees per hectare when tapping begins. It then falls progressively through tree mortality due to root rots, fungal diseases of the tapping panel, and other accidents (in one study 200 trees per hectare remained even after 40 years). When tapping becomes unprofitable, the agroforest is clearfelled, burnt, and the site is replanted with food crops and new rubber seedlings. Because replanting and concomitant loss of income from the surviving rubber trees is a major investment for small farmers, plantation is often delayed; moreover some agroforests have reached even 80 years of age. In some cases, farmers try to regenerate the light-demanding rubber trees in small clearings. At present, these traditional systems are being progressively replaced by more intensive practices, such as planting monoculture rubber and oil palm (Gouyon *et al.*, 1993; Michon, 2005). In the Amazon, the temporal dynamics of rubber agroforestry have not been studied to the same extent as that in Indonesia, but it is clear that they also can be, to a great extent, more than 50 years old, and the system appears to be less cyclical than the Indonesian equivalent, probably because of lower population pressure (Schroth *et al.*, 2003). As mentioned above, rubber trees have also been integrated in shaded cocoa systems in Bahia, Brazil, as a way of intensifying management and increasing revenues. Rubber has become a common diversification option for cocoa farmers in West and Central Africa, although more commonly through planting in separate plots rather than interplanting with cocoa (Ruf, 2013).

Rattan (*Calamus* spp.), a genus of climbing palms, is another example of a perennial crop that has been successfully



Figure 5 Rubber agroforest of unknown age in the Tapajós National Forest, Brazilian Amazon. Old tapping marks are visible on several trees in the left half of the picture. Reproduced from (with kind permission from Island Press) Schroth, G., da Fonseca, G.A.B., Harvey, C.A., *et al.*, 2004b. Introduction: the role of agroforestry in biodiversity conservation in tropical landscapes. In: Schroth, G., *et al.* (Eds.), Agroforestry and Biodiversity Conservation in Tropical Landscapes. Island Press, Washington, pp. 1–12.

integrated into the shifting cultivation cycle in Indonesia, especially Eastern Kalimantan, where it has become the second most important forest product of the country after timber. The rattan seeds or seedlings are added to slash-and-burn plots with dryland rice and they grow as part of a commercial fallow vegetation when the food crop fields are abandoned. Canes can be harvested after 7–10 years for 50 or more years, until the plot is slashed and burned again for a new cycle. This practice is now threatened by the expansion of oil palm as well as periodic droughts to which rattan is poorly adapted (Michon, 2005).

Rattan and rubber agroforests in Indonesia, and to a lesser extent rubber agroforests in the Amazon, can be considered long-cycle rotational systems that involve periodic events of clearfelling and replanting – in fact a type of economically enriched fallow. Their invention is a remarkable case of farmer innovation. Through the integration of tree crops into their slash-and-burn systems, farmers in Indonesia and the Amazon solved several problems at the same time. The planting of tree seeds or seedlings with food crops required a little extra labor during the first few years, when the seedlings were most vulnerable. In contrast to the practice used in industrial plantations of planting tree crops with cover crops, it also ensured food security while the tree crops were not yet productive. Furthermore, the agroforests had a much higher density of useful trees than natural forest, where the tree crops were native (e.g., several hundred rubber trees per hectare in agroforests as compared with less than five per hectare in natural forest in the Amazon), thereby again increasing the productivity of labor as well as land. And finally, by associating tree crops with native vegetation, these economically enriched fallows regenerated the fertility of the site, enabling a new cycle of food and tree crops when the old tree crops had been exhausted.

Other CMSAF that are planted in slash-and-burn plots can become permanent through regeneration in canopy gaps, as in natural forest. Remarkable among these are the agroforests based on damar trees (*S. javanica*), a resin producing dipterocarp species that occupy more than 50 000 ha in southern Sumatra (Michon, 2005). Permanent damar agroforests were invented by farmer extractivists in southern Sumatra in response to the overexploitation of damar trees in the native forest when market demand for their resin increased in the early twentieth century. The new practice resulted in a remarkable case of 'reagroforestation' of a slash-and-burn landscape (Michon *et al.*, 2000). Dipterocarp trees are considered difficult to regenerate but are successfully planted by the local farmers in slash-and-burn plots with rice, coffee (*C. canephora*), pepper (*Piper nigrum*), and fruit trees. The coffee is cultivated for 8 years, and then the damar and fruit trees grow together with natural regrowth. Resin tapping begins after 20–25 years and after 40–50 years, when the agroforests reach their full production. Dead trees are replaced under the canopy, but there is usually no replanting of the whole plot. Although most of the large trees in mature agroforests are damar trees, these are associated with many other useful tree species such as durian (*D. zibethinus*) and timber trees. The large durian trees that produce a popular and commercially important fruit as well as timber are also a common or dominant component of other types of Indonesian agroforests, sometimes with other fruit and various spice trees in the lower strata (Michon, 2005). In a comparison of rubber, damar, and durian agroforests in Sumatra, Thiollay (1995) found that damar agroforests were structurally most similar to primary forest with an often continuous canopy of 35–45 m height. The canopy of rubber agroforests was lower (20–30 m) and their understorey denser than that of the damar agroforests. Durian agroforests had a more open canopy at 30–45 m height composed of durian and other fruit and timber trees and a lower stratum of smaller trees such as clove (*Syzygium aromaticum*), cinnamon (*Cinnamomum* sp.), nutmeg (*Myristica fragrans*), and coffee (**Figure 6**).

The benzoin (*Styrax parallelloneurum*) agroforests in the highlands of northern Sumatra, Indonesia, are another intermediate subtype of CMSAF that are rotational but do not involve clearfelling. They are established by planting benzoin seedlings in the understorey of thinned primary or secondary forest. These seedlings eventually become tall trees growing in a matrix of remnant forest trees and forest regeneration. Tapping of the fragrant benzoin resin starts after approximately 8 years and can continue for 60 years, although yields decrease after 30 years. When tapping and the associated management of the ground vegetation are discontinued, the site reverts gradually into forest and the cycle can recommence several decades later. Benzoin rotations involving a slash-and-burn phase with rice cultivation are also known from Sumatra and Laos (Michon, 2005).

Intensively Managed Mixed Systems

In the CMSAF discussed so far, tree crops are associated with a substantial amount of spontaneous vegetation, some of it valuable and retained on purpose or even nursed, whereas some are merely tolerated, reflecting a strategy of low management intensity and temporary abandonment. Spontaneous vegetation often dominates in the less intensively managed strata: the shade canopy where the main commercial species are understorey crops or the lower and middle strata where the main commercial species are tall trees. Economically, these systems may be highly focused on a single, dominant tree crop species, even if they have high species diversity from a biological point of view.

However, high species and structural diversity can also result from intensive management, usually of relatively small plots, as in the case of tropical homegardens, where CMSAF are built largely from planted species. Homegardens have been defined as "intimate, multistorey combinations of various trees and crops, sometimes in association with domestic animals, around homesteads" (Kumar and Nair, 2004). Although individual homegardens are typically small, they can occupy significant areas in densely settled regions. For example, 20% of the arable land in the island of Java, Indonesia, has been estimated to be under homegarden use, and the state of Kerala in India has approximately 5.4 million homegardens, both densely populated areas with more than 800 people per square kilometre. Homegardens have a tradition dating back several thousand years in both regions. Although homegardens have been studied more frequently in Asia, they are also common in

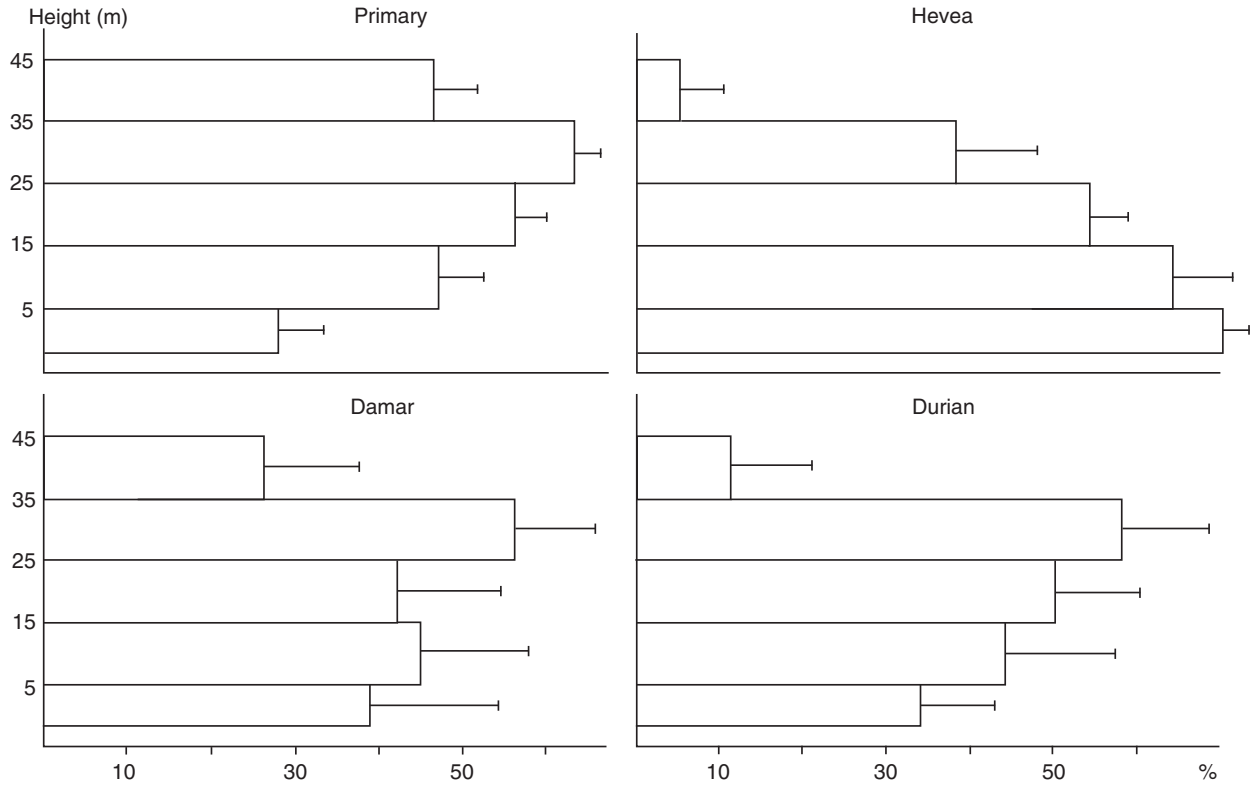


Figure 6 Height profiles of mean foliage cover in primary forest and agroforests based on rubber, damar, and durian in Sumatra. Reproduced from (with kind permission from Island Press) Schroth, G., Harvey, C.A., Vincent, G., 2004c. Complex agroforests – their structure, diversity, and potential role in landscape conservation. In: Schroth, G., *et al.* (Eds.), Agroforestry and Biodiversity Conservation in Tropical Landscapes. Island Press, Washington, DC, pp. 227–260 and Thiollay, J.-M., 1995. The role of traditional agroforests in the conservation of rain forest bird diversity in Sumatra. Conservation Biology 9, 335–353.

Africa, Central America, and the Amazon. In the Amazon, homegardens are common on anthropogenic Dark Earths and may have been sites of early plant domestication by Amerindians (Fraser *et al.*, 2010). The number of species in individual homegardens can range from a few to more than 70, and the homegardens of West Java collectively harbor more than 600 species, although some varieties have reportedly been lost over the past few decades (Kumar and Nair, 2004). The transition from homegardens to other crop fields or more extensively managed CMSAF is often gradual. For example, in the Tapajós region of the Brazilian Amazon, there is often a gradual transition from clean-weeded, homegarden-like systems composed essentially of planted species, such as rubber trees, cupuaçu trees (*Theobroma grandiflorum*), and açai palms (*Euterpe oleracea*) in the proximity of the homestead, to extensively managed, secondary forest-like rubber agroforests at greater distance from the communities (Schroth *et al.*, 2003, **Figure 5**). Homegardens can contribute significantly to household food needs, especially of fruits and vegetables and during lean times, although they are usually complemented by annual crop fields in the farming system. Homegardens can also be significant sources of timber, fuelwood, and a range of nontimber products including medicine, as well as animal products such as milk and eggs, and generate cash through the sale of part of their production (Kumar and Nair, 2004).

Forest-Enrichment Systems

Homegardens represent the intensive end of CMSAF, characterized by a dominance of cultivated species, whereas forest-enrichment systems are the extensive end and transition into extractively used natural forests (wild harvesting). In these systems, useful plants are integrated into more or less disturbed natural forest, for example, in clearings or along water courses, but in contrast to the systems discussed earlier, the natural forest vegetation remains dominant. Hunter-gatherers in the Amazon appear to have enriched forest around campsites with useful palms and other trees for several thousand years (Politis, 2001), which is similar to the practice in Indonesia, whereas the transfer of forest species to areas around campsites was an early form of plant domestication (Michon and de Foresta, 1999). More recent practices in the Amazon include the sowing of açai palms in riparian forests (Schroth and da Mota, 2007, **Figure 7**) or the enrichment of natural rubber groves with rubber seeds or seedlings to counteract the decline of the tapped mature trees (Dean, 1987). The planting of clusters of rattan palms into thinned forest can be found in Kalimantan, Indonesia (Michon, 2005). If natural forest with high densities of useful trees whose regeneration was facilitated by human disturbance were included in the concept of CMSAF, then this would reportedly be applied to some 11% of the Brazilian Amazon, where such human-modified forests are



Figure 7 Riparian forest enriched with açai palms (*E. oleracea*) in the Tapajós-Arapiuns Extractive Reserve, Brazilian Amazon. Reproduced from (with kind permission from Island Press) Schroth, G., da Mota, M.S.S., 2007. Tropical agroforestry. In: Scherr, S.J., McNeely, J.A. (Eds.), Farming with Nature – the Science and Practice of Ecoagriculture. Island Press, Washington, pp. 103–120.

thought to prevail (Scoles and Gribel, 2011). Examples include the oligarchic forests dominated by açai palms – in fact transitional systems between extractivism and agroforestry – in the Amazon estuary (Muniz-Miret *et al.*, 1996); forest fallows with high densities of tucumã palms (*Astrocaryum tucuma* syn. *Astrocaryum aculeatum*) that produce valuable fruits in the central Amazon (Schroth *et al.*, 2004a); and probably forests with high density of Brazil nut trees (Scoles and Gribel, 2011).

Environmental Functions

The environmental functions of CMSAF have mostly been studied at the scale of the plot or farm and with a short-term focus, but ultimately to determine their true relevance to global environmental issues, they need to be considered at the scale of the landscape and over timescales of years or decades. In view of the ongoing forest loss in many tropical countries, of particular interest is whether CMSAF replace forest or help conserve forest, or even help to restore forest functions where these have previously been lost. From an environmental point of view, especially in view of global climate change and biodiversity loss, the replacement of primary or advanced secondary forest by tree crops, even if managed as CMSAF, is much less desirable than the sustainable intensification of existing agroforests (see Section Production and Intensification) and their expansion on already cleared agricultural or fallow land. Where the conversion of native forest is inevitable, the efficient and sustainable use of the cleared land is paramount (Schroth *et al.*, 2011a). Unfortunately, some tree crops such as cocoa have a history of often being planted as pioneer crops on recently cleared forest land where soils are fertile, weed and pest pressures low, and the microclimate favorable, although the sustainable management, intensification, and replanting of existing farms have been neglected (Gockowski and Sonwa, 2011; Ruf and Schroth, 2004). When remnant trees were retained or allowed to regenerate in such systems, outstanding examples of CMSAF such as the cabrucas of Brazil, the cocoa agroforests of southern Cameroon, or the coffee agroforests of Kodagu, India, have resulted, but at the cost of forest conversion. A major environmental achievement of these CMSAF that were built from standing forest is to have conserved more of the forest cover and functions than would have been possible if forest had been converted into simpler agricultural systems. For example, the fact that Brazil's main cocoa production region in southern Bahia, one of the most biodiversity-rich parts of the Atlantic Forest Biome, is still largely forested and enjoys high levels of species conservation despite the fact that natural forest has been reduced to less than 10% of its original extent is due to the dominance of cocoa agroforests in the agricultural landscape (Schroth *et al.*, 2011b). Despite these favorable environmental characteristics of shaded tree crop systems, the conversion of forest into CMSAF should only be considered where options of replanting and intensification on existing agricultural land have been exhausted.

However, where CMSAF are built by restoring agroforest vegetation on previously cleared agricultural or even savannah land, the environmental benefits are unambiguous. Indonesian and Amazonian rubber agroforests are examples of CMSAF that replaced natural forest fallow in slash-and-burn systems. Although these agroforests are eventually cleared and replanted, this happens at relatively long time intervals and would also happen with normal forest fallows. It has been shown that the expansion of rubber agroforests in Borneo occurred at the expense of secondary rather than primary forest, and as a consequence the total area of secondary and agroforest cover (including rubber agroforests) may have locally increased (de Jong, 2001). Rubber agroforests in Sumatra, however, seem to have expanded during the twentieth century at the expense of primary forest (Feintrenie and Levang, 2009). Permanent agroforests that are planted on agricultural land but require no subsequent slash-and-burn events for replanting, as in the case of damar agroforests in southern Sumatra, are another environmental quantum leap in the reagroforestation of agricultural land. Because the continuous regeneration of damar trees imposes no age restriction on these agroforests, their structure approaches that of primary forest even more closely than that of rotational forms of CMSAF does (**Figure 6**); moreover, their biodiversity value is very significant (Michon and de Foresta, 1999). However, in the absence of effective forest conservation measures, such

permanent agroforests can also expand into forest land and thus indirectly help natural forest loss as agricultural land becomes scarce (Kusters *et al.*, 2008).

Ecological significance is also associated with cases where farmers have used agroforestry practices in savannah areas to create CMSAF by planting tree crops that usually pertain to a forest environment, thereby effectively expanding the forest domain. One such case was described from the forest–savannah transition zone of central Cameroon, where farmers progressively established multilayered systems of food and tree crops on savannah land to suppress competitive grasses, and then inserted cocoa seedlings in the understorey. Subsequent increases in soil carbon contents showed the power of trees to restore soil fertility (Jagoret *et al.*, 2012). Other examples of the 'agroforestation' of savannah land include coffee agroforests around villages in Guinea (Correia *et al.*, 2010).

Although not as good as natural forest, there is now an increasing body of research demonstrating the value of CMSAF for biodiversity conservation where they can be a valuable complement for natural forest and very much better than agricultural monocultures. Although all agroforests are somehow disturbed and therefore unable to harbor certain sensitive forest specialist species, the value of agroforest habitat for many rare and endangered species that would not be able to survive in open agricultural landscapes is firmly established (Cassano *et al.*, 2009; Estrada *et al.*, 2012; Schroth *et al.*, 2004c). Agroforests are also often used by forest species as movement corridors (**Figure 8**). Many authors have, however, stressed the need to conserve forest remnants even in landscapes with high agroforest cover in order to conserve the full suite of native species (Faria *et al.*, 2007; Schroth and Harvey, 2007; Schroth *et al.*, 2004c).

Other environmental functions of these land use systems have less often been quantified. Owing to the presence of large trees, CMSAF have higher carbon stocks in the vegetation than fields of annual crops and generally more than most other agroforestry systems. For example, in the cocoa agroforests of southern Cameroon, a total biomass of 304 Mg ha^{-1} has been measured, 56% of the biomass of primary forest (541 Mg ha^{-1}) at that site, whereas food crop fields only had 85 Mg ha^{-1}, or 16% of the biomass of primary forest (Duguma *et al.*, 2001). Because aboveground carbon stocks are concentrated in large trees, they should be highest in farms that retain large remnant forest trees soon after clearing and should decrease as these forest trees die or are sold off. The conservation and regeneration of large forest trees in CMSAF is thus an important measure for conserving the carbon stocks (and also the biodiversity) of agroforests. In a global review of carbon stocks in coffee production systems, Méndez *et al.* (2012) found average carbon stocks in the vegetation decreasing in the sequence: traditional coffee polycultures that contained large forest trees > commercial polycultures that associate coffee with a range of fruit trees > coffee monocultures with a simple shade stratum of legume trees > unshaded coffee monocultures. Belowground C stocks of tree crops are often approximately 20–30% of aboveground C stocks but can vary considerably and reach values of 1 and higher for species that are often pruned, for example, for the extraction of hearts of palm (Schroth *et al.*, 2002). When farms are very extensively managed or even temporarily abandoned, tree cover and presumably their biomass per hectare can increase. For example, an increase in tree density (and presumably carbon stocks) has been found by recent inventories in cocoa agroforests in southern Bahia, Brazil, compared with inventories carried out in the 1960s. This has been interpreted as an effect of the cocoa crisis and reduced management intensity of the past 20 years (Sambuichi *et al.*, 2012). Such increases may, however, be temporary and be lost when conditions improve and farm management intensifies.



Figure 8 Sumatran orangutan visiting a durian (*D. zibethinus*) tree in a rubber agroforest several kilometers from the nearest natural forest in Batang Toru, North Sumatra. (Photo: Schroth, G., unpublished)

In permanent agroforests that were established on slash-and-burn plots, total system biomass should increase over time approaching that of natural forest, although probably never reaching it owing to the absence of very large trees that can take several hundred years to grow. In rotational systems, such as certain rubber and rattan agroforests, however, the system biomass is periodically 'reset' through slashing, burning, and replanting and is best characterized through a time average, similar to that of monocyclic forest plantations. In Indonesia, Hairiah *et al.* (2001) reported carbon stocks of 89 Mg ha^{-1} in old rubber agroforest and a time average of 46 Mg C ha^{-1} in a rubber agroforest cycle between two slash-and-burn events, compared with 306 Mg C ha^{-1} in primary forest. Schroth *et al.* (2011a) reported C stocks of 143 (SD = 63) Mg ha^{-1} for eight old rubber agroforests in Brazil; primary forest was not measured at that site.

As CMSAF often form the transition between more intensively managed agricultural land and natural forest, they may also contribute to the conservation of forest carbon stocks by reducing the use of fire at the agriculture–forest interface. For example, in northern Thailand, the presence of tea agroforests in watersheds has reportedly reduced the use of fire in the same watersheds for fear of affecting the valuable tea plantings if fire went out of control. It has also been suggested that the presence of rubber agroforests on forest boundaries in the Tapajós region of the Amazon may have protected forest edges by encouraging a more careful use of fire, to which rubber trees are very sensitive, in slash-and-burn plots (Schroth *et al.*, 2004c). Other edge effects that commonly contribute to tree mortality and the degradation of forest boundaries, such as

strong winds, have been shown to be mitigated by secondary forests growing on forest boundaries and the same would be expected from agroforests, but this has not been specifically demonstrated. Agroforests are also often used for hunting because of the presence of fruit trees that attract wildlife. However, it is not known whether this diverts hunting effort from the forest, thereby protecting forest fauna, or attracts forest fauna into agroforests where it is more vulnerable. The net effect may be site dependent (Wilkie and Lee, 2004).

Hydrological services of CMSAF have rarely been quantified, although Philpott *et al.* (2008) showed that, like natural forest, coffee agroforests in the Sierra Madre de Chiapas in southern Mexico reduced the average size of landslides in comparison with simpler structured agricultural systems (**Figure 9**). Because CMSAF very often occupy sloping lands above irrigated plots and villages in the valleys, it can be assumed that they play a considerable role in filtering water and regulating water flows, functionally expanding the forests higher up in the mountains. In a study in Sumatra, Verbist *et al.* (2010) showed that on sensitive volcanic soils, shade coffee systems had lower surface run-off and erosion rates than sun coffee systems, although they cautioned that much of the catchment sediment yield was derived from river banks, footpaths, and roads and was unrelated to farm practices.

An indirect but potentially very significant environmental service role of CMSAF is to make land use in protected areas (where these are inhabited), or their buffer zones, more sustainable. Especially in Latin America, inhabited protected areas, such as biosphere reserves, extractive reserves, sustainable development reserves, and indigenous lands, occupy millions of hectares. Although these areas usually have restrictions on the types of land use that are permitted, the practice of slash-and-burn agriculture and cattle pasture within protected areas is quite common. Especially where CMSAF are traditional forms of land use in these reserves, they can be environmentally and socially more sustainable alternatives to slash-and-burn agriculture and pasture. For example, in the biosphere reserves of the Sierra Madre de Chiapas, Mexico, coffee agroforests are an important land use activity, especially at higher elevations (Cortina-Villar *et al.*, 2012), whereas in the Tapajós-Arapiuns Extractive Reserve in the Brazilian Amazon, rubber agroforestry and a more recent adaptation, agroforests based on timber and nontimber trees, are alternatives to the production of cassava flour in slash-and-burn agriculture (Schroth *et al.*, 2011a; Schroth and da Mota, 2013). CMSAF may also have value for tourism, but apart from some bird-watching tourism in shade coffee farms mostly in northern Latin America, this potential has been little explored.

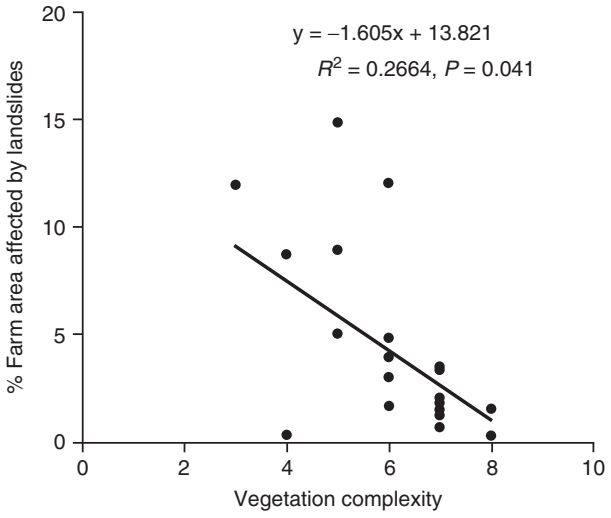


Figure 9 Percent coffee farm area affected by landslides as a function of vegetation complexity in coffee farms in the Sierra Madre de Chiapas, Mexico. Rustic and traditional polyculture farms have higher vegetation complexity scores (7–8), commercial polycultures mid-range scores (5–6), and coffee farms with simple shade have lower scores (3–4). Reproduced from (with kind permission from Springer Science and Business Media) Schroth, G., Läderach, P., Dempewolf, J., *et al.*, 2009. Towards a climate change adaptation strategy for coffee communities and ecosystems in the Sierra Madre de Chiapas, Mexico. Mitigation and Adaptation Strategies for Global Change 14, 605–625.

Production and Intensification

CMSAF are an important form of land use in many parts of the tropics. In Indonesia, a country with a long history and strong tradition in tree crop agroforestry, CMSAF has been estimated to occupy 6–8 million hectares, provide 80% of the rubber latex, 80% of dipterocarp resins, 95% of the benzoin, 60–75% of the main tree spices (clove, cinnamon, and nutmeg), and approximately 95% of the fruits and nuts, as well as significant quantities of bamboos, rattans, fuelwood, handicraft materials, and medicinal plants traded or used in the country (Michon, 2005). CMSAF are responsible for most of the cocoa area of southern Bahia, Brazil's main cocoa region, as well as 30% to 60% of cocoa farms in West and Central Africa, where most of the world's cocoa is produced (Gockowski and Sonwa, 2008). Despite the widespread simplification of shade canopies in recent decades, CMSAF are still an important form of coffee farming in Mesoamerica and the northern Andes, as well as Kodagu, from where 30% of India's coffee come (Garcia *et al.*, 2010). Homegardens provide a range of timber and nontimber (including food) products to millions of households throughout the tropics. For many farmers practicing CMSAF, these are their main source of income and products for domestic use, even if almost everywhere they are complemented by fields of food crops.

However, Michon (2005) stated that a weakness of complex agroforests in Indonesia is their apparently lower profitability compared with intensive production systems, and therefore, many of these traditional forms of CMSAF are under threat or even in the process of being replaced by more intensive land use forms such as monocultures of clonal rubber or oil palm. The same is true for other tropical regions. The rubber agroforests of the Tapajós, Brazilian Amazon, were probably always most typical of the river margins but have now lost any relevance on the flat plateau soils with the recent expansion of mechanized soybean agriculture (Schroth *et al.*, 2003). As mentioned before, Ruf (2011) observed a trend of progressive replacement of shaded cocoa farms by little or unshaded cocoa farms in West Africa, whereas many homegardens in Kerala and elsewhere have been replaced by simple

tree crop plantings and have lost many species and varieties (Kumar and Nair, 2004). Significant traditional shade coffee areas in Mesoamerica, northern South America and the Caribbean have been lost through conversion into lightly or unshaded systems (Perfecto *et al.*, 1996). In Kodagu, India, traditionally high shade levels in coffee farms have been reduced with the introduction of irrigation and crop diversification (especially pepper) and farmers increasingly use exotic trees (*Grevillea robusta*) instead of diverse native trees for shade (Garcia *et al.*, 2010).

Michon (2005) suggested that the apparently low profitability of many Indonesian agroforests which leads to their replacement by simpler land use systems is in part due to their management for diversification rather than intensification. However, extensive management and consequently low productivity is also characteristic of many CMSAF that are not particularly diversified from an economic point of view but are dominated by a single crop species (e.g., rubber or cocoa). Apparently, CMSAF lose ground as market conditions encourage greater specialization and more intensive management of a single or small number of currently most profitable crops. This is what will be seen if rubber agroforests are replaced by monocultures of clonal rubber trees in Indonesia or if homegardens are replaced by coconut plantations in Kerala, India. Cultural and societal changes such as increased urbanization and changing food preferences, certainly, also play a role (Kumar and Nair, 2004). Agricultural policies have also for many years encouraged monoculture practices, such as the replacement of traditional shade coffee and cocoa systems with less shaded systems, although farmers have not always followed these recommendations (Johns, 1999).

Considering the fluctuations of commodity prices on international markets and the numerous environmental risks to which producers of tree crops are exposed, switching to monoculture practices may not always be in the best long-term interests of local farmers, who may not have the financial and technical means to engage in such drastic changes of their traditional land use systems. Ruf and Schroth (2013) present a series of case studies illustrating a current trend toward diversification among tree crop farmers in regions that had previously been dominated by a single (often pioneer) tree crop such as cocoa, coconut, or coffee. This trend is motivated in part by severe price shocks affecting commodities such as coffee and cocoa during the past two decades and in part by environmental pressures such as pests and diseases, declining soil fertility, and climate variability. This diversification may take place at the plot, farm, or landscape level and does not necessarily result in CMSAF, but suggests that interest in diversified farming systems is again on the rise, counteracting to some extent the overspecialization that was a hallmark of the Green Revolution.

Where CMSAF are in decline not because of their diversification but because of their low productivity and profitability, research is needed into ways to increase their output while still preserving essential elements of these traditional, site-adapted systems. The following examples are intended to illustrate that the conservation, intensification, and promotion of CMSAF are multidimensional tasks which need to consider the dynamics of markets and society, in addition to agronomic and ecological questions, without attempting to be exhaustive.

Williams *et al.* (2001) studied the possibility of introducing grafted rubber seedlings in canopy gaps of Indonesian rubber agroforests in order to progressively increase their productivity without incurring the costs of clearfelling and replanting of entire plots. Although based on a traditional practice, this system has limitations in so far as rubber trees are light demanding and the seedlings are exposed to various risks (including damage from pigs and monkeys) when growing in canopy gaps. Schroth *et al.* (2004d) sought to increase the productivity of rubber agroforests in the Amazon and found that although some seed-grown trees in these agroforests were surprisingly productive despite the infertile, sandy soil, and extensive management, most trees had low productivity (**Figure 10**). However, farmers seemed to be reluctant to use grafted rubber seedlings even where this technology was available on nearby commercial plantations and this was interpreted as a risk avoidance strategy. For farmers who wanted to plant rubber but did not have access to, or were reluctant to use, grafted seedlings, a possible solution of intermediate intensity was to plant seeds from productive trees at higher-than-normal density, test-tap them at the age of 1–2 years, and then eliminate those saplings that showed the lowest potential. An adaptation of the traditional agroforestry practice whereby timber and nontimber trees were planted in slash-and-burn plots instead of (or in addition to) rubber trees was adopted by several hundred families (Schroth *et al.*, 2011a; Schroth and da Mota, 2013). Very recently, interest in rubber has increased in the area with increased market prices for rubber supplemented by a government subsidy. The impacts on cultivation practices remain to be seen.

In most parts of the tropics, cocoa is produced in systems of relatively low productivity, including in CMSAF. Examples include the cabrucas of southern Bahia, Brazil, which was once the second largest cocoa producer in the world but production fell precipitously in the 1990s through a combination of economic recession and the introduction of the witches' broom fungus (*Moniliophthora perniciosa*) of cocoa from the Amazon to which extension services initially had no appropriate response. Today, average cocoa productivity levels are approximately 250–300 kg ha^{-1} (Midlej and Santos, 2012); there is lack of qualified labor, and farm owners are indebted and unable to raise capital to invest in their farms. Therefore, although more disease-resistant and productive cocoa varieties for replanting and grafting of the old farms are now available, the crisis perpetuates itself. Legal restrictions on the felling of native trees prevent to some extent land use change, but also complicate the management of shade canopies. The cabrucas are of high value for the conservation of the exceptional biodiversity of this part of the Atlantic Forest biome and are part of the local culture (Schroth *et al.*, 2011b). Their maintenance will require an increase in productivity and probably also the development of additional forms of revenue from this traditional land use practice.

Coffee-based CMSAF in the highlands of Mesoamerica and the Andes have long been under pressure from agricultural extension services that favored monoculture practices. Now they are increasingly under threat from global climate change because the quality of Arabica coffee, and thus its price, is sensitive to high temperature. In addition, parts of the region will become drier and may suffer from an increase in extreme

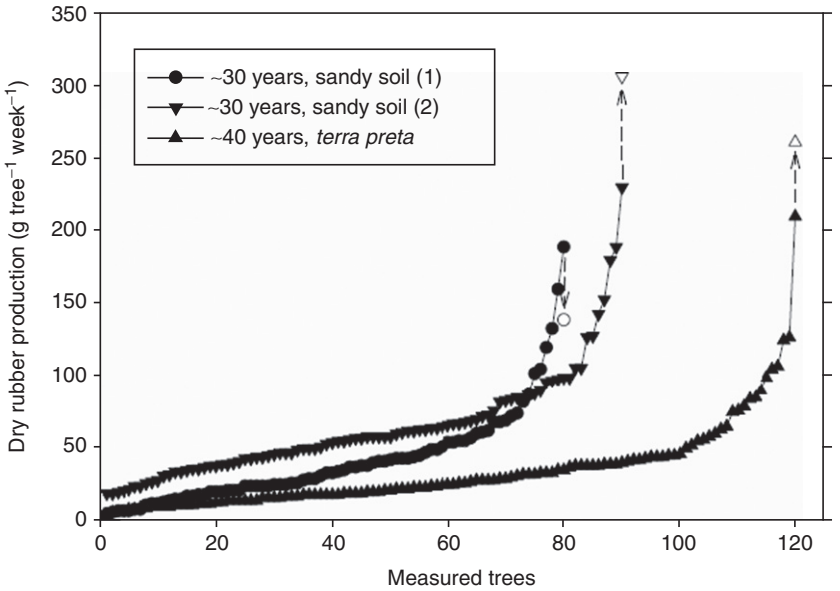


Figure 10 Productivity of individual rubber trees in three rubber agroforests in the Tapajós region of the Brazilian Amazon. Closed symbols show the productivity per tree at the beginning of the tapping season, and open symbols show the average productivity of the highest producing tree over the tapping season. Reproduced from (with kind permission from Elsevier) Schroth, G., Moraes, V.H.F., da Mota, M.S.S., 2004d. Increasing the profitability of traditional, planted rubber agroforests at the Tapajós river, Brazilian Amazon. Agriculture, Ecosystems and Environment 102, 319–339.

weather events such as hurricanes (Schroth *et al.*, 2009). A decrease of the profitability of coffee agroforests in areas such as the Sierra Madre de Chiapas, Mexico, might lead to their replacement with cattle pasture and consequently an increase in the use of fire, which has been a threat to the area's forests and coffee farms during drought years. Moreover, coffee agroforests have been shown to afford better protection against landslides than more simply structured land use forms (Philpott *et al.*, 2008). Increased diversification of the coffee farms with other tree crops has been among the recommendations to reduce the vulnerability of the farms to climate hazards (Schroth *et al.*, 2009), complemented by carbon trading and a government scheme of payments for environmental services to incentivize tree planting and forest conservation on the coffee farms and in the wider landscape (Cortina-Villar *et al.*, 2012; Schroth *et al.*, 2011a).

Although homegardens and similar types of agroforests have been early sites of tree domestication in several parts of the tropics, CMSAF are mostly made up of plants that have been relatively little improved through selection and breeding and therefore have relatively low and variable productivity. This is often true for the main crop species (e.g., cocoa or rubber planted from local seed) but even more so for secondary planted species and especially naturally grown species that were retained for their usefulness. One way to intensify cocoa CMSAF is to domesticate these 'companion trees' for the improved production of indigenous fruits and nuts (Leakey *et al.*, 2005). This approach is well advanced in Cameroon, where trees are selected for higher and more homogeneous productivity and greater product quality. It is being recognized as an important way to increase the incomes of rural communities (Leakey *et al.*, 2012). Likewise, Schroth *et al.* (2004a) have described a simple and low-cost management approach for improving the fruit quality and productivity of an Amazonian palm species, *A. aculeatum* syn. *A. tucuma*, that regenerates abundantly in disturbed sites (such as agroforests, crop fields, and fallows) but is very difficult to germinate and plant.

Futures of CMSAF

Change is normal in agricultural systems. Some CMSAF, such as homegardens, are thousands of years old and may have been sites of early plant domestication. Other CMSAF were invented by tropical farmers within the past hundred years, responding to an increased demand for commodities that extractive systems were not able to support or taking advantage of new crops and integrating them into their traditional land use systems. Some CMSAF reflect strategies of occupying land and taking it into production at relatively low cost, whereas others are carefully built and managed systems where a variety of crops occupy different ecological niches within a farming system. During the second half of the twentieth century, many CMSAF came under pressure from agronomists who favored intensive, monoculture production systems in the style of the Green Revolution. More recently, under the pressure of years of low commodity prices and increased risks from global climate change, the advantages to tropical farmers of producing several different outputs than depending on a single product has been more commonly recognized among farmers and agricultural policy makers (Ruf and Schroth, 2013). However, globalization and increasing global demands for commodities such as rubber and oil palm provide farmers with strong incentives to specialize and intensify their production systems, at least where inputs are affordable and markets and policies are

perceived as reliable. Changing availability of land and labor and changes in cultural norms also influence land use systems, but predicting these effects is not straightforward. Although the replacement of homegardens by simpler tree crop systems in Asia has been explained with a lack of labor to maintain them (Kumar and Nair, 2004), the same factor currently contributes to maintaining extensively managed cocoa agroforests in Brazil.

A novelty for the past 20 years is the increasing recognition of environmental services provided by land use systems such as CMSAF, including their biodiversity (Schroth *et al.*, 2004c). Certification systems such as 'Bird-friendly coffee' have been created to attract premiums and prevent the simplification of shade canopies that are used by resident and migratory birds, whereas shade coffee has been included in governmental and nongovernmental payments for environmental services programs in Mexico (Schroth *et al.*, 2011a) and Costa Rica. In some areas, CMSAF farms attract foreign tourists and Fair Trade premiums. In Brazil, legal restrictions on tree felling are a factor maintaining CMSAF besides increasing the cost and reducing the potential revenue from their management (sustainable or otherwise). However, government subsidies for tree products from the Amazon (such as rubber) are intended to benefit extractive systems but will also benefit CMSAF.

In view of these diverse forces, it is difficult to predict the future of CMSAF and most likely there will be different futures depending on region and type of practice. It is predicted that CMSAF have the best prospects to remain part of the landscape in areas where there are specific government policies for conserving land use practices of intermediate intensity, such as in inhabited protected areas (Cortina-Villar *et al.*, 2012; Schroth *et al.*, 2011a; Schroth and da Mota, 2013) and probably in a more intensively managed version in periurban areas with high demand for a range of fruits and other tree products. However, where environmental, market, and policy conditions are favorable for intensive agricultural production of single commodities, such as rubber or oil palm, CMSAF are likely to be replaced by more intensively managed monocultures.

See also: Agroforestry: Hydrological Impacts. Agroforestry: Practices and Systems. Agroforestry: Participatory Domestication of Trees. Climate Change: Agricultural Mitigation

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Agroforestry: Conservation Trees and Erosion Prevention

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Glossary

Agroforestry A managed land use that combines elements of agriculture and forestry, sometimes described as a two-tiered farming system.
Earthflow A downslope viscous flow of soil and rock material saturated with water under the pull of gravity. Earthflows are a shear above a failure plane in underlying rock. They can be deep flowing with the failure plane deeper than the rooting depth of trees.
Gully An eroding landform created by running water. Gullies in hill sides can be very large and difficult to stabilize, notably where the bedrock is exposed. Subterranean gullies are called tunnel gullies.
Loess A type of silty or loamy soil arising from wind deposition of the parent material, which because of its loose or uncompacted nature is very prone to rapid erosion, notably wind erosion.
Regolith The layer of loose material that sits atop bedrock. It includes soil and unconsolidated rock material.
Shallow landslide The downward falling or sliding of a mass of soil, often because of saturation with water. Shallow landsliding can be reduced substantially where soil is reinforced by tree roots.
Silvopastoralism A form of agroforestry where the agricultural element is pastoral farming; cf. arable farming.
Slump A collapse of the regolith initially triggered by some catastrophic event, for example, an earthquake, a flooded stream undermining the base of a hill slope, or an exceptional rainstorm. Initial rapid collapse is followed by slower ongoing movement often for several years.

Introduction

Soil is one of the most precious resources. The loss of soil, particularly through the land degradation processes of wind and water erosion, is one of the most serious environmental problems the world is faced with, as it reduces the means of producing food. Approximately 80% of the world's agricultural land was reported, almost 20 years ago, to suffer moderate to severe soil erosion and 10% to suffer slight to moderate erosion (Pimentel *et al.*, 1995). These statistics are unlikely to have improved since 1995, as farm sizes have increased, woody vegetative boundaries have been removed, and more sloping land has been brought into pastoral and arable cultivation to feed and fuel an increasing world population. Erosion rates on sloped arable land are of an order higher than rates on forested slopes (Cerdan *et al.*, 2010; Pimentel *et al.*, 1995). Land-use change following deforestation of sloped land is generally from forest to arable agriculture, with its accelerated risk of soil erosion. The negative effects of soil erosion include water pollution and siltation, crop yield depression, organic matter loss, and reduction in water storage capacity (e.g., Pimentel *et al.*, 1995; Bakker *et al.*, 2004; Cerdan *et al.*, 2004; Boardman and Poesen, 2006), which may lead to fundamental social challenges, such as land abandonment and the decline of rural communities (Bakker *et al.* 2005).

Water and Wind Erosion

Water erosion is the removal of soil by water and transportation of the eroded materials away from the point of removal. Water action due to rain erodes the soil and causes activities like gully, rill, and stream erosion leading to the downstream effects of flooding and sedimentation. The severity of water erosion is influenced by slope, soil type, soil water storage capacity, nature of the underlying rock, vegetation cover, and rainfall intensity and period.

Wind erosion is caused by the action of the wind on the soil surface and is the process by which fine soil particles are carried away. Wind erosion is a serious problem in many parts of the world, especially in arid and semiarid regions. It affects agricultural land in much of Northern Africa and the Near East; parts of Southern, Central, and Eastern Asia; Australia; Northwest China; Southern South America; and North America.

The severity of wind erosion is influenced by wind speed, the condition of the soil surface, and the amount of vegetation cover present. Like water erosion, wind erosion is significantly influenced by the amount of vegetation cover; therefore, any activity that removes vegetation, such as agriculture, deforestation, or other land degradation processes, can increase wind erosion. Wind erosion creates problems far from the initiation point with dust storms reducing air quality in urban areas and in adjoining countries in some cases.

Factors Contributing to Erosion Risk

Increased risk of erosion and sediment shift is associated with high soil erodibility; little ground cover; steep, long, and continuous slopes; high intensity storms; high drainage density of the slope; and proximity to natural waterways. Planting vegetation is one of the most effective and cost-saving strategies of reducing soil erosion, particularly on slopes. Trees

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have the capability through their root architecture, protective canopy, ability to divert and disrupt air flow, and reshaping of the landscape to reduce the erosion of soil from vulnerable landscapes.

Agroforestry as a Technology to Reduce Soil Erosion on Agricultural Land

Agroforestry and silvopastoralism are promoted as technologies that include trees in an arable or pastoral farming system to add economic value to the farming operation. Reduction of soil erosion can be a significant consequence of developing such two-tiered farming systems, particularly where the region is prone to high wind run or heavy rainfall and where the soils are thin and are easily transported by wind or water. Deforestation and overgrazing have been identified as significant contributors to soil loss in many regions of the world, and the replacement or planting of trees has become a high priority for the retention of soil on slopes or where wind erosion is causing significant soil loss.

The combination of trees and agriculture in the temperate region has become less common in modern agricultural practice, as the trees have been viewed as an impediment to intensifying agriculture (Tsonkova *et al.*, 2012). However, the increased knowledge of negative consequences originating from conventional agriculture, for example, soil erosion, water pollution, and biodiversity loss, has restored the interest in agroforestry practices within many regions of the world (Reisner *et al.*, 2007). The challenge facing the adoption of agroforestry practices is whether they will provide the same economic outcomes as conventional agriculture. This is equally true in temperate and tropical agricultural systems (Abdi *et al.*, 2013; Meena *et al.*, 2012). Ecological outcomes through prevention of soil erosion are often not considered significant enough to introduce a silvopastoral or agroforestry component to agricultural systems. Deforestation has generally been carried out to develop pastoral or arable land to feed communities and improve the local economy, to source lumber, or to open up the land for mining (Kusimi, 2008). Consequently, the economic value of afforestation must match the economic value of the land, without trees, for agriculture. Trees provide fuel, fodder, and timber, and uptake of agroforestry increases where this providence is important to the landowners. In the present context of reducing soil erosion on agricultural land a number of examples demonstrate the efficacy of this approach. The forest soils of San Pedro Mixtepec, Oaxaca, Mexico became prone to water erosion following the loss of plant coverage. This was due to opening of sloped lands to cultivation and overgrazing in lands with slopes $>27^{\circ}$. The establishment of an agroforestry system with *Leucaena leucocephala* (Lam.) de Wit and *Moringa oleiferous* (Lam.) in terraces reduced removal of soil by water erosion from 16.67 to 2.17 Mg ha^{-1} $year^{-1}$, compared with unprotected slopes (Sanchez-Bernal *et al.*, 2013). The same trend was reported by Saha *et al.* (2011) in Northeast India following the introduction of agroforestry to shifting cultivation practices.

Sourabh *et al.* (2013) observed that retention of trees were included in a variety of technological innovations used by indigenous communities in Northeast India for making the system more productive, less degradative, and able to generate cash income for modern living. Agroforestry is one of the preferred land-use options for smallholder farms in the Philippines due to its ability to increase land productivity and protect soil from erosion (Delgado and Canters, 2012). Their modeled predicted soil loss showed higher risks on sloped lands under nonagroforestry use.

Widespread erosion and landslides following rapid conversion of sloping lands in Democratic People's Republic of Korea, in association with heavy rainfall events, have led to the promotion of agroforestry at a policy level to conserve soil. Timber (*Larix leptolepis*) and fruit (aronia berry: *Aronia melanocarpa*) trees are the preferred options planted as contour strips (Xu *et al.*, 2012). Meena *et al.* (2012) stressed the importance of the economic benefits, additional to soil conservation, of agroforestry in the semiarid and arid regions of Northern India, if there were to be uptake of the technology. Technical advice on management of trees for the maintenance of pasture and for saleable products was identified as a key factor. The delayed economic benefits of trees planted for erosion control is a sufficient barrier to agroforestry in some rural societies (e.g., Jos Plateau, Nigeria, see Thapa and Yila, 2012). To expedite the wider adoption of these technologies and to halt and reverse soil degradation, it is suggested that farmers initially be supported with economic incentives to compensate their short-term economic loss (Das and Bauer, 2012).

Using Trees to Manage Mass Movement Erosion Forms on Agricultural Land

The water-driven erosion forms discussed below are illustrated using examples and management strategies used for pastoral agrosystems in New Zealand. The two most suitable conservation tree species used for soil erosion management in New Zealand are poplar (*Populus* spp.) and willow (*Salix* spp.). The use of trees in pastoral agrosystems is best described as silvopastoralism.

Shallow Landslide Erosion

Shallow landslides, referred to as slips below, are the rapid flowing or sliding movements of soil and regolith exposing a slip surface. These can be shallow and parallel to the surface or deeper and more concave. They are caused by water infiltrating into the soil until it meets an impermeable layer when it flows downslope. Sufficient hydraulic pressure lifts the soil and turf mat, which then flows/slides downslope creating a debris tail over pasture, sometimes reaching the valley bottom or the stream (**Figure 1(a)**). Slips occur on a variety of rock types ranging from sandstones to mudstones and in loess deposited over hard rocks, such as limestone.

Studies have shown that following slippage, production on the eroded surface will only recover to approximately 80% of the uneroded surface (e.g., Rosser and Ross, 2011). It is, therefore, important from an economic perspective for farmers to minimize this loss of productivity.

To prevent the slip occurring, willow or poplar poles (vegetative cuttings, 2–3 m long) are planted up to 18 m apart



(a) (b)

Figure 1 (a) Severe slipping on soft mudstone in eastern North Island, New Zealand. (b) Young space planted willows reducing the risk of further erosion on an unstable slope. Photos McIvor, I.

across the slope in a regular pattern or, more usually, where the slipping is considered most likely to occur (Figure 1(b)). Slip-prone soils are often shallow and exposed to climatic extremes. The recommended practice is to plant a mix of clones, protect the new poles with sleeves, and actively manage them (e.g., replace dead trees and no cattle exposure for 2–3 years) for the first 5 years of growth to insure that a healthy tree develops. Where the potential for slip erosion is very severe to extreme, a closed canopy tree cover is recommended. However, this requires permanent retirement from pasture, a change many farmers are not willing to undertake.

Earthflow Erosion

Earthflow is a flow of soil and underlying regolith, generally characterized by retention of a pastured cover and often broken by tension cracks and smaller secondary movements. Such flows do not result in a separate slip scar and debris. Earthflows range from shallow to deep (1 to >70 m), from fast-moving to a very slow and discontinuous creep, and from retaining a continuous turf mat to having a broken surface with secondary movements. They may even have gullies cutting through them, increasing their instability. Earthflows move when the whole regolith is wetted up and the frictional resistance is at a minimum. This is generally later in winter and not usually in response to intense rainstorms.

The control measures applied depend on the type of earthflow. The measures rely on removing surface water to minimize infiltration by surface smoothing and constructing diversion banks, tying together the surface with willow roots, pair planting willows where gullies are most likely to form, and planting at the toe of the movement to hold up the toe (essential when the toe is being undercut by a waterway).

Both poplars and willows are used for managing earthflows (Figures 2 and 3). Willows are preferable to poplars for halting earthflows, as their roots form thick mats when in a wet environment. This holds the poorly structured mudstone better than poplar roots, which do not have this matting characteristic.

The willows are planted across the flow in a regular pattern at 8–15 m spacing. The regular pattern allows cultivation between the rows if any breakouts occur or for pasture renewal. As with poplars, silviculture is necessary to create an appropriate form and to reduce shading.

Slump Erosion

Slump erosion occurs where there is a backward rotation of a significant area of land. This erosion type is relatively uncommon, as most occur as a secondary feature following a flow or large slip leaving an exposed headwall which then collapses with a backward tilt. Slump erosion events are usually sufficiently large (Figure 4) that tree planting alone cannot control them. They need to have surface dam water drained the surface smoothed, and the area retired and close planted in trees. Once in trees, the slumps need to be closely managed, as continuing movement overturns or topples trees requiring clearing to keep drainage open and replanting. Over time movement reduces.

Fluvial Erosion Forms

Fluvial erosion occurs where the soil or regolith is exposed to running water, resulting in tunnel gully erosion or gully erosion.

Tunnel Gully Erosion

Tunnel gully erosion is an insidious process where subsurface soil layers are removed by water. The water moves down through the soil profile until it reaches a less permeable layer where it concentrates to flow downslope removing soil particles in its path and forming tunnel. These tunnels either partially or totally collapse over time. They occur in a wide variety of hill country environments ranging from strongly



(a) (b)

Figure 2 (a) Mudstone earthflow on pastoral land with protected poplar poles space planted to control the movement and (b) shallow earthflow on mudstone with movement halted by successful poplar planting. Photos Eyles, G.



Figure 3 Deep earthflow on mudstone in the East Cape region of New Zealand, stabilized by a combination of mechanical surface and diversion banking and willow and poplar planting. Photo G. Eyles.



Figure 5 Harvesting poplars that have successfully controlled tunnel gullies in strongly weathered claystones in Northland, New Zealand. Photo R. Cathcart.



Figure 4 Major slump event on the Maraetotara Heights, Hawke's Bay, New Zealand, which first moved in the early 1970s and is still moving today despite tree planting. Photo D. Miller.

weathered claystone, siltstone, and loessial hill country to uncemented ignimbrites.

Where climate allows and trees can grow, tunnel gullies can be controlled by planting a poplar or willow pole in the collapsed tunnels. The tree roots hold up the sediment gradually filling up the holes. Tunnel erosion is managed by identifying the characteristic sunken drainage lines and planting poles in these. In this way the tunnels fill up with sediment before any collapses (Figure 5).

Gully Erosion

Gully erosion (Figure 6) occurs where concentrated surface water scour out the regolith and underlying rock with the debris being either deposited downslope or transported into river systems creating major downstream problems. The gully

form and severity is very dependent on the rock type. The very severe to extreme gully erosion is restricted to argillites (crushed), mudstone, and fine siltstones with each rock type having its characteristic gully shape.

Prevention is much more effective than repair as once the erosion is into the bedrock it is very difficult to get trees (or any other plant material) established. The large gullies cannot be repaired. The whole catchment needs to be retired from grazing and planted in closed canopy trees with the eroding surfaces repeatedly planted with willow wands to create a vegetated surface. These sites take many generations before they are repaired.

The construction of debris dams (Lancaster and Grant, 2006) at intervals up the gully coupled with pair planting of willows has successfully controlled erosion from small gullies.



Figure 6 This gully formed overnight in 1900-year-old uncemented ignimbrite west of Taupo, New Zealand. In this environment, as an erosion prevention measure all drainage lines in pastured hill country are pair planted with tree willows at 15–20 m spacing and measures taken to insure the grassed surface is not broken, so allowing a gully head to form. Terrace edges need to be protected and either grassed waterways developed or flumes constructed.

The willow root mats grow across the gully bed and over the surface of the dam covering and protecting the eroding surface (Figure 7(b)). Tree pairs are spaced from 8 to 15 m up the gully depending on severity. Discontinuous gullies (Figure 7 (a)) are very common in hill country. Large erosion events fill the valley bottoms and smaller events begin to scour them. Prevention is by pair or single planting of willows up the valley bottom at 15–20 m spacing and at weak points developing a planted block with 2–3 rows of willows planted at 1.5 m spacing across the valley bottom and in an area fenced out from grazing.

Rill Erosion

Pasture renewal in easy hill country is often on a 5 to 10 year cycle involving desiccation of the existing pasture followed by surface disking, planting of a fodder crop, and then oversowing with an improved pasture spp. mix. Rill erosion when the surface is exposed can lead to severe soil loss (Figure 8).



Figure 8 Rill erosion on hill country cultivated for pasture renewal. Zero tillage techniques or strip cultivation will reduce the risk of soil loss. Photo Eyles, G.



(a) (b)

Figure 7 (a) A discontinuous gully and (b) gully control achieved by stabilizing the base level through construction of debris dams supported by willows. Note the willow root mat grown over the dam structure. Photos G. Eyles.

The risk of this is best minimized by zero or minimum tillage management systems that do not put the soil at risk. If cultivation is required, strip cultivation leaving grassed strips each 20 m on the contour across the slope will reduce the risk.

Stream Bank Erosion

In hill country, storm events can create flash floods in streams that scour out the side walls, deepen the profile, and cause gullies to form. This can be avoided by planting willows along the banks (Figure 9). The roots stabilize the banks and protect the stream floor from degrading.

Using Trees to Reduce Soil Loss from Wind Erosion

Wind erosion is a significant source of soil loss in many parts of the world (Figure 10) and its contribution to desertification and the loss of productive farmland is of international concern. Although wind erosion has been documented in China for centuries, in recent years the climate in these areas has become drier and as a consequence the problem has been getting worse (Shi *et al.*, 2004). Windbreak forest belts in desert areas in China are being used to effectively control soil erosion (Figure 11) and promote accumulation of organic matter and clay in the soil and formation of crust at soil surface, thus fixing drifting sands and accelerating formation of eolian sandy soil (Li *et al.*, 2012). Su *et al.* (2010) reported that shelterbelts of *Populus gansuensis* increased soil organic carbon by 14.6 times and 17.0 times after 7 and 32 years, respectively, compared with unprotected shifting sand land. Large shelterbelt schemes cover more than 11 million ha of wind erosion-prone land.

Windbreaks are one of the oldest agroforestry systems in North America. In the Canadian prairies, more than 43 000 km of windbreaks have been planted since 1937, protecting 700 000 ha. These windbreak plantings were initiated in response to large-scale generation of dust storms in the Dust Bowl during the 1930s. New policies and practices were



Figure 10 Tree roots exposed by erosive removal of soil by wind.



Figure 11 Triple rows of poplar trees planted on four sides of a 25 ha field to reduce wind erosion in Inner Mongolia, China. Photo I. McIvor.



(a) (b)

Figure 9 (a) Effective control of hill country stream bank erosion can often be achieved by bank planting of willows. (b) Mature poplars providing stability and shade for a now stable stream. Photos G. Eyles.

developed to conserve soil and livelihoods, in which windbreaks were a key component. In 1987, approximately 858 000 windbreaks in the United States, mostly in the north central and Great Plains areas, spanned 281 000 km and protected 546 000 ha (Williams *et al.*, 1997). Agroforestry approaches to combating wind erosion and desertification have been reported for Egypt (El-Flah, 2009), the Sudan (Dafa-Alla and Al-Amin, 2011), and Pakistan (Akram *et al.*, 2006), with varying degrees of success.

National Policy and Erosion-Control Practices

Erosion-control practices are reported from most countries where soil erosion in agrosystems occurs. Many of these practices are reported at an experimental level. Uptake of new technologies continues to be a challenge, particularly where the present economic situation of the landowner is at risk. Policies applied at a national or regional level often require financial incentives for uptake of the technology or practice. For farmers, soil loss is not necessarily equated with economic loss, because it can be offset by application of fertilizers or a change of crop.

The benefits of being able to apply national and regional policies on soil conservation and reduction of erosion as developed in the People's Republic of China are described in the next section. China has many examples of programs operating on a large scale that are highly successful in reducing wind- and water-induced soil erosion.

Illustrative Case Studies – China

Slope Erosion on Pastoral and Arable Land

Erosion is a prominent ecoenvironmental problem in China. The total land area suffering from water and wind erosion is 2 949 000 km^2, accounting for 30% of the national territory area (Table 1). The total area of territories suffering from water erosion is 1 293 000 km^2 and the total area of territories suffering from wind erosion hits 1 656 000 km^2. The west region of China experiences the most serious erosion, accounting for 80% of the total erosion area.

Table 1 Summary statistics of total erosion areas due to water and wind erosion

Types of soil erosion	*Degree of erosion*	*Area (10 000 km^2)*
Water erosion	Slight erosion	66.76
	Moderate erosion	35.14
	High erosion	16.87
	Severe erosion	7.63
	Extreme erosion	2.92
	Total	129.32
Wind erosion	Slight erosion	71.6
	Moderate erosion	21.74
	High erosion	21.82
	Severe erosion	22.04
	Extreme erosion	28.39
	Total	165.59

In China, soil and water erosion takes place mainly in eight regions. These regions have different geographical features, so they suffer different types of erosion (Table 2).

The black soil region of Northeastern China is very important to the soybean industry. Indeed, 45% of the soybean production in China is from this region. Although the restoration history of this region is shorter than that of other areas, accelerated erosion is known to be widespread across the black soil area. This widespread erosion has occurred because much of the cropland is located on long rolling slopes. Specifically, the black soil layer of black soil in the region has been reduced from 70–100 to 16–70 cm, and the level of soil organic matter has been reduced from 6% to 15% to 2% in the period from the 1950s to the 1980s. The accelerated erosion in this region led to a remarkable reduction in the effective soil depth. The Loess Plateau and upper reaches of the Yangtze and other rivers in Southwestern China suffer serious soil and water loss from slope farmland.

The Chinese government has enacted several laws and regulations for water and soil conservation, such as the provisional outline of soil and water conservation (1952), the act of soil and water conservation (1982), and the law of water and soil conservation (1991, 2010). During this time, the related departments and local governments have also established some regulations for water and soil conservation.

In the long term, water and soil conservation practices in China benefit from collecting together local experiences. The most important practice is comprehensive management of small watersheds. By the end of 2011, the total area of territories benefitting from water and soil conservation measures reached 992 000 km^2, among which 200 000 km^2 benefited from structural measures (terracing and silt retention dams), 779 000 km^2 from biological measures (afforestation, shelterbelts, and planting of shrubs and grasses), and 13 000 km^2 from other measures (tillage practices, restricting land use, and relocating population). A total of 58 446 silt retention dams have been built, with a silted land area of 928 km^2. Among them, 5655 backbone silt retention dams, with a storage capacity from 500 000 to 5 million m^3, provide a total storage capacity of 5.7 billion m^3. The producing and living conditions of the residents living in the work zones have become better. Approximately 150 million people benefit from the works of water and soil conservation and approximately 20 million poor people become richer.

Use of Conservation Trees in Erosion Prevention

Since these reforms and the opening up of policy, the Chinese government has launched several key forestry programs (Table 3). Simultaneously, other policies and regulations were promulgated. These key forestry programs greatly ease the ecoenvironmental problems of water and soil erosion in China. Five of these programs (Sloping Land Conversion Program, Three North Shelterbelt Program, Beijing–Tianjin Sand Storm Source Control Project, Loess Plateau Comprehensive Control Project, and Rocky Desertification Comprehensive Treatment Project) are focused on reducing water and soil erosion. The remaining programs also contribute to water and soil conservation; however, their main targets are other aspects of forestry.

Table 2 The main regions of China suffering from water and soil erosion

Region	*Geographical scope*	*Geographical features*	*Situation of erosion*
Black soil region of Northeastern China	• Heilongjiang • Jilin • Liaoning • Inner Mongolia	• Rolling hill regions with black soil • Downslope tillage	• Top soil loss
Mountainous region of Northern China	• Beijing • Hebei • Shangdong • Liaoning • Shanxi • Henan • Anhui	• Shallow soil • Bare rock • Steep slopes	• Easy to form torrential flood
Loess plateau	• Shanxi • Shaanxi • Gansu • Inner Mongolia • Ningxia • Henan • Henan	• Soil layer deep and loose • Ravines and gullies crisscross	• Soil erosion amount reaches to approximately 5000 t km^{-2} $year^{-1}$
Agropastoral interlaced region of Northern China	• Inner Mongolia • Hebei • Shaanxi • Ningxia • Gansu	• Excess land reclamation • Overgrazed	• Wind erosion and water erosion
Upper reaches of the Yangtze and other rivers in the Southwestern China	• Sichuan • Yunnan • Guizhou • Hubei • Chongqing • Shaanxi • Gansu • Tibet	• Complicated geological structure • Frequent geological activity • High mountains and steep slopes • Downslope tillage	• Mud-rock flow and landslips.
Karst region in Southwestern China	• Guizhou • Yunnan • Guangxi	• Unproductive soil • Bare rock • Steep slopes	• Rock desertification
Red soil regions of Southern China	• Jiangxi • Hunan • Fujian • Guangdong • Guangxi • Hainan	• Low mountain and hilly area • Broken topography • Steep slopes	• Slope disintegration
Steppe region of Western China	• Inner Mongolia • Shaanxi • Gansu • Qinghai • Ningxia • Xinjiang	• Excess land reclamation • Overgrazed	• Degradation and desertification of grassland

In China, the following six key forestry programs covered 97% of the counties of the whole nation.

The Natural Forest Protection Program covers the headwaters of the Yangtze River (the Three Gorges region as the boundary, including the provinces of Sichuan, Guizhou, Chongqing, Hubei, and Tibet), the Upper and Middle Yellow River (Xiaolangdi Reservoir as the boundary, including the provinces of Shaanxi, Gansu, Qinghai, Ningxia, Inner Mongolia, Shanxi, and Henan), and the state-owned forest area in Northeast of China (including the provinces of Jilin, Heilongjiang, Inner Mongolia, Hainan, and Xinjiang). Since the inception of the program 2.7 million ha of plantations have been established, 3.2 million ha of forests have been established by aerial seeding, 12 million ha of newly enclosed

Table 3 Key afforestation programs in China addressing soil and water erosion

Project name	*Project profile*
Sloping Land Conversion Program	● Duration: 1999–2010 ● Geographical scope: 25 Provinces and Xinjiang production and construction corps ● Relevant laws and regulations: Recommendations for Further Improving Sloping Land Conversion Policy (2002), The Regulations on Sloping Land Conversion (2002) ● Primary target: Solving the problem of water and soil erosion in key regions ● Present situation: From 1999 to 2011, the completed construction area covers 289 000 km^2, among which 92 000 km^2 from returning farmland to forest, 170 000 km^2 from afforestation in barren hills, and 27 000 km^2 from closed forest. The forest coverage in the construction area has undergone a 3% increase
Three North Shelterbelt Program	● Duration: 1978–2050 ● Geographical scope: 13 Provinces ● Relevant laws and regulations: Recommendations for Further Improving the construction of the three north shelterbelt system (2009) ● Primary target: Effectively controlling the hazards of sand storms and water and soil erosion. Constructing a shelter–forest network for fields in the plains ● Present situation: By the end of 2012, the total area of afforestation covered 265 000 km^2. The forest coverage in construction area now reaches 12.4% of the land area
Beijing–Tianjin Sand Storm Source Control Project	● Duration: 2001–10 ● Geographical scope: 5 Provinces ● Relevant laws and regulations: Project Planning of Beijing–Tianjin Sand Storm Source Control (2002) ● Primary target: Effectively controlling the desertification of the land ● Present situation: The forest coverage in construction area increased from 12.4% in 2000 to 18.2% in 2009
Loess Plateau Comprehensive Control Project	● Duration: 2010–30 ● Geographical scope: 7 Provinces ● Relevant laws and regulations: Planning of Loess Plateau Comprehensive Management (2010) ● Primary target: Controlling the water and soil erosion and reducing the quantity of sediment flowing into the Yellow river ● Present situation: The area of afforestation covers 78 000 km^2. The forest coverage in construction area increased from 11% in 1977 to 19.6% in 2012
Rocky Desertification Comprehensive Treatment Project	● Duration: 2008–15 ● Geographical scope: 8 Provinces ● Relevant laws and regulations: Planning of Rocky Desertification Comprehensive Treatment 2006–15 (2008) ● Primary target: Controlling and preventing the spread of stony deserts and water and soil erosion. Conversion of the slope land ● Present situation: By the end of 2011, the area of afforestation reached to 8000 km^2. The area of stone desertification reduced by 9600 km^2 from 2005 to 2011
Natural Forest Protection Program	● Duration: 1998–2020 ● Geographical scope: 17 Provinces ● Relevant laws and regulations: Implementation Plan of Natural Forest Protection in Upper Reaches of Yangtze River and Upper and Middle Yellow River (2000), Implementation Plan of Nature Forest Protection in the Key State-Owned Forest Areas in the Northeastern China and Inner Mongolia (2000) ● Primary target: Prohibiting the cutting of natural forest in upper reaches of the Yangtze River and upper and middle Yellow River. Reducing the forest harvest in the key state-owned forest areas in the Northeastern China and inner Mongolia ● Present situation: The forest coverage in construction area has a 3.7% increase
Plain Farmland Shelterbelts Program	● Duration: 1988–2020 ● Geographical scope: 26 Provinces ● Relevant laws and regulations: Greening Standard of Plain Counties In Northern and Central China (1987), Greening Standard of Plain Counties in Southern China (1987), Planning of Reaching Nation Standard in Greening the Plain Counties (1988), Program Planning of Plain Farmland Shelterbelt 2006–10 (2006)

(*Continued*)

Table 3 Continued

Project name	*Project profile*
	● Primary target: Perfect the plain farmland shelterbelt system and forest ecosystem. Greening along the highways, railways, and waterways. Improving the quality of the forest in plain area. Insure stable grain production ● Present situation: By the end of 2010, the area of afforestation reached 71 000 km^2. The forest coverage in construction area increased from 7.3% in 1987 to 15.8% in 2010
Yangtze River Basin Shelter Forest System Project	● Duration: 1989–2020 ● Geographical scope: 17 Provinces ● Relevant laws and regulations: First-Stage Project Planning of Yangtze River Basin Shelter Forest System Construction (1986), Second-Stage Project Planning of Yangtze River Basin Shelter Forest System Construction 2001–2010 (2000) ● Primary target: Improving the deteriorative ecoenvironment in the Yangtze River Basin ● Present situation: From 2002 to 2011, the area of afforestation reached to 11 700 km^2. By the end of 2011, the forest coverage in construction area reached to 45.4%
Sanjiangyuan Ecological Protection and Construction Project in Qinghai Province	● Duration: 2004–20 ● Geographical scope: Qinghai Province ● Relevant laws and regulations: Overall Planning of Ecological Protection and Construction in Sanjiangyuan (2005), Overall Development Scheme of Sanjiangyuan National Comprehensive Experimental Area of Ecological Protection in Qinghai Province (2011) ● Primary target: Improving the construction of ecological protection and infrastructure ● Present situation: The vegetation coverage had a 3.08% increase in construction area

nonforested land and open forest land has been set aside for natural regeneration, 101 million ha of forest has been taken into management and protection, and 621 500 foresters have been resettled in other locations.

The Shelterbelt Forest System Project covers the Northwest, Northeast, and the North of China; the middle and lower reaches of the Yangtze River; the coastal area; the Pearl River Basin; the Huai River Basin; Taihang Mountain area; and the plain area. By establishing farmland shelterbelt forest and planting trees on barren land, by the end of 2008, 24.5 million ha of forest had been conserved by the program and the forest coverage in the three northern regions had increased from 5.1% in 1978 to 10.5% in 2008. The program has overseen the improvement of 270 000 km^2 of sandy lands and the stabilization of 380 000 km^2 of water and soil erosion areas. Since 2000, the river basin programs within this project have collectively established 4.3 million ha of plantation.

The Sloping Land Conversion Program involves 25 provinces (Beijing, Tianjin, Hebei, Shanxi, Inner Mongolia, Liaoning, Jilin, Heilongjiang, Anhui, Jiangxi, Heinan, Hubei, Hunan, Guangxi, Hainan, Hongqing, Sichuan, Guizhou, Yunnan, Xizang, Shanxi, Gansu, Qinghai, Ningxia, and Xinjiang) and Xinjiang Production and Construction Corps. According to the principle of highlighting the key points, the upper reaches of the Yangtze River, the upper and middle reaches of the Yellow River, Beijing–Tianjin sand source district, critical lake watersheds, the Hongshui River Basin, the Hei River Basin, and the Tarim River Basin are the focal points of the program. This program began in 2000 after massive flooding was caused in part by land clearing and focuses on China's largest source of soil erosion and flood risk – arable farms on steep slopes. The program is a land retirement program that aims to reduce soil erosion by returning cropland on steep slopes back to forest or grassland. Farmers are recompensed for giving up farming this land. Between 2000 and 2009, 4.8% of the cropland had been converted into forest land in Guyuan, according to regional experts. In Ansai County, the implementation of the grain for green program increased the newly forested land substantially to 21.4% of the study area by 2010 at the cost of both cropland and shrub–grassland, which decreased by 46.3% and 18.8%, respectively, from 1995 to 2010. Consequently, the coverage of forested land (both older forest and newly forested land) increased from 12.4% in 1995 to 37.7% in 2010.

The Beijing–Tianjin Sand Storm Sources Control Project ranges from Damao Banner in Inner Mongolia in the west, Ar Horqin Banner in Inner Mongolia in the east, Dai County in Shanxi Province in the south, and East Ujimqin Banner in Inner Mongolia in the north, including Beijing, Tianjin, Hebei, Shanxi, and Inner Mongolia. This program was launched in 2001 and by the end of 2009, 8.2 million ha of desertified land had been treated through various means, including 5.3 million ha of afforestation, 2.0 million ha of grass establishment, and 784 000 ha of small water basin treatment at a cost of US$3.5 billion.

The Wildlife Protection and Nature Reserve Development Program involves eight regions, which are mountain and plains area in Northeast China, desert region in Mengxin Plateau, plain and Loess Plateau in North China, high-cold region in Qinghai–Tibet plateau, alpine and gorge region in Southwest China, hilly area in south central China, hilly and plain area in East China, and hilly area in South China. In 2010 there were 2349 nature reserves of various types in China, accounting for 15.2% of total land area, among which 1706 were managed by the forestry sector. The nature reserves established by the forestry sectors alone have put 90% of terrestrial ecosystem, 45% of natural wetland, 85% of wild animal populations, 65% of higher plant communities, and 20% of natural high-quality forest under effective protection.

Table 4 Tree species used in three of the soil erosion-control programs in China

Program	*Environmental situation*	*Species used*	*Region*
Plain Farmland Shelterbelts Program	Wind erosion	*Populus tremula*	Northeast China, East China, Yangtze River Basin, and Northwest China
	Strong Siberian wind	*Ulmus rubra*, *Larix gmelinii*, and *Picea asperata*	Bashang and Hebei
	Wind and sand fixation	*Salix matsudana* Koidz and *Artemisia desertorum*	Mu Us Sandland
Sloping Land Conversion Program	Wind erosion	*Robinia pseudoacacia*, *Platycladus orientalis*, *Pinus tabulaeformis*, *Pinus armandii*, *P. asperata*, *Populus davidiana*, and *Ulmus pumila*	Loess plateau
	Water and soil conservation	*R. pseudoacacia*, *Photinia serrulata*, *Phyllostachys pubescens*, *Pinus massoniana*, *Pinus elliottii*, *Dalbergia hupeana*, *Liquidambar formosana* Hance, *Corylus chinensis*, and *Phoebe bournei*	Hunan
Rocky Desertification Comprehensive Treatment Project	Soil conservation	*Pyrus pyrifolia* and *Hylocereus undatus*	Fuyuan, Xingren, and Guangxi

Plantation programs for the forestry industry, mainly composed of fast-growing and high-yield plantations, cover 18 provinces (Hebei, Inner Mongolia, Liaoning, Jilin, Heilongjiang, Jiangsu, Zhejiang, Anhui, Fujian, Jiangxi, Shandong, Henan, Hunan, Hubei, Guangdong, Guangxi, and Yunnan). The planned area of establishment was 4.7 million ha by 2005, 9.2 million ha by 2010, and 13.3 million ha by 2015; funded by a public–private partnership. Progress to date is uncertain.

In China, the general principles governing the choice of tree species include the following: matching species with site, giving priority to indigenous tree species, and unifying the economic benefit and ecological benefit. Based on different program objectives and different geographical locations, different tree species are being used. Examples of the range of species selected, together with the ways in which they are used in different programs, are given in Table 4.

The Tree North Shelterbelt Program has attracted international attention as the largest and most distinctive artificial ecological engineering project in China (Li *et al.*, 2012). Shelterbelt types used in the Tree North Shelterbelt Program include pure forest belts, roadside tree belts, mixed tree–shrub belts, mixed deciduous tree–shrub belts, mixed deciduous conifer tree belts, among others (Xu *et al.*, 1998). Efforts since 1977 have brought multiple benefits to local people by providing firewood and livestock fodder. The environment has benefitted especially in the form of farmland protection, soil and water conservation, wind reduction, and sand dune fixation (Li *et al.*, 2012). Li *et al.* (2012) warned that improvement of water use efficiency is important in these arid and semiarid regions, so careful choice of ecotype/clone within tree species is critical when establishing shelterbelts.

In the Plain Farmland Shelterbelts Program, *Populus tremula* is the main tree used. In Fujian province, *Phoebe bournei* cultivated as a monoclonal forest is a priority choice. It, however, requires better lands (lower slopes rather than upper slopes). Initial planting densities of 1500–1800 saplings per hm^2 are later thinned to final densities of 600–900 saplings.

To reduce the area of monoclonal forest in China, the planting of mixed species forest is recommended. Some examples are given below. In Fujian province, for cultivating the excellent timber tree *Manglietia yunnanensis*, 1800 saplings per hm^2 are planted at first, followed by later planting of mixes in the proportion 3–4:1. Mixes of *Cunninghamia lanceolata* and *M. yuyuanensis* are suitable in Fujian. In South China, *C. lanceolata* and *Pinus massoniana* are common mixed forest tree species. The former one mixed with *P. massoniana*,, *Cryptomeria fortunei*, *Cinnamomum camphora*, and *Schima superba* results in excellent timber yields. In North China, *Pinus koraiensis* mixed with *Fraxinus mandshurica* and *Lespedeza bicolor* Turcz,, and *Pinus tabuliformis* mixed with *Platycladus orientalis*, Oak, *Robinia pseudoacacia*, and *Amorpha fruitcosa* are recommended.

In stage II of the Greening Taihang Mountain Program in the middle of China, mixed forests are planted, in which *Acer truncatum* Bunge, Chinese honey locust, *Rhus typhina*, etc. are dominant tree species. The mixed forests account for 19.3% of the forest land in construction areas. In Beijing, Hebei, Shanxi, and Henan the proportion are 24.8%, 28.0%, 14.2%, and 10.1%, respectively.

Techniques and Species employed in the Establishment of Shelterbelt Trees in the programs

In Inner Mongolia, most of the shelterbelts are planted so as to form 400 × 400 m meshes (Figure 11), with each of the belts comprising three parallel lines of trees planted at 3 × 2 m intervals. This results in a porous structure that provides

maximum effective protection with reduced wind damage and debris buildup at the edges of the belt. The species used for the shelterbelts are fast-growing, medium-sized crown varieties that give good resistance in the prevailing soil and weather conditions. *Populus canadensis* Moench, *Populus euroamericana*, *Populus beijingensis*, and *Populus xianohei* are among the most widely used species, whereas a single row of *Amorpha fruticosa* is often planted on each side of the tree belt to provide understory protection.

Traditional planting approach for poplars was of 1-year-old rooted cuttings planted into pits within a 0.4 m trench. This technique was effective but costly. A newer technique planting unrooted 80–240 cm cuttings into a 70–220 cm slit or augured hole in the soil (depending on the depth to the water table) made by a mechanical device, either in spring (and buried over winter) or in autumn, provides good survival and subsequent growth. It is replacing the traditional technique. The conifer selection program has favored local provenances of *Pinus sylvestris* var. *mongolica* planted into raised beds *in situ* followed by taproot pruning. Selection programs continue to improve poplar and pine selection options particularly with improved survival and water use efficiency.

Effectiveness of Conservation Trees in Erosion Prevention

The implementation of the key forestry programs to some extent works to solve the water and soil erosion problem in China. The following section shows the effectiveness of Chinese key forestry programs in erosion prevention.

The area of water and soil erosion reduces year by year. After the implementation of the Natural Forest Protection Program, the area of erosion decreased 20% in Chongqing. In Hunan province, the erosion area reduced from 6000 km^2, before the implementation of the Yangtze River Basin Shelter Forest System Project, to 4700 km^2. Under the effectiveness of the Tree North Shelterbelt Program and Loess Plateau Comprehensive Control Program, approximately 230 000 km^2 of the erosion area is governed, which accounts for 50% of the total erosion area in Loess Plateau. By the end of 2010, Sanjiangyuan Ecological Protection and Construction Project in Qinghai Province brought approximately 750 000 km^2 erosion area under control.

The quantity of sediment flowing into the Yellow River and the Yangtze River reduces year by year. After the implementation of the Natural Forest Protection Program in 1998, the sediment concentration of the Yangtze River detected in Yichang in 2008 was 10% less than that in 1998 and the rate is reducing at approximately 1% per year. The sediment concentration of the Yellow River detected in Huyankou hydrometric station in Henan province reduced by 38% from 2000 to 2007. After the implementation of the Yangtze River Basin Shelter Forest System Project, the sediment concentration of Mianjiang, the trunk river of Ruijin in Jiangxi province, reduced from 0.32 kg m^{-3} 10 years ago to 0.27 kg m^{-3} now, in the rainy season.

The desertification of land has been under preliminary control. In eight provinces (Shanxi, Gansu, Ningxia, Inner Mongolia, Qinghai, Shaanxi, Hebei, and Heilongjiang), which are under the management of Tree North shelterbelt program, the area of desertification was reduced by 7300 km^2 from 2000 to 2007. The trend of desertification in three sand lands (Mu Us, Khorchin, and Hulun Buir) has been slowed, and initiatives are now focused on rebuilding and utilizing the desert. After the implementation of the Beijing–Tianjin Sand Storm Source Control Project, the density of PM10 (atmospheric particle matter with diameter of 10 μm or less) in Beijing reduced from 0.16 mg m^{-3} in 2000 to 0.11 mg m^{-3} in 2010. The number of the days when the ambient air quality attained Grade II (the national ambient air quality standard for urban residential, commerce–traffic mixed, common industrial, and rural areas in China) increased from 177 in 2000 to 285 in 2009.

The stony desertification of land has been under preliminary control. From 2005 to 2011, under the implementation of Rocky Desertification Comprehensive Treatment Project, there was approximately 19 800 km^2 rocky desertification land attaining effective governance. In Guizhou province, there were 14 400 km^2 karst area and 4800 km^2 rocky desertification area attaining effective governance from 2008 to 2012. A shift from arable farming to fruit farming has enabled farmers to stay on their land and farm economically while reducing soil erosion. As an example, in the Longhe Eco-Demonstration Area, through technical training for demonstration households, large areas of Pitaya (dragon fruit) plantations have been established. The Pitaya orchards, combining water-saving irrigation technology and interplanting grass technology, model a more sustainable way of farming that integrates new ways of land management with local culture. The introduction of 'ecological orchards' of fruit trees, such as Pitaya, has changed the land use from arable farming to agroforestry, has brought more economic stability to farmers, and improved the local ecological environment.

Other Benefits of Conservation Trees in the Landscape

Natural forest provides effective erosion protection and the forest resource base has increased gradually. Under the implementation of the Natural Forest Protection program, the timber production has reduced approximately 220 million m^3 and from this the reduction in forest resource consumption has reduced by approximately 380 million m^3. The stand volume has increased by approximately 725 million m^3. Given the percentage of cut-turn of 63%, this increased forest resource could convert into approximately US$58 billion, which is approximately 3 times the program investment.

The habitat of animals and plants has improved and the biological diversity is increasing. During the construction period of Sanjiangyuan Ecological Protection and Construction Project in Qinghai Province (2004–2010), there were population increases for the large mammals: Tibetan wild ass, Tibetan antelope, wild yak, and Bharal (blue sheep). For example, the total number of Tibetan antelope in Qinghai Province increased to 60 000 in 2010 from 30 000 in 1980.

As a consequence of the Ecological Protection and Construction Project, there have been changes in the industrial structure. According to data from state forest administration,

People's Republic of China, of 44 counties in the construction area of Natural forest protection program, the relationship between the primary, secondary, and tertiary industries changed from 86:3:11 in 2003 to 62:18:20 in 2009. The degree of dependency on timber production reduced from 90% at the beginning of the program to 52% at the end of 2010. Simultaneously, the forestry industry has diversified its activities and increased production value at a rate of 20% per year. The five provinces involved in the project had an increase in gross domestic product from US$16 billion in 1999 to US$97 billion in 2010.

Soil conservation programs have improved grain security. The implementation of Three North Shelterbelt Program effectively converted 'crop failure' to 'grain harvest.' In Northeastern China, Northern China, and the bend of the Yellow river approximately 225 000 km^2 of farmland is sheltered by forest. Under the implementation of the Plain Farmland Shelterbelts Program, 930 000 km^2 of the farmland in Henan province is protected by shelterbelts. In 2006 and 2007, production of grain in Henan province passed the billion kilogram mark. In Qihe country, Shangdong province, the grain output increased from 481 million kg in 2003 to 862 million kg in 2006.

Summary

Soil is one of the most precious resources. The loss of soil, particularly through the land degradation processes of wind and water erosion, is one of the most serious environmental problems the world is faced with, as it is reducing the means of producing food. Approximately 80% of the world's agricultural land was reported, almost 20 years ago, to suffer moderate to severe soil erosion and 10% to suffer slight to moderate erosion (Pimentel *et al.*, 1995). It is possible to alter the impact of these forms of erosion through the development and implementation of national policies and effective technologies, coupled with changes in land use and alternative economic opportunities for affected local communities. Without economic protection, soil degradation is most likely to continue in some other locality. Restorative technologies incorporating trees in the agricultural landscape have been developed in New Zealand and China and other countries to reduce soil loss. Where these technologies are being applied, they are proving to be effective in reducing erosion to low levels, thereby retaining both soil quantity and quality for the future.

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Agroforestry: Fertilizer Trees

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Glossary

Coppicing Cutting trees close to the ground level to produce regrowth from the remaining stump.
Deep capture The extraction of nutrients by tree roots from soil depths beyond the reach of crop roots.
Pollarding Cutting back the crown of a tree but leaving the main trunk with the objective of harvesting wood and browse, producing regrowth beyond the reach of animals, or reducing the shade cast by the crown.
Protein (fodder) bank Stands of trees or shrubs established within a farm or pasture area to serve as a supplementary source of protein-rich fodder for livestock.
Silvopastoral Land use system in which trees are integral part of pasture land.

Introduction

Much of the world's agricultural land is degrading rapidly, and losing its productivity due to soil erosion and nutrient mining associated with continuous cropping without nutrient inputs and soil conservation. An estimated 24% of the world's land area has been degrading over the past 25 years, directly affecting the livelihoods of 1.5 billion people (Bai *et al.*, 2008). Approximately 19% of the degraded land is cropland (Bai *et al.*, 2008). According to the Global Assessment of Human-induced Soil Degradation, soil erosion affects 83% of the global degraded area (Bai *et al.*, 2008). Soil degradation by erosion alone affects 1966 million hectares worldwide (Lal, 2007). In Africa, the annual average nutrient (NPK) loss is estimated at 9–58 kg ha^{-1} $year^{-1}$ in 28 countries and 61–88 kg ha^{-1} $year^{-1}$ in the remaining 21 (Chianu *et al.*, 2012). Recent global analyses show that N limitation is particularly widespread in all ecosystems (LeBauer and Treseder, 2008; Liu *et al.*, 2010). The global average N recovery rate is 59%, indicating that nearly 41% of N inputs are lost in ecosystems (Liu *et al.*, 2010). Almost 80% of African countries experience N deficit or N stress problems, which, along with poverty, cause food insecurity and malnutrition (Liu *et al.*, 2010). In total, 29% of the global cropland area experiences P deficits (MacDonald *et al.*, 2011).

Conventionally in modern agriculture, increased productivity has been achieved mainly through application of synthetic inorganic fertilizers. However, the increasing price of synthetic fertilizers and the inability of poor farmers to gain access to them pose severe constraints on their widespread use. Although organic matter may be an alternative source of nutrients, neither animal manure nor green biomass is usually found in adequate quantities to meet the high application rates (10–40 Mg ha^{-1} $year^{-1}$) required to meet the nutrient requirements of crops (Mafongoya *et al.*, 2006). Some authors have therefore argued that improving fertilizer use efficiency by a combination of organic and inorganic nutrients is vital to the long-term sustainability of global agriculture. Within this important goal there is great potential for the more effective utilization of biological N-fixation (BNF), which is virtually without cost. BNF accounts for 60% of N production (Zahran, 1999) and 16% of the current global N input (Liu *et al.*, 2010). However, in Africa and South America, BNF is the single largest N source, accounting for 32–34% of the N input (Liu *et al.*, 2010). In this respect its further use would, at the least, ease the pressure for land through the rehabilitation of degraded areas (Herridge *et al.*, 2008). However, BNF can also play a greater role in sustainable agriculture as it increases N recovery rates in addition to reducing the need for synthetic fertilizers. In this article, the authors present a review of options for more efficiently harnessing BNF for improved food security within the important debate about the future of global agriculture. They specifically explore the potential role that N-fixing trees can play in land rehabilitation for food crops and pastures and the improved productivity of saline and impoverished soils. In this context it is interesting that with the advent of high-yielding crop varieties requiring full sunlight, the tendency has been to remove trees including N-fixers from many food and cash cropping systems.

Fertilizer Trees: Definition

The term 'fertilizer trees' is commonly used to refer to the utilization of N-fixing leguminous trees in cereal production systems to improve the availability of N to crops (Ajayi *et al.*, 2011; Akinnifesi *et al.*, 2010; Mafongoya *et al.*, 2006), but this usage has generally excluded the use of such trees in pastures

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Table 1 Cereal yield response to fertilizer trees summarized from studies across sub-Saharan Africa

Cereal crop	*Species*	*Number of studies (N)*	*Mean yield (Mg ha^{-1} ± SE)*	*Yield increase (Mg ha^{-1} ± SE)*	*Increase[f] (% ± SE)*
Maize	Pigeon pea[a,b]	24 (69)	2.1 ± 0.2	0.7 ± 0.1	89.8 ± 13.2
	Tephrosia[a,b]	28 (177)	2.1 ± 0.1	0.9 ± 0.1	206.3 ± 42.6
	Leucaena[b,c]	6 (78)	2.5 ± 0.2	1.0 ± 0.1	94.5 ± 12.2
	Sesbania[a,b]	42 (262)	3.0 ± 0.1	1.7 ± 0.1	318.1 ± 82.5
	Gliricidia[d]	15 (127)	3.2 ± 0.1	2.2 ± 0.1	295.9 ± 27.8
	Faidherbia[e]	12 (88)	4.5 ± 0.2	2.5 ± 0.2	184.6 ± 33.9
	Synthetic fertilizer	72 (384)	3.8 ± 0.1	2.2 ± 0.1	383.8 ± 40.5
Sorghum	Gliricidia[d]	4 (10)	1.5 ± 0.1	−0.1 ± 0.1	93.8 ± 5.3
	Faidherbia[e]	5 (14)	1.0 ± 0.2	0.3 ± 0.1	144.4 ± 22.8
	Sesbania[a,b]	2 (24)	1.8 ± 0.1	0.6 ± 0.1	180.44 ± 19.1
Millet	Vachellia[e]	3 (11)	0.7 ± 0.1	−0.04 ± 0.1	107.8 ± 14.4
	Faidherbia[e]	5 (13)	1.2 ± 0.1	0.4 ± 0.1	149.3 ± 14.4

[a]Relay cropping.
[b]Improved fallow.
[c]Alley cropping.
[d]Intercropping.
[e]Parkland.
[f]Increase over the no-input control.
Abbreviation: N = number of data points representing either sites or years within a study.
Note: The yield increase is the difference between the treatment and the control (no input) on the same site. The percent increase is increase in yield over the control in percentage terms, and this was calculated as 100*(yield increase)/control yield.

and for the rehabilitation of degraded land. The so-called 'N-fixing tree' is a tripartite symbiotic system involving an association between the plant, N-fixing bacteria, and mycorrhizae-forming fungi (Nygren *et al.*, 2012). Atmospheric N-fixation by symbiotic, single-celled bacteria (*Rhizobium*) in root nodules is common in 340 species of the family Leguminosae. N-fixation also occurs in over 200 nonleguminous plants species in 25 genera of 8 families associated with *Frankia* (Actinomycetes), which are filamentous bacteria (Franche *et al.*, 2009; Russo, 2005). The broader definition of 'fertilizer' trees used here includes the legume–*Rhizobium* as well as nonlegume–*Frankia* symbioses.

There are a large number of agroforestry practices that capitalize on BNF from fertilizer trees for the supply of N and organic matter to annual and perennial crops. These include alley cropping, improved fallows, cereal-tree legume intercropping, relay cropping, biomass transfer, fodder banks, multistrata agroforestry, parklands, and silvopastoral systems. Among the widely used fertilizer trees are acacia (*Acacia* spp.), acaciella (*Acaciella* spp.), albizia (*Albizia* spp.), alder (*Alnus* spp.), calliandra (*Calliandra calothyrsus*), casuarina (*Casuarina equisetifolia*), erythrina (*Erythrina* spp.), faidherbia (*Faidherbia albida*), flemingia (*Flemingia* spp.), gliricidia (*Gliricidia sepium*), inga (*Inga edulis*), leucaena (*Leucaena* spp.), sesbania (*Sesbania* spp.), parkia (*Parkia biglobosa*), tagasaste (*Chamaecytisus palmensis*), tephrosia (*Tephrosia* spp.), tamarind (*Tamarindus indica*), and vachellia (*Vachellia* spp.). Hereafter reference will be limited to these common names.

Benefits of Fertilizer Trees

Increased Crop Productivity

Several studies have reported the beneficial effects of fertilizer trees on yields of food crops. According to a meta-analysis of 94 peer-reviewed publications across sub-Saharan Africa (Sileshi *et al.*, 2008a), maize yields increased by 0.7–2.5 Mg ha^{-1} over the no-input control, which translates to an 89–318% increase (**Table 1**). Under similar conditions, the recommended rate of synthetic fertilizer led to 384% increases over the control (**Table 1**). Robust estimates indicate that the 95% confidence intervals of maize yield increased by faidherbia (2.0–2.7 Mg ha^{-1}), gliricidia (1.8–2.4 Mg ha^{-1}), and synthetic fertilizer (1.9–2.3 Mg ha^{-1}) overlap completely. Recent analyses (Sileshi *et al.*, 2011, 2012) also showed that maize yields are more stable in maize intercropped with leucaena and gliricidia than in fully fertilized sole maize at sites in Malawi, Zambia, and Nigeria. In terms of increased crop yields, synergistic effects of synthetic fertilizer and fertilizer trees were noted. Yield increases from fertilizer trees were substantial even when associated with 25–50% of the recommended dosages of synthetic fertilizer (Sileshi *et al.*, 2011, 2012).

Although fewer data are available for millet and sorghum (mostly short term in nature), increases in yields relative to the control have been substantial with fertilizer trees (**Table 1**). An important gain that is usually under-reported is the stover yield. Stover is a critical fodder in cereal-livestock mixed farming systems in Africa. Using empirical distributions of stover to grain fresh weight ratios of 0.8:1.0 the authors estimate that an additional 0.2–2.0 Mg ha^{-1} year^{-1} of stover can be produced by the use of fertilizer trees (**Table 1**), an important contribution to livestock feed when grass is in short supply. These yield increases are also associated with large variability attributable to tree species, site conditions (soils, rainfall, elevation), and management factors (Bayala *et al.*, 2012; Sileshi *et al.*, 2008a, 2010). Although in the short term crop yields may be reduced due to tree competition, in the long term favorable soil conditions are expected to improve crop productivity.

Through biomass transfer, fertilizer trees can also be used to increase vegetable productivity. Biomass transfer is

Table 2 Vegetable yield[a] response to biomass transfer using fertilizer tree prunings from sub-Saharan Africa

Crop	*Tree species (biomass)*	*Country*	*Mean yield (Mg ha^{-1})*	*Yield increase[b] (Mg ha^{-1})*	*(%)*	*References*
Cabbage[c]	Gliricidia (8 ton ha^{-1})	Zambia	43.1	26.1	154	Kuntashula *et al.* (2004)
	Gliricidia (12 ton ha^{-1})		53.6	36.6	215	Kuntashula *et al.* (2004)
	Leucaena (12 ton ha^{-1})		32.6	15.6	92	Kuntashula *et al.* (2004)
	Fertilizer (800 kg ha^{-1} NPK)		57.6	40.6	239	Kuntashula *et al.* (2004)
Onion[d]	Gliricidia (8 ton ha^{-1})		68.3	40.2	143	Kuntashula *et al.* (2004)
	Gliricidia (12 ton ha^{-1})		79.8	51.7	184	Kuntashula *et al.* (2004)
	Fertilizer (800 kg ha^{-1} NPK)		57.1	29	103	Kuntashula *et al.* (2004)
Cabbage	Gliricidia (8 ton ha^{-1})		51.1	28.4	125	Kuntashula *et al.* (2006)
	Fertilizer (800 kg ha^{-1} NPK)		55.0	32.3	142	Kuntashula *et al.* (2006)
Onion	Gliricidia (8 ton ha^{-1})		49.7	26.7	116	Kuntashula *et al.* (2006)
	Fertilizer (800 kg ha^{-1} NPK)		40.8	17.8	78	Kuntashula *et al.* (2006)
Cabbage	Gliricidia (8 ton ha^{-1})	Zambia	59.7	27.9	88	Kuntashula *et al.* (2006)
	Synthetic fertilizer		80.8	48.9	153	Kuntashula *et al.* (2006)
Rape	Leucaena	South Africa	7.6	6.7	784	Muchecheti *et al.* (2012)
	Vachellia		5.0	4.1	481	Muchecheti *et al.* (2012)
	Calliandra		3.0	2.1	249	Muchecheti *et al.* (2012)
	Fertilizer (150 kg N ha^{-1})		10.0	9.1	106	Muchecheti *et al.* (2012)
Paprika	Gliricidia (8 ton ha^{-1})	Malawi	0.32	0.10	43.1	Sileshi *et al.* (2011)
	Gliricidia+50% Synth fertilizer		0.41	0.19	84.2	Sileshi *et al.* (2011)
	Synthetic fertilizer (100% recom.)		0.24	0.02	9.4	Sileshi *et al.* (2011)

[a]This represents fresh weight in the case of cabbage, rape, and onion, whereas dry weight in the case of paprika.
[b]Increase over the no-input control.
[c]Average of 31 farmers' fields.
[d]Average of 12 farmers' fields.
Note: The yield increase is the difference between the treatment and the control (no input) on the same site. The percent increase is increase in yield over the control in percentage terms, and this was calculated as 100*(yield increase)/control yield.

essentially moving tree biomass (prunings) produced in one part of the farm (e.g., in protein banks, fallows, etc.) to another (e.g., a vegetable garden). Usually 4–12 Mg ha^{-1} of the leafy biomass (on dry matter basis) is applied to crops, and this has been shown to increase yields of cabbage, rape, onion, tomato, and garlic in trials on research stations as well as farmers' fields in Africa (Table 2).

Increases in productivity have been demonstrated in cash crops associated with fertilizer trees. For example, shade trees reduce the stress on crops such as coffee and cacao by ameliorating adverse climatic conditions and nutritional imbalances, thus increasing overall system productivity in multistrata agroforestry (Beer *et al.*, 1998). In Western Ghana, Isaac *et al.* (2007) found higher above ground cocoa biomass (39.6 Mg ha^{-1}) under albizia canopies compared to 22.8 Mg ha^{-1} for sole cocoa. Above-ground dry matter of cocoa also declined along a spatial gradient away from albizia trees (Isaac *et al.*, 2007). In India, the agronomic yield of large cardamom doubled under 5–15-year-old alder stands and peaked between 15 and 20 years of age (Russo, 2005).

Soil Rehabilitation Services

To understand how the above yield benefits are achieved one needs to examine how adding fertilizer trees into the agricultural landscape restores soil fertility and promotes the biological processes and ecological functions that together rehabilitate degraded land. These are the critical processes that benefit the farmer in particular and society in general. Among these important services are nutrient cycling, increased availability of macronutrients (extractable N, P, and K), cations and improvement in soil pH, increased organic matter (SOM), enhanced biological activity, improved soil physical properties, and better water relations.

Improvement in soil nutrient cycling

Fertilizer trees have potential to provide N in quantities sufficient to support moderate crop yields through (1) N inputs from biological N_2 fixation and retrieval of nitrate from deep soil layers and (2) cycling of N from plant residues and manures (Buresh and Tian, 1998). However, fertilizer trees cannot produce new resources of other nutrients, although they can increase their availability and uptake by crop plants through different mechanisms. The cycling of P from organic materials is also normally insufficient to meet the P requirements of crops (Buresh and Tian, 1998). As they access deep water reserves beyond reach of annual crops, tree roots act as a safety net to capture nutrients leached from the topsoil and return these to the soil surface as litter. The presence of trees improves nutrient use efficiency by providing a safety net to recover nutrients leached from the topsoil during intense rainfall and return them to the surface horizons on which crop roots primarily depend, in a manner analogous to the hydraulic lift of water.

N availability and uptake

The percentage of N derived from the atmosphere (NDFA) is more than 59% according to a recent analysis of 38 cases using N isotopic analyses (Nygren *et al.*, 2012). Under humid and sub-humid conditions, on average NDFA was 69% in

young trees and 63% in periodically pruned trees compared to 54% in free-growing (nonpruned) trees (Nygren *et al.*, 2012). The average N-fixation for 16 variable fertilizer tree species was found to be 246 kg N ha^{-1} $year^{-1}$, but much higher (300–650 kg N ha^{-1} $year^{-1}$) in improved fallows and protein banks where trees are managed by pruning or coppicing (Nygren *et al.*, 2012). These values are much higher than the global estimates (23–176 kg N ha^{-1} $year^{-1}$) for food legumes and herbaceous pasture and fodder legumes (Herridge *et al.*, 2008). Among the nonlegume–*Frankia* associations, N-fixation has been estimated at 40–320 kg N ha^{-1} $year^{-1}$ for alder (Russo, 2005) and casuarina 73 kg N ha^{-1} $year^{-1}$ (Nygren *et al.*, 2012). Although the annual N inputs vary widely between species and even among provenances of the same species across different locations and stand age, the amounts reported are enough to fulfill crop N needs for sustained yield (Nygren *et al.*, 2012).

In Latin American coffee and cacao agroforestry, pruning residues and litter fall from shade trees have been shown to contribute 60–340 kg N ha^{-1} $year^{-1}$ (Beer *et al.*, 1998). In coffee plantations in Costa Rica, erythrina contributed over 300 kg N ha^{-1} $year^{-1}$ (Kass *et al.*, 1997). Various studies across the globe have documented significant increases in N stocks under fertilizer trees compared to crop monocultures (**Table 3**). According to a study on cacao agroforestry in Ghana the ammonium sulphate fertilizer equivalence of albizia leaves is 21–72 kg N ha^{-1}; thus, the leaves could substitute 29–63% of fertilizer when applied to soil at 2.5 Mg ha^{-1} (Anim-Kwapong, 2006). In a silvopastoral system with king grass in Costa Rica, erythrina contributed 266 kg N ha^{-1} $year^{-1}$ (Kass *et al.*, 1997). Direct below-ground transfer of N fixed by legume trees to associated non-N-fixing crops and forage grass has been widely documented (Nygren *et al.*, 2012; Sierra and Nygren, 2006). This can take place via root exudates or common mycorrhizal networks (Nygren *et al.*, 2012). In coffee agroforestry approximately 30% of the N effectively fixed by leucaena, calliandra, and erythrina was transferred to the associated coffee trees (Snoeck *et al.*, 2000). In Sri Lanka, up to 21% of N in grass was derived from transfer of N fixed by gliricidia and leucaena (Jayasundara *et al.*, 1997).

A review of studies in parklands across Africa shows that N availability is higher under faidherbia than in the open field (**Table 3**). N availability can also be increased significantly under improved fallows and alley cropping of fertilizer trees compared to control plots without trees (**Table 3**). In gliricidia-maize-pigeon pea intercropping in southern Malawi 191–302 kg N ha^{-1} could be realized from gliricidia prunings (Akinnifesi *et al.*, 2010).

Although N inputs from fertilizer trees may be high, the N recovery by crops is usually 10–30% of the N applied as prunings per season, depending on the quality of residues. Much of the N from organic inputs (50–80%) is not used by the crop. Low N recovery is partly caused by a lack of synchrony between the N release and demand by the associated crop. Nevertheless, N use efficiency by cereals is higher from fertilizer trees than from synthetic fertilizer. For example, in alley cropping in Nigeria, N use efficiency of synthetic fertilizer was 10–22% compared to 49% in gliricidia and 59% in albizia

Table 3 Increase (%) in N and P stocks due to fertilizer and nutrient uptake by crop relative to crop monoculture or areas outside tree influence

	Agroforestry (crop)	*Tree species*	*Increase (%)*	*Country*	*Reference*
N stocks	Cacao	Albizia	5–10	Ghana	Isaac *et al.* (2007)
	Parkland	Faidherbia	15–156	Sahel	Boffa (1999)
			200	Niger	Kho *et al.* (2001)
			50–90	Sudan	Rhoades (1995)
			100–150	Ethiopia	Kamara and Haque (1992)
			5–29	Malawi	Rhoades (1995)
		Tephrosia	20	Viet Nam	Fagerström *et al.* (2002)
N uptake	Parkland (millet)	Faidherbia	139.2	Niger	Kho *et al.* (2001)
	Alley cropping (maize)	Albizia	126.6	Nigeria	Okogun *et al.* (2000)
		Gliricidia	159.6	Nigeria	Okogun *et al.* (2000)
		Leucaena	170.4	Nigeria	Okogun *et al.* (2000)
		Leucaena	50–114	Nigeria	Akinnifesi *et al.* (1997)
	Alley cropping (sorghum)	Albizia	100–300	USA	Rhoades *et al.* (1997)
	Intercropping (maize)	Gliricidia	156	Malawi	Mweta *et al.* (2007)
	Improved fallow (maize)	Sesbania	299	Zambia	Mafongoya (unpublished)
		Tephrosia	76	Zambia	Mafongoya (unpublished)
		Gliricidia	160	Zambia	Mafongoya (unpublished)
		Leucaena	99	Zambia	Mafongoya (unpublished)
P stocks	Cacao	Albizia	2.3–4.5	Ghana	Isaac *et al.* (2007)
	Parkland	Faidherbia	18–134	Sahel	Boffa (1999)
			30	Niger	Kho *et al.* (2001)
			44–125	Ethiopia	Kamara and Haque (1992)
			5–29	Malawi	Rhoades (1995)
	Intercropping	Gliricidia	160.7	Malawi	Mweta *et al.* (2007)
P uptake	Intercropping	Gliricidia	92	Zambia	Mafongoya (unpublished)
		Leucaena	110	Zambia	Mafongoya (unpublished)
		Gliricidia	121	Malawi	Mweta *et al.* (2007)

(Okogun *et al.*, 2000). N uptake by crops is usually improved when cereals are associated with fertilizer trees (**Table 3**). Soil amendment with small dosages of inorganic fertilizer (25–50% of recommended rate) further increases N uptake. For example, N uptake increased by over 245% when the maize crop in the alleys between these trees was amended with 40–80 kg N ha^{-1} of synthetic fertilizers in Nigeria (Okogun *et al.*, 2000). Similarly, N uptake significantly increased when gliricidia plots were amended with synthetic N and P fertilizers (Mweta *et al.*, 2007).

The question arising from all of the above is: To what extent can fertilizer trees substitute for inorganic N fertilizers? The answer it seems depends on the desired crop yield. Typically, smallholder farmers in SSA have maize yields of 1–2 Mg ha^{-1}. 1 Mg ha^{-1} maize crop requires 20 kg N ha^{-1}. Tree pruning applied at 5 Mg ha^{-1} provides N input of 60–150 kg ha^{-1} (Palm, 1997), and this can support maize yields of up to 4 Mg ha^{-1} without any added synthetic fertilizer. In gliricidia-maize intercropping in Malawi, it is possible to reduce synthetic fertilizer use by 48 kg N ha^{-1} $year^{-1}$ (Dong-Gill, 2012) while still maintaining yields of up to 4 Mg ha^{-1} (Akinnifesi *et al.*, 2010). For higher yields, although BNF may supply adequate N, supplementation with inorganic fertilizers may be required to provide sufficient P and K.

P availability and uptake

Fertilizer trees can contribute to P availability, either directly by releasing tissue P during decomposition and mineralization or indirectly by acting on chemical processes that regulate P adsorption–desorption reactions. Compared to annual crops, tree root systems are more extensive. This increases the exploration of larger soil volumes, resulting in enhanced uptake of P and other nutrients. Trees may also access soil P from relatively recalcitrant pools not utilized by crops (Buresh and Tian, 1998). The symbiotic association between fertilizer trees and mycorrhizal fungi can also improve the capacity of the plant to take up P. A number of empirical studies have documented higher soil P concentrations and uptake by crops in the presence of fertilizer trees (**Table 3**). However, it is important to note that fertilizer tree innovations will not eliminate the need for P inputs in P deficient soils. Plant materials, even when added in large amounts, may provide less P than that required to obtain adequate crop yields. This inadequacy is due to a low concentration of P (<3 g kg^{-1}) in plant residues. For example, >18 kg P ha^{-1} is required to produce maize yield of 2 Mg ha^{-1}. However, application of even high-quality residues at 5 ton ha^{-1} adds only 15 kg P ha^{-1} crop (Palm *et al.*, 1997). Therefore, soil amendment with soluble mineral P fertilizers or phosphate rocks is required to obtain adequate crop yields in P-limited soils (Buresh and Tian, 1998). The added P can be recycled through fertilizer trees in their leaf litter and root turnover.

Cation concentrations and improvement in soil pH

Increases in cations and soil pH and decrease in aluminium saturation and improvement in the conditions for plant growth in acid soils have been associated with application of tree prunings (Mafongoya *et al.*, 2006). Increases in soil cation concentrations usually results from recycling through the biomass fertilizer trees. Several studies in parklands in the Sahel indicate that exchangeable K in the 0–10 cm soil is 43–133% higher under faidherbia than in the open (Boffa, 1999). Similarly, Ca was 2–270% higher, while Mg was 0–78% higher under faidherbia than in the open. In Ethiopia, Kamara and Haque (1992) found that K concentrations were higher by 150–178% beneath faidherbia than in the open. Fertilizer trees could minimize nitrate leaching and soil acidification both by decreasing drainage and recycling leached nutrients. Thus, in acid soils fertilizer tree prunings could be used as a 'liming' material, thus providing resource-poor farmers with an inexpensive biological means for alleviating soil acidity.

Increased soil organic matter

Fertilizer trees enhance soil organic matter (SOM) both through production of SOM and reducing losses due to erosion. A compilation of studies in parklands of West Africa (Boffa, 1999) indicates 11–100% higher SOM under faidherbia trees than in open areas. In Ethiopia, SOM under faidherbia was 69–107% higher than in the open (Kamara and Haque, 1992). Increased soil organic carbon (SOC) content, particularly in the light fraction, is known to improve aggregate stability, porosity, hydraulic conductivity, and soil structures that resist erosion.

Improvement in soil biological properties

The impact of fertilizer trees on soil biological properties may be assessed by changes in abundance, diversity, and community structure of soil fauna and flora, microbial biomass, enzyme activity (e.g., respiration), and soil pests and weeds. Soil fauna play a key part in litter decomposition through their interactions with plants and soil microbial communities. During decomposition, the organic forms of nutrients in the litter are converted to inorganic forms that can be absorbed by the growing plants. In addition, the activities of soil fauna improve soil water infiltration and storage, which is becoming increasingly important in agricultural sustainability in arid climates (Sileshi and Mafongoya, 2006; Tian *et al.*, 2001).

Even in highly degraded soils, fertilizer tree species have been shown to restore soil fauna in a relatively short time (Sileshi and Mafongoya, 2006; Sileshi *et al.*, 2008b; Tian *et al.*, 2001). At two sites in eastern Zambia, earthworm densities were found to be significantly higher in maize intercropped with vachellia, calliandra, gliricidia, and leucaena compared with fully fertilized sole maize (Sileshi and Mafongoya, 2006). In another study in eastern Zambia, earthworm abundance was 2–3 times higher in maize planted after sesbania +tephrosia and pure pigeon pea fallows compared with sole maize (Sileshi *et al.*, 2008b).

N-fixing trees have been shown to modify populations of microflora, microbial biomass, and enzyme activity (Mafongoya *et al.*, 1997; Tian *et al.*, 2001; Wick *et al.*, 1998). For example, at Domboshawa in Zimbabwe, fungal and actinomycetes populations differed with the quality and quantity of fertilizer tree biomass as well as the method of application. Actinomycetes populations were six to nine times higher where vachellia and calliandra biomass was surface-applied than when incorporated in the soil (Mafongoya *et al.*, 1997).

The microbial biomass is also part of the active SOM pool, and has been proposed as an indicator of state and change of total SOM. Enzyme activity in the soil is an indicator of soil

biological status. For example, phosphatases are important in the P cycle because they provide P for plant uptake by releasing PO_4, and acid phosphatase can provide a potential index for a soil to mineralize organic P. β-glucosidase catalyzes the conversion of cellulose to glucose, and as such important energy sources for micro organisms. In long-term experiments carried out at three sites in southern Nigeria (Wick *et al.*, 1998), β-glucosidase increased by 41–119% with leucaena relative to continuous cropping of maize/cassava (Wick *et al.*, 1998). Alkaline phosphatase increased by 24–149% with leucaena relative to the control (Wick *et al.*, 1998).

Fertilizer trees in certain agroforestry practices can also reduce soil insect pests and weeds (Sileshi *et al.*, 2008c). For example, termite damage to maize was reduced by improved fallows involving fertilizer trees in Zambia (Sileshi *et al.*, 2005). One of the most important aspects is the control of problematic weeds such as spear grass (*Imperata cylindrical*). In Nigeria, hedgerows of leucaena and gliricidia reduced the population of spear grass by 51−67%, above-ground biomass by 78−81%, and below-ground rhizomes by 90−96% compared to a bush fallow (Anoka *et al.*, 1991). In a study at Pucallpa in the Peruvian Amazon, weed biomass was 40–63% less in inga fallows compared to natural fallows (Lojka *et al.*, 2012). In alley cropping, albizia and gliricidia have been shown to reduce weed in Nigeria (Okogun *et al.*, 2000).

Fertilizer tree fallows have also been shown to reduce the parasitic witch weeds (*Striga* spp.) problem, which is usually associated with low soil fertility in Africa (Gacheru and Rao, 2001; Sileshi *et al.*, 2008c). Sesbania was better than many other species in reducing *Striga asiatica* infestation in maize in eastern Zambia (Sileshi *et al.*, 2008c). The reduction in infestation was significantly influenced by the quantity of biomass from fertilizer trees (Sileshi *et al.*, 2008c). In East Africa, reduction of *Striga hermontica* infestation by legume fallows depended on the rate of decomposition and nitrogen mineralization of organic residues (Gacheru and Rao, 2001). Reduction in weed problems is due to shading and smothering of the weeds by trees and the thick mulch layer formed by the leaf litter from the trees subsequently depleting the weed seed-bank. Many legume species release a wide range of allelochemical compounds, which can inhibit weed seed germination or reduce weed vigor (Sileshi *et al.*, 2008c).

Improvement in soil physical properties

Among the commonly used indicators of soil physical properties are soil depth, bulk density, aggregate stability, infiltration rates, water-holding capacity, and penetration resistance. Soil bulk density is a direct measure of soil compaction. Soils with low bulk density, although open-textured and porous, are susceptible to erosion, poor water retention, and oxidation of SOM and loss of SOC. In contrast, soils with high bulk density have lower porosity. Various studies indicate improvement in bulk density, aggregate stability, and porosity due to fertilizer trees. In sandy loam soil in the pre-Amazon region of Brazil, bulk density, total porosity, and soil aeration were substantially improved in alley cropping with leucaena, pigeon pea, acacia, and their mixtures over a period of three years (Aguiar *et al.*, 2010). In gliricidia, leucaena, Vachellia, and sesbania rotational fallows in Zimbabwe and Zambia soil bulk density was up to 12% lower and aggregate stability was higher by 18–36% compared to sole maize crops (**Table 4**). Pore density was also significantly higher in vachellia and sesbania fallows (285–443 m^{-2}) compared to continuous maize (256 m^{-2}). The pore density was significantly higher in Vachellia and sesbania fallows (4521–8911 m^{-2}) compared to continuous maize (2689–3938 m^{-2}). The mean pore sizes were lower in continuous maize and higher in the fertilizer tree fallows (Nyamadzawo *et al.*, 2008a). The mean pore sizes at 5 cm tension were 0.07–0.12 mm in fallows relative to continuous maize, which were 0.03 mm.

The improvement in soil structure was also associated with increased drainage, especially during wet periods. In eastern Zambia and Zimbabwe, steady-state infiltration rates were 42–600% higher when maize was rotated with gliricidia, leucaena, vachellia, sesbania, and tephrosia compared to continuously grown sole maize (**Table 4**). Time to water runoff was also longer by 40–133% and drainage was improved by 88–900% compared to continuous sole maize. The soil in maize planted following improved fallows had lower penetration resistance compared with monoculture maize at various sites in eastern Zambia (**Table 4**).

Reduced penetrometer resistance and increased water infiltration imply reduced water runoff and soil erosion. The improvement under fertilizer trees was evident from the longer time to runoff measured in maize fertilizer tree rotations compared to sole maize in Zambia and Zimbabwe (**Table 4**). Land under fertilizer trees has been shown to be less susceptible to runoff and erosion than continuous maize. According to Fagerström *et al.* (2002), in an upland rice cropping system in northern Vietnam, tephrosia fallows and hedgerows effectively prevented nutrient losses by erosion. Runoff and soil losses were also lower in maize grown with fertilizer trees compared to continuous maize in Zimbabwe (**Table 4**). Soil loss was 30–100% higher under continuous maize than under fertilizer tree fallows (Nyamadzawo *et al.*, 2006; Nyamadzawo *et al.*, 2012).

As they increase hydraulic conductivity and reduce runoff losses, fertilizer trees improve water retention, storage, and availability to associated crops. At Domboshawa in Zimbabwe 75–80% of the total available water was retained at suction <33 kPa in the top 0–15 cm depth under vachellia fallows (Nyamadzawo *et al.*, 2012). Soil water stored in 2-year sesbania-improved fallows was greater than in continuously cropped fertilized or unfertilized maize in eastern Zambia (Phiri *et al.*, 2003). In parklands in Ethiopia, the amount of available water under faidherbia was twice that outside the tree canopy (Kamara and Haque, 1992). Similarly, in Malawi, soil moisture in the 0–15 cm soil was 4–53% higher under faidherbia than outside the tree canopy (Rhoades, 1995). The trees canopy also intercepts water and channels it down to the soil, thus contributing soil water recharge through macropores created by roots and increased microbial activities. Phiri (2002) recorded greater rainfall interception by sesbania tree canopies indicated by increased moisture storage and sub-soil moisture recharge.

The role of fertilizer trees in improving water use efficiency (WUE) has recently been demonstrated with long-term field studies in Africa (Sileshi *et al.*, 2011). In rain-fed agriculture, rain use efficiency (RUE) defined as the ratio of above-ground net primary production to annual rainfall provides

Table 4 Changes in soil physical properties (0–20 cm) due to fertilizer trees (FT) in improved fallow and the control (sole maize) and the % change (%Δ) at Msekera, Kagoro, and Kalunga sites in Zambia and Domboshawa in Zimbabwe

Variable	*Tree species*	*Site*	*FT*	*Control*	*(%Δ)*	*Reference*
Bulk density ($Mg\ m^{-3}$)	Gliricidia	Msekera	1.39	1.53	−9.2	Sileshi and Mafongoya (2006)
			1.40	1.42	−1.4	Mafongoya *et al.* (2006)
	Leucaena		1.35	1.53	−11.8	Sileshi and Mafongoya (2006)
	Vachelia	Domboshawa	1.33	1.41	−5.7	Nyamdzawo *et al.* (2008)
	Sesbania	Msekera	1.35	1.42	−4.9	Mafongoya *et al.* (2006)
			1.59	1.66	−4.2	Phiri (2002)
		Domboshawa	1.36	1.41	−3.5	Nyamdzawo *et al.* (2008)
Aggregate stability (mm)	Sesbania	Msekera	83.3	61.2	36.1	Chirwa *et al.* (2004)
			65.0	55.0	18.2	Phiri (2002)
			38.0	32.0	18.8	Phiri (2002)
	Pigeon pea		80.0	61.2	30.7	Chirwa *et al.* (2004)
Infiltration rate ($mm\ hr^{-1}$)	Gliricidia	Kagoro	4.4	2.9	51.7	Chirwa *et al.* (2003)
		Msekera	16	4.0	300.0	Mafongoya *et al.* (2006)
	Leucaena	Kagoro	3.7	2.9	27.6	Chirwa *et al.* (2003)
	Vachelia	Kagoro	5.5	2.9	89.7	Chirwa *et al.* (2003)
		Domboshawa	>35	5.0	600.0	Nyamdzawo *et al.* (2007)
	Sesbania	Msekera	20.0	4.0	400.0	Mafongoya *et al.* (2006)
			0.13	0.08	62.5	Phiri (2002)
			4.4	2.1	109.5	Chirwa *et al.* (2004)
		Kagoro	9.5	2.9	227.6	Chirwa *et al.* (2003)
	Sesbania	Kalunga	21.0	7.0	200.0	Nyamadzawo *et al.* (2006)
		Msekera	8.0	5.0	60.0	Nyamadzawo *et al.* (2006)
		Domboshawa	12	5.0	140.0	Nyamadzawo *et al.* (2007)
	Pigeon pea	Msekera	5.2	2.1	147.6	Chirwa *et al.* (2004)
	Tephrosia	Kalunga	16.0	7.0	128.6	Nyamadzawo *et al.* (2006)
		Msekera	7.1	5.0	42.0	Nyamadzawo *et al.* (2006)
Time to runoff (min)	Vachelia	Domboshawa	30.0	15.0	76.5	Nyamadzawo *et al.* (2006)
	Sesbania	Kalunga	21.0	9.0	133.3	Nyamadzawo *et al.* (2006)
		Msekera	7.0	3.0	133.3	Nyamadzawo *et al.* (2006)
		Domboshawa	21.0	15.0	40.0	Nyamadzawo *et al.* (2006)
	Tephrosia	Kalunga	14.0	9.0	55.6	Nyamadzawo *et al.* (2006)
	Tephrosia	Msekera	7.0	3.0	133.3	Nyamadzawo *et al.* (2006)
Drainage (mm)	Sesbania	Msekera-1a	56.4	15.8	257.0	Phiri (2002)
		Msekera-1b	10.9	1.0	990.0	Phiri (2002)
		Msekera-2a	61.1	7.6	703.9	Phiri (2002)
		Msekera-2b	10.7	5.7	87.7	Phiri (2002)
Penetrometer resist (Mpa)	Gliricidia	Kagoro	0.6	1.2	−50.0	Chirwa *et al.* (2003)
	Leucaena	Kagoro	0.8	1.2	−33.3	Chirwa *et al.* (2003)
	Vachelia	Kagoro	1.0	1.2	−16.7	Chirwa *et al.* (2003)
	Sesbania	Kagoro	0.9	1.2	−25.0	Chirwa *et al.* (2003)
		Msekera	2.2	3.2	−31.3	Chirwa *et al.* (2004)
	Pigeon pea	Msekera	2.9	3.2	−9.4	Chirwa *et al.* (2004)
Runoff loss (%)	Vachelia	Domboshawa	0	57.0	−100.0	Nyamadzawo *et al.* (2006)
	Sesbania	Domboshawa	21.0	57.0	−63.2	Nyamadzawo *et al.* (2006)

information similar to WUE. Sileshi *et al.* (2011) analyzed variations in RUE with leucaena in three long-term experiments conducted in Zambia and Nigeria. At the two sites in Zambia, maize intercropped with leucaena achieved 191–197% higher RUE compared to sole maize continuously cropped without nutrient inputs. At the Nigerian site, RUE was 139–202% higher in maize planted between leucaena hedgerows compared to the control (Sileshi *et al.*, 2011). According to another study at Makoka (Chirwa *et al.*, 2007), WUE was higher in maize intercropped with gliricidia than in the sole maize and maize+pigeon pea intercropping. At another site in eastern Zambia, WUE was 202% higher in sesbania fallows compared to continuous sole maize (Phiri, 2002).

Carbon Sequestration and Greenhouse Gas Mitigation Potential

A growing number of studies have also demonstrated that fertilizer trees can sequester significant amounts of C both in the soil and in their woody biomass and mitigate greenhouse gas (GHG) emissions. In Mali, Takimoto *et al.* (2008) estimated 70.8 Mg C ha^{-1} in the top 40 cm of the soil in parklands dominated by faidherbia. SOC increases of 3–70% under faidherbia canopy have also been reported in the Sudan (Rhoades, 1995). At several sites in Malawi, SOC was 3–30% higher under faidherbia canopy than in the open (Rhoades, 1995). According to Sierra and Nygren (2006), gliricidia trees

in pastures contributed 16–18 Mg C ha^{-1} to soil over 12 years. In a 19-year-old gliricidia alley cropping in Costa Rica, the SOC pool was 16–23% higher than the sole crop (Oelbermann *et al.*, 2004). In the 19th year of alley cropping, SOC was significantly higher in the alley crop (3.2%) compared to the sole crop (2.4%) (Oelbermann *et al.*, 2004). Similarly, in a 19-year-old alley cropping with erythrina in Costa Rica, C inputs from tree prunings were 4.01 Mg C ha^{-1} $year^{-1}$ (Oelbermann *et al.*, 2006). The input from crop residues was significantly greater in the erythrina alley crop for maize (1.34 Mg ha^{-1} $year^{-1}$) and beans (0.35 Mg ha^{-1} $year^{-1}$) compared to the sole crop (Oelbermann *et al.*, 2006). Nygren (1995) showed that C input from prunings of erythrina in Costa Rica ranged from 2.3 to 5.2 Mg ha^{-1} $year^{-1}$ at a tree density of 625 trees ha^{-1}. In alley cropping with leucaena in Nigeria, SOC increased by 108% in the 0–15 cm soil as compared to the control without a hedgerow (Kang *et al.*, 1999). In Zimbabwe, SOC was 1.7 times higher in Vachellia fallows than continuous sole maize (Nyamadzawo *et al.*, 2008b). SOC stocks within 0–30 cm depth under 5-year-old rotational woodlots (15.8–25.6 Mg ha^{-1}) were higher than in soils that had been continuously cropped for the same time period (13 Mg ha^{-1}) in Tanzania (Kimaro *et al.*, 2011). According to Kaonga and Coleman (2008) SOC stocks under tephrosia, sesbania, and pigeon pea were higher (27.3–31.2 Mg ha^{-1}) than under fully fertilized sole maize (26.2 Mg ha^{-1}) and unfertilized sole maize (22.2 Mg ha^{-1}) in eastern Zambia. The above-ground plant C input was estimated at 2.8 Mg C ha^{-1} $year^{-1}$ for tephrosia, 2.7 Mg ha^{-1} $year^{-1}$ for sesbania, and 2.5 Mg ha^{-1} $year^{-1}$ for pigeon pea, which was comparable to 2.7 Mg ha^{-1} $year^{-1}$ recorded for fully fertilized sole maize (Kaonga and Coleman, 2008). In Malawi, Makumba *et al.* (2007) found that soil C in a gliricidia–maize intercropping roughly doubled after 7 and 10 years compared to sole maize. A more recent reanalysis of the data from Makumba *et al.* (2007) found an annual net gain of 3.5 Mg C ha^{-1} $year^{-1}$ in the soil (Dong-Gill, 2012). With the potential for N_2O mitigation of 0.12–1.97 kg N_2O–N ha^{-1} $year^{-1}$) the gliricidia–maize intercropping was estimated to mitigate 3.5–4.1 Mg CO_2 eq. ha^{-1} $year^{-1}$ (Dong-Gill, 2012).

Estimates of above-ground C storage are also substantial. In cacao agroforestry in Indonesia, C stock in biomass was estimated at 31.4 Mg C ha^{-1} in 15-year-old gliricidia (Simley and Kroschel, 2008). Similarly, in Costa Rican cacao agroforestry, erythrina stored 40 Mg C ha^{-1} (Oelbermann *et al.*, 2006). In 5-year rotational woodlots in Tanzania, carbon sequestered in wood of fertilizer trees ranged from 11.6 to 25.5 Mg ha^{-1} (Kimaro *et al.*, 2011). Wood C accumulation rates ranged from 2.3 to 5.1 Mg C ha^{-1} $year^{-1}$ in acacia species (Kimaro *et al.*, 2011). A 6-year stand of faidherbia in Tanzania accumulated 9.4 Mg ha^{-1} of wood C at a 5 m by 5 m spacing (Okorio and Maghembe, 1994). In parkland in Mali, faidherbia accumulated 20.3 Mg ha^{-1} (Takimoto *et al.*, 2008). This can play a critical role in mitigation of climate changes as they favor nutrient recycling and C sequestration in crop and pasture land. However, the potential for accumulation of ecosystem C by fertilizer trees depends on site characteristics and planting densities. Therefore, accurate methods are required to determine change in C with the inclusion of fertilizer tree innovations in the various farming systems.

Provision of Products

Most N-fixing trees provide various products including wood, fruits, edible seeds, and fodder that are rich in protein and increase pasture productivity.

Wood and Wood Products

Several studies have indicated production of substantial amounts of firewood and timber from fertilizer trees planted on farmland (**Table 5**). In acid soils in Peru, inga produced up to 8–12 Mg ha^{-1} $year^{-1}$ of wood (Lojka *et al.*, 2012). Russo (2005) reported wood production of 15–20 m^3 ha^{-1} $year^{-1}$ in alder. A stand of 30-year-old trees with a density of 35 trees ha^{-1} yielded 70 m^3 ha^{-1} of timber, 18.3 Mg ha^{-1} of dry fuelwood (Russo, 2005). Several studies have also indicated production of substantial amounts of firewood in Africa (**Table 5**). Assuming per capita dried firewood consumption of 486 kg (0.67 m^3) $year^{-1}$ (Ndayambaje and Mohren, 2011), wood yields of the various species would be sufficient to meet the household fuelwood demands for 1–17 families of 6 people (**Table 5**). Such high wood yields exemplify the potential of fertilizer trees in meeting local firewood demands, especially in Africa where the population depends on extraction of wood from forests due to lack of alternatives in energy supply. As forest resources continue to degrade, access to firewood declines, and rural women have to walk increasingly longer distances in search of firewood. Planting of fertilizer trees on farmland can increase access to firewood by women, and thus the time and labor spent in search of firewood can be reallocated to food production and childcare.

Fruits and Edible Seeds

Some fertilizer trees (e.g., tamarind, parkia, pigeon pea, *Tetrapleura tetraptera*, etc.) produced edible seeds or kernels. For example, pigeon pea seeds are a rich source of protein, carbohydrates, minerals, and vitamins, making it an ideal supplement to the traditional starch-based diets of Africa and Asia, which are generally protein-deficient (Odeny, 2007). The edible pulp of tamarind is consumed fresh or used to make syrup, juice concentrates, and exotic food specialities such as chutney, curries, pickles, and meat sauces. In the Sahel, parkia seeds are a valuable source of condiment locally called 'soumbala,' which is an important source of protein (Kalinganire *et al.*, 2008).

Fodder and Pasture

Scarcity of forage and lack of access to high-quality feed are major constraints to livestock productivity, especially in the semiarid areas. Silvopastoral management including protein (fodder) banks and grazing systems involving fertilizer trees may partly overcome these problems. Protein banks allow animals to be stall-fed with fodder from trees such as gliricidia, calliandra, or various species of leucaena, pterocarpus, and others grown in blocks on farmland. Alternatively, grazing systems allow livestock to graze on pasture under widely

Table 5 Potential annual harvestable fuelwood produced from fertilizer trees planted in contour strips, woodlots, or rotational fallows

Tree species	*Age (years)*	*Quantity (Mg ha^{-1} yr^{-1})*	*Sufficient for N families of 6*	*Country*	*References*
Calliandra	4.5	3.2	1.1	Tanzania	Mwihomeke and Chamshama (2004)
Casuarina	4.5	1.8	0.6		Mwihomeke and Chamshama (2004)
Acacia crassicarpa	5	22.4	7.7		Otsyina (1999)
A. crassicarpa	4	19–24.0	8.2		Otsyina (1999)
Vachellia nilotica	7	1.2	0.4	Tanzania	Nyadzi *et al.* (2003)
Senegalia (Acacia) polycantha	7	10.1	3.5		Nyadzi *et al.* (2003)
Leucaena	7	12.7	4.4		Nyadzi *et al.* (2003)
Acacia crassicarpa	5	51.0	17.5	Tanzania	Kimaro *et al.* (2007)
A. mangium	5	40.0	13.7		Kimaro *et al.* (2007)
Senegalia (Acacia) polycantha	5	39.0	13.4		Kimaro *et al.* (2007)
Vachellia nilotica	5	27.0	9.3		Kimaro *et al.* (2007)
Gliricidia	5	30.0	10.3		Kimaro *et al.* (2007)
Leucaena	3	9.7	3.3	Zambia	Ngugi (2002)
Sesbania	3	8.0	2.7		Ngugi (2002)
Gliricidia	3	7.0	2.4		Ngugi (2002)
Sesbania	1–3	7.3	2.5		Kwesiga and Coe (1994)
Sesbania	Na	2.0	0.7	Rwanda	Ndayambaje and Mohren (2011)
Alder	Na	7.0	2.4		Ndayambaje and Mohren (2011)
Casuarina	Na	11.0	3.8		Ndayambaje and Mohren (2011)
Leucaena	Na	10.0	3.4		Ndayambaje and Mohren (2011)
Tagasaste	Na	11.0	3.8		Ndayambaje and Mohren (2011)
Leucaena single row	2.7	21.2	7.3	Kenya	Jama and Getahun (1991)
Leucaena double row	2.7	18.2	6.2		Jama and Getahun (1991)

spaced trees (e.g., alley farming) or scattered trees (e.g., parklands).

In the more extensive grazing areas of South America, Asia, Australia, and Africa, fertilizer trees are increasingly being planted in association with improved grasses to increase carrying capacity and/or enhance the productivity of grazing cattle. In high-elevation areas of Centra1 America and the Andean region, alders are prominent components of such systems. For example, in Costa Rica, alder stands in pasture grasses cover over 50 000 ha (Kass *et al.*, 1997), whereas the drier espinales of Chile (2 million ha), Bolivia, and Argentina are dominated by *Vachellia* (*Acacia*) *caven* (Muñoz *et al.*, 2007). Similarly, in the over grazed, semi arid chaco of Argentina, Bolivia, and Paraguay (more than 1.2 million km^2) fertilizer trees in the legume genera *Vachellia* and *Acaciella* (formerly *Acacia*), *Leucaena*, *Mimosa*, *Prosopis*, *Pithecellobium*, and *Sesbania* provide N for grass growth and browse (Abril and Bucher, 2001; Muñoz *et al.*, 2007). In the more intensively managed areas in Brazil, Venezuela, Colombia, Mexico, parts of Central America, and the Caribbean, trees such as leucaena are planted in pasture or protein banks (Argel *et al.*, 1998). In Southeast Asia, leucaena and gliricidia are widely used in silvopastures. In Indonesia alone leucaena occurs in >79 000 ha of pasture land (Shelton *et al.*, 2005). In Queensland in Australia >100 000 ha of leucaena in pastures provides valuable forage for large-scale beef production (Shelton *et al.*, 2005). In Western Australia, >50 000 ha of tagasaste is grown in wide-spaced alleys or dense plantations to both provide fodder and reduce salinity by lowering the water table (Lefroy *et al.*, 1992). These are used as the sole source of feed during seasonal periods of nutritional shortage even on commercial farms.

In the parklands and in African savannahs, trees act as 'islands of fertility,' and grass growing under the canopy has better quality and yield than in the open areas (Treydte *et al.*, 2007). For example, grass productivity under faidherbia and parkia canopies was two to six times higher than in open areas in West African parklands (Boffa, 1999). Similarly, in Kenya grass productivity under acacia (now *Vachellia tortilis*) canopies was 1.5–2.3 times higher than outside the tree canopies (Weltzin and Coughenour, 1990). At Pakchong in Thailand, dry matter yield over 840 days was 30–41.5 Mg ha^{-1} in a mixture of grass and leucaena compared to 25–36.8 Mg ha^{-1} in grass alone (Tudsri *et al.*, 2002). Similarly, at Turrialba in Costa Rica, production of star grass was 16.9 Mg ha^{-1} year^{-1} with Erythrina compared to 11.7 Mg ha^{-1} year^{-1} in grass monoculture (Kass *et al.*, 1997).

In the parklands in the Sahel, pods of faidherbia provide a valuable source of dry season fodder. Parkia, locally called Néré, is also a valuable source of fodder in the Sahel, where its branches are lopped by farmers and fed to livestock in the dry season when grass is scarce. Supply of protein, which is the most important nutrient for cattle production on rangelands, can also be improved through fodder supplements from the legume genera *Acacia*, *Vachellia* (*Acacia*), *Leucaena*, etc. (Lefroy *et al.*, 1992; Mapiye *et al.*, 2011). As a result, meat and milk production is significantly improved. An analysis of results from experiments in Latin America and Australia indicated >70% increase in live weight gain and beef production using leucaena pastures (Jones, 1994).

Trade-offs

Under certain circumstances, the benefits of fertilizer trees could be offset by tree-crop competition for light, nutrients and other resources, soil acidification, or gaseous emissions

(Dick *et al.*, 2006). For example, root competition between trees and crops is a major problem, especially where fast-growing tree species are used without knowledge of optimum planting densities and management requirements. In a study on root development in a cassava-based cropping system in southern Bénin, Lose *et al.* (2003) compared annually planted pigeon pea alleys, perennial alleys, and blocks of gliricidia, flemingia, parkia, and millettia mixture. Annual alleys of pigeon pea had less interference with cassava, whereas block arrangement of the tree mixtures had detrimental effects on the cassava growth in the adjacent rows (Lose *et al.*, 2003). Even with intimate mixtures, competition may not be a problem under optimum tree densities and appropriate management such as pruning, lopping, and coppicing. Pruning offers one of the most direct and adaptable methods of controlling competition. Pruning intervals and intensities can be modified to regulate above- and below-ground competition and to match various production goals. For example, deleteriously competition for water did not exist in gliricidia-maize-pigeon pea intercropping when gliricidia was pruned before and during the cropping season in southern Malawi (Chirwa *et al.*, 2007). Water use studies in southern Africa also show minimal or no competition for moisture between the tree and crops. However, these studies have mostly been restricted to areas with relatively high rainfall (>900 mm) in normal years. In drier areas, competition may be severe.

Agroforestry has great potential for optimizing nutrient cycling and managing soil acidity under appropriate management. However, continuous removal of plant biomass (depending on ash alkalinity) may result in soil acidification. The amount of acidity generated by product removal is equal to the ash alkalinity carried by the product. If the bulk of the leguminous plant biomass is allowed to decompose on site after harvest, then the ash alkalinity is released and soil acidification minimized (Wong *et al.*, 2002). Management of soil acidification under legumes in low-input agroecosystems should therefore minimize the removal of biomass from the site of production and nitrate leaching. Localized acidification may be beneficial in circumstances where alkalinity accumulates down in the soil profile or in localized parts of the landscape. In these circumstances, the use of acidifying legume allows the alkalinity to be accessed and made available in the form of biomass with high ash alkalinity. The acid-ameliorating effect of this biomass can then be used in more acid parts of the landscape or in the more acid top soil. Using low-acidifying fertilizer tree species (provenances) may also reduce the risk of acidification. High genotypic variability within tropical legumes allows selection of genotypes.

Some of the N from legume biomass not taken up by plants and microbes in the soil can contribute to N_2O emissions (Chikowo *et al.*, 2004; Hall *et al.*, 2006), especially after rainfall events. As N addition rates progressively increase beyond the capacity of soil microbes to utilize N, the rate of N_2O production would slow down and finally reach steady state; under this stage, soil C availability would presumably control N_2O production and emission (Dong-Gill *et al.*, 2012). In a semi arid condition in Mali, Hall *et al.* (2006) found six times more N_2O emission from gliricidia plots than from continuous cultivation of sorghum without fertilizer. In a wet tropical soil, Seneviratne and Van Holm (1998) found over 5900 times more N_2O emission from soil without mulch than from plots that received gliricidia mulch. In the same experiment, N_2O emission from urea fertilizer was over 25 000 times higher than from plots that received gliricidia mulch (Seneviratne and Van Holm, 1998).

Conclusions

This review suggests that diversification of agro-ecosystems with fertilizer trees can optimize indigenous soil N supply and increase productivity of the land. Fertilizer trees have an added advantage: ensuring a multifunctional agriculture that provides timber, fodder, shade, soil improvement, and watershed management. Unlike synthetic N sources, fertilizer trees ensure greater internal nutrient recycling and water availability, thus contributing to greater nutrient use efficiency. Therefore, they can make a major contribution to sustainable agriculture by minimizing external inputs, particularly N fertilizers, increasing resource and land use efficiency, and slowing down erosion. The savings on synthetic fertilizer costs and GHG mitigation potential could also be substantial. Unlike synthetic fertilizers, fertilizer trees may play a significant role in reducing N leaching, which is particularly important during periods of reduced ground cover by herbaceous plants, such as between cropping seasons. The advantage of organic inputs over synthetic fertilizers is that much of the N from organic inputs not used by the crop is usually incorporated into various SOM pools, or assimilated by the associated trees, thus remaining in the system for other uses. N from inorganic pools not taken by the crop is subjected to higher levels of leaching and denitrification. Thus, the accumulation of N in SOM pools over time is more sustainable compared to synthetic N fertilizer, which releases nutrients rapidly. The potential of inorganic fertilizers to ameliorate the physical and biological degradation of poorly buffered soils is limited. Synthetic fertilizers, however, will remain a necessary input to agriculture to feed the increasing human population. Therefore, the focus of this article is not just whether fertilizer trees are better or worse than mineral fertilizers, because both play an important (and complementary) role in food production. The authors strongly believe that smallholder farmers would benefit if development planners were to emphasize the merits of different fertility replenishment approaches and take advantage of the synergy between fertilizer trees and mineral fertilizers rather than focusing on the 'organic versus inorganic' debate.

Although the rate of adoption of fertilizer trees has been lower than anticipated in many regions of the world, there have been notable successes in other parts. In the traditional production systems, the adoption of fertilizer trees has been driven by local tradition, economic factors, and land ownership. These traditional systems are being degraded and losing their productivity, but they may be a source of inspiration in the design of new land management practices where fertilizer trees can play a greater role in increasing food, forage, and fibre production. However, a longer-term vision and significant investment in research and development are needed. Screening of candidate tree species and development of innovations appropriate to specific conditions are important where these do not exist.

Where appropriate innovations already exist, barriers to adoption and risks that the adoption presents need to be identified.

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See also: Agroforestry: Complex Multistrata Agriculture. Agroforestry: Fodder Trees. Agroforestry: Hydrological Impacts. Agroforestry: Practices and Systems

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Agroforestry: Fodder Trees

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Glossary

Agroforestry The cultivation of trees and crops in interacting combinations.
Alley farming A method of planting, in which rows of a crop are sown between rows or hedges of nitrogen-fixing plants, the roots of which enrich the soil.
Climate change mitigation Actions to limit the magnitude and rate of long-term climate change. Climate change mitigation generally involves reductions in human emissions of greenhouse gases.
Germplasm A collection of genetic resources for a plant, often stored as a seed collection.
Ideotypes Characteristics of model trees for maximizing economic yield in a particular environment for producing well-defined end products.
Legume A plant in the family Leguminosae. Legumes are notable in that most of them have symbiotic nitrogen-fixing bacteria in structures called root nodules that enrich the soil.

Introduction

Livestock are key components of farming systems throughout the world. Although livestock are often associated with wealth in many countries, approximately 1 billion head of livestock are held by more than 600 million poor smallholders, comprising approximately 70% of the world's rural poor (IFAD, 2004).

Low quality and quantity of feeds are major constraints limiting animal productivity. Feeding livestock has become particularly problematic in the developing world because of rising population growth increasing the demand for livestock products. In both developing and developed countries, the supply of livestock feed has become more scarce because of diminishing land availability due to the reduction in the quantity and quality of rangeland and natural grasslands. Changing cropping patterns, such as the recent increase in the area under crops for biofuels, further exacerbates feed availability (FAO, 2001; Ayantunde *et al.*, 2005; IFPRI, 2008).

Fodder trees and shrubs (the terms trees and shrubs are used interchangeably) are both old and new solutions to feed problems. They can be characterized as 'old' solutions because farmers have fed tree foliage to their livestock for centuries, using wild browse or trees that grow naturally on their farms (Le Houérou, 1980). They can be considered as 'new' solutions in that in recent years, there have been significant movements of germplasm and increased cultivation of fodder shrubs in many areas of the world. Moreover, nearly all fodder trees can be considered to be multipurpose, in that they provide many benefits to the farmer, the farming system, and the environment (**Table 1**; Shelton, 2005).

This article reviews the role of fodder trees in agroforestry systems in which trees and crops are deliberately grown in interacting combinations (Nair *et al.*, 2004). Thus, the many rangeland or forest systems in which pastoralists rely on wild fodder trees, or systems in which fodder trees are grown in monocropped plantations is not reviewed. As in many other agroforestry systems, fodder trees can interact with adjacent crops or enterprises; for example, competing for moisture, light, and soil nutrients or for farmers' scarce resources: land, labor, and capital.

First the main fodder tree species grown in different parts of the world are introduced. Next, practices for growing fodder trees including seeds and tree establishment, tree management, harvesting, and animal productivity are assessed. Finally, benefits and impacts and present challenges for enhancing the contributions of fodder shrubs to improved productivity, farm intensification, and livelihoods are reviewed.

Two key limitations of this review are required to be mentioned here. First, the authors were greatly restricted by the fact that they only consulted publications in English. Regions, such as Latin America, Francophone West Africa, and East and Southeast Asia are thus underrepresented. Second, many of the references do not say whether the fodder trees they discuss are part of agroforestry systems, that is, either planted or deliberately retained, or are wild browse. As this article focuses on fodder trees in agroforestry systems, the authors have not included references to fodder trees where their origin/location is not clear.

Fodder Tree Species

Eleven of the most widely planted fodder tree species are depicted in **Table 2**. There is a considerable variation in the adaptation of the leading species to different environments. All of the species listed are grown in the humid and subhumid tropics; a few such as *Gliricidia sepium*, *Leucaena pallida*, and Mulberry (*Morus alba*) are also grown in the semiarid tropics. Two are also grown in cooler tropical/subtropical areas: mulberry and tree lucerne (*Chamaecytisus palmensis* also called *Chamaecytisus prolifer*). Ten of the species are legumes; the only exception is mulberry, which, though not a legume, is still high in protein. The species are adapted to different conditions, such as drought, frost, poor drainage, and soil acidity (**Table 2**). Nine are considered to be of higher feed quality, whereas three are of lower quality, based on factors such as

Table 1 The value of fodder trees in agroforestry systems

For livestock
- Valuable source of high quality, protein-rich forage for subsistence, and commercial production of livestock, including cattle, sheep, goats, rabbits, poultry, fish, and bees
- Able to supply foliage during dry periods when herbaceous species are not productive
- Being deep rooted, they are drought tolerant and thus are important components of adaptation strategies to climate change
- Living fences, around homesteads and fields
- Some species have important medicinal attributes for treating livestock health issues

For farming systems
- Source of nitrogen-rich mulch for cropping systems
- Enhance the sustainability of farming systems due to fertility enhancement, longevity, soil cover, and control of soil erosion
- Timber for trellises and stakes for climbing crops
- Source of fruit, vegetables, and medicines

For people and the environment
- Opportunity to intensify sustainable agricultural production
- Means to stabilize sloping lands against soil erosion, due to their deep-rooting habit and permanent soil cover
- Often an important source of timber, firewood, and charcoal, particularly for domestic consumption
- Habitat for wildlife
- As woody perennials, a sink for CO_2 and contributor to climate change mitigation and adaptation
- Source of cash income when sold as forage or when seed are marketed
- A means to lower water table and to limit rise in salinity

Source: Adapted from Shelton, H.M., 2005. Forage tree legume perspectives. In: Reynolds, S.G., Frame, J. (Eds.), Grasslands: Development Opportunities Perspectives. Boca Raton, FL: Science Publishers, pp. 81–108.

Table 2 Characteristics of selected fodder trees

Species	*Countries planted*[a]	*Altitude range (m)*	*Mean annual rainfall (mm)*	*Frost tolerance*[b]	*Tolerance to poor drainage*[b]	*Tolerance to acidity*[b]	*Feed quality*[c]
Acacia angustissima	Tanzania and Zimbabwe	0–2600	900–2800	M	NT	T	M
Calliandra calothyrsus	Burundi, Indonesia, Kenya, Philippines, Rwanda, Tanzania, and Uganda	0–2200	>800	NT	NT	M	M
Chamaecytisus palmensis	Australia, Ethiopia, Kenya, and South Africa	1500–3000	600–1600	T	NT	NT	H
Cratylia agentea	Brazil	180–930	1000–4000	NT	NT	T	H
Gliricidia sepium	Indonesia, Philippines, and Mali	0–1600	600–3500	NT	NT	M	H
Leucaena diversifolia	Burundi, Philippines, Rwanda, Tanzania, and Uganda	<2000	1500–3500	NT	NT	NT	H
Leucaena leucocephala	Australia, Indonesia, Kenya, Philippines, Tanzania, Thailand, and Malawi	0–1900	650–1500	NT	NT	NT	H
Leucaena pallida	Tanzania	1000–2000	500–2000	M	NT	NT	M
Leucaena trichandra	Kenya	700–2000	1000–1800	NT	M	M	H
Morus alba	Costa Rica, France, Guatemala, Honduras, India, Kenya, Korea, Pakistan, and Uganda	0–4000	250–2500	T	M	M	H
Sesbania grandiflora	Indonesia	0–800	800–4000	NT	T	NT	H
Sesbania sesban	Ethiopia and Kenya	100–2500	>500	M	T	T	H

[a]List of countries is indicative, not exhaustive.
[b]NT, not tolerant; M, moderate tolerance; T, tolerant.
[c]M, medium; H, high.

Source: Reproduced from Roshetko, J.M., Dagar, J.C., Puri, S., *et al.*, 1996. Selecting species of nitrogen fixing trees for fodder production. In: Roshetko, J.M., Gutteridege, R.C. (Eds.), Nitrogen Fixing Trees for Fodder Production. A Field Manual. Morrilton, Arkansas: Winrock, pp. 23–43; Shelton, H.M., 2005. Forage tree legume perspectives. In: Reynolds, S.G., Frame, J. (Eds.), Grasslands: Development Opportunities Perspectives. Boca Raton, FL: Science Publishers, pp. 81–108; World Agroforestry Centre, Agroforestree data base. Available at: http://www.worldagroforestry.org/resources/databases/agroforestree (accessed 27.05.13); Devandra, C., Sevilla, C.C., 2002. Availability and use of feed resources in crop-animal systems in Asia. Agroforestry Systems 71, 59–73; CIAT, 2013. Tropical Forages Database. Available at: http://www.tropicalforages.info/index.htm (accessed 16.06.13); and Sanchez, M.D., 2000. World distribution and utilization of Mulberry. In: Potential for Animal Feeding 2000 FAO Electronic Conference on Mulberry for Animal Production, Rome FAO. Available at: http://www.fao.org/AG/AGa/AGAP/FRG/Mulberry/home.htm (accessed 02.07.13).

intake of digestible dry matter, presence of antinutritive compounds, and crude protein (Shelton, 2005). Shelton (2005) reports that only approximately 20 fodder tree legumes are in significant use (that is used on large numbers of farms) out of the several hundred fodder tree legume species regarded as having potential as a feed source.

There is much debate over whether to use exotic or indigenous species. Indigenous species are widely used in many farming systems; for example, there are reports of 29 indigenous fodder tree species used by farmers in Dendi and Jeldu districts, West Shewa Zone, in central Ethiopia (Kindu *et al.*, 2006), whereas in Burkina Faso, farmers were found to use 70 tree species for fodder across three land use systems (Sibiri *et al.*, 2000). Farmers in the Solma area of Nepal use more than 90 species, subspecies, and land races of trees for fodder (Thapa *et al.*, 1997). Moreover, they have considerable knowledge about their qualities. Thorne *et al.* (1999) have confirmed that Nepalese farmers' knowledge of tree fodder quality is quite consistent with the information that nutritional researchers generate from laboratory analyses. But scientists and development practitioners make relatively little use of local species; they tend to draw on the exotics, for which seed and information is readily available. Certainly, more research is needed on indigenous species in many countries to increase the knowledge base for scientists, development practitioners, and farmers. However, it seems to be common for exotic species to out-yield indigenous ones. For example, Atta-Krah *et al.* (1986) reported that a 2-year study of 22 native fodder species in Nigeria was abandoned because none were nearly as productive as *G. sepium* or *Leucaena leucocephala*.

There is considerable discussion in the literature on ideotypes, that is, characteristics of model trees for maximizing economic yield in a particular environment for producing well-defined end products (Smith, 1992; Dickman *et al.*, 1994; Leakey and Page, 2006). The discussion involves yield/quality differences between species as well as within species (between individual trees, progenies, and provenances). Characteristics of model trees vary by location and environment but some of the most frequently cited characteristics include:

- Easy establishment.
- High productivity under repeated cutting, grazing, or browsing.
- Resistance to pests and diseases.
- High seed production ability or reliable vegetative propagation.
- High production of good quality forage in terms of protein, minerals, palatability, and digestibility.
- Suitability to different environments (e.g., temperature, rainfall, soil acidity, drainage, or salinity).

Fodder Tree Practices

Niches and Planting Arrangements

In Africa, fodder trees are widely grown in some areas of the subhumid East African highlands, including Kenya, Uganda, Tanzania, and Rwanda, primarily among dairy farmers (Wambugu *et al.*, 2011). *Calliandra calothyrsus*, *Leucaena diversifolia*, *Leucaena trichandra*, and *Sesbania sesban* are the most important species. Farmers plant the trees in neglected niches, such as around the homestead, along crop and field boundaries, and along the contour to protect the soil against erosion. This way they do not need to take scarce crop land out of production. Few farmers report that the trees reduce yields of adjacent food crops (Franzel and Wambugu, 2007), but experiments often show otherwise (Garcia-Barrios and Ong, 2004). However, experiments have shown that *Calliandra* intercropped with Napier grass (*Pennisetum purpureum*) does not depress grass yields (Nyaata *et al.*, 1998).

Farmers in other areas of Africa plant in different arrangements. In the Ethiopian highlands, *S. sesban* is the most important planted fodder tree and is generally grown in home gardens (Mekoya *et al.*, 2008). In the subhumid East and Central Mashonaland provinces of Zimbabwe, farmers plant *L. leucocephala*, *Acacia angustissima*, *L. diversifolia*, and *L. pallida* in pure stands, whereas others intercrop them with food crops or other fodder crops (Hove *et al.*, 2003; Mapiye *et al.*, 2006). In the semiarid Sahelian zone of West Africa, only small numbers of farmers plant fodder trees but many purposely allow emerging seedlings to grow on their crop lands so as to harvest fodder from them (Boffa, 1999). Most fodder trees are multipurpose, providing other products such as firewood and fruits or services such as shade and soil erosion control (**Table 1**). In many instances these 'other' products may be the tree's primary use.

Similarly, in Asia a wide range of planting arrangements is found. In Cagayan de Oro, Philippines, farmers planted their improved forage species, mainly *G. sepium*, in fodder banks, along boundaries or on contour lines (Bosma *et al.*, 2003). They used combinations of improved fodder grasses and trees to increase their incomes from livestock, including cows, buffalos, and goats for milk and meat production and rabbits and chickens solely for meat production.

In other areas of Philippines, various fodder trees are used in a conservation farming practice called sloping agricultural land technology (Devandra and Sevilla, 2002). It is a form of alley farming with crops grown in bands 4–5 m wide between contoured rows of leguminous fodder shrubs such as *C. calothyrsus*, *L. leucocephala*, *L. diversifolia*, *G. sepium*, and *Flemingia macrophylla*. Leaves are fed primarily to goats. In the islands of Nusa Tenggara Timur, Indonesia, *L. leucocephala* is the main fodder tree and is grown as a fallow rotation for maize and as a food source for tethered cows and housed goats (Piggin, 2007). In central Java, *C. calothyrsus*, *G. sepium*, and *L. leucocephala* are the most important species and are grown along field boundaries as a live fence and for feeding dairy cows (Kragten and Burgers, 2000); Chen *et al.* (1992) report the planting of fodder trees in Bangladesh on bunds, paths, and homesteads for feeding ruminants. They also note that in semiarid Pakistan, farmers plant *Acacia* spp. in rows 10–12 m apart and crops in between, until the trees mature. The trees' main use is for fuel but leaves and pods are fed to livestock.

In Latin America, Murgueitio *et al.* (2011) reported intensive sylvopastoral systems involving the planting of fodder shrubs (*Tithonia diversifolia* and *L. leucocephala*) at high densities (10 000 per ha) intercropped with pastures and timber trees. The system is used in beef cattle and dairy farms in the Tolima and Eje Cafetero regions of Columbia, in Michoacan

and San Luis Potosi areas of Mexico, and in three provinces in Panama. Shrubs and pastures are directly grazed.

Fodder shrubs also feature in agroforestry systems in some developed countries. In semiarid western Australia, *Chamaecytisus proliferus* features in two grazing systems: alley farming and plantations (Abadi *et al.*, 2003). In alley farming, *C. proliferus* is planted in lines in annual pastures, with 60 m between rows. The trees are ready for browsing in the second year and cattle graze in the fields for 6 months, every other year. In the *C. proliferus* plantations, there is an understory of annual pasture. Chriyaa (2005) reported the use of fodder trees planted at wide spacings in barley and other crop fields in Spain, Morocco, and Syria, to allow for mechanical cultivation and harvesting of the crops.

Seeds, Tree Establishment, and Management

The quality and reliability of germplasm used for planting fodder shrubs is generally low throughout the tropics. High-quality seed may be available from formal sources, such as national tree seed centers but such seed is often expensive and inaccessible to farmers. Most farmers obtain seed or other planting material (e.g., seedlings or cuttings) from local sources, without any information of provenance origins and quality or the importance of genetic diversity.

A key problem characterizing most new introductions of fodder trees to areas has been the narrow genetic base of the source of seed (often only a single or very few trees). The result is that the germplasm in the most widespread use is often of inferior quality. For example, Stewart *et al.* (1996) reported that the introduction of *G. sepium* from Trinidad into Sri Lanka was based on seed from a single tree. The lack of genetic diversity in many such introduced populations leaves them highly susceptible to damage from pests and diseases and inbreeding depression lowering yield.

Lillesø *et al.* (2011) claimed that lessons from the evolution of smallholder crop seed delivery systems indicate that a commercial, decentralized model holds most promise for sustainability in promoting smallholder agroforestry systems. However, current emphasis in agroforestry is often on government and nongovernmental organization (NGO) models of delivery, which hinder the development of a commercial, decentralized system. Graudal and Lillesø (2007) reported that an efficient seed and seedling supply is only likely to be achieved if considered as part of a commercial commodity chain in a market that encourages the operation of small, competitive seed and seedling retailers. They also warn of severe market distortions caused by free seed, which is often made available by NGOs and projects, which suppresses the emergence of private sector suppliers.

In the highlands of East Africa, fodder shrub seeds are planted in nurseries, either bare-rooted or in polythene pots, and then transplanted on farm 3 months later at the onset of the rains. Others plant seed directly in their fields. An evaluation of bare-rooted *Calliandra* seedlings in western Kenya reported 34% higher survival rates than direct seeding but the cost per surviving seedling was 24% higher, due to nursery labor costs (Swinkels, 1994). Bare-rooted seedlings cost less to produce than potted seedlings but are more susceptible to drought after transplanting. The choice among alternative techniques depends on the species involved, the available resources and farmers' skills.

In the East African highlands, trees are first pruned 9–12 months after transplanting to a height of approximately 80 cm. They are pruned approximately 4–5 times per year and generally kept at a height of below 1 m, in order to minimize the effect on adjacent crops.

Much less is known about the farmer-managed natural regeneration of fodder trees and how these trees are managed once mature. In an area of eastern Kenya ranging from subhumid to semiarid, researchers identified 160 such species that farmers used for fodder. Farmers' most preferred species were *Triumfetta tomentosa*, *Aspilia mossambicensis*, and *Melia volkensii*. Among the 15 that farmers ranked highest in importance, only one, *Commiphora zimmmermanii*, was planted and its main use appeared to be as a live fence. Most were scattered in crop land. Harvesting methods varied included coppicing, pruning branches, cutting soft twigs only, or allowing animals to browse (Roothaert and Franzel, 2001).

Fodder Yields

Yields of fodder trees depend on several factors including variety, soil and light characteristics, tree density, moisture availability, and harvesting management (e.g., cutting intensity and frequency) (Chen *et al.*, 1992; Smith, 1992). Little information is available on the yield of fodder trees and most available data are from experimental rather than farm conditions. *Calliandra* yields 1.5 kg dry matter per tree per year on farms in central Kenya, grown in hedges pruned at 0.6–1 m height, five times per year (Patterson *et al.*, 1998; Wambugu *et al.*, 2011). In Zimbabwe, where many farmers plant in pure stands, *Calliandra* yields range from 2.5 to 5.6 t ha^{-1} $year^{-1}$ and *A. angustissima*, *L. leucocephala*, and *G. sepium* produce more than 3 t ha^{-1} $year^{-1}$ when cut a single time at the end of the wet season (Hove *et al.*, 2003). In the semiarid areas around Segou, Mali, *G. sepium* yields 2 t ha^{-1} $year^{-1}$ and *Pterocarpus* spp. yields 0.5 t ha^{-1} $year^{-1}$. Mulberry yields up to 20 t ha^{-1} $year^{-1}$ (dry leaves) in Tanzania and 45 t ha^{-1} $year^{-1}$ (total yield) in Costa Rica (Sanchez, 2000).

In Indonesia, Devandra and Sevilla (2002) reported dry matter yields of *S. grandiflora* at 215–412 g per tree or 9–11 t ha^{-1} and those of *G. sepium* at 1–1476 g per tree or 13–27 t ha^{-1}. *Calliandra* yields range from 0.8 to 3.3 kg per tree, and *L. leucocephala*, at 15.4 t ha^{-1}. Chen *et al.* (1992) reported dry weight leaf yields of *L. leucocephala* in Asia and the Pacific ranging from 4 to 15 t ha^{-1} $year^{-1}$.

Animal Productivity

The feed value of a forage is a function of its nutrient content and digestibility, its palatability and the associative effects of other feeds (Smith, 1992). These factors interact among themselves and with the health and breed of the animal to determine the effective feed value of the material.

On average, fodder trees are richer in protein than tropical grasses, such as *Panicum maximum* or *Pe. purpureum*. This is

especially true during the dry season, when crude protein content of many tropical grasses drops below the minimum 6% required for maintenance. In contrast, many fodder trees remain green with high protein content, often in the range of 15–24% (Smith, 1992). Fodder shrubs can be used to improve quality of crop residues and by-products (Larbi *et al.*, 1993).

The nutritive value of fodder trees cannot be accurately determined without indication of their digestibility. Leaves of fodder trees degrade fairly well and rapidly but digestibility values may not be a good indicator of the feed value of fodder because of such factors as metabolic attributes, which may reduce intake or bind nutrients. Because of such attributes, it has been generally recommended that fodder tree leaves should be less than 30% of a cow's diet and for some tree species, less than 15%. Evaluations of feed value should also be complemented by feeding trials and, if possible, ones under or simulating farmer management and conditions (Smith, 1992).

Considerable evidence on fodder shrubs' effect on milk yields comes from research on *Calliandra* in East Africa. A farmer in East Africa needs approxiamtely 500 *Calliandra* trees to feed a dairy cow throughout the year at a rate of 2 kg dry matter per day. One kilogram of dried *Calliandra* (24% crude protein and digestibility of 60% when fed fresh) has about the same amount of digestible protein as 1 kg of dairy meal (16% crude protein and 80% digestibility) (Roothaert *et al.*, 2003). Two kilograms of dried *Calliandra* provide an effective protein supplement to the basal feed of Napier grass and crop residues, according to on-farm feeding trials from Embu District, Kenya (Paterson *et al.*, 1998) and Masaka District, Uganda (Kabirizi *et al.*, 2006). Under farmers' management, milk production increased by 0.6–0.75 kg milk per kg dried *Calliandra*. Surveys also reported farmers' estimates of the milk response to *Calliandra* feedings. In one, farmers estimated that the mean response was 0.80 kg milk per kg dry *Calliandra* (Franzel and Wambugu, 2007) slightly above the range of the findings from the on-farm trials. In the other, in which farmers reported amounts of tree fodder fed and milk produced, the response was 0.35 kg milk per kg dried *Calliandra* (Place *et al.*, 2009). One of the trials also investigated the effect of *Calliandra* on butter fat and found a positive, but not statistically significant effect (Paterson *et al.*, 1999). A study in Kenya showed that intake of Napier grass increased due to supplementation with *L. leucocephala* leaves, which resulted in significant increases in milk yields. Milk yield increased over control treatment by 20% (Muinga *et al.*, 1992). *Sesbania sesban* has shown a similar effect on feed intake when used as supplement for sheep in Ethiopia (Khalili *et al.*, 1994).

Only one study was found assessing the effect of fodder trees on nondairy cattle in Africa, which confirmed the effectiveness of *L. leucocephala* as a dry season supplement for grazing steers in semiarid western Tanzania (Kakengi *et al.*, 2001).

Dairy goats are an important and rapidly growing smallholder enterprise in East Africa. Many farmers grow fodder trees to feed their goats (Place *et al.*, 2009) and studies confirm their significant impact on milk yields (Kirurio *et al.*, 1999), Niang *et al.*, 1996). Ewes supplemented with *S. sesban* in Ethiopia showed a 13% increase in milk production over ewes supplemented with concentrates (Mekoya, 2008). Numerous experiments have confirmed the effectiveness of fodder trees in increasing the productivity of sheep and goats. Sheep gained 79–90 g day^{-1} in live weight from being fed *Calliandra* in Kenya (Kirurio *et al.*, 1999; Niang *et al.*, 1996). Concerning dairy goats, supplementation with *Mimosa scabrella* in the highlands of Rwanda enabled goats to gain 50 g day^{-1} compared with 31 g day^{-1} for grass alone. Six other tree species also increased body weight (Niang *et al.*, 1996).

Benefits and Impacts

Fodder trees contribute to improved livelihoods in various ways, as discussed below (**Figure 1**).

Increased Production and Income From Cattle

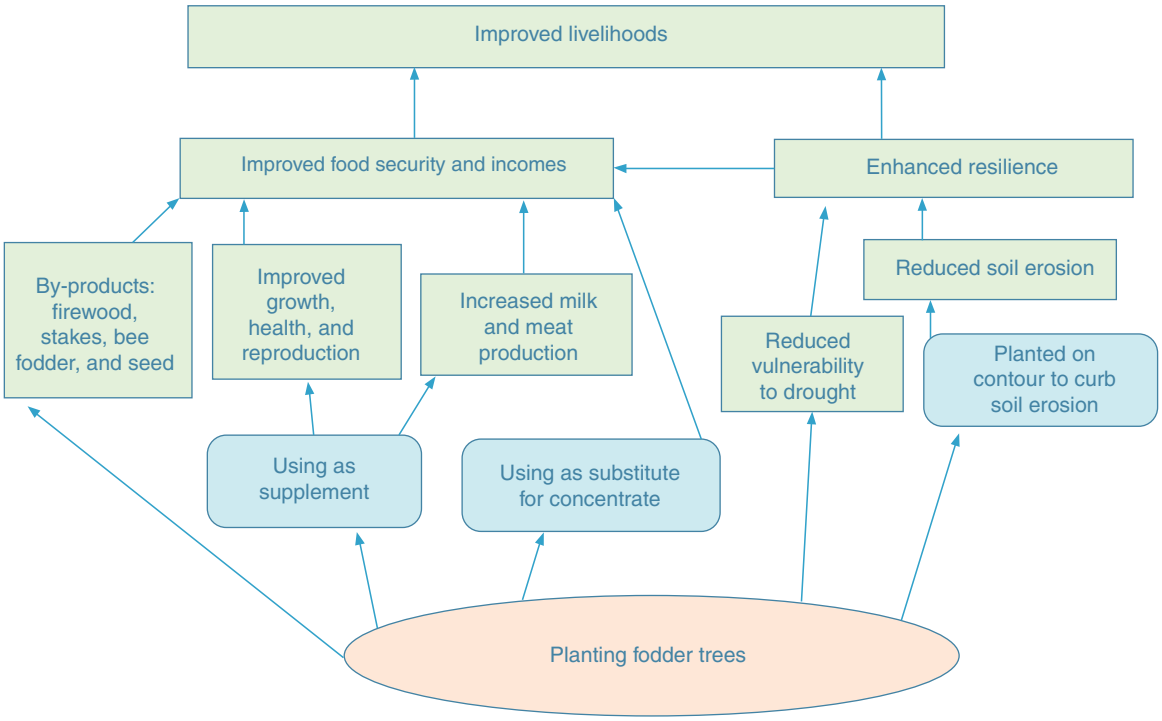
In Cagayan de Oro, Philippines, fodder trees were the most important feed source during the dry season and ranked second to fodder grasses during the wet season. The profitability of the combined and improved fodder species (trees, grasses, and herbaceous legumes) was assessed and they were found to increase net incomes from livestock production from US$68 to US$503 per household. The forages increased crop production by a further US$22.50, based on farmer estimates of increased crop yields. Further, the improved forages reduced farm labor, especially for herding and tethering, valued at US$36 per year (Bosma *et al.*, 2003).

Considerable evidence on income from fodder shrubs also involves *Calliandra*. Farmers use it both as a supplement to increase milk production and as a substitute for dairy meal. It can be fed fresh or stored and fed dry, which does not significantly reduce nutritive quality (Tuwei *et al.*, 2003). Net returns in 2002 and 2003 ranged from US$62 to US$122 per year across four sites in Kenya and Uganda for a farmer with 500 trees. Farmers' actual numbers of trees were usually fewer, ranging from means of 130 trees per farm in western Kenya to 560 trees per farm in southwestern Uganda, resulting in net returns ranging from US$30 to US$114 per year (Wambugu *et al.*, 2006). Net returns varied across sites primarily because of differences in numbers of trees and in milk prices. An estimate in 2009 found mean net returns to be US$35 per year in central Kenya (Place *et al.*, 2009). The lower amount was primarily due to lower estimates of amounts fed and response of milk yields.

An economic analysis from Chikwaka District, Zimbabwe, found that the use of fodder trees (*L. leucocephala*, *A. angustissima*, *L. diversifolia*, and *L. pallida*) in smallholder dairy had gross margins of US$13–334 and benefit–cost ratios of 1.12–3.03. The margins and ratios varied depending mainly on the amount of tree fodder fed; higher use led to higher returns (Moyo and Ayuk, 2001).

In semiarid western Australia, cattle graze on annual grasses (*Brassica* spp.) and tree legumes (*C. proliferus*) in two grazing systems: alley farming and plantations (Abadi *et al.*, 2003).

These systems earn a net present value (the present value of a stream of future costs and benefits occurring over a period of years) of approximately US$303 per ha (using a discount rate of 7%) and an annual equivalent return of US$24 per ha. In alley farming, *C. palmensis* is planted in 6 m wide belts, with



Food security, income, and livelihoods are grouped together in this diagram but contributing to one does not necessarily contribute to the other, as when an increase of cash income is taken by the male head of household for his own use.

Figure 1 Principal ways that fodder trees contribute to improved food security, incomes, and livelihoods. Reproduced from Franzel, S., Carsan, S., Lukuyu, B., Sinja, J., Wambugu, C., 2014. Fodder trees for improving livestock productivity and smallholder livelihoods in Africa. Current Opinion in Environmental Sustainability 6, 98–103.

60 m between rows. The trees are ready for browsing in the second year and cattle graze in the fields for 6 months, every other year. In the *C. palmensis* plantations, there is an understory of annual pasture. Compared to annual pastures, *C. palmensis* alley farming and plantations increase net present values by US$65 and US$124 per ha, respectively. Incremental annual equivalent returns are US$5 and US$10, respectively (Abadi *et al.*, 2003). These numbers appear low but as ranching is extensive, a small per-hectare increment can add substantially to farm income.

Increased Production and Income from Small Ruminants

The only economic analysis involving fodder trees and small ruminants in Africa is from Segou, Mali. In on-farm trials, *G. sepium* and *Pterocarpus* spp. were evaluated on their contributions to sheep growth and on the time they saved farmers from having to collect fodder off the farm. Fodder shrubs were found to be profitable only under conditions where alternative options were expensive (Hamer *et al.*, 2007). Although not a formal economic analysis, a study from Ethiopia found that farmers in three land use systems made widespread use of *S. sesban* for feeding sheep, and had strong positive perceptions of the tree's effect on weight gain and reproductive performance in two of them (Hess *et al.*, 2006; Mekoya *et al.*, 2008).

Other Benefits as Feeds

Few studies report on the marketing of fodder tree leaves or their use in commercial feeds. In the Tanga area of northeastern Tanzania, *L. leucocephala* leaf meal is widely marketed, primarily to urban dairy producers. Most is from wild populations but some is cultivated on farms. Leaf meal is also an ingredient of one of the country's major mineral supplements (Franzel *et al.*, 2007). Analyses of the use of leaf meal in mineral blocks for sheep in Nigeria have been conducted but use at the farm level is not reported (Aye and Adegun, 2010). *Leucaena leucocephala* leaf meal is widely sold along road sides in eastern Thailand (S. Franzel, pers. comm.).

Sonaiya and Swan (2004) reported that tree leaves are an important component of poultry feeds in many countries and specifically recommend *Leucaena* spp., *Calliandra* spp., and neem (*Azadirachta indica*). They report on a study from Pakistan that found that a 20% ration of fresh neem leaves increases feed intake and egg production in layers. Farmers in East Africa also report feeding tree biomass to poultry (primarily to make yolks brighter yellow, which increases egg prices), rabbits, and fish (Place *et al.*, 2009).

The above analyses do not take into account many other benefits of fodder shrubs as cited by farmers in Kenya and Uganda (**Table 3**). These include the provision of products (firewood, stakes, bee forage, and seeds, which are sometimes sold) and services (fencing, soil fertility improvement, soil

Table 3 Benefits of fodder shrubs, other than inceased milk production, according to dairy farmers in two African farming systems

Type of benefit	*Percentage of farmers mentioning in*	
	Embu area, Kenya (N = 60)	*Kabale area, Uganda (N = 93)*
Firewood	50	72
Soil fertility improvement	48	72
Improvement in animal health	38	5
Soil erosion control	18	20
Improved creaminess of milk (increase in butter fat)	18	6
Fencing	18	76
Revenue from sale of seedlings	13	9
Stakes	9	70

Note: Percentages sum to greater than 100 because many farmers mentioned more than one benefit.
Source: Reproduced from Franzel, S., Carsan, S., Lukuyu, B., Sinja, J., Wambugu, C., 2014. Fodder trees for improving livestock productivity and smallholder livelihoods in Africa. Current Opinion in Environmental Sustainability 6, 98–103.

erosion control, and improvement in animal health and reproduction) (Franzel and Wambugu, 2007). Few estimates of the quantities and values of these products and services were found. In Kenya, hedges combining Napier grass and *Calliandra* or *L. trichandra* reduced runoff and soil erosion while not reducing adjacent maize yields (Angima *et al.*, 2002; Mutegi *et al.*, 2008). Fodder trees can also help farmers adapt to and mitigate climate change (Badege *et al.*, 2013). For adaptation, they are deep rooted, resistant to drought, and maintain high protein levels during the dry season, when high-quality feed is scarce (Wambugu *et al.*, 2011). For mitigation, fodder trees improve livestock productivity, which helps reduce methane emissions per unit of output and helps reduce carbon emissions by substituting for commercially manufactured concentrates. But no studies were found that explicitly quantify the contributions of fodder trees to climate change adaptation or mitigation.

Gender Considerations

There is widespread recognition that women are disadvantaged in the agricultural sector of many developing countries (World Bank, 2012; Kiptot and Franzel, 2012). This has led to research and development initiatives to try to redress the imbalance. Some of these initiatives have deliberately targeted women groups to impart knowledge and technology to them, to ensure that extension activities address different interest groups, holding separate meetings for men and women and training more women extension officers, particularly to serve communities that have strong traditions that prohibit male extension officers from interacting with women farmers. Research on gender and fodder trees has shown that women in Africa can benefit considerably from planting fodder shrubs, for several reasons (Kiptot and Franzel, 2011). First, women in many countries are responsible for collecting fodder off the farm. Growing fodder on farms can thus reduce their time spent searching for fodder, freeing up labor for attending to their families or engaging in other productive enterprises. Second, because women are often cash-constrained, they are unable to purchase concentrates for feeding their livestock. Fodder shrubs can provide protein at a much lower cost than purchased concentrates. Third, female households head plant fodder shrubs at about the same rate as male heads of households and are able to manage the trees as effectively (Kiptot and Franzel, 2011). Finally, research has shown that women in East Africa have access to cash earned from dairy. In Tanzania and Uganda, women managed and controlled 39.8% of the income from milk, and 70.4% of the income if sold in informal markets (Njuki *et al.*, 2011). Planting fodder shrubs will increase animal productivity and hence the income that they access from milk.

Key Challenges for Enhancing Fodder Trees' Benefits

Three key constraints limiting the uptake and benefits of fodder shrubs are as follows:

Species diversification: There is a lack of species appropriate to different agroecological zones, particularly high altitude (>2000 m) and semiarid zones. In humid and subhumid zones, species are needed that provide more nutritious biomass than some of the species in widespread use, such as *Calliandra*, and that are resistant to psylids (*Heteropsylla cubana*), jumping plant lice, which prevent farmers from planting *L. leucocephala*. More research is also needed on indigenous species. Efforts should be made to integrate the huge amount of indigenous knowledge about indigenous species with scientific methods to screening and testing them.

Lack of functioning seed supply systems: Emerging seed markets have facilitated adoption in some countries (e.g., Kenya; Acharya *et al.*, 2010) but are yet to emerge in other countries. Main constraints include policies of government seed centers, plant health regulatory agencies, and NGOs that distribute free seed (Franzel and Wambugu, 2007). Decentralized, commercial models provide greater potential than government or NGO-led models (Lillesø *et al.*, 2011).

Weak extension support: Although fodder trees require relatively little land, labor, or capital, they are a knowledge-intensive practice as farmers need to acquire new skills such as nursery establishment, tree pruning, and seed collection. As weak as extension systems are in most developing countries, agroforestry extension is nearly nonexistent. Promoting innovative approaches such as farmer to farmer extension, civil

society campaigns, and facilitative policies can help promote widespread adoption (Wambugu *et al.*, 2011).

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See also: Agroforestry: Fertilizer Trees. Agroforestry: Practices and Systems

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Agroforestry: Hydrological Impacts

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Glossary

Competition Occurs when trees exploit the same resources as crops.
Complementarity Occurs when trees acquire resources that crops cannot acquire.
Hydraulic lift Upward transfer of water through roots from wetter soil at depth to surface horizons.
Leafing phenology Seasonal trend in leaf flushing and leaf drop.
Resource capture The capture of essential growth resources (light, water, and nutrients) by plants.
Sap flow Measurement of water movement in stems or roots using heat as a tracer.
Water-use efficiency The ratio of the total amount of biomass produced to crop water use.

Introduction

In addition to their social and economic value, forests and agroforestry (AF) have been widely promoted as a viable solution to overcome the loss of ecosystem functions associated with the conversion of natural landscapes for human use (Jose, 2009). AF systems vary in the density and configuration of trees in farming landscapes from a few scattered trees or line plantings to dense and complex agroforests. However, the relationship between tree cover and water supply is not straightforward and forest/agriculture policies are often at odds with scientific understanding. In the tropics, forest/farming and water policies were often based on the assumption that tree-covered landscapes are the most appropriate way to maximize water yield, regulate seasonal flows, and ensure high water quality under all hydrological and ecological situations (Calder *et al.*, 2007). According to this assumption, conserving or extending tree cover in upstream watersheds is the most effective way to enhance water availability for agricultural, industrial, and domestic use and prevent floods in downstream areas. Various national agencies, often with international cofunding, are spending vast sums of money on tree planting and soil conservation efforts based on the belief that 'more trees mean more water'.

However, forest hydrology research in the 1980s and 1990s suggests a different picture and has implications for AF. Although the important role of upstream forest cover in ensuring the delivery of high-quality water has been confirmed, earlier assumptions regarding its benefits in terms of providing more temporally dispersed downstream seasonal and annual flows were generally overestimated (Bruijnzeel, 2004). Furthermore, in arid and semiarid ecosystems, forests and savannah woodlands do not provide the best land cover to increase downstream water yield. It is now recognized that the protective role of forest cover in regulating extreme flow in tropical ecosystems has been overestimated, particularly in connection with major events such as floods affecting large-scale watersheds or river basins (FAO and CIFOR, 2005).

According to van Noordwijk *et al.* (2006), current approaches to AF solutions to watershed problems require four basic steps: (1) diagnosis of problems at the watershed scale, (2) comparing land-use options on the basis of buffering functions, (3) modeling biophysical degradation and rehabilitation processes in the analysis of tradeoffs between profitability and watershed functions, and (4) negotiations between stakeholders of solutions based on tradeoffs. They concluded that the criteria and indicators of watershed functions such as the timing and quality of river flows are influenced by a combination of effects, including the green and brown cover provided by plant canopies and surface litter layers, soil surface properties and structure, and the landscape drainage network. Using data from two contrasting watersheds at Mae Chaem (1500 mm annual rainfall) in Northern Thailand and Way Besai (2500 mm rainfall) in Lampung, Indonesia, they found that the changes in land cover have relatively little effect on low river flow. Instead, they showed that changes in soil structure tend to dominate long-term opportunities to keep watersheds productive, as well as providing quality water at the desired time.

Impact of Trees on Water Balance

Water balance represents the balance between inputs from rainfall and/or irrigation and the sum of evapotranspiration, stream flow, and losses to groundwater. Contour-planted hedgerows are frequently recommended for sloping land in the tropics because they increase infiltration and improve soil conservation (Young, 1997). An estimated 500 million people practice unsustainable forms of subsistence agriculture on marginal hillsides, exacerbating the problems of erosion. To understand how trees influence the hydrology of individual

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fields or farms, it is necessary to understand the processes involved. To begin it is examined how the introduction of trees may improve on-farm water balance by reducing losses. Evidence from analyses of farmers' fields around the world shows that, on average, only 30% of rainfall is used for crop growth and emitted to the atmosphere as transpiration (Rockstrom *et al.*, 2007); the remainder is lost as runoff, evaporation and drainage. In humid zones, rainfall greatly exceeds that required to sustain crop transpiration and the main losses are due to runoff and drainage. In arid and semiarid areas, transpiration ranges between 5% and 40% of rainfall, suggesting that there is ample scope to increase agricultural productivity because water is wasted. Although poor agricultural production is often attributed to low rainfall, other factors such as low soil fertility or poor land management are often even more important. In the case of AF, integration of trees can theoretically increase productive use of rainfall by reducing runoff, drainage and soil evaporation by maintaining partial leaf cover following crop harvest.

Perhaps the best example of the effectiveness of this approach to water management in farming systems is in Southern Australia, where trees are used to manage excess water that has accumulated in rising water tables since the native perennial vegetation was cleared. This problem exacerbates salinization, a major constraint to agriculture in this area. The hypothesis is that the introduction of trees creates a much higher year-round leaf area than annual cropping systems, thereby combating secondary salinization by increasing the extraction of groundwater and enhancing drainage below the crop rooting zone (Lefroy and Stirzaker, 1999). Evidence for young eucalypts or tagasaste fodder hedgerows has shown that their roots remove water from below the crop rooting zone between the tree belts. Furthermore, strategic placement of trees in the landscape minimizes the land area required to be planted to induce the desired effect on local hydrology (Brooksbank *et al.*, 2011a). Eucalyptus is renowned for its high water consumption, competitiveness, fire risk and suppression of biodiversity, and is rarely recommended for AF. Unsurprisingly, its high productivity and demand for water are raising concerns over declining water yield in catchments in South Africa, Kenya, and India (Ong, 2003). However, despite these problems, eucalyptus is highly prized as a cash crop in countries experiencing severe deforestation such as Ethiopia, India, and China.

Although the moderating effects of forests on stream flow have been reevaluated, evapotranspiration from forests nevertheless has an important influence on rainfall. Recent work combining remote sensing data for rainfall and vegetation with atmospheric transport trajectories demonstrates that forest cover increases tropical rainfall on a regional scale, an effect which may extend for hundreds and thousands of kilometers downstream of forested areas (Spracklen *et al.*, 2012).

Complementary and Competitive Interactions for Resources

AF is known to increase overall system productivity and enhance soil structure, nutrient recycling, and sustainability, while producing timber, firewood, fruit, fodder, and green manure in addition to annual food crops (Young, 1997). However, the potential benefits depend on complex spatial and temporal interactions between the biological, physical, hydrological, and climatic components of the system; these include the tree and crop species involved, soil type, depth and fertility, quantity and distribution of rainfall, solar radiation, and air temperature and atmospheric humidity (Ong *et al.*, 2002, 2006; Lott *et al.*, 2009). A major aspect affecting the overall outcome of integrating trees in farming systems is the increasing competitiveness of trees as they establish and grow larger (Lott *et al.*, 2000a,b).

Tree roots extend to much greater lateral distances and depths than those of crops (Stone and Kalisz, 1991), thereby exploiting a much greater soil volume. There is therefore the potential for both complementarity and competition depending on the distribution and activity of tree and crop roots in the soil profile. Rooting depth is potentially unlimited in deep soils lacking impenetrable hardpans or stony horizons and the roots of some tree species may reach depths of 20–30 m in search of deepwater reserves.

Complementarity may be either spatial or temporal. Spatial complementarity occurs when trees exploit deep reserves of water and nutrients, satisfying the central tenet of AF that trees must exploit resources which crops cannot access if the system is to succeed (Cannell *et al.*, 1996). For example, stable isotope studies in Niger have shown that neem trees (*Azadirachta indica*) extracted groundwater at a depth of 6 m at Majjia Valley but not at Sadore, where the water table was too deep to be accessible (35 m; Smith *et al.*, 1997). By contrast, temporal complementarity occurs when trees make their primary demand for resources at different times to crops, for example, during the dry season after crops have been harvested. This has been illustrated in studies of hedgerow intercrops containing *Leucaena leucocephala* at Hyderabad, India, which showed that the trees continued to grow during the dry season when 20% of the annual rainfall was received (Black and Ong, 2000).

An interesting agronomic solution to achieving temporal complementarity is to use trees that are fully or partly deciduous (leafless) during the cropping season (Broadhead *et al.*, 2003a,b; Muthuri *et al.*, 2005). This complementary leafing phenology means they are less competitive than evergreen trees which utilise resources throughout the year. However, adoption of less competitive tree species may be incompatible with the objectives of farmers as they are often less productive than fast-growing trees producing economically valuable products. If farmers wish to plant more fast-growing species, management practices such as root and/or shoot pruning may be needed to control competition for below-ground resources and reduce shading of crops.

Trees Improve Infiltration of Water and Reduce Evaporation and Runoff

The use of improved fallows is an important AF practice for improving soil fertility as it avoids direct competition between

trees and crops. This is illustrated by the bench terraces used on steep hillsides in Kabale District, Southern Uganda, where repeated downslope cultivation and soil creep during heavy rain draw topsoil to the front of the terrace, exposing the infertile subsoil on the upper terrace. The upper terrace is therefore less productive, providing only 5% of the total yield when the entire terrace is planted with sole crops. However, tree fallows containing *Alnus acuminata* (alnus), *Calliandra calothyrsus* (calliandra), *Sesbania sesban* (sesbania), or a mixture of all three species planted on the upper part of the terrace produce a range of tree-based products and improve soil structure and fertility, whereas food crops such as beans and maize continue to be grown on the lower terrace (Siriri *et al.*, 2010, 2012).

In this study, measurements of soil water content (θ_w) when sesbania trees were 31–39 months old and alnus and calliandra were 37–45 months old showed that unpruned sesbania increased θ_w by 14% and 18%, respectively, on the upper terrace, where the trees were grown, and in the cropping area on the lower terrace. The equivalent increases for alnus were 15% and 9%, whereas the more competitive calliandra reduced θ_w by 3% and 15%, respectively, on the upper and lower terrace. In parallel with these effects on θ_w, soil evaporation (E_s) comprised 53% of rainfall under sole maize compared with 38%, 37%, and 29% in the *Sesbania*, *Calliandra*, and *Alnus* systems following periods of high rainfall (Siriri *et al.*, 2012). *Alnus* and, especially, *Sesbania* therefore increased the available soil moisture and reduced the proportion of unproductive rainfall. Moreover, tree fallows reduced runoff from 17% to 4% of seasonal rainfall (Siriri *et al.*, 2006). These findings suggest that *Sesbania* and *Alnus* may be integrated on smallholdings without compromising water supplies for crops, although alnus must be pruned to sustain crop yield. By contrast, although *Calliandra* reduced E_s, the water saved was absorbed by its extensive root system, depriving crops of water and suggesting that *Calliandra* fallows are inappropriate because the crop yield was reduced even after pruning (Siriri *et al.*, 2010).

In addition to accessing deep water reserves beyond the reach of annual crops, tree roots act as a safety net to capture nutrients leached from the topsoil and return these to the soil surface as litter (Rowe *et al.*, 1999). Nitrogen (N) is the most limiting nutrient for crop production in much of sub-Saharan Africa, but the high cost of inorganic fertilisers often precludes their use by poor farmers. This has increased interest in low input AF systems containing leguminous tree species whose leafy biomass provides green leaf manure (GLM) to supply N to crops (Okogun *et al.*, 2000). Crop yield is typically strongly correlated with preseason mineral N concentration (NO_3^-+NH_4^+) in the topsoil and mineralisation of organic matter following improved fallows or in mixed cropping systems containing leguminous species (Ikerra *et al.*, 1999). Application of *Gliricidia* GLM leads to almost immediate release of N, with 30% being released within 7 days and up to 60% within 24 weeks. If inorganic fertiliser is also added, *Gliricidia* GLM releases up to 60% of its N within 3 weeks and 70% within 24 weeks (Itimu, 1997; Phombeya, 1999). Significant improvements in maize yield were apparent in tree-based systems after 2 years, when approximately 3.0 t ha^{-1} of grain was obtained, which is triple that for unfertilised sole maize (Chirwa *et al.*, 2003). However, although application of GLM increased preseason soil mineral N levels, these declined rapidly during early crop growth when the plants were too small to exploit the available N (Chirwa *et al.*, 2006). In such circumstances, the presence of trees improves nutrient use efficiency by providing a safety net to capture nutrients leached from the topsoil during intense rainfall and return them to the surface horizons on which crop roots primarily depend, in a manner analogous to the hydraulic lift of water described later.

The greatest opportunity for simultaneous tropical dryland AF systems appears to be exploitation of complementary interactions between trees and crops grown for their marketable products (Ong and Leakey, 1999). Although trees provide valuable ecosystem services, these are not usually the primary reason why farmers retain, manage, or plant them. Thousands of tree species are cultivated for valuable products such as poles, fruit, fodder, firewood, and medicinal compounds, as illustrated by the World Agroforestry Centre's Database. Tradeoffs often exist between valuable tree products and the ecosystem services trees bring. For example, fast-growing eucalypts are highly prized in highly degraded countries such as Ethiopia, where they are by far the most popular tree species with farmers and attempts to introduce more benign species have been disappointing.

Species with outstanding hydrological properties and excellent complementarity of water use are often neglected by farmers. Many native tree species are ideally suited for planting with annual crops but either of low value or have slow growth rates. An exceptional case of successful avoidance of competition in simultaneous AF systems is the traditional use of *Faidherbia albida*, now a target species of the farmer-managed natural regeneration program (FMNR) in the Sahelian parklands. Its high degree of complementarity results from its unusual reverse canopy phenology as it is leafless during the cropping season and leafy during the dry season. Many authors have reported increased crop yields under *F. albida* trees (the 'albida effect'), which have been attributed to improved availability of water and essential macronutrients, particularly nitrogen and phosphorus, although the relative importance of these factors varies seasonally and depends on soil water and nutrient status at specific sites (Rhoades, 1995; Kho *et al.*, 2001).

However, the 'albida effect' would require 20–40 years to develop in Ethiopia (Poschen, 1986), a timescale well beyond the planning horizon of most farmers. Of course, it would be ideal to match valuable trees with crops so reductions in crop yields are more than offset by valuable products from the trees. One example is the *Melia volkensii*–millet system used in semiarid Kenya (Ong and Leakey, 1999). A recent approach is to promote and assist FMNR of useful trees such as *F. albida* (Garrity *et al.*, 2010). FMNR began in Niger during the 1980s due to the failure of massive conventional reforestation projects in the Sahel. An analysis of satellite imagery has revealed that 4.8 m ha of *F. albida*-dominated farmlands have spread through the Maradi and Zinder regions through this practice (Reij *et al.*, 2009). Further research is needed to understand fully how FMNR promotes rapid tree growth in Niger.

Why Tree Root Distribution Matters

Historically, much research has focused on the more visible above-ground competition between trees and crops, and in understanding the effects of tree canopies on crops resulting from shading and rainfall interception. However, below-ground competition, determined primarily by the distribution and activity of tree and crop roots, is at least as important, but much less well understood, because the required research is more difficult. Below-ground aspects of competition are invisible to farmers, who often attribute competition to shade rather than for water and nutrients. In practice, crop yield is determined by the balance between the above- and below-ground elements of competition, depending on the prevailing limiting factors for growth. Disentangling these issues is challenging.

The use of soil water by trees and crops in AF systems depends on many factors, but is optimized when use of below-ground space is maximized both spatially and temporally. This involves consideration of both the architecture and activity of tree and crop roots at different developmental stages. Annual crops and perennial grasses are relatively shallow-rooted, occupying the surface horizons where soil water content is most variable and responds rapidly to rainfall. In contrast, tree roots can extend deep below the soil surface and laterally into the crop rooting zone, well beyond the edge of the tree canopy (Stone and Kalisz, 1991; Schroth, 1998). The main structural roots of trees are long lived and provide the framework on which the fine roots (<2 mm diameter), which are active in water and nutrient acquisition, are deployed; these are short lived and their turnover makes a considerable contribution to soil carbon accumulation. Although deep tree roots can tap into ground water, evidence from sap flow studies (Brooksbank *et al.*, 2011c) indicates that trees preferentially access water from surface zones when this is available. Thus, trees usually compete with crops during the rainy season as their preexisting rooting framework provides a competitive advantage over the emerging roots of germinating crops. Though tree species vary in rooting architecture and root biomass, this is not necessarily reflected by their growth or competitiveness (Wajja-Musukwe *et al.*, 2008). An evaluation of the ratio of root number in the top 1.8 m of soil to trunk volume has shown that *Casuarina equisetifolia* and *Markhamia lutea* had significantly higher ratios than *A. acuminata*, *Maesopsis eminii*, and *Grevillea robusta*; *Casuarina* and *Maesopsis* were most competitive with crops, whereas *Markhamia* and *Grevillea* were least competitive. Tree propagation method also affects root architecture, and hence, potentially, competition (Mulatya *et al.*, 2002; Asaah *et al.*, 2010, 2012).

Several options are available to farmers to manage below-ground water resources (Schroth, 1998; Rao *et al.*, 2004). Their decisions depend on the relative value of products from trees and crops, labour supplies, and availability of soil resources. In some situations, trees and crops may be temporally segregated using rotational fallows, but in simultaneous AF systems competition can be controlled using appropriate tree/crop combinations and planting configurations, or tree management practices involving root and/or crown pruning to control water demand and zones of water uptake. An agronomic approach to achieve temporal complementarity is to use trees with complementary leafing phenology; for example, species that are fully or partly deciduous are less competitive with crops than the evergreen species that capture resources throughout the year (**Figure 1**; Broadhead *et al.*, 2003a,b; Muthuri *et al.*, 2005).

Pruning offers a direct and adaptable method of controlling competition and has been the focus of several studies in East Africa (Tefera, 2003; Rao *et al.*, 2004; Wajja-Musukwe *et al.*, 2008; Namirembe *et al.*, 2009; Siriri *et al.*, 2010, 2012). This practice enables farmers to grow the tree species they prefer by managing their growth. Crown pruning varies in intensity and ranges from removing the lower branches to raise the tree canopy to the removal of almost all branches of trees or hedgerows (pollarding). Crown pruning has the added advantage of yielding animal fodder, fuel, and small wood and provides an ongoing and flexible source of nontimber products and income before the trees are harvested. Root pruning may be achieved by tillage as the normal process of land preparation disrupts the fine roots of trees in the surface soil horizons. As these rapidly regrow, longer lasting effects can be achieved by severing all lateral roots close to the trunk with a machete or hoe at the start of the cropping season. This enforces spatial separation of tree and crop roots, but yields no direct product unless farmers are sufficiently fuel-hungry to excavate cut roots. The ease of the first cut depends on the age of the trees but, if repeated annually, the cutting of root regrowth requires little effort and is easily integrated into land preparation. Although root pruning is an attractive option in some circumstances, practitioners must be aware that, if this is incomplete, the activity of the remaining uncut lateral roots is increased so that no overall improvement in crop yield is obtained (Wajja-Musukwe *et al.*, 2008). **Figure 2** illustrates the potentially substantial beneficial effect of root pruning on crop growth: maize has attained full height adjacent to the tree on the pruned side, but in this situation of 'incomplete' pruning, the competition effect is exaggerated on the unpruned side.

The influence of pruning trees on associated crops varies between species. In the study of bench terraces in Uganda, mentioned earlier (Siriri *et al.*, 2010), in which three tree species were grown on the infertile upper third of terraces and annual crops were planted on the lower terrace, shoot pruning of trees <2 years old was sufficient to maintain crop yield, but a combination of crown and root pruning was required as trees grew larger. *Calliandra calothyrsus* was more competitive than *A. acuminata* and *S. sesban*, whereas beans (*Phaseolus vulgaris*) were more sensitive to competition than maize (*Zea mays*). Measurements of sap flow through the trunks of trees can be used to determine diurnal and longer term patterns of water use and the impact of pruning. Such studies revealed that root pruning greatly reduced diurnal water use in *G. robusta* in Kenya (**Figure 3(a)**; Anyango, 2005), and that shoot or root pruning both reduced sap flow in *Alnus* and *Sesbania*, whereas only root pruning was effective in reducing water use by *Calliandra* in Uganda (**Figure 3(b)**; Siriri, 2013).

Tefera (2003), working on boundary-planted trees (*C. equisetifolia*, *G. robusta*, *M. lutea*, and *Eucalyptus grandis*) in Kenya, observed that pruning (pollarding, root pruning, and pollarding plus root pruning) increased the survival and productivity of intercropped maize compared with unpruned

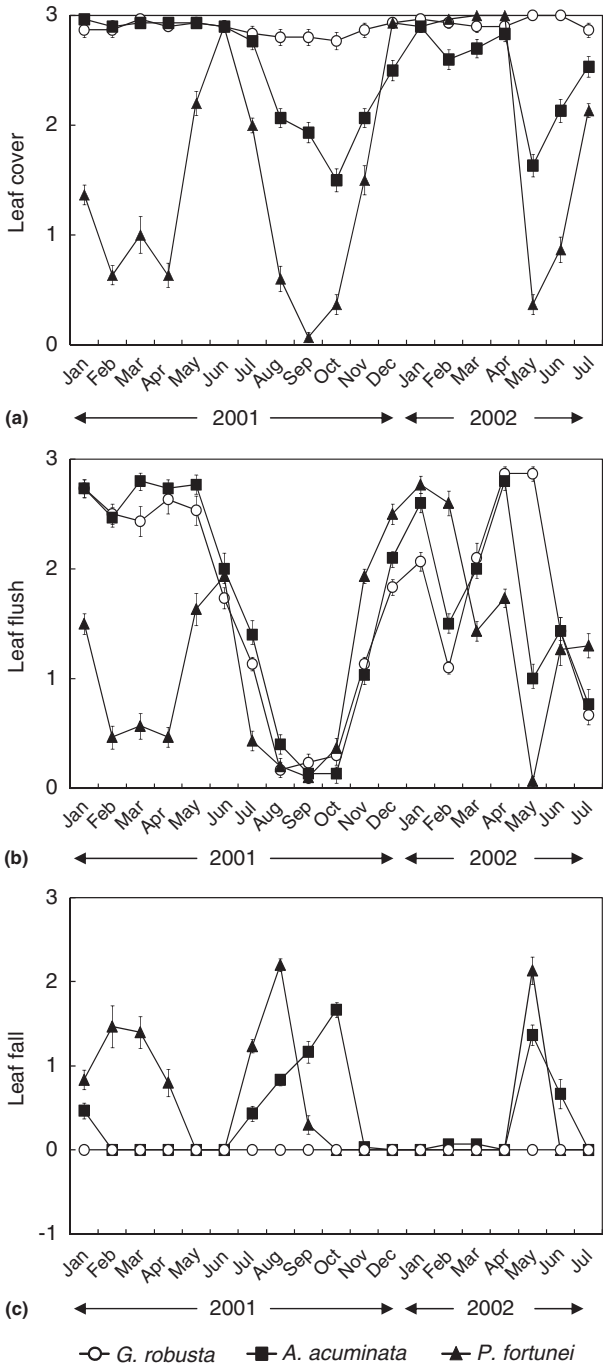


Figure 1 Time courses for (a) leaf cover, (b) leaf flush, and (c) leaf fall in *Grevillea robusta, A. acuminata,* and *Paulownia fortunei* trees at Thika, Kenya, between January 2001 and July 2001. Adapted from Muthuri, C.W., Ong, C.K., Mati, B.M., van Noordwijk, M., 2005. Modeling the effects of leafing phenology on growth and water use by selected agroforestry tree species in semi-arid Kenya. Land and Water Resources Research 4, 1–11. Vertical bars show double standard errors of the mean. Scores were ascribed using a four-point scale ranging from 0 (absent), 1 (low), 2 (intermediate) to 3 (high).

control plots, although effects varied between species (Figure 4). Two years after pruning, sap flow was lowest in pollarded *C. equisetifolia* and *G. robusta* trees and highest in



Figure 2 Influence of root pruning on one side of the *Grevillea robusta* tree row 2 years previously (far side of the tree row) on the growth of maize in Western Kenya. Note that growth was greatly reduced by competition for below-ground resources on the unpruned side of the tree row (foreground).

root-pruned trees (Figure 5), indicating that these were using alternative deep sources of soil water to support the transpirational demand of the canopy. These data indicate that root pruning can redirect water uptake by trees to deeper soil layers, thereby avoiding stomatal closure and enabling them to continue to grow; however, if the canopy is not pruned, it will continue to compete with crops through shading and rainfall interception. Such effects are likely to vary with site, tree species, and planting density.

It is important to recognize that management for complementarity of water use by root pruning may detract from other potential advantages of tree-crop combinations, such as N fixation in root nodules by rhizobial bacteria and nutrient uptake by symbiotic mycorrhizal fungi associated with roots and proteoid roots, as these functions are more closely associated with surface than with deep roots.

Importance of Hydraulic Lift

Hydraulic lift is defined as the passive movement of water through the roots of trees from deeper and wetter soil layers to shallower and drier horizons along a gradient of soil water potential (Richards and Caldwell, 1987). This not only occurs nocturnally when transpiration is low, but may also occur during the day along water potential gradients induced by variation in soil salinity. This process redistributes water to topsoil, where it can be reabsorbed during subsequent periods of rapid transpiration. Hydraulic lift may be an important mechanism for avoiding drought stress by increasing daytime water supplies. This allows the stomata to remain open, enhancing assimilate production and growth in water-limited environments (Kizito *et al.*, 2012). Hydraulic lift has been demonstrated for more than 50 species from a variety of climates. Reverse hydraulic lift may also occur when downward movement of water between surface and deeper soil horizons occurs through roots (Jackson *et al.*, 2000). This process allows

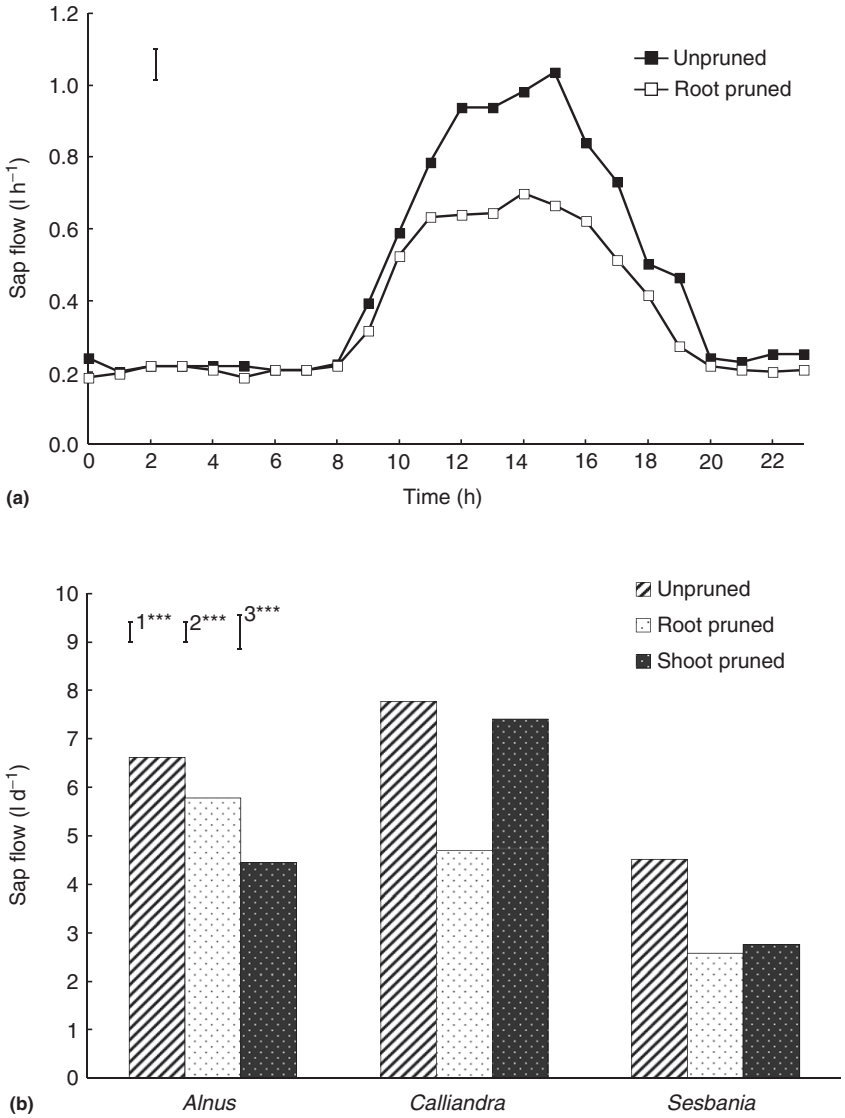


Figure 3 (a) Diurnal time courses of sap flow in unpruned and root-pruned *Grevillea robusta* trees shortly after root pruning was completed; vertical bar shows standard error of the difference (SED) (Anyango, 2005) and (b) influence of tree species and pruning treatment on mean daily sap flow rates for *A. acuminata*, *C. calothyrsus*, and *S. sesban*; vertical bars 1, 2, and 3 show SED values for species, pruning treatment, and tree-pruning treatment interaction. ***Denotes significance at $p < .001$ (Siriri, 2013).

a more rapid rehydration of deeper horizons when the topsoil is rewetted by rainfall than could be achieved by normal gravitational percolation.

In Africa, hydraulic lift amounted to 20% and 17.5% of the total volume transpired by *Vitellaria paradoxa* and *Parkia biglobosa*, respectively, in a semiarid Sahelian Parkland environment (Bayala *et al.*, 2008). In Australia, measurements for *Eucalyptus kochii* have shown that water redistributed by hydraulic lift contributes up to 27% of daily transpiration (Brooksbank *et al.*, 2011a); planting deep rooting trees that are able to exploit groundwater via hydraulic lift increased water use and biomass production by up to sixfold and tenfold, respectively, because roots were able to reach the relatively shallow water table (Brooksbank *et al.*, 2011a, 2011b, 2011c). The dimorphic root system of *F. albida* has both vertical and lateral roots, which allow it to tap groundwater to substantial depths, while still exploiting the surface horizons where nutrient supplies are greatest, suggesting the existence of hydraulic lift (Roupsard *et al.*, 1999). In Tanzania, Ludwig *et al.* (2003) observed that hydraulic lift only occurred during unusually wet years and was largely absent in *Acacia tortilis* during severe drought.

Thus, hydraulic lift may have a critical role in delaying soil drying and protecting fine roots in the topsoil from loss of hydraulic conductivity (Caldwell *et al.*, 1998). However, in the savannas of East Africa, the potentially beneficial effect of redistributing large quantities of water by acacia trees was offset by competition in the upper soil horizons (Ludwig *et al.*, 2004). Thus, the advantage of hydraulic lift depends on soil moisture content and other factors, such as soil depth, which are known to shape inter- and intraspecific interactions between plants.

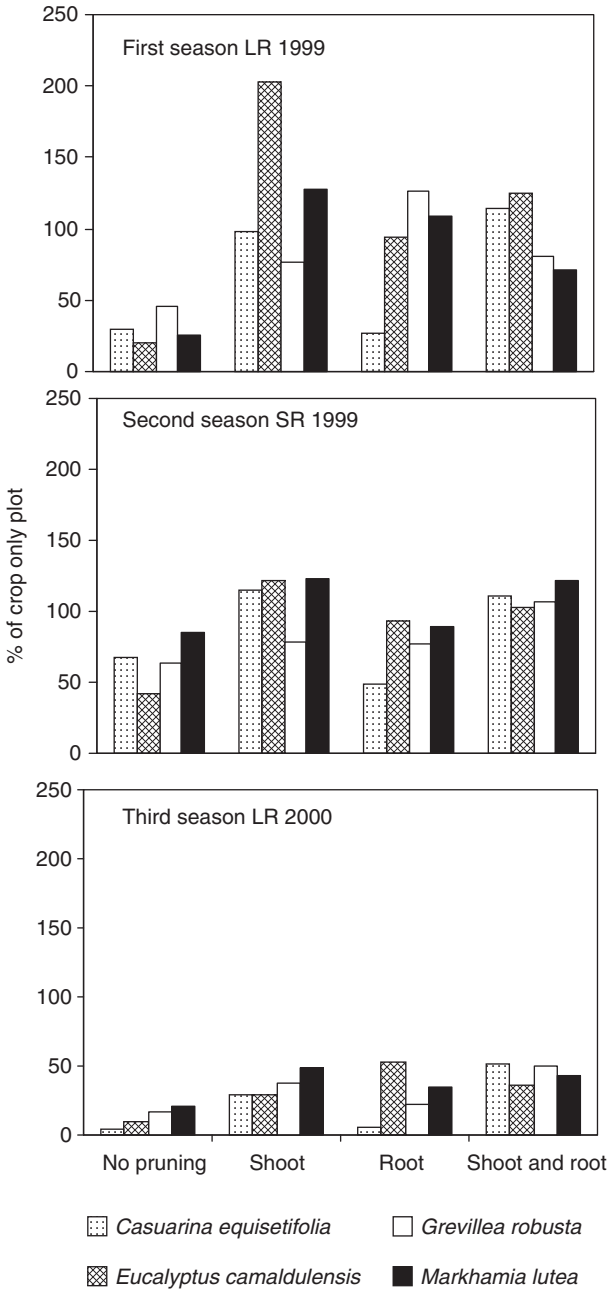


Figure 4 Effects of shoot, root, or shoot plus root pruning on maize yield relative to sole maize crops for four tree species. Data are for the first three cropping seasons after pruning at Siaya, Western Kenya. LR and SR represent long and short rains (Tefera, 2003). Reproduced with permission from Rao, M.R., Schroth, G., Williams, S.E., *et al.*, 2004. Managing below-ground interactions in agroecosystems. In: van Noordwijk, M., Cadisch, G., Ong, C.K. (Eds.), Below-Ground Interactions in Tropical Agroecosystems: Concepts and Models with Multiple Plant Components. Wallingford, UK: CABI Publishing, pp. 309–328.

Modeling the Impacts of Agroforestry

An overall assessment of whether AF systems use rainfall more effectively than a combination of woodlots and open fields can only be made when all components of the water balance are understood and compared. Furthermore, as it is not possible to make direct measurements of all possible tree and crop combinations, it is necessary to combine direct measurements with modeling. For example, analysis of water use in a *G. robusta*–maize AF system in semiarid Kenya has shown that approximately 59% of rainfall was lost by soil evaporation in the absence of a tree canopy, compared with approximately 44% under a tree canopy. This represents a substantial saving of approximately 117 mm year^{-1}, which was directly related to canopy cover, clearly demonstrating the potential improvement in water use that can be achieved by increasing ground cover in rain-fed agriculture (Wallace *et al.*, 1999).

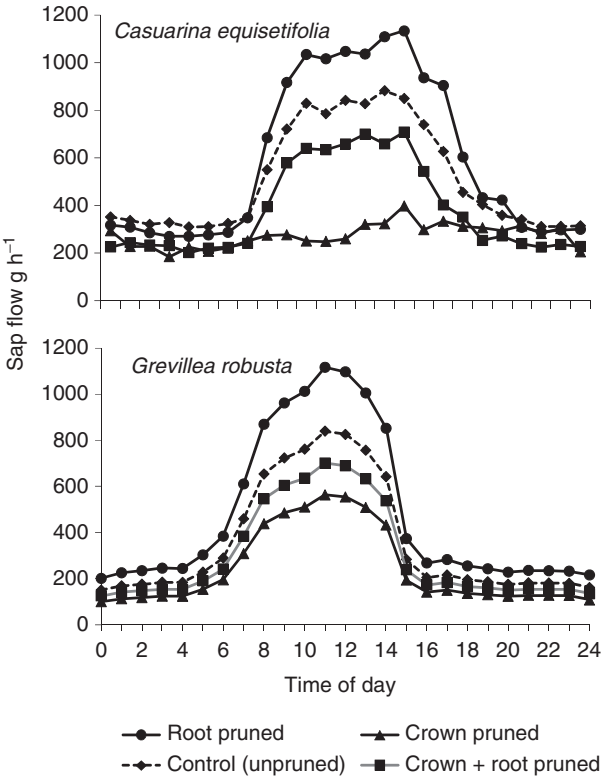


Figure 5 Effect of pruning treatment on mean daily time courses of sap flow for *Casuarina equisetifolia* and *Grevillea robusta* trees 2 years after tree pruning (Tefera, 2003).

The water, nutrient and light capture (WaNuLCAS) model developed by van Noordwijk and Luisana (2000) provides a convenient means of illustrating the impact of trees on water use at the landscape level when combined with sap flow measurements for individual trees. The impact of evergreen and deciduous trees in the drylands of East Africa was modeled using WaNulCAS (Muthuri *et al.*, 2005) to evaluate the impact of tree leafing phenology on crop performance and soil water balance. The hypothesis that deciduous trees, which shed their leaves for much of the dry season, would reduce water requirements was tested using three species, *G. robusta* (evergreen), *A. acuminata* (semideciduous), and *Paulownia fortunei* (deciduous). The leafing phenology of each species was categorized using three criteria: leaf flush, leaf fall, and leaf cover (Figure 1). The model output suggested that (1) leafing phenology is one of the most important tree attributes with respect to water consumption; (2) lower water use by

deciduous species should increase stream flow compared with evergreens; and (3) deciduous tree species are suitable for the semiarid areas examined and provide viable alternatives to evergreen species such as *Grevillea*.

Conclusions

This article shows that trees may have both beneficial and detrimental hydrological impacts at farm and watershed levels. Temporal complementarity in the use of rainfall occurs if residual water is available after the crop is harvested or rainfall occurs when there is no scope for cropping. The most remarkable example of temporal complementarity in water use is the unusual phenology of the Sahelian tree, *F. albida*, which is leafy during the dry season and sheds its leaves during the rainy season. Improved soil water and nutrient status has been reported under mature tree canopies in the savanna areas of Africa, Central America, and North America. In theory, trees can enhance soil water content beneath their canopies if the water saved through decreases in soil evaporation caused by shade and reduced runoff exceeds the quantity of water removed by their root systems. Hydraulic lift by tree roots may also redistribute water from moist zones deep in the soil profile to the surface horizons. However, spatial complementarity in water use is rare as tree and crop roots often exploit the same surface soil horizons and rainfall seldom recharges horizons below the crop rooting zone, although there is clear evidence of spatial complementarity when groundwater is accessible to tree roots.

Containing competition for water, nutrients, and light between trees and crops in AF systems remains a major challenge in the semiarid tropics, especially in the search for an acceptable substitute for eucalyptus. In Southern Australia, the greatest challenge is to find tree species that provide valuable products and improve the poor drainage, which is responsible for inducing salinity in millions of hectares of profitable farm land, with minimal loss of crop yield.

Finally, there is an urgent need to consider the impact of climate change on water use by trees, which has received surprisingly little attention. Previous studies of watershed functions of forests and AF systems have focused on reward schemes to upstream communities for providing environmental services to downstream users, whereas Clean Development Mechanism schemes in Africa have focused chiefly on global benefit. Rewards may well be an efficient and fair way of investing international funds in climate-change adaptation, which will have profound hydrological impacts on AF at both local and global scales (van Noordwijk *et al.*, 2011).

See also: Agroforestry: Fertilizer Trees. Agroforestry: Practices and Systems. Climate Change: Agricultural Mitigation

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Agroforestry: Participatory Domestication of Trees

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Glossary

Apical dominance The process which regulates branching in plants.
***Circa situ* conservation** It is conservation through wise use.
Cultivar A cultivated variety.
Ideotype The combination of a number of genetic traits that confer superiority in quality or yield.
Participatory rural appraisal Identification of the needs of local communities through dialog.

Introduction

The domestication of agroforestry trees is a technique for the intensification of agroforestry as a low-input farming system delivering multifunctional agriculture for the relief of poverty, malnutrition, hunger, and environmental degradation in tropical and subtropical countries (Leakey, 2010, 2012a).

In the past, tree products were gathered from natural forests and woodlands to meet the everyday needs of people living a subsistence lifestyle. With the advent of the Industrial Revolution and, more recently, the intensive modern farming systems of the Green Revolution, the resource of these trees has declined. This has been due to increased population pressures for agricultural land and the escalation of deforestation. To rebuild and improve this useful resource, the concept of tree domestication for agroforestry was proposed in 1992 (Leakey and Newton, 1994) and subsequently implemented by the World Agroforestry Centre (International Centre for Research in Agroforestry (ICRAF)) as a global initiative from 1994 (Simons, 1996). Great progress has been made in the first two decades of this initiative (Leakey *et al.*, 2005, 2012; Tchoundjeu *et al.*, 2006, 2008), which have encouraged local entrepreneurship in the processing and marketing of agroforestry tree products (AFTPs). This has had beneficial impacts on farmers' livelihoods (Tchoundjeu *et al.*, 2010).

Strategy

Domestication through cultivar development relies on three processes: selection, testing, and breeding. Selection identifies certain genotypes for cultivar development, testing exposes the new cultivars to appropriate environments, and breeding creates new genetic variability.

As in animals, plant domestication is a continuous process that, in crops like wheat, rice, maize, oranges, and apples, started thousands of years ago and continues today. In trees, two basic approaches are used to effect genetic improvement: the seed-based breeding approach typical of forestry and the clonal approach typical of horticulture, but the domestication strategies are not dissimilar. In agroforestry, Leakey and Akinnifesi (2008) have suggested a strategy based on the establishment of three interlinked tree populations (**Figure 1**):

- Gene resource population.
- Selection population.
- Production population.

The gene resource population is basically the wild population from which new selections can be derived. The selection population is the collection of selected provenances, progenies, or individual trees which are being tested and used to develop clonal cultivars or integrated within breeding programs to create the next generation of breeding stock. A wide range of genotypes may be kept in this population as long as each one has at least one characteristic of possible future interest. The production population consists of the highly selected clones, progenies, or provenances which are currently being planted by farmers.

In their strategy paper, Leakey and Akinnifesi (2008) specifically highlighted the development of a clonal approach to the domestication of high value trees, particularly the traditionally important indigenous fruits and nuts. However, the key element of the tree population strategy is equally applicable to less valuable tree species grown for their environmental services and propagated by seed. It is important to remember that the practice of domesticating a species is cyclical and thus continuous. For this reason, commercial plantings have to be made with whatever material is best at a given time, knowing that they will be superseded later.

The strategy being implemented by ICRAF and others to domesticate high-value indigenous trees for agroforestry, such as those producing marketable fruits and nuts, is based on participatory processes involving local communities. A participatory tree domestication strategy involves the consultation with and participation of farmers to (1) determine their priority species for domestication (Franzel *et al.*, 1996, 2008) (2) make an inventory of the natural resource, (3) implement a program of genetic selection and mass propagation aimed at the sustainable production of AFTPs for food, tree fodder, medicinals and nutriceuticals, timber, wood and fibers, etc., and (4) sell and trade the products in local traditional and new emerging markets further afield. Such strategies also recognize the importance of the wise use and conservation of genetic resources; the reduction of deforestation and restoration of degraded land. Participatory approaches have numerous advantages (Leakey *et al.*, 2003) such as building on tradition and culture and promoting rapid adoption by growers to enhance livelihoods and environmental benefits (Simons and Leakey, 2004). This participatory approach to domestication, therefore, differs from the more common scientific approach that has typically been implemented to develop most food crops. Therefore these approaches can be thought of as the 'farm' and the 'research station' pathways to domestication. In

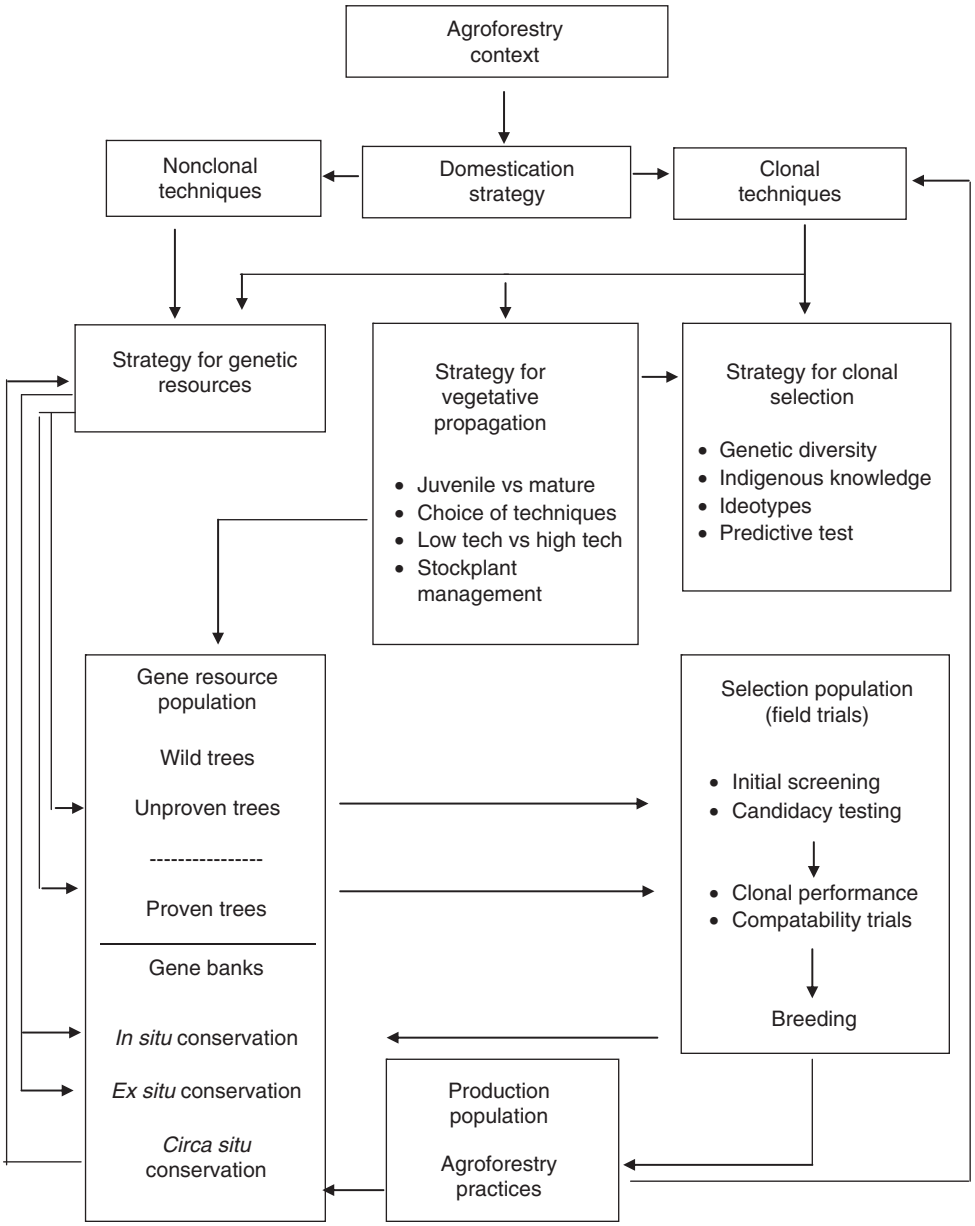


Figure 1 The agroforestry tree Domestication Strategy and the relationships between a Genetic Resources Strategy and the Strategies for Vegetative Propagation and Clonal Selection. Reproduced from Leakey, R.R.B., Akinnifesi, F.K., 2008. Towards a domestication strategy for indigenous fruit trees in the tropics. In: Akinnifesi, F.K., Leakey, R.R.B., Ajayi, O.C., *et al.* (Eds.), Indigenous Fruit Trees in the Tropics: Domestication, Utilization and Commercialization. Wallingford, UK: CAB International, pp. 28–49.

agroforestry, these two pathways have been integrated (Figure 2) in a way that ensures that the participating farming communities can benefit from the close involvement of researchers as mentors both to the communities and the Nongovernmental Organizations (NGOs) implementing the domestication program.

Biological Components of the Strategy

Propagation of superior trees

The choice of mass propagation by the clonal approach has a number of advantages stemming from the use of vegetative propagation to capture and fix desirable traits, or combinations of traits, found in individual trees (Leakey and Simons, 2000). The main advantage arises from the fact that by taking a cutting, or grafting a scion onto a rootstock, the new plant which is formed has an exact copy of the genetic code of the plant from which the tissue was taken and is, therefore, genetically identical to the stockplant or 'mother' plant . The clone so formed can be mass produced by further vegetative propagation.

The capture of the first asexual propagule from proven and mature field trees that have already expressed their genetic traits is typically done in the field by air-layering/marcotting shoots on the mother tree or by collecting scions or buds from it for grafting or budding onto seedlings in the nursery.

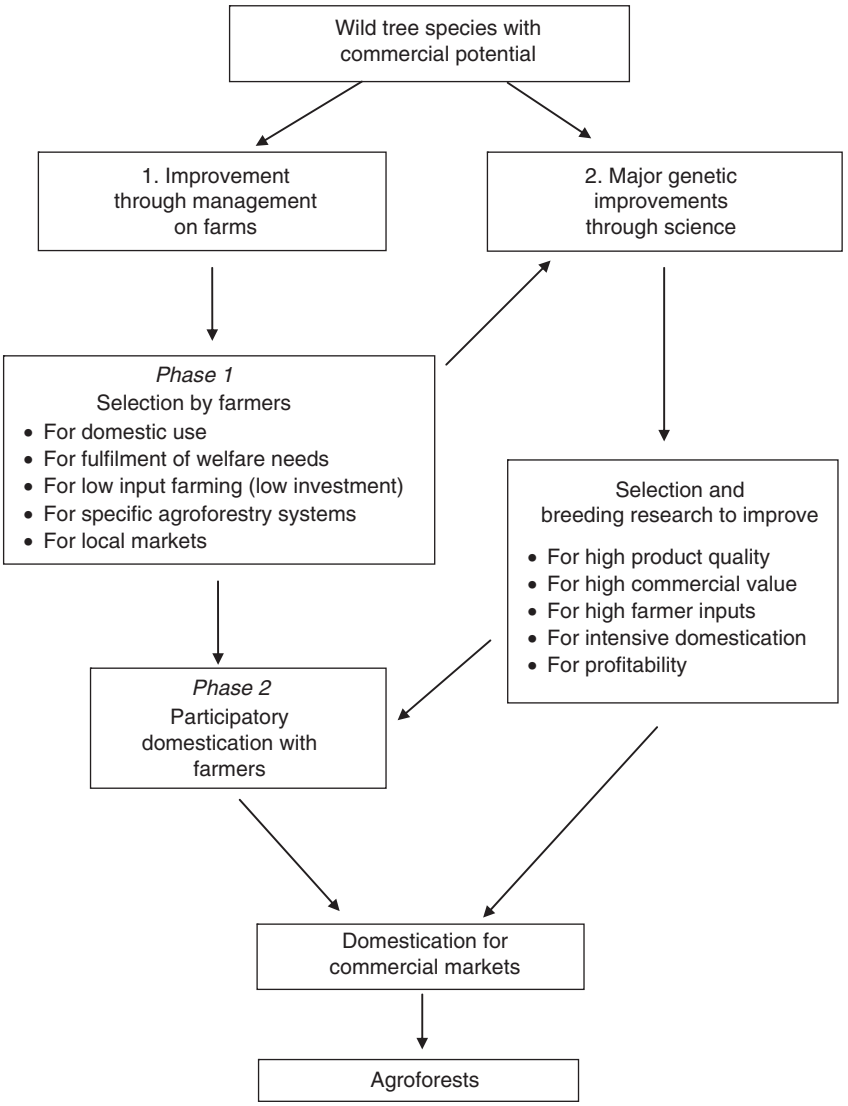


Figure 2 Tree domestication pathways. Reproduced from Leakey, R.R.B., Akinnifesi, F.K., 2008. Towards a domestication strategy for indigenous fruit trees in the tropics. In: Akinnifesi, F.K., Leakey, R.R.B., Ajayi, O.C., *et al.* (Eds.), Indigenous Fruit Trees in the Tropics: Domestication, Utilization and Commercialization. Wallingford, UK: CAB International, pp. 28–49.

Alternatively, the tree can be felled and the stump left to coppice to provide juvenile material for propagation by stem cuttings. The latter is preferable for clonal timber production from trees with a well-formed juvenile stem, whereas the former is more suitable for trees producing fruits on mature branches (Leakey and Akinnifesi, 2008). The advantage of propagating fruit trees from mature branches is that they already have the reproductive capacity to form flowers and fruits. This means that they are productive within a few years, thus reducing the time taken to produce economic returns. Plants propagated from mature tissues will also have a lower physical stature, making the harvesting of fruits easier (**Figure 3**).

Once the clone has been formed by one or other of the above techniques, the best strategy is to mass produce the clone, or cultivar, by rooting cuttings in the nursery. For this process, inexpensive and simple nonmist propagators have been developed (Leakey *et al.*, 1990). This simple, low-technology strategy allows the process to be implemented in remote areas without electricity or running water. These propagators are also extremely effective and meet the needs of most developing country tree domestication projects in both the moist and dry tropics.

The above strategy of capturing the genetic superiority of mature trees in the field may not always be possible or acceptable, making it necessary to develop clones from seedling plants in the nursery. Basically, this adds an additional genetic selection step to the overall domestication program, which can take many years to complete. Nevertheless, there are three reasons why the use of seedlings may be preferable (Leakey and Simons, 2000):

1. The population of mature trees can be dysgenic (genetically depleted) because the elite specimens have been removed by loggers or farmers. In this case, the seedling progeny

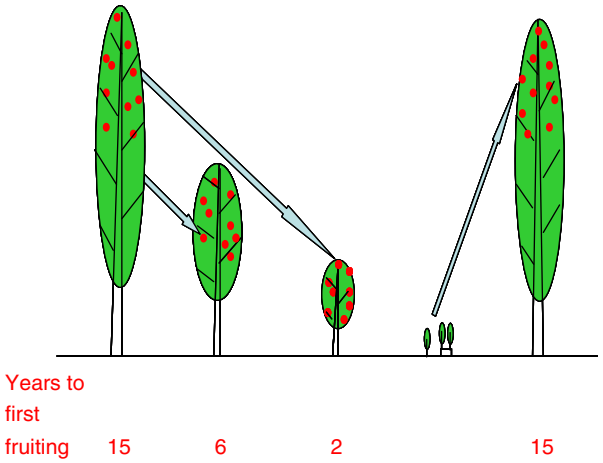


Figure 3 Designing trees of different sizes for different uses by selecting the source of the propagation material *vis-à-vis* the state of maturation in the tree. Reproduced from Leakey, R.R.B., 2012b. Living with the Trees of Life – Towards the Transformation of tropical Agriculture. Wallingford, UK: CABI, 200 pp.

derived from such populations will probably have a better array of genetic variation during reproduction due to the remixing of genes during the segregation phase of meiosis.

2. The felling of large numbers of the most desirable mature trees for the purpose of generating cultivars may not be acceptable to the owners. In addition, felling the mature trees may not be environmentally acceptable.
3. The use of seedlings allows the screening of far larger populations, with much more diverse origins, thus maintaining genetic diversity among the cultivars.

Through the improvement of tree yield and product quality, tree domestication becomes a strategy for the intensification of agroforestry (Leakey, 2012a), something which is further enhanced when many of the different trees within the farming systems are domesticated in parallel.

Genetic resource issues

One of the important requirements of an appropriate strategy is to conserve a substantial proportion of the genetic variability for future use in selection programs and, subsequently, through breeding to broaden the genetic base of the cultivars in the Production Population. This also serves as a risk aversion strategy should it be necessary in the future to breed for resistance to pests and diseases. There are three actions which each contribute to genetic conservation:

- Establishing a Gene Bank (*ex situ* conservation).
- Wise utilization of the genetic resource in cultivation (*circa situ* conservation).
- Protecting some wild populations (*in situ* conservation).

Ex situ gene banks containing randomly sampled populations from across the natural range of the species should be replicated within a site and across a number of sites. This replication is both for security and to ensure that the sites embrace any climatic or edaphic variation within the region. They should also be located in areas offering long-term protection from external threats, for example, deforestation and wild fires.

Regarding *circa situ* conservation and the wise use of genetic resources, it is important to recognize that there is a trade-off between accuracy of genetic value estimation and intensity of selection (i.e., greater accuracy generally comes at the expense of reduced numbers of families, individuals per family, or clones). In long-lived tree crops, there is also the problem that many of the traits on which selection is based are not visible until the trees are nearing their productive age at the end of a long period of growth. Consequently, in timber trees, for example, much selection is done on early rates of growth and assumptions that this will relate to yield. In the case of the West African tree *Triplochiton scleroxylon*, a Predictive Test was developed on the basis of apical dominance (the process controlling the formation of branches) in very young plants in the nursery. This was to take advantage of a strong relationship between this physiological process and branching frequency in the nursery and then between branching frequency in the field and stem volume or timber yield (Leakey and Ladipo, 1987). A quick and early test like this allows much larger populations to be screened than would be either practical or economically justifiable through long-term field trials.

The trade-off between the intensity of selection and number of plants also affects the diversity of the genetic base – the gene resource population. This diversity should be rigorously enforced as one of the objectives of a domestication program. This, therefore, involves a good sampling protocol both of the natural population as well as for any existing provenances and progenies from a breeding program. In this respect, it is important to remember that it is not uncommon for there to be a few elite trees in provenances and progenies which may, however, on average, be poor. This is especially important if a clonal domestication program is being developed, as these elite individuals from poor populations may be genetically unique.

As the selection process intensifies with time, new traits will be introduced into the domestication program (e.g., seasonality of production, early fruiting, disease and/or pest resistance, drought tolerance, etc.). After the initial phases of clonal selection, the opportunity will arise for controlled pollinations between proven elite clones as has been done in *Ziziphus mauritiana* (Kalinganire *et al.*, 2012) in the Sahel and *Dacryodes edulis* in Cameroon (Makueti *et al.*, 2012). In this way, it should be possible to take advantage of specific-combining ability in unrelated superior clones and to produce progeny with heterosis in desirable traits that exceed what is found in the wild populations. The vegetative propagation of these new genotypes can become a second clonal generation.

Environmental Components of the Strategy

Different agroforestry practices typically involve a range of different species producing environmental/ecological services such as soil fertility enhancement, erosion control, or different products ranging from low-value fuel wood to high-value marketable products for food, cosmetic, and pharmaceutical industries. Different approaches to domestication will probably be followed for these different species. Likewise, these

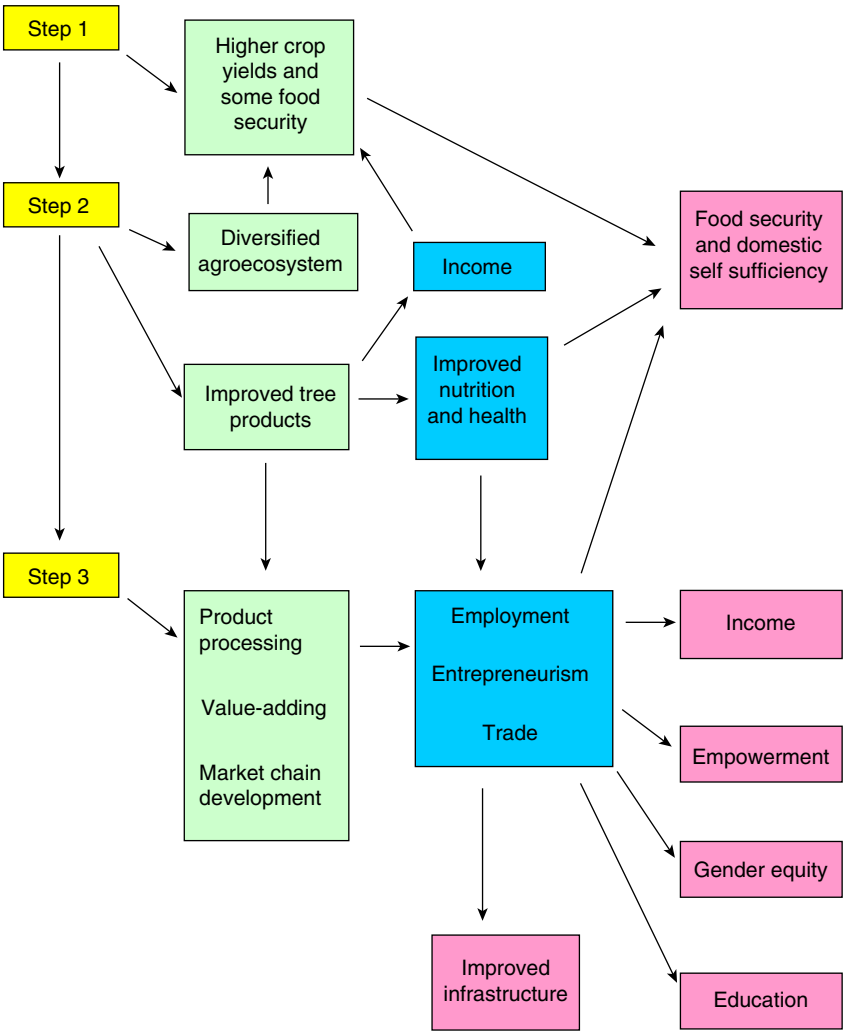


Figure 4 The delivery of multifunctional agriculture by three agroforestry steps. – Step 1. Land rehabilitation with leguminous trees and shrubs, Step 2. Domestication with indigenous trees producing marketable products, and Step 3. Marketing, processing, and value-adding indigenous tree products (see **Table 1**). Modified from Asaah, E.K., Tchoundjeu, Z., Leakey, R.R.B., *et al.*, 2011. Trees, agroforestry and multifunctional agriculture in Cameroon. International Journal of Agricultural Sustainability 9, 110–119.

different species will probably fill different spatial and temporal niches in the landscape and be planted in different configurations and densities within farming systems. This is all part of the diversification of the agroecosystem which is an important component of enhancing agroecosystem functions for the rehabilitation of degraded farmland (Leakey, 1999a, 2012b).

The domestication of indigenous trees producing high-value products, such as traditional foods and medicines, is one component of a novel strategy for the intensification (Leakey, 2012a) and diversification (Leakey, 2010) of smallholder farming systems in the tropics and subtropics through agroforestry. In environmental terms, the diversification with long-lived perennial plants is important because it is the way to rebuild the ecological functions of agroecosystems and landscapes. Soil and land rehabilitation is crucial if agriculture is to use land already cleared of forest rather than abandoning it and cutting down more forest (Leakey, 2012b).

Tree domestication and the commercialization of tree products also create incentives for farmers to plant agroforestry trees as they generate income and promote business, trade, and employment opportunities. When added to agroecosystem rehabilitation, tree domestication can be seen as step two in a generic model of how agroforestry can deliver environmentally desirable multifunctional agriculture (Leakey, 2010; Leakey, 2013; **Figure 4**) – a model with high adaptability to different climatic and edaphic situations (Leakey, 2012b).

Social Components of the Strategy

Many of the biological components described in the Section Biological Components of the Strategy are not specific to Participatory Domestication and would apply to more centralized and top-down programs led by research scientists. In

contrast, the social components are central to the philosophy of Participatory Domestication.

The prime objective of the participatory approach is to involve the target communities in all aspects of the planning and implementation of the program so that they fully understand it and can 'buy-in' and have ownership of the program. In addition, the purpose of this strategy is also to ensure that all engaged members of the community, whether male or female, are empowered by the program and are the beneficiaries of the outputs of their own initiatives and labor. This should enhance the livelihoods of the community members in general and promote social equity.

In the longest-running example of participatory domestication in agroforestry trees, the researchers have fed their outputs to NGO partners through training-of-trainers courses and by acting as mentors to the NGO-managed farmer-training schools (or Rural Resource Centers) established in pilot villages (Tchoundjeu *et al.*, 2002, 2006, 2010; Asaah *et al.*, 2011). As it will be seen in the Section Techniques, the farmers in this partnership have contributed their knowledge about the use and importance of local species, the range of variation in different traits of relevance to genetic selection, and their traditional knowledge (TK) about the role of these species in local culture and tradition. They have also contributed their time and labor. Furthermore, and crucially, they have also made available some of their trees for research and training in domestication techniques.

In implementing this strategy, it is of great importance to recognize the legal and socially important communal rights of local people to their TK and local germplasm (Lombard and Leakey, 2010) and to ensure that they benefit from their use and are rewarded for sharing them for the wider good. Because of the sensitivity arising from past commercial exploitation of these rights by individuals, companies, academics, international agencies, and government, it is very clear that the partners in domestication programs have to earn the trust of local communities before TK and germplasm is made freely available. Ideally, to ensure that benefits flow back to the farmers and communities, the recipients of TK and germplasm should enter into formal 'Access and Benefit Sharing' agreements (ICRAF, 2012) in which the rights of the holders of knowledge and genetic resources will be legally recognized.

Commercial Components of the Strategy

With poverty alleviation as one of the objectives of the domestication of agroforestry trees, it is clear that incentives for and approaches to income generation are important in the overall strategy. Consequently, improving and expanding the markets for agroforestry trees and their products are central to the strategy.

The first opportunity is the creation of demand for agroforestry trees, whether for environmental and ecological services or for AFTPs. This, certainly, involves the dissemination of the importance of agroforestry for soil fertility replenishment, watershed protection, reduction of erosion, demarcation of boundaries, as well as for the production of wood for fuel and other uses, timber, extractives, medicines, fodder, food, and numerous nonfood products (Leakey, 2012b). The experience of the past 10–15 years indicates that the first income stream from agroforestry projects is derived from the sales of plants from village nurseries to neighboring communities, especially the sale of seedlings of nitrogen-fixing or the so-called 'fertilizer' trees (Asaah *et al.*, 2011; Leakey and Asaah, 2013). This is because the loss of soil fertility due to frequent cropping without access to artificial fertilizers is recognized as one of the main constraints to agricultural production. In addition, the benefit flow from these trees is obtained relatively quickly (1–3 years). However, it generally takes longer to obtain returns from the production of AFTPs.

The strategy for increased income generation from AFTPs is, in the first instance, to build local markets and trade. This is particularly important in the case of traditional foods and medicines as local people are familiar with the use of these products and the demand typically exceeds supply. In the longer term, however, some of these products may have regional and even international markets, firstly with expatriates from tropical countries living in Europe and America, and then as products become more widely known or better processed with global customers.

A secondary reason for focusing on local and regional rather than international markets is that if the demand expands too fast there is a risk that large-scale entrepreneurs may enter the marketplace and outcompete local business people (Leakey and Izac, 1996) thus, undermining the use of tree domestication as a development strategy. Having said that there are a few interesting and potentially very important initiatives in which multinational companies are becoming engaged with local communities in tropical countries in Public–Private Partnerships (Leakey, 2012b). These are generally operating in a way that is contrary to the trend of globalization in which all the economic benefits flow to industrial countries rather than at least some remaining in the tropical country.

Some tree products, notably fruits, are produced seasonally and have a very short shelf life. To overcome this constraint to year-round marketing, it is necessary to investigate opportunities for processing and value adding. This can take many forms such as drying and airtight packaging; preservation in oil, brine, or syrup; and freezing, etc. Generally, this involves the need for a level of scale outside the capacity of a smallholder farmer, although 'cottage' industries can be a possibility. If this approach to extending the marketing season has to involve industrial companies, then new issues arise. One of these is to involve the companies in the domestication process so that traits which are important in the processed product are included in the genetic selection program (Leakey, 1999b). Later, issues of trading agreements that also result from the involvement of processing companies in marketing will be considered.

An alternative approach to processing can be to seek the generally rare plants that flower and fruit outside the normal seasonal pattern and then to develop these as cultivars. Although this can be quite simple to achieve, these out-of-season plants may not have quality or yield traits that are as good as those fruiting within the normal season. In this case, developing cultivars which expand the productive season may need to also involve a breeding program.

As the commercialization process involves more players and becomes more complex, the risks that the producers will

be exploited and inadequately rewarded for their products and innovations increase. Entering into any market will expose suppliers to competition. Commentators have suggested that this will undoubtedly jeopardize the rights of farmers or communities in the supply chain. To shut out casual and opportunistic competitors, it is obviously important to do as much as possible to ensure that the supply chains leading up to the manufacture of the products are efficient, competitive, and as well protected as possible. Innovative approaches to ensuring that farmers and local communities are rewarded for their innovations have been developed by PhytoTrade Africa (Lombard and Leakey, 2010). It has been engaged in addressing the sustainable commercialization of natural products produced by indigenous plants, especially the trees of the Miombo woodlands. PhytoTrade Africa believes that the risks of exploitation can be minimized if the primary producers are able to secure long-term access to the markets developed for their products. Thus, they have worked to ensure that markets can be secured so that supply chains can emerge so that as wild harvesting leads to domesticated or farmed sources, the initial producers are protected as much as possible. The approach involves working with indigenous communities and helping them to secure long-term access to local and even international markets in ways which reward them and protect their intellectual property rights. Experience to date indicates that these approaches can result in critically important supplementary income of otherwise poor and marginalized farmers and producers. This, in turn, significantly improves their livelihoods.

This partnership approach between producers and the local-to-global cosmetic, food, beverage, herbal medicine, and pharmaceutical industries is based on four areas of intervention aimed at the propoor commercialization of the traditionally important products:

- Product development.
- Market development.
- Supply chain development.
- Institutional development.

Such partnerships are developed by carefully constructing commercial agreements with leaders in the relevant sector. Critically, this involves the establishment of strong and viable trade associations that are forward thinking and market oriented. Through these partnerships, it is possible to ensure long-term relationships and supply agreements which ensure that the farmers and local community producers remain in the value chain. The achievement of this can, under certain circumstances, also create a barrier to entry for plantation developers who might wish to outcompete small-scale producers and farmers.

One important consideration in developing these partnerships is the selection of appropriate species. It is critical that the abundance of the resource, and the ownership over the resource by the target producers, is sufficient to ensure sustainable and reliable supply of the products. To date, small-scale producers have depended on wild harvesting to supply the local markets. Although this provides a supply-related barrier to large scale trade that favors small-scale producers, it also imposes constraints to the market expansion that is needed to raise these producers out of poverty. For example, wild products are highly variable in quality, often with unreliable levels of production. However, the focus on naturally occurring wild resources is now changing with the recent emergence of highly compatible propoor participatory domestication technologies for indigenous fruit and nut trees. This offers great opportunities to improve product quality through tree selection and cultivar development. Creating these new crops should also greatly increase the supply of very marketable produce. Thus, by realizing the importance of 'commercialization for domestication' and 'domestication for commercialization,' there is considerable opportunity for agroforestry to alleviate poverty, malnutrition, and hunger in marginalized agricultural communities of developing countries. Thus, the symbiotic relationship between domestication and commercialization is a very important aspect of the strategy needed to ensure real impact on the big socioeconomic issues affecting the world. The overall outcome of such developments arising from improved agricultural production and enhanced livelihoods should, therefore, be improved access to clean water, better diets, healthcare, education, etc. Just as it is seen above regarding adaptability to different environmental situations, this model case has great adaptability to different socioeconomic situations (Leakey, 2012b).

Thus, in conclusion, when the social and commercial components of the strategy that have been developed for participatory domestication strategy are added to the agroecosystem benefits from the adoption of agroforestry for land rehabilitation, the emergence of a three-step generic model for the delivery of a socially and economically desirable multifunctional agriculture by agroforestry can be seen (**Figure 4**, **Table 1**).

Before moving on, however, it is important to recognize that the trade in some new products will require regulatory approval for European Union (EU) and American markets. It is, however, possible to tie the approval of these products to the target producers, as has been achieved by PhytoTrade Africa's successful application to have Baobab fruit approved as a novel food ingredient in the EU under Regulation (EC) 258/97 and by Unilever Deutschland GmbH for *Allanblackia* seed oil (European Food Security Authority No EFSA-Q-2007-059.

Techniques

Biological Components of the Techniques

Genetic selection

The domestication process is basically about the cultivation of plants with superior genetic traits. In trees, two techniques can be used to assist in the identification of superior mature trees (sometimes called 'elite' or 'plus trees') producing timber and wood, indigenous fruits and nuts, or otherwise useful everyday domestic products. In forestry for timber and wood production, genetic improvement is typically done by selection of a population with inherent genetic quality (a provenance) and by making seed collections from that population. Alternatively, when more is known about the genetic quality of individuals within a population, seeds (a progeny) are typically collected from the best mother tree(s). The same

Table 1 The 3-step model for multifunctional agriculture

- Step 1: Adopt agroforestry technologies such as two year 'Improved fallows' or 'Relay cropping' with nitrogen-fixing shrubs that improve maize yields from approximately 1 ton ha^{-1} per hectare up to approximately 4–5 tons ha^{-1}. This allows the farmers to both improve food security and reduce the area of their holdings planted with maize and thus make space for other crops, perhaps cash crops which would generate income. An additional benefit arising from improved fallows with leguminous shrubs is the reduction of parasitic weeds like *Striga hermontica* and the reduced incidence of insects pests like the stem borers of maize.
- Step 2: Diversify the farming system by the inclusion of species producing marketable products or fodder for livestock. The adoption of participatory approaches to the domestication of traditionally important indigenous food plants is a good way to rapidly create new cash crops that generate income, improve nutritional security through diversified diets, enhance gender equity, provide diversified diets rich in micronutrients, empower communities toward self-sufficiency in products of day-to-day domestic importance, and maintain culture and traditions. The sale of these products would allow the purchase of fertilizers and thus, potentially, the increase of maize yields up to 10 tons ha^{-1}. Consequently, the area under maize could be reduced further to allow more cash cropping. The integration of fodder trees and livestock into a farm is one of the elements of diversification that could be part of this step.
- Step 3: Promote entrepreneurship and develop value-adding and processing technologies for the new tree crop products, thus increasing availability of the products throughout the year, expanding trade, and creating employment opportunities. All of these are outputs which should help to reduce the incidence of poverty and enhance gender equity.

Source: Modified from Leakey, R.R.B., 2010. Agroforestry: A delivery mechanism for multifunctional agriculture. In: Kellimore, L.R. (Ed.), Handbook on Agroforestry: Management Practices and Environmental Impact. Environmental Science, Engineering and Technology Series. New York, USA: Nova Science Publishers, pp. 461–471 and Leakey, R.R.B., 2013. Addressing the causes of land degradation, food/nutritional insecurity and poverty: A new approach to agricultural intensification in the tropics and sub-tropics. In: Hoffman, U. (Ed.), UNCTAD Trade and Environment Review 2012. Geneva, Switzerland: UNCTAD. Available at: www.unctad.org/Templates/Page.asp?intItemID=3723&lang=1 (accessed 16.09.12).

approach is used in agroforestry when cultivating trees for soil fertility enrichment or for wood products such as poles or wood fuel (i.e., environmental services or low-value products). However, in agroforestry, trees are also cultivated for high-value useful or marketable products like fruits, nuts, medicines, or other chemical ingredients. In this case, domestication is often done using vegetative propagation to develop cultivars or clones, and participatory approaches involving local communities are appropriate.

In the participatory domestication of trees producing indigenous foods two approaches to genetic selection can be adopted. The first is to seek the knowledge of local people about which trees produce the best products (see 'social components of the techniques' given below as to how to ensure that their traditional rights are recognized). The second, more scientific, technique involves the quantitative characterization of many traits of fruits, kernels, and leaves, which are associated with size, flavor, nutritional value, etc. This characterization also determines the extent of the tree-to-tree variation. This more scientific approach can be used to 'backstop' or enhance the indigenous knowledge approach by adding new knowledge about marketable or commercially important traits to enrich the indigenous knowledge. Over the past two decades, much scientific knowledge has been acquired to support the participatory domestication initiatives being implemented around the world (see review by Leakey *et al.*, 2012; Leakey, 2012b).

In the scientific approach to selection, modern laboratory techniques are being increasingly used to examine traits which are not visible to the naked eye. For example, to quantify genetic variation in the chemical and physical composition of marketable products such as polysaccharide food-thickening agents, nutritional content (protein, carbohydrate, oils, fiber, vitamins, minerals, etc.) by proximate analysis, medicinal factors like antiinflammatory properties, the composition of essential oils and fatty acids, the determination of wood density, strength, shrinkage, color, calorific value, and other important wood properties correlated with tree growth (Leakey *et al.*, 2012). In addition, molecular characterization

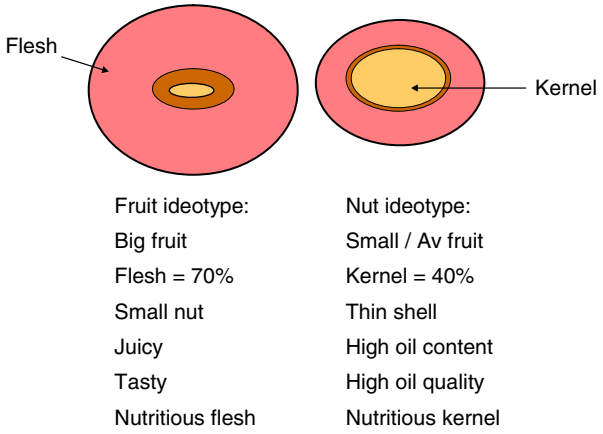


Figure 5 Some traits of different trees which can be combined to form the ideal tree for fresh fruit or kernel production – an Ideotype.

of the genetic code is being used to determine the structure of genetic variation in natural, managed, and cultivated tree stands and to devise appropriate management strategies that benefit users (Jamnadass *et al.*, 2009). This information is used to determine the proportion of a species' genetic variation that is available at a local geographical scale, whether or not cultivated stands are of local or introduced origin, and to ensure that domesticated populations have sufficient genetic diversity to avoid future problems from inbreeding (Pauku *et al.*, 2010).

The above scientific inputs to the understanding of genetic variation can then inform the process of farmer selection and help to provide guidance of how best to meet the needs of different market opportunities. To achieve this, the concept of 'ideotypes' developed for the breeding of cereals has been modified in order to assist tree selection (Leakey and Page, 2006). An ideotype is the ideal combination of traits for a cultivar to produce a product that meets the needs of a particular market (**Figure 5**). So, for example, an ideotype for a fresh fruit would have a lot of flesh (and small seeds/nuts/kernels), be sweet, juicy, tasty, nutritious, and look attractive.

However, a nut ideotype would have a large kernel(s) (and probably little flesh), have a thin shell so that it is easily cracked, be rich in edible oil with an appropriate fatty acid profile, or have other characteristics meeting the needs of the cosmetic or pharmaceutical industries. In both instances, these quality traits are ideally associated with a high yield of fruits or nuts, so that the cultivar can be said to have a high 'harvest index' – a large amount of 'ideal' harvestable product.

An obvious trait for inclusion in the selection of all cultivars for food products is their nutritional quality. Although it is known that the tree-to-tree variation is substantial in these traits, and indeed in antinutritional factors such as phenolic content, there is a lack of knowledge on the extent of this variation in most species. Instead, most researchers have published the average values per species. This allows some comparison between species but is not useful when seeking to select cultivars from within a species. Likewise, there is very little information about tree-to-tree variation in taste, but again it is known that it is complex and substantial (Kengni *et al.*, 2001).

Vegetative propagation and stockplant management

The vegetative propagation of elite trees is central to the domestication strategy for indigenous trees producing valuable and marketable products (Leakey and Akinnifesi, 2008). A key element of this strategy is that the domestication is done by local people in their communities so that they are the beneficiaries of their work. This means that the vegetative propagation techniques have to be appropriate for implementation in remote villages by people with little, if any, formal education. For this reason, the techniques must be simple, robust, and must not be dependent on an electricity supply or running water. The achievement of this has been described by Leakey (this volume and 2004). One aspect of this is the way in which stockplants are managed. Thus, the long-term success of a cloning program is heavily dependent on the nursery management and the skills of the nursery staff.

Nursery management

Good nursery management involves many skills and attention to detail. The process starts with acquisition of high-quality germplasm of known origin (accession records) and recorded genetic quality, supported by documents recognizing the rights of the supplier (Access and Benefit Sharing agreements) – for example, see the Agroforestry Tree Genetic Resources Strategy of the World Agroforestry Centre (ICRAF, 2012). Furthermore this germplasm must have been appropriately stored and handled to avoid loss of viability. Germplasm can be of two types: seeds and vegetative propagules. Seeds also are of two main types: those that can be stored by drying or freezing (orthodox) and those which cannot be (recalcitrant). Both the latter and the vegetative propagules are short lived (from a few days to at most a few weeks). They have to be very carefully and rapidly handled to avoid water or temperature stress and any physical damage.

Accession records must be stored safely and the origin of every plant in the nursery must be labeled or in some other way traceable back to these records. Plants of unknown origin are of zero importance in a domestication program.

Successful plant production is dependent on rapid germination of seeds and propagation of vegetative propagules and their subsequent growth in good, free-draining potting compost well supplied with nutrients and organic matter. During early growth, some shade is usually desirable to prevent wilting and water stress. Usually, daily watering is required during dry weather. Once growing in the nursery, potted plants must be regularly maintained so that they do not become root bound and consequently the roots do not escape from the pot into the soil below (if this happens, it is very difficult to subsequently establish this plant as its roots will be left in the nursery). Plants should not be kept in the nursery so long that their root systems become coiled. Attention should be paid to weeds and pests.

Plants which are poorly managed in the nursery usually struggle to perform well once planted out in the field. The standards of nursery management are clearly visible to a visitor and are an excellent indicator of the interest and enthusiasm of the nursery staff and manager. Consequently, they are also a good indicator of the likely success of the subsequent planting program.

Predictive test for domestication of timber trees by vegetative propagation

One of the difficulties facing anyone involved in tree domestication is their longevity and long regeneration cycle. Many trees do not reach sexual maturity for 10–20 years and especially in the case of timber they do not display their yield potential and commercially important qualities until they are large trees. This makes tree breeding a slow business, but it also means that clonal forestry is difficult as juvenile trees which have not had time to display their potential are the easiest to propagate by cuttings. To get around this problem, large trees can be felled and allowed to develop coppice shoots, although this too is less likely from very old trees.

In *Triplochiton scleroxylon*, a West African timber tree conforming to Rauh's Model of branching architecture, a technique to predict which seedlings in a given population were more likely to grow to form the trees with the best form (branching frequency) and yield has been developed (Leakey and Ladipo, 1987; Ladipo *et al.*, 1991). This is based on the fact that the trees developing the greatest stem volume had been found to be those producing a few branches in each branch whorl and no branches between whorls – so allocating biomass to stem rather than to branches. The technique is based on an assessment of the 'strength' of apical dominance, the process regulating the formation of branches, by decapitating young seedlings and following the pattern of sprouting and the reassertion of dominance by the upper shoot (Ladipo *et al.*, 1992). This nursery-based screening technique in seedlings on 3–6 months old allows the rapid selection of those likely to produce the best stems to enter a program of clonal propagation. Conversely, because the leaves of this species are eaten as a vegetable by local people in Nigeria, the trees producing the most branches can be selected and managed as a hedge for leaf production.

Nursery management strategy

Farmers who manage tree nurseries can adapt their management to best meet their needs. For example, if their priority is to meet their own domestic food demands, they can plant the majority of the trees they produce in their own farm rather than selling them or multiplying them up by harvesting successive batches of cuttings or scions. Alternatively, if income

generation through the development of a tree nursery business for the sale of plants to other farmers is the priority, they can take 3–4 crops of cuttings off every plant per year for a few years and so very rapidly build up a large stock of plants for sale. This strategy should result in the greatest income generation in the long term but has the disadvantage that there are no financial returns in the first few years. An even longer term commercial strategy would be to do a long period of plant multiplication before large-scale planting. In addition to these individual strategies, there are, certainly, many possibilities of intermediate or mixed options.

Environmental Components of the Techniques

As a low-input farming system based on long-lived perennial trees, agroforestry provides many environmental benefits. Tree domestication is normally an approach to make these farming systems more productive and more profitable – in other words to intensify the agroforestry system. Many aspects of this will also have indirect environmental benefits in more rapid cover of the soil, greater root penetration, and lateral spread with consequently better protection and improvement of the soil and agroecosystem function. Rapid tree growth is associated with high water use. Although this may have negative impacts on the growth of associated crops, it can also reduce the impacts of salinization by lowering the water table.

Recent data in *Dacryodes edulis* show that vegetatively propagated cultivars have lower fine root density in the crop rooting zone and hence are more likely to be less competitive with crops (Asaah *et al.*, 2012). In addition, the perennial nature of trees also assists in carbon sequestration for the mitigation of climate change, and emerging evidence suggests that vegetatively propagated cultivars store more carbon than seed propagated individuals in their primary roots and shoots – an unexpected benefit of tree domestication (Asaah, 2012).

One important aspect of these environmental impacts is their quantification. This requires Baseline surveys based on randomized controlled trials – described by Barrett *et al.*, (2010) as providing solutions to development economics issues with weak causal factors. If applied to agroforestry, this approach should help to determine the scale of the impact at the plot, farm, landscape, and regional level.

Social Components of the Techniques

To maximize the social and economic benefits flowing from tree domestication, a participatory approach has been taken by the World Agroforestry Centre and some other organizations and their local partners to identify the farmers' preferences in terms of the tree species they would like to cultivate. Interestingly, in most of the places around the world where this has been done, the farmers have identified indigenous fruits, nuts, and leaves for uses as foods or medicines (Franzel *et al.*, 2008). As mentioned in the Section Social Components of the Strategy, participatory domestication has typically followed the identification of priority species, with farmers contributing their knowledge about the traits they would like to see incorporated within a selection program and the usefulness of the tree products to local households.



Figure 6 A village satellite nursery in Bangoua, Cameroon.

To encourage and assist the farmers, the agroforestry scientists and NGO partners in Cameroon have provided training and knowledge through specially constituted Rural Resource Centers in pilot villages in different regions of the country (Tchoundjeu *et al.*, 1998, 2006, 2010; Asaah *et al.*, 2011). These Rural Resource Centers provide opportunities for hands-on training in critical nursery management, vegetative propagation, agroforestry practices, and enterprise development in a community nursery (**Figure 6**). The focus of this training is that it is appropriate for implementation in often remote village nurseries without piped water and electricity. The farmers are then encouraged to set up similar facilities in their own farm or community, thus creating satellite nurseries which help to spread the techniques and concepts to neighboring communities. To encourage this kind of farmer-to-farmer technology transfer, exchange visits, demonstrations, and competitions covered by radio and television are organized. In time, these village and community nurseries become self-sufficient and independent.

In recent years, the range of topics presented in training programs has been expanded to include the wise use of microfinance and financial management, product marketing, business development, infrastructure development, and community organization. In parallel to this, artisans in neighboring towns have been trained in the fabrication of simple equipment and tools for product drying, processing, and packaging, whereas entrepreneurs and women's groups have been helped to develop businesses in food product processing and value adding aimed at improving the quality of products for the marketplace and increasing market demand. As these processes expand, it is expected that some people will cease to be farmers and producers and instead enter the cash economy as business men and women providing employment to others and developing new enterprises.

Although much progress has been made in developing, implementing, and expanding the participatory domestication of a wide range of agroforestry trees and commercializing their products, there is still much to do to quantify the socioeconomic impacts. A critical component of this is the establishment of statistically viable baseline surveys so that accurate assessments can be made in years to come as the concepts are disseminated and scaled up to new communities. This process

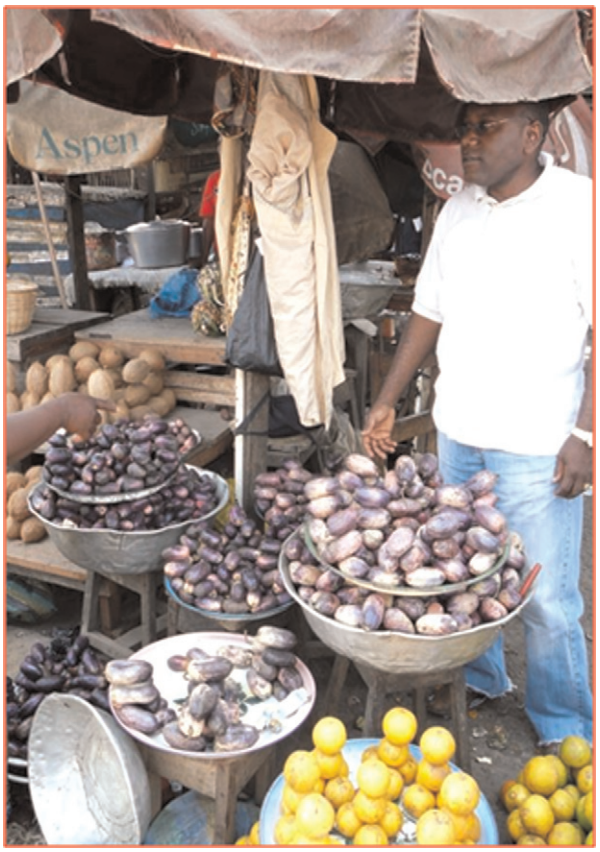


Figure 7 A market stall in Makanéné in Cameroon, selling *D. edulis* fruits.

has begun, but to date, the results are preliminary. Likewise, it is still too early to say much about the implementation of work to recognize and protect the rights of farmers and rural entrepreneurs to their innovations.

Commercial Components of the Techniques

Ultimately, as it can be seen from Figure 4, it is the commercialization of the sustainably grown products that potentially delivers the really important impacts from agroforestry and multifunctional agriculture. However, it is also recognized that commercialization can pose the greatest risks affecting the success or failure of the overall initiative. One study (Wynberg *et al.*, 2003) has examined the 'Winner or Loser' qualities of different approaches to the commercialization of an indigenous fruit (*Sclerocarya birrea* – Marula) in southern Africa (Table 1). It basically found that bottom-up community initiatives had the greatest chance of being Winners, although top-down commercialization involving large multinational companies could also be Winners if the company recognized the importance of buying raw products from local smallholder producers, rather than from large-scale plantation growers.

Focusing first on tree domestication can encourage the positive aspects of commercialization from producers practicing agroforestry. The expansion of markets beyond the traditional market or roadside stall (Figure 7) requires increased product quality, uniformity, and regular supply. The longer the value chain from local to global market, the more important are the attributes of quality, uniformity, and regularity of supply (Figure 8). Hence, the development and cultivation of vegetatively propagated cultivars selected for year-round

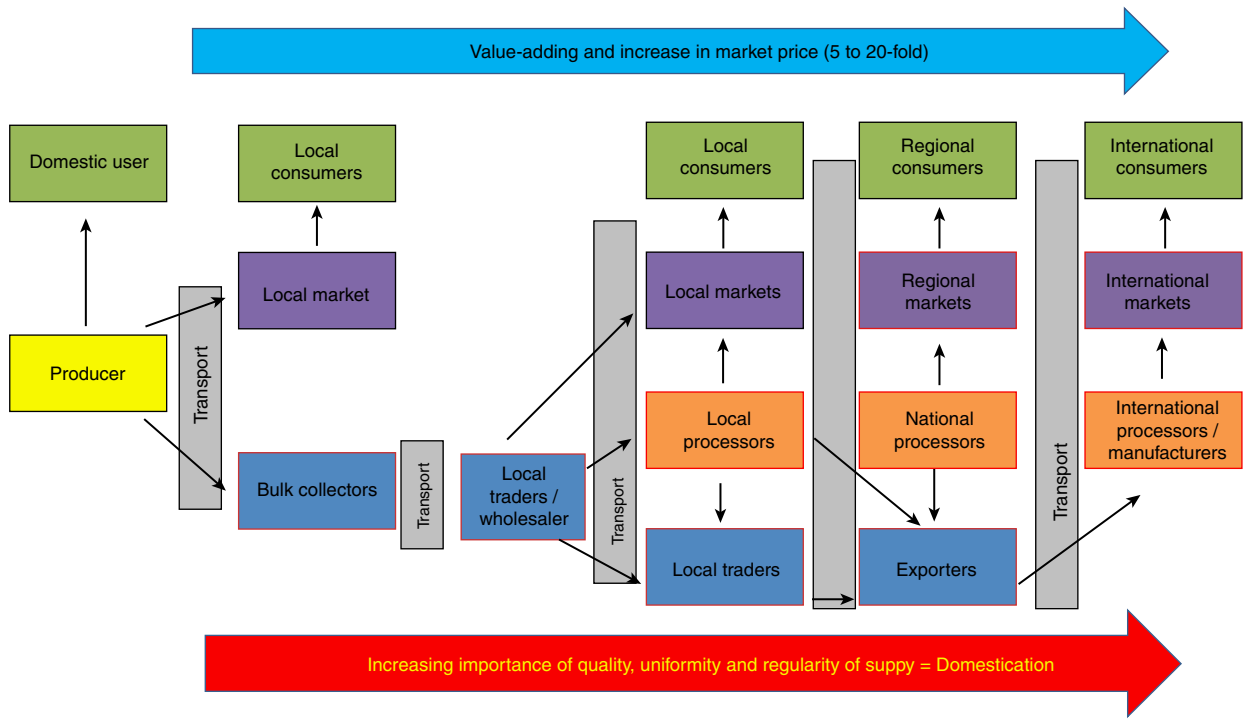


Figure 8 The increasing importance of domestication in the value chain of an agroforestry tree product.

production and other commercially desirable traits makes a quantum leap in the marketability of the products, as it means that traders and wholesalers can purchase a large volume of uniform, high-quality product from a recognized and named cultivar. In return, hopefully the producer will receive a higher price, as it is clear that consumers are willing to pay more for the more desirable varieties (**Figures 9** and **10**).

The above demand for uniformity and quality makes the ideotype concept more important, especially at upper end of the value chain where processing and value addition increase the value of the marketable products (**Figure 11**). With the increasing importance of the ideotype, the identification of the specific traits that confer market acceptability and market exclusivity and distinctiveness become more and more critical. This, therefore, is the reason for increasingly sophisticated research, mentioned in the Section 'Biological components of the technique' earlier, to determine the genetic variation found in different tree populations in the chemical, physical, and medicinal properties of the raw products. This, certainly, will lead to the need for stronger linkages between agroforestry researchers and partners in industry (Leakey, 1999b).

Food crop domestication over thousands of years has been credited with the advance of civilization as witnessed in industrialized countries (Diamond, 1997). However, domestication and commercialization are both part of this force for development, as one is considerably weakened without the other. Leakey (2012b,d) has recognized that in the tropics there is a need for a 'new wave of domestication,' but this too has to be supported by market growth along the value chain. Thus, one of the important components in this 'new wave' is the processing and value addition that extends the shelf life of products, expands market demand, and makes them more valuable. In Cameroon, the development of cottage industries to dry and package AFTPs has started (Asaah *et al.*, 2011), but this enterprise development and its up-scaling needs considerable expansion – recognizing the characteristics of Winners in the development process (**Table 1**). In this regard, one interesting development in recent years has been the involvement of a few multinational companies in Public–Private Partnerships with rural communities engaged in production of agroforestry products in tropical countries (Jamnadass *et al.*, 2011; Leakey, 2012b). Although associated with risks, this also offers great opportunities for the future development of agroforestry tree crops if the strategies and practices can be developed appropriately.

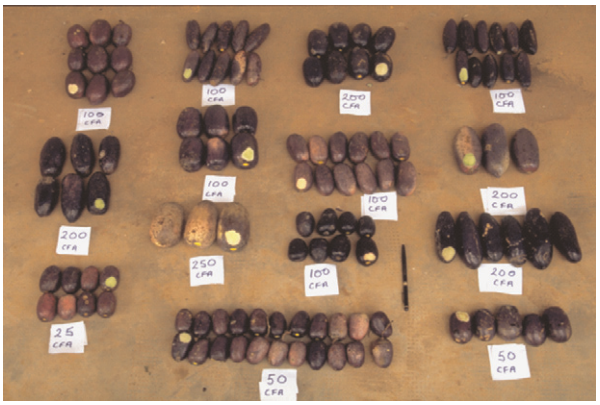


Figure 9 Fruits of *D. edulis* from market stalls showing the retail price in Central African francs (CFA) and illustrating consumer preferences for fruits from certain trees. Reproduced from Leakey, R. R.B., 2012b. Living with the Trees of Life – Towards the Transformation of tropical Agriculture. Wallingford, UK: CABI, 200 pp.

Outcomes

To date, studies on the environmental and socioeconomic impacts of tree domestication have not been based on randomized controlled trials. Nevertheless, comparisons based on household surveys have indicated that integrated rural development based on agroforestry, tree domestication, and local market initiatives with small-scale enterprises have

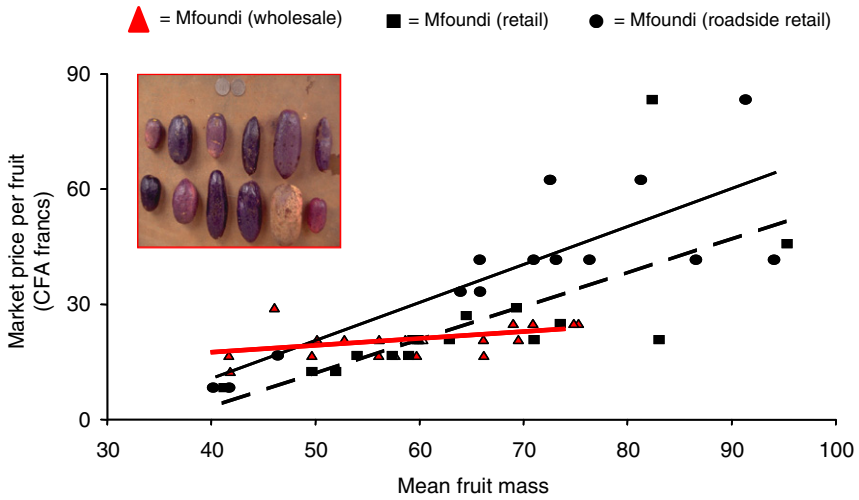


Figure 10 Relationship between mean *D. edulis* fruit mass and market price per fruit ($1 = 750CFA francs). Modified from Leakey, R.R.B., Atangana, A.R., Kengni, E., *et al.*, 2002. Domestication of *Dacryodes edulis* in West and Central Africa: Characterisation of genetic variation. Forests, Trees and Livelihoods 12, 57–71.



Figure 11 Value-added products developed from agroforestry tree species. Reproduced from Leakey, R.R.B., 2012b. Living with the Trees of Life – Towards the Transformation of tropical Agriculture. Wallingford, UK: CABI, 200 pp.

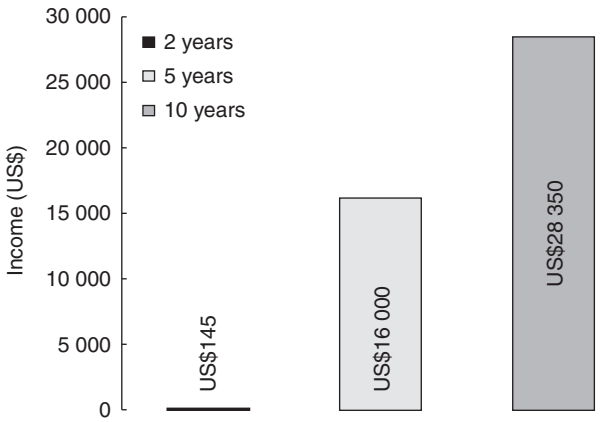


Figure 12 Income generated from plant sales at Rural Resources Centers in Cameroon after 2, 5, and 10 years. Reproduced from Leakey, R.R.B., Asaah, E.K., 2013. Underutilised species as the backbone of multifunctional agriculture – The next wave of crop domestication. Acta Horticulturae 979, 293–310.

positive impacts on the lives of farming households in participating communities (Figure 12 and Table 2). Together these impacts illustrate that agroforestry can deliver what the International Assessment of Agricultural Knowledge, Science and Technology for Development (IAASTD) called Multifunctional Agriculture (Table 3). Currently, the impacts are only on a local/household/farm/village scale and there is much to be done to upscale and outscale the agroforestry initiatives before the scales are extended (Table 4).

Biological Components of the Outcomes

The major outcome of participatory tree domestication, as expected, is new tree crop cultivars with improved product quality and greater market demand. This is happening in many places around the tropics in more than 50 species but is most advanced in Cameroon, where these cultivars have been developed by local farmers for cultivation in their own farms to meet household needs. However, as the supply of product increases, it is expected that both these cultivars and their products will be sold – at first locally and then more widely (Tchoundjeu *et al.*, 2010; Asaah *et al.*, 2011; Leakey, 2012b). The cultivation of these new cash crops is leading to the diversification of farming systems and this is expected to result in healthier agroecosystems. Another biological finding with likely impacts on agroecosystems is that vegetatively propagated trees allocate their dry matter differently, with less in fine root and more in primary roots and shoots. Consequently, clonal cultivars are more likely to be less competitive with annual crops (Asaah, 2012; Asaah *et al.*, 2010, 2012).

Environmental Components of the Outcomes

One important outcome expected from more sustainable land use systems that rehabilitate degraded land is better access to productive land for staple food crop production and hence the opportunity to diversify into other crops with market potential. This diversification either as mixed cropping or as landuse mosaics should improve the agroecosystem functions and thus lower the need for inputs such as pesticides. The increased tree

Table 2 The social, marketing, and natural resource qualities that determine whether or not the impacts of commercializing indigenous fruits, nuts, and other tree products are positive or negative

Winner qualities	*Loser qualities*
In individuals, households, and enterprises	
• Individuals organized as a group	• Poorly organized group structure
• Well informed about markets	• Poorly informed of markets
• Good access to transport	• Poor access to transport
• Coordinated production	• Uncoordinated production
• Small 'Input cost:Revenue received' ratio	• Large 'Input cost:Revenue received' ratio
• Consistently good quality products	• Variable quality products
• Skilled in bargaining	• Unskilled in bargaining
• Well networked with good partnerships	• Poorly networked
• Easy and equitable access to resource	• Uncertain and restricted access to resource
• Fits with other livelihood strategies and sociocultural norms	• Competes with other livelihood strategies and sociocultural norms
In product marketing	
• Commercial opportunities	• Undeveloped/poor market interest
• Diversity of end markets	• Limited markets
• Diversity of end products	• Fad or single niche products
• Positive marketing image	• No or negative marketing image
• Unique characteristics of product	• Many other substitutes
• Raw product quality well matched to market	• Raw product requires processing
• Many buyers of raw materials and products	• A monopsony – only one buyer of raw materials
• Many sellers of raw materials and products	• A monopoly – only one seller
• Buyers aware of product or brand	• Buyers ignorant of product or brand
In the tree resource	
• Abundant resource	• Rare resource
• Plant part used is readily renewable	• Slow replacement of harvested product
• Harvesting does not destroy the plant	• Destructive and damaging harvesting
• Easily propagated	• Difficult to propagate
• Genetically diverse with potential for domestication	• Genetically uniform or little potential for selection
• Multiple uses for products	• Narrow use options
• High yield of high-quality product	• Low yielding and/or poor-quality product
• Valuable product	• Low-value product
• Consistent and reliable yield from year to year	• Inconsistent and unpredictable production
• Already cultivated within farming system	• Wild resource which is difficult to cultivate
• Already being domesticated by local farmers	• Totally wild resource
• Fast growing	• Slow growing
• Short time of production of product	• Long time to production
• Compatible with agroforestry land uses	• Competitive with crops, labor intensive, etc.
• Hardy	• Sensitive to adverse environmental conditions
• Widely distributed	• Only locally distributed

Source: Reproduced from Leakey, R.R.B., Tchoundjeu, Z., Schreckenberg, K., Shackleton, S.E., Shackleton, C.M., 2005. Agroforestry tree products (AFTPs): Targeting poverty reduction and enhanced livelihoods. International Journal in Agricultural Sustainability 3, 1–23.

cover, especially if arranged along the contours of hillsides, protects the soil and reduces the risks of serious erosion and can also protect watersheds. The hydrological impacts are most fragile in dryland environments.

The perennial nature of trees also assists in carbon sequestration for the mitigation of climate change, and emerging evidence suggests that vegetatively propagated cultivars store more carbon in their primary roots and shoots than by seed-propagated individuals – an unexpected benefit of tree domestication (Asaah, 2012).

Social Components of the Outcomes

One of the original purposes of initiating participatory tree domestication was to improve the livelihoods of poor farmers, especially income generation to reduce poverty; food security to reduce hunger; better nutrition and diet to reduce malnutrition; and better equity to improve the lot of women and children in society. It was envisioned that indirectly this would also improve health and education opportunities and that the overall package would empower individuals and communities, allowing them to be more self-sufficient in order to transform their lives, giving them hope for the future. Early indications (Table 2) are that these outcomes are starting to emerge in the participating communities. Furthermore, when associated with microfinance, business training and access to simple equipment for the processing and packaging of raw products, there is now evidence of rural people engaging in small businesses either as entrepreneurs or as employees.

Table 3 The impacts reported by farmers engaged in a participatory domestication program for agroforestry trees in Cameroon

Positive impacts
Increased number of farmers adopting agroforestry and the domestication of indigenous trees
Increased production of tree products
Increased income from tree sales by nurseries
Increased income from sale of tree products
Increased income from better farming practices
Increased income from eligibility for microfinance
Increased income used for schooling and school uniforms
Increased income used for medicines and healthcare
Increased income used for home improvements – for example, installation of water and electricity in the home, new buildings, etc.
Increased income used for farm improvement – for example, livestock, wells, agricultural inputs, etc.
New employment opportunities from nurseries
New employment opportunities from processing both agricultural crops (such as cassava) and new markets for processed agroforestry products (fruits, spices, herbs, and medicinals)
New employment opportunities in the emerging workshops producing small tools and appropriate mechanized equipment to service the need for food processing equipment
New employment opportunities from marketing as traders of processed products and the food processing equipment
New employment opportunities in transport from producers to markets and to the processors of agricultural produce
Retention of youths in the villages due to career opportunities by domesticating trees in their village nurseries
Tree domestication has led to better diets and improved nutrition
Luxury food items consumed
Improved health from potable water
Piped water supplies for irrigation and use in nurseries
Increased livestock rearing due to tree fodder
Increased use of traditional medicines and better health
Increased honey production and processing
Reduced drudgery in women's lives from not having to collect water from rivers and farm produce from remote farms, as well as from mechanical processing of food crops
Reduced drudgery gives more time to look after their families and engage in farming or other income-generating activities
Improved marketing for food and agroforestry products
Improved soil fertility from improved fallows has increased crop yields 2- to 3-fold with better weed control
Improved tree fodder for goats and cattle
Having more time as a result of better farming methods, farmers had more time for marketing and new farming activities
Community feeling empowered, stronger, and optimistic for the future in ways that they could sustain
Knowledge has empowered the Rural Resource Centers as an agent of change
Negative impacts
Increased jealousy and theft
New roads lead to deforestation and land degradation as a result of the expansion of farming activities to more remote areas

Significantly, one of the outcomes mentioned by young people in the participating communities is that this now means that they can see a future for themselves if they remain in the village rather than feeling that they have to migrate to towns and cities for a better life (Table 2).

Table 4 The characteristics of the participatory domestication of agroforestry trees important for the delivery of multifunctional agriculture

The features that agroforestry brings to multifunctional agriculture to enhance social, economic, and environmental resilience in agriculture and rural development are:

- Based on TK and culture
- Based on participatory techniques to ensure relevance to local people
- Based on integrated natural resources management and sustainable land use
- Based on knowledge of the natural resource

The above features mean that multifunctional agriculture can:

- Empower subsistence farmers to control their destiny
- Enhance food security and rural/urban livelihoods, reducing hunger
- Enhance nutrition security and health, reducing malnutrition and diseases
- Enhance opportunity for income generation, reducing poverty
- Diversify farming system at the local and landscape scale, enhancing watershed services and sustainable production
- Create new agricultural commodities
- Diversify market economy and buffer commodity price fluctuations
- Decentralize business opportunities to the villagers
- Create employment in processing and marketing
- Build social responsibility from the 'grassroots'
- Enhance international public goods and services, reducing climate change and loss of biodiversity
- Offer opportunities for new policy interventions to combat deforestation, desertification, and land degradation
- Breakdown the disconnects between disciplines and organizations responsible for policy and its implementation in rural development

Source: Reproduced from Leakey, R.R.B., 2012b. Living with the Trees of Life – Towards the Transformation of tropical Agriculture. Wallingford, UK: CABI, 200 pp.

Commercial Components of the Outcomes

The important commercial outcomes have been the development of Rural Resource Centers that deliver both education and training in agroforestry and tree domestication, as well as in community development and business management so that the villagers can earn money from the sale of plants and raw products. This money is then being used to make infrastructure developments, such as roads and clean water supplies, as well as to reduce the drudgery of the women (Table 2). The consequence of this has been that poor farmers are starting to generate income and enter the cash economy and so begin to climb out of poverty (Figure 11). In bigger villages and small towns, local people are also developing cottage industries and engaging more in marketing and trade. This relationship between enhanced farm production and urban life is important for the rural economy and the overall alleviation of poverty. It is an example of farm production being the 'engine of growth.'

Future Impact

In the long term, the application of these strategies should lead to benefits, which encompass many of the rural development goals of development agencies, as specified in the Millennium Development Goals of the United Nations. At the community

level, some of these goals have been achieved, but to date, it is still only talked about several thousand participating farmers. Achieving these benefits will, however, require the large-scale adoption of the techniques and strategies presented here in ways that will meet the needs of the farmers and those of new and emerging markets (Leakey *et al.*, 2012). This makes it important to get the messages about good domestication strategies to policy makers (e.g., Wynberg *et al.*, 2003).

Clearly, the challenge is to scale up the application of agroforestry and tree domestication to the huge numbers needed to have meaningful impact of national, regional, and global scales.

Biological Components of the Impact

The vision of what could be achieved with the widespread adoption of the domestication of trees and the associated trade of the products in numerous different industries is perhaps best exemplified by the domestication of the wolf to give large numbers of breeds of dogs of all sorts of shapes, sizes, and appearances, to be both pets and working partners with farmers, policemen, entertainers, blind people, etc. These dog breeds have arisen by breeders teasing out the genetic traits present in the wolf genome. If the same is done for trees, there could be a large number of different cultivars meeting the needs of many food, cosmetic, medicinal, perfume, fiber, and wood markets – not just in one species but in hundreds of species. This, in turn, would lead to a highly diversified, intensified, and more productive Multifunctional Agriculture (Leakey, 2012b).

Integrated Environmental, Social, and Economic Components of the Impact

The restoration of degraded land by Multifunctional Agriculture could make productive land available for an expansion of overall farm production to fill the Yield Gap (Leakey, 2012b) and meet the needs of a growing human population without the need for further deforestation and without future negative impacts on erosion, flooding, climate change, etc. A healthier environment could lower the risks of disasters due to flooding, drought, landslides, pest and disease epidemics, etc.

The achievement of even greater success than foreseen by the Millennium Development Goals could lead to greatly improved local and national economies and the gradual transition of developing countries toward developed countries.

See also: Agroforestry: Fertilizer Trees. Agroforestry: Hydrological Impacts. Agroforestry: Practices and Systems. Biodiversity and Ecosystem Services in Agroecosystems. Biodiversity: Conserving Biodiversity in Agroecosystems. Climate Change: Agricultural Mitigation. Domestication of Plants. Ecoagriculture: Integrated Landscape Management for People, Food, and Nature. Food Security: Yield Gap. Land Use: Restoration and Rehabilitation. Plant Cloning: Macropropagation. Publicâ Private Partnerships in Agroforestry

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Agroforestry: Practices and Systems

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Glossary

Agroforestry Purposeful growing of trees, crops, sometimes with animals, in interacting combinations for a variety of objectives. Agrisilviculture = trees + crops; Silvopasture = trees + pasture/animals; Agrosilvopasture = trees + crops + animals/pasture.

Alley cropping Growing crops in the interspaces between rows of planted trees or shrubs. In the tropics, crops are grown in the alleys between trees or regularly pruned hedgerows of planted, usually nitrogen-fixing, shrubs or trees. In temperate zones, crops are grown in the alleys of widely spaced timber trees.

Community forestry A form of social forestry, where tree-planting activities are undertaken by a community of people on common or communally owned land.

Fallow Land resting from cropping, which may be grazed or left unused, often colonized by natural vegetation. An improved fallow refers to deliberate planting of fast-growing species for rapid replenishment of soil fertility.

Farm forestry Tree planting on farms, usually as woodlots.

Homegarden A subsistence farming system consisting of integrated mixtures of multipurpose trees and shrubs in association with crops and sometimes livestock around homes, the whole unit managed intensively by family labor.

Multipurpose tree (and shrub) A tree/shrub that is grown for multiple products and/or services.

Multistoried or multistrata system An arrangement of plants forming distinct layers from the lower (usually herbaceous) layer to the uppermost tree canopy.

Social forestry Tree planting to pursue social objectives.

Introduction: A Brief History of the Development of Agroforestry

Agroforestry is perhaps as old as agriculture itself. The practice has been prevalent for many centuries in different parts of the world, especially under subsistence farming conditions. For example, homegardening is reported to have been associated with fishing communities living in the moist tropical region approximately 10 000 BC (Kumar and Nair, 2004; Nair and Kumar, 2006), and in Europe, domestic animals were introduced into forests to feed approximately 4000 BC (Mosquera-Losada *et al.*, 2012). It has, however, been only during the past 35 years that these indigenous forms of growing trees and crops/animals together were brought under the realm of modern, scientific land-use scenarios.

Several factors contributed to the above-stated development. When the newly independent nations of the developing world were faced with the problem of feeding their millions during the 1950s and 1960s, the policy makers thought the best solution was to focus on the model of modern intensive monocultural agriculture that was successful in the industrialized world. Several food-production technologies were consequently developed with emphasis on production of preferred species of crops in monocultural or sole-crop stands with heavy input of agrochemicals (fertilizers, insecticides, herbicides, etc.), mechanization, and irrigation. In the 1970s, these efforts, collectively called the Green Revolution, resulted in substantial gains in food production and helped avert large-scale hunger in some regions of the world. At that time, most of the international agricultural research centers (IARCs) of the Consultative Group on International Agricultural Research (CGIAR) system and the national programs focused on a few individual food crops and their production technologies for sole-crop production systems. However, for a variety of reasons, many farmers, especially the poorer ones in the tropics and subtropics, were often continuing their traditional practices of cultivating crops in mixed stands for more than one season, and were commonly nurturing trees in their cropping systems. In such circumstances, the production technologies developed for individual crops were not wholly applicable to these systems. Similar patterns of single-species stands of trees were also adopted in plantation forestry and fruit orchards in many parts of the tropics and that resulted in significant gains in wood and fruit production. Typically, the traditional, mixed production systems of raising food crops, trees, and animals together as well as exploiting a multiple range of products from natural woodlots did not fit into this 'modern' single-commodity paradigm, and were discouraged. Serious doubts began to be expressed in the 1960s and 1970s about the relevance of the single-commodity strategies and policies promoting them. In particular, there was concern that the basic needs of the poorest farmers were neither being considered nor adequately addressed. Soon it became clear that many of the technology packages that contributed to the Green Revolution, such as irrigation systems, fertilizers, and pesticides, were not affordable by the poor farmer on the one hand, and their large-scale application had serious environmental consequences on the other. It was also recognized that most tropical soils, which are poorer and more easily degraded than temperate-zone soils, were unable to withstand the impact of high-input technologies. The disastrous consequences of increasing rates of deforestation in the world's tropical regions also became a matter of serious concern. It was clearly understood that a major cause of deforestation was the expansion of agricultural land to provide food and fuelwood for the rapidly increasing populations. Faced with these problems, land-use experts and institutions intensified their search for appropriate strategies that would be socially acceptable, enhance the sustainability of the production base, and meet the need for production of multiple outputs. These collective efforts led to taking a new look at the age-old practices based on combinations involving trees, crops, and livestock on the same

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land unit. The inherent advantages of traditional land-use practices involving trees – sustained yield, environmental conservation, and multiple outputs – were recognized quickly. Agroforestry thus began to come of age in the late 1970s. The establishment of the International Council (Centre, since 1991) for Research in Agroforestry (ICRAF), now known as the World Agroforestry Centre, in 1977, in Nairobi, Kenya, signified the institutionalization of agroforestry and heralded the beginning of the era of agroforestry as a multidisciplinary science (Nair and Garrity, 2012).

In the temperate, industrialized regions, the evolution of 'modern' agroforestry was slower than in the tropics. J. Russell Smith's classical work Tree Crops: A Permanent Agriculture (Smith, 1950) is considered to have created a 'new' wave of interest in agroforestry; he argued that "an agricultural economy based almost entirely upon annual crops such as corn and wheat is wasteful, destructive of soil fertility and illogical." However, it was not until the late 1970s to early 1980s that the push for ecologically and socially friendly management approaches such as integrated natural resource management, the principles of which are encompassed in agroforestry, gathered momentum. It started with the understanding about the undesirable environmental consequences of high-input agriculture and forestry practices that focused solely on the economic bottom line (Brown, 2004). Their demand for environmental accountability and application of ecologically compatible management practices increased when it became clear that the land-use and land-cover changes associated with the removal and fragmentation of natural vegetation for establishment of agricultural and forestry enterprises led to adverse ecological consequences (Garrett, 2009). Agroforestry initiatives have also sprung up and moved forward in several industrialized regions of the world including Europe (Rigueiro-Rodriguez *et al.*, 2008; Mosquera-Losada *et al.*, 2012) and Australia and New Zealand (Polglase *et al.*, 2008).

Agroforestry: Concepts, Principles, and Characteristics

Agroforestry is a loosely defined term. Several definitions – long and short – and descriptions have been proposed for agroforestry, and innumerable discussions have taken place in professional and technical meetings and conventions on the definition quagmire, especially during the early stages of the development of the discipline in the 1970s and 1980s. Over time, the enthusiasm to define and describe the term subsided. A consensus has since emerged that agroforestry is one of the terms – including agriculture, forestry, and several subsets within them – that cannot be defined exactly, and that the concept is more important than the definition.

At present, there is a general understanding that agroforestry refers to the purposeful growing of trees and crops in interacting combinations for a range of objectives including both a variety of products or commodities and a vast array of environmental and other ecological services. Basically, it involves the deliberate admixture of trees and shrubs, collectively called woody perennials or trees, on the same unit of land as agricultural crops or animals, either in some form of spatial arrangement or temporal sequence. In the resulting systems, there is significant ecological and economical interaction between the woody and the nonwoody components. Thus, an agroforestry system normally involves two or more species of plants (or, plants and animals), at least one of which is a woody perennial. The system has two or more outputs and a production cycle of more than 1 year, and both its ecology and economics are more complex than in a monocultural system of agriculture or forestry. Gold and Garrett (2009) describe the essence of agroforestry in four key 'I' words: intentional, intensive, interactive, and integrated. The term 'intentional' implies that systems are intentionally designed and managed as a whole unit, and 'intensive' means that the systems are intensively managed for productive and protective benefits. Toward this end, it has been argued that agroforestry intensification involves the inclusion of genetically superior (domesticated) trees (Leakey, 2012a). The biological and physical interactions among the system's components (tree, crop, and animal) are implied in the term 'interactive,' and 'integrative' refers to the structural and functional combinations of the components as an integrated management unit. It is often emphasized that all agroforestry systems (AFS) are characterized by three basic sets of attributes: productivity (production of preferred commodities as well as productivity of the land's resources), sustainability (conservation of the production potential of the resource base), and adoptability (acceptance of the practice by the farming community or other targeted clientele). These different concepts of agroforestry are captured in ICRAF's characterization: "Agroforestry is a dynamic, ecologically sound system of natural resource management. By integrating trees on farms and in the agricultural landscape, it helps diversify and sustain production for enhanced economic, environmental and social benefits" (World Agroforestry Centre, 2008).

As noted in the Section Introduction: A Brief History of the Development of Agroforestry, the motivations for initiatives in agroforestry research were different in the tropics and the temperate regions. Given that the structure and management of land-use systems are determined not only by the biological components, but also by the site-specific ecological features and the local social and cultural characteristics, such differences between the tropics and the temperate zones are common in all forms of land use, be it agriculture, including animal production, or forestry. These ineluctable differences manifest themselves in the nature, characteristics, objectives, and expectations of agroforestry practices in the two broad geographical regions; nevertheless, the practices in both regions encompass the same concepts and principles.

In addition to agroforestry, several other terms with 'forestry' endings became prominent in the late 1970s and 1980s as a consequence of increasing global interest in tree-planting activities. These include Community Forestry, Social Forestry, and Farm Forestry. Although these terms have also not been defined precisely, they emphasize people's participation in tree-planting activities, not necessarily in association with agricultural crop and/or animals as in agroforestry, but with the social objectives ranking equally in importance with production objectives. Social forestry refers to using trees and/or tree planting specifically to pursue social objectives, usually betterment of the poor, through delivery of the benefits of tree products and/or tree

planting to the local people. Community forestry, a form of social forestry, refers to tree-planting activities undertaken by a community on communal lands or the so-called common lands; it is based on the local people's direct participation in the process, either by growing trees themselves, or by processing the tree products locally. Farm forestry, a term used mainly in Asia, refers to tree planting on farms. The major distinction between agroforestry and these other terms is that whereas agroforestry emphasizes the interactive association between woody perennials and agricultural crops and/or animals for multiple products and services, the other terms refer to tree planting, often as woodlots. Several other terms and initiatives such as permaculture, agroecology, and farming systems that encompass the concept of integrated land use (with or without trees) have also become prominent since the 1970s. In practice, however, all these activities and practices that include trees directly or indirectly refer to growing and using trees to provide food, fuelwood, fodder, medicines, building materials, and cash income. Only blurred lines, if any at all, separate them, and they all encompass agroforestry concepts and technologies. Therefore, in common land-use parlance, these different terms are often used as synonyms, and sometimes out of context.

Agroforestry: Practices and Systems

A wide range of traditional land-use systems that fit the concept of agroforestry as outlined in the Section Agroforestry: Concepts, Principles, and Characteristics has been identified from different parts of the world (Nair, 1989) and others being practiced may still remain to be identified. The most organized effort to understand the complexity, diversity, and extent of indigenous AFS in the tropics has been a global inventory undertaken by ICRAF between 1982 and 1987. That activity was aimed at systematically collecting, collating, and evaluating data pertaining to a large number of such systems around the tropics (Nair, 1989). It assembled, for the first time, a substantial body of information on a large number of AFS including their structure and functions, and their merits and weaknesses. Based on this comprehensive database, Nair (1985; 1989) proposed a classification scheme for AFS based on several criteria:

1. Structure of the system: based on the nature and arrangement of the three major groups of components:
   a. Agrisilviculture (trees + crops).
   b. Silvopasture (trees + animals).
   c. Agrosilvopasture (trees + crops + animals).
2. Primary functions of the system:
   a. Production of basic needs such as food, fodder, fuelwood, and cash.
   b. Protection or service functions (such as soil fertility build-up, environmental amelioration, wind-protection, and erosion control).
3. Spatial arrangement of components, i.e., time sequence pattern of component arrangement:
   a. Simultaneous (trees intercropped with crops or livestock).
   b. Sequential (trees and crops rotated in sequence).
4. Level of management:
   a. Subsistence to commercial.
   b. Household consumption to market-oriented.

Other classification schemes of AFS have also been proposed (e.g., Sinclair, 1999); but essentially they are all based on the above criteria and concepts. Various characterizations and descriptions of AFS such as agrisilvicultural systems for fuelwood production in semiarid lands, silvopastoral systems for animal production in sloping lands, multistrata homegardens in humid tropics, etc., are common in agroforestry literature. Moreover, descriptions of existing systems as well as recommendations of potential agroforestry technologies for specific agroecological zones include a mixture of various forms of agroforestry in terms of the nature and arrangement of components, and several AFS can be found within the same ecological regions. Thus, in general, any specific agroforestry practice cannot be identified exclusively to a specific ecological region, and vice versa.

The nature, complexity, and objectives of agroforestry vary considerably between the tropics and the temperate region. **Table 1** presents a list of the major tropical practices. Local adaptations and manifestations of these (and other) practices exist as innumerable AFS with site-specific characteristics in different parts of the tropics and subtropics (Nair, 1989; 1993).

Compared with the tropics, agroforestry practices and systems in the temperate zone are less diverse and complex. The Association for Temperate Agroforestry (AFTA) has recognized five major agroforestry practices in North America: alley cropping, forest farming, riparian buffer strips, silvopasture, and windbreaks (**Figure 1**). Other temperate-zone AFS include the ancient tree-based agriculture involving a large number of multipurpose trees such as chestnuts (*Castanea* spp.), oaks (*Quercus* spp.), carob (*Ceratonia siliqua* L.), olive (*Olea europa* L.), and figs (*Ficus* spp.) in the Mediterranean region (Nair *et al.*, 2008; Rigueiro-Rodriguez *et al.*, 2008). The dehesa system, grazing under oak trees with strong linkages to recurrent cereal cropping in rangelands, is also a very old European practice (Rigueiro-Rodriguez *et al.*, 2008; Howlett *et al.*, 2011; Mosquera-Losada *et al.*, 2012).

AFS Subgroups

To further streamline AFS nomenclature and reduce the number of major groups, Nair (2012a) arranged the systems into five major subgroups with major types of AFS identified under each, as listed below. These are followed in this article:

1. Multistrata systems
   - Homegardens (including mixed fruit and spice tree gardens): Intimate multistory combinations of several trees – especially fruit- and nut-producing species – and crops in homesteads; livestock may or may not be present; the size of the garden is small (< 1 ha) and the garden is managed intensively usually by family labor.
   - Shaded perennials: Growing shade-tolerant species such as cacao (*Theobroma cacao* L.) and coffee (*Coffea* sp.) under or in between overstory shade-, timber-, or other commercial tree crops.
   - Other multistrata agroforests: Various other forms of complex multistrata agroforests and multilayer tree gardens exist in different tropical humid lowland regions of Southeast Asia and parts of Africa and Latin

Table 1 Major agroforestry practices in the tropics

Agroforestry practice	*Brief description*
Tropical agroforestry	
Alley cropping (hedgerow intercropping)	Fast-growing, preferably leguminous, woody species grown in crop fields; the woody species pruned periodically to a low height (<1.0 m) to reduce shading of crops; the prunings applied as mulch into the alleys as a source of organic matter and nutrients, or used as animal fodder.
Homegardens	Intimate multistory combinations of a diverse and large number of trees and crops in homesteads; livestock may or may not be present.
Improved fallow	Fast-growing, preferably leguminous, woody species planted and left to grow for short periods (2–3 years) of fallow between cropping periods for soil fertility enhancement; woody species may yield economic products.
Multipurpose trees (MPTs) on farms and rangelands	Fruit trees and other MPTs scattered haphazardly or planted in some systematic arrangements in crop or animal production fields; trees provide products such as fruits, fuelwood, fodder, and timber.
Silvopasture:	Integration of trees in animal production systems:
• Grazing systems	○ Cattle grazing on pasture under widely spaced or scattered trees.
• Cut-and-carry system (Protein banks)	○ Stall-feeding of animals with high-quality fodder from trees grown in blocks on farms.
Shaded perennial-crop systems	Growing shade-tolerant species such as cacao and coffee under or in between overstory shade-, timber-, or other commercial tree crops.
Shelterbelts and windbreaks	Use of trees to protect fields from wind damage, sea encroachment, floods, etc.
Taungya	Growing agricultural crops during the early stages of establishment of forestry (timber) plantations.

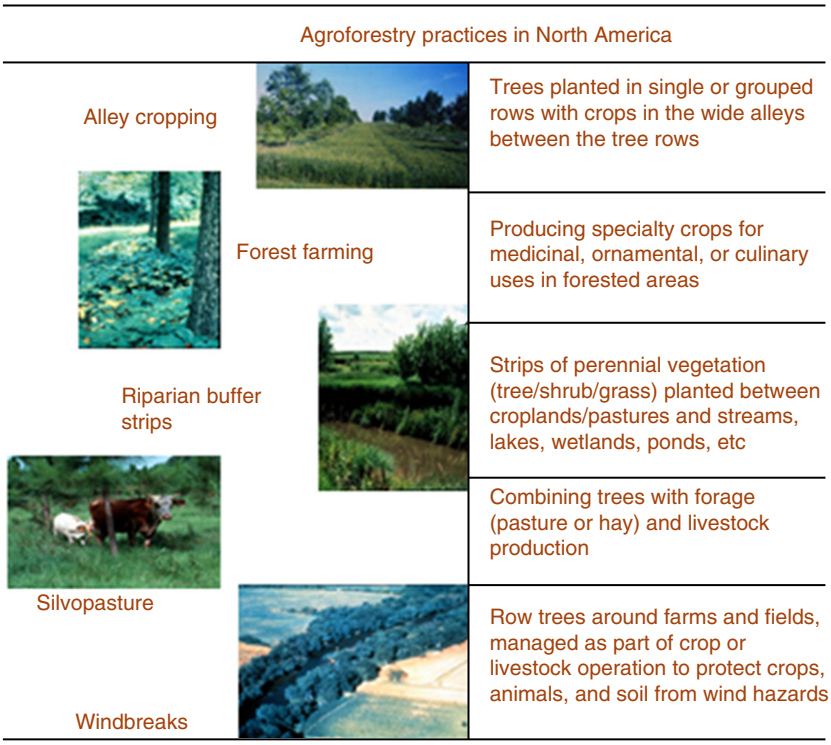


Figure 1 Agroforestry practices in North America.

America, involving a variety of tree species such as damar (*Shorea* spp.), cinnamon (*Cinnamomum zeylanicum*), and jungle rubber (*Hevea* sp.) that are exploited for their for nonwood products.

2. Tree intercropping
   - Alley cropping: Fast-growing, preferably leguminous, woody species grown in crop fields as a hedgerow with close (~0.5 m) in-row spacing and wide (4 m or more) between-row spacing; the woody species pruned periodically at low height (<1.0 m) to reduce shading of crops; the prunings applied as mulch into the alleys as a source of organic matter and nutrients, or used as animal fodder.
   - Multipurpose trees on farmlands: Fruit-, fodder-, fuelwood-, and timber trees scattered or planted in some systematic arrangements in crop- or animal-production fields.

3. Silvopasture (trees in support of crop production)
   - Grazing under scattered or planted trees.
   - Tree-fodder systems (fodder banks).
4. Protective systems
   - Boundary planting, windbreaks, shelterbelts, soil conservation hedges: Use of trees to protect fields from wind damage, sea encroachment, floods, etc.
5. Agroforestry woodlots
   - Block planting of preferred tree species for specific purposes such as reclamation of salt-affected lands, eroded lands, acid soils, waterlogged soils, etc.

Geographical Distribution and Area under AFS

The nature and intensity of the type of agroforestry practiced in a locality or region is determined primarily by its ecological potential and socioeconomic conditions. Humid lowlands and other tropical regions of the world that are not constrained by climatic limitations such as extreme temperatures and long dry seasons are home to a large diversity of plant species and therefore numerous and diverse AFS. Moreover, socioeconomic factors such as human population pressure, greater availability of labor, smaller land-holding size, complex land tenure, and lack of proximity to markets often support more and diverse AFS in such regions. In general, small family-farms, subsistence food crops, and emphasis on the role of trees in improving soil quality of agricultural lands are characteristic of tropical AFS. However, environmental protection is the main motivation for agroforestry in the industrialized nations, where intensive, mechanized monocultural production systems of agriculture and forestry have contributed to reduced biodiversity and loss of forest resources and wildlife habitat, and increased environmental hazards such as erosion, nonpoint source pollution of ground water and rivers, and greenhouse-gas emissions.

As noted above, multistrata systems (homegardens, shaded perennial systems, and multilayer tree gardens) are common in tropical regions with high human population, whereas less intensive systems are common in areas with lower population density. In the moist tropical and dry regions also, the nature of AFS is influenced by climate and population pressure: homegardens and multilayer tree gardens are found in the relatively wetter areas; tree intercropping systems such as multipurpose trees on crop lands, silvopastoral (grazing) systems, and protective systems of windbreaks and shelterbelts are common in these regions. In the tropical montane regions that have favorable rainfall regimes, sloping lands and rolling topography make soil erosion an issue of major concern; consequently, soil conservation is one of the main objectives of agroforestry in these regions. Shaded perennial systems, use of woody perennials in soil conservation, and silvopastoral systems are the major forms of agroforestry in such tropical highlands. Several other specific systems also exist in the tropics such as apiculture with trees, aquaculture involving trees and shrubs; but, again, information on them was too meager to warrant their inclusion here.

Estimating the area under AFS on a farm in itself is a challenge because of the lack of clarity and proper procedures for delineating the area influenced by trees in a mixed stand of trees and crops (Nair *et al.*, 2009). In simultaneous systems, the entire area occupied by multistrata systems such as homegardens and shaded perennial systems and intensive tree-intercropping situations can be listed as agroforestry. However, most AFS are rather extensive, where the components, especially trees, are not planted at regular spacing or density; for example, the parkland system and extensive silvopastures. Such situations exist also in Europe and other temperate regions where the mosaics of intensive field systems, with hedgerows and patches of woodland, are common features of agricultural landscapes. The problem of estimating the area under agroforestry is more difficult in the case of practices such as windbreaks and boundary planting where although the trees are planted at wide distances between rows (windbreaks) or around agricultural or pastoral parcels (boundary planting), because the influence of trees both above and below ground extends beyond the obviously visible area of trees. For windbreaks, the rule of thumb is that the area protected from wind erosion extends laterally to 10 times the height (H) of trees in the central core of windbreaks. The problem has a different dimension of difficulty when it comes to sequential tropical systems such as improved fallows and shifting cultivation. In such situations, the beneficial effect of trees and other woody vegetation (in the fallow phase) on the crops that follow them (in the cropping phase) is believed to last for a variable length of time (years). Despite these temporal and spatial issues, a recent ICRAF survey using high-resolution remote-sensing (Zomer *et al.*, 2009) quantified the areas of agricultural landscapes with at least 10% tree cover worldwide as nearly a billion hectares. Considering the prevalence of agroforestry practices in nonagricultural lands, Nair (2012a) estimated the global area currently or potentially under agroforestry as 1.6 billion ha (**Table 2**).

Brief Description of Major Agroforestry Practices

Intercropping (Alley Cropping and Other Forms of Tree Intercropping)

In the tropics, alley cropping was developed by researchers in the 1970s and 1980s in an attempt to find alternatives to the long-term fallows of shifting cultivation. The main motivation and rationale for alley cropping was the perceived soil-improving potential of fast-growing, leguminous woody species and their ability to withstand repeated cutting. It was hypothesized that by integrating these woody species into food crop production systems in simultaneous combinations, some of the benefits of natural long-term fallows such as recycling nutrients, suppressing weeds, and controlling erosion on sloping land could be realized without having to keep the land out of agricultural production. The practice consists of growing arable crops between hedgerows of planted shrubs and trees, preferably leguminous species that are periodically pruned to prevent shading to crops (**Figure 2**). The biomass obtained by pruning the trees and shrubs during the crop-growing season is put back to the alleys as a source of mulch and green manure. Besides, leguminous woody species add nitrogen to the system through biological nitrogen fixation.

Table 2 Global distribution and area under different agroforestry system subgroups[a]

AFS subgroup	*Major AF practices*	*Distribution (major agro-ecological/geographical regions)*[b]		*Approximate area (million ha)*[b]	
		Tropical	*Temperate*	*Tropical*	*Temperate*
Multistrata systems	Homegardens	Humid: wet, moist, and montane (rainfall >1000 mm year^{-1})	Forest farming	100	
	Shaded perennials				
Tree intercropping	Alley cropping	Rainfall >800 mm year^{-1}	n/a	50	50
	Trees on farmlands	Throughout tropics	n/a	550	50
Silvopasture	Cut-and-carry and browsing	Wet and moist; rainfall >1000 mm year^{-1}		300	150
	Grazing under trees	Semiarid to arid	North America, Europe, subtropical highlands		
Protective systems	Windbreaks, shelterbelts	Semiarid and arid lands; coastal areas	North America, Europe, China	200	100
	Soil conservation hedges	Sloping lands in higher rainfall areas	North America (Riparian buffer strips)		
	Boundary planting	Throughout	Windbreaks		
Agroforestry woodlots	Firewood and fodder	Drylands		50	
	Land reclamation	Degraded lands (eroded, salt-affected)			
Total				1250	350

[a]Estimates based on the reported values in literature.
[b]Including potential areas for adoption.
Source: Reproduced from Nair, P.K.R., 2012a. Climate change mitigation and adaptation: A low hanging fruit of agroforestry. In: Nair, P.K.R., Garrity, D.P. (Eds.), Agroforestry: The Future of Global Land Use. Dordrecht, The Netherlands: Springer, pp. 31–67.



Figure 2 Tropical alley cropping. Fast-growing, coppicing, nitrogen-fixing shrubs and trees are grown in rows 4–8 m apart in crop fields and pruned periodically (4–6 week intervals); the succulent and easily decomposable tree biomass so obtained is returned to the cropped alleys as a source of nutrient for crops. The photo shows *Gliricidia sepium* grown with maize (*Zea mays*), a practice followed by thousands of farmers in eastern and southern Africa. Photo credit: ICRAF, Nairobi, Kenya.

Many studies on alley cropping, of both biophysical and socioeconomic nature, were undertaken in various parts of the tropics during the 1980s and 1990s. Indeed, alley cropping was the most widely researched topic in tropical agroforestry during that period. In interpreting the results of these studies, some experts have used the data to defend alley cropping, others to denigrate it. But, the merits or demerits of alley cropping or, for that matter, any agroforestry technology cannot be judged on the basis of any single criterion or short-term result. Benefits other than crop yield, such as soil fertility improvement, the yield and economic returns from multiple products such as fuelwood and fodder, and the possibility of avoiding the risk associated with monocultural production systems must be carefully weighed against drawbacks.

Key issues concerning alley cropping are its ecological adaptability and labor demand. The provision of nutrients through decomposing mulch, a basic feature of alley cropping, depends on the quantity of the mulch as well as on its quality and time of application. If the ecological conditions do not favor the production of sufficient quantities of mulch (as is the case in dry tropics), there is no perceptible advantage in practicing alley cropping (Rao *et al.*, 1998). The issue of high labor demand is associated with the pruning of the shrubs and the incorporation of the biomass in the field. There are also some issues of pest management problems of mixed species stands as well as newly introduced species, and tree–crop competition for growth resources such as nutrients, water, and light. All these issues have contributed to poor rates of farmer adoption of the alley-cropping technology.

Another agroforestry technology that has been promoted, especially in nutrient-depleted African soils, is improved fallow with 'fertilizer trees.' Basically, one or a few (mixed) tree species, usually biological nitrogen fixers, are planted at high density as a substitute to natural fallow, to achieve the benefits of the latter in a shorter time of 2–3 years versus 15–20 years of natural fallow (Buresh and Cooper, 1999). The production of biomass in planted fallows as well as the potential of planted fallows to ameliorate soil fertility is controlled by several factors: environmental conditions, soil type,

land degradation, length of the fallow period, density of tree planting, tree management, and soil and climatic conditions. Improved fallows are reported to sequester substantial amounts of C in plants and soil in the short term (Sanchez, 1999; Albrecht and Kandji, 2003), and enhance the stabilization of water-stable aggregates, which in turn decreases the risk of erosion in subsequent crop periods, thus contributing to the sustainability of the system (Mutuo, 2005).

In the temperate region as well as Australia, alley cropping refers to growing herbaceous (agricultural) crops in the alleys between rows of widely planted trees that are planted in single or grouped rows (**Figure 1**). This tree-row and alley arrangement allows the use of farm machinery and equipment and reduces the need for manual labor. Black walnut (*Juglans nigra*), a valuable timber- and nut-producing tree is the species most widely used in alley cropping in North America (**Figure 3**). The common spacing adopted is 12.5 m between tree rows and 3 m between trees within a row (270 trees ha^{-1}). The driving force behind most temperate-zone alley cropping is economic benefits from the intercrop. Soil conservation in gently sloping lands could be an additional advantage. Various aspects of this practice have received considerable research attention in the eastern and midwestern USA and Canada (Garrett, 2009). Other similar systems in the temperate regions include the traditional intercropping practice used in the establishment of fruit and nut trees including olive (*Olea* spp.) and grapes (*Vitis* spp.) in Europe, with pecan (*Carya illinoensis*) trees in southeastern USA, and with paulownia (*Paulownia* spp.) trees in China.

The most widespread form of agroforestry, in terms of the area involved, is perhaps the extensive intercropping under-scattered stand of trees, particularly in the semiarid regions of sub-Saharan Africa and Asia. The so-called parkland system of sub-Saharan Africa (**Figure 4**) extends across the entire semiarid belt from Senegal in the west to Ethiopia and Kenya in the east (Boffa, 1999). It originated from the practice of the traditional shifting cultivation in which farmers conserved in their fields the trees that are desirable for shade, fodder, fruits, and medicines. The trees that are most common include *Faidherbia albida*, *Parkia biglobosa*, and *Vitelleria paradoxa*. The understory species include both crops (millet, cassava, cotton, maize, and others depending on climatic and soil conditions) as well as grasses for animal grazing, where animals are let loose for grazing over crop residues and grasses. The practice is therefore considered as extensive intercropping or silvopasture.



Figure 3 Temperate alley cropping. A pine (*Pinus* sp.) – cotton (*Gossypium* sp.) alley cropping in northwest Florida, USA. Photo credit: Shibu Jose, The Center for Agroforestry, University of Missouri.

Multistrata Systems

Intensive, multispecies, tree-based farming systems such as homegardens, shaded perennial stands, and other complex agroforests are common agroforestry practices in the humid and subhumid parts of the tropics, especially in the lowlands (**Figure 5**). The structural and functional diversity and various other characteristics of these systems have been well described and reviewed (Nair, 1989; Kumar and Nair, 2006). Homegardens have a long tradition of providing food and nutritional security as well as environmental sustainability in smallholder production systems, often in heavily populated regions of lowland humid tropics in south- and southeast Asia, and to a small extent in other tropical and subtropical regions. Although a few systems that have some similarities to tropical homegardens can be found in parts of the temperate regions as well (e.g., the satoyama system in Japan: Ichikawa and Toth, 2012), intensive multispecies homegardens are a unique agroecosystem of the tropics.

Shaded-perennial systems that involve growing tree crops such as coffee (*Coffea* sp.) and cacao (*T. cacao*) under the shade of overstory tree species (**Figure 6**) represent another traditional example of high-intensity crop combination that has some unique ecological features and commercial value. In addition to coffee and cacao, several of the tropical fruit- and nut-producing tree species that are harvested annually or at shorter intervals are often grown in association with understory- or overstory species (Elevitch, 2006, 2011; Gama-Rodrigues *et al.*, 2010). In some situations, the species combinations and management features of these systems are very similar to those of homegardens such that, at the landscape- and village level, there is a continuum of plant associations from



Figure 4 Parkland system. A mature stand of maize (*Zea mays*) under a sparse stand of *Faidherbia albida* trees in Malawi. Reproduced from Ajayi, O.C., Place, F., 2012. Policy support for large-scale adoption of agroforestry practices: Experience from Africa and Asia. In: Nair, P.K.R., Garrity, D.P. (Eds.), Agroforestry: The Future of Global Land Use. Dordrecht, The Netherlands: Springer, pp. 175–201.



Figure 5 Homegarden. Homegardens that consist of intimate, multistory combinations of various trees and crops around homesteads provide food- and cash security as well as social and esthetic benefits to millions of farm households around the tropics. The picture shows a homegarden with coconut palms (*Cocos nucifera*); various fruit- and nut-producing trees such as jackfruit tree (*Artocarpus* sp.), mango (*Mangifera indica*), and nutmeg (*Myristica fragrens*); and food crops such as plantains (*Musa* spp.), cassava (*Manihot esculenta*), and rice (*Oryza sativa*) in the foreground, in a Kerala homegarden, southwestern India.



Figure 6 Shaded perennial system. Shaded perennial-crop systems involve growing shade-tolerant commercial species such as coffee (*Coffea* sp.) and cacao (*Theobroma cacao*) under overstory shade trees. The photo shows a coffee field with Erythrina poeppigiana as the shade tree in Costa Rica. Photo: E. Somarriba, CATIE, Costa Rica.

homegardens nearer homes to multistrata tree gardens away from the homes.

Characterized as the epitome of sustainability, these multispecies tree–crop combinations are excellent examples of efficient land-management systems by smallholder farmers. With heavy reliance on human (often family) labor for the farm operations, conventional tillage operations involving machinery are minimal or absent in such systems. Some of the distinguishing ecosystem sustainability features of these systems include efficient and 'closed' nutrient cycling facilitated by continuous litter fall and decomposition and very little export of nutrients from the system by way of harvested products, the reliance on organic manure and plant materials with consequent avoidance of chemical-fertilizer use, and predominance of deep-rooted trees, which collectively contribute to the high levels of C sequestration and climate-change mitigation in these systems, as evidenced by the recent studies by Saha *et al.* (2010) in the homegardens of Kerala, India, and Gama-Rodrigues *et al.* (2010) in the shaded cacao systems of Bahia, Brazil.

Protective AFS

These systems encompass the use of trees and shrubs for exploiting their ecosystem-protection benefits by planting them as windbreaks, riparian buffers, soil conservation hedges, and similar other configurations. Windbreak practices include shelterbelts, timber belts, and hedgerows, and are planted and managed as part of a crop or livestock operation. Field windbreaks are used to protect a variety of wind-sensitive row, forage, tree, and vine crops, to control wind erosion, and to provide other benefits such as improved bee pollination of crops and wildlife habitat (Brandle *et al.*, 2009). For livestock, windbreaks help reduce animal stress and mortality, feed and water consumption, and odor, whereas timber belts are managed windbreaks designed to increase the value of the forestry component. Shelterbelts are also planted along the coastal areas to reduce the impact of sea encroachment and protect crops from salt-water damage. Riparian and 'upland' buffers are strips of permanent vegetation, consisting of trees, shrubs, and grasses that are planted and managed together. Riparian buffers are placed between agricultural land (usually crop land or pasture land) and water bodies (rivers, streams, creeks, lakes, wetlands, etc.) to reduce runoff and nonpoint source pollution, stabilize stream banks, improve aquatic and terrestrial habitats, and provide harvestable products (**Figure 7**). Upland buffers are placed along the contour within agricultural crop lands to reduce runoff and nonpoint source pollution, improve internal drainage, enhance infiltration, create wildlife habitat and connective travel corridors, and provide harvestable products (Schultz *et al.*, 2009). As discussed under alley cropping, frequently pruned rows of trees and shrubs planted across the contour in crop production fields help reduce soil erosion and the pruned biomass serves as a source of nutrient to crops or can be transported away to be used as animal fodder.

Riparian buffers are a common feature of the landscape in the US north central region in particular (Jose *et al.*, 2012), as well as in Canada (Thevathasan *et al.*, 2012). In addition to the benefit of C sequestration, these protective systems can provide additional C benefits due to improved crop and livestock production and energy savings (Kort and Turnock, 1999). Recognizing that agricultural runoff as a key contributor to nonpoint source pollution (NPSP) of water including hypoxia in the Gulf of Mexico, riparian buffer strips are a heavily subsidized agroforestry practice by US Federal cost-share programs such as the Conservation Reserve Program, Environmental Quality Incentives Program, Forest Stewardship Program, Wetlands Reserve Program, and Wildlife Habitat Incentives Program (Jose *et al.*, 2012).



Figure 7 Riparian buffer. Bear Creek National Restoration Watershed (designated under the Clean Water Action Plan, 1999) and the USDA designated Bear Creek National Research and Demonstration Site. The pictures are of various kinds of riparian buffers along Bear Creek. Photo credit: The Iowa State University NREM Riparian Buffer Team, ISU, USA.



Figure 8 Silvopasture. Beef cattle grazing on *Brachiaria brizantha* (grass) grown under *Eucalyptus* hybrid trees on a farm in Minas Gerais, Brazil.

Silvopasture

Silvopasture that combines trees, forages, and shrubs with livestock operations is another type of agroforestry practice that is popular in both the tropics and the temperate regions. Broadly, there are two major forms of silvopasture: grazing- and tree-fodder systems. In grazing systems, cattle are allowed to graze on pasture under widely spaced or scattered trees (**Figure 8**), whereas in the tree-fodder systems, the animals are stall-fed with fodder from trees or shrubs grown in blocks (fodder banks) on farms (Nair *et al.*, 2008; Kiptot and Franzel, 2012). Most silvopastoral systems in Africa and other developing regions of the world involve extensive open grazing by free-roaming animals under scattered natural stands of trees and shrubs mostly in semiarid to arid areas, as in the parklands of sub-Saharan Africa. More intensive grazing systems of silvopasture are practiced in Latin America where animals are penned in parcels of land with barbed-wired living-fence, and grazing is regulated (Somarriba *et al.*, 2012). Such 'organized' silvopastoral systems are also becoming popular in the extensive Cerrado region of Brazil (Nair *et al.*, 2011). The most intensive silvopastoral system is the stall feeding of animals by fodder from trees grown elsewhere, which is a very common practice in smallholder farming systems as described by Kiptot and Franzel (2012). The grazing system of silvopasture has recently gained prominence as an environmentally desirable approach to managing degraded pasture lands in the industrialized countries (Rigueiro-Rodriguez *et al.*, 2008; Garrett, 2009).

Silvopasture embodies the goals of desirable management practices for climate-change mitigation (especially in terms of grazing and manure addition) and C sequestration.

Additional benefits of silvopasture include water quality improvement (Michel *et al.*, 2007), soil conservation, esthetics, and providing shade to cattle (Garrett, 2009). Alternative land uses including sustainable forest management, outdoor recreation, and ecotourism, and most encouragingly silvopasture, are considered highly compatible with traditional ranching and include several elements of best management practices for ranchers (Garrett, 2009).

Tree Woodlots and Specialty Crops

These terms are used to denote agroforestry practices that are undertaken for special situations and needs. Examples include growing tree woodlots as fodder banks (for production of cut-and-carry tree-fodder), boundary planting of trees for production of firewood, small timber, poles and fence posts; tree planting for reclamation of degraded lands such as saline soils and mined land (Quinkenstein *et al.*, 2012); establishing tree woodlots for biomass and bioenergy production such as in the Canadian prairies (Kort and Turnock, 1999; Thevathasan *et al.*, 2012) growing specialty products such as ornamentals, honey, and high-value crops for niche markets; and a whole host of such 'nonconventional' land-use systems. The extent of people and areas involved and the economic benefits derived from such activities are seldom documented. Among these activities only large-scale tree woodlots would count as major activities in terms of carbon sequestration and climate change mitigation, although all would be important for their economic, social, and cultural benefits.



Figure 9 Fallow regeneration. Farmer-managed natural regeneration of fallow in Burkina Faso. Reproduced from ICRAF.

One of the best ways of reclaiming areas degraded by severe soil erosion, acidity, salinity or alkalinity, and other forms of land degradation is by planting tree species that are adapted to such conditions and leaving the land under the tree woodlot for several years (20 or more, depending on local conditions) before it is opened up for planting crops or fodder grasses. Several such programs, under the banner 'wasteland development,' supported by various government agencies and with the involvement of nongovernmental organizations and local communities are popular in India. Another example of large-scale implementation of protective agroforestry is the 'fallow regeneration' that is gaining momentum in different parts of arid and semiarid sub-Saharan Africa (**Figure 9**). For example, the recent rejuvenation of the centuries-old parkland AFS of the Sahel through the spread of farmer-managed natural regeneration has been documented to have occurred on nearly 5 million hectares by 2008 in Niger alone (Reij *et al.*, 2009; Garrity, 2012).

Role of Agroforestry in Land Management in the Twenty-first Century

Agroforestry began to attract the attention of the international development and scientific community in the 1980s as a means for increasing and sustaining agricultural production in marginal lands and remote areas of the tropics that were not benefited by the Green Revolution. Thanks to the research and development efforts at various local, regional, and global levels, agroforestry is at present recognized as having the potential to offer much toward sustainable land management and environmental integrity in poor and rich nations alike. Discussing the role of agroforestry in land management in the twenty-first century, Nair and Garrity (2012) identified food security, climate change mitigation and adaptation, and other ecosystem services as the key areas where the impact of AFS could be conspicuous in the immediate future.

Food Security

In sub-Saharan Africa, which is home to three-quarters of the world's 'ultra-poor' (less than US$0.50 per day), approximately 218 million people, roughly 30% of the continent's total population, struggle with hunger daily (United Nations, 2010). Soil-fertility depletion, exacerbated by continuous cropping without nutrient inputs in the inherently poor soils, is a major challenge in the dryland ecosystems that dominate these regions. Reversing this trend and restoring soil health in the smallholder African farming systems has become a major development policy issue on the continent. The most urgent need is to increase biomass production in the farming system with richer sources of organic nutrients to complement whatever amounts of inorganic fertilizers that a smallholder farmer can afford to apply. The integration of 'fertilizer trees' such as *Calliandra*, *Gliricidia*, *Sesbania*, and *Tephrosia* as improved fallows into food crop agriculture is a promising, but underappreciated, approach to accomplishing this.

Recent advances in agroforestry based on the use of fertilizer trees and other trees have produced a range of promising approaches to accomplishing this through a portfolio of options, now referred to as Evergreen Agriculture (Swaminathan, 2012). Evergreen Agriculture emphasizes the application of sound, tree-based management practices, and the knowledge to adapt these to local conditions, to optimize fertilizer and organic resource-use efficiency for greater crop productivity. It is also compatible with reduced tillage, increased residue retention on the soil surface, and other principles of conservation agriculture, in situations where these practices are feasible and appropriate. Currently, *F. albida* is showing promise as a cornerstone of Evergreen Agriculture for fallow regeneration and restoration of soil fertility in dry areas (Garrity, 2012).

The important role of fruit- and other food-producing trees in providing food security especially to low-income households is another important issue to be considered in this context. A large number of such trees grown in intimate association with herbaceous crops in homegardens and intercropping systems (Elevitch, 2006; Kumar and Nair, 2006, Leakey, 2012b) provide food security as well as nutritional security to millions of households throughout the tropics. Scientific efforts to domesticate and improve traditionally important, but underutilized, trees as a means to intensifying AFS are currently receiving deserved research attention in agroforestry (Leakey *et al.*, 2012). Domestication and improvement of the multitude of such indigenous agroforestry trees offer enormous opportunities to enhance food- and nutritional security as well as generating household income, especially in the tropical and subtropical developing regions.

Pathways to increasing food security also include the ability to increase livestock production in integrated crop-livestock-tree systems, which are dependent on greater sustainable sources of high-quality fodder (Herrero *et al.*, 2010). The impact of fodder tree production and income among smallholder dairy farmers in East Africa has emerged as a major area of agroforestry impact (Kiptot and Franzel, 2012). Additional pathways to smallholder food security are also achieved through the production of higher-value products that are sold for increased income, and the husbandry of tree crops, such as timber, also increases the farm asset base (Garrity, 2004). The integration of trees into crop- and livestock-production systems opens up opportunities for all these pathways on the small-scale farm.

Table 3 Estimates of carbon sequestration in agroforestry systems in different ecological regions of Africa and Asia

Agroforestry system subgroup	*Major AF practices*	*Estimated C stock range (Mg ha^{-1})*		*C Seq Potential (CSP) in new areas (Mg ha^{-1} yr^{-1})*	
		Above ground	*Below ground (especially soils)*	*Above ground*	*Below ground (soils)*
Multistrata systems	Homegardens	2 to 18	Up to 200	0.5–3	1.5–3.5
	Shaded perennials	5 to 15	Up to 300	1–4	1.0–5
Tree Intercropping	Alley cropping	Up to 15	Very low to 150	0.5–4	1.5–3.5
	Multipurpose trees on farmlands	Up to 12	Very low to 150	0.2–2.5	1.5–3.5
Silvopasture	Tree fodder (browsing, cut-and-carry)	1.8–3	Very low to 80	0.3–4	1.0–2.5
	Grazing under trees	1.5–8	Very low to 60	0.3–2	0.4–1.0
Protective systems	Windbreaks, shelterbelts, soil conservation hedges, boundary planting	1.5–7	Very low to 60	0.7–2	0.4–1.0
Agroforestry Tree woodlots	Woodlots for firewood, fodder, land reclamation	1.5–7	Very low to 60	1–5	1.0–6.0

Source: Reproduced from Nair, P.K.R., 2012b. Carbon stocks in agroforestry systems: A global appraisal. Presented at the ASA/CSSA/SSSA International Annual Meetings, 21–24 October 2012, Cincinnati, OH, USA. Available at: www.agronomy.org/annualmeetings2012 (accessed 10.05.13).

Climate Change Adaptation and Mitigation

Agroforestry is a key approach to the integration of climate change adaptation and mitigation objectives, often generating significant cobenefits for local ecosystems and biodiversity (Matocha *et al.*, 2012). Synergies between climate change adaptation and mitigation actions are particularly likely in situations involving income diversification with tree and forest products. These options also reduce the susceptibility of land use systems to extreme weather events, enhance soil fertility, and favor the conservation and restoration of forest and riparian corridors. Evaluating the role of agroforestry in climate change adaptation and mitigation, Nair (2012a) concluded that whereas existing multistrata and tree intercropping systems will continue to provide substantial climate change mitigation benefits, large-scale initiatives in grazing land management, working trees in drylands, and the establishment of vegetative riparian buffer and tree woodlots are the most promising agroforestry pathways for both adaptation and mitigation.

Sequestration of carbon in soils and in the biota, along with payments to resource-poor farmers for the ecosystem services rendered, would be a timely win-win strategy in the fight against food-insecurity and global warming (Lal, 2010). The role of agroforestry in carbon sequestration is now well articulated (Nair *et al.*, 2010) for many AFS (**Table 3**). Consequently, there is considerable interest in the creation of biocarbon investment funds to channel carbon offset payments from developed countries to stimulate more carbon sequestration while simultaneously enhancing the livelihoods of smallholders and the environment. These investments will encourage development pathways resulting in higher landscape-level carbon stocks (Garrity *et al.*, 2010).

Ecosystem Services

Exploiting nitrogen fixation by tropical legumes, enhancing the efficiency of nutrient cycling, and benefitting from the deep-capture of nutrients are recognized as the primary bases of the soil sustainability advantages of such systems. The focus of soil-improving qualities of multipurpose trees that dominated agroforestry research agenda during the 1980s and 1990s was on realizing these benefits at the farm or local level. Since the 1990s, other ecosystem services of trees that transcend from local to global levels such as climate change mitigation through carbon sequestration and biodiversity conservation have received increasing attention. The biodiversity conservation attributes of agroforestry stem from the species diversity and complexity of such systems. The trend toward major public investments for rewarding farmers for the ecosystem services their enterprises provide to society, in both the developed world and the emerging economies such as China and India, suggests that the integration of trees into agricultural systems will be a major opportunity in the succeeding decades.

Conclusions

Modern agricultural systems have resulted in significant gains in agricultural production worldwide and averted large-scale hunger over the past half century. Yet, many developing regions of the world, notably sub-Saharan Africa, lag behind the rest of the world in food production and other aspects of development. This is because the input-intensive agricultural technologies of the Green Revolution have turned out to be unsuitable for Africa's infertile soils, unforgiving climate, weak infrastructure, and sociocultural traditions. During the past 35 years, research and development efforts have widely demonstrated the positive role of AFS in addressing some of the major problems of Africa and other parts of the world such as food- and nutritional insecurity, soil degradation, desertification, and climate change; yet agricultural development efforts have vastly ignored the values of such time-tested integrated systems and their social values.

Conventionally, one has treated agriculture and forestry separately although these sectors are often interwoven on the

landscape and share many common goals. These disconnects are one of the main causes of failure of land-use systems to meet the needs of the people in ways that confer sustainability. Agroforestry offers the opportunity to exploit the potential of the multitude of indigenous plants that provide multiple products and ecosystem services and incorporate them into widely adoptable land-use systems to improve the lives of millions of people and our environment.

See also: Agroforestry: Complex Multistrata Agriculture. Agroforestry: Fertilizer Trees. Agroforestry: Fodder Trees. Agroforestry: Hydrological Impacts. Agroforestry: Participatory Domestication of Trees. Biodiversity and Ecosystem Services in Agroecosystems. Biodiversity: Conserving Biodiversity in Agroecosystems. Ecoagriculture: Integrated Landscape Management for People, Food, and Nature. Food Security: Yield Gap. Soil: Nutrient Cycling

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Air: Confined Animal Facilities and Air Quality Issues

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Glossary

Air Pollutant Foreign and/or natural substances occurring in the atmosphere that may result in adverse effects to humans, animals, and/or the surrounding environment.

Ammonia (NH_3) A colorless gaseous compound of nitrogen and hydrogen that is highly soluble in water and has the ability to react with oxides of nitrogen to form ammonium nitrate, a particulate matter that contributes to air pollution and the resulting health implications.

Anaerobic digestion A biochemical process in which bacteria break down biodegradable organic material, such as manure, in an oxygen-free environment. The breakdown of organic materials results in the production of biogas, typically a mixture of methane and carbon dioxide.

Anthropogenic Originating from human activity.

Confined Animal Feeding Operation (CAFO) Agricultural operations where animals are kept and raised in confined areas, where animals feed, manure, and production operations are on a small land area. Usually, feed is brought to animals in CAFOs rather than the animals grazing. The US Environmental Protection Agency (EPA) separates CAFOs into three categories (large, medium, and small) based on the number of animals in a facility.

Criteria pollutant Six emissions identified and regulated by the EPA, including: sulfur dioxide, nitrogen dioxide, particulate matter, carbon monoxide, ozone, and lead.

Enteric fermentation The digestive process in ruminant animals, such as beef and dairy cattle, sheep, and goats, by which feed is broken down by microorganisms (bacteria, protozoa, and archaea) into simple molecules for absorption into the bloodstream. Byproducts of enteric fermentation include gaseous compounds (methane, carbon dioxide, etc.), which are expelled from animals via eructation.

Odors A substance giving off a smell, caused by one or more volatilized chemical compounds. In animal production, odorants are a major concern for the general public, as urban encroachment of agricultural land increases.

Particulate matter (PM) Any material that exists in the solid or liquid state in the atmosphere. The size of PM can vary from coarse, windblown dust particles to fine particles. Coarse particles (PM_{10}) range between 2.5 and 10 μm in diameter. Fine particles ($PM_{2.5}$) are less than 2.5 μm in diameter. Both PM_{10} and $PM_{2.5}$ can affect human and animal health and can contribute to smog and ozone formation.

Volatile organic compounds (VOCs) Carbon-containing compounds that evaporate into the air. These compounds contribute to the formation of smog and odor.

Introduction

The world population is expected to grow from today's 7 billion people to 9.3 billion people by 2050 (United Nations, 2009). Although the human population shows this dramatic growth, the amount of arable agricultural land needed to grow food to nourish these people is limited and can only increase moderately. Furthermore, increasing disposable income in developing and emerging countries leads to higher per capita consumption of animal protein, leading to an expected increase in global dairy and meat consumption of 74% and 58%, respectively (UNFAO, 2012). Thus, food production must become more efficient and intensification is one of the most viable solutions. In general, concentrated animal feeding operations (CAFOs) allow the production of relatively low cost food; however, there are externalities associated with CAFOs, such as air and water pollutants, and greenhouse gas (GHG) emissions.

Over the past decades, there has been a shift from traditional, rather low input, and extensive farms to CAFOs in the US and throughout much of the developed world. Owing to the increase in the number of CAFOs and the air quality issues surrounding them, the US Environmental Protection Agency (EPA) has created nationwide specifications for what constitutes a CAFO as well as what emissions from these operations must be monitored and mitigated.

For an animal operation to be considered a CAFO, it must first meet the definition of an animal feeding operation (AFO). An AFO is an 'operation where animals have been, are, or will be stabled or confined and fed or maintained for a total of 45 days or more in any 12-month period and where vegetation is not sustained in the confinement area during the normal growing season' (USEPA, 2012b). 'Maintained' in this case means that the animals are confined in the same area where waste is generated or concentrated and can include areas where animals are fed, watered, cleaned, groomed, milked, or medicated (USEPA, 2012b). This definition also distinguishes AFOs from pasture- or grazing-based systems; therefore, animals raised on pasture are not considered to be produced in an AFO.

AFOs are defined as either medium- or large-sized CAFOs if a series of EPA specifications apply. Most significantly, an AFO is considered a CAFO if it is determined to be 'a significant contributor of pollutants to waters of the US' (USEPA, 2012b). Dairy and beef cattle, veal calves, swine, chickens, turkeys, ducks, horses, and sheep can all fall within the CAFO designation if specific threshold numbers are met. This article presents three types of CAFOs, namely those for large ruminants (beef and dairy cattle), swine, and poultry (broiler and layer).

Among the benefits of CAFOs are that they show decreases in animal mortality rates, improved feed efficiencies, and improved productivity (ASABE, 2006). However, CAFOs also have externalities including the production and emissions of nuisances, air pollutants, and GHGs. Emissions from CAFOs that contribute to poor air quality can vary in severity between the types of animals being produced (NRC, 2003); however, the key issues related to air quality remain the same across livestock production systems. Air emissions associated with CAFOs can include odorous, gaseous, and particulate compounds. This article will highlight the major air quality issues associated with CAFOs.

Air Pollutants

Air pollutants affect human and animal health as well as ecosystem health and visibility (Pope *et al.*, 2009; Cambra-Lopez *et al.*, 2010). Criteria pollutants that are regulated in the US and that have the greatest effects on air quality include carbon monoxide (CO), lead (Pb), nitrogen dioxide (NO_2), particulate matter (PM) of less than 10 μm in diameter (PM_{10}), PM of less than 2.5 μm in diameter ($PM_{2.5}$), ground level ozone (O_3), and sulfur dioxide (USEPA, 2001). These criteria pollutants and some of their precursor compounds are regulated under the Clean Air Act and enforced by the USEPA, to address direct public health concerns (USEPA, 2012a). The National Research Council (NRC, 2003) provided a list of air emissions, which contribute most significantly to air quality concerns (**Tables 1** and **2**). In CAFOs, the primary air pollutants of concern are PM, ammonia (NH_3), hydrogen sulfide (H_2S), volatile organic compounds (VOC), and odors. Although NH_3, H_2S, VOCs, and odors are not directly regulated from most environmental agencies (with the exception of central and southern California), it is important to minimize these emissions because they can lead to the formation of criteria pollutants and often constitute nuisances. For example, ammonia can contribute to secondary PM formation (Pinder *et al.*, 2007), VOCs can contribute to O_3 formation (Shaw *et al.*, 2007; Sun *et al.*, 2008), and both NH_3 and VOCs contribute to odor production, a growing concern for policymakers as well as the general public. Additionally, there is an association between exposure to PM and adverse human and animal health effects in livestock CAFOs (Aneja *et al.*, 2009). Human exposures to $PM_{2.5}$ have been associated with pulmonary disease (Pope *et al.*, 2009) and those to PM_{10} with decreased lung function, cardiac arrhythmia, heart attacks, and premature death (Madden *et al.*, 2008). PM also contributes to impaired atmospheric visibility by scattering and absorbing light (Boylan *et al.*, 2006), issues which are discussed in other article.

The following section discusses air quality issues emitted across all CAFO types.

Ammonia

Livestock is estimated to be the single largest source of NH_3 emissions in the US, producing 71.3% of annual emissions (USEPA, 2000). Ammonia primarily results from manure degradation and forms when urease, an enzyme present in animal feces, catalyzes the hydrolysis of urea from urine (Sun *et al.*, 2008). The formation of ammonia occurs as follows:

$$(NH_2)\bullet 2CO + H_2O \rightarrow CO_2 + 2NH_3$$

Ammonia emissions are dependent on the amount of urea nitrogen (urea-N) and degree of mixing between urine and feces (Bussink and Oenema, 1998) and as a result, there are great variations in NH_3 emissions between farms (James *et al.*, 1999; VandeHaar and St-Pierre, 2006), manure land-application methods (Amon *et al.*, 2006), and time of year (Bussink and Oenema, 1998). The production rate of urea-N, and subsequently NH_3, is directly related to the concentration of nitrogen ingested by animals. Urea in ruminants is produced in the liver (detoxification of ammonia from blood circulation) and excreted in the urine. Overfeeding protein in the diet commonly leads to increased urea excretions, which affects NH_3 formation (Burgos *et al.*, 2010). The volatilization of NH_3 from any CAFO can be highly variable depending on the total NH_3 concentration in the solid or liquid phase, temperature, pH, and manure storage time. Emissions depend on how much of the N in solution reacts to form NH_3 versus ionized ammonium ($NH4^+$), which is nonvolatile (i.e., a nongaseous compound) (USEPA, 2001).

In general, NH_3 loss to the atmosphere can lead to PM formation, soil acidification, and eutrophication of surface waters (Fangmeier *et al.*, 1994; Krupa, 2003; CAST, 2011) and decreased livestock performance (Drummond *et al.*, 1980).

Table 1 Ranking of the importance of Animal Feed Operation (AFO) emissions at global and local scales

Emissions	*Global, national, and regional*	*Local, property line, and nearest dwelling*	*Primary effects of concern*
Methane (CH_4)	Significant[a]	Insignificant	Global climate change
Nitrous oxide (N_2O)	Significant	Insignificant	Global climate change
Ammonia (NH_3)	Major	Minor	Atmospheric deposition
Volatile organic compounds(VOCs)[b]	Insignificant	Minor	Quality of human life
Particulate matter	Insignificant	Significant	Health, haze
Odor	Insignificant	Major	Quality of life

[a]Ranking of the importance of each emissions based on NRC recommendations for the potential impact of emissions, both locally and nationally. Rank order from high to low is as follows: major, significant, minor, and insignificant.

[b]According to the NRC, 2003, compared with other sources, VOC emissions from AFOs are considered to be insignificant; however, recent research may warrant changes in this classification.

Source: Adapted from National Research Council (NRC), 2003. Air Emissions from Animal Feeding Operations: Current Knowledge, Future Needs. Washington, DC: National Academies Press.

Table 2 Classification of air emissions from Animal Feed Operations (AFOs)

Emissions	*Criteria pollutant*	*Hazardous air pollutant*	*Greenhouse gas*	*Regulated air pollutant*
CH_4	–	–	X	–
N_2O	–	–	X	–
NH_3	–	–	–	X
Volatile organic compounds	Precursor of ozone	X	X	X
Particulate matter	X	–	–	–
Odor	–	–	–	X

Source: Adapted from National Research Council (NRC), 2003. Air Emissions from Animal Feeding Operations: Current Knowledge, Future Needs. Washington, DC: National Academies Press.

Hydrogen Sulfide

Hydrogen sulfide (H_2S) and other reduced sulfur compounds are produced as manure decomposes anaerobically, resulting in the breakdown of organic matter. Hydrogen sulfide can arise from storage, handling, and decomposition of animal waste. There are two primary sources of sulfur in animal manures: (1) the sulfur amino acids present in animal feed and (2) inorganic sulfur compounds, such as copper sulfate and zinc sulfate, which are used as feed additives to supply animals with trace minerals and serve as growth stimulants for animals (USEPA, 2001; NRC, 2003). Although sulfates are used as trace mineral carriers in all sectors of animal agriculture, their use is more extensive in the poultry and swine industries. A possible third source of sulfur in some locations is trace minerals in drinking water (USEPA, 2001; NRC, 2003). Under anaerobic conditions, any excreted sulfur that is not in the form of H_2S will be reduced microbially to H_2S. Therefore, manure managed in liquid form or slurries are potential sources of H_2S emissions. The magnitude of H_2S emissions is a function of liquid phase concentration, temperature, and pH. Temperature and pH affect the solubility of H_2S in water. The solubility of H_2S in water increases at pH values above 7. Therefore, as pH shifts from alkaline to acidic, the potential for H_2S emissions increases (Snoeyink and Jenkins, 1980; USEPA, 2001). Under anaerobic conditions, livestock and poultry manures are acidic, with pH values below 5.5 (USEPA, 2001). In addition, H_2S causes respiratory problems (Donham *et al.*, 1986) and may lead to adverse effects on workers' health (Mitloehner and Calvo, 2008). Hydrogen sulfide is toxic and can be highly dangerous especially when it is suddenly released in high concentrations from stored manure in a confined area and has caused human and animal mortalities (Ni *et al.*, 2012).

Volatile Organic Compounds

VOCs vary in their reactivity and contribution to O_3 formation (Carter, 1994), and many of the VOCs emitted from fermented animal feeds have low ozone-formation potentials relative to other anthropogenic sources (Howard *et al.*, 2010a,b); however, the quantity of VOC emissions produced from CAFO feed (dairy facilities in particular) generates a valid air quality concern. VOCs are formed as intermediate metabolites in the degradation of organic matter in feed and manure (USEPA, 2001). Under aerobic conditions, any VOC formed is rapidly oxidized to carbon dioxide and water. Under anaerobic conditions, complex organic compounds are degraded microbially to volatile organic acids and other VOCs, which in turn are converted into methane and carbon dioxide by methanogenic bacteria (USEPA, 2001). When the activity of the methanogenic bacteria is optimal, virtually all of the VOCs are metabolized to simpler compounds, such as CH_4, and the potential for VOC emissions is minimal (USEPA, 2001). Other effects of VOC emissions include odor production, PM formation, O_3 formation, and ecosystem degradation (Cambra-Lopez *et al.*, 2010; Pinder *et al.*, 2007). Additionally, VOC emissions can lead to adverse health effects, such as ear, nose, and throat damage (Mitloehner and Calvo, 2008). VOCs encompass a wide range of compounds.

Odors

Odors from CAFOs are a major nuisance and have the potential to negatively impact the quality of life for the nearby residents (Fournel *et al.*, 2012). Gaseous compounds associated with odor vary greatly in molecular weight and odorant strength making it challenging to quantify and compare odors. As a result, the concept of an 'odor unit' (OU) was developed as a way to normalize the specific odor-related effect of an odor or mixture of odors. There are six major groups of odorous compounds, as identified by Mackie *et al.* (1998), which includes the previously discussed air pollutants, NH_3 and VOCs, and several sulfur-containing compounds.

Large Ruminant Facilities

Large ruminant facilities include both dairy and beef cattle operations. In 2009, US dairy and beef industries produced 85.9 billion kilogram of milk and 11.8 billion kilogram of beef, respectively (USDA, 2010). Both the industries span the continental US and range from small- to large-scale operations. Although there are still extensive, pasture-based dairy and beef operations in the US and around the world, this article focuses on intensive dairy and beef CAFOs. Typically, dairy CAFOs are integrated, freestall operations, whereas beef CAFOs are feedlots. This section provides a brief description of both dairy and beef CAFOs and the air quality issues surrounding these facilities.

Most freestall dairies are integrated, which means that they house calves, growing heifers, and dry and lactating cows on the same farm. Animals in dairy CAFOs are typically housed and fed in confinement and manure is removed from housing areas daily. Most feedstuffs are piled up on the farm premises and mixed to assemble a total mixed ration (TMR) for the

cows. On dairy CAFOs, calves are typically fed milk or milk replacer, and diets are supplemented with grain. Calves are housed individually in calf hutches for approximately 2 months, until animals are weaned. Heifers are group housed and fed a forage-based TMR, and are managed to calve at approximately 2 years of age. Dry cows are fed a high-forage TMR for a 60-day period between lactations in order to recover before the next lactation. Finally, lactating cows are fed a high-nutrient, well-balanced TMR to optimize milk production.

The most intensive sector in beef cattle production is the finishing phase. This is the final phase of beef production and involves housing cattle in dirt-floored drylot corrals known as feedlots. The time an individual steer or heifer spends in a feedlot depends on its entering weight, rate of gain, and desired weight at slaughter. Cattle typically enter feedlots at 350–400 kg, with the exception of male dairy calves, which enter at 150 kg (Stackhouse *et al.*, 2011). On average, cattle are housed for a total of 4–6 months until a slaughter weight of approximately 550 kg is reached (Stackhouse *et al.*, 2011). Feedlot cattle are fed a high-concentrate diet containing 75–90% corn, soybean meal, dried distiller's grains, etc. and 10–25% roughage.

Manure management in large ruminant CAFOs is critical due to the sheer size of these animals and associated amounts of excreta. An adult bovine excretes 41–60 kg of feces and urine daily (Davis *et al.*, 2002; CAST, 2011). Typical manure management in dairy CAFOs involves scraping excreta from dirt-floored corrals and piling it into dry storage piles. Manure from concrete floored freestall barns in which mainly lactating cows are housed can occur by either scraping or flushing. Most modern dairies prefer the latter and manure is flushed into liquid storage structures, which are often referred to as lagoons. If managed inappropriately (e.g., by overloading with nutrients), lagoons can be major sources of NH_3, H_2S, and odor emissions. In addition, manure lagoons are large contributors of GHG emissions in dairy CAFOs. Although land-application practices of dairy manure can vary, most large dairies use flood irrigation of liquid manure from the lagoons to fertilize crops on the surrounding fields. In beef CAFOs, manure from a corral is typically removed every 4–6 months, namely after a cattle group is leaving to be slaughtered. During the time cattle reside in the corrals a manure pack is formed, which can be a source of odor and PM emissions. Scraped manure from cattle corrals are mostly land applied to crops as fertilizer. Management of manure in dairy CAFOs can affect the chemical and physical properties of manure, including chemical composition, microbial populations, oxygen content, pH, biodegradability, and moisture content (MC). Manure storage allows for conservation of nutrients present in manure, which can then be utilized for application onto cropland, biodigesters, or composting.

In addition to manure management, there are several other air emission sources that result from beef and dairy CAFOs. Both dairy and beef CAFOs contribute to air pollution through emissions from animals (also known as enteric fermentation), manure, cropping systems, and feed management. This section covers the major air pollutants contributing to air pollution from dairy and beef CAFOs, namely NH_3, H_2S, VOCs, and odors.

Ammonia

The main sources of NH_3 emissions from dairies are fresh manure, long-term manure storage, and land application of manure (Bussink and Oenema, 1998). Similarly, primary emissions from beef CAFOs are from corrals, manure storage, and field-applied manure (Stackhouse-Lawson *et al.*, 2012). Both dairy and beef cattle have the unique ability, being ruminants, to recycle N back to rumen bacteria that would otherwise be excreted as urinary urea-N. Although this physiological process reduces N losses, an excess of dietary crude protein (CP) beyond the animal's nutritional needs leads to an increase in urinary urea-N content (Marini and Van Amburgh, 2005). As mentioned in the Section Air Pollutants, NH_3 emissions can be very variable depending on the climate, time of year, etc. For example, NH_3 emissions from dairies were found to be two to three times greater during the summer compared with winter (Todd *et al.*, 2008; Bluteau *et al.*, 2009). Emissions of NH_3–N from feedlots has been estimated to be as low as 9% and as high as 56% of N fed to animals (Faulkner and Shaw, 2008; Todd *et al.*, 2008; CAST, 2011). Total NH_3 losses at dairy CAFOs can range from 17 to 40 kg N per year per cow (Bussink and Oenema, 1998) or between 20 and 40 g NH_3–per day per AU (animal unit) in freestall areas (Groot Koerkamp *et al.*, 1998; Snell *et al.*, 2003). Diet can be altered to reduce the amount of NH_3 emissions from manure (James *et al.*, 1999; VandeHaar and St-Pierre, 2006). Through optimization of N content of a diet, N excretion per unit of product, and the related NH_3 emissions, can be reduced (de Boer *et al.*, 2011). The use of precision feeding that closely matches the nutritional needs of an animal can help to minimize the emissions from manure (Tylutki *et al.*, 2008). Through precision feeding, producers can avoid the expenses associated with overfeeding animals and minimize nutrient excretion that can lead to emissions. This is especially beneficial when monitoring CP content of the diet because it avoids excess N being converted to urea-N, thus avoiding extra emissions of NH_3 to the environment, as mentioned above.

Manure management in dairy and beef CAFOs can also result in variability of NH_3 emissions. For example, ammonia emissions from scraped or dirt-floored corrals have been found to be three times greater than those from flushed systems (Kroodsma *et al.*, 1993). Additionally, with short-term manure storage, solid manure has been found to have significantly higher NH_3 emission rates than liquid manure; however, long-term storage of manure has a reverse effect (Dewes, 1999). In the case of lagoons, a cover provided by either crust or tarp reduces NH_3 compared with uncovered manure storage structures (Sommer *et al.*, 1993). One method to control emissions from manure is through the use of additives. Manure additives include commercially available products that are intended to reduce ammonia volatilization from manure. The additives are typically mixed with water and poured evenly into the manure slurry but effectiveness is variable (USEPA, 2001).

Hydrogen Sulfide

The most significant source of H_2S in dairy and beef CAFOs is from stored manure. When manure is stored in anaerobic

lagoons (as is the case in many dairies) and undergoes microbial degradation, both NH_3 and H_2S are produced (Xue and Chen, 1999). Hydrogen sulfide is the result of anaerobic decomposition of sulfur-containing amino acids within these lagoons. Hydrogen sulfide emissions also contribute to the formation of odorous pollutants, which is further discussed in the Odor Section below.

Volatile Organic Compounds

Among large ruminant CAFOs, dairies are believed to be one of the largest sources of VOC emissions (Malkina *et al.*, 2011). Emissions of VOCs in dairy CAFOs originate predominantly not only from fermented feedstuff before it is ingested (Howard *et al.*, 2010a), but also by manure and from dairy cattle directly via enteric fermentation (Filipy *et al.*, 2006; Shaw *et al.*, 2007; Alanis *et al.*, 2010). Fluxes of VOCs from cows and waste include methanol, acetone, propanal, dimethylsulfide, and acetic acid (Shaw *et al.*, 2007). Additionally, when assessing manure alone from dairies, the most abundant VOC fluxes were found to be methanol and acetic acid (Hobbs *et al.*, 2004; Shaw *et al.*, 2007). Fermented feeds, such as silage, are major sources of VOC and they require large amounts of fossil fuel inputs for production (de Boer, 2003; Schils *et al.*, 2007).

Silage production has recently been identified as a major source of VOCs from dairies (Alanis *et al.*, 2008) and might show to be the leading agricultural source in locations like Central California (Howard *et al.*, 2010a). In a recent study, Chung *et al.* (2010) identified 48 VOCs from dairy sources, which included sources from silage and TMRs, whereas Malkina *et al.* (2011) identified 24 VOCs from silage and TMR emissions.

Odor

According to the National Research Council (2003) the main sources of odors emitted from dairy CAFOs result from silage mounds, barns, waste storage facilities, or land-applied manure. The greatest contributors of odors in livestock CAFOs are several groups of VOCs, including sulfur-containing compounds (hydrogen sulfide), volatile fatty acids (VFAs), phenols, and indoles (Shabtay *et al.*, 2009). Odor emissions from beef cattle fattening operations are affected by life stage and manure management (Shabtay *et al.*, 2009). In dairies, VOCs have the greatest impact on odors. Additionally, land application of manure, storage of manure, and dairy housing have been found to produce odor emissions of 1.5–90, 5.1–32, and 1.3–3.0 OU s^{-1} m^{-2}, respectively (Pain *et al.*, 1991; ASABE, 2006). Techniques to minimize odor from manure storage include covering lagoons, either with a natural crust or an artificial membrane, aerating storage basins (Westerman *et al.*, 2000), or utilizing anaerobic digestion of manure (Powers *et al.*, 1997).

Swine Facilities

To optimize production efficiency, the majority of swine facilities use enclosed and ventilated barns for housing. The hog production cycle has three main phases consisting of farrowing, nursing, and growing/finishing. Swine CAFOs can consist of one or two of these phases per barn but most commonly encompass all three in a farrow-finish production program (USEPA, 2001). In swine CAFOs, emissions are primarily generated from anaerobic microbial decomposition of organic matter in manure and spoiled feedstuff occurring either in barns, manure storage structures, or during manure land application (CAST, 2011). As with other livestock species, swine diet composition has a significant impact on the concentration and type of emissions coming from animal manure. There are various management methods utilized in swine production settings. In the US, swine are mainly intensively managed indoors on bedded or slatted floors. Bedding, such as straw, cornstalks, or sawdust, is used to collect solid manure and this bedding along with the manure is applied to cropland as fertilizer. There are four principal types of waste management systems used with confinement housing in the swine industry: deep-pit, pull-plug pit, pit recharge, and flush systems (**Table 3**). These differ depending on the state of manure collection and frequency of cleaning and draining. All of these systems use slatted floors (USEPA, 2001). The pit system allows the animal waste to fall through the slats directly into a pit and is collected in liquid form (Hamon *et al.*, 2012). Manure storage is in either an anaerobic lagoon or an external storage facility. In the pit systems, the space may be cleaned from daily to annual intervals, depending on the type utilized. In flush systems, manure is removed several times a day (USEPA, 2001). The pull-plug system removes manure from the pit after being stored for about a week and is then moved to outside storage facilities. This keeps emissions lower within the swine facilities but not necessarily with the later storage of removed manure (Cole *et al.*, 2000). These storage practices result in the decomposition of manure and formation of biogas. Ammonia, hydrogen sulfide, and VOC emissions may be higher in flush systems than from pit recharge and pull-plug pit systems due to turbulence during flushing.

Ammonia

The major air quality concern from swine CAFOs is NH_3 emissions from manure (Cole *et al.*, 2000). Ammonia

Table 3 Summary of emissions from Swine Model Farms (tons per year per 500 animal unit farm)

Type of manure	*Ammonia (NH_3)*	*Hydrogen sulfide (H_2S)*	*Volatile organic compounds*
Flush	15	2.6	0.6
Pit recharge	15	0.9	0.6
Pull-plug with lagoon	15	0.9	0.6
Pull-plug with storage tank	11	NA	NA
Deep pit	12	0.3	NA

Source: Adapted from US Environmental Protection Agency (USEPA), 2001. Emissions from Animal Feeding Operations. EPA 68-D6-0011. Research Triangle Park, NC: USEPA.

concentrations inside confined swine facilities varies widely, from 1.9 ppm to as high as 25.9 ppm and is dependent on the cleanliness of the facility (Duchaine *et al.*, 2000) as well as the time of year and barn ventilation rate (Heber *et al.*, 2000, 2004, 2005). Ammonia emission rates can be affected by housing type, animal size and stage of production, manure management, storage and treatment, feed nitrogen content, and climatic variables (Leneman *et al.*, 1998; Arogo *et al.*, 2003). Ammonia emissions have been found to vary by stage of production. For example, farrowing rooms and nurseries have lower NH_3 emissions than gestation or grow-finish facilities (Zhu *et al.*, 2000; Jacobson *et al.*, 2006). This is due to the higher protein requirement for growing/finishing animals. Zahn *et al.* (2001) studied the ammonia emission rates from 29 swine manure storage systems. These studies showed that deep-pit and pull-plug systems emitted NH_3 at a rate of 57 g NH_3 per square meter per day. On average, lagoons released 85 g NH_3 per square meter per day. Earthen, concrete-lined steel tanks emitted NH_3 at a rate of 144 g NH_3 per square meter per day. These external storage tanks release a significant amount more than the other two systems. The USEPA (2001) confirmed this large NH_3 formation in external manure storage facilities. In general, one of the greatest issues around ammonia in swine production are its effects on the respiratory system leading to irritation of the eyes, skin, mucous membranes, and upper respiratory system.

Hydrogen Sulfide

Hydrogen sulfide forms in deep-pit, pull-plug pit, and in external manure storage management systems (USEPA, 2001). According to Zahn *et al.* (2001), on average, lagoons emitted 0.25 g H_2S per square meter per day; deep-pit and pull-plug systems emitted 0.32 g H_2S per square meter per day; and the eternal tanks emitted 0.95 g H_2S per square meter per day. Once again, the external tanks emitted a significant amount more than the lagoons, and deep-pit and pull-plug systems. In addition to being a health hazard and air pollutant in swine facilities, H_2S contributes to odors, as outlined in the following Odors Section.

Volatile Organic Compounds

In addition to NH_3 and H_2S, Zahn *et al.* (2001) investigated VOC emission rates in 29 manure storage systems. The lagoons systems averaged 63.8 g per VOC syterm per hour; the deep-pit and pull-plug systems emitted 89.9 g per VOC system per hour; and the steel tanks emitted 394 g per VOC system per hour. Other studies have also been performed to quantify VOC emissions from swine facilities. Bicudo *et al.*, 2002 measured the mean VOC emissions at three different swine facilities and found that an 8000-head nursery emitted 204 $\mu g\, s^{-1}\, m^{-2}$, a 2000-head finishing facility emitted 291 $\mu g\, s^{-1}\, m^{-2}$, and a 3000-head finishing facility emitted 258 $\mu g\, s^{-1}\, m^{-2}$. Compared with all manure storage systems, anaerobic lagoons emit the least VOCs and noxious odors (USEPA, 2001).

Odor

Odors from swine CAFOs are primarily comprised of NH_3 and H_2S emissions (Cole *et al.*, 2000; Hamon *et al.*, 2012). Emissions of odors are dependent on seasonal and climatic parameters, as is the case with other CAFOs. Anaerobic processes can also release VFAs that can be considerably more offensive than ammonia or hydrogen sulfide. In terms of manure management, odors increase as the animal manure decomposes (Cole *et al.*, 2000). H_2S creates a very pungent and noticeable sulfur odor. In addition to odor contributions from NH_3 and H_2S emissions, feed composition also plays a direct role in the quantity and intensity of the odors produced (Gralapp *et al.*, 2002). Although NH_3 and H_2S are abundant odors in terms of concentrations in swine CAFOs, approximately 400 different odorous compounds have been identified (Hamon *et al.*, 2012).

Poultry Facilities

Poultry CAFOs include both broiler (chickens used for meat production) and layer (chickens used for egg production) facilities. Broilers are typically produced in littered floor systems, where birds are kept in a closed structure (termed a house) with space to move and access to feed and water systems. Bedding for broiler housing varies by geographical location, but material can include rice hulls, wheat or rye hulls, sawdust or wood shavings, peanut shells, sand, chopped straw, or corn stalks. The bedding used in broiler houses is referred to as litter when it is mixed with feces (USEPA, 2001). Most of the litter is reused (also known as built-up litter) over multiple flocks of production (CAST, 2011). Alternatively, caked litter (i.e., litter that has a wet and hardened surface layer, usually found along the feed and water lines where much of the manure is deposited) is removed between each flock (CAST, 2011; USEPA, 2001). Layer chickens are primarily raised in cage systems, where the birds are housed in cages with a relatively limited amount of space. These can either be in high-rise (HR) (65–70% of cage systems), or manure-belt (MB), (25–30% of cage systems) housing systems (CAST, 2011; Xin *et al.*, 2010) but alternative cage-free housing systems do exist and are increasingly popular. Manure in HR facilities is typically stored in the lower level of the house for 1 year and removed as solid manure in the fall for cropland application. Manure in MB houses is removed daily to weekly, via the MB, and can be stored either on-site, in separate storage, or a composting facility (Xin *et al.*, 2010).

As with other livestock facilities, emissions vary depending on housing and manure management systems. Although a substantial amount of research has been performed to determine air quality emissions associated with on-site production and storage of manure, there is limited data on emissions associated with land-applied poultry manure (a common practice for poultry facilities). Air quality in poultry CAFOs is an area of concern; however, most research is on NH_3, whereas data on other air pollutants, such as PM and VOCs is limited.

Mitigation techniques in poultry facilities are utilized mainly by manure management. Dietary manipulation (Roberts *et al.*, 2007), topical application of chemical or mineral

additives to poultry manure (Li *et al.*, 2008), treatment of exhaust air via a biofilter or wet scrubber (Melse and Ogink, 2005; Manuzon *et al.*, 2007; Shah *et al.*, 2008), and faster application of land-applied manure have been investigated as possible mitigation techniques to minimizing emissions associated with manure from poultry CAFOs. Through direct incorporation, or injection, of manure into soil with immediate tillage there is the potential to minimize emissions from land-applied manure (CAST, 2011). Injection of manure during land application can minimize odors, NH_3, and VOC emissions. In layer facilities specifically the use of MB systems should be used for manure management because they significantly reduce odors and NH_3 emissions (Fournel *et al.*, 2012).

Ammonia

Among both layer and broiler CAFOs, NH_3 is the major noxious gas produced. The primary source of NH_3 from poultry is from manure, both in-house and off-site. Manure excreted from poultry has a high MC and as the moisture evaporates, NH_3 is emitted (USEPA, 2001). The generation and concentration of indoor NH_3 is influenced by housing and manure management practices, as with other livestock CAFOs. Broiler manure storage is in-house, so continuous airflow from ventilation systems is used to help minimize the amount of NH_3 exposure for animals, as NH_3 is emitted year round (USEPA, 2001). However, this does not minimize NH_3 emissions; rather it likely leads to elevated emissions of NH_3 to the atmosphere (CAST, 2011). Manure management in layer housing systems that utilize manure belts allows manure to dry to between 30% and 60% MC, making it easier to transport and creating less NH_3 emissions (Xin *et al.*, 2010). Ammonia concentrations in MB housing are generally lower than in other housing systems (Green *et al.*, 2009) due to the higher frequency of manure removal (Green *et al.*, 2009). Long-term broiler manure storage with high MC can further mineralize organic nitrogen to NH_3 (USEPA, 2001). Though only a small amount of research has been performed in regard to land-applied poultry manure, NH_3–N losses from land-applied poultry manure (expressed as a percentage of manure nitrogen content) have been estimated at 7% for dry laying-hen manure (Lockyer and Pain, 1989), 41.5% for wet laying-hen manure (Lockyer and Pain, 1989), and 25.1% for broiler litter (Cabera *et al.*, 1994). Prolonged exposure to elevated NH_3 concentrations adversely affects bird health, such as the respiratory system and productivity (e.g., feed intake, bodyweight gain, egg production, and feed conversion) (CAST, 2011). For poultry housing, the recommended indoor NH_3 concentration is less than 25 ppm (MidWest Plan Service, 1990; United Egg Producers, 2010).

Hydrogen Sulfide

With dry manure collection from poultry and the associated manure storage facilities, any sulfur excreted should be oxidized to nonvolatile sulfate, thus making H_2S production negligible (USEPA, 2001). Hydrogen sulfide emissions are varied because of MC, the time manure stays in the facility, the ventilation rate, and incidence and duration of storage (USEPA, 2001). In broiler facilities, daily mean H_2S concentrations have an inverse relationship to house ventilation rates and molting of birds causes these H_2S concentrations to decrease (Ni *et al.*, 2012). There is little information about H_2S emissions from layers but averages of 19.7 ppb H_2S have been reported for commercial layer houses, 26.4±17.6 and 24.9 ±19.0 ppb for HR houses, and 40.0±21.1 and 41.2±31.5 ppb MB houses (Lim *et al.*, 2003; Ni *et al.*, 2012, respectively). Higher concentrations of H_2S have been reported to be approximately 40–100 ppb in some broiler facilities (Zhu *et al.*, 2000). Poultry H_2S emissions are much lower than those from other livestock, such as swine (Zhu *et al.*, 2000). If there is residual H_2S in poultry manure at the time of land application, it is oxidized to sulfate but with transient saturated soil conditions sulfate can be reduced back to H_2S and be aerosolized (USEPA, 2001).

Volatile Organic Compounds

Poultry manure is also a contributor to VOCs which, as mentioned in the Section Air Pollutants, can contribute to ozone and odor formation. The high MC of poultry manure leads to the production of VOCs (USEPA, 2001). Poultry manure forms different dienes, ketones, aldehydes, and aromatics, with an overall contribution of 36.43±26.57 ug m^{-3} of total VOC from animal sources (Howard *et al.*, 2010b). The overall contribution from poultry has been found to be significantly less than contributions from cattle or swine (Howard *et al.*, 2010b). Poultry litter composting also contributes to VOC emissions. Composting of poultry litter has been found to emit high amounts of alkanes and alkylated benzenes, with much lower emissions of aldehydes, terpenes, and ketones (Turan *et al.*, 2007). The greatest production of VOC emissions occur early during the composting process and declines rapidly thereafter with the maximum production of VOCs obtained within the first 5 days (Turan *et al.*, 2007).

Odor

Odor associated with poultry is often a result of manure and the most noxious odor has been identified as ammonia (CAST, 2011). Although there is odor associated with poultry CAFOs, its incidence is much less than that of swine facilities and is produced at constant concentrations throughout the day (Zhu *et al.*, 2000). In layer facilities the use of MB systems, both forced air drying and natural drying, reduces odor emissions, respectively, by 37% and 42% compared with odor emissions from a deep-pit technique (Fournel *et al.*, 2012). MB systems also produce less odor than deep-pit systems due to their frequent manure removal (Fournel *et al.*, 2012). Odor incidence in poultry increases as a result of higher temperatures during summer months, and odor varies depending on the age of birds and the season (Fournel *et al.*, 2012; Hayes *et al.*, 2006). Odor from broiler facilities is associated with litter and worsens when the litter is damp (Hayes *et al.*, 2006). Broiler house odors of the same concentration are perceived as more intense than odors emitted from pig slurry and there is a greater correlation between poultry manure odor intensity and

concentration than in swine (Misselbrook *et al.*, 1993). Composting of litter also produces odor as organic compounds can be volatilized during composting (Turan *et al.*, 2007).

Conclusion

As the global human population rises and the degree of affluence in developing nations grows, people demand more food and in particular more high quality animal protein. This demand for protein requires intensification of animal facilities in order to maximize production on limited land. CAFOs have become the main mode for efficient animal production in the US. However, the high stocking density of CAFOs leads to greater amounts of air pollutants and a rise in associated concerns. Additionally, manure and feed storage and management have been a recurring contributor to air quality issues in all three CAFOs. Dairy, beef, swine, and poultry CAFOs all emit NH_3, H_2S, VOCs, and odors, and these air pollutants can impact human and animal health. Numerous approaches to mitigate emissions are currently being studied and include improvements of animal production efficiency, herd health, nutrition, and feed production, as well as manure management strategies.

See also: Air: Greenhouse Gases from Agriculture. Beef Cattle. Climate Change: Animal Systems. Dairy Animals. Dust Pollution from Agriculture. Poultry and Avian Diseases. Swine Diseases and Disorders

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Air: Greenhouse Gases from Agriculture

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Introduction: Agriculture and Land Use

The earth's climate is warming as a consequence of the accumulation of greenhouse gases in the atmosphere. The most important greenhouse gases contributing to this warming are carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O). Although these gases are present in the atmosphere naturally, human activity has been responsible for a rapid increase in their concentration over the past century. Greenhouse gases are released by a variety of processes, the most important of which is fossil fuel consumption, which currently adds more than 9 billion tons of CO_2–C to the atmosphere each year. However, other activities make a significant contribution to greenhouse gas emissions, including agriculture. Approximately 31% of annual global greenhouse gas emissions resulted from agriculture and land use according to the Intergovernmental Pannel on Climate Change's fourth assessment report (IPCC, 2007). Globally, agricultural land occupies approximately 40% of the earth's ice-free land area. This land includes land used for crop and livestock production, managed grassland, agroforestry, and bioenergy crop production. But agriculture is currently at a crossroad, challenged by the demands to produce more food for a growing global population, but in ways which reduce environmental impacts, and at a time of water and energy shortages, climate change, and limited availability of new land (Godfray *et al.*, 2010).

The predicted rise in the human population to more than 9 billion people by 2050, as well as changing global diets, will lead to an increased demand in the amount and type of food produced. This will, in turn, lead to the possibility of increased greenhouse gas emissions. One solution to the problem of producing more food (and one that has been used in the past) would be to bring more land into agricultural production. However, the availability of land is limited and there is competition for land to provide other ecosystem services such as the provision of habitats for biodiversity, carbon storage, and cycling of water and nutrients. Small areas of land will undoubtedly be converted for agricultural use, but this will not form the basis for any significant increase in the world's food supply. Instead, more food should be produced from the current agricultural areas and it should be done in ways that reduce environmental impact. The concept has been described as Sustainable Intensification (Godfray *et al.*, 2010) and is proposed as a guiding principle that addresses the twin concerns of maintaining production in ways that will contribute to long-term sustainability in farming systems and thus include greenhouse gas mitigation.

The greenhouse effect is a natural process without which life on the earth would not be possible because the average global temperature would be well below 0 °C. Carbon dioxide and other greenhouse gases absorb infrared radiation from the sun, which causes the greenhouse gas molecules to vibrate. The infrared radiation from the sun is converted into heat energy and is reemitted back into the atmosphere. The heat energy is trapped in the earth's atmosphere and oceans, causing the earth to warm up. There has always been a balance between processes which produce and remove CO_2 from the atmosphere; thus, the earth's temperature has remained relatively stable. Recently, humans have altered this balance, resulting in increasing levels of CO_2 in the atmosphere. This has resulted in more heat energy becoming trapped in the earth's atmosphere, leading to a rise in average global temperatures (IPCC, 2007).

This article focuses specifically on the relationships between agricultural production and greenhouse gas emissions. The management and reduction of greenhouse gas emissions from agriculture makes a critical contribution to sustainable land use, because such management can influence both the production and environmental impact of the system. Farming is responsible for the production of three greenhouse gases: CO_2, N_2O, and CH_4 (**Figures 1(a)** and **(b)**). Each gas contributes to the warming up of the atmosphere; however, the warming potential of each gas varies. Nitrous oxide, although produced in small quantities, has the largest warming potential with a value 298 times greater than that of CO_2 over a 100-year period. Methane's warming potential is 25 times greater than that of CO_2 over a 100-year period. By comparing the ability of each gas to contribute to warming of the atmosphere, their collective impact can be compared by converting the warming potential of each gas to CO_2 as CO_2 equivalents or CO_{2e}.

Carbon dioxide production from agricultural sources is mainly derived from land-use change. A change from forest or permanent pasture to cultivated croplands often involves a loss of soil carbon, as soil organic matter is decomposed and released to the atmosphere as CO_2. Atmospheric CH_4 concentrations are partly driven by agricultural activity and CH_4 is mainly a product of manure, ruminants, and rice cultivation; since the early 1990s, growth rates of the gas have declined (IPCC, 2007). Agriculture is the primary driver of increased N_2O emissions, through the use of synthetic fertilizers increasing available nitrogen supply to agricultural systems (Reay *et al.*, 2012). A shift in diet toward higher meat consumption has lead to an increased need for intensification of land management practices and expansion to produce increased feed needed for consumption by livestock. Between 1967 and 1997, meat demand in developing countries has more than doubled, rising from 11 to 24 kg per capita per year (Smith *et al.*, 2007). This pattern is expected to continue particularly in countries such as China, linked to economic growth and shifting lifestyles, which will lead to a large increase in greenhouse gas emissions. A shift to higher meat consumption would also increase emissions of CH_4 due to its association with ruminants. A combination of shifting diet and increased demand for food due to population growth are expected to drive an increase in future greenhouse gas emissions from agriculture. Mitigation measures may help to buffer these emissions.

The total global emissions of greenhouse gases from agriculture in 2012 has been estimated to be 4.68×10^{15} g CO_{2e}

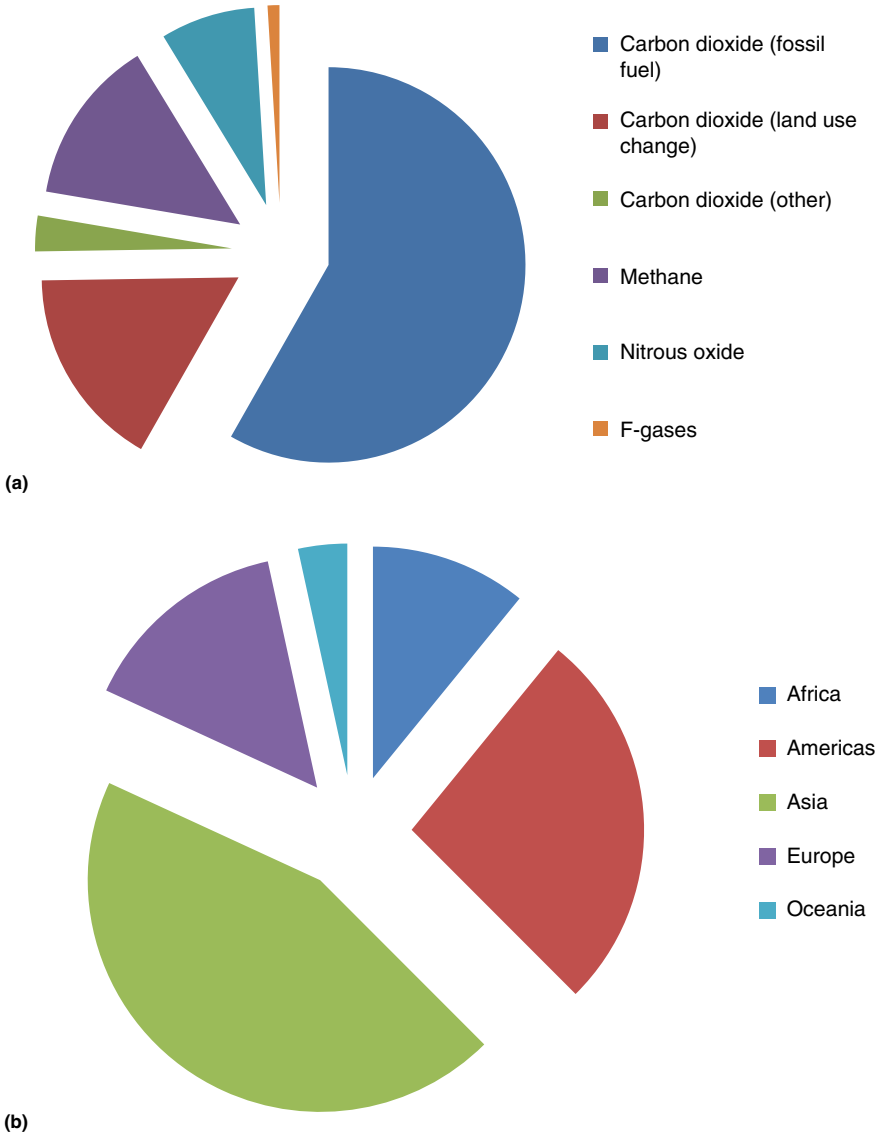


Figure 1 (a) Total global greenhouse gas emissions in 2004 and (b) global emissions from agriculture between 2000 and 2010 (FAO, 2012). F-gases, fluorinated gases. Reproduced from Food and Agriculture Organisation's Statistical Database; FAOSTAT. Rome. Reproduced from data reported by the IPCC (2007). Summary for policymakers. In: Solomon, S., Qin, D., Manning, M., *et al.* (Eds.), Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, UK and NY, USA: Cambridge University Press.

(FAO, 2012). This has grown by 13% over the two decades between 1990 and 2010. However, the rate of growth has been highly uneven, with strong growth in emissions from agriculture from non-Annex 1 countries (including Asia and South America), occurring at the same time as Annex 1 countries (that includes North America and Europe) showed a small decline in emissions (Figure 2).

Reporting

The reporting of emissions of greenhouse gases from agriculture and other emission sources is guided by methodologies developed by the IPCC (2006). In accordance with these guidelines, emissions from sources are calculated on the basis of emission factors or coefficients, which provide estimates of emissions from typical management practices and activity data describing fertilizer use, livestock numbers, etc. Varying levels of sophistication are possible, depending on the availability of national data and information. The estimation of emissions of greenhouse gases from agricultural activities presents particular challenges that are a consequence of the interactions between the environment and the underlying biological processes responsible. Emissions represented by such calculations inevitably represent an approximation and could be considered to be at best an average over a given time period. The emissions are reported to the United Nations

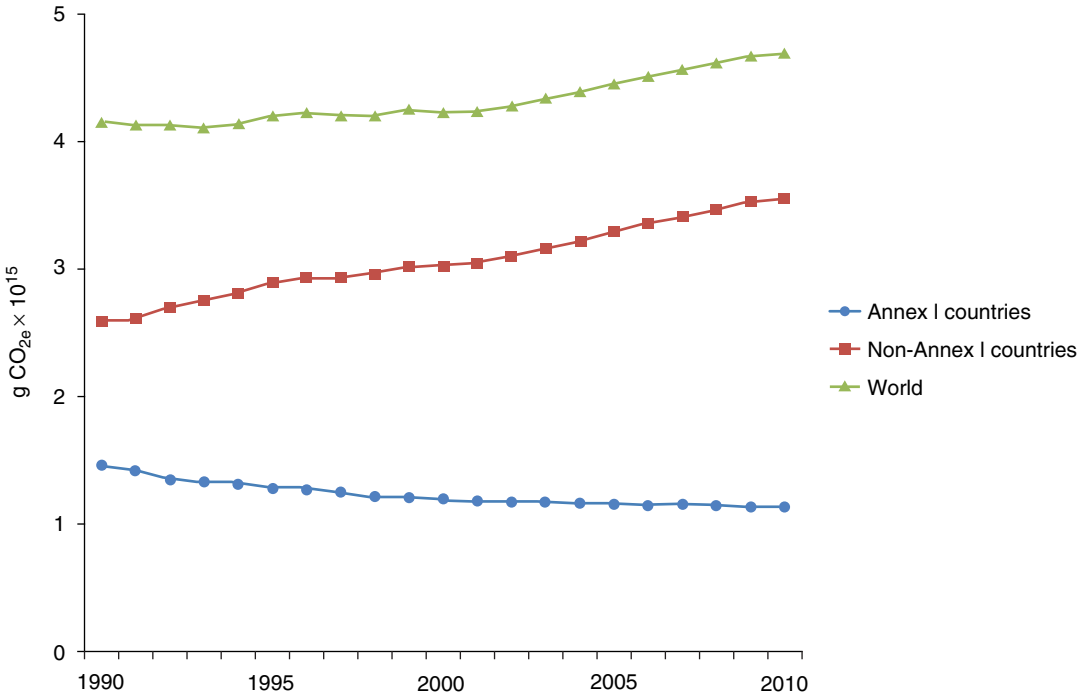


Figure 2 The changes in emissions of total greenhouse gases from agriculture at a global scale between 1990 and 2010. Annex I, North America and Europe; Non-annex I, Asia and South America. Reproduced from FAO, 2012. Food and Agriculture Organisation's Statistical Database, FAOSTAT. Rome. Available at: http://faostat3.fao.org/ (accessed 24.01.14).

framework on climate change and synthesized to produce reports on global emissions.

The diversity of processes contributing to greenhouse gas emissions from agriculture, and their biological sources, makes direct measurement difficult. However, because of the significance of agriculture in contributing to global greenhouse gas emissions, a significant amount of work has been undertaken to develop methodologies that can be used to make direct measurements of emissions. This work helps us to quantify more accurately the magnitude of emissions, to develop models that are better able to represent such emissions, and to devise mitigation strategies that are effective both in terms of reducing greenhouse gas emissions and maintaining productivity.

Measurement/modeling

A variety of methodologies are available for the measurement of greenhouse gases from agriculture, ranging from small-scale measurements from individual sites in fields to atmospheric measurements across regions. For example, emissions of N_2O can be made by placing sealed chambers at the ground surface and measuring the accumulation of gases over a short period of time (usually less than 1 h). An alternative (micrometeorological) approach is to use sensors attached to masts above the ground surface, coupled with measurements of instantaneous wind speed and then calculate fluxes using an appropriate model (Jones *et al.*, 2011). Measurement of methane emissions from livestock can be undertaken by direct sampling of animal breath and also by using the micrometeorological approach described for N_2O. An alternative methodology that has been valuable in quantifying livestock emissions is to use chambers within which animals can be housed, and then measure changes in gaseous composition of the atmosphere passing through them.

Accurate measurements of greenhouse gas emissions are critically important in developing predictive models of greenhouse gas emissions. These vary in complexity from simple empirically based models estimating individual emissions associated with specific management practices to complex whole ecosystem models that represent interactions between management and the environment to simulate emissions of CO_2, N_2O, and CH_4.

Nitrous Oxide

Nature of Gas

The trace gas N_2O makes a significant contribution to the earth's greenhouse gas balance, and agriculture is its main source (Reay *et al.*, 2012). Concentrations of N_2O have increased steadily in the atmosphere in recent decades, primarily as a consequence of emissions from soils that are caused by microbial transformations of fertilizer nitrogen compounds contained in synthetic fertilizers and organic manures (**Figure 3**). There is a smaller contribution from manure management and biomass burning.

Nitrous oxide is a powerful greenhouse gas with approximately 300 times the global warming potential of CO_2 per molecule (Robertson and Vitousek, 2009); however, it is not emitted at the same magnitude. Nitrous oxide directly contributes to approximately 10% of the total greenhouse gas effect, but atmospheric N deposition also influences the

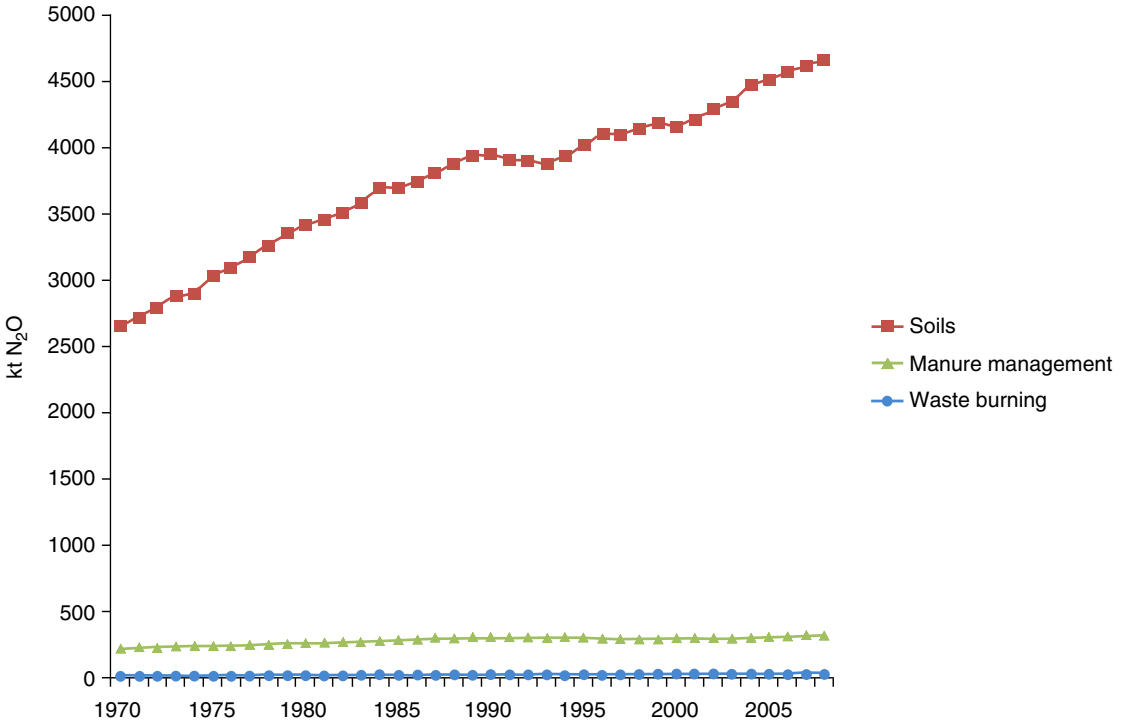


Figure 3 Global emissions of nitrous oxide from agriculture between 1970 and 2008, partitioned by source. Reproduced from European Commission, Joint Research Centre (JRC)/Netherlands Environmental Assessment Agency (PBL), 2011. Emission Database for Global Atmospheric Research (EDGAR), release version 4.2. Available at: http://edgar.jrc.ec.europa.eu (accessed 24.01.14).

greenhouse gas budget more widely through indirect effects on the cycling of C. Although N_2O does absorb the earth's outgoing infrared radiation, it is not chemically reactive in the troposphere (the lower layer of the atmosphere). However, its chemical reactivity increases as it enters the stratosphere (the layer of the atmosphere between 12 and 46 km above the earth's surface), where it plays a major role in stratospheric ozone depletion. Nitric oxide and nitrogen dioxide (collectively referred to as NO_x) are produced from the dissociation of N_2O in the atmosphere; these compounds then react readily with ozone, leading to its depletion in the stratosphere (Ravishankara *et al.*, 2009). Somewhat paradoxically, NO_x is also responsible for the production of ozone in the troposphere, which causes many environmental problems for the health of flora (including crops) and fauna (including humans). Ozone at ground level also leads to photochemical smog, which can be a problem in both urban and rural areas.

The emission of N_2O is, therefore, of critical importance in both tropospheric and stratospheric chemistry and is an important source of air pollution (Sutton *et al.*, 2011). The residence time of N_2O in the atmosphere is quite long (approximately 120 years) and wind currents can transport the gas to vast distances. Air pollution is not limited by national boundaries.

Cycling (Sink Source)

The nitrogen cycle involves large-scale global transfers of N between the atmosphere and the biosphere. Nitrogen inputs to the biosphere occur both as a consequence of natural processes (biological fixation and lightening) and industrial fixation (**Figure 4**). Nitrogen is ultimately returned to the atmosphere as nitrogen gas, but the processes of microbial transformation of N result in the release of small quantities of N_2O. There are natural and anthropogenic contributors to atmospheric N_2O emissions, both of which occur primarily as a consequence of microbial transformation of N in soils and water. Natural sources result from nutrient cycling processes in unmanaged ecosystems, whereas anthropogenic sources are derived from microbial transformations of N applied to agricultural land in fertilizers, manures, and crop residues.

Other agricultural practices also influence the output of N_2O from cultivated or grazed lands, such as water management, aeration, application of alternative fertilizers (ammonium nitrate, urea, cattle slurry, chicken manure, and sludge pellets) burning, biological nitrogen fixation, grazing, tillage, crop rotation, and decomposition of crop residue. The application of nitrogen to land is used to support both arable crops and pastures.

Nitrous oxide is produced as an intermediate during the microbial processes of nitrification and denitrification. The microbial transformation of inorganic nitrogen is the main source of N_2O in the soil, and so substrate supply is a determinate factor in emission rate (Butterbach-Bahl *et al.*, 2011). Nitrification involves the oxidation of ammonium (NH_4^+) to nitrate (NO_3^-), whereas denitrification is a reductive process resulting in the reduction of NO_3^- to N_2 gas via a series of intermediates during microbial respiration. Nitrous oxide emitted from the soil can be an outcome of

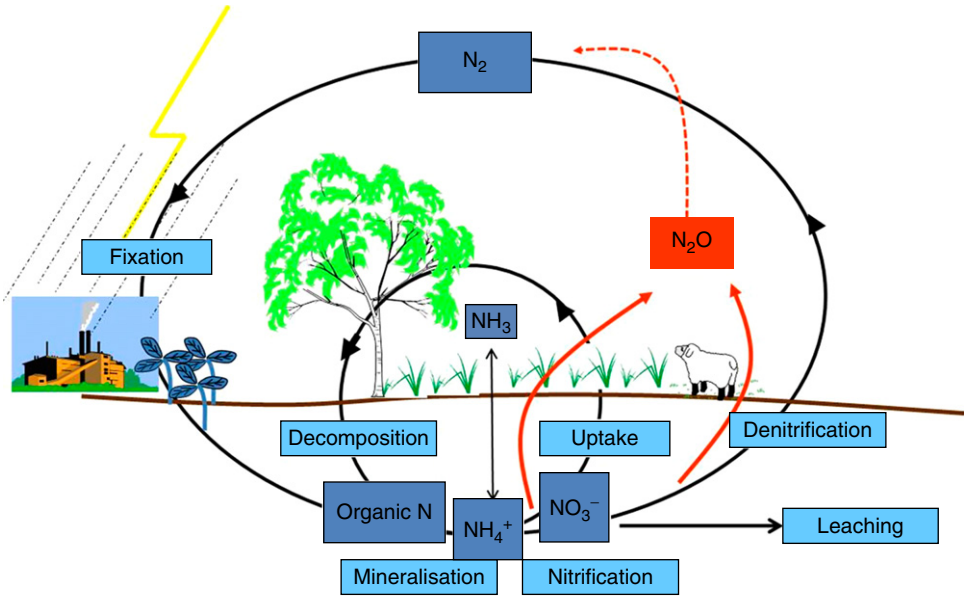


Figure 4 A simplified schematic diagram of N cycling in agricultural systems. Nitrogen pools are represented by the purple boxes and processes are indicated by the light blue boxes.

nitrification, denitrification, or a combination of the two. The denitrification process ultimately leads to the complete reduction of N_2O to N_2 in the atmosphere. Numerous variables regulate the transformation reaction as well as the proportionality of gas products, such as soil pH, oxygen content of the soil, temperature, carbon availability, and nitrate or nitrite concentrations (Butterbach-Bahl *et al.*, 2011). Addition of fertilizer directly increases available nitrogen leading to higher nitrification and denitrification rates and so enhanced rates of N_2O production by the system (Mosier *et al.*, 1998). Emissions are greatly increased immediately after nitrogen application to crops and soils, when a large outward flux of nitrous oxide occurs. Rates of N_2O production and subsequent emission from the soil to the atmosphere are heterogeneous, both spatially and temporally (Rees *et al.*, 2012). Site-specific variables are determinate factors in the rate and magnitude of N_2O emissions, such as soil water content, texture, and compaction. The availability of nutrients, microbial activity, soil temperature, and soil aeration status are all determined variably by soil water content and so effect N_2O emissions from the soil.

The IPCC (2007) reported that global atmospheric N_2O concentrations had increased from a preindustrial value of approximately 270–319 ppb in 2005. Anthropogenic sources account for less than half global N_2O emissions globally; however, they are the primary driver in emission growth. Global reactive N supply has approximately doubled relative to the preindustrial average through the manufacturing of synthetic fertilizers, use of manure, and the enhancement of biological nitrogen fixation as well as industrial uses (Reay *et al.*, 2012). Manure usage would have been the predominant source of N_2O production before the Second World War. The subsequent rapid increase in synthetically manufactured fertilizers in the second half of the twentieth century led to a rapid increase in N_2O emissions. During the past 40 years, unprecedented additions of nitrogen have been made to agricultural systems (Erisman *et al.*, 2008). In 2005, 100 Tg of synthetic N was applied to the world's agricultural systems. However, only 17 Tg of N was consumed by humans in food, indicating that much of the applied N is lost through various pathways to the environment (Erisman *et al.*, 2008). As the global human population continues to rise, food must be produced to sustain it, but it will be increasingly important to use added nitrogen more efficiently.

Geography and Emission Intensity

The patterns of fertilizer consumption and associated production of N_2O vary considerably on a global basis. Over the past 40 years, India and China have shown a strong growth in emissions, whereas those from developed nations such as the United States of America and the United Kingdom remain stable (**Figure 5**). N_2O emissions derived from agricultural source are expected to rise from approximately 87 Tg N_2O–N per year in 2000 to 236 Tg N_2O–N per year by 2050, representing a 270% increase (Tilman *et al.*, 2001), primarily derived from increased nitrogen fertilizer use in non-OECD Asia, Latin America, and Africa (Reay *et al.*, 2012), as well as a potential increase in biofuel usage. Regional variability in N_2O emissions is expected to continue, with Asia being the primary contributor due to its population levels (Rees, 2011). Projected shifts to a higher meat consumption diet will also contribute to higher emissions, particularly from Asia. There are currently large differences in sources of N_2O emissions across the world regions. In Europe, Asia, North America and, Central and South America, direct emissions from soils dominate contributions, but in Africa and Oceania, manure and pasture management are the primary contributors. Fertilizer application patterns show clear geographic trends. Higher application rates are apparent in Asia, Europe, and North America, whereas lower rates occur in Africa, Latin America, and Oceania. Lower application rates are associated with more extensive areas of land management but may also indicate

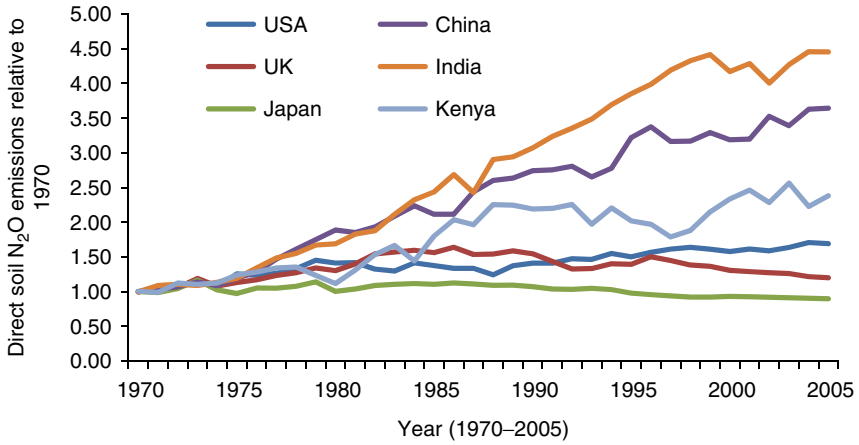


Figure 5 Comparison of N_2O emissions for different nations relative to 1970. levels. Reproduced from European Commission, Joint Research Centre (JRC)/Netherlands Environmental Assessment Agency (PBL), 2011. Emission Database for Global Atmospheric Research (EDGAR), release version 4.2. Available at: http://edgar.jrc.ec.europa.eu (accessed 24.01.14).

lower productivity. The relationship between emissions and the population size of a given region can be expressed by dividing total national emissions by the population size. Asia has the lowest N_2O emissions per capita of all continents at 623 g, which is very low relative to North America's 2167 g per capita. Per capita emissions are largely related to meat consumption, which explains the extent of North America's per capita emissions; this trend is expected to develop in Asia in the future due to the association of meat consumption with an expected increase in wealth (Rees, 2011).

Mitigation

Mitigation options for N_2O emissions generally aim to increase the efficiency with which fertilizer N is used by crops and thereby reduce the potential for losses. This can be achieved by improving soil conditions, for example, by improved drainage and soil structure. Other approaches focus on reducing the presence of available N in soils by altering the timing of fertilizer applications to better match crop demand or by reducing overall N inputs. The use of a winter crop cover and species introductions can also help to reduce emissions by making more efficient use of added N. Legumes offer an important opportunity to reduce greenhouse gas emissions, because they are able to fix atmospheric nitrogen biologically and release less N_2O than fertilizer nitrogen. Another interesting approach has been to use inhibitors that slow down the nitrification process and therefore have the potential to both reduce N_2O production and increase crop N uptake. Although such additives are expensive, they have been widely used in New Zealand to reduce N_2O emissions and increase fertilizer-use efficiency.

Demand side measures also have the potential to reduce N_2O emissions, because meat consumption is strongly linked to N_2O production. Improved efficiency of the food system and avoiding food loss and wastage are viable options which could substantially reduce emissions. To assess both the potential magnitude of results as well as the cost of different mitigation options, marginal abatement cost curves can be utilized (MacLeod *et al.*, 2010). Different mitigation approaches have differential impacts on emissions, as well as incurred cost, with some measures saving both money and emission. Mitigation strategies should integrate measures in order to achieve maximum reductions; not overlooking that cost-effectiveness of specific strategies may change over time as well as not overlooking a possible interaction between measures. The effectiveness of mitigation measures are often site specific, which can cause difficulties when scaling up; there is high variability in response to measures by different soil type and climate. To overcome this, spatially explicit farm management practices (precision farming) can allow the integration of mitigation measures to achieve maximum reductions overcoming problems of spatial heterogeneity (Rees *et al.*, 2013).

Methane

Nature of the Gas

Methane (CH_4) is a principal component of natural gas. It is a simple molecule that consists of four hydrogen and one carbon atom, and at 1.8 ppm, it is the most abundant non-CO_2 greenhouse gas in today's atmosphere (Montzka *et al.*, 2011). Methane is a powerful greenhouse gas with a global warming potential 25 times greater than that of CO_2, and it plays a central role in tropospheric chemistry. Like N_2O, concentrations of CH_4 have increased significantly in recent decades (**Figure 6**). However, unlike N_2O, CH_4 is produced by a much wider variety of sources. Methane is relatively stable in the atmosphere and remains there for approximately 9–15 years.

Sources

A major source of CH_4 emissions from agriculture is the enteric fermentation of ruminant livestock (IPCC, 2007). In domesticated ruminant livestock, CH_4 is generated as a result of the complex microbiological fermentation in the rumen and the large intestine and is released via the mouth or nostrils. The process of enteric fermentation is a microbial

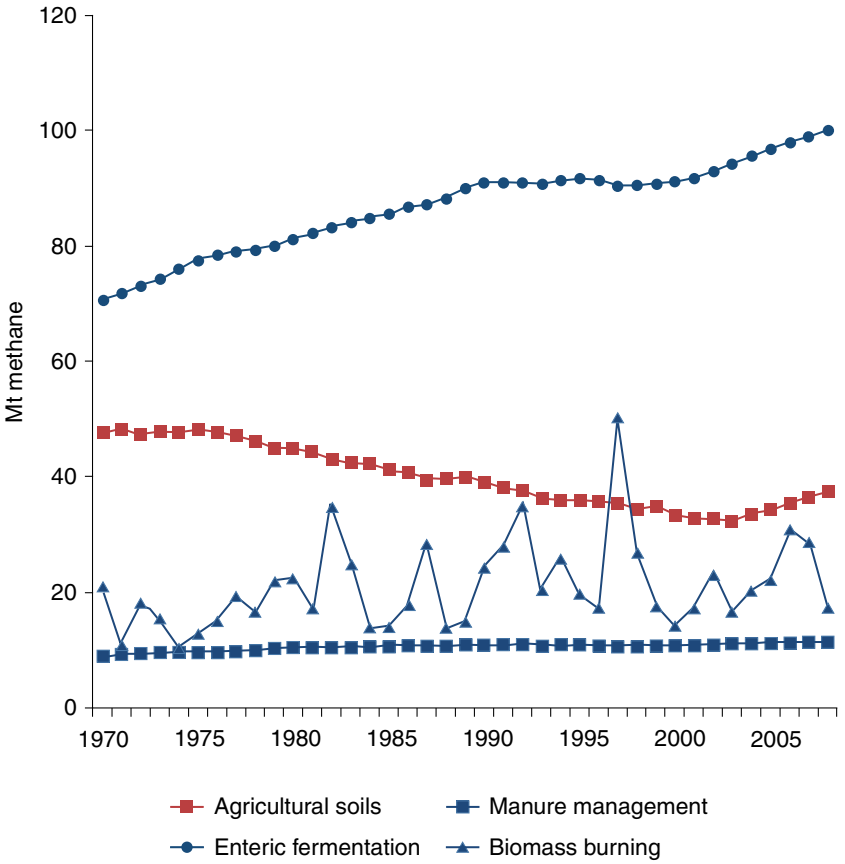


Figure 6 Global methane emissions from agricultural sources apportioned by source between 1970 and 2008.

fermentation process that produces methane as a by-product. The pattern and magnitude of these emissions may vary with grazing behavior and diet (USEPA, 2006). Methane emissions from ruminant livestock have increased significantly in recent years as a consequence of larger numbers of livestock on a global basis (**Figure 6**).

Another major source of CH_4 results from rice cultivation by the anaerobic decomposition of organic matter in soil (Li *et al.*, 2005). Soils that are flooded are ideal environments for the production of CH_4 as they have high levels of organic substrates in anaerobic conditions, with high levels of moisture. These conditions promote anaerobic respiration, which is the process responsible for CH_4 production. The magnitude of emissions may vary with soil conditions, production practices, and the climate.

Methane emissions released by biomass burning result from an incomplete combustion of organic substrates and encompass a wide variety of sources (i.e., woodlands, peat lands, and agricultural waste) (Cloy *et al.*, 2012). Higher CH_4 emissions may result from the burning of the latter two, due to a high water content and low oxygen availability common to the combustion of these fuel sources (USEPA, 2006).

Another source of CH_4 is produced from livestock manure management systems, when organic material is decomposed in anaerobic conditions. In particular, liquid manure management systems (i.e., lagoons or holding tanks) that are often used in larger swine and dairy operations, can contribute significantly to CH_4 emissions (USEPA, 2006). Methane is also produced from buried wastes in landfill sites and as a result of leakage from gas production and transport. There are also significant natural sources of methane from termites and wetland ecosystems.

Sinks

Once methane is released, it is removed from the atmosphere by atmospheric consumption processes or sinks. The amount of CH_4 released and removed ultimately determines atmospheric CH_4 concentrations and thus how many years they will remain in the atmosphere. Global CH_4 sinks arise primarily from the oxidation by chemical reaction with hydroxyl radicals (OH) in the atmosphere (IPCC, 2007). In the tropospheric layer of the atmosphere, CH_4 reacts with OH to produce CH_3 and water.

Methane is also removed from the atmosphere (though in smaller amounts) through stratospheric oxidation. From both processes, small amounts of CH_4 are destroyed by reacting with the OH in the atmosphere, and this accounts for approximately 90% of methane removal from the atmosphere (IPCC, 2007). Other CH_4 sinks include the microbial uptake in soils as well as reaction with chlorine atoms in the atmosphere. These sinks contribute an estimated 7% and 2% of the total methane removal, respectively.

Growth Rate

Records of ice sheets indicate that CH_4 is more abundant in the earth's atmosphere now than at any time during the past 400 000 years (IPCC, 2007). Global average atmospheric concentrations of CH_4 have increased since 1750, from approximately 700 to 1745 parts per billion by volume (ppbv) in 1998, which equates to a 150% increase. Since 1998, CH_4 emissions have increased, but the overall rate of CH_4 growth has reduced. A recent study by Bergamaschi *et al.* (2010), highlights that atmospheric CH_4 has been at a relatively steady state of 1751 ppbv between 1999 and 2002. The IPCC (2007) estimated that CH_4 emissions increased by approximately 17% between 1990 and 2005, with an average annual increase of 58 Mton CO_2 equivalents per year.

Anthropogenic sources account for less than half global CH_4 emissions; however, they are the primary driver in emission growth. Agriculture is the largest man-made source of CH_4, which contributes approximately 43% toward total anthropogenic emissions of CH_4 (Cloy *et al.*, 2012). This can be accounted for by an increase in population pressure (also an increase in demand for food, hence more meat and dairy products), technological change, public policy, and economic growth (increased gross domestic product particularly in some developing countries) (IPCC, 2007). These emissions mainly derive from large sources such as enteric fermentation by ruminant animals (25%) and rice cultivation (12%), with minor contributions from animal waste (3%) and savannah (biomass) burning (3%) (Cloy *et al.*, 2012).

Future projections highlight the potential for further increases in CH_4 emissions. For example, the Food and Agriculture Organization has estimated that if emissions increase in proportion to increases in livestock numbers, then global livestock-related methane production is expected to increase by up to approximately 60% (Steinfeld *et al.*, 2006). This prediction is feasible, particularly in developing countries such as South America, as cattle population has increased from 176 to 379 M head between 1961 and 2004 (IPCC, 2007). Further, all other livestock categories have increased in the order of 30–600% since 1961, which has been primarily due to food demand and is projected to increase further in the future years. The USEPA (2006) predicts that combined CH_4 emissions from enteric fermentation and manure management will increase by 21% between 2005 and 2020.

Geography and Emission Intensity

Methane emissions from developing regions such as Africa, Asia, and Latin America have recently shown strong growth, whereas in Europe and North America, emissions remain relatively stable (with smaller fluctuations). Emissions are projected to increase by as much as 60% by 2030 (USEPA, 2006). This is more likely to be accounted for by emissions from Asia, which are expected to show an increase from animal sources, a 153% increase from enteric fermentation and 85% increase in manure management in particular from 1990 to 2020 (IPCC, 2007, USEPA, 2006). Latin America is expected to contribute significantly toward the global increase of CH_4 emissions as it is projected to increase emissions by 51% between 1990 and 2005 (USEPA, 2006). This is largely due to increased food demand and population pressures that will most likely result in increased emissions from agriculture.

The only region where, according to the USEPA (2006), CH_4 emissions are projected to decrease to 2020 is Western Europe. This is associated with numerous emission reduction policies (such as the Kyoto Protocol) that legally bind countries to reduce emissions and other environmental policies (IPCC, 2007).

Mitigation

Opportunities for mitigating CH_4 emissions include effective management of livestock, as more efficient use of feeds often reduces amounts of CH_4 produced (Clemens and Ahlgrimm, 2001). More intensive feeding regimes with a carefully tailored feed (e.g., augmenting the volume of starches in the diet greatly reduces CH_4) and high-quality forage management practices (e.g., livestock grazing on mixed alfalfa-grass pasture) can reduce per capita emissions by up to 50% (Thorpe, 2009). One strategy for reducing methane emissions is to inhibit the production of methanogenesis within the animal husbandry system. Such options include the application of ionophores, methane oxidizers, and probiotics (Thorpe, 2009). However, this method is unlikely on its own to achieve significant mitigation of emissions, may prove uneconomic in the long term (Patra, 2012), and is currently outlawed in the EU. One of the most straightforward CH_4 emissions mitigation opportunities occurs as a consequence of herd reduction, although a less drastic option involves genetic selection and the use of breeds with lower CH_4 emissions (Thorpe, 2009; Bell *et al.*, 2011). The developed world has seen a general decline in herd numbers over the past 20 years. This is a result of increasing concerns over meat consumption and health scares, coupled with concerns over the nature of production (ibid, 2008). Strategies to mitigate emissions from rice cultivation include draining the wetland twice during the growing season, as this can effectively reduce CH_4 release from 10% to 80% (Smith *et al.*, 2008). Kai *et al.* (2011) found that changes in agricultural practices such as new high-yield rice species, coupled with greater application of fertilizers, often require shorter inundation periods which, in turn, can reduce CH_4 emissions.

Carbon Dioxide

Nature of Gas

Carbon dioxide (CO_2) is a naturally occurring color- and odorless chemical compound which exits as a gas at room temperature. The chemical structure of CO_2 consists of a single carbon atom covalently bonded to two oxygen atoms. It has a molecular mass of 44.01 g mol^{-1}, a density of 1.98 kg m^{-3}, and boiling and melting points of −57 and −78 °C, respectively. The ability of CO_2 to dissolve in water makes it a factor contributing to ocean acidification by the formation of carbonic acid (H_2CO_3). The main environmental concern, however, is over CO_2 acting as a greenhouse gas, which is a significant factor contributing to global warming.

Carbon dioxide is widely used by humans throughout many different industries. Common uses are in carbonated drinks (soft drinks and beer), decaffeinated coffee production,

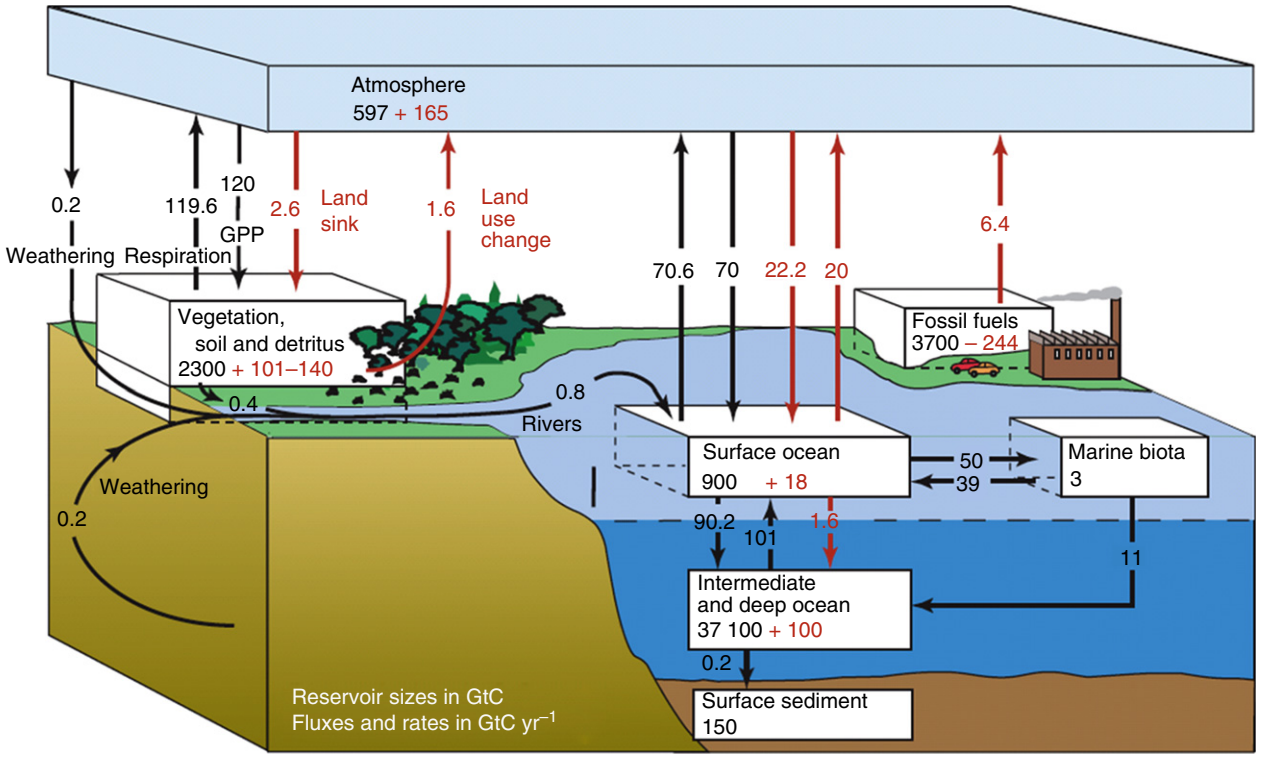


Figure 7 The global carbon cycle (IPCC 2007). Figures in black represent natural processes and pools, whereas those in red represent the contribution of anthropogenic influences. GPP, gross primary production (http://www.ipcc.ch/graphics/ar4-wg1/jpg/fig-7-3.jpg, with permission from IPCC).

wine making, fire extinguishers, as a refrigerant, and to enhance plant growth in greenhouses.

Cycling (Source/Sink)

Carbon moves naturally between land, oceans, and atmosphere via the carbon cycle (Figure 7). The timescales for carbon transformation vary greatly from seconds, such as during fixation of CO_2 via photosynthesis, to more than millions of years, as in the case of fossil carbon formation. Not only are humans responsible for emitting large amounts of greenhouse gases into the atmosphere through the combustion of fossil fuels, but soils also make a significant contribution. The proportion of greenhouse gas emissions from different sectors illustrates that CO_2 emissions directly attributable to agriculture are relatively small, but agriculture, together with land-use change, contributes to almost one-third of global emissions. Despite this large loss of CO_2, there is the ability to use land as a means of reducing atmospheric CO_2 levels by sequestering it in soils. This brings the additional benefit of improved soil quality from organic matter, leading to enhanced agricultural production. Agriculture and forestry are unique in that they can provide both a source and a sink for CO_2.

The two main sources of CO_2 associated with agriculture are the relatively small contribution made by the use of fossil fuels and land-use change. Fossil fuels are needed in agriculture as fuel for farming machinery, in the manufacture of agricultural equipment, and during the production of agrochemicals. Fossil fuel use in agriculture is low in relation to societies' overall energy use, representing only 3–4.5% of the total energy budget of industrialized countries using high intensity farming (Sauerbeck, 2001). The amount of fossil fuel and subsequently CO_2 emissions attributable to agriculture increases dramatically when including food processing, preservation, packaging, and transport. Increasingly, food is being transported further away from where it was grown to where it is consumed.

By contrast, land use change, second only to energy production, is one of the biggest sources of anthropogenic CO_2 into the atmosphere. Deforestation, conversion of forests, grasslands, and drainage of wetlands for agricultural purposes are the largest sources of CO_2 associated with agriculture. Net cumulative emissions of CO_2 from land-use change, from 1850 to 2000, amount to approximately 156 Pg C (Houghton, 2003). Land-use change to agriculture leads to CO_2 being emitted because some of the carbon fixed in the plants during photosynthesis is removed when harvested, resulting in less plant litter and biomass being returned to the soil. This causes disruption of the soil's aggregates and enhanced microbial decay of organic matter, leading to CO_2 release via respiration. Disruption of soil aggregates can cause loss of the carbon-rich topsoil due to an enhanced susceptibility to erosion. Burning organic matter in the form of plant residues during agricultural practices such as slash and burn also causes the release of significant amounts of CO_2.

Agriculture can also act as a sink for CO_2. In carbon-depleted agricultural soils, organic carbon can be enhanced by increasing the addition of carbon in soil from plant litter or crop residues and by reducing the rates of microbial decomposition. Where land has been depleted in carbon, reversion to forestry or pasture can restore carbon stocks and

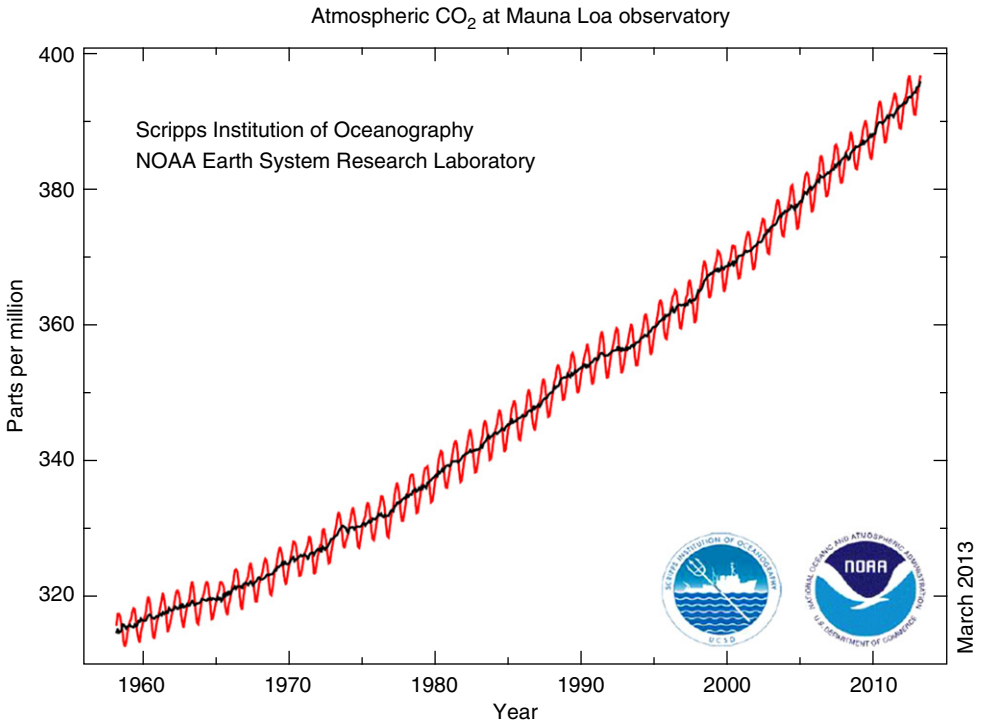


Figure 8 The carbon dioxide data (red curve), measured as the mole fraction in dry air, on Mauna Loa. The black curve represents the seasonally corrected data (www.esrl.noaa.gov/gmd/ccgg/trends/ (accessed 01.07.13)).

contribute to a net removal of CO_2 from the atmosphere. The ability of agricultural soils to act as a CO_2 sink is unlikely to continue indefinitely as they approach equilibrium with inputs and losses of carbon in a given environment. Carbon levels in soil can start to decrease in circumstances where management increases loss rates.

Growth Rate

Measurements of atmospheric CO_2 concentrations are very reliable and have demonstrated a long period of annual increase in atmospheric CO_2 concentrations. However, there are uncertainties in the accuracy and quantification of terrestrial and oceanic CO_2 sinks. Growth rates in atmospheric CO_2 concentrations have been recorded in Mauna Loa in the Pacific Ocean since 1958 and were initiated by C. David Keeling of the Scripps Institution of Oceanography in March of 1958 at a facility of the National Oceanic and Atmospheric Administration (Keeling *et al.*, 1976). They show a continuous increase from less than 320 ppm in 1958 to nearly 400 ppm in 2013 (**Figure 8**). Since 1958, the average rate of increase in the atmospheric concentration of CO_2 has been approximately 1 ppm per year (2 PgC per year). In 2005, the atmospheric CO_2 concentration was approximately 380 ppm, which is an increase of approximately 35% since preindustrial times. Between 1959 and 2008, 43% of each year's CO_2 emissions remained in the atmosphere (Le Quere *et al.*, 2009). However, in recent years, this amount has been thought to have risen to up to 45% due to climate change effects. Increasing CO_2 concentrations correlate well with fossil fuel combustion and land-use change patterns.

Emissions per Country

In 2011, China, the United States, the European Union, India, the Russian Federation, and Japan were the top six emitting countries of CO_2, representing 28%, 16%, 11%, 7%, 5%, and 4% of global emissions, respectively (Global Carbon Project, 2012). A large proportion of CO_2 emissions originates from fossil fuel consumption rather than from agriculture (Le Quere *et al.*, 2009).

Since 2002, there has been a 150% increase in total CO_2 emissions from China. However, there is great uncertainty in the accuracy of CO_2 emission reporting from China, with uncertainty levels of 10%, whereas most other industrialized countries have an uncertainty level of 5%. At a global level, large increases in emissions can be linked to thermal power generation, steel production, and cement production. There was a small decline in emissions linked to the economic slowdown of 2008–09, but growth in emissions soon recovered after that reaching more than 9 billion tons of CO_2–C by 2010 (Peters *et al.*, 2012).

In 2011, the Organisation for Economic Co-operation and Development (OECD) countries accounted for one-third of global CO_2 emissions, the same amount as that of China and India combined. In 2011, CO_2 emissions from developed countries decreased. The European Union, the United States, and Japan experienced decreases in CO_2 emissions of 3% to 3.8 billion tons, 2% to 5.4 billion tons, and 2% to 1.2 billion tons, respectively. The decrease in emissions is thought to have been due to weak economic conditions, mild winter weather, and high oil prices (Andres *et al.*, 2012). Despite this, developing countries increased emissions by 6% on average in

2011. Australia, Spain, Russia, and Canada experienced increases of 8%, 2%, 1%, and 7%, respectively. Economies in Transition countries also experienced an increase in emissions such as in Ukraine, where emissions increased by 7%. Total CO_2 emissions for all industrialized countries that had quantitative greenhouse gas mitigation targets under the Kyoto Protocol decreased in 2011 by 0.7%. Figure 4 shows CO_2 emissions per capita from combustion of fossil fuels and cement production of the top 5 emitting countries in 2011. China and the European Union have similar per capita emissions.

Mitigation

Reducing increases in atmospheric CO_2 accumulation as a result of agriculture and land-use change requires a commitment to avoiding land-use change that will release large amounts of soil carbon. In particular, this must address deforestation, cultivation of pasture, and degradation of peaty and organic soils. Such actions would help to avoid the increases in atmospheric CO_2 that have been a characteristic of the past century of human development; however, this also requires recognition of the range of functions that land supports in addition to food production.

The management of agricultural soils also provides an opportunity to increase the quantities of carbon stored in soils that are used on a continuous basis for agricultural production. These include improved nutrient management, reduced tillage, improved agronomy, the use of composts and manures, improved rotations, and bioenergy crops. The efficiency of different management options varies according to climate and baseline agricultural practices; however, it has been estimated that in Europe, there is a potential through improved agricultural management to sequester between 90 and 120 Mton carbon per year, with benefits in terms of greenhouse gas mitigation and improved soil quality (Smith, 2004).

Conclusions

Agriculture, and the land use associated with agricultural production systems, contributes significantly to global greenhouse gas emissions. Most emissions are associated with N_2O emissions from N fertilizers and manures and from CH_4 emissions from ruminant livestock and rice cultivation. A smaller amount of emission is also associated with CO_2 loss from soils converted into croplands from forests and pastures. There is an urgent need to improve the efficiency of farming systems in order to ensure that productivity is maintained or increased at the same time as their environmental impact (particularly greenhouse gas emissions) are reduced. Many management options are available to reduce the emissions of individual greenhouse gases in the crop and livestock sectors. The implementation of such management practices alongside protection of forests and permanent pasture from conversion to croplands can be expected to significantly reduce emissions of greenhouse gases from the agriculture and land-use sectors.

See also: Edaphic Soil Science, Introduction to. Farm Management. Food Security: Development Strategies. Land Use: Restoration and Rehabilitation. Soil: Carbon Sequestration in Agricultural Systems. Soil: Conservation Practices. Soil Fertility and Plant Nutrition. Soil Greenhouse Gas Emissions and Their Mitigation. Soil: Nutrient Cycling

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Analyses of Total Phenolics, Total Flavonoids, and Total Antioxidant Activities in Foods and Dietary Supplements

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Abbreviations

ABAP	2,2′-Azobis(2-samidinopropane) dihydrocholoride
ABTS	2,2′-Azinobis-(3-ethylbenzothiazoline-6 sulfonic acid)
CAA	Cellular antioxidant activity
CVD	Cardiovascular disease
DCF	Dichlorofluorescein
DCFH	2′,7′-Dichlorofluorescin
DCFH-DA	Dichlorofluorescindiacetate
DPPH	2,2-Diphenyl-1-picrylhydrazyl radical scavenging capacity
FCR	Folin–Ciocalteu reagent
FRAP	Ferric reducing antioxidant power
GAE	Gallic acid equivalents
HAT	Hydrogen atom transfer
KMBA	α-Keto-gamma-methiolbutyric acid
ORAC	Oxygen radical absorbance capacity
PSC	Peroxyl radical scavenging capacity
RMCD	Randomly methylated α-cyclodextrin
SBC	Sodium borohydride/chloranil
SET	Single electron transfer
TEAC	Trolox equivalent antioxidant capacity
TOSC	Total oxyradical scavenging capacity
TRAP	Total radical-trapping antioxidant parameter
USDA	United States Department of Agriculture

Introduction

Previous epidemiologic studies have consistently shown that diet plays a crucial role in the prevention of chronic diseases (Temple, 2000; Willett, 1994). Consumption of fruits and vegetables, as well as grains, has been strongly associated with reduced risk of cardiovascular disease, cancer, diabetes, Alzheimer disease, cataracts, and age-related functional decline (Temple, 2000; Willett, 1994; Willett, 1995). This convincing evidence suggests that a change in dietary behavior such as increasing consumption of fruits, vegetables, and whole grains is a practical strategy for significantly reducing the incidence of chronic diseases (Liu, 2003).

Phytochemicals are the bioactive nonnutrient plant compounds such as the carotenoids, flavonoids, isoflavonoids, and phenolic acids in fruits, vegetables, whole grains, and other plant foods. Thousands of phytochemicals have been identified in foods, yet there are still many that have not been identified. They have been linked to reductions in the risk of major chronic diseases (Liu, 2003). For example, phytochemicals may inhibit cancer cell proliferation, regulate inflammatory and immune response, and protect against lipid oxidation (Hollman and Katan, 1997; Liu, 2003). A major role of the phytochemicals is the protection against oxidation (Boyer and Liu, 2004).

Cells in humans and other organisms are constantly exposed to a variety of oxidizing agents, some of which are necessary for life. These agents may be present in air, food, and water, or they may be produced by metabolic activities within cells. The key factor is to maintain a balance between oxidants and antioxidants to sustain optimal physiologic conditions in the body. Overproduction of oxidants can cause an imbalance, leading to oxidative stress (Liu and Hotchkiss, 1995). Oxidative stress can cause oxidative damage to large biomolecules such as proteins, DNA, and lipids, resulting in an increased risk of cancer and cardiovascular disease (Ames and Gold, 1991; Ames *et al.*, 1993).

Humans, and all animals, have complex antioxidant defense systems, but they are not perfect and oxidative damage will occur. To prevent or slow down the oxidative stress induced by free radicals, sufficient amounts of antioxidants need to be consumed (Ames *et al.*, 1993; Boyer and Liu, 2004). Because prevention is a more effective strategy than treatment for chronic diseases, a constant supply of phytochemical-containing foods with desirable health benefits beyond basic nutrition is essential to furnish the defensive mechanism to reduce the risk of chronic diseases in humans (Liu, 2004). Recent research has also shown that, through overlapping or complementary effects, the complex mixture of phytochemicals in fruits and vegetables provides a better protective effect on health than single phytochemicals (Eberhardt *et al.*, 2000; Liu, 2004). This perspective has been strengthened by the occurrence of inconsistent results in human clinical trials using single antioxidants.

Antioxidant research has been expanded dramatically since the mid-1990s with the development of several assays measuring the total antioxidant activity of pure compounds, foods, and dietary supplements (Cao *et al.*, 1993; Cao *et al.*, 1995; Ou *et al.*, 2001; Prior *et al.*, 2003).

Several assays, such as the trolox equivalent antioxidant activity (TEAC) and oxygen radical absorbance capacity (ORAC) assays, as well as 2,2-diphenylpicrylhydrazyl (DPPH) scavenging and ferric reducing antioxidant power (FRAP) are commonly used to study the antioxidant activities *in vitro* (Arts *et al.*, 2004; Prior *et al.*, 2005; Sharma *et al.*, 2007; Huang *et al.*, 2005). These assays provide a relative measure of antioxidant activity, but often the radicals scavenged have little relevance to those present in biological systems (Perron and Brumaghim, 2009).

However, these total antioxidant activity assays in test tubes do not necessarily reflect the cellular physiological conditions

and do not consider the bioavailability and metabolism issues. In addition, the mechanisms of action of antioxidants go beyond the antioxidant activity of scavenging free radicals in disease prevention and health promotion (Liu, 2004). Animal models and human studies are expensive and not suitable for the initial antioxidant screening of foods and dietary supplements. The best solution is the cell culture models, which support antioxidant research prior to animal studies and human clinical trials (Liu and Finley, 2005). These models provide an approach that is cost-effective, relatively fast, and address some issues of uptake, distribution, and metabolism (Wolfe and Liu, 2007).

The objective of this article is to review the current literature for analyses of antioxidants and antioxidant activities, including assays for total phenolics, total flavonoids, and total antioxidant activities.

Analysis of Total Phenolics in Foods and Dietary Supplements

Phenolic Compounds

Phenolic compounds are compounds that have one or more hydroxyl groups on the aromatic skeleton. Phenols represent group of compounds that have more than one phenolic hydroxyl group attached to one or more benzene rings (Liu, 2004; Dobes *et al.*, 2013; Khoddami *et al.*, 2013; Khatiwora *et al.*, 2010; Ng, 2009).

Phenolics are the products of secondary metabolism in plants, providing essential functions in the reproduction and the growth of the plants; acting as defense mechanisms against pathogens, parasites, and predators; as well as contributing to the color of plants. In addition to their roles in plants, they have been reported to have multiple biological effects, including antioxidant activity, to prevent heart disease, reduce inflammation, lower the incidence of cancers and diabetes, as well as to reduce rates of mutagenesis in human cells (Liu, 2004; Khoddami *et al.*, 2013; Khatiwora *et al.*, 2010).

These compounds may be classified into different groups as a function of the number of phenol rings that they contain and of the structural elements that bind these rings to one another (Liu, 2004). Distinctions are thus made between the phenolic acids, flavonoids, stilbenes, and lignans. The flavonoids, which share a common structure consisting of 2 aromatic rings (A and B) that are bound together by 3 carbon atoms that form an oxygenated heterocycle (ring C), may themselves be divided into 6 subclasses as a function of the type of heterocycle involved: flavonols, flavones, isoflavones, flavanones, anthocyanidins, and flavanols (catechins and proanthocyanidins). In addition to this diversity, polyphenols may be associated with various carbohydrates and organic acids, and with one another (Manach *et al.*, 2004).

Phenolics are widely distributed in plants, spices, vegetables, fruits, whole grains, green and black teas, coffee, fruit juices, olive oil, red and white wines, and chocolates (Perron and Brumaghim, 2009); and are found in medium to high milligram quantities per serving for all of these foods, although measurements of the precise concentrations of phenolic compounds in each type of food often vary. Thus, people with diets rich in fruits and vegetables may consume one or more grams per day of these compounds, based on the recommendation of 5 servings per day of colorful fruits and vegetables by the Centers for Disease Control and Prevention (Perron and Brumaghim, 2009; Gardner *et al.*, 2007; Vison, 1998; Nardini *et al.*, 2002; Vinson *et al.*, 2001; Mertens-Talcott *et al.*, 2006; Seeram *et al.*, 2008; Garcia-Alonso, *et al.*, 2007; Gil *et al.*, 2000; Oboh and Rocha, 2007; Gutierrez *et al.*, 2001; Visioli *et al.*, 1998; Makris *et al.*, 2003; Vinson *et al.*, 1999).

Fruits, vegetables, and beverages such as tea and red wine constitute the main sources of dietary phenolics. Certain phenolics such as quercetine are found in all plant products (fruits, vegetables, cereals, leguminous plants, fruit juices, tea, wine, infusions, etc.), whereas others are specific to particular foods (flavanones in citrus fruit, isoflavones in soya, and phloridzin in apples). In most cases, foods contain complex mixtures of phenolics, which are often poorly characterized (Manach *et al.*, 2004).

Folin–Ciocalteu Assay

The Folin–Ciocalteu (F–C) assay is one of the most popular assays for phenolic analysis (Singleton and Rossi, 1965; Singleton *et al.*, 1999). The principle of the F–C assay is the reduction of the Folin–Ciocalteu reagent (FCR) in the presence of phenolics resulting in the production of molybdenum–tungsten blue that is measured spectrophotometrically at 760 nm and the intensity increases linearly with the concentration of phenolics in the reaction medium as described by Swain and Hillis (1959).

The FCR (Folin and Ciocalteu, 1927) provides an improvement over the Folin–Denis reagent with the addition of lithium sulfate to the reagent. The lithium salts reduce the amount of precipitate that can form when high concentrations of reagent are used to increase the assay's reactivity.

The F–C assay is simple and widely used to determine total phenolics in fruits and vegetables (Chu *et al.*, 2002; Dewanto *et al.*, 2002a,b; Sun *et al.*, 2002; Vinson *et al.*, 2001; Wolfe *et al.*, 2003; Liu *et al.*, 2005; Sun and Liu, 2006).

The common protocol is performed according to Singleton *et al.* (1999) with some modifications according to Dewanto *et al.* (2002a,b). Volumes of 0.5 ml of deionized water and 0.125 ml of diluted fruit extracts were added to a test tube. FCR (0.125 ml) was added to the solution and allowed to react for 6 min. Then, 1.25 ml of 7% sodium carbonate solution was aliquoted into the test tubes, and the mixture was diluted to 3 ml with deionized water. The color was developed after 90 min, and the absorbance was read at 760 nm.

Advantages and Limitations

The F–C method has the advantages of being easy, quickly, and highly reproducible (with a lower coefficient of variation); highly used as screening method for fruits, vegetables, whole grains, and plants.

The F–C assay has a limitation. The reagents for this method do not react specifically with only phenolics but also react with other oxidizable compounds like ascorbic acid, aromatic amines, reducing sugars, and aromatic amino acids (Khoddami *et al.*, 2013; Hatch *et al.*, 1993).

The presence of proteins also interferes in the assay. As a solution for this problem, Hatch *et al.* (1993) proposed using acetone–trichloroacetic acid solution that precipitates proteins.

Yates and Peckol (1993) described the use of polyvinytpolypyrrolidone (PVPP) to alleviating this interference. Phenolic compounds bind to nonsoluble PVPP under acidic conditions and can then be removed from solution by filtering or centrifuging. The remaining oxidizable species are then quantified with a Folin–Ciocalteu or Folin–Denis assay and subtracted from the results of the assay before the addition of PVPP. However, if all the phenolics are not removed by the PVPP, phenolic concentrations are underestimated.

Analysis of Total Flavonoids

Flavonoid Compounds

Flavonoids have a 15-carbon skeleton, which consist of 2 aromatic rings (A and B rings) linked by 3 carbons that are usually in an oxygenated heterocyclic ring, or C ring. Differences in the generic structure of the heterocyclic C ring lead to their classification as flavones, flavonols, flavonones, flavononols, isoflavonoids, flavanols (catechins), and anthocyanidins (Liu, 2004). Flavonols (quercetin, kaempferol, and myricetin), flavones (luteolin and apigenin), flavanols (catechin, epicatechin, epigallocatechin, epicatechin gallate, and epigallocatechin gallate), flavonones (hesperetin and naringenin), anthocyanidins, and isoflavonoids (genistein and biochanin A) are common flavonoids found in the human diet. Flavonoids are most frequently found in nature as conjugates in glycosylated or esterified forms but can occur as aglycones, especially as a result of food processing. These compounds are a class of plant secondary metabolites derived from the condensation of cinnamic acid with three malonyl-CoA groups. (Khoddami *et al.*, 2013; Liu, 2004; Hollman and Arts, 2000).

Flavonoids are the most common group of phenolic compounds that are found ubiquitously in plants (Khatiwora *et al.*, 2010; Ng, 2009), fruits, vegetables, whole grains, bark, roots, stems, flowers, tea, and wine (Liu, 2004; Nijveldt *et al.*, 2001). The concentration of total flavonoids for some samples were described by He *et al.* (2008), blueberry showed the total flavonoid content of 689.5 ± 10.7 mg of quercetin equivalent per 100 g of sample, cranberry 341.5 ± 23.4 mg per 100 g, apple 170.5 ± 7.9 mg per 100 g, broccoli 116.5 ± 8.2 mg per 100 g, and red pepper 73.2 ± 1.9 mg per 100 g.

Flavonoids play an important role in human health (Liu, 2004). They have been reported to have many health benefits including antioxidant activity, antiinflammation, antibacterial and antiviral effects, antiallergenic reaction, and antimutagenic and anticancer properties (Liu, 2004; Liu, 2003; Hanasaki *et al.*, 1994; Hertog and Hollman, 1996; Hertog *et al.*, 1994; Hertog *et al.*, 1993).

Methods Description

The total flavonoids method can be used in fruits, vegetables, whole grains, dietary supplements, and nutraceutical products. First, the quantitative methods of flavonoids were based on the colorimetric F–C assay (Singleton *et al.*, 1999; Singleton and Rossi, 1965), high performance liquid chromatography (HPLC) method (Vaya and Mahmood, 2006; Bloor, 2001), and $AlCl_3$ colorimetric test, but now the most used method to quantify the total flavonoids is the sodium borohydride/chloranil (SBC) assay (He *et al.*, 2008).

The F–C assay is commonly used to quantify the total phenolics. However, this method is not specific to flavonoids because it detects compounds with active hydroxyl group(s) including phenolic acids, flavonoids, ascorbic acid, reducing sugars, some amino acids, and aromatic amines (He *et al.*, 2008).

The usage of HPLC to quantify the flavonoids compounds is specific and sensitive. However, the problem with this method is the numbers of pure standard compounds available and the separation capacity of the HPLC column. In addition, there are more than 4000 flavonoids that have been identified, but a large percentage of them remain unknown (Liu, 2004). Therefore, it is not a good option to choose HPLC method to quantify the total flavonoid compounds.

The general technique mostly employed previously for quantification of flavonoids is based on the spectrophotometric determination of complex flavonoid–$AlCl_3$, which provides a bathochromic displacement and the hyperchromic effect (Mabry *et al.*, 1970). Although, there are some analytic limitations on this method described by Christ and Muller (1960), one of the problems of this method is when the total flavonoids are quantified in the fruits and vegetables, because some flavonoids containing C-glycosides do not undergo acid hydrolysis, and they are discarded in the aqueous phase during the liquid–liquid extraction due to the polarity from glucosyl residue (Ortega and Silva, 2001). Other factors have been revealed as crucial during the formation of the flavonoid–$AlCl_3$ complexes such as: the reaction time, the concentration of the reagent ($AlCl_3$ and flavonoid content/plant materials), and the chemical structure of the phenolic (Ortega and Silva, 2001). The $AlCl_3$ colorimetric test for flavonoids does not measure those flavonoids that do not bear the characteristic chelating functional groups for Al binding. Essentially flavones (e.g., chrysin, apigenin, luteolin, etc.) and flavonols (e.g., quercetin, myricetin, morin, rutin, etc.) react with Al(III), whereas flavanones and flavanonols do not form complex to the same extent (Chang *et al.*, 2002).

The SBC assay was developed in the lab and it has been used by many scientists to quantify the total flavonoids (He *et al.*, 2008). This method has the advantage of detecting all types of flavonoids, including flavones, flavonols, flavonones, flavononols, isoflavonoids, flavanols, and anthocyanins. The flavonoids with a 4-carbonyl group were reduced to flavan-4-ols using sodium borohydride catalyzed by aluminum chloride. Then the flavanols were oxidized to anthocyanins by chloranil in acetic acid solution (He *et al.*, 2008).

The SBC assay is used to quantify total flavonoids content in foods, vegetables, whole grains, herbal products, dietary supplements, functional foods, and nutraceutical products foods to support flavonoid-related health claims and to provide more accurate data for future epidemiological studies and human clinical trials. This assay is accurate, precise, and specific for total flavonoids and is a powerful tool in antioxidant research (He *et al.*, 2008).

The principle of the SBC method to quantify total flavonoids content is: flavonoids with a 4-carbonyl group (flavones, flavonols, flavonones, flavononols, and isoflavonoids) were reduced to flavan-4-ols (catechins) using sodium borohydride (Sweeny and Iacobucci, 1977a). This reaction was catalyzed by the addition of aluminum chloride to achieve a high yield of flavan-4-ols. The flavanols (catechins) were oxidized to anthocyanins by chloranil in acetic acid solution (Sweeny and Iacobucci, 1977b; Sweeny and Iacobucci, 1981; Jurd, 1966). The anthocyanins generated in the reaction were quantified spectrophotometrically at 490 nm after the addition of vanillin and concentrated hydrochloric acid (Sarkar and Howarth, 1976; Broadhurst and Jones, 1978).

The protocol for total flavonoids test is performed according to the method described by He *et al.* (2008). Briefly, 4 ml extracts of tested samples were added into test tubes, then dried to dryness under nitrogen gas, and reconstituted in 1 ml of THF/EtOH (1:1, v/v). Catechin standards (0.1–8.0 mM) were prepared fresh each day before use in 1 ml of THF/EtOH (1:1, v/v). To each test tube with 1 ml of sample solution or 1 ml of catechin standard solution, 0.5 ml of 50 mM NaBH4 solution and 0.5 ml of 74.56 mM $AlCl_3$ solution were added. The mixture was shaken in an orbital shaker at room temperature for 30 min. Then an additional 0.5 ml of $NaBH_4$ solution was added into each test tube with continuing shaking for another 30 min at room temperature. Cold acetic acid solution (2.0 ml of 0.8 M, 4 °C) was added into each test tube, and the solutions were kept in the dark for 15 min after a thorough mix. Then, chloranil (1.0 ml, 20 mM) was added into each tube, which was heated at 100 °C with shaking for 60 min in a reciprocal shaking bath. The reaction solutions were cooled using tap water, and the final volume was brought to 4 ml using methanol. Then, 1 ml of 1052 mM vanillin was added into each tube, followed by mixing. Concentrated HCl (2.0 ml, 12 M) was added into each tube, and the reaction solutions were kept in the dark for 15 min after a thorough mix. Aliquots of the final reaction solutions (200 µl) were added into each well of a 96-well plate, and absorbances were measured at 490 nm.

Chemical Total Antioxidant Activity Assays

Techniques that measure total antioxidant activities of foods can be valuable in studying the relationship between dietary factors and chronic disease prevention, as well as providing vital information for selecting good dietary sources of antioxidants. This has led to the development of diverse new or improved methods applied to all kinds of plant-based foods (Ou *et al.*, 2001; Ou *et al.*, 2002; Pulido *et al.*, 2000; Naguib, 2000; Arnao *et al.*, 2001; Aldini *et al.*, 2001; Huang *et al.*, 2002).

Over 20 methods are used for assessment of antioxidant capacities (Frankel and Meyer, 2000). The significance of the measured values and mutual comparison of the results gained by individual method is still an unresolved problem.

The measurement of antioxidant activity is an important screening method to compare the oxidation/reduction potentials of fruits and vegetables and their phytochemicals in various systems. Many chemistry methods are currently in wide use, including the ORAC (Cao *et al.*, 1993), total radical-trapping antioxidant parameter (TRAP) (Ghiselli *et al.*, 1995; Wayner *et al.*, 1985), TEAC (Miller *et al.*, 1993), total oxyradical scavenging capacity (TOSC) (Winston *et al.*, 1998), and the peroxyl radical scavenging capacity (PSC) assays, the latter of which was developed by our laboratory (Adom and Liu, 2005). FRAP assay (Benzie and Strain, 1996) and the DPPH free radical method (Brand-Williams *et al.*, 1995) measure the ability of antioxidants to reduce ferric iron and DPPH, respectively.

For the methods based on similar principles of electron transfer (ET), there are the TEAC, FRAP, and DPPH. For the hydrogen atom transfer methods (HAT), there are the ORAC method, TRAP, TOSC, and the PSC assays (Stratil *et al.*, 2007; Badarinath *et al.*, 2010).

Ferric Reducing Antioxidant Power Assay

This is a colorimetric assay that measures the ability of plasma to reduce the intense blue ferric tripyridyltriazine complex to its ferrous form, thereby changing its absorbance (Benzie and Strain, 1999).

The advantages of this method are simple, speedy, and inexpensive, and do not required specialized equipment. It can be performed using automated, semiautomated, or manual methods (Benzie and Strain, 1999). But the disadvantages are that FRAP cannot detect species that act by radical quenching (H transfer), particularly SH group containing antioxidants like thiols, such as glutathione and proteins (Prior and Cao, 2000; Huang *et al.*, 2005; Cao and Prior, 1998).

The FRAP assay was done according to Benzie and Strain (1996) with some modifications. The stock solutions included 300 mM acetate buffer (3.1 g $C_2H_3NaO_2 \cdot 3\ H_2O$ and 16 ml $C_2H_4O_2$), pH 3.6, 10 mM TPTZ (2,4,6-tripyridyl-s-triazine) solution in 40 mM HCl, and 20 mM $FeCl_3 \cdot 6\ H_2O$ solution. The fresh working solution was prepared by mixing 25 ml acetate buffer, 2.5 ml TPTZ solution, and 2.5 ml $FeCl_3 \cdot 6\ H_2O$ solution and then warmed at 37 °C before use. Fruit or vegetable extracts (150 ml) were allowed to react with 2850 ml of the FRAP solution for 30 min in the dark condition. Readings of the colored product (ferrous tripyridyltriazine complex) were then taken at 593 nm. The standard curve was linear between 25 and 800 mM Trolox. Results are expressed in mM Trolox equivalents (TE) per gram fresh mass.

Trolox Equivalent Antioxidant Capacity

This assay is based on the ability of molecules to scavenge the stable free radical of 2,2′-azinobis-(3-ethylbenzothiazoline-6 sulfonic acid)(ABTS) in comparison with Trolox, a water-soluble analog of vitamin E. The activity of a compound is, therefore, expressed as TEAC units. This technique has not been widely applied, which limits the possibility to compare results from different studies. All the other assays have been applied in plasma reproducibility (Badarinath *et al.*, 2010).

For TEAC or ABTS assay, the procedure followed the method of Arnao *et al.* (2001) with some modifications. The stock solutions included 7.4 mM $ABTS^+$ solution and 2.6 mM potassium persulfate solution. The working solution was then

prepared by mixing the two stock solutions in equal quantities and allowing them to react for 12 h at room temperature in the dark. The solution was then diluted by mixing 1 ml $ABTS^+$ solution with 60 ml methanol to obtain an absorbance of 1.1 ± 0.02 units at 734 nm using the spectrophotometer. Fresh $ABTS^+$ solution was prepared for each assay. The extracts (150 ml) were allowed to react with 2850 ml of the $ABTS^+$ solution for 2 h in a dark condition. Then the absorbance was taken at 734 nm using the spectrophotometer. The standard curve was linear between 25 and 600 mM Trolox. Results are expressed in mM TE per gram fresh mass.

2,2-Diphenyl-1-Picrylhydrazyl

DPPH is a stable free radical at room temperature, which produces a violet solution in methanol. When the free radical reacts to an antioxidant, its free radical property is lost due to chain breakage and its color changes to light yellow (Badarinath *et al.*, 2010).

DPPH method was commonly used because it is a very simple, sensitive, and rapid method, which was very convenient for the screening of many samples of different polarity (Koleva *et al.*, 2002).

DPPH protocol was described by Brand-Williams *et al.*, (1995). Ethanolic solutions in different concentrations were prepared by adding 1000 µl of DPPH (0.004% w/v), and the final volume was brought to 1200 µl with ethanol. Each tube was incubating for 30 min at room temperature in the dark. The same procedure was taken for gallic acid. The control was prepared as above without any extract, and ethanol was used for the baseline correction. The DPPH solution was freshly prepared daily, stored in a flask covered with aluminum foil, and kept in the dark at 4 °C between measurements. The percent decrease in absorbance was recorded for each concentration and percent quenching of DPPH was calculated on the basis of the observed decrease in absorbance of the radical. Changes in the absorbance of the samples were measured at 517 nm.

Total Oxyradical Scavenging Capacity

Winston *et al.* (1998) developed the TOSC. The substrate that is oxidized in this assay is α-keto-gamma-methiolbutyric acid, which forms ethylene. The time course of ethylene formation is followed by head space analysis of the reaction cell by gas chromatography, and the antioxidant capacity is quantified by the ability of the antioxidant to inhibit ethylene formation relative to a control reaction.

The advantage of the TOSC method is that it permits the quantification of the antioxidant capacity toward three oxidants, that is, hydroxyl radicals, peroxyl radicals, and peroxynitrite (Regoli and Winston, 1999). At the same time, the disadvantage of this method is not readily adaptable for high-throughput analyses required for quality control in that it requires multiple injections from a single sample into a gas chromatograph to measure the production of ethylene (Lichtenthaler and Marx, 2005).

Peroxyl radicals were generated by the thermal homolysis of ABAP at 35 and 39 °C. Reactions were carried out in 10 ml rubber septum-sealed vials in a final volume of 1 ml. The reactions were initiated by injection of 100 ml of 200 mM ABAP in water directly through the rubber septum. Ethylene production was measured by gas-chromatographic analysis of 1 ml aliquots taken directly from the head space of the reaction vials. By staggering the starting times for each vial, 8–10 serial samples can be monitored in sequence at 12-min intervals. Analyses were performed with a gas chromatograph equipped with a flame ionization detector.

Measurement of Oxygen Radical Scavenging Capacity

ORAC assay is an HAT assay first developed by Cao *et al.* (1993) to measure total antioxidant capacity of secondary antioxidants. The assay is based on the fluorescence method for peroxy radicals developed by DeLange and Glaze in 1989. ORAC assay has been one of the most commonly used antioxidant activity assays in research and food industries (Caldwell, 2001). But the disadvantage is that it requires fluorometers, which may not be routinely available in analytical laboratories. Temperature control decreases reproducibility (Badarinath *et al.*, 2010).

The protocol for ORAC method is performed according to Prior *et al.*, 2003. Briefly, 20 µl of blank, Trolox standard, or food extracts in 75 mM potassium phosphate buffer, pH 7.4, was added to triplicate wells in a black, clear-bottom, and 96-well microplate. The triplicate samples were distributed throughout the microplate and were not placed side by side, to avoid any effects on readings due to location. A volume of 200 µl of 0.96 µM fluorescein in working buffer was added to each well and incubated at 37 °C for 20 min, with intermittent shaking, before the addition of 20 µl of freshly prepared 119 mM ABAP. The microplate was immediately inserted into a plate reader at 37 °C. The decay of fluorescence at 538 nm was measured with excitation at 485 nm every 5 min for 2.5 h. The areas under the fluorescence versus time curve for the samples minus the area under the curve for the blank were calculated and compared to a standard curve of the areas under the curve for 6.25, 12.5, 25, and 50 µM Trolox standards minus the area under the curve for blank.

Rapid Peroxyl Radical Scavenging Capacity

PSC method is a rapid, simple, and reliable approach for measuring both hydrophilic and lipophilic antioxidant capacity of pure antioxidant compounds, food extracts, and biological fluids toward biologically relevant radicals, based on the oxidation of 2′,7′-dichlorofluorescin (DCFH) by peroxyl radicals (Adom and Liu, 2005).

The reaction mechanism for PSC assay is as follows: Thermal degradation of ABAP produces peroxyl radicals (ROOH) (Pryor *et al.*, 1993; Winston *et al.*, 1998), which oxidize nonfluorescent DCFH to fluorescent dichlorofluorescein (DCF). The degree of inhibition of DCFH oxidation, by antioxidants that scavenge peroxyl radicals, was used as the basis for calculating antioxidant activity.

The protocol for PSC method is performed according to the method of Adom and Liu (2005). Just before use in the reaction, 80 µl of 2.48 mM DCFH-DA was hydrolyzed with

900 µl of 1.0 mM KOH for 3–5 min in a vial to remove the diacetate (DA) moiety and then diluted to 6 ml total volume with 75 mM phosphate buffer (pH 7.4). DCFH-DA was stable to oxidation, whereas DCFH was very slowly oxidized at ambient conditions without ABAP. ABAP (200 mM) was prepared fresh in buffer, and each batch was kept at 4 °C between runs. In a run, 100 µl of pure compounds or food extracts appropriately diluted in 75 mM phosphate buffer (pH 7.4) was transferred into reaction cells on a 96-well plate, and 100 µl of DCFH was added. The 96-well plate was loaded into the plate reader and the solution in each cell was mixed by shaking at 1200 rpm for 20 s. The reaction was then initiated by adding 50 µl of ABAP. The reaction was carried out at 37 °C, and fluorescence was monitored at 485 nm excitation and 538 nm emission with the fluorescent spectrophotometer. The buffer was used for control reactions. Reaction conditions were all optimized from preliminary studies for the control reaction to be completed (to reach maximum fluorescence) in 40 min.

Using randomly methylated α-cyclodextrin (RMCD) simplifies the preparations steps and most importantly ensures enhanced solubility of lipophilic compounds without any interfering side reactions, because RMCD is chemically inert in this reaction. Use of both hydro-PSC and lipo-PSC assays extends the applicability of this method to include both hydrophilic and lipophilic antioxidant capacities of foods. Results from such analyses should give more complete information on the antioxidant protection offered by a large diversity of foods (Adom and Liu, 2005).

Special Considerations for Chemical Total Antioxidant Activity Assays

Most of the data presented in the literature have been on antioxidant activities of water-soluble food extracts. Of additional interest, however, is the antioxidant activity of lipid-soluble components of foods, which are becoming very important in combating specific types of radicals and diseases. Lipophilic antioxidants play unique roles in the body (Bernstein *et al.*, 2001; Snodderly, 1995; Beatty *et al.*, 2000; Landrum and Bone, 2001; Burton and Ingold, 1986). Therefore, measurement of their contributions to the total antioxidant activity of foods can assist in elucidating the role these compounds play in disease prevention and health promotion. Information on total antioxidant capacity (both lipophilic and hydrophilic) would therefore give a more complete spectrum of protection provided by foods and their contribution toward disease prevention.

Most current antioxidant capacity assays are performed in aqueous solutions and are not suitable for lipophilic antioxidant capacity measurements. Another major improvement in measuring antioxidant capacity has been the introduction of fluorescein dyes as fluorescent probes for monitoring the reaction (Huang *et al.*, 2002; Ou *et al.*, 2002). Incorporation of fluorescent probes and cyclodextrin into antioxidant capacity assays have extended the application and usefulness of data generated from such experiments. For example, the methods of Ou *et al.* (2001) and Huang *et al.* (2002) were recently adopted by Wu *et al.* (2004) to measure the hydrophilic and lipophilic antioxidant capacities of over 100 common foods in the US market.

The PSC assay generates results comparable to similar more modern assays using fluorescein derivatives as probes and may even have certain additional advantages. For instance, with the hydroxyl radical averting capacity (HORAC) assay, it was observed that the intercept of the linear standard curves keep changing with each run, suggesting that, to eliminate the uncertainty of the intercept, it may be necessary to obtain standard curves within the run to compute final values (Ou *et al.*, 2002). The PSC assay does not require a linear standard curve, and for practical purposes using a concentration range that includes the EC_{50} produces accurate and reproducible results. The PSC assay is also very sensitive, being able to run in the low micromolar range. Adapting the PSC assay to run in a 96-well plate and also using a fluorescent dye allows the assay to be performed on simple fluorescent spectrophotometers. The method can be easily automated as has been done for the ORAC assay (Huang *et al.*, 2002).

Among all methods described in the literature for determining the antioxidant potential *in vitro*, the ORAC and PSC methods are commonly used because of the physiological relevant radicals. The PSC method has lower variation due to the incorporation of the fluorescence probe DCFH allowing for less interference, and can be used to evaluate the effects of processing and storage on antioxidant activities of fruits, vegetables, and food products (Adom and Liu, 2005).

Limitations of Chemical Antioxidant Activity Assays

Despite wide usage of these chemical antioxidant activity assays, their ability to predict *in vivo* activity is questioned for a number of reasons. Some are performed at nonphysiological pH and temperature, and none of them take into account the bioavailability, uptake, and metabolism of the antioxidant compounds (Liu and Finley, 2005). The protocols often do not include the appropriate biological substrates to be protected, relevant types of oxidants encountered, or the partitioning of compounds between the water and lipid phases and the influence of interfacial behavior (Frankel and Meyer, 2000).

Bioavailability and metabolism are two important questions that need to be addressed in the study of the biological effects of antioxidants (phytochemicals) in foods. The form of antioxidants found in foods is not necessarily the same as the form found in the blood or the targeted tissues after digestion, absorption, and metabolism. To study the mechanisms of action of antioxidants in the prevention of chronic disease, two important questions to be asked are the following: Are these antioxidants (phytochemicals) bioavailable? Are these original antioxidants or their metabolites the bioactive compounds? It is crucial to understand the bioavailability and metabolism of these compounds to gain knowledge of what compounds and how much of these compounds actually reach target tissues. In some cases, the original phytochemicals may be excreted or metabolized and never actually reach target tissue, and the active compounds may not be the original antioxidant compounds found in foods but rather their metabolites. Till date, many studies did not address the bioavailability and metabolism of phytochemicals from whole foods (Liu and Finley, 2005; Wolfe and Liu, 2007).

Examining the bioavailability of compounds from food sources can be challenging, because there are many factors that may influence bioavailability. Foods contain a wide variety of phytochemicals, and interactions with other chemicals in the food may affect bioavailability. Phytochemicals may be bound to different sugars (glucosides, xylosides, rhamnosides, or galactosides) or to other compounds (fibers) that may affect the compound's bioavailability. Other factors, such as digestion, food processing, and stage of harvest, may also affect phytochemical bioavailability. Although much progress has been made in understanding the bioavailability and further metabolism of pure compounds, more work is needed to further comprehend the bioavailability of phytochemicals from complex food sources (Liu and Finley, 2005).

A good *in vitro* model would be beneficial in this area of study in evaluating the bioavailability of phytochemicals from foods by offering a simple method to screen for factors that may affect intestinal absorption of phytochemicals, such as the food matrix, food processing, digestion, and interactions with other foods. Human and animal models can be expensive and time-consuming, whereas a cell culture model allows for rapid, inexpensive screenings. The Caco-2 cell culture model has the potential to be a good model to measure the bioavailability of antioxidants, such as carotenoids and flavonoids, from whole foods (Liu *et al.*, 2004; Boyer *et al.*, 2004; Boyer *et al.*, 2005; Garrett *et al.*, 1999; Deprez *et al.* 2001).

Popular antioxidant activity/capacity assays, such as ORAC (Cao *et al.*, 1993), TRAP (Ghiselli *et al.*, 1995), TEAC (Miller *et al.*, 1993), TOSC (Winston *et al.*, 1998), PSC (Adom and Liu, 2005), and FRAP (Benzie and Strain, 1996), all have the limitation of the inability to represent the complexity of biological systems. They measure chemical reactions only, and these reactions cannot be interpreted to represent activity *in vivo*, as they cannot account for the bioavailability, stability, tissue retention, or reactivity of the compounds under physiological conditions (Huang *et al.*, 2005).

The importance of using a more biologically relevant model in the determination of antioxidant activity is highlighted by the differences between the results of pure chemistry assays and those based in cell culture.

Cell-Based Total Antioxidant Assay

Biological systems are much more complex than the simple chemical mixtures employed, and antioxidant compounds may operate through multiple mechanisms (Liu, 2004). The different efficacies of compounds in the various assays attest to the functional variation. The best measures are from animal models and human studies; however, these are expensive, time-consuming, not suitable for initial antioxidant screening of foods and dietary supplements (Liu and Finley, 2005).

Cell culture models provide an approach that is cost-effective, relatively fast, and address some issues of uptake, distribution, and metabolism. Wolfe and Liu (2007) developed a cell-based antioxidant activity assay to screen foods, phytochemicals, and dietary supplements for potential biological activity. This method named cellular antioxidant activity (CAA). It was developed in the response to a need for a more biologically representative method than the chemistry antioxidant activity assays commonly used to screen antioxidant materials for potential biological activity (Wolfe and Liu, 2007).

It has been suggested that the following should be considered in choosing appropriate methods to measure antioxidant activity: physiologically relevant substrates; conditions that mimic biological systems; low levels of oxidants that represent all stages of oxidation; measurement of different compounds at comparable concentrations and use of plant extracts where the phenolic composition is known; and quantification based on induction period, percent inhibition, rates of product formation/decomposition, or median effective dose (Frankel and Meyer, 2000).

In CAA method, the probe, DCFH-DA, is taken up by HepG2 human hepatocarcinoma cells and deacetylated to DCFH. Peroxyl radicals generated from ABAP lead to the oxidation of DCFH to fluorescent DCF, and the level of fluorescence measured upon excitation is proportional to the level of oxidation. Pure phytochemical compounds and food extracts quench peroxyl radicals and inhibit the generation of DCF. Thus, the CAA assay uses the ability of peroxyl radicals, reactive products of lipid oxidation, to induce the formation of a fluorescent oxidative stress indicator in the cell culture and measures the prevention of oxidation by antioxidants (Wolfe and Liu, 2007).

The protocol for CAA method is performed according to the method described by Wolfe and Liu (2007). Briefly, human hepatocellular carcinoma HepG2 cells were seeded at a density of 6×10^4 per well on a 96-well microplate in 100 µl of growth medium/well. Twenty-four hours after seeding, the growth medium was removed, and the wells were washed with PBS. Wells were treated in triplicate for 1 h with 100 µl of treatment medium containing tested fruit extracts plus 25 µM DCFH-DA. Then 600 µM ABAP was applied to the cells in 100 µl of HBSS, and the 96- well microplate was placed into a plate reader at 37 °C. Emission at 538 nm was measured after excitation at 485 nm every 5 min for 1 h. Each plate included triplicate control and blank wells. Control wells contained cells treated with DCFH-DA and ABAP. Blank wells contained cells treated with DCFH-DA and HBSS. Results were expressed as µmol quercetin equivalents (QE) per 100 g of fresh fruit.

Conclusions

Increased consumption of fruits, vegetables, whole grains, and other plant-based foods has been linked to the reduced risk of developing chronic diseases. Public interest in dietary antioxidants has been increased dramatically, and antioxidant researches have been boosted in recent decades. Many chemistry-based assays have been developed to measure the antioxidants and total antioxidant activities in food samples and dietary supplements, such as total phenolic analysis assay and SBC assay, ORAC assay, TRAP assay, TOSC assay, PSC assay, TEAC assay, DPPH assay, and FRAP assay. However, these chemistry-based assays do not reflect the complexity of biological systems and physiological conditions, and do not consider the issues of bioavaibility and metabolisms (Liu and Finley, 2005; Wolfe and Liu, 2007; Wolfe and Liu, 2008). CAA assay is a newly developed antioxidant assay based on a cell

culture model to test antioxidant activities of food samples and dietary supplements *in vitro* and generates test results that are more biologically relevant (Wolfe and Liu, 2007). As the cell-based antioxidant activity assays better take bioavailability and metabolism of antioxidants into consideration at the physiological conditions, they open a new field and may lead the direction for future studies in antioxidant research.

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Animal Health: Ectoparasites

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Glossary

Anorexia A symptom that reflects the lack of appetite. It could induce weight loss that is considered unhealthy.

Ataxia A nonspecific neurological sign that consists of lack of voluntary coordination of muscle movements. It could be as a result of dysfunction of the cerebellum, the loss of sensitivity to the positions of joint and body parts (proprioception), or to dysfunction of the vestibular system (disequilibrium).

Dyspnea A symptom of breathlessness commonly associated to respiratory distress.

Enzootic Organism that is native to a place or a specific fauna.

Fomite Any object or substance capable of carrying infectious organisms and able to transfer them from one individual to another.

Leucopoenia A condition of a decreased number of leukocytes (commonly referred to as white blood cells) in the blood. It is also known as leukopenia, or leuokopoenia, and is one of the most important indicators of infection risk.

Recombinant DNA vaccine A vaccine that uses viruses or bacteria into which harmless genetic material from disease-causing organisms are inserted using genetic engineering techniques. Recombinant vaccines aim to create a strong antibody and T-cell immune response leading to protection against the targeted disease.

Sylvatic A pathogen or disease that affects only wild animals.

Thrombocytopenia A condition of a decreased number of platelets in the blood.

Transhumance The seasonal movement of people with their livestock. It is also known as nomadic movement.

Introduction

Ectoparasites and vectorborne diseases have a major impact on the productivity and welfare of livestock and wildlife and represent a constant risk for the survival and well-being of major human groups throughout the world (McDermott *et al.*, 1999; Perry and Sones, 2007; Herrero *et al.*, 2010; Thornton, 2010; Gachohi *et al.*, 2011; Rich and Perry, 2011; FAOSTAT, 2012; Grace *et al.*, 2012).

Recent surveys have estimated that the livestock population worldwide has reached 24 billion in 2012 (FAOSTAT, 2012). Analysis of the Food and Agriculture Organization of the United Nations Statistical Program (FAOSTAT) indicates that there are five major groups of livestock with major economical and welfare impact for humans worldwide: cattle/buffaloes, sheep/goats, chickens, swine, and horses (**Table 1**). Cattle and buffaloes with 1.6 billion heads worldwide are mostly concentrated in Asia (32% with more than 520 million animals), followed by South America (20%), Africa (15%), North America (14%), and Europe (10%). Similarly, sheep/goats with more than 2000 million animals worldwide are mainly distributed in Asia (>670 million), Africa (>250 million), and Oceania (>100 million).

Ectoparasites, such as ticks, fleas, biting flies, ked, mites, midges, lice, and mosquitoes, could impose a heavy burden to livestock affecting productivity. Blood loss, irritation, and discomfort could induce damage to the animal skin (hides and wool), reduce milk production, decrease immunity response, and cause retarded growth rates. In addition, ectoparasites represent a constant threat to livestock due to their competence (either as amplifiers or mechanically) for the transmission of a large number of pathogens with high morbidity and mortality implications. In addition to the worldwide economic toll caused by ectoparasites, livestock health has direct implications of sustainability of a large percentage of the world population (Kristjanson *et al.*, 2009). From the more than 6 billion people inhabiting the earth, more than a billion are living in poverty depending partially or totally on livestock (referred to as poor livestock keepers). The subsistence of these groups, most of them concentrated in Asia (600 million), East and West Africa (300 million), and South America (100 million), is constantly jeopardized by many livestock diseases, such as Bluetongue, Anaplasmosis, East Coast fever, babesiosis, Trypanosomiasis, and Rift Valley fever, that have a devastating impact, irrespective of whether they are through animal deaths, through the loss of markets and income, or because of the zoonotic potential on human health.

The increased activities toward intensification of agricultural practices and of livestock production, along the increasingly sale of live animals for food or pets, landscape modification, poor ecosystem protection, and the extensive transportation networks, create host populations conducive to evolution and persistence of parasites and vectors. This has a much greater impact in developing or poor countries of the tropical and subtropical regions, where climatic conditions favor parasite's survival and transmission or where there are the major economical impediments for adequate control of parasites, or where the systems for disease control and reporting are relatively weak (Grace *et al.*, 2011).

Ectoparasites are arthropods organisms that could seriously limit the production on livestock and so lowering the income from milk and meat sales and less access to liquid capital, could serve as potential for several zoonotic diseases, and could threat livelihoods of key household assets. The economic losses due to the direct and indirect consequences of ectoparasites in cattle production in Africa alone are estimated

Table 1 Worldwide distribution of the major livestock species

Region	*Country*	*Livestock*[a] total	*Cattle/buffaloes*	*Sheep/goats*	*Horses*	*Swine*	*Chicken*
Asia	India	559.1	321	228	0.5	9.6	774
	China	875.8	108	285	6.8	476	4803
	Pakistan	153.4	65	88	0.4	NA	321
	Bangladesh	76.2	24.4	51.8	NA	NA	228
North America	USA	177.4	94	8.6	9.8	65	2100
	Mexico	71.5	32.6	17	6.4	15.5	506
South America	Brazil	281.9	210.7	26.7	5.5	39	1239
	Argentina	75	49	20	3.7	2.3	96
	Colombia	36.5	28	4.6	2.1	1.8	157
West Africa	Nigeria	115.7	16	92	0.2	7.5	192
	Gabon	0.5	NS	0.3	NS	0.2	3.2
	Ghana	10.6	1.5	8.6	NS	0.5	47.8
East Africa	Sudan	138	42	96	NS	NS	43
	Ethiopia	103.7	53.4	48.3	2	NS	49
Oceania	New Zealand	42.9	9.9	32.7	NS	0.3	14
	Australia	101.9	26.7	72.6	0.3	2.3	83
SE Asia	Vietnam	37.6	8.8	1.3	0.1	27.4	218
	Indonesia	51	15.6	27.8	0.4	7.2	1623
	Philippines	23.6	5.8	4.2	0.2	13.4	159
Europe	France	43.8	19.6	9.3	0.4	14.5	124
	Germany	42.2	13	2.2	0.5	26.5	114
	United Kingdom	46.2	10.1	31.2	0.4	4.5	164

[a]Numbers do not include poultry.

Abbreviations: NA, data not available; NS, not significant numbers.

Note: Numbers are in million.

Source: Reproduced from FAOSTAT, 2012. Available at: http://faostat3.fao.org/home/index.html (accessed 15.04.14).

between US$1000 and US$1200 million annually (UNEP, 2012), with a total loss of US$4 750 000 year^{-1} in terms of agricultural gross domestic product.

There are four major groups of ectoparasites that affect livestock (Table 2): ticks (responsible for major losses amongst livestock worldwide), biting flies, mites, and lice.

Direct Consequence of Ectoparasites in Livestock

'Discomfort,' induced by intense itching and scratching, could lead to skin and hide damage. If intense enough, it could lead to a decreased productivity (either as a result of reduce feeding or due to erratic behavior) and depreciated value of skins (hides, wool, and leather) or the livestock as commodity. Chicken mites could cause papules on any part of the bird, could be debilitating, and could result in skin irritation, stunted growth, loss of vigor, reduced egg production, anemia, and even death. The cattle follicle or the goat follicle mite could cause lesions on the neck, shoulders, and axillary region of the animal. Papulonodular demodicosis can occur in pregnant or lactating animal where nodules could form over time ranging from a pin head to a chicken egg in size. These nodules can rupture and produce skin damages (sores) that can lead to defects in raw leather and economic losses in the hide industry. The scabies mite could cause adverse effects to the host by depositing feces into the burrows they live in, producing papules, puritus, and hair loss, where the skin may become thickened crusted and where secondary infection occurs. In extreme infestations, sensitive animals may experience weight loss, eating difficulty, hearing impairment, blindness, exhaustion, and death. Similarly, psoroptic ear mite infestation could cause scaling, crusting, inflammation, and hair loss of the ear as well as accumulation of wax, ear scratching, head shaking, and rubbing of the head and ears. Chronic infestations can lead to anemia and weight loss and in extreme cases can be fatal.

Early reports on losses caused by lice in the United States, for example, estimate that lice cause a 68 lb per head weight loss in 12% of the cattle slaughtered, representing an estimated cost of more than US$126 million (Drummond, 1985). The losses in weight gain, hide values, and even those associated with the type of housing, including damage of fences, hay racks, and buildings, due to rubbing are very dependent on variables, such as sex, age, and immunity (Michel *et al.*, 1979; Geden and Stoffolano, 1980; Lancaster *et al.*, 1982; Meyer *et al.*, 1982; Gibney *et al.*, 1985; Lancaster, 1986).

'Anemia' due to blood intake could result in animals with high parasitism. Some examples include mosquitoes that could cause painful bites, loss of weight, and reduction of milk production; sucking lice infestation that could result in loss of weight, poor performance, and reduction of milk production due to blood loss; and the lethargy associated with the dullness, nervousness, and irritation induced by the lice-feeding activity. Ticks that bite may induce inflammation, itching, and swelling and potentially induce secondary infections.

Ticks have a negative impact on cattle as they cause weight loss in animals and decrease the milk production. Some estimates showed that infestation with large number of engorged *Boophilus* female ticks could reduce the annual weight by up to 0.5 kg per animal and decrease the annual milk production by up to 200 l per animal.

Table 2 Major parasite groups, species (scientific and common names) and their impact on the hosts

Parasite	*Species*	*Common name*	*Host*	*Consequences*
Biting flies	*Simulium* spp.	Black flies, buffalo gnat, turkey gnat, or white socks	Cattle, horses, and livestock	Annoyance, tissue damage, blood loss, anaphylactic shock, and death
	Melophagus ovis	Sheep ked	Sheep	Annoyance, leading it to rub, producing both loss and damage of the wool. It also produces hard nodules on the skin (known as cockle) which reduce the value of the hide
	Tabanus spp.	Horse flies, breeze flies, clegs or clags, deer flies, gad flies, stable flies, and zimbs	Horse, cattle, and other livestock	They are vicious painful biters that feed on blood during daytime interfering with the animal behavior. They could induce poor performance in animals, and a decrease in weight gain and milk production. Infection may also predispose animals to secondary infections if present in large numbers
	Haematobia irritans	Horne fly	Cattle, horses, sheep, and goats	Annoyance, blood loss, reduction in milk production, growth rate, and weight gain. Could induce also secondary infections, including myiasis by other flies species
	Oestrus ovis	Sheep bot flies	Sheep, deer, goat, cattle, and horses	Annoyance and discomfort, leading to reducing grazing lose weight and in some cases death. The area most affected by larvae deposition is the nose, causing irritation to the mucosa, swelling of the internal membranes of the nose, possibly impairment of breathing. In extreme infections, it could cause septic sinusitis and the possibility of death from general septicemia
	Hypoderma spp.	Warble fly, heel flies, bomb flies, or gad flies	Cattle and deer	Typically the laid eggs are deposited on the foreleg and are ingested by licking. After an internal cycle involving the passing through the esophagus muscles and spinal cord, the larvae reemerge, causing subcutaneous swellings ('warbles') and skin damage (holes) reducing the skin value. If the infestation is severe, the injure on the tissues due to the migrating larvae, may seriously slow growth rate, decrease milk production and weight gain, and so reduce the profitability of livestock production on both meat or hide.
	Gasterophilus spp.	Horse bot flies	Horses, caribou, and donkeys	Larvae from eggs laid around the mouth, eyes, nose, and chin (by *Gasterophilus nasalis*) travel to the sinus cavities or the brain. Fly eggs laid or around the lower legs and shoulders (by *Gasterophilus intestinalis*) hatch by licking and travel to the mouth and into the intestines. The larvae affect the animal by interfering with feeding, causing stomach lesions that can become a site of secondary infection and by causing restlessness when the larvae are in the rectum before passage. Horses with large numbers of bots become run down and unthrifty.
	Cochliomyia hominivorax	Screw-worm fly	Cattle, sheep, and other livestock	Parasitic fly whose larvae (maggots) eat the living tissue. Fly lays eggs on wounded tissues (as a consequence of barbed wire cuts, flea bites, branding, castrating, dehorning, or tailing of the host animal) and after hatching, larvae will burrow deeper perpendicular to the skin surface eating into live flesh
	Cuccoides spp. and *Leptoconops* spp.	Sand flies, biting midges, noseeums, and punkies	Cattle, sheep, and deer	Annoyance and blood loss. They could also induce suffocation, if present in large numbers

(*Continued*)

Table 2 Continued

Parasite	*Species*	*Common name*	*Host*	*Consequences*
	Hippobosca spp.	Forest fly,	Sheep, goats, red deer, camels, and rabbits	Annoyance and blood loss
Ticks	*Ornithodoros* spp. and *Otobius* spp.	Soft tick	Swine, cattle, sheep, antelope, deer, camels, and poultry birds	Annoyance and blood loss
	Hyalomma spp., *Ixodes* spp., *Dermacentor* spp., *Amblyomma* spp., *Boophilus* spp., and *Rhipicephalus* spp.	Hard tick	Cattle, sheep, deer, and goat	Even in general not painful, hard tick bites could cause inflammation at the wound, followed by acquired immune reactions in the skin. Biting stress could cause lameness, anorexia (loss of appetite), blood loss, and reduced weight gain and milk production. Damage to the skin and hide due to the scar may remains for years reducing the value of the leather. Some species may also induce some toxic effects on the host (such as eczema, alopecia, fever, or paralysis)
Lice	*Damalinia* spp.	Cattle biting louse	Cattle, sheep, goats, and horses	Annoyance, interfering with normal animal behavior and decreasing weight gain and milk. Large numbers cause intense pruritis and irritation and chronic dermatitis due to scratching, rubbing, and biting of infested areas
	Haematopinus spp., *Linognathus* spp., and *Solenopotes* spp.	Sucking louse, cattle tail louse, long-nosed cattle louse, and little blue cattle louse	Cattle, sheep, goats, horses, and donkeys	Annoyance and blood loss. They can interfering with normal animal behavior, decreasing weight gain and milk production. Large numbers cause severe dermatitis and secondary infections. Animals may die, and pregnant cows may abort
	Bovicola spp.	Goat biting louse and angora goat biting louse	Sheep and goats	Annoyance and blood loss. They can interfere with normal animal behavior, decreasing weight gain and milk production. Large numbers cause severe dermatitis and secondary infections
Mites	*Sarcoptes* spp., *Psoroptes* spp., *Psorobia* spp., *Demodex* spp., and *Dermanyssus* spp.,	Scarbies mite, sheep itch mite, cattle follicle mites, goat follocle mite, chicken mite, chorioptic scab mite, and psoroptic ear mite	Cattle, sheep, goat, and poultry	Annoyance, skin/hide/wool damage, anemia, mal nutrition and death. They can interfere with normal animal behavior. Large numbers cause severe dermatitis and secondary infections and also decrease production

'Parasitism' in general refers to flies laying eggs in open wounds or where larvae invade unbroken skin or enter the body through the nose or ears. They could be divided into two categories: myiasis and pseudomyiasis. Myiasis is caused by flies that need a host for larval development or by flies' larvae that can develop in a host if open wounds or sores are present. Pseudomyiasis is referred to as the accidental deposit of eggs on oral or genitourinary openings caused by flies that have no preference or need to develop in a host. The impact of myiasis could be devastating. In 1989, more than 2.7 million animals distributed in 25 000 km^2 between the Mediterranean Sea and the Sahara Desert were infested in a single outbreak episode.

Indirect Consequence of Ectoparasites: Vector Transmission of Zoonotic Diseases

Among the wide variety of ectoparasites that could affect livestock, flies, and ticks are by far recognized as the major pests due to their competence as vector of several zoonotic diseases whose etiological agents may be protozoal, bacterial, or viral (Table 3). Unfortunately, from the increasing number of pathogenic vectorborne agents that can affect livestock throughout the world, relatively few are recognized as being of economic significance.

The following is a brief summary of the major vectorborne diseases in livestock worldwide.

Heartwater (Cowdriosis)

Heartwater is a septicemic, infectious tick-transmitted disease of cattle, sheep, goats, and other ruminants caused by *Ehrlichia ruminanti*um (Health, 2012). All domestic and wild subclinical-infected ruminants, including cattle, buffalo (*Syncerus caffer*), black wildebeest or white-tailed gnu (*Connochaetes gnou*), oryx (*Taurotragus oryx oryx*), giraffe (*Giraffe camelopardalis*), sable antelope (*Hippotragus niger*), Rusa deer (*Rusa*

Table 3 Major parasites groups as vectors of diseases: Vector species names, host, diseases, etiological agent, and occurrence. Information about the potential zoonotic transmission to humans is indicated

Vector	*Species*	*Host*	*Diseases*	*Etiological agent*	*Occurrence*	*Human*
Soft ticks	*Otobius* spp.	Cattle, sheep, goats, and rabbits	Q-fever	Coxiella burnetii	Worldwide	Yes
	Otobius spp.	Horses, cattle, sheep, goats, and rabbits	Tularemia	Francisella tularensis	Worldwide	Yes
	Ornithodoros porcinus	Domestic pig (*Sus domestica*), Warthog (*Phacochoerus aethiopicus*), wild boar (*Sus scrofa*), bush pig (*Potamochoerus* sp.), forest pig (*Hylochoerus meinertzhagen*)	African Swine fever	African Swine fever virus (*Asfarvirus* sp.)	Worldwide	
Hard ticks	*Rhipicephalus* spp., and *Ixodes* spp.	Cattle, water buffalo (*Bubalus bubalis*), African bufalo (*Syncerus caffer*), deer (*odocoeleus virginianus*), and reideer (*Rangifer tarandus*)	Bovine babesiosis (redwater)	*Babesia bovis*, *B. bigemina*, *B. divergens*	Worldwide	
	Dermacentor spp., *Hyalomma* spp., and *Rhipicephalus* spp.	Horses, mules, donkeys, and zebras	Equine babesiosis (piroplasmosis)	*Theileria equi* and *Babesia caballi*	Worldwide	
	Amblyomma spp.	*Bovidae* and *Cervidae* spp.: cattle, sheep, goats, deer, camelids, antelopes, giraffe, and wild ruminants	Heartwater	*Ehrlichia ruminantium*	Worldwide	
	Rhipicephalus spp., and *Hyalomma* spp.	Bovidae and Cervidae species: cattle, sheep, goats, deer, camelids, antelopes, giraffe, and wild ruminants	Theileriosis, East Coast Fever, Mediterranean theileriosis	*Theileria parva*, *Theileria annulate*	Worldwide, Africa, Mediterranean basin to China	
	Rhipicephalus spp., *A. variegatum*, and *Haemaphysalis* spp.	Sheep, goats	Nairobi sheep disease, Crimean Congo hemorrhagic fever	Nairobi sheep disease virus (NSD), Ganjam virus, Hazara virus	Africa and India	Yes
	Boophilus spp., *Dermacentor* spp., *Rhipicephalus* spp., *Ixodes* spp., *Hyalomma* spp., and *Ornithodoros* spp.	Cattle, sheep, deer, and goats	Bovine *Anaplasmosis* (gall sickness)	*Anaplasma marginale*, *A. centrale*, *A. ovis*, *A. bovis*, *A. caudatum*, *A phagocytophilum*	Tropical and subtropical regions	Yes
Mosquitoes, biting midges	*Aedes* spp., *Anopheles* spp., *Culex* spp., *Deinocerites* spp., *Mansonia* spp., *Psorophora* spp., *Coquiletidia* spp., *Ochlerotatus* spp., and *Simulium* spp.	Horses, donkeys, and zebras	Easter Equine Encephalitis (EEE), Venzuelan Equine encephalitis (VEE), Western Equine Encephalitis (WEE), West Nile Virus (WNV), Japanese Ecephalitis (JE)	Arbovirus (VEE, EEE, WEE, JE), Flavivirus (WNV)	North, Central and South America and the Caribbean (VEE and EEE) or USA (WEE), worldwide (WNV), and Japan (JE)	Yes

(*Continued*)

Table 3 Continued

Vector	*Species*	*Host*	*Diseases*	*Etiological agent*	*Occurrence*	*Human*
	Culicoides spp.	Cattle, sheep, goats, deer, camelids, antelopes, equines, and wild ruminants	Bluetongue, bovine ephemeral fever (Three Day Sickness), african horse sickness	*Orbivirus* spp., Ephemerovirus virus, Schmallenberg virus	Worldwide, Europe	
	Culex spp.	Sheep and goats	Nairobi sheep disease, Crimean Congo hemorrhagic fever	Nairobi sheep disease virus (NSD), Ganjam virus, Hazara virus	Africa and India	Yes
	Aedes spp., *Culex pipiens*, *Anopheles* spp.	Bovidae and *Cervidae* spp.: cattle, sheep, goats, deer, camelids, antelopes, wild ruminants	Rift Valley Fever	*Phlebovirus* spp.	Africa	Yes
	Aedes spp., and *Culex* spp.	cattle, sheep, goats, camelids, giraffe, antelope	Lumpy skin disease, sheep pox, goat pox	*Capripoxvirus* spp.	Africa, Middle east	
	Aedes spp.	cattle, sheep, goats, deer, camelids, horses, donkeys, swine	Vesicular stomatitis	*Vesiculovirus* spp.	Americas, Europe, and Africa	Yes
Biting flies	*Tabanus* spp., *Musca* spp., *Lyperosia* spp., and *Atylotus* spp.	Bovidae and Cervidae spp.: cattle, sheep, goats, deer, camelids, antelopes, wild ruminants	*Trypanosomiasis* (surra, nagana, Peste-boba, Tahaga)	*Trypanosoma evansi*, T. equinum, T. brucei, T. *vivax*, T. *congolense*	Worldwide	Yes
	Melophagus ovinus	Sheep	Bluetongue	*Orbivirus* spp., Ephemerovirus virus		
	Stomoxys calcitrans and *Biomyia mirificens*	Cattle, sheep, goats, camelids, giraffe, antelope	Lumpy skin disease, sheep pox, and goat pox	*Capripoxvirus* spp.	Africa, Middle east	
	Phlebotomus spp., and *Lutzomyia* spp.	Cattle, sheep, goats, deer, camelids, horses, donkeys, and swine	Vesicular stomatitis	*Vesiculovirus* spp.	Americas, Europe, and Africa	Yes

unicolor), white-tailed deer (*Odocoileus virginianus*), sitatunga (*Tragelaphus spekii*), steenbok (*Raphicerus campestris*), and lechwe (*Kobus leche kafuensis*), can serve as reservoir of the parasite.

Heartwater is transmitted by ticks of the genus *Amblyomma*. There are 13 species that can transmit the disease: *Amblyomma variegatum*, the tropical bont tick, is the most important vector due to its worldwide distribution. Other species are *Amblyomma hebraeum*, *Amblyomma gemma*, *Amblyomma lepidum*, *Amblyomma astrion*, *Amblyomma pomposum*, *Amblyomma cohaerans*, *Amblyomma marmoreum*, *Amblyomma sparsum*, *Amblyomma tholloni* (mainly distributed in southern, eastern and western African countries) and *Amblyomma maculatum* (the Gulf Coast tick), *Amblyomma cajennense* (the Cayenne tick), and *Amblyomma dissimile* (North America and the Caribbean).

The clinical pathologies associated with heartwater involve fever, anorexia, dyspnea, diarrhea, accumulation of reddish fluid in the pericardium (hydropericardium and hydrotorax), mediastinal and pulmonary edema, and submucosal and subserosal hemorrhages. In addition, tremors of superficial muscles and aggressive or anxious behavior may be present (OIE, World Organization for Animal Health, 2012; Health, 2012).

- No commercial vaccines are available at present. Attenuated bacterial strains used as vaccines (such as Gardel, Senegal, or Welgevonden strains) confer protection against homologous lethal challenges, but they induce limited or nonprotection against heterologous strain challenges. Inactivated vaccines using the Gardel or Mbizi strain or recombinant DNA vaccines do not prevent infection but rather confer some protection and reduction of death on animals exposed to a wide variety of live strains.
- As for many tick-transmitted infectious diseases, the most effective prophylaxis is the eradication or control (repellents and acaricides) of the tick vector.

African Swine Fever

African swine fever (ASF) is an enzootic tick-transmitted disease in domestic pigs (*Sus domestica*), European wild boar, and American wild pigs. The disease is caused by the ASF virus (ASFV), a DNA virus in the genus *Asfivirus* (Asfarviridae family) (Health, 2012). The natural reservoir of the virus are wild hogs, warthogs (*Phacochoerus aethiopicus*), bush pigs (*Potamochoerus* sp.), or the giant forest hogs (*Hylochoerus meinertzhageni*). Nevertheless, infected survivors, such as domestic swine, are virus carriers for life. The disease is transmitted by ticks of the genus *Ornithodoros*, but it can also be transmitted directly by contact between sick and healthy animals, by fomites (infected premises, vehicles, implements, and clothes), or by feeding on garbage, blood, tissues, secretions, or excretions of infected sick and dead animals (ASFV can remain infectious for 6 months in uncooked pork products).

The ASFV is endemic to the sub-Saharan Africa, including Madagascar. In Europe, it has been eradicated from Spain and Portugal, but it is present in Italy (Sardinia), Georgia, Azerbaijan, Armenia, and Russia. The ASFV was also reported in the Caribbean (Haiti and the Dominican Republic) and South America (Brazil), even though it was successfully eradicated.

The pathologies associated with the disease depend on the form (virulence) of the virus.

'Acute form' (highly virulent virus): fever, anorexia, diarrhea, vomiting, leucopoenia, thrombocytopenia, and abortion are common (OIE, World Organization for Animal Health, 2012). Reddening of the skin, especially in the tips of the ears, chest, abdomen, tail, and distal extremities may occur. Mortality rate in domestic swine may reach 100%. 'Subacute form and Chronic form' (moderately virulent virus): fever, light anorexia with weight loss, and abortion are common. Pericarditis, swellings over joints, and chronic skin lesions (ulcer and necrosis) have also been reported. The mortality rate in domestic swine is low and may vary between 30 and 70% (Health, 2012).

- As there is no vaccine or treatment for the disease, rapid slaughtering of all infected animals and proper disposal of cadavers and litter, as well as thorough cleaning, disinfection, and sterilization of garbage, are essential. Strict import or animal movement policy for animals and animal products from endemic or infected areas should be enforced.

Anaplasmosis

Anaplasmosis in ruminants (also known as bovine anaplasmosis and Gall sickness) is an infectious hemotropic disease of ruminants caused by several species of bacteria of the genus *Anaplasma*: *Anaplasma marginale*, *Anaplasma centrale*, *Anaplasma ovis*, *Anaplasma bovis*, *Anaplasma caudatum*, and *Anaplasma phagocytophilum* (Health, 2012). Cattle, sheep, or goats that have recovered from the clinical disease or other species of ruminants, such as water buffalo (*Bubalus bubalis*), white-tailed deer, mule deer (*Odocoileus hemionus hemionus*), black-tailed deer (*Odocoileus hemionus columbianus*), pronghorn (*Antilocapra americana americana*), Rocky Mountain Elk (*Cervus elaphus nelsoni*), bighorn sheep (*Ovis canadensis canadensis*), black wildebeest (*Connochaetes gnu*), blesbuck (*Damaliscus albifrons*), and duiker (*Sylvicapra grimmi grimmi*), can serve as reservoir. These pathogens are transmitted by several hard tick species of the genera *Boophilus* spp., *Dermacentor* spp., *Rhipicephalus* spp., *Ixodes* spp., *Hyalomma* spp., and *Ornithodoros* spp. In addition, athropods such as horse flies (*Tabanus* spp.) and mosquitoes (*Psorophora* spp.) (Blouin *et al.*, 2000; Kocan *et al.*, 2000, 2001, 2002, 2003, 2004a,b; de la Fuente *et al.*, 2002; Kocan and de la Fuente, 2003; De La Fuente *et al.*, 2004; de la Fuente *et al.*, 2005) and fomites (such as needles and surgical instruments that were in direct contact with blood-infected materials) could also be responsible for the transmission. Anaplasmosis is present in most tropical, subtropical, and in some temperate areas, which account for its worldwide distribution.

Anaplasmosis in characterized in the acute form by fever, anemia, weakness, anorexia, constipation, yellowing of the mucous membranes, dehydration, dyspnea, reduced or poor performance and milk production, and weight loss. Mortality could be as high as 70% (OIE, World Organization for Animal Health, 2012; Health, 2012).

- Several anaplasmosis immunization methods, using killed vaccine, attenuated live vaccine, or live *A. centrale* vaccine, have been used to protect cattle against anaplasmosis in countries where the disease is endemic with varying results (McHardy and Simpson, 1973; McHardy, 1974; McHardy *et al.*, 1980; Kocan *et al.*, 2001).
- Treatment of anaplasmosis depends on early diagnosis and prompt administration of an appropriate drug.
- As for many tick-transmitted infectious diseases, the most effective prophylaxis is the eradication or control (repellents and acaricides) of the tick vector.

Bluetongue

Bluetongue is a viral disease in sheep and cattle caused by several species of the genus *Orbivirus* (Health, 2012). There are 24 recognized serotypes of the bluetongue virus (BTV). The virus affects a wide range of ruminants, such as sheep, goats, cattle, buffaloes, white-tailed deer, pronghorn (*Antilocapra americana*), bighorn sheep (*Ovis canadensis*), African antelope, and other Artiodactyla species such as camels. Ruminants seem not to be the natural reservoir for the virus, because it does not establish persistent infections. The survival of the agent in the environment may be associated with insect or potentially with an unknown reservoir. The virus is transmitted among sheep and cattle by biting midges of the genus *Culicoides* and perhaps the wingless biting fly *Melophagus ovinus* (among sheep). Transmission occurs when midges feed on viremic animals and then on healthy individuals. Bluetongue is not a contagious disease; however, the virus can be spread mechanically on surgical equipment and needles. The distribution and prevalence of the disease is mostly associated with environmental factors (i.e., high rainfall, temperature, and humidity) and has a seasonal occurrence. The BTV has been found in many parts of the world, including Africa, Europe, the Middle East, Australia, the South Pacific, North and South America, and parts of Asia (Holbrook *et al.*, 1985; Osburn *et al.*, 1985; Parsonson *et al.*, 1985; OIE, World Organization for Animal Health, 2012).

The pathological signs and the severity of the infection varies widely, from asymptomatic to fatal, depending on factors related to agent, host, and environment. Some common lesions associated with the disease may include fever, congestion, edema, hemorrhages, and ulcerations of digestive and respiratory mucosae. Mucopurulent nasal discharges, excessive salivation, depression, dyspnea, and hyperemic of the muzzle, tongue, lips, face, eyelids, and ears are also common in susceptible animals. The tongue may become edematous and cyanotic protruding from the mouth. This symptomatology is what the disease is named after. In addition, hypertrophy of lymph nodes and splenomegaly have also been commonly reported. Morbidity in sheep can reach 100% with mortality between 30% and 70% in more susceptible breeds. In wild ruminants, especially white-tailed deer and pronghorn antelope, morbidity rate could reach 100%, with a mortality rate that can reach 90% (Health, 2012). It is estimated that the annual losses due to morbidity and mortality of animals, trade embargoes, and vaccination costs worldwide may be as high as US$3 billion (Anderson *et al.*, 1985; Holbrook *et al.*, 1985; Osburn *et al.*, 1985; Parsonson *et al.*, 1985; Osburn, 1994; Ward *et al.*, 1994; Osburn *et al.*, 1996; MacLachlan and Osburn, 2006). The estimated cost in the US cattle and sheep industry due to the loss of trade and the cost associated with diagnostic testing reaches US$125 million annually.

- Live attenuated and inactivated virus vaccines are available; however, they showed to be serotype specific. Nevertheless, attenuated or live vaccines should be used cautiously because the viruses in attenuated vaccines can be transmitted to unvaccinated animals and could reassort with field strains, resulting in new viral strains. In addition, vaccines can cause fetal malformations in pregnant ewes.
- As for most arboviral infections, the most effective control is to limit the spread or the occurrence of the disease by quarantine or limit the movement (housing) of animals; preventive vector control with insecticides such as synthetic pyrethroids or organophosphates is recommended.
- No treatment is available for infected animals.

Bovine Babesiosis

Babesiosis, or tick fever, is a febrile tick-transmitted disease of domestic and wild animals caused by several species of the genus *Babesia* (*Babesia bovis*, *Babesia bigemina*, *Babesia divergens*, *Babesia major*, *Babesia ovata*, *Babesia occultans*, and *Babesia jakimovi*), a protozoan parasite distributed worldwide (Barnett, 1974; Health, 2012). The natural reservoirs of the protozoan are subclinical infected ruminants, such as cattle, buffalo (*Bufalus bubalis* and *Syncerus caffer*), reindeer (*Rangifer tarandus*), and white-tailed deer. The protozoan does not survive outside of its hosts and is transmitted mainly by two genera of hard tick: *Rhipicephalus* spp. (*Rhipicephalus microplus*, *Rhipicephalus annulatus*, *Rhipicephalus decoloratus*, *Rhipicephalus geigyi*, and *Rhipicephalus evertsi*), which are vectors of *B. bovis* and *B. bigemina*; and *Ixodes ricinus*, which is vector of *B. divergens*.

Bovine babesiosis is found in areas where its arthropod vector is distributed, especially tropical and subtropical regions, including Africa, Asia, Australia, the Caribbean, and Central and South America (Montenegro-James, 1992; OIE, World Organization for Animal Health, 2012).

The pathologies associated with the disease depend on the parasite species and the age and immune status of the host. In general terms, clinical sings involve fever, anorexia, hemolytic anemia, hemoglobinuria, hepatosplenomegaly (enlarged spleen and liver), and production of dark red- or brown-colored urine. Ataxia, incoordination, and signs of general circulatory shock are common in *B. Bovis*-infected animals, where parasitemia generally does not exceed 1%. Hemoglobinuria and anemia are typical clinical signs of *B. Bigemina*- and *B. divergens*-infected animals, with reports of parasitemia levels of up to 30% (Health, 2012).

- Although vaccination is available through live vaccine (*B. bovis* and *B. bigemina*), the most effective prophylaxis is the eradication or control (repellents and acaricides) of the tick vector.

Theileriosis (East Coast Fever) and Tropical Theileriosis

East Coast fever and tropical theileriosis are tick-transmitted diseases caused by the protozoan parasites of the genus *Theileria* (OIE, World Organization for Animal Health, 2012; Health, 2012). Several ruminant species, including cattle, African buffalo (*Syncerus caffer*), Indian water buffalo (*B. bubalis*), and waterbuck (*Kobus* spp.), can be infected and can serve as reservoir, even though ticks can remain infected on the pasture for up to 2 years depending on the climatic conditions. The hard ticks of the genus *Rhipicephalus* are main vector for *Theileria*. There are six identified *Theileria* spp. that infect cattle. *Theileria parva* and *T.* mutants, the most important etiological agents of the East Coast fever, can be transmitted by *R. appendiculatus*, *Rhipicephalus zambeziensis*, and *Rhipicephalus duttoni*. East Coast fever is enzootic in East Africa and has been reported in Tanzania, Kenya, Uganda, Mozambique, South Africa, Rhodesia, Zaire, Rwanda, Burundi, Malawi, the Sudan, and most likely Ethiopia, Zambia, and Southern Somalia. *Theileria annulata*, the etiological agent of the tropical theileriosis, is transmitted by ticks of the genus *Hyalomma* and has a broader geographical distribution, including the Mediterranean Basin, North Africa, southern republics of the former USSR, the Middle East, and Asia. Other pathogenic *Theileria* species, such as *Theileria lestoquardi* (*Theileria hirci*), infect small ruminants in the Mediterranean Basin (Southern Europe and North Africa) as well as Asia (Barnett and Brocklesby, 1971; Brocklesby and Barnett, 1972; Morzaria *et al.*, 1974).

The most common pathological signs are in general nonspecific and mimic many other diseases. Clinical signs include fever, anorexia, lacrimation, corneal opacity, nasal discharge, terminal dyspnea, diarrhea, emaciation, dehydration, reduced or poor performance, and weight loss. In susceptible animals mortality could reach 100% (Health, 2012).

'The East Coast fever' is characterized by a generalized lymphadenopathy due to lymphocyte infection. Hyperplastic, hemorrhagic, edematous, and necrotic lymph nodes have been observed in acute cases of the infection. In addition, interlobular emphysema and severe pulmonary edema have also been reported. Lymphoid cellular infiltrations appear in the liver and kidney and hemorrhages and ulceration may be seen throughout the gastrointestinal tract.

'The tropical theileriosis' is characterized by macrophage infection that causes the release of cytokines (TNFα), anemia, and the presence of macroschizonts in infected macrophage-type cells.

- Immunization using live attenuated species (*T. parva* and *T. annulata*) or recombinant DNA vaccines seems to be reliable and robust against homologous challenges (Cunningham *et al.*, 1989).
- Treatment against *T. parva* and *T. annulata* can be done using chemotherapeutic agents, such as buparvaquone. Nevertheless, treatments with these agents do not completely eradicate infections. In those cases, animals become carrier. Interestingly, animals treated for *T. annulata* (but not for *T. parva*) develop complete cross-protection against most *Theileria* strains.
- As for many tick-transmitted infectious diseases, the most effective prophylaxis is the eradication or control (repellents and acaricides) of the tick vector (Minjauw *et al.*, 1998).

Trypanosomiasis

Trypanosomiasis, also known as surra, nagana, Peste-boba, Tahaga, Kaodzera, Baleri, Gambian horse sickness, Cachexial fevers, Dourine, mal de las caderas, etc., is a disease in cattle, buffaloes, sheep, goats, deer, camelids, antelopes, lamas, donkeys, horses, mules, deer, llamas, pigs, and elephants caused by a several flagellated protozoan species of the genus *Trypanosoma*: *Trypanosoma evansi*, *Trypanosoma equinum*, *Trypanosoma brucei*, *Trypanosoma vivax*, and *Trypanosoma congolense* (FAO–WHO, 1969; Takken *et al.*, 1988; Dargie *et al.*, 1993; Cecchi *et al.*, 2009; Ilemobade, 2009; Health, 2012). It is transmitted from animal to animal mechanically by hematophagous flies, including *Tabanus* spp., *Musca* spp., *Lyperosia* spp., *Stomoxys*, and *Atylotus* genera. In addition, hemophagous bats in South and Central America can serve as hosts, reservoirs, and vectors of *T. evansi* by transmitting the protozoan mechanically from animal to animal with their saliva or through biting flies (*Tabanus* spp., *Musca* spp., *Lyperosia* spp., and *Atylotus* spp.). Species such as *T. congolense*, *T. vivax*, *T. brucei*, *Trypanosoma Uniforme*, and *Trypanosoma simiae* are known as tsetse-transmitted trypanosomiasis where more than 23 species of Tsetse fly (*Glossina* spp.) act as biological vector. The tsetse-transmitted trypanosomiasis is the most economically important livestock disease in Africa, especially in cattle, affecting more than 37 countries with an estimated annual overall loss of US$6 billion year^{-1} (FAO–WHO, 1969; Dargie *et al.*, 1993; Hendrickx *et al.*, 1999; Cecchi *et al.*, 2008; Cecchi *et al.*, 2009).

The disease in characterized by the presence of a nonregenerative anemia, intermittent fever, edema, lacrimation, and enlarged lymph nodes, liver, and spleen. Infected animals also show decreased fertility, loss of appetite, affected body condition and productivity, emaciation, and early death (OIE, World Organization for Animal Health, 2012; Health, 2012).

- There is no vaccine available for trypanosomiasis.
- Treatment against trypanosomiasis may include diminazene aceturate and quinapyramine methylsulfate. Other drugs such as isometamidium chloride and quinapyramine sulfate and chloride can be used as prophylactic during transhumance or high seasonal parasitic pressure.
- For many tick-transmitted infectious diseases, the most effective prophylaxis is the eradication or control (repellents and acaricides) of the tick vector.

Eastern Equine Encephalitis, Venzuelan Equine Encephalitis, Western Equine Encephalitis, Japanese Encephalitis, and West Nile

Eastern, Western, and Venezuelan equine encephalomyelitis and the West Nile are mosquito-borne infections caused by several viral species and viral subtypes of the genera Alphavirus

(McConnell, 1972; Bigler and McLean, 1973; Gibbs, 1976; de Bellard *et al.*, 1989; Tsai, 1991; MacKay *et al.*, 2000; Castillo-Olivares and Wood, 2004; Anishchenko *et al.*, 2006; Davis *et al.*, 2008; Gibney *et al.*, 2011; Health, 2012). A common factor for all of them is that viruses normally cycle in bird populations and are transmitted mainly by mosquitoes. The Eastern equine encephalitis virus (EEEV) may also be able to persist in a wide range of animals, including mammals, birds, reptiles, and amphibians. The Venezuelan equine encephalitis virus (VEEV) seems also to be maintained in the sylvatic rodents or marsupials population (OIE, World Organization for Animal Health, 2012).

Eastern Equine Encephalomyelitis Virus

There are two variants for the EEEV, the North America and the Caribbean variant (more pathogenic) and the South and Central America variant (less pathogenic). The enzootic cycle of the infection is maintained most predominantly by mosquitoes of the genera *Culiseta*, a mosquito that primarily feeds on birds. Bridge vectors for EEEV include several species of mosquitoes of the genera *Coquilletidia*, *Aedes*, *Ochlerotatus*, and *Culex*. Mammals, including horses, humans, cattle, and small rodents, are considered to be incidental (dead end) hosts.

The maintenance and transmission of the virus inside the bird population (flock) can also occur by means of other vectors, such as in chicken lice, chicken mites (*Dermanyssidae*), and assassin bugs, or by direct transmission through feather picking and cannibalism.

Western Equine Encephalomyelitis Viruses

The Western equine encephalomyelitis virus (WEEV) is closely related to some other alphaviruses, including Sindbis, Ft. Morgan Aura virus, and the Highlands J viruses. WEEV has been isolated from Argentina to Western USA and Canada. The enzootic cycle of the infection with WEEV in maintained most predominantly by mosquitoes of the genera *Culex* and *Aedes*, which primarily cycles the virus between passerine birds and a variety of mammals, such as black-tailed jackrabbits (*Lepus califomicus*) acting as potential incidental hosts, or reptiles, such as snakes, frogs, and tortoises, which may serve as reservoir.

Venezuelan Equine Encephalomyelitis Viruses

The Venezuelan equine encephalomyelitis complex contains at least six viral subtypes. The VEE complex viruses (VEEV) are divided into epizootic (or epidemic) and enzootic (or endemic) groups. The epizootic viruses, which could be transmitted by several mosquito genera including *Aedes*, *Anopheles*, *Culex*, *Mansonia*, *Psorophora*, and possibly *Ochlerotatus*, are amplified in equines (horses, donkeys, and zebras) that serve as primary source of the virus during an outbreak. The epizootic group has been isolated in South and Central America.

The enzootic (sylvatic) subtypes are generally found in limited geographic areas, where they usually occur in natural cycles between rodents and mosquitoes. The enzootic subtypes, transmitted mainly by species of the *Culex* genera, are not amplified in equines and they are considered less pathogenic. The viruses of these subtypes have been isolated in South, Central, and North America.

In addition to mosquitoes, other vectors such as Black flies and mites can also mechanically transmit the epizootic viruses, meanwhile ticks of the genera *Amblyomma* and *Hyalomma* can be infected by both enzootic and epizootic VEEV strains.

West Nile Encephalomyelitis Virus

Mosquitoes of the genera *Culex*, *Aedes*, and *Anopheles* are the main vectors for the transmission of the West Nile encephalitis virus (WNEV) from wild birds. Humans and other small mammals (such as dogs) may harbor WNEV after being bitten; however, they are inefficient transmitters because viral titers are relatively low, and WNE viremia is in general short lived. The WNEV is endemic in Eastern Europe, the Middle East, Africa, and Asia, but it has been spreading to North America as recently as in 1999.

Clinical presentation of the infection involves lymphopenia, leukopenia, and fever as a result of the viral replication in macrophages and neutrophils. As the viral replication occurs in other tissues, such as in ancreas, adrenal cortex, heart, liver, and vasculature walls, variable degree of lesions, ranging from no lesion to extensive necrosis with hemorrhages, could be observed. As the infection progresses toward the central nervous system, neurological signs, such as sensitivity to sound, anxiety, periods of excitement, and restlessness, occur. Drowsiness, drooping ears, circling, aimless wandering, head pressing, inability to swallow, abnormal gait, and paralysis and death may follow as brain lesions appears. Mortality rates among horses could range from 70% to 90% (Health, 2012).

- Attenuated and inactivated virus vaccines are available for a number of combinations of viruses (EEEV/VEEV, EEEV/WEEV/VEEV, EEEV/WEEV/VEEV/tetanus toxoid, and EEEV/WEEV/VEEV/WNEV/tetanus toxoid.
- There is no cure for any of these viral diseases, but supportive measures (treating symptoms) are present. They may include antiinflammatory treatment (corticosteroids), anticonvulsants, intravenous fluids, tracheal intubation, and antipyretics.
- As for most arboviral infections, the most effective control to limit the spread or the occurrence of the disease is quarantine or limit the movement (housing) of the primary amplifiers (equids), preventive vaccination of animals, or the use of repellents or fans to limit the presence of mosquitoes.

Final Remarks

Ectoparasites and vectorborne pathogens will continue to present significant threats to human and animal health worldwide. On a global basis and especially in poor or developing countries, where they are the major economical impediments to efficient parasite control and efficient livestock production, the economic toll caused by ectoparasites and vectorborne diseases is staggering. The outbreaks of endemic disease, the threats of exotic disease introduction, and fears of

potential changes in arthropod distribution associated with climate change and animals movement have been the main reasons for changes in the nature of animal husbandry and parasite control. The livestock industry loses millions of dollars annually due to just external parasites control and prevention alone. Unfortunately, providing affordable and accessible parasite control and animal healthcare to producers in developing countries or poor livestock keepers worldwide remains a challenge.

A better understanding of the current distribution, prevalence, and control of ectoparasites coupled with a better domestic and international capability to detect, identify, and report vectorborne diseases would contribute substantially to improved meat and milk production worldwide.

See also: Climate Change and Plant Disease. Climate Change: Animal Systems. Food Safety: Emerging Pathogens

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Animal Health: Foot-and-Mouth Disease

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Glossary

Antivirals/biotherapeutics Class of medication to treat or prevent viral infections.
Immunity (adaptive) The mechanism of defense against pathogens found in vertebrates that is acquired after exposure to pathogens creating immune memory. Adaptive immunity is triggered by vaccines and foreign pathogens.
Immunity (innate) The mechanism of defense against pathogens present in plant and animal cells that functions in a nonspecific manner. This type of immunity is induced very rapidly after exposure to pathogens and before the adaptive immune response.
Interferons Proteins made and released by mammalian cells in response to the presence of pathogens including viruses, bacteria, parasites, or tumor cells. Interferons allow for communication between cells triggering protective defenses against pathogens or tumors.
Outbreak Occurrence of disease greater than expected in a particular time and place.
Surveillance Refers to an epidemiological practice by which the appearance and spread of disease is monitored in order to control it as fast as possible and to establish patterns of progression.
Transcription The first step in gene expression in which a particular segment of DNA is copied into RNA by the enzyme RNA polymerase.
Translation The process by which ribosomes decode messenger RNA (mRNA) into proteins.
Vaccines Biological preparation that confers immunity to a particular disease. A vaccine typically contains a weakened or killed form of the pathogen, or portions of the pathogen such as its surface proteins or toxins.
Virulence factors Molecules expressed and secreted by pathogens responsible for causing disease. Virulence factors allow the pathogen to colonize the host, evade immunity, and sometimes persist for long times.

Introduction

Foot-and-mouth disease (FMD) is one of the most contagious diseases of animals (Grubman and Baxt, 2004). The causative agent, FMD virus (FMDV), is the type species of the genus *Aphthovirus* within the *Picornaviridae* family (Grubman and Baxt, 2004). The virus is antigenically variable and consists of seven serotypes, A, O, C, Asia-1, South African Territories 1–3 (SAT1-3), and numerous subtypes and strains within each serotype.

More than 70 species of domestic and wild cloven-hoofed animals including cattle, swine, sheep, and goats are affected by FMD (Bachrach, 1968). The disease generally causes fever, lameness, and vesicular lesions on the tongue, snout, feet, and teats of susceptible animals often resulting in sloughing off of the epithelium and rupture of vesicles releasing copious amounts of virus (**Figure 1**). Disease signs can vary among species. In particular, sheep do not show overt signs of FMD (Alexandersen *et al.*, 2002d) and as a result an unnoticed infection of this species can spread an outbreak as rapidly as wild fire as it occurred in the United Kingdom in 2001 (Mahy, 2004).

FMD does not result in high mortality, except when young animals are infected. However, the disease can have significant debilitating effects including weight loss, reduced milk production, loss of draft power and mobility, resulting in a decline in productivity for a period of time. Infection of young animals can cause myocarditis and death as it occurred in the 1997 FMD outbreak in Taiwan, which caused an approximately 100% fatality rate in suckling pigs (Yang *et al.*, 1999).

Historically, FMD was probably first recognized in 1546 when the Franciscan monk, Hieronymus Fracastorius, described an outbreak in cattle in Italy that caused clinical signs similar to FMD (Fracastorius, 1546). Subsequently, in 1897 Loeffler and Frosch (1897) demonstrated for the first time that a filterable agent caused an animal disease, i.e., FMD. In the nineteenth and early twentieth centuries large numbers of FMD outbreaks occurred in many countries in Europe leading to the establishment of several institutes to study this disease. A vast amount of information has been obtained concerning FMD in more than 100 years since the seminal discovery by Loeffler and Frosch. As a result researchers have developed protocols and reagents to detect and control the disease and they continue to design novel approaches to improve disease control (see Section Disease Control Measures). However, despite this progress FMD continues to ravage many parts of the developing world, as well as causing frequent outbreaks in previously FMD-free countries. Moreover, after the 11 September 2001 attacks on the United States there is concern that FMD can be used as a weapon for bioterrorism.

FMD is currently present in many areas of the world including Africa, Asia, the Middle East, and a few countries in South America, whereas North America, Central America, Western Europe, Australia, and New Zealand are FMD free (**Figure 2**). The presence of the disease has a significant effect on the international trade of susceptible animals and their products. In particular the widespread presence of FMD in developing countries in Asia, Africa, and the Middle East has a substantial effect on the economies of many of these countries because a large proportion of their population lives in rural areas and depends on livestock for food and income (Cheneau *et al.*, 2003). Furthermore, the ability to block the spread of FMD to disease-free countries has become more difficult

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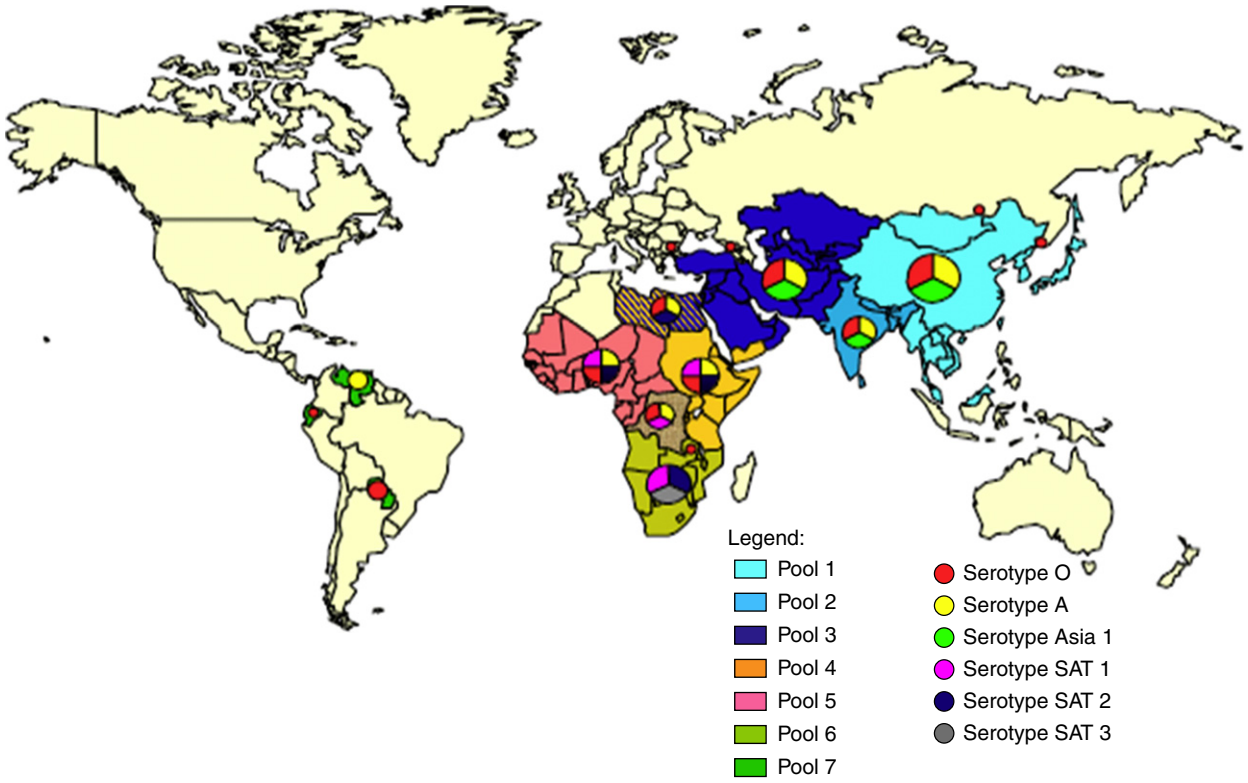


Figure 1 Countries affected by foot-and-mouth disease virus (FMDV). World map showing the different countries that reported an outbreak of FMDV between January 2010 and February 2013. Each color represents the different FMDV serotypes that affected the indicated region. Reproduced from Food and Agriculture Organization of the United Nations (FAO). European Commission for the control of FMD. Foot-and-Mouth Disease Situation. February 2013.

because of the globalization of trade and the rapid movement of goods and people worldwide. Thus, there are efforts led by the United Nations Food and Agriculture Organization (FAO) and the World Organization for Animal Health (OIE) to enhance veterinary service capabilities in developing countries so as to initiate disease surveillance programs and improve disease detection. In addition, there is also an urgent need to supply and deliver vaccines to these countries, which requires financial and human resources from developed countries and animal health organizations such as the FAO and the OIE.

In this article, the authors discuss many aspects of FMD including the molecular biology of the virus, disease pathogenesis, host immune response, disease outbreaks, and various approaches to disease control. The authors aim to make the reader aware of the severity of this disease and its impact on both animal and human health.

The Agent

Genome Organization

FMDV contains a positive-sense single-stranded ribonucleic acid (RNA) genome of approximately 8500 nucleotides (nt) covalently linked at the 5′ end to a virus-encoded protein (3B, also known as VPg) and packed into a nonenveloped icosahedral capsid. Figure 3 shows a schematic diagram of the FMDV genome displaying the predominant protein products that have been identified (Mason *et al.*, 2003). The FMDV genome displays a long open reading frame (ORF) flanked by highly conserved and structured untranslated regions (5′ and 3′ UTRs). The 5′ UTR of approximately 1300 bases contains five specific regions including the S fragment, poly(C) tract, pseudoknots (PKs), cre, and the internal ribosome entry site (IRES), which are required for efficient replication and translation (Grubman and Baxt, 2004; Mason *et al.*, 2003). Translation of the viral polyprotein begins after the IRES, at two alternative AUG codons and yields a large polyprotein of approximately 2300 amino acids that is co- and post-translationally processed by virus-encoded enzymatic activities into many precursor and mature products (Clarke and Sangar, 1988; Kirchweger *et al.*, 1994; Medina *et al.*, 1993; Ryan *et al.*, 1991; Vakharia *et al.*, 1987). Mature products include four structural (1A (VP4), 1B (VP2), 1C (VP3), and 1D (VP1)) and eight nonstructural (NS) proteins (L^{pro}, 2A, 2B, 2C, 3A, 3 copies of 3B (VPg), $3C^{pro}$, and $3D^{pol}$). The L protein is a cysteine protease (L^{pro}) that cleaves itself from the growing polypeptide chain and also cleaves many cellular factors playing a critical role in viral pathogenesis (Belsham *et al.*, 2000; Brown *et al.*, 1996; Falk *et al.*, 1990; Kirchweger *et al.*, 1994; Kleina and Grubman, 1992; Strebel and Beck, 1986). The P1 region encodes the four structural proteins, whereas P2 and P3 are precursors for the NS proteins that are mostly involved in viral RNA replication (Mason *et al.*, 2003). $3C^{pro}$ is the virus-encoded cysteine protease responsible for the majority of proteolytic cleavages in P1, P2, and P3 that result in



Figure 2 Common lesions of FMDV in cattle and swine. Vesicular lesions in the tongue and coronary bands of cattle (a and b) and pigs (c and d). (a) Ruptured vesicles on the tongue and along upper gum with sharp margins of lesions and red raw appearance of exposed dermis. (b) Foot of a steer with an unruptured vesicle in the heel-bulb. (c) Mouth of pig showing single, 1-day-old, unruptured vesicle at edge of tongue. (d) Swine feet with vesicles along the coronary bands of main and supernumerary digit with clear presence of sero-fibrinous in-filling.

mature viral products (Bablanian and Grubman, 1993; Vakharia *et al.*, 1987), and $3D^{pol}$ is the viral RNA-dependent RNA polymerase (RdRp).

Following the ORF there is a relatively short 3′ UTR of approximately 90 nt that folds into a specific stem-loop structure followed by a poly (A) tract of variable length. The 3′ UTR is also required for virus infectivity and replication (Pilipenko *et al.*, 1996; Saiz *et al.*, 2001; van Ooij *et al.*, 2006).

The three-dimensional structure of several FMDV serotypes has been determined by X-ray crystallography (Acharya *et al.*, 1989; Curry *et al.*, 1996; Fry *et al.*, 1999; Lea *et al.*, 1995; Lea *et al.*, 1994). The virus displays an icosahedral shape formed by 60 copies each of the four structural proteins. Although VP4 is buried on the inside of the particle, VP1 contains a prominent surface exposed loop, G–H loop, involved in the interaction between the virus and the integrin family of receptors in the host (O'Donnell *et al.*, 2005; Pierschbacher and Ruoslahti, 1984a,b). In comparison to other picornaviruses FMDV is quite unstable at a pH lower than 6.5 (Curry *et al.*, 1995; Ellard *et al.*, 1999), a feature that probably plays a role in targeting the virus to specific tissues and organs in susceptible hosts.

Virus Infectious Cycle

Several studies on the mechanism of FMDV entry have been reported (Grubman and Baxt (2004) and references therein). In tissue culture, FMDV can bind to four members of the αv subgroup of cellular integrins, $\alpha v\beta 1$, $\alpha v\beta 3$, $\alpha v\beta 6$, and $\alpha v\beta 8$, via the highly conserved RGD motif located on the G–H loop of VP1 (Monaghan *et al.*, 2005; O'Donnell *et al.*, 2009). However, the virus can utilize other membrane-bound molecules as receptors. Some FMDV field strains can be adapted to tissue culture by acquiring the ability to bind to cell surface heparan sulfate (HS) or other uncharacterized molecules (Baranowski *et al.*, 1998; Jackson *et al.*, 1996; Martinez *et al.*, 1997; Neff *et al.*, 1998; Sa-Carvalho *et al.*, 1997; Zhao *et al.*, 2003). *In-vivo* studies in cattle have shown that FMDV localizes only on epithelial cells of susceptible tissues that constitutively express

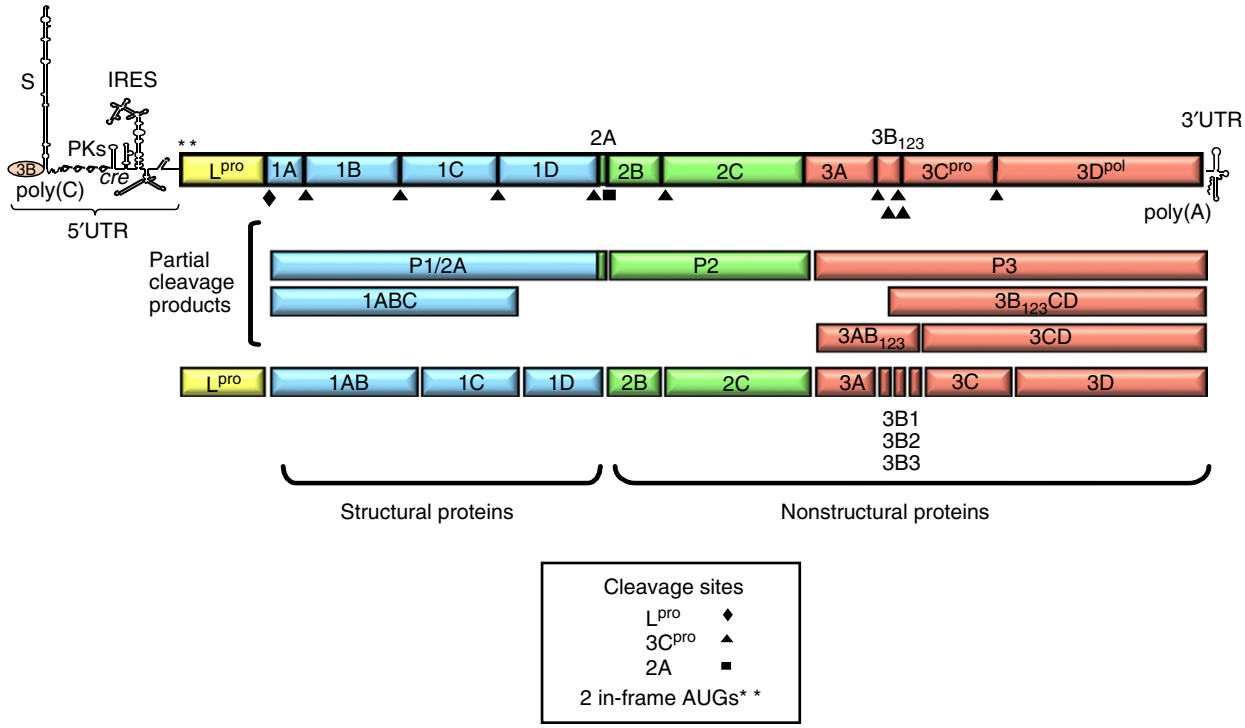


Figure 3 Genome organization of FMDV. RNA elements are shown at the 5′ and 3′ untranslated regions (UTR) and are represented as thin lines. The 5′ UTR consists of S fragment, poly (C) tract, pseudoknots (PKs), cis-acting replicative element (cre) and internal ribosome entry site (IRES). The ORF is depicted as outlined-open boxes. Filled triangles, squares, and diamonds indicate processing sites for $3C^{pro}$, 2A, and L^{pro}, respectively. Posttranslational proteolytic cleavages are shown as partial products as described in the text. Asterisks describe the two AUG initiation codons. The 3′ UTR consists of a short stretch of RNA and a poly (A) sequence. 3B (VPg) protein is shown as covalently linked to the 5′ end of the genomic RNA.

high levels of $\alpha v\beta 6$ integrin, suggesting that these molecules primarily mediate virus entry in the animal host (Brown *et al.*, 2006; Monaghan *et al.*, 2005; O'Donnell *et al.*, 2009).

With respect to the mechanism of virus entry, studies in cell culture expressing $\alpha v\beta 6$ integrins have demonstrated that FMDV serotypes A, O, and C use clathrin-dependent endocytosis (Berryman *et al.*, 2005; Martín-Acebes *et al.*, 2007; O'Donnell *et al.*, 2005). However, other mechanisms, such as caveola-mediated endocytosis, mediate internalization of FMDV through the HS receptor, indicating that the mechanism of entry depends on the specificity of receptor usage (O'Donnell *et al.*, 2008). Recently, it has been proposed that independently of the receptor utilized during cell entry, FMDV-induced autophagy facilitates infection (Berryman *et al.*, 2012).

On entry and uncoating of the viral RNA, the 5′ bound VPg protein is cleaved by a cellular enzymatic activity (Ambros and Baltimore, 1980; Ambros *et al.*, 1978; Gulevich *et al.*, 2002; Rozovics *et al.*, 2011) and translation begins at the IRES element (Belsham and Brangwyn, 1990; Kuhn *et al.*, 1990). IRES-dependent initiation of translation represents an alternative to the cap-dependent initiation mechanism that operates for most cellular messenger RNA (mRNAs) (Kozak, 1978). FMDV efficiently takes over the host translation apparatus by L^{pro}-dependent cleavage of the translation initiation factor eIF-4G (Devaney *et al.*, 1988; Kirchweger *et al.*, 1994). By 2–4 h postinfection cap-dependent cellular translation is basically shutoff and viral proteins are the major products detected in cell extracts.

As previously mentioned, the viral polyprotein is processed by three virus-encoded enzymatic activities including L^{pro}, 2A, and $3C^{pro}$ (Birtley *et al.*, 2005; Grubman and de los Santos, 2012a; Grubman *et al.*, 1995; Guarne *et al.*, 1998; Ryan *et al.*, 1991; Strebel and Beck, 1986). Following translation and polyprotein processing, the FMDV genome is replicated by the viral polymerase $3D^{pol}$ (Ferrer-Orta *et al.*, 2009; Ferrer-Orta *et al.*, 2006; Mason *et al.*, 2002; Nayak *et al.*, 2005; Pathak *et al.*, 2008; Paul *et al.*, 1998). RNA synthesis occurs within the cellular vesicles that derive from rearranged membranes of the endoplasmic reticulum and Golgi and contain most of the FMDV NS products and many associated host factors (Lawrence and Rieder, 2009; Martinez-Salas *et al.*, 2001; O'Donnell *et al.*, 2009; Pacheco *et al.*, 2009; Rozovics and Semler, 2010).

The final steps of the replication cycle involve encapsidation of the viral genomic RNA and maturation of the capsid. Only viral genomic RNA (plus strand) can be encapsidated and after encapsidation, the virion matures when the precursor VP0 is processed into VP2 and VP4 by an unknown mechanism (Curry *et al.*, 1995; Curry *et al.*, 1997; Knipe *et al.*, 1997; Nugent *et al.*, 1999).

Antigenic Variation

FMDV displays seven serotypes and multiple subtypes. New variants continuously arise due to the number of animal species that are susceptible to the virus, the different

environments the virus has adapted to, and the fact that viral replication relies on RdRps. RdRps are rapid and highly processive enzymes but display a fairly low fidelity resulting in high mutation rates (Ng *et al.*, 2008). This high error rate leads to significant differences of replicated genomes from the parental genome generating 'quasispecies' or 'cloud of mutants,' a phenomenon that has explained the evolution of replicating RNA molecules (Domingo *et al.*, 2002; Domingo *et al.*, 1980; Eigen, 1971). Most of the nucleotide changes in FMDV occur in the capsid-coding region and lead to antigenic variation. Some mutations may occur under immune pressure (Borrego *et al.*, 1993), whereas others become fixed even in the absence of immune pressure (Domingo *et al.*, 1993).

In addition to variation caused by mutation, FMDV has been shown to undergo RNA recombination in tissue culture and in field isolates (Jackson *et al.*, 2007; King *et al.*, 1985; Wilson *et al.*, 1988).

Antigenic variation is more common in the field and increases with time, probably as the result of repeated exposure and immune selective pressure of a highly diverse population of infected and vaccinated host species (Martinez *et al.*, 1992; Vosloo *et al.*, 1996).

Pathogenesis

FMDV infects a large variety of cloven-hoofed animals including many wild animals such as antelope, camel, deer, elephant, elk, giraffe, and llama. However, most pathogenesis studies have been focused on cattle, swine, sheep, and goats, given the serious economic consequences that an FMD outbreak may pose to the livestock industry. The ability of these viruses to infect such a variety of animal species challenges the analysis of the complex interactions between this agent and the host (Arzt *et al.*, 2011a,b).

Dissemination in the Host

In cattle and sheep the main route of infection is the respiratory tract. Swine are less susceptible to aerosolized virus and become infected by direct contact perhaps through abrasions on the vesicles present on the skin or mucous membranes of infected animals (Alexandersen *et al.*, 2003; Arzt *et al.*, 2011a, b; Grubman and Baxt, 2004). Virus is excreted into the milk (Burrows, 1968; Hyde *et al.*, 1975; Ray *et al.*, 1989) as well as in semen, urine, and feces (Donaldson, 1987; Kitching, 1992). The incubation period is dependent on the serotype, amount, and route of infection, but it is generally about 2 days or more.

A number of studies in cattle have shown that when animals are experimentally exposed to FMDV by aerosol, the virus primarily infects tissues of the upper respiratory tract (Alexandersen *et al.*, 2003; Brown *et al.*, 1992; Brown *et al.*, 1996; Sutmoller *et al.*, 1968). Arzt *et al.* (2010) have shown that tissues of the nasopharynx, dorsal soft palate, and to a lesser extent the lungs are the initial sites of FMDV replication. By 24 h postinfection the virus disseminates throughout the body and, although it reaches all organs, replication preferentially occurs at the sites where typical vesicular lesions appear including the coronary bands of the hooves, the mouth, the heart, and the adrenal glands (Arzt *et al.*, 2011a). Infected cattle also aerosolize large amounts of virus, which can infect naive cattle in addition to other species (Sorensen *et al.*, 2000).

In contrast to cattle, pigs are more refractory to aerogenous infection, but they are more susceptible to infection via the gastrointestinal route and generate greater quantities of aerosolized virus (Alexandersen *et al.*, 2002a; Alexandersen and Donaldson, 2002b; Alexandersen *et al.*, 2002d; Arzt *et al.*, 2011b). Pigs develop fever, viremia, and lesions on the feet and snout and young animals may develop fatal myocarditis.

Clinical disease in small ruminants is also characterized by lesions on the feet and mouth, fever, and viremia; however, disease is often subtle and can go undiagnosed (Kitching and Alexandersen, 2002). Although the specific sites of primary infection in sheep have not been well documented, it is likely that distinct phases within the upper and lower respiratory tract may occur as has been demonstrated in cattle (Arzt *et al.*, 2010; Arzt *et al.*, 2011b).

Carrier State

Similar to many other viruses, FMDV has evolved mechanisms to persist in the natural host. In general, the acute phase of infection is resolved within 14 days; however, some animals, mostly ruminants, experience a long asymptomatic chronic infection that can occur in both vaccinated and nonvaccinated animals (Alexandersen *et al.*, 2002c). These animals are referred to as carriers or persistently infected animals and by definition those are animals from whom infectious virus can be recovered from esophageal–pharyngeal fluids at 28 days or later after infection (Sutmoller *et al.*, 1968). However, it is not clear whether carrier animals transmit infection to naïve animals or what are the mechanism(s) that mediate the establishment and maintenance of such a state (Moonen and Schrijver, 2000; Salt, 1993; Sutmoller and Casas, 2002; Sutmoller *et al.*, 1968; Woodbury, 1995).

The carrier state has been documented for cattle, African buffalo, water buffalo, and to a lesser extent in sheep, goats, and other wild ruminants (Sutmoller and Casas, 2002). In cattle, FMDV can be detected in the epithelium of the pharynx and soft palate and in the light zones of the germinal centers in lymphatics of the pharyngeal region after the viremic period (Juleff *et al.*, 2008; Zhang and Kitching, 2001).

Studies in swine have shown that viral RNA could be detected in tissues at 28 days or longer postinfection, after viremia had been resolved (Mezencio *et al.*, 1999; Mohamed *et al.*, 2011; Zhang *et al.*, 2009); however, as no infectious virus could be recovered, by definition those animals were not considered carriers. More recently, Rodriguez-Calvo *et al.* (2011) have proposed a 'pseudopersistence state' in swine. Infectious FMDV C-S8c1 was isolated from different lymphoid tissues and the coronary band epithelia at 17 days postinfection; however, more studies are required in this species to evaluate if transmission to naïve animals is possible at later times.

Little is known about the mechanism that is involved in FMDV persistence, but involvement of the innate and adaptive responses have been suggested (Alexandersen *et al.*, 2002c; Baxt and Mason, 1995; Childerstone *et al.*, 1999; Guzylack-Piriou *et al.*, 2006; Mason *et al.*, 1993; Mason *et al.*, 1994);

Table 1 Involvement of nonstructural FMDV proteins in virulence

FMDV factors	*Affected process*	*Viral counter-mechanism*
L^{pro}	Translation and transcription	• eIF-4G-1 cleavage (de los Santos *et al.*, 2006, 2007; Devaney *et al.*, 1988; Kirchweger *et al.*, 1994) • Gemin5 cleavage (Pineiro *et al.*, 2012) • Decreased amounts of IFN-β (de los Santos *et al.*, 2007) • Degradation of NF-κB (de los Santos *et al.*, 2007) • Inhibition of RANTES (de los Santos *et al.*, 2006) • Deubiquitination of proteins involved in type I interferon pathway (TBK1, TRAF3, TRAF6)
2B + 2C and or 2BC	Membrane rearrangements, secretion and trafficking, and autophagy	• Inhibition of major histocompatibility complex class I surface expression and secretion of antiviral cytokines (Moffat *et al.*, 2005, 2007; Sanz-Parra *et al.*, 1998) • Modulation of cytophathogenicity (Arias *et al.*, 2010) • Induction of autophagy (O'Donnell *et al.*, 2001; Berryman *et al.*, 2012)
3A	Host tropism/viral RNA replication	• Unknown (Beard and Mason, 2000; Giraudo *et al.*, 1990; O'Donnell *et al.*, 2001; Sagedahl *et al.*, 1987)
3B	Viral RNA replication	• Primer for RNA synthesis. Sequence requirements in $3B_3$ (Arias *et al.*, 2010; Falk *et al.*, 1992; Pacheco *et al.*, 2003; Pacheco and Martinez-Salas, 2010)
$3C^{pro}$	Transcription and translation	• Histone H3 cleavage (Falk *et al.*, 1990) • eIF-4G and eIF-4A cleavage (Belsham *et al.*, 2000) • Sam68 clevage (Lawrence *et al.*, 2012) • NEMO cleavage (Wang *et al.*, 2012)

Robinson *et al.*, 2011). In any case, the role of carrier animals in the spread of virus in the field is controversial. As pharyngeal fluids contain virus and have high levels of neutralizing antibodies, it is unlikely that persistently infected animals could be the source of infectious virus (Bergmann *et al.*, 1996). The only direct evidence of transmission from African buffalo to cattle was reported during outbreaks in Zimbabwe in the late 1980s and early 1990s (Dawe *et al.*, 1994a) and in one study in which transmission from buffalo to cattle was experimentally obtained (Dawe *et al.*, 1994b). However, thus far, there is no conclusive evidence demonstrating that persistence plays a major role in FMDV transmission.

Virulence Factors

Virulence factors enable the virus to establish a niche for effective colonization and successfully evade the immune system. Several FMDV NS proteins and RNA regions of the genomic UTRs are known to disrupt or hijack cellular factors ultimately favoring virus replication and dissemination in the host (see **Table 1**).

Nonstructural Proteins

Virulence of L^{pro} was determined by developing a leaderless virus (Piccone *et al.*, 1995a) that was found to be highly attenuated in both cattle and swine (Brown *et al.*, 1996; Chinsangaram *et al.*, 1998; Mason *et al.*, 1997). Studies targeted to understand the attenuating effect of the leaderless virus demonstrated that L^{pro} is involved in blocking the innate immune response by interfering with translation and transcription of type I interferon (IFN-α/β) (Chinsangaram *et al.*, 2001; Chinsangaram *et al.*, 1999; de los Santos *et al.*, 2006; de los Santos *et al.*, 2007). Although blocking of host translation is primarily mediated by L^{pro}-specific cleavage of the translation initiation factor eIF-4G (Devaney *et al.*, 1988; Kirchweger *et al.*, 1994), inhibition of host transcription depends of the complex interplay of L^{pro} with several host factors.

A functional genomics approach using microarray technology and comparing the profiles of leaderless versus wild-type virus infected cells added supporting evidence. Thirty-nine out of 22 000 analyzed genes were differentially expressed in leaderless as compared with wild-type virus-infected cells and mostly included genes involved in the immune response (Zhu *et al.*, 2010). Apparently, this effect results from L^{pro}-dependent degradation or inhibition of activation of transcription factors that play key roles in immunity such as nuclear factor κB (NF-κB) and interferon regulatory factor 3/7 (IRF-3/7) (de los Santos *et al.*, 2007); Wang *et al.*, 2011a). Additionally, L^{pro} exhibits a deubiquitinase (DUB) function that affects many molecules involved in the regulation of type I IFN signaling pathways (Wang *et al.*, 2011b). Identification of L^{pro} cellular binding partners has been instrumental in the understanding of FMDV pathogenesis. Several cellular proteins such as eIF-4G, cyclin A and B, Gemin 5 and Daxx have been identified as direct interactors and targets of L^{pro} cleavage (Pacheco *et al.*, 2009; Pineiro *et al.*, 2012; Ziegler *et al.*, 1995). Thus, further exploration of these molecular interactions should provide additional insights into the L^{pro} function within highly complex cellular systems.

Similar to other viruses, FMDV can target and inhibit proteins that travel through the secretory pathway and are driven through the ER and Golgi organelles. Blockage of this pathway is common within the *Picornaviridae* family and is crucial for virus survival and evasion of the host immune system (Cornell *et al.*, 2006; Doedens and Kirkegaard, 1995; Netherton *et al.*, 2007). Overexpression of FMDV NS proteins 2B or 2BC induces membrane rearrangements thus hindering protein secretion (Moffat *et al.*, 2005, 2007; Pena *et al.*, 2008).

Interestingly, it has been reported that FMDV infection results in the downregulation of cell membrane attached MHC class I molecules, which play a key role in antigen presentation (Sanz-Parra *et al.*, 1998). Protein 2C has also been found in membranous aggregates along the periphery of FMDV-infected cells (Tesar *et al.*, 1989) and has been directly implicated in FMDV RNA synthesis and cytopathogenicity (Arias *et al.*, 2010; Caliguiri and Tamm, 1968).

The 3A protein plays a critical role in FMDV replication (Falk *et al.*, 1992; O'Donnell *et al.*, 2001). Attenuated strains containing partial deletions in 3A can be obtained by repeated passage of FMDV in chicken embryos (Giraudo *et al.*, 1990; Sagedahl *et al.*, 1987). Interestingly, a similar deletion was detected in the FMDV strain that caused a devastating outbreak in Taiwan in 1997 (O/TAW/97) mainly affecting swine but not cattle (Beard and Mason, 2000; Dunn and Donaldson, 1997). These results suggested that the NS 3A protein plays a critical role in FMDV pathogenesis and host restriction. The NS protein 3B is also critical for virus replication. FMDV contains three copies of 3B (VPg 1–3) and although viruses can be obtained with only one copy of VPg multiple copies are required for full infectivity (Arias *et al.*, 2010; Falk *et al.*, 1992; Pacheco and Martinez-Salas, 2010; Pacheco *et al.*, 2003). The role of FMDV $3C^{pro}$ in viral pathogenesis results from cleaving several host proteins. FMDV $3C^{pro}$ processes the host cell histone H3, leading to a block in cellular transcription (Falk *et al.*, 1990). In addition, $3C^{pro}$ targets the translation initiation factors eIF-4G and eIF-4A contributing to the L^{pro}-dependent shutoff of host cell translation (Belsham *et al.*, 2000), and the RNA-binding protein Sam68, which is required for efficient viral replication (Lawrence *et al.*, 2012). Interestingly, $3C^{pro}$ has been also shown involved in processing the NF-κB-essential modulator (NEMO) protein thus impairing IFN synthesis (Wang *et al.*, 2012). Cleavage of many host-specific proteins adds complexity to the multiple strategies FMDV has evolved to disarm the host immune response.

Untranslated Regions

The 5′ UTR of FMDV is more than 1300 bases in length (Forss *et al.*, 1984) and folds in complex secondary and tertiary structures that are involved in many aspects of viral replication and translation (see Section The Agent). Many host cellular proteins have been found to interact with the 5′ UTR and include PTBP, ITAF45, PCBP2, and nucleolin (Andreev *et al.*, 2007; Luz and Beck, 1990; Pacheco and Martinez-Salas, 2010; Pilipenko *et al.*, 2000). These proteins regulate IRES activity providing cell type specificity and determining virus spread, and some are cleaved during infection (Rodriguez-Pulido *et al.*, 2007). Other IRES-binding proteins, such as Gemin5, downregulate translation, but this effect is neutralized by L^{pro} (Pacheco *et al.*, 2009; Pineiro *et al.*, 2012). An additional host factor that binds specific sequences at the 5′ UTR is the RNA helicase A (RHA), which is required for viral replication (Lawrence and Rieder, 2009).

The RNA region located between the two AUG initiation codons (inter AUG) has been shown to be critical for the initiation of viral translation (Lopez de Quinto and Martinez-Salas, 1999; Piccone *et al.*, 1995a) although this effect can be cell type and serotype dependent (Belsham, 2013). Indeed, clinical studies have demonstrated that this region constitutes a virulence factor because disruption of the inter-AUG significantly reduced virulence of aerosolized FMDV A24 in cattle (Piccone *et al.*, 2010).

An important role of the 5′ UTR in virulence has also been demonstrated by testing the antiviral effect of antisense DNA oligomers targeting different regions of the IRES (Fajardo *et al.*, 2012; Vagnozzi *et al.*, 2007). However, these compounds have not been tested *in vivo* in the natural host.

In contrast to the 5′ UTR, the role of the 3′ UTR in virulence is limited. This region, which only spans 90 nucleotides, can fold into stable structures and presumably bridges the 3′ and 5′ UTRs during viral replication (Barton *et al.*, 2001; Herold and Andino, 2001; Pilipenko *et al.*, 1992). Although no molecular studies have confirmed this hypothesis, a role of the FMDV 3′ UTR in virulence has been proposed as viruses could not be recovered from genomes harboring a particular deletion of 74 bases in the 3′ UTR of serotype O1K (Saiz *et al.*, 2001). However, other studies have shown that viruses containing a 57 nucleotide insertion in the 3′ UTR of serotype A24 are fully virulent in cattle provided that conserved RNA structures are not affected by the insertion (Piccone *et al.*, 2009).

Autophagy and Virulence

Autophagy is a cell-regulated pathway that degrades and recycles long-lived proteins and cellular components (He and Klionsky, 2009). Unexpectedly, autophagy can be beneficial for viruses by providing specialized membranes for virus replication. It has been demonstrated by confocal microscopy that during FMDV infection, NS proteins 2B, 2C, and 3A and the structural protein VP1 colocalize with double-membrane (autophagosome) markers (O'Donnell *et al.*, 2011). Specifically, FMDV 2C has been associated with the autophagic markers Beclin-1 and vimentin (Gladue *et al.*, 2012; Gladue *et al.*, 2013). These findings suggest that autophagy plays a critical role in viral replication and could potentially promote persistent infection in relevant tissues where nonlytic release of the virus occurs (Alexandersen *et al.*, 2002c; Salt, 1993).

Host Immune Responses to Foot-and-Mouth Disease Virus

As a successful pathogen, FMDV has developed several mechanisms to evade the host innate and adaptive immune response. Understanding the host/pathogen interaction and the contributions of innate versus adaptive immune responses has become a central topic in FMDV research in order to be able to design new successful control strategies.

Innate Immunity

Foot-and-mouth disease virus is susceptible to interferon

IFNs are the first line of the host innate immune defense against viral infection in mammals (Ank *et al.*, 2006; Basler and Garcia-Sastre, 2002; Frese *et al.*, 2002). Pretreatment of cell cultures with all three types of IFN (I, II, and III) (Fensterl

and Sen, 2009) can dramatically inhibit replication of FMDV and it was shown that type I IFN can inhibit replication of all seven FMDV serotypes (Chinsangaram *et al.*, 2001; Chinsangaram *et al.*, 1999; Díaz-San Segundo *et al.*, 2011; Moraes *et al.*, 2007). FMDV counteracts the innate immune response, at least in part, by blocking the expression of IFN as a result of L^{pro} activity (see Section Virulence Factors). The action of the different types of IFN against FMDV is also very effective in the natural host (see Sections Disease Control Measures – Antivirals/Biotherapeutics).

Preliminary studies to understand the molecular mechanisms induced by IFN treatment that result in protection against FMDV challenge showed a correlation with specific IFN-stimulated gene (ISG) upregulation and tissue-specific infiltration and partial maturation of dendritic cells (DCs) in the skin and natural killer (NK) cells in draining lymph nodes (Diaz-San Segundo *et al.*, 2013b; Diaz-San Segundo *et al.*, 2010; Moraes *et al.*, 2007). Cell culture studies with IFN demonstrated that at least two ISGs, double-stranded-RNA-dependent protein kinase and 2′, 5′ oligoadenylate synthetase/RNase L, are involved in this process (Chinsangaram *et al.*, 2001; de los Santos *et al.*, 2006; Moraes *et al.*, 2007). Furthermore, the 10-kDa IFN-γ-inducible protein (IP-10) is also directly involved in the protection conferred by type I IFN as demonstrated using a mouse IP-10 knockout model treated with IFN-α before FMDV challenge (Diaz-San Segundo *et al.*, 2013a).

Foot-and-mouth disease virus interacts with cells of the innate immune system

During the course of infection, the virus interacts with different DC populations (Bautista *et al.*, 2005; Diaz-San Segundo *et al.*, 2009; Lannes *et al.*, 2012; Nfon *et al.*, 2008; Nfon *et al.*, 2010; Ostrowski *et al.*, 2005; Reid *et al.*, 2011; Robinson *et al.*, 2011), NK cells, and macrophages either by direct infection or as a consequence of DCs phagocytosing the virus in peripheral tissues for antigen presentation (Merad and Manz, 2009; Vivier *et al.*, 2011).

FMDV can infect conventional DCs (cDCs) *ex vivo*, although in most cases this interaction is abortive and no virions are produced (Diaz-San Segundo *et al.*, 2009; Ostrowski *et al.*, 2005). However, it has been demonstrated in cattle that the presence of specific anti-FMDV antibodies enhances infection through the interaction of virus–antibody complexes with FcγR receptors located on the surface of cDCs resulting in productive infection and cell death (Robinson *et al.*, 2011). In addition, FMDV can modulate adaptive immune responses as a result of its interaction with DCs. During acute infection, the virus stimulates DCs to produce interleukin (IL)-10, thus directing adaptive immunity toward the development of a stronger humoral response (Diaz-San Segundo *et al.*, 2009; Robinson *et al.*, 2011). Although it has been shown that interaction of FMDV with bovine cDCs *in vitro* results in productive infection, attempts to recover virus from DCs derived from FMDV-infected swine have been unsuccessful. Nevertheless, FMDV affects monocytes extracted from pigs during acute stages of FMDV blocking their ability to differentiate into mature cDCs (Diaz-San Segundo *et al.*, 2009) and to respond to stimulation with toll-like receptor (TLR) ligands (Nfon *et al.*, 2008).

Swine Langerhan cells (LCs) are also affected by FMDV (Bautista *et al.*, 2005; Nfon *et al.*, 2008). *Ex-vivo* studies demonstrated that FMDV is able to attach and become internalized in these cells; however, there is no evidence of viral RNA replication or production of viral proteins (Bautista *et al.*, 2005). Furthermore, LCs from FMDV-infected pigs showed a reduction in IFN-α production after *ex-vivo* stimulation, although their ability to present antigen is unaffected (Nfon *et al.*, 2008). Clearly, DC antigen presentation is preserved during FMDV infection resulting in a rapid and strong adaptive immune response and virus clearance.

Plasmacytoid DCs (pDCs) are poorly activated by FMDV *in vitro* (Lannes *et al.*, 2012), although when live virus is internalized as part of immune complexes bound to FcγRII surface receptors, the activation is more efficient for either porcine or bovine cells (Guzylack-Piriou *et al.*, 2006; Reid *et al.*, 2011). In any case, the level of IFN-α induction is highly serotype dependent and uptake of these complexes results in abortive virus replication. Furthermore, it has been demonstrated that the level of systemic type I IFN increases during FMDV infection in cattle and is mainly produced by pDCs (Reid *et al.*, 2011). Nfon *et al.* have found that during acute FMDV infection in swine, the pDC population is depleted in blood, although there is a peak of IFN in serum at the same time of the peak of viremia (Nfon *et al.*, 2010). However, *ex-vivo* production of IFN after the stimulation of pDCs with TLR ligands from infected animals is inhibited (Nfon *et al.*, 2008). These results suggest that the pDC response in animals infected with FMDV vary depending on the animal species and the specific FMDV serotype involved.

Macrophages are fundamental for rapid 'clean up' of viral pathogens at the sites of infection. Similar to DCs, FMDV also utilizes an antibody-dependent internalization process via the FcγRII receptor to enter macrophages (Baxt and Mason, 1995; McCullough *et al.*, 1988). Interestingly, it has been reported that, in the absence of productive infection of porcine macrophages, FMDV remains infectious for 10–24 h after internalization by macrophages (Ridgen *et al.*, 2002). Implications of these observations favor the role of macrophages as transporters and disseminators of viable virions to distant sites of the body where the virus can infect and replicate in other cells.

NK cells occupy a critical position during the initial host response against pathogens, particularly during viral infections (Vivier *et al.*, 2011). It has been demonstrated that during FMDV infection of swine there is a reduced capacity of NK cells to lyse target cells and secrete IFN-γ (Toka *et al.*, 2009). NK cell dysfunction during the viremic phase of acute FMDV infection suggests that the virus can effectively block NK function and evade the host's immune response allowing the virus to replicate and disseminate within the host. However, the mechanism involved in this blockage remains unclear.

Adaptive Immunity

Humoral responses

It is well established that the clearance of FMDV occurs through an early potent secretion of neutralizing antibodies starting from day 4 after viral infection. The early B-cell response to FMDV infection in cattle is characterized by the

presence of IgM in lymphoid organs of the upper respiratory tract and serum by 4 days postinfection followed by the detection of IgA and then IgG peaking 1–2 weeks later (Collen *et al.*, 1989; Juleff *et al.*, 2009; Pega *et al.*, 2013; Salt *et al.*, 1996). In infected swine, a similar response is detected (Pacheco and Martinez-Salas, 2010). Interestingly, several groups have demonstrated that the production of antibodies is T-cell independent (Borca *et al.*, 1986; Collen *et al.*, 1989; Juleff *et al.*, 2009; Pega *et al.*, 2013).

T-cell response

Swine develop severe but transient lymphopenia and lymphoid depletion in all the lymphoid organs during the acute phase of FMDV infection. All T-cell subsets, as well as B cells, are affected and depletion of lymphocytes correlates with the appearance of viremia (Bautista *et al.*, 2003; Diaz-San Segundo *et al.*, 2006). In addition, the function of T cells during this early stage of infection is significantly impaired. Thus, FMDV rapidly induces an immune-depressed state in infected swine that recovers by 4–7 days after infection when viremia is abating. These early events provide very favorable conditions for the virus to both spread systemically and shed into the environment. Although lymphopenia is a well-characterized event in swine, the mechanisms involved are not completely understood. It has been reported that infection of lymphocytes is a possible cause of lymphopenia in both swine and cattle (Diaz-San Segundo *et al.*, 2006; Joshi *et al.*, 2009). However, other groups have failed to detect productive infection of peripheral blood mononuclear cells during the course of FMD (Bautista *et al.*, 2003). Nfon *et al.* (2008) have proposed that lymphopenia in swine can be caused by an increase in the amount of systemic IFN during FMDV infection. However, this IFN production was not reproducible for all FMDV serotypes. Finally, it is possible that the diminished T-cell responses could be related to the elevated amounts of IL-10 produced by the cDCs during infection (Diaz-San Segundo *et al.*, 2009; Ostrowski *et al.*, 2005), as IL-10 has been reported to have a role in inducing immunosuppression *in vivo* (Brooks *et al.*, 2006). Similarly, lymphopenia and inhibition of T-cell response to mitogen has also been demonstrated in cattle (Joshi *et al.*, 2009; Perez-Martin *et al.*, 2012), although immunocompetency throughout the FMDV infection has been also reported (Windsor *et al.*, 2011). Apparently, strain- and species-specific immune responses may account for the differences in the observed responses.

Disease Outbreaks

In Disease-Free Countries

FMD was first described in Italy in 1546 (Fracastorius, 1546) and subsequently outbreaks were reported in France, Germany, and the UK in the from the seventeenth to the nineteenth centuries (Mahy, 2004). The earliest reports of FMD in South America, North America, Asia, and Africa were in the nineteenth century. In the United States, the first FMD outbreak was reported in 1870 and subsequently there were eight additional outbreaks with the last occurring in 1929. During this period, disease control consisted of inhibition of animal movement, stamping-out of infected and in-contact animals, and disinfection of affected premises.

In the early 1950, some countries in Western Europe experienced thousands of outbreaks, which were not controlled by existing strategies. As a result, vaccination with an inactivated whole-virus antigen was introduced and resulted in a dramatic decrease in the number of outbreaks. By 1992, The European Union had adopted a no-vaccination policy (Brown, 1992). However, from the late 1990s to the early twenty-first century a number of outbreaks occurred in developed countries that had been FMD free for many decades. These outbreaks were mainly the result of the spread of FMDV type O viruses. In 1997, an outbreak occurred in Taiwan, which had been FMD free for 68 years, spreading to almost the entire island in less than 3 weeks (Yang *et al.*, 1999). Eventually, slaughter and vaccination were required to control the disease and the outbreak resulted in the culling of more than 4 million pigs at a cost of approximately US$6 billion. Unfortunately, Taiwan has never regained its FMD-free status and continues routine FMD serological surveillance. As recently as May 2013, an outbreak of serotype O was reported.

In the next few years, FMDV type O outbreaks occurred in South Korea and Japan for the first time in 66 and 92 years, respectively. The South Korean outbreak was relatively large affecting approximately 500 000 animals, and was controlled by slaughter and vaccination (Joo *et al.*, 2002), whereas the outbreak in Japan was limited and controlled by slaughter (Sakamoto and Yoshida, 2002). In February 2001, an outbreak was discovered in the UK. By the time the outbreak was detected it had already spread to many counties and ultimately resulted in the culling of approximately 6.5 million animals with an estimated cost of US$12–14 billion (Scudamore and Harris, 2002). Subsequently, the virus spread to Northern Ireland and France, presumably as a result of the presence of infected sheep imported from the UK, but the disease only affected a few farms and was controlled by slaughter. In March 2001, the disease was confirmed in The Netherlands (Pluimers *et al.*, 2002). Approximately 200 000 animals were vaccinated and slaughtered. In contrast the UK controlled the disease only by inhibition of animal movement and slaughter of infected animals. As a result of the slaughter of large numbers of animals in these outbreaks, many of which were disease free, the public questioned the validity of this policy. In response to this concern the OIE in 2002 changed their recommended policy on vaccination and allowed a country to regain FMD-free status after vaccination without slaughter in 6 months rather than 12 months, whereas countries that slaughtered or vaccinated and then slaughter can regain FMD-free status in 3 months. Nevertheless, the new OIE policy increased the likelihood that countries would utilize alternative approaches other than culling to control FMD.

Uruguay had been declared FMD free without vaccination in 1996, but outbreaks occurred in 2000 and early 2001 (Sutmoller *et al.*, 2003). The first outbreak was limited and controlled by stamping-out. The second outbreak was quickly detected and initially animals on the affected farms were depopulated, but the disease spread and a 'ring-vaccination' program was soon implemented followed by national vaccination of all cattle. In contrast to the UK, only a small number of animals were destroyed, and Uruguay's beef exports

resumed within a year. The cost of the control program was approximately US$14 million.

In 2007, another FMD outbreak occurred in the UK close to the Pirbright facility, which houses both the Merial FMD vaccine production plant and the Institute of Animal Research which conducts basic and applied research (Cottam *et al.*, 2008). The outbreak strain, type O1 BFS 1860, was traced to ongoing work at both Pirbright laboratories, and was contained to just eight farms surrounding the Pirbright facility because of rapid identification of the disease. Even though the disease was limited it still resulted in an estimated loss of greater than £100 million.

In April, 2010 a large FMD outbreak caused by type O virus occurred in Japan (Nishiura and Omori, 2010). A number of FMD-susceptible species were infected and more than 276 000 animals were culled including seed bulls on a farm that supplied 90% of the sperm used for cattle production in the Miyazaki prefecture. Although veterinarians initially reported disease signs in buffalo at the end of March and disease in cattle on another farm it was not until 3 weeks later that FMDV was confirmed by laboratory analysis. Initially, culling and a ban on livestock movement were imposed to control the disease, but because the number of infected farms rapidly increased emergency vaccination of all FMD-susceptible farm animals around the infected premises was started. FMDV had reemerged in South Korea in 2010 and again in the winter of 2010–11 and was the result of serotypes A and O, respectively (Park *et al.*, 2012; Yoon *et al.*, 2012). The later outbreak was the largest ever recorded in South Korea and was closely related to the type O virus that caused the 2010 Japanese outbreak. The disease affected cattle, pigs, sheep, and goats. Initially, infected farms were depopulated, but subsequently emergency vaccination was used.

The outbreaks in Taiwan in 1997, the UK in 2001, and in Japan in 2010 again demonstrated that if there is a delay in recognizing FMD it is extremely difficult to adequately limit and control its spread, whereas the rapid identification of the disease in the 2007 outbreak in the UK clearly limited its spread.

In Enzootic Countries

FMD is currently enzootic in many Asian, African, and Middle-Eastern countries. Many of these countries do little to control the disease because of the lack of resources. In 2013 alone numerous outbreaks have occurred in China, Russia, Taiwan, Tanzania, Zimbabwe, Botswana, and other countries. Of particular concern is the spread of some serotypes to geographical areas in which these viruses have not previously been reported and therefore the susceptible animal population has no immunity. For example, the movement of the SAT-2 virus from Southern Africa to Saudi Arabia in 2000 was the first report of this serotype in Saudi Arabia. More recently in 2012, SAT-2 was reported in Egypt and caused a large outbreak in cattle.

Disease Control Measures

Surveillance

Control of FMD requires a concerted effort by the individual livestock owner, private veterinarians, and by the country's veterinary services. Since FMDV replicates and spreads extremely rapidly it is essential that infected animals are detected very quickly requiring both vigilance on the part of the livestock owner as well as knowledge of disease signs. Unfortunately, even in developed countries with presumably knowledgeable livestock owners and a trained veterinary service, FMD outbreaks may still go undetected until the disease has spread beyond the initial site of infection. This can partially be due to infection of sheep or goats that often do not show easily detectable disease signs, due to a delay in reporting the index case, or due to a lack of reporting because of illegal feeding of swine with improperly treated swill (Mahy, 2004). In the 2001, UK FMD outbreak the first infected animals were pigs on a farm in Northumberland that were not reported for approximately 3 weeks and in the mean time resulted in the subsequent infection of sheep on the neighboring farms that were moved to various parts of the country without showing apparent clinical sings (Scudamore and Harris, 2002).

Diagnostics

An essential component of a disease control strategy is the use of diagnostic assays to rapidly confirm or eliminate clinically suspect animals. For FMD this is especially important as there are a number of diseases including swine vesicular disease, vesicular stomatitis, and vesicular exanthema of swine, which cause vesicular lesions in swine and cattle that cannot be distinguished from FMD (Bachrach, 1968). After positive diagnosis of FMD, it is also necessary to identify the serotype and strain of the virus as this information is necessary to choose the appropriate antigen to use in vaccination-to-slaughter or vaccination-to-live campaigns. Sensitive diagnostic assays are also needed to distinguish infected animals from vaccinated animals and perform epidemiological surveillance to confirm the naïve status of animals in the field in order to allow for resumption of international trade.

Currently, the OIE suggests the use of a number of diagnostic techniques depending on the type of field samples obtained. The recommended tissue of choice is epithelium or vesicular fluid, but other samples including serum or esophageal–pharyngeal (OP) fluids can also be used. Virus isolation, virus neutralization, reverse-transcription polymerase chain reaction (RT-PCR), enzyme-linked immunosorbent assay (ELISA), or complement fixation assays can be used to identify FMDV. More recently, lateral flow devices are being developed to allow for rapid pen-side testing.

The need for rapid diagnosis is critical. Currently, FMD is confirmed by ELISA, which takes approximately 3–4 h. A negative result must be confirmed by virus isolation in tissue culture, which can take up to 4 days and is not compatible with a rapid response. Therefore, more recently RT-PCR and real-time RT-PCR assays have been developed. Results from the later assay can be obtained in 2 h (Callahan *et al.*, 2002). To differentiate infected animals from vaccinated animals a number of tests have been developed. These are all based on the premise that infected or convalescent animals have antibodies to the viral NS proteins as well as the viral structural proteins, whereas vaccinated animals should only have

antibodies to the viral structural proteins. Unfortunately, this later observation is not necessarily correct as the current inactivated vaccine may contain various amounts of NS proteins depending on the degree of purity of the vaccine preparation (Doel, 2003; Lubroth *et al.*, 1996). A currently validated ELISA uses *E. coli* or baculovirus produced NS protein 3ABC to differentiate infected animals from vaccinated animals. Another assay uses more than one NS protein to unambiguously identify infected animals. This assay, developed by scientists at the OIE Reference laboratory in Rio de Janeiro, is a Western blot of five viral NS proteins expressed in *E. coli* (Berger *et al.*, 1990; Bergmann *et al.*, 1993; Bergmann *et al.*, 2000).

Vaccines

The current FMD vaccine is an inactivated whole-virus preparation that is formulated with various adjuvants before use. As FMDV is an antigenically variable virus, different vaccines are required for each serotype and often different vaccines are necessary to protect against various strains or subtypes within a serotype. The vaccine is produced by infection of suspension cultures of BHK-21 cells with live virus and therefore production requires a high-containment facility. In-depth reviews by Doel (Doel, 2003) and Barteling (Barteling and Cassimi, 2004) discuss the history, production, and testing of inactivated FMD vaccines.

Various countries have established regional FMD vaccine banks that maintain vaccines against circulating viruses (Doel, 2003; Grubman and Baxt, 2004). The United States, Canada, and Mexico in 1982 established the North American FMD Vaccine Bank which is located at the Plum Island Animal Disease Center (PIADC) off the coast of Long Island, NY and is jointly administered. Initially, vaccines were stored as formulated antigen that only had approximately a 1-year shelf life. More recently, vaccine banks store concentrated antigen in the gaseous phase of liquid nitrogen (Doel, 2003) to increase antigen shelf life (Doel and Pullen, 1990). However, to be used in the field the concentrated antigen has to be shipped back to the manufacturer for formulation and returned to the country where the outbreak is occurring. To maintain concentrated FMD antigen that will be protective against circulating FMDV strains it is necessary to continually monitor virus in the field and determine if these strains are sufficiently related to available vaccine antigen. If not appropriate, new vaccine strains have to be produced.

Although inactivated FMD vaccines have been effective in eliminating FMDV from Western Europe and some countries in South America, there are a number of concerns with their use and as a result vaccination has often not been used as part of an FMD disease control approach. (1) As already mentioned production of inactivated FMD vaccines requires expensive high-containment facilities and effective virus inactivation. Unfortunately, the 2007 FMD outbreak in the UK was the result of escape of live virus from the Pirbright FMD facility. (2) Vaccine production requires passage of live virus in BHK-21 cells. There is evidence that passage of virus in cell culture can result in the selection of antigenic variants with altered receptor binding, antigenic structure, and virulence (Bolwell *et al.*, 1989). (3) Depending on the purity of the vaccine antigen produced by various manufacturers it can be difficult to serologically distinguish infected animals from vaccinated animals (Grubman and Baxt, 2004). To address this concern new animal vaccines require markers that allow for differentiation of infected animals from vaccinated animals (DIVA). (4) Vaccinated cattle can become long-term carriers following contact with FMDV-infected animals. (5) The United States cannot produce FMD vaccine as the current Federal law only allows work with FMDV to be conducted at the PIADC and this facility does not have a high-containment manufacturing plant. Thus, in the event of an FMD outbreak in the United States, Canada, or Mexico the correct concentrated antigen present in the bank would have to be shipped overseas to the manufacturer for formulation and bottling and shipped back for distribution. (6) The current vaccine can only induce protection in approximately 7 days. Thus, there is a window of susceptibility if vaccinated animals are exposed to live virus before the induction of an adaptive immune response.

Owing to these limitations, for the past 40 years researchers have attempted to develop new vaccines that can address some or all of these concerns (as reviewed in Doel, 2003; Fowler and Barnett, 2012; Grubman, 2003; Mason and Grubman, 2009; Parida, 2009; Rodriguez and Grubman, 2009). In this article, the authors mainly focus on the latest developments in the most advanced vaccine approaches. Importantly, all of the new vaccine approaches described includes DIVA markers.

New subunit vaccine candidates

The initial attempts to produce vaccines that addressed some of the limitations of the inactivated vaccine included inoculation of susceptible animals with viral structural protein VP1 or a fragment of VP1 (Bachrach *et al.*, 1975; Kleid *et al.*, 1981; Strohmaier *et al.*, 1982; see Grubman and Baxt, 2004 for references). This approach and its limitations have been extensively reviewed (Grubman, 2003; Taboga *et al.*, 1997). In another approach researchers have attempted to utilize empty virus particles as the immunogen. Empty viral capsids or virus-like particles contain all of the epitopes present on intact virus, but lack the infectious nucleic acid. These capsids are natural products of FMDV infection, are antigenically similar to virions, and are as immunogenic as infectious virus in animals (Grubman *et al.*, 1985; Rowlands *et al.*, 1974; Rweyemamu *et al.*, 1979). The empty viral capsids can be produced in various expression systems and then delivered to the animal. Alternatively, the DNA encoding the capsid-coding region and the $3C^{pro}$ required for capsid polypeptide processing can be delivered to the animal via DNA or viral vectors and the capsids synthesized in the animal. This latter approach has a potential advantage as compared with delivery of preformed empty capsids to the animal as the synthesis of the immunogen in the animal should induce both antibody as well as cell-mediated immune responses.

Li *et al.* (2008) used a silkworm–baculovirus expression system to produce FMDV Asia-1 empty capsids and vaccinated cattle with the hemolymph from infected silkworms. Four of the five animals were protected from homologous virus challenge. One potential limitation in the use of empty capsids as vaccine candidates is that in the absence of virion RNA they are less thermostable than the natural virus particle and therefore may be less immunogenic (Curry *et al.*, 1997). Porta *et al.*

(2013) attempted to enhance stability of baculovirus-expressed FMDV A22 empty capsids and also reduce expression of the toxic $3C^{pro}$. The mutated capsids were more stable than the WT capsids to both heat and acid and 3C expression and catalytic activity was reduced. Two of the four cattle vaccinated twice with WT empty capsids and an oil adjuvant and three of the four animals inoculated with mutant capsids were protected from challenge with homologous virulent virus (Porta *et al.*, 2013).

Other investigators have used viral vectors, including poxvirus, pseudorabies virus, and replication-defective human adenovirus (Ad5), as delivery vehicles (Grubman and Baxt, 2004; Zhang *et al.*, 2011). Thus far, the most efficacious viral-vectored delivery vehicle is the Ad5 system. The Ad5-FMDV A24 (Ad5-A24) vector constructed by Grubman and colleagues (Moraes *et al.*, 2001) is protective, after one inoculation, as early as 7 days postvaccination in both swine (Moraes *et al.*, 2002) and cattle (Grubman *et al.*, 2010; Pacheco *et al.*, 2005). More recent studies with second-generation vectors containing the NS protein 2B coding region demonstrated enhanced efficacy in challenge studies in swine (Pena *et al.*, 2008) and cattle (Moraes *et al.*, 2011). Furthermore, by changing the route and sites of inoculation the protective dose could be significantly reduced (Grubman *et al.*, 2012b). The US Department of Agriculture (USDA) in collaboration with the US Department of Homeland Security and GenVec Inc. have produced this vaccine on the US mainland in BSL2 facilities and tested it in cattle following the requirements of the Center for Veterinary Biologics of the Animal Plant and Health Inspection Service, USDA, which included safety testing of the vaccine in cattle at three sites on the US mainland. In June 2012 this vaccine was granted a conditional license for inclusion in the US National Veterinary Vaccine Stockpile for use in cattle in the United States in the event of an emergency situation.

Live-attenuated vaccines

A number of reviews have described early attempts to develop live-attenuated FMD vaccines (Bachrach, 1968; Brooksby, 1982; Mason and Grubman, 2009). These vaccines are economically cost effective to produce, should cause only mild or no disease, and theoretically can induce both adaptive and cell-mediated immune responses. Live-attenuated FMD viruses were developed by passage of WT virus in nonpermissive hosts including mice, rabbits, and embryonated eggs until their virulence for cattle was attenuated. However, although this approach has been successful in the development of very effective vaccines against yellow fever and polio, it has not been successful against FMD. Field studies in various countries demonstrated that although the attenuated strains could induce a degree of protection in a particular species it was often virulent in other susceptible species. In addition, there is concern that attenuated viruses created in this manner can revert to virulence.

More recently, scientists have used reverse genetics to mutate selected portions of the viral genome. McKenna *et al.* (1995) removed a portion of the region of VP1 required for binding to cells. This virus did not induce disease in inoculated swine or cattle and protected cattle from challenge with virulent FMDV. In another approach Piccone *et al.* (1995a) constructed a serotype A virus lacking the entire L^{pro} coding region, leaderless virus. Although this virus was infectious in BHK-21 cells, it grew to lower titers in primary cells, was attenuated in both swine and cattle, and induced a significant neutralizing antibody response (Chinsangaram *et al.*, 1998; Mason *et al.*, 1997). However, upon challenge animals vaccinated with this virus developed delayed and reduced disease signs as compared with naïve challenged animals. Similarly, a chimeric leaderless virus with a capsid from serotype O in a type A background was avirulent in cattle, but caused limited clinical disease in swine (Almeida *et al.*, 1998). Although, as already discussed (see Section Virulence Factors) L^{pro} is an important virulence factor it is clear that other regions of the viral genome are also involved in pathogenesis. Infection of cells with a virus with mutations in a conserved domain of L^{pro}, SAP domain (see Section Virulence Factors), does not result in cleavage of NF-κB (SAP virus). This virus was attenuated in swine, but induced a significant neutralizing antibody response (Diaz-San Segundo *et al.*, 2012). Furthermore, swine vaccinated with SAP virus were protected from challenge with the virulent parental virus as early as 2 days postvaccination.

New marked inactivated virus vaccines

Although live-attenuated FMD vaccines have thus far not been successful, a number of groups have tested these viruses as potentially safer DIVA inactivated vaccine candidates. Chinsangaram *et al.* (1998) showed that swine vaccinated with an oil-adjuvanted inactivated leaderless A12 virus or inactivated WT A12 virus induced very significant neutralizing antibody responses and protected the animals from homologous virus challenge. Utilizing the leaderless virus platform Uddowla *et al.* (2012) constructed an A24 leaderless virus with two negative markers. This virus was avirulent in cattle and swine and was not transmitted to naïve animals. In addition, an ELISA targeted to the negative markers was developed that successfully differentiated infected animals from vaccinated animals. Furthermore, cattle vaccinated with the oil-adjuvanted inactivated A24 leaderless negative marker virus developed an FMDV-specific neutralizing antibody response and were protected from clinical disease when challenged 21 dpv.

Fowler *et al.* (2011) observed that a negative marker inactivated vaccine could address the concern about differentiating infected animals from vaccinated animals. They isolated a virus, after passage of an Iranian vaccine strain in cell culture, lacking a 13 amino acid portion of the G–H loop of VP1 and developed an ELISA that could distinguish animals vaccinated with this immunogen from infected animals. Vaccinated cattle were protected from homologous WT virus infection.

Antivirals/Biotherapeutics

Inactivated and Ad5-FMD vaccines can only induce complete protective immunity by 7 days postvaccination (Golde *et al.*, 2005; Moraes *et al.*, 2002). Thus, before 7 days vaccinated animals exposed to virulent FMDV are still susceptible to the disease. As FMDV replicates and spreads very rapidly it is important, especially in an outbreak in an FMD-free country, to

quickly limit its dissemination. Ideally, a biotherapeutic agent in combination with a marked FMD vaccine could induce both rapid nonspecific protection and specific long-term vaccine-induced protection (Grubman, 2003).

As already discussed, type I and III IFNs are one of the first lines of host defense against viral infection and can inhibit FMDV replication in cell culture (Ahl and Rump, 1976; Chinsangaram *et al.*, 2001; Díaz-San Segundo *et al.*, 2011). On the basis of these findings and the clinical use of type I IFN in the treatment of various diseases including hepatitis C or B, Chinsangaram *et al.* (2003) constructed Ad5 vectors containing the gene for porcine IFN-α (poIFN-α). Swine inoculated with this vector and challenged 1 day later with virulent FMDV serotype A24 were clinically protected. Subsequently, this group demonstrated that protection could last for 3–5 days (Moraes *et al.*, 2003) and that swine challenged with FMDV O1 Manisa or Asia-1 1 day postinoculation were also protected, and that protection was induced by Ad5-poIFNβ treatment as well (Dias *et al.*, 2011). However, cattle treated with Ad5 containing bovine IFN-α were not completely protected, but developed delayed and less severe disease as compared with naïve challenged animals (Wu *et al.*, 2003).

More recently, Diaz-San Segundo *et al.* (Díaz-San Segundo *et al.*, 2011) constructed Ad5 vectors containing boIFN-λ (type III IFN) and demonstrated it has anti-FMDV activity in cell culture. After inoculation of cattle this vector induced upregulation of ISGs in the upper respiratory tract, which is the initial site of FMDV infection. Cattle administered Ad5-boIFNλ and challenged 1 day later with either FMDV A24 or O1 Manisa had significantly delayed and reduced severity of disease (Perez-Martin *et al.*, 2012).

It has also been demonstrated that type II IFN (IFN-γ) has antiviral activity against FMDV in cell culture (Moraes *et al.*, 2007; Zhang *et al.*, 2002). Using an Ad5-poIFNγ construct Moraes *et al.* (2007) showed that a combination of Ad5 vectors delivering both type I and type II poIFNs could protect swine from challenge 1 day later at lower doses than either alone. More recently, it was shown that poly ICLC, a synthetic dsRNA mimic and a potent inducer of IFN, could protect swine when challenged 1 day later with FMDV (Dias *et al.*, 2012).

In cell culture studies investigators have examined a number of antiviral compounds targeted to specific viral proteins including L^{pro} (Kleina and Grubman, 1992) and 3D (Rai *et al.*, 2013). In addition, antisense and RNA interference technologies (Chen *et al.*, 2004; de los Santos *et al.*, 2005; Fajardo *et al.*, 2012; Rosas *et al.*, 2003; Vagnozzi *et al.*, 2007) have been shown to block virus replication in cell culture. However, these technologies have not yet been tested in naturally susceptible animals.

Concluding Remarks

A wealth of new information has been obtained on FMDV at the molecular level, including many of the functions of the viral-encoded proteins, the interaction of the virus with the host, the pathogenesis of the disease, and the effect of infection on the host immune response. This information and the tools of reverse genetics and immunology have allowed us to develop new approaches to more rapidly detect and potentially better control this disease. New diagnostic assays, some of which can be used pen-side, should result in the rapid detection of disease. Likewise, new serological assays may allow a more rigorous differentiation of infected animals from vaccinated animals. A better understanding of the immunogens necessary to induce protection has resulted in the development of novel vaccine candidates that do not require high-containment facilities for production and allow for unequivocal DIVA assays. The demonstration that biotherapeutic approaches, such as the delivery of IFN genes, can rapidly induce protection before vaccine-induced immunity has opened additional possibilities of disease control. Nevertheless, the recent outbreaks of FMDV in a number of developed countries and the continued presence of FMD in many developing countries demonstrate the difficulty in controlling this disease.

Unlike rinderpest, which was the first eradicated animal disease, FMDV is antigenically diverse and infects many animal species including wild animals making it a much more difficult disease to control. FMD is still widespread in many developing countries, which do not have the infrastructure or the resources to effectively control the disease. Various international organizations including the FAO and OIE as well as regional organizations and developed countries have attempted to enhance aspects of disease control in developing countries. Most recently, the FAO and OIE have sponsored Global FMD Conferences in Paraguay in 2009 and in Bangkok in 2012. The outcome of these conferences has been the development and adoption by FAO and OIE of a multistep approach termed 'The Progressive Control Pathway (PCP)' to systematically help control FMD in countries in which it is enzootic. This approach requires both the affected countries and FMD-free countries, with knowledge and resources, to work together to increase the level of control so that countries will be able to gain OIE recognition as FMD free with or without vaccination (Sumption *et al.*, 2012).

It is clear that in a globalized world with an increasing population the need for more food including animal products is critical. Thus, the control of FMD is not only a problem for veterinary services and the livestock sector of the economy, but also has direct consequences on human health. It is, therefore, imperative for governments as well as private organizations to work together to continue to develop a more comprehensive understanding of FMD and to allocate sufficient funds to use this information to control and limit disease spread in all countries. Undoubtedly, if this type of global effort is not undertaken and sustained, all countries will suffer because of the continued presence of FMD.

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See also: Advances in Animal Biotechnology. Animal Welfare: Stress, Global Issues, and Perspectives. Beef Cattle. Dairy Animals.

Food Safety: Emerging Pathogens. Food Security: Food Defense and Biosecurity. Genomics of Food Animals. Investments in and the Economic Returns to Agricultural and Food R&D Worldwide. Small Ruminants in Smallholder Integrated Production Systems. Swine Diseases and Disorders. Vaccines and Vaccination Practices: Key to Sustainable Animal Production

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Animal Health: Global Antibiotic Issues

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Glossary

Antibiotic resistance A form of drug resistance in which certain microorganisms could survive after exposure to one or more antibiotic treatment.

Foodborne illness Any disease resulting from the consumption of food contaminated by pathogens, viruses, parasites, or toxins.

Prebiotics Nondigestible food ingredients that stimulate the growth or activity of bacteria (probiotics) in the digestive system and eventually benefit the host.

Probiotics Live bacteria that could have health benefits on the host.

Withdrawal periods Time required after administration of antibiotics in agricultural animals needed to ensure that antibiotic residues in meat, egg, or milk products is below the determined maximum residue limit.

Zoonotic pathogen Pathogenic bacteria that could cause an infectious disease that is transmitted between species from animals other than humans to humans, or from humans to other animals.

Introduction

Antibiotics are antimicrobial compounds that can inhibit and even destroy bacterial and fungal growth. Some compounds, such as aminoglycosides and penicillins, are isolated from living organisms, whereas others, such as oxazolidinones, quinolones, and sulfonamides, are produced by chemical synthesis. Accordingly, antibiotics can be classified based on their origin as natural origin, semisynthetic origin, or synthetic origin. Most of the common antibiotics used today are semisynthetic modifications of a variety of natural compounds. These antibiotics are used in both human medicine and animal agriculture to reduce incidences of diseases. They are usually administered by injection or orally via feed and water.

Antibiotics used for growth promotion in livestock and poultry not only allow the growth of healthier and more productive farm animals through improved weight gain and feed conversion efficiency, but they are also effective against animal diseases (Dibner and Richards, 2005). However, low-dose or specific employment of antibiotic as growth promoters that may involve bacterial antibiotic resistance and the replacement of these antibiotics with some natural products are under pressure.

Antibiotics widely administered in preharvest farm animals also help to reduce foodborne pathogens and prevent foodborne illness, which causes high morbidity and mortality rates worldwide. Currently, broad-spectrum antibiotics are commonly employed as feed additives for the preslaughter inhibition of foodborne pathogens. Owing to difficulties in determining specific agents targeting specific pathogen at the farm animal level, antibiotics have been shown to lower foodborne illness, and thus reduce morbidity and mortality, in humans (Callaway *et al.*, 2003). Other nonantibiotic antimicrobials are also used in foodborne pathogen prevention. These strategies include vaccination and the use of bacteriocins, bacteriophages, enzymes, probiotics, prebiotics, and organic acids.

As an essential strategy for controlling animal diseases, antibiotics have been employed in agricultural farming for therapeutic purposes. Multiple antibiotics have been approved for use against livestock diseases, including respiratory disease, enteric disease, and mastitis (Radostits *et al.*, 2007), as well as necrotic enteritis, chronic respiratory diseases, gangrenous dermatitis, fowl cholera, and avian influenza commonly seen in poultry (Pattison, 2008), as will be elaborated in this article.

Based on Page and Gautier's most recent study, commonly used classes of antibiotics in farm animals all over the world are summarized in **Table 1** (Page and Gautier, 2012).

Although the employment of antimicrobial agents has multiple significant benefits in animal agriculture, the appropriate use of these agents, including how to select the right ones, how to administrate them, and how to assess their risks, is a highly complex issue and continues to be a challenge for most growers and farmers. Knowledge and understanding of the common infectious diseases in multiple farm animals and guidelines for antimicrobial use in animal and animal products are crucial (Radostits *et al.*, 2007).

Some important topics addressed in this article include the patterns of antimicrobial use, preharvest and postharvest, therapeutic and subtherapeutic, nutritional, and for treatment. In addition, alternative antimicrobials and their appropriate employment in farm animals will also be discussed.

Antibiotics Used as Growth Promoters

Since the 1950s, antibiotics have been used as growth promoters in agricultural animal production in the United States, Australia, and several European countries (Dibner and Richards, 2005). Generally, 'growth promoter' refers to products that help to grow an animal faster for the same unit amount of feed consumed in a given period of time. Several researchers have shown that low-concentration (usually 2.5–50 mg kg^{-1}) addition of antibiotics to animal feed results in an accelerated growth rate and improved feed conversion efficiency in agricultural animals such as cattle, pigs, sheep, and poultry (Amy *et al.*, 2007). The improvement in average growth rate was estimated to be between 4% and 8%, and feed utilization was improved from 2% to 5% in 1994 (Ewing and Cole, 1999); a majority of recent studies have shown larger

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Table 1 The most commonly employed antibiotics in farm animals worldwide

Country	*Year*	*Livestock*	*Poultry*
Australia	2006	Macrolides, penicillins, sulphonamides, and tetracyclines	–
Belgium	2009	Colistin, macrolides, penicillins, and tetracyclines	Macrolides and penicillins
Canada	2008	Lincosamides, macrolides, penicillins, and tetracyclines	–
Denmark	2010	Caphalosporin, macrolides, penicillins, penicillin-aminoglycoside, pleuromutilins, and tetracyclines	Macrolides, penicillins, and tetracyclines
Finland	2009	Aminoglycosides, beta-lactams, cloxacillin, fluoroquinolones, penicillin, and tetracyclines for all terrestrial species	
France	2010	Macrolides, penicillins, polymyxins, and tetracyclines	Penicillins, polymyxins, and tetracyclines
Germany	2005	Beta-lactams, sulphonamides, and tetracyclines for all species	
Japan	2004	Aminoglycosides, cephalosporins, macrolides, penicillins, sulphonamides, and tetracyclines	Aminoglycosides, macrolides, and tetracyclines
Kenya	2004	Aminoglycosides and penicillins for all farm species	
Netherlands	2009	Aminoglycosides, cephalosporins, colistin, neomycin, penicillins, penicillin-aminoglycoside, and tetracyclines	Colistin, fluoroquinolones, neomycin, penicillins, and tetracyclines
New Zealand	2009	Aminoglycosides, cephalosporins, macrolides, penicillins, penicillins sulphonamides, and tetracyclines	Bacitracin
Norway	2010	Aminoglycosides, penicillins, and sulphonamides for all terrestrial species	
South Africa	2004	Macrolides, penicillins, sulphonamides, and tetracyclines for food-producing species	
Sweden	2010	Macrolides, penicillins, pleuromutilins, and tetracyclines	Penicillins
Switzerland	2005	Aminoglycosides, penicillins, polymyxins, sulphonamides, and tetracyclines	Aminoglycosides, penicillins, sulphonamides, and tetracyclines
USA	2010	Macrolides, penicillins, sulphonamides, and tetracyclines for food-producing species	
UK	2010	Penicillins and tetracyclines for food-producing species	

benefits, up to 10% gain in both weight and feed conversion efficiency (JETACAR, 1999).

The exact mechanisms of growth promotion by antibiotics are still speculative. But, based on recent *in vivo* animal experiments, the antibactericidal effect of antibiotics is the most likely explanation for growth promotion. Antibiotics may help concentrate nutrients by reducing the amount of several intestinal bacteria that are able to divert nutrition away from an animal's body. In addition, antibiotics could also inhibit release of toxins in the gut by intestinal bacteria. Antimicrobial growth promoters could also help increase the availability and absorption of nutrients and energy by maintaining the composition of gut microflora, thus thinning the barrier in small intestine and at the same time assisting the digestion of grain-based high-energy diets.

Current Use of Antibiotic Growth Promoters

In the United States, beta-lactam antibiotics, especially penicillins and lincosamides, as well as macrolides, especially erythromycin and tetracyclines, are commonly used as growth promoters in pigs (Peter and John, 2004). Multiple other antimicrobial compounds are also used in US swine production to stimulate growth. These include arsenical compounds, bacitracin, flavophospholipol, pleuromutilins, quinoxalines, and virginiamycin (Peter and John, 2004). In Australia, similar antibiotics are employed in animal agriculture. Such growth promoters include arsenical compounds, flavophospholipol, macrolides (especially kitasamycin and tylosin), olaquindox, and streptogramin (especially virginiamycin) (JETACAR, 1999). Compared to the United States and Australia, the application of antibiotics in growth promotion in the European countries is relatively limited. In pig production, avilamycin, flavophospholipol, and ionophores, especially monensin and salinomycin, are among the few approved growth promoters in use in Europe (Angulo, 2004).

In the cattle industry, major antibiotics including flavophospholipol, monensin, and virginiamycin are commonly used as growth promoters in the United States (Peter and John, 2004). Owing to the high energy requirements of cattle, growth promoters may play an important role by stimulating muscle formation and improving milk productivity (Peter and John, 2004). However, the use of growth promoters can have several side effects in cattle. The most common harmful effect is lactic acidosis, which both impairs milk production and debilitates cattle. To counteract this side effect and maintain a balance between benefit and harm, administration of lasalocid and monensin are probably the safest and most effective antibiotic growth promoters due to their activity in inhibiting most of the lactate-producing bacterial species without harming the major lactate fermenters. Australian cattle farmers also employ flavophopholipol, lasalocid, and monensin (JETACAR, 1999). Other cattle growth promoters used in Australia include narasin, oleandomycin, and salinomycin. The use of glycopeptide avoparcin was no longer permitted after 2000. In the European Union, the same types of ionophores – monensin and salinomycin – are used in cattle. However, the use of

pristinamicin and quinupristin has been banned since 2000 (Dibner and Richards, 2005).

For the poultry meat and egg industries, specific growth promoters such as flavophospholipol and virginiamycin are employed in the United States (Peter and John, 2004). In Australia, poultry producers use arsenical compounds, flavophospholipol, bacitracin, and virginiamycin (JETACAR, 1999). Growth promoters are not allowed to be used in layer farms in Australia. In Europe, major growth promoters used in the poultry industry include avilamycin, avoparcin, bacitracin, and virginiamycin. According to several recent studies, a 10 mg per kg dose of avoparcin is able to improve feed conversion efficiency by 2.96%, increase the growth rate of meat chickens by 2.37%, and increase 1.33 net cents per kg liveweight; 17.6 mg per kg dose of virginiamycin, similarly, is able to increase these three values by 3.48%, 3.19%, and 1.48%, respectively (Mehdi *et al.*, 2011).

The Future of Antibiotic Growth Promoters

In 2000, the World Health Organization (WHO) recommended several global principles, including rapidly phasing out all antibiotic growth promoters from agricultural animal production, specifically those that are used in the treatment of human diseases (World Health Organization, 2000). Four years later, WHO also recommended for assessment of risk and surveillance of antibiotic growth promoters used in agricultural animals and the pattern of antimicrobial resistance in various animal and human bacterial pathogens (World Health Organization, 2004).

Though the relationship between application of antibiotics in farm animal production and the trend of antimicrobial resistance in human bacterial pathogens is still under debate, the idea of antibiotic-free animal production is based on an emotional level instead of a legislative level. In fact, from the point of view of many consumers, the use of antibiotics as growth promoters has negative effects on public health, and a certain percentage of consumers want to reduce or control the use of antibiotics in food animals, regardless of their practical advantages. The use of antibiotics as growth promoters is being curtailed under consumer pressure. The replacement of these antibiotics/antimicrobials with some consumer-friendly and natural organic bioactive components is a potential area of research interest worldwide.

The Potential Alternatives to Antibiotics for Growth Promotion

In light of the declining demand for antibiotic growth promoters, more and more research has been focused on developing alternatives to growth stimulation and improving feed utilization and efficiency. Since the benefits of growth promotion may result from the alteration of gut microflora, alternatives to antibiotic growth promoters may be required to improve animal intestinal gut flora through natural and organic bioactive and functional feed supplements. Therefore, research interest has concentrated on following the five approaches: in-feed enzymes, probiotics, prebiotics, organic acids, bioactive phytochemicals, and competitive exclusion of pathogens by-products being administered via water or feed. So far, none have been proved to replace the use of antibiotics in growth stimulation thoroughly and successfully, and thus further research is needed. The possibilities of using these potential alternatives to synthetic antibiotics are explored below.

In-feed enzymes

Feed enzymes have been employed extensively in both livestock and poultry feed for more than 15 years, especially in wheat- or barley-based diets (Choct, 2002). In-feed enzymes are usually produced by fermentation of fungi and bacteria, after which these are used to stimulate growth as additives in animal feeds. Several studies have investigated the effectiveness of in-feed enzymes as a substitute for antibiotic growth promoters for improving nutrient absorption and digestibility, gaining body weight, and animal performance. Based on recent studies, it was demonstrated that in-feed enzymes often have activities in promoting digestion of feed components that are normally poorly digested or totally undigested in agricultural animals (Hedemann *et al.*, 2009). The mechanism by which in-feed enzymes promote digestion of feed components is believed to involve the breakdown of those hard-to-digest chemical components in the grains and meals such as nonstarch polysaccharides, especially arabinoxylans and beta-glucans, phytates, and proteins (Gerard *et al.*, 2011). Added routinely to the feed of livestock and poultry, these enzymes are efficient at maximizing feed conversion efficiency, and more importantly they have no or very few side effects. As a consequence, numerous researchers are now focusing on improving the quality of existing enzymes, intending to broaden the range of feed ingredients in which they could be used as alternative growth promoters.

Competitive exclusion products

Owing to the increasing concerns about the role of chemical antibiotics in bacterial resistance in both agricultural animals and humans, and following Darwin's competitive exclusion principle, many researchers are seeking biological alternatives to replace antibiotic growth promoters with competitive exclusion products. Competitive exclusion products are usually processed from and composed of various species of undefined or partially defined bacteria isolated from the gastrointestinal tracts of agricultural animals. Products such as Broilact™, Avigard™, and Preempt™ are often administered to newborn animals, especially poultry, and have shown their effectiveness in animal growth promotion, gut health maintenance, and even the control of pathogenic infection (Alaeldein, 2013). Several studies have found that a significant improvement of animal feed conversion ratio using Avigard treatment results from the reduction in feed intake and also the prevention of pathogenic colonization such as *Salmonella* and *Campylobacter* from the gut (Gerard *et al.*, 2011). At the same time, multiple competitive exclusion products can also help reduce diarrhea and mortality levels, but the mechanisms remain unclear.

Probiotics

Similar to competitive exclusion products, probiotics are defined as directly fed mono- or mixed cultures of living microorganisms that can compete with undesired microbes

and benefit the host by improving the properties of the indigenous microbiota (Fuller, 1992). Available probiotics can be divided into two main categories. One category is colonizing species such as *Lactobacillus, Lactococci,* and *Enterococcus*; the other is free-flowing noncolonizing species, which include both *Bacillus* and *Saccharomyces cerevisiae*. These beneficial microbes are able to ameliorate the overall health of animal by improving the gut microbial balance; however, their exact mechanism is still under investigation. One major hypothesis for their actions could involve their influence on intestinal metabolic activities, including the improvement of bacteriocins, propionic acid, and vitamin B12 production, and increasing the villous length and nutrient absorption (Christina *et al.*, 2009). Other possible mechanisms include competitive exclusion of pathogenic microorganisms and their immunostimulatory activities.

Probiotics are also effective in helping boost weight gain and feed conversion rates in newborn animals. However, several questions about the active strains, the maximum dosage, the effective delivery system, and the potential risks remain unanswered and need to be further investigated. One more potential danger of using live probiotics refers to their antibiotic resistance. A report from the Scientific Committee on Animal Nutrition (2001) concerning the safety of probiotic products found that *Lactobacillus plantarum* and *Pediococcus acidilactici* were tetracycline-resistant. As a consequence, the use of probiotics could possibly put the whole food chain and the environment at risk. Moreover, the permanent establishment of probiotics in animal gastrointestinal tracts is difficult. Several studies have indicated that gut microflora are active and efficient in preventing new organisms from colonizing and becoming established (Jonsson and Conway, 1992). Finally, the high cost and high dosage of administration required for probiotics for growth promotion might also be a serious drawback to their widespread application in animal agriculture.

Prebiotics

Prebiotics are nondigestible feed ingredients that are able to provide selective stimulatory effects on both the growth and metabolic activity of certain gut microflora, including the probiotics mentioned above. Their effects are based on the nature of the compound, but essentially they could exert the same or similar actions as probiotics. Unlike probiotics, which are foreign microorganisms introduced into the gut competing with colonic communities which have already become established, the chief advantage of employing prebiotics in improving gut function is that their target bacteria are already commensal with the large intestine (Macfarlane *et al.*, 2008). However, prebiotics cannot be effective if the targeted beneficial bacteria are not in the gut due to, for example, antibiotic therapy or intestinal diseases. One potential area of future research would be examining the combined effect of both probiotics and prebiotics, known as 'synbiotics,' for the replacement of antibiotic growth promotants (Louise, 2009).

Organic acids

Some evidence has shown that in the presence of organic acids, mainly short-chain fatty acids such as acetic, butyric, and propionic acids, there is significant increased growth of gut mucosa. Butyric acid, the metabolic product of *Lactobacillus*, is one of the representatives of organic acids that could potentially be used as alternative growth promoters. Butyric acid exerts multiple effects on the intestinal function of both animals and humans, including acting as a vital energy source for intestinal cells, stimulating epithelial cell proliferation and differentiation (Dalmasso *et al.*, 2008), and inducing antiinflammatory effects (Hodin, 2000). In addition, by stimulating the expression of tight junction proteins and the production of antimicrobial peptides in mucosa, butyric acids are also able to strengthen the gut mucosal barrier (Schauber *et al.*, 2003; Bordin *et al.*, 2004; Peng *et al.*, 2007).

Bioactive phytochemicals

A variety of plant-derived agents are employed worldwide as feed additives in farm animals. As a substitute for antibiotics, these plant-derived compounds also exert production-enhancing effects, including the improvement of dairy weight gain, enhancement of feed conversion efficiency, and increasing milk and egg production (Halldor, 2012). As the secondary metabolites of flowering plants, essential oils have been used as nonantibiotic antimicrobials as animal feed additives for the purpose of both growth stimulation and bacterial inhibition (Hammer and Carson, 2011). Para-thymol, an isomeride of thymol, with higher antibacterial activity and lower volatility, has been found to be safer and exerts even better growth-promoting effects than thymol and carvacrol (Peng *et al.*, 2011). Other bioactive phytochemicals patented worldwide include isoflavone, produced by *Fabaceae* family, diaryheptanoid from the bark of the Japanese shrub alder *Alnus pendula*, *Curcuma aromatica* Salisb extracted from ginger, saponin extracted from yucca, alkaloids from plume poppy, and lignocellulose obtained from *Magnolia*, all of which have been claimed to effectively modulate gut microflora, improve immune function, and promote both absorption and digestion of nutrients by livestock and poultry (Halldor, 2012).

Antimicrobials for Pre-harvest Foodborne Pathogens Reduction in Food Animals

According to the Centers for Disease Control and Prevention (CDC), an estimated 48 million illnesses, 128 000 hospitalizations, and 3000 deaths are caused by foodborne pathogens annually (Centers for Disease Control and Prevention, 2012). Zoonotic pathogens colonized in the gastrointestinal tract of food animals can be shed in feces. Fecal contents play a significant role in carcass cross-contamination and are likely to reach consumers and food processors. In addition, fecal content is a direct source for pathogens in water, soil, vectors, and crops. As a consequence, it remains a major public health concern to reduce the foodborne pathogenic bacteria populations at the farm level. A broad range of preharvest intervention strategies have been employed, and some are still under development. Owing to increased worldwide concern about the transmission of antibiotic resistance from farm animals to humans, the preharvest use of antibiotics has been limited and even gradually prohibited. Though the reduced preslaughter use of antibiotics to reduce foodborne pathogens in farm animals has been partially offset by an increased use of

prescribed antibiotics for therapeutic purposes, the direct use of several common antibiotics and alternative natural antimicrobial agents as a substitute for antibiotics is urgently needed. Major potential natural strategies include using bacteriocin, vaccination, introducing bacteriophages, adding enzymes or organic acids as feed supplements, and the enhancement of competition by introducing substrate-adapted competitive products such as probiotics and prebiotics. Parallel and simultaneous application of more than one preharvest strategy could be a promising strategy to synergistically lower the incidence of foodborne illness.

Selected Antibiotics Registered for Preslaughter Use in Agricultural Animals

Foodborne illness is a significant factor contributing to mortality and morbidity not only in the United States but throughout the world. Various agents such as viruses, bacteria, fungi, and parasites are responsible for more than 200 known foodborne diseases. Among the numerous and various threats, *Salmonella*, *Escherichia coli* O157:H7 (EHEC), *Campylobacter*, and *Listeria* are the leading causes of meat products–related illness and deaths in the United States. Most of these foodborne pathogens are able to live on the skin or in the gastrointestinal tract of food animals such as cattle, swine, sheep, and poultry, especially chickens and turkeys, and in the farm environment where the soil is fertilized with composted animal manure (D'Aoust *et al.*, 2008; Meng *et al.*, 2008; Nachamkin, 2008; Swaminathan *et al.*, 2008). Thus, antibiotics have been widely employed in preharvest use in farm animals and in humans to reduce foodborne pathogens and to prevent foodborne illness. In spite of the widespread use of antibiotics in animals, it is often difficult to choose a specific antibiotic which could target specific pathogens because the microbes usually fall into diverse groups. As a result, broad-spectrum antibiotics are usually employed in preharvest animals. Based on recent research, antibiotic treatment for controlling gastrointestinal pathogens has been found to disrupt the gut microbial ecosystem and thus impair animal health, meat or milk production, and even food safety. Despite the potential shortcomings of antibiotic preharvest treatment, recent research at the farm animal level has shown that antibiotics do have the potential to kill foodborne pathogens inside the body and thus improve food safety.

Most of the antibiotics are routinely administered through animal diets to exert their antimicrobial activities. For example, monensin, one antibiotic in the ionophore class, which might not induce or increase antibiotic resistance and is also not therapeutically used in humans, is approved for use in food animals in the preharvest reduction of foodborne pathogenic bacterial populations.

Poultry

Antibiotics have been put into widespread use in poultry farms for disease prevention and treatment since the 1940s. Campylobacteriosis in humans is frequently acquired via the consumption of undercooked poultry meat contaminated with *Campylobacter jejuni*, identified and isolated from multiple farm animals but most commonly in poultry meat products (Vugia *et al.*, 2007). Effective antibiotics such as erythromycin can be administered in feed or drinking water. Because fluoroquinolones and erythromycins belong to the classes of antimicrobials, these are also used in human campylobacteriosis treatment. The preharvest use of these two antibiotics in poultry needs to be carefully evaluated. Some researchers have pointed out that *Campylobacter* is resistant to macrolides and fluoroquinolones due to the inappropriate use of these antibiotics (Nachamkin, 2008).

Human listeriosis is caused by infections of the bacterium *Listeria monocytogenes*, which result from the consumption of contaminated poultry or ready-to-eat poultry products. Its resistance to many commonly used antibiotics makes treatment of *L. monocytogenes* more difficult. However, a study has found that pediocin and enterocin were more active against *L.monocytogenes* than nisin (Cintas *et al.*, 1998).

Colonization by *Salmonella enterica* serovars Enteritidis and Typhimurium in poultry is relatively common and a major public health concern. Transmission of enteric salmonellosis to humans usually occurs through consumption of contaminated poultry and poultry products, specifically eggs. Owing to the presence of multiple antibiotic-resistant strains of *Salmonella*, antibiotic treatment against this pathogen has been compromised at least to some extent. One major concern is the strain of *Salmonella enterica* serovar Typhimurium (DT104) commonly found in poultry and eggs. DT104 is demonstrated to be resistant to at least five antibiotics – ampicillin, chloramphenicol, streptomycin, sulfonamides, and tetracycline. Preharvest control of DT104 continues to be a significant challenge due to its increased virulence by alterations of inherent pathogenic characteristics and treatment failures resulting from the inappropriate use of antibiotics (Besser *et al.*, 2000). However, combined use of trimethoprim and sulfonamide at the preharvest level might be effective in reducing *Salmonella* in chicken gut. Other possible choices include fluoroquinolones and the third-generation cephalosporins (D'Aoust *et al.*, 2008); **Table 2** shows the preslaughter FDA-approved antibiotics commonly used in the poultry industry (Teshome *et al.*, 2007).

Cattle

EHEC causes infection and various diseases, especially hemorrhagic colitis, in humans with a relatively low infectious dose (Lee and Greig, 2010). EHEC is mainly harbored in the gastrointestinal tracts of healthy cattle and is shed in their feces. The major source of EHEC was traced to ruminant manure, but undeniably, EHEC was also identified in some nonruminant farm animals including swine and fowl due to the cross-contamination spread by ruminant manure. But, since bovine manure is the major source of EHEC contamination in the farm environment and animal meat products, effective preharvest control targeting reduced prevalence and quantity of fecal EHEC excretion by live cattle is crucial. EHEC does not typically exhibit the drug resistance to the use of multiple antibiotics which is frequently found in enteropathogenic *E. coli* and other foodborne pathogens like *Campylobacter* and *Salmonella*, though the use of ionophores does not show significant influence on the prevalence of EHEC (Edrington *et al.*, 2003; LeJeune and Kauffman, 2006). However, it has been shown that almost all EHEC isolates are

Table 2 FDA-approved antibiotics for preharvest subtherapeutic purpose in poultry

Antibiotics	*Dosage in feed (mg head^{-1} day^{-1})*	*Main treatment purpose*	*Withdrawal time (days)*
Arsanilic acid	75–120	Feed efficiency and growth	5
Avilamycin	5–10	Feed efficiency and growth	None
Avoparcin	7.5–15	Feed efficiency and growth	None
Bacitracin	4–50	Feed efficiency and growth	None
Bambermycins	1–20	Feed efficiency and growth	None
Chlortetracycline	10–100	Disease control	None
Lincomycin	2–4	Feed efficiency and growth	None
Oxytetracycline	5–50	Disease control	0–3
Penicillin	2–50	Feed efficiency and growth	None
Roxarsone	23–46	Feed efficiency and growth	None
Spiramycin	5–20	Feed efficiency and growth	None
Avoparcin	7.5–15	Feed efficiency and growth	None
Tylosin	10–110	Feed efficiency, growth, and disease control	None
Virginiamycin	>25	Disease control	None

Table 3 FDA-approved antibiotics for preharvest subtherapeutic use in cattle

Antibiotics	*Dosage in feed (mg head^{-1} day^{-1})*	*Main treatment purpose*	*Withdrawal time (days)*
Bacitracin zinc	35–70	Feed efficiency and growth	None
Bambermycins	1–5	Growth	None
Chlortetracytcline	350	Disease control	2
Laidlomycin	5–10	Feed efficiency and growth	None
Lasalocid	10–30	Feed efficiency and growth	None
Monensin	5–30	Growth and Disease control	None
Oxytetracycline	75	Disease control	None
Tylosin	8–10	Disease control	None
Virginiamycin	10–25	Disease control	None

susceptible to neomycin sulfate (Mora *et al.*, 2005). Neomycin sulfate is an approved antibiotic used in cattle, where it has been demonstrated to significantly decrease the fecal excretion of EHEC (Elder *et al.*, 2002; Woerner *et al.*, 2006). Given appropriate use and quick withdrawal, neomycin appears to be a promising candidate for preharvest use in the cattle industry. **Table 3** shows the commonly used FDA-approved preslaughter antibiotics in the cattle industry (Teshome *et al.*, 2007).

Swine

Antibiotics and other antimicrobial agents have been widely used as preharvest feed additives in the swine industry since the early 1950s. In addition to effectively stimulating swine growth rates and improving reproductive performance, preharvest use of antibiotics is also able to reduce the populations of foodborne pathogens including *Campylobacte*r, EHEC, *Listeria*, and *Salmonella*. Currently, preslaughter use of carbadox, cephalosporins, lincosamides, macrolides, penicillins, pleuromutilins, polypeptides, quinolones, sulfonamides, and tetracyclines is cleared by the Food and Drug Administration in swine feed (Morrison, 2001). Among these approved antibiotics, the feeding of chlortetracycline and tylosin decreased fecal shedding in swine artificially infected with EHEC, and the feeding of spectinomycin in pigs under 4 weeks old and weighing less than 15 lb effectively controlled the infectious bacterial enteritis caused by *E. coli* and salmonella (Friendship, 2006). However, bacitracin did not exert significant antimicrobial effects on EHEC (Irwin *et al.*, 2003). **Table 4** shows the commonly used FDA-approved preslaughter antibiotics in the swine industry (Teshome *et al.*, 2007).

Nonantibiotic Antimicrobials Used in Preharvest Reduction of Foodborne Pathogens in Farm Animals

Because of the increased concern among consumers about antibiotic resistance, several nonantibiotic antimicrobials have been developed and introduced for use by farmers to inhibit preharvest foodborne pathogens. The major potential agents include bacteriocin, bacteriophages, chlorate, vaccines, organic acids, and other plant- or animal-derived products. Some of their advantages and disadvantages will be discussed in this part.

Bacteriocins

Bacteriocins are proteins or peptides with antimicrobial activities produced by certain bacteria for the purpose of inhibiting the growth of their competitive bacterial strains in the environment. Such antimicrobial proteins are able to inhibit the growth of several major foodborne pathogens including EHEC, *Salmonella*, and *Listeria* (Stahl *et al.*, 2004; Patton *et al.*,

Table 4 FDA-approved antibiotics for preharvest subtherapeutic use in swine

Antibiotics	*Dosage in feed (mg head^{-1} day^{-1})*	*Main treatment purpose*	*Withdrawal time (days)*
Apramycin	150	Disease control	28
Arsanilic acid	45–90	Feed efficiency and growth	5
Bacitracin methylene disalicyrate	10–30	Feed efficiency and growth	None
Bacitracin zinc	20–40	Feed efficiency	None
Bambermycins	2–4	Growth	None
Carbadox	50	Disease control	42
Chlortetracycline	>50	Disease control	None
Lincomycin	40–200	Disease control	None
Oxytetracycline	22	Disease control	5
Penicillin	10–50	Feed efficiency and growth	None
Roxarsone	182	Disease control	5
Tiamulin hydrogen fumerate	35–200	Disease control	2–7
Tilmicosin	181–363	Disease control	7
Tylosin	10–110	Feed efficiency, growth, and disease control	None
Virginiamycin	>25	Disease control	None

2007). The application of bacteriocin isolated from *Lactobacillus salivarius* and *Paenibacillus polymyxa* in chicken intestinal tracts has been shown to induce a dramatic reduction in broiler chicken cecal *Campylobacter* colonization (Svetoch and Stern, 2010). Nisin has already been found to be effective in spoilage bacteria reduction in meat and milk, and encapsulated nisin is able to inhibit the growth of *L. monocytogenes* (da Silva Malheiros *et al.*, 2010), although nisin's preharvest application is still under research. However, under the basic principle of bacteriocin, by protecting bacteriocins from ruminal or gastric degradation, once reaching the lower gut, bacteriocins exert their antimicrobial activities by disrupting the cell membranes of target foodborne pathogens. Owing to their nontoxic characteristics on eukaryotic host cells, bacteriocins are considered safe for consumption of meat and meat products.

Bacteriophages

Because they are highly specific in recognizing and injecting 'disrupting DNA' into a host bacterium, bacteriophages can be active against specific bacterial strains. Specificity allows bacteriophages to be used against targeted foodborne pathogens in a mixed population without disturbing the composition of normal gut microflora. In 2007, a phage spray produced by Omnilytics (Salt Lake City, UT), specifically against EHEC in preharvest live cattle, was approved by the FDA. Other studies have also tested the short-term reduction of *Salmonella* colonization in poultry and swine (Callaway *et al.*, 2008). Several researchers have also tested the oral consumption of large doses of bacteriophages and found it to be harmless to animals. Owing to their rapid replication and high level of specificity, bacteriophages can serve as a potential preharvest strategy against foodborne pathogens in agricultural animals. However, the efficacy of bacteriophages against infecting bacteria should be tested in the lab before application. The specificity of bacteriophages is also a disadvantage when a need to target multiple pathogens or causative agents of disease is not confirmed (Inal, 2003). In addition, compared to antibiotics, bacteriophages are more complex organisms that are able to transfer genes between bacteria and induce pathogenic mutation. Only by careful selection of strictly lytic bacteriophages and sequencing their hereditary materials can cross-gene transfer be prevented (Inal, 2003). In comparison with antibiotics, the administration of bacteriophages requires trained personnel, which makes the application of bacteriophages much more difficult for farmers.

Chlorate

Chlorate is the analog of nitrate reductase, both of which can catalyze the conversion from nitrate to nitrite for the anaerobic respiration of *Salmonella* and *E. coli*. The accumulation of chlorite, degraded from chlorate, in the cytoplasm is able to kill bacteria (Stewart, 1988). Some studies have demonstrated that chlorate administered in drinking water significantly reduces EHEC populations in both cattle and sheep in the rumen, intestine, cecum, and feces (Callaway *et al.*, 2003). In addition, preliminary studies examining the use of chlorate in broilers and in turkeys have also yielded promising results (Byrd *et al.*, 2003; Moore *et al.*, 2006). Addition of chlorate to swine diets reduced experimentally inoculated *Salmonella* and EHEC fecal and intestinal populations (Anderson *et al.*, 2001a, b). Currently, chlorate has been licensed as a product but needs evaluation in its application.

Vaccination

Vaccination is the method of inhibiting pathogens by inducing the defense mechanisms of animals' own immune systems. Some specific vaccination has already shown great efficacy in reducing the levels of foodborne pathogens in agricultural farm animals. Vaccines against *Salmonella* strains have been developed for use in swine and dairy cattle (House *et al.*, 2001). More recently, a vaccine designed to inhibit fecal EHEC in cattle has also been developed (Fox *et al.*, 2009). Based on these research efforts, the use of vaccination in preslaughter reduction of foodborne pathogens seems to hold promise. Vaccines made from any one bacteria serovar cannot confer cross-protection against another serovar, no matter how much antigenic similarity there is between them, but more than 2500 serovars of *Salmonella* are found in animals and humans. *Campylobacter jejuni*, *Campylobacter hyointestinalis*, *Campylobacter*

upsaliensis, *Campylobacter lari*, and *Campylobacter fetus* are also found in farm animals (Singh, 2009). As a consequence, super-high specificity and additional costs prevent vaccination from being commonly used in agriculture.

Other natural antimicrobial agents as feed supplements

Organic acids are gradually being employed in animal nutrition for both their nutritional value and their antimicrobial effects. Organic acids produced by the anaerobic microflora of the large intestine include acetate, lactate, malate, and propionate. Some of them have been shown to exhibit antimicrobial activity against gram-negative bacteria such as EHEC, *Salmonella*, and *Campylobacter* (Huyghebaert *et al.*, 2011).

Various plant products can also serve as antimicrobial agents. For example, pasteurized blueberry juices have been shown to have antimicrobial effects on multiple major foodborne pathogens such as *Salmonella* Typhimurium, *C. jejuni*, *L. monocytogenes*, and EHEC (Biswas *et al.*, 2012). Other organics such as cocoa, peanut skin, and the pomace of blueberry and blackberry have also shown antimicrobial activity but need further study. Multiple fruits and vegetables contain phenolic compounds, such as lignins and tannins, both of which are able to affect the gastrointestinal tract via antimicrobial activity (Cueva *et al.*, 2010). Tannins have been found to significantly reduce the population of EHEC in cattle (Wang *et al.*, 2009). Another study showed that highly lignified forages could reduce the shedding period of EHEC (Wells *et al.*, 2005). In addition, most of the essential oils such as citrus oil usually exert their antimicrobial effects by disrupting the cell membrane of bacteria (Turgis *et al.*, 2009). As a result, both organic acids and bioactive phytochemicals have been proposed as potential preharvest agents against foodborne pathogens in farm animals.

Multiple animal-derived products have also been documented as being effective in foodborne-pathogen inhibition. Chitosan, isolated from the exoskeletons of crustaceans and arthropods (insects, spiders, millipedes, and centipedes), has been shown to inhibit the growth and reduce trans-shell penetration of mold and several foodborne pathogens including *S.* Enteritidis, *E. coli*, and *L. monocytogenes* (Leleu *et al.*, 2011). A heat-stable and salt-tolerant peptide, pleurocidin, could be isolated from myeloid cells and mucosal tissue of both vertebrates and invertebrates, whose inhibitory effect against different foodborne pathogens such as *L. monocytogenes* and EHEC has already been documented (Jung *et al.*, 2007). Other products such as defensin, lactoferrin, lactoperoxidase, lysozyme, and ovotransferrin have all shown their potential in meat or the preservation of milk products and in reducing multiple foodborne pathogens, but their application in preharvest control of foodborne pathogens in farm animals needs to be studied further.

Antibiotics Used as Veterinary Medicine

The therapeutic treatment of individual sick animals with antibiotics or other effective antimicrobials is essential and is employed all over the world. In 2007, global sales of animal health products included: Western Europe (US$110 million), North America (US$725 million), the Far East (US$435 million), Latin America (US$275 million), Eastern Europe (US $150 million), and the rest of world (US$80 million) (Evans *et al.*, 2008). Antibiotics used for veterinary therapy are often administered orally through feed and water, or by injection, in order to relieve animals' suffering and reduce production losses. However, if certain livestock or poultry are sick, the whole herd or flock needs to be treated to prevent the spread of disease. In these cases, antibiotic treatment is usually given in high doses, intermittently within a relatively short period of time. Broad-spectrum or combinations of antibiotics are commonly used in such situations when the specific pathogens of concern are unidentified or in doubt. Worldwide estimated sales of antibiotic products in 2007 include macrolides (US$629 million, 22.7%), penicillins (US$550 million, 19.8%), tetracyclines (US$533 million, 19.2%), quinolones (US$531 million, 19.1%), and sulphonamides (US $118 million, 4.3%), with the leading products being oxytetracycline (US$272 million), enrofloxacin (US$259 million), chlortetracycline (US$257 million), ceftiofur (US$200 million), florfenicol (US$114 million), and tulathromycin (US $90 million) (Evans *et al.*, 2008). However, a narrow-spectrum antibiotic able to target a specific pathogen involved in animal disease should be the first choice and could also lower the risk level of antibiotic resistance. The major animal diseases requiring therapeutic use of antibiotics are respiratory and enteric diseases in calves and pigs, necrotic enteritis in poultry, and mastitis in dairy cattle.

Approved Antibiotics against Livestock Diseases

Antibiotics are commonly used therapeutically against a broad range of infectious diseases in livestock, including cattle, pigs, sheep, and horses, but currently treatment using antibiotics is becoming more pathogen-specific under the supervision of veterinarians. There are three major therapeutic patterns of antibiotic use in livestock: prophylaxis, which targets exposed healthy animals before onset of risk diseases; metaphylaxis, which is the mass treatment of animal populations currently suffering from diseases before the onset of blatant illness; and treatment for animals experiencing acute clinical diseases. The dose regimen for these three therapeutic uses of antibiotics relies on the expected minimum inhibitory concentration of the target pathogens expected to be implicated.

Three of the most prevalent infectious diseases in livestock are respiratory disease, enteric disease, and mastitis (Giguère *et al.*, 2006; Radostits *et al.*, 2007; Zimmerman *et al.*, 2012).

Mannheimia, *Pasteurella*, and *Haemophilus* are three major pathogens responsible for respiratory disease in cattle, and they constitute one of the biggest health challenges for dairy cattle (Barrett, 2000; Rerat *et al.*, 2012). Tetracyclines, especially chlortetracycline and oxytetracycline, are commonly added to feed and water to treat cattle respiratory disease (Apley and Coetzee, 2006). Other approved antibiotics for bovine respiratory disease treatment include aminoglycosides, especially spectinomycin and neomycin, macrolides in the form of tilmicosin and erythromycin, tylosin, penicillins (amoxicillin and ampicillin), cephalosporin especially ceftiofur, and sulfonamides (sulfamethazine and sulfadimethoxine). Besides

these, florfenicol and enrofloxacin are also approved by the FDA (Apley, 2001).

Apart from respiratory disease, enteric disease involving *E. coli* and *Salmonella* is also common in livestock. Neomycin, in the aminoglycoside class, is commonly used as a water additive against these enteric disease. Chlortetracycline and oxytetracycline under the tetracycline class are also approved by the FDA for the treatment of these enteric bacterial pathogens (Apley, 2001). Infectious agents include rotavirus, coronavirus, and cryptosporidium, for which antimicrobials are still under research.

Mastitis is a major problem in dairy cattle and can impair normal lactation. Pathogens including *Pseudomonas*, *Staphylococcus*, *Mycoplasma*, *Pasteurella*, *E. coli*, and *Streptococcus* cause mastitis (Kandasamy *et al.*, 2011). Novobiocin, pirlimycin, and streptomycin are FDA-approved therapeutics for treatment of mastitis. Any of these antibiotics can be used alone or in combination with penicillin (Wagner and Erskine, 2006). Other approved intramammary antibiotics against mastitis are amoxicillin, cephapirin, cloxacillin, hetacillin, and lincomycin (Wagner and Erskine, 2006). Erythromycin is also approved by the FDA in the form of an injectable antibiotic. In addition to these, beta-lactams, cephalosporins, neomycin, and tetracyclines are also recommended.

In addition to these three major livestock diseases, footrot, metritis, pleuropneumonia, and colitis are also common in farm animals. In the case of footrot (infectious pododermatitis), ceftiofur, injectable oxytetracyclines, tylosin, erythromycin, and trimethoprim-sulfonamide combinations are FDA-approved antibiotics. Metritis is also a common disease in dairy cows. Tylosin and injectable oxytetracycline are the only two products approved by the FDA for the treatment of metritis. Procaine penicillin, amoxycillin, tetracyclines, trimethoprim, and tilmicosin are usually used for treatment of pleuropneumonia in swine (Constable *et al.*, 2008). For colitis, caused by *Serpulina*, dimetridazole, tiamulin, and lincomycin are three common antibiotics being used currently (Friendship, 2006; Burch *et al.*, 2008). For effective control of lactic acidosis in the lambs, virginiamycin is used as a feed additive, though therapeutic use of antibiotics is relatively rare in sheep or goat production due to the high cost. For horses, gentamicin is injected routinely for foal sepsis, whereas virginiamycin is given in feed against laminitis (Apley, 2001).

Approved Antibiotics against Poultry Diseases

Since the 1940s, antibiotics have also been used in poultry farming for both therapeutic and prophylactic purposes. But due to recent improvements in husbandry, hygiene conditions, and farm management, bacterial diseases in poultry have been better controlled with less reliance on antibiotics. However, antibiotic therapy is still useful and required when alternative disease control methods such as vaccination fail. Important and common poultry diseases include necrotic enteritis, chronic respiratory diseases, gangrenous dermatitis, fowl cholera, and avian influenza (Pattison, 2008; Saif *et al.*, 2008). Antibiotic treatments for these diseases are predominantly done through supplementation in either water or feed. Most of the effective and common antibiotics are being used as therapeutic intervention in poultry diseases (Hofacre, 2006).

Necrotic enteritis is the most common infectious disease in modern poultry farms and can result in huge financial losses. *Clostridium perfringens* is the major causative bacteria of necrotic enteritis. However, the occurrence of this disease is always associcated with the outbreak coccidial infection, which induces the gut to be more susceptible to *C. perfringens* (Dahiya *et al.*, 2006). Tetracycline, streptomycin, neomycin, bacitracin, and avilamycin in feed are the four most common antibiotics targeting necrotic enteritis (Wages, 2001). Control of *C. perfringens* infection together with prevention of coccidiosis could be accomplished by adding antibiotics such as virginiamycin (20 g ton^{-1}), bacitracin (50 g ton^{-1}), and lincomycin (2 g ton^{-1}) to feed (Wages, 2001). The ionophore classes of anticoccidial compounds are also effective in preventing coccidial infections. In addition, probiotics administration is also used as an effective method to both prevent and treat clinical necrotic enteritis.

Controlling respiratory disease in poultry is important to ensure maximum economic profits. Respiratory disease in poultry is induced by several complex factors including viral presence, stress, and dietary changes, but *Mycoplasma gallisepticum* infection is responsible for most respiratory diseases in poultry (Animal Health National Program, 2007). A variety of antibiotics such as tylosin, tiamulin, tilmicosin, aivlosin, tetracyclines (mainly doxycycline, chlortetracycline, and oxytetracycline), spiramycin, erythromycin, gentamicin and ketasamycin, neomycin, and colistin are used, both alone and in various combinations, to control and cure respiratory disease in poultry (Loehren *et al.*, 2008). But fluoroquinolones (enrofloxacin, danofloxacin, norfloxacin, flumequin, etc.) are used in the withdrawal phase.

Gangrenous dermatitis is caused by contamination of more than one type of bacteria including *Clostridium septicum*, *Staphylococcus aureus*, and *E. coli* (Li *et al.*, 2010). Owing to the involvement of various bacterial pathogens in gangrenous dermatitis, broader-spectrum antibiotics are needed for the treatment and control of this disease. Preferred effective antibiotics include erythromycin, penicillin, and tetracycline, especially oxytetracycline (Wages, 2001).

Pasteurella multocida is the causal agent of fowl cholera (Siti and Robert, 2000). This contagious bacterial disease usually results in high morbidity and mortality rates. Sulfonamides are commonly used for early treatment (Wages, 2001). Sulfaquinoxaline sodium, together with sulfamethazine and sulfadimethoxine in feed or water, is commonly used to control fowl cholera in poultry (Loehren *et al.*, 2008). Tetracycline and norfloxacin administered via feed and water or administered parenterally are also helpful in controlling fowl cholera. And combination streptomycin-dihydrostreptomycin injection is effective in ducks.

Other useful antibiotics include lincomycin, virginiamycin, spectinomycin, tylosin, and erythromycin, which are mainly used as gram-positive antimicrobials. In addition, gentamicin and ceftiofur are the most commonly used in *in ovo* injectable antibiotics (Loehren *et al.*, 2008). In the case of protozoan diseases, which include coccidiosis caused by *Eimeria* and histomoniasis caused by *Histomonas meleagridis*, coccidiostats and histomonostats in the form of feed additives are used as effective antimicrobials (Wages, 2001).

Limitations of Antibiotic Use in Animals

Antibiotics employed for infectious disease prevention and treatment in large groups of farm animals such as cattle, swine, and chicken are usually administered orally in drinking water or as feed additives, and sometimes also via intramammary infusions. These antibiotics are likely to result in residue in edible tissues such as milk and eggs. Multiple antibiotic residues are harmful during the development of human organs, as well as the nervous and reproductive systems. As a result, infants and young children are most susceptible to these residue compounds because of their weak body protection. By establishing preslaughter withdrawal periods, restricting certain antibiotics used in laying hens, and discarding milk produced after intramammary infusions of antibiotics in lactating animals, these harmful antibiotic residues could be reduced or even eliminated (Page and Gautier, 2012).

Public Health Concerns about Antibiotic Resistance

The use of antibiotics, first introduced in the mid-twentieth century, was considered the single most effective medical strategy for dramatically reducing morbidity and mortality in both humans and animals (Andersson and Hughes, 2010). However, the overuse of antibiotics has caused increased antibiotic resistance among multiple human pathogens. Whether or not the pool of resistance genes generated by use of antibiotics in farm animals has induced the prevalence of failures in therapy for human infectious diseases is compounded by the widespread use of antibiotics in livestock and poultry is still controversial. So far, judging from numerous journal articles, reviews, conference reports, newspapers, and TV reports, the inappropriate use of antibiotic in farm animals and its potential risk to human health have become the greatest public health concern among both consumers and scientists. Governments worldwide have already sought regulatory and legal authority in order to restrict or even abolish the nontherapeutic use of antibiotics (Page and Gautier, 2012).

Conclusion

Antimicrobial substances, especially antibacterial agents, are commonly employed worldwide to improve the performance, health, and production of livestock, dairy cattle, and poultry. These agents are used to protect against illness, help reduce significant agricultural losses, and prevent foodborne infections in humans. For the subtherapeutic use of antimicrobials, preharvest treatment for both promotion of animal growth and inhibition of colonization and cross-contamination of foodborne pathogens have drawn great attention because of the urgency of the situation as well as the effectiveness of antibiotics in human disease treatment. However, some agents used in animal agriculture belong to classes also employed in human medicine, such as macrolides, penicillins, sulphonamides, and tetracyclines. This dual use of antibiotics and the common concern of multiple antibiotic resistance in human pathogens and the potential impact of antibiotic residues in food on public health are controversial and have raised concerns. As a result, efforts to develop alternatives such as plant-derived antimicrobial agents and biopreservatives are underway. Although the thoughtful and measured therapeutic use of antibiotics or other effective antimicrobials is essential to livestock producers, regulatory bodies, and consumers, narrow-spectrum antibiotics remain the first choice, and a comprehensive understanding of the use of narrow-spectrum antibiotics in preharvest-level farm animal production, along with proper guidance from the veterinary profession, are vital to solving this complex issue.

See also: Food Safety: Emerging Pathogens. Food Security: Postharvest Losses. Poultry and Avian Diseases. Vaccines and Vaccination Practices: Key to Sustainable Animal Production

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Animal Health: Mycotoxins

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Glossary

Adducts A chemical compound that forms from the addition of two or more substances. The product of an addition reaction.
Bioavailability The degree to which a drug or other substance becomes available to the target tissue after administration.
Carcinogenicity The ability or tendency to produce cancer.
Fatty degeneration The accumulation of fat globules within the cells of an organ, such as the liver or heart, resulting in deterioration of tissue and diminished functioning of the affected organ.
Hyperestrogenism An abnormally high presence of estrogen. Condition characterized by and caused by excessive secretion or intake of estrogen.
Teratogenic Of, relating to, or causing malformations of an embryo or a fetus.
Water activity The ratio between the vapor pressure of a material (p) and the vapor pressure of pure water under the same conditions. Water activity values range from 0 (zero) to 1 (one).

Main Toxigenic Fungi and Mycotoxins

Mycotoxins are organic compounds of low molecular weight, produced as secondary metabolites by several species of fungi, showing various chemical structures (**Figure 1**) and occurring in agricultural commodities, especially in cereal products. Human and animal diseases caused by mycotoxins are called mycotoxicoses, which are diffuse syndromes mainly caused by lesions in organs, such as liver, kidneys, epithelial tissue (skin and mucous membranes), and central nervous system, depending on the type of the toxin (Diaz, 2005).

About 100 000 fungi species have already been identified, from which more than 200 may be considered potentially toxic, but only about 5% are known to produce toxic compounds or classes of compounds that cause adverse effects in animals and humans in different parts of the world (Gompertz *et al.*, 2008). However, the most important mycotoxins are aflatoxins, fumonisins, ochratoxins (OT), zearalenone, and trichothecenes, because of their frequent occurrence in feedstuffs and the high toxigenic potential demonstrated in domestic animals.

Contamination of feedstuffs with toxigenic fungi may occur in different phases of production and processing, from sowing to transportation and storage. Besides, as mycotoxins are generally highly chemically stable, they may remain in feedstuffs even after fungi are removed by usual processing and packaging processes.

Mycotoxicoses may be observed in different animal species, and the symptoms of intoxication vary depending on the type of mycotoxin, as presented in **Table 1**. However, the toxicity of some individual mycotoxins can be enhanced in a synergistic or additive manner when they occur as cocontaminants and are consumed by different animal species (Grenier and Oswald, 2011).

The economic impact of mycotoxins in animal health includes mortality of domestic animals, increased costs with veterinary care, and decreased production efficiency. Acute mycotoxicoses are rare in animal production, and chronic exposure to low levels of mycotoxins is responsible for reduced productivity and increased susceptibility to infectious diseases (Oswald *et al.*, 2005).

Toxigenic Fungi

The name fungi is given to a group of living organisms including microfungi (molds and yeasts) and macrofungi (mushrooms). Filamentous microfungi (molds) are the ones that produce mycotoxins. Yeasts are not known to produce mycotoxins, although they are of considerable interest in the food industry. Unlike plants, fungi do not contain chlorophyll, do not accumulate starch, and do not have cellulose in their cell walls. However, they resemble animal cells for being able to store glycogen, and contain chitin, a polymer that is a glucose derivative. Thus, all fungi live a heterotrophic existence in nature, either as parasites or saprobes, dependent on living or dead organic matter for their nutrients.

There are a number of essential phases in the life of a fungus: spore germination, mycelium vegetative growth, spore-bearing development, spores production, liberation, and dispersal. The reproductive structures of fungi, called spores (propagules), are able to reproduce and generate new cells in favorable environmental conditions. According to their origin, spores can be sexual or asexual. Fungi are classified according to their morphology and chemistry and, more recently, to their molecular biology. One of the most current core features show four groups in the Kingdom fungi: Chytridiomycota, Zygomycota, Basidiomycota, and Ascomycota. Micotoxigenic species are mostly found in the Ascomycota Division; however, mushrooms are found within the Basidiomycota Division (macrofungi), producers of mycetisms.

The main mycotoxin-producing fungi species belong to the genera *Aspergillus*, *Penicillium*, *Fusarium*, *Alternaria*, *Claviceps*, *Myrothecium*, *Stachybotrys*, *Phoma*, *Trichotecium*, *Cephalosporium*, *Trichoderma*, *Cladosporium*, and *Pithomyces*. However, the

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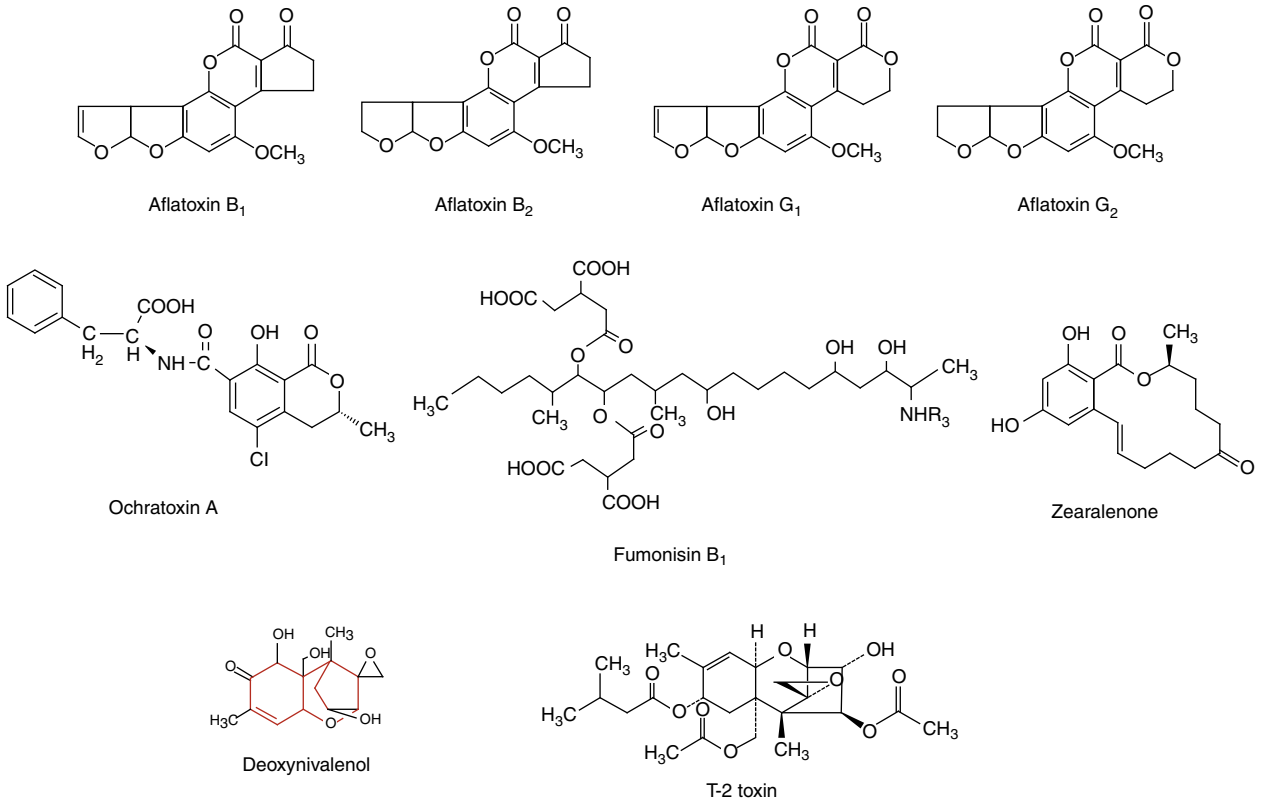


Figure 1 Chemical structures of main mycotoxins.

Table 1 Main toxigenic fungi, mycotoxins, and respective biological effects in susceptible species

Fungi species	*Mycotoxin*	*Biological activity*	*Main susceptible animals*
Aspergillus flavus and *Aspergillus parasiticus*	Aflatoxins	Hepatotoxicity and carcinogenicity	All species
Fusarium graminearum and *Fusarium culmorum*	DON (Vomitoxin)	Dermatotoxicity and immunosuppression	Swine
Fusarium sporotrichioides	Toxin T-2	Alimentary Toxic *Aleucia* (ATA)	Swine and poultry
Fusarium verticillioides	Fumonisins	Leucoencephalomalacea, pulmonary edema, and carcinogenicity	Swine and equine
Penicillium verrucosum and *Aspergillus ochraceus*	Ocratoxin A	Nefrotoxicity	Swine and poultry
Fusarium graminearum	Zearalenone	Estrogenic	Swine and bovine

genera *Aspergillus*, *Penicillium*, and *Fusarium* are considered the most important producers of mycotoxins. In general, these species have worldwide distribution, although some of them are specific to certain countries due to climate differences and local agricultural practices. Microscopic structures of the three genera are illustrated in Figure 2.

The development of toxigenic fungi and mycotoxin production are dependent on complex factors such as: (1) type of substrate; (2) physical factors: water activity, temperature, pH, aeration, and relative humidity; and (3) biological factors: genetic potential to produce mycotoxin, viable spores, presence of insects and mites, fungi interaction, mechanical damage, and storage time (Figure 3). However, humidity and temperature are the most influential factors in mycotoxin production. The water existing in foods is not always available to the fungus. Some substrates strongly retain water, impairing its absorption by the fungus. In others, water may be almost fully available and can be measured for each substrate. This measure is called water activity of the substrate.

The dependence of fungal growth on water availability is variable, with some species growing at water activity from 0.97 to 0.58. The minimum water activity necessary for the growth of the main toxigenic fungi is 0.76, and the minimum water activity for the growth of *Aspergillus flavus* and *Fusarium verticillioides* is 0.78 and 0.87, respectively. It is noteworthy that Aw values for the production of mycotoxins are often higher than those needed for the growth of the producer fungi. Table 2 shows temperatures and minimum water activity requirements for growth and mycotoxin production by the major toxigenic fungi.

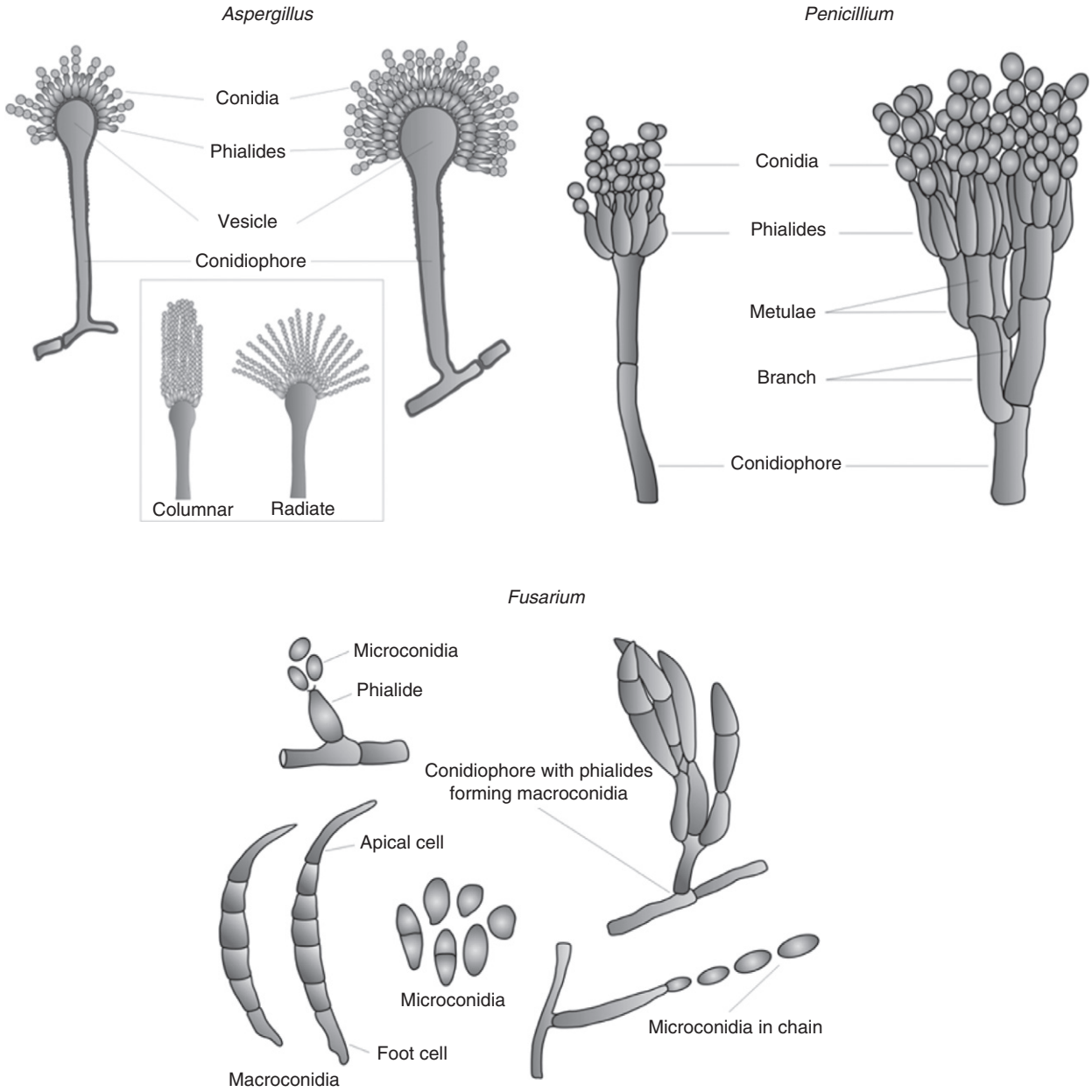


Figure 2 Microscopic structures fungi of genera *Aspergillus*, *Penicillium*, and *Fusarium*.

Toxigenic fungi may be present in food without producing any toxin. Thus, the demonstration of mold contamination is not the same as that of mycotoxin contamination. In relation to aflatoxins, some authors point out that, in average, 50% of isolated strains are producers of aflatoxins in foods (Geisen, 1998). It is noteworthy that the absence of visible signs of mold formation does not necessarily mean that the food is free of toxins, since they can remain in the product even after the fungus disappears. A particular mycotoxin can be produced by more than one species of fungi. For example: aflatoxin can be produced by *A. flavus*, *Aspergillus parasiticus* and *Aspergillus nomius*. The same species of *Fusarium* can produce more than one toxin. Thus, *F. verticillioides* can produce fumonisins, zearalenone, and moniliformin.

Aflatoxins

Aflatoxins are produced by fungi in the genus *Aspergillus*, mainly species *A. flavus* and *A. parasiticus*. These toxins were discovered in 1960, after an outbreak in turkeys in England (Turkey X disease). In this outbreak, thousands of birds died after the intake of Brazilian peanut meal. Nowadays, 20 similar compounds are called aflatoxins, although the most important types are aflatoxins B_1, B_2, G_1, and G_2. Aflatoxin B_1 (AFB_1) is the most frequent type naturally found in cereals, and the one with the greatest toxigenic power, followed by G_1, B_2, and G_2. Aflatoxin M_1 (AFM_1), a detoxification product present in milk as a result of AFB_1 biotransformation, is also as toxic as AFB_1.

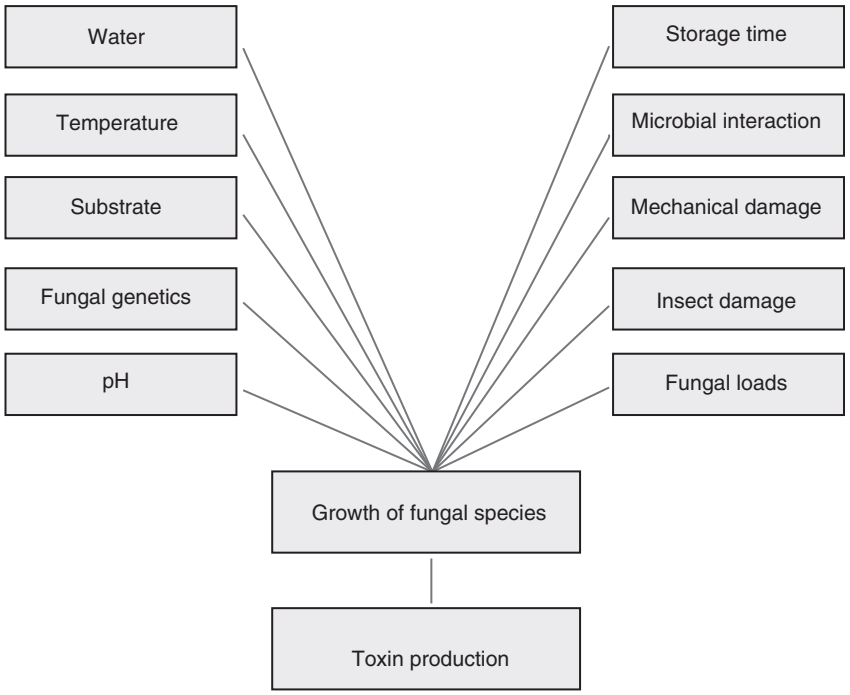


Figure 3 Factors affecting fungal growth and production of mycotoxins.

Table 2 Temperature and minimal water activity (a_w) on fungal growth and mycotoxin production by mean toxigenic fungi

Fungi	*Temperature (°C)*		*Minimum Aw for*		*Toxin*
	Range	*Optimum*	*Growth*	*Toxin production*	
Aspergillus flavus	10–45	33	0.78–0.80	0.83–0.87	Aflatoxins type B
Aspergillus parasiticus	12–42	32	0.78–0.82	0.87	Aflatoxins types B, G
Aspergillus ochraceus	10–35	25	076–0.81	0.83–0.87	Ochratoxin A
Penicillium verrucosum	0–31	20	0.81	0.83–0.90	Ochratoxin A
Penicillium expansum	25–30	25	0.83–0.85	0.99	Patulin
Fusarium verticillioides	2–37	15–30	0.87	0.90	Fumonisins Zearalenone Moniliformin Zearalenone
F. graminearum	5–35	24–26	0.90	0.99[a]	DON, DAS Moniliformin
F. poae	2–39	22–28	0.89	0.98[a]	T-2, DAS Nivalenol

[a]Optimum for toxin production.
Abbreviations: DON, deoxynivalenol; DAS, diacetoxyscirpenol.

Aflatoxins are characterized by their high toxicity. All domestic and laboratory species are sensitive to the acute toxic, mutagenic, or carcinogenic effects of these compounds, whose target organ is the liver. Aflatoxins are also a great public health concern, as they are involved in the etiology of liver cancer in humans following the ingestion of contaminated foodstuffs.

The genus *Aspergillus* and their toxins are distributed worldwide in foodstuffs and animal feed, but may predominantly be found in tropical and subtropical climates. Plants get contaminated by means of contact with fungal spores in the environment, mainly in the soil, during harvesting and drying. The use of inadequate agricultural practices that increase contact of the products with soil, as well as insect damage to the surface of grains, and inadequate storage in humid and unventilated conditions are pointed out as the main causes that favor contamination and growth of toxigenic fungi.

It is important to emphasize that aflatoxin concentration tends to increase throughout the chain of production and commercialization of animal feed. Jones *et al.* (1982) analyzed raw material and feed production, and the same feed stored in the poultry facilities. They observed that mean contamination was equal to 1.2, 6.0, and 8.8 $\mu g\,kg^{-1}$ aflatoxin, respectively. The same study showed a strong correlation between the period of storage in the poultry facility and aflatoxin frequency

and concentration in the feed. These authors reported that optimal conditions for aflatoxin production in stored feed were 70–89% relative humidity, and temperatures between 19 and 27 °C.

Ochtatoxin A

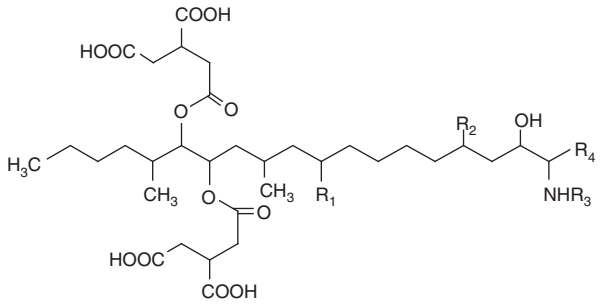
OT belongs to a large family of mycotoxins that encompasses more than 20 different metabolites among which ochratoxin A (OTA) is the most naturally occurring and the most toxic one. OTs are produced by *Aspergillus* species, mainly by *A. ochraceus* and *A. westerdijkiae*, which are usually found on coffee, cocoa, spices, and dried fruits in tropical regions of the globe. Many *Penicillium* species also produce OTs, such as *Penicillium verrucosum*, which develops on cereals during storage in temperate regions of the world, and *P. nordicum*, which is found on cheese and fermented meat. One of the main features of OTs is that they are not degraded during most food-processing steps, such as fermentation and cooking, and they are thus frequently encountered in food and feed. Cereals, wine, beer, and pork meat are, in this order of importance, the main sources of human exposure to OTs. In addition, another important feature of OTs is that they readily bind to proteins and therefore have also been detected in milk.

OTs are composed of a pentaketide dihydroisocoumarin moiety linked to the amino acid phenylalanine by an amide bond at C7. There is a chlorine atom on one of the hydroisocoumarin rings that strongly contributes to toxicity. Ochratoxin B, which is the dechlorinated form of OTA, is at least 10 times less toxic than OTA.

Fumonisins

Fumonisins constitute a large family of mycotoxins mainly produced by *F. verticillioides*, *Fusarium proliferatum* and other *Fusarium* species. These fungi species are important pathogens of corn responsible for '*Fusarium* kernel rot' or 'pink ear rot.' Fumonisins have also been isolated from cultures of *Alternaria alternata* and *Aspergillus niger* and mainly contaminate grapes. Contamination can occur at different stages, such as crop growth, harvesting, or storage, depending on temperature and humidity. However, development of *Fusarium* species mainly occurs before harvest or in the early periods of storage, when humidity levels are still high ($a_w > 0.9$). Human exposure to fumonisins is of greater importance in countries of South America, Asia, and Africa due to weather and storage conditions, and to higher consumption of maize-based products, as well.

The fumonisin family encompasses 28 structurally related metabolites that can be classified in four series: A, B, C, and P. All of them share a long carbon chain backbone with an amine, but have different hydroxyl, methyl, and tricarboxylic acid side chains (Figure 4). The A series has an acetylated terminal amine group in C2 position, whereas B and C series have free amino groups, and P series have a 3-hydroxypiridinium moiety at this position. C series differ from the rest in that their acyl chain is condensed with glycine instead of an alanine residue, and these compounds have a C19 backbone chain instead of C20. One particular feature of



	R_1	R_2	R_3	R_4
A_1	OH	OH	CH_2CO	CH_3
A_2	H	OH	CH_2CO	CH_3
B_1	OH	OH	H	CH_3
B_2	H	OH	H	CH_3
B_3	OH	H	H	CH_3
B_4	H	H	H	CH_3
C_1	OH	OH	H	H
C_3	OH	H	H	H
C_4	H	H	H	H

Figure 4 Chemical structures of fumonisins.

fumonisin structure is the presence of two tricarbollylic esters on C14 and C15, which are rare in natural products. Type B fumonisins are the most abundant in naturally contaminated commodities. Esterification of the backbone structure produces FB_4, and further oxidation produces FB_2, FB_3, and FB_1. Among type B fumonisins, fumonisin B_1 (FB_1) represents 70% of total fumonisin content, and FB_2 generally accounts for up to 25%. Concerning the other series, only C fumonisins have been detected in corn samples, but at much lower concentrations.

Zearalenone

These are a group of mycotoxins produced by several *Fusarium* species, such as *Fusarium graminearum*, *Fusarium culmorum*, *Fusarium crookwellense*, *Fusarium equiseti*, *Fusarium cerealis*, and *Fusarium semitectum*. In fact, they are produced by most of the toxigenic *Fusarium* species and therefore they are usually detected in combination with other fusariotoxines, such as trichothecenes and fumonisins. As they are produced by *Fusarium* species, zearalenones are mostly encountered in temperate and warm countries on cereal crops, especially on corn, as well as on wheat, oats, and soybean. Production of these mycotoxins mainly takes place in the field, but may also occur during improper cereal storage. Human exposure to zearalenones is essentially caused by consumption of contaminated raw maize and, to a lesser extent, of corn- and wheat-derived products, and beer. The main concern related to exposure to zearalenones is due to the fact that they are one of the most potent families of nonsteroidal naturally occurring estrogens. Zearalenones have a resorcinol moiety fused to a 14-member macrocyclic lactone. There are six major members of this family: zearalenone, α-zearalenol, β-zearalenol, α-zearalanol, β-zearalanol, and zearalanone (Figure 5).

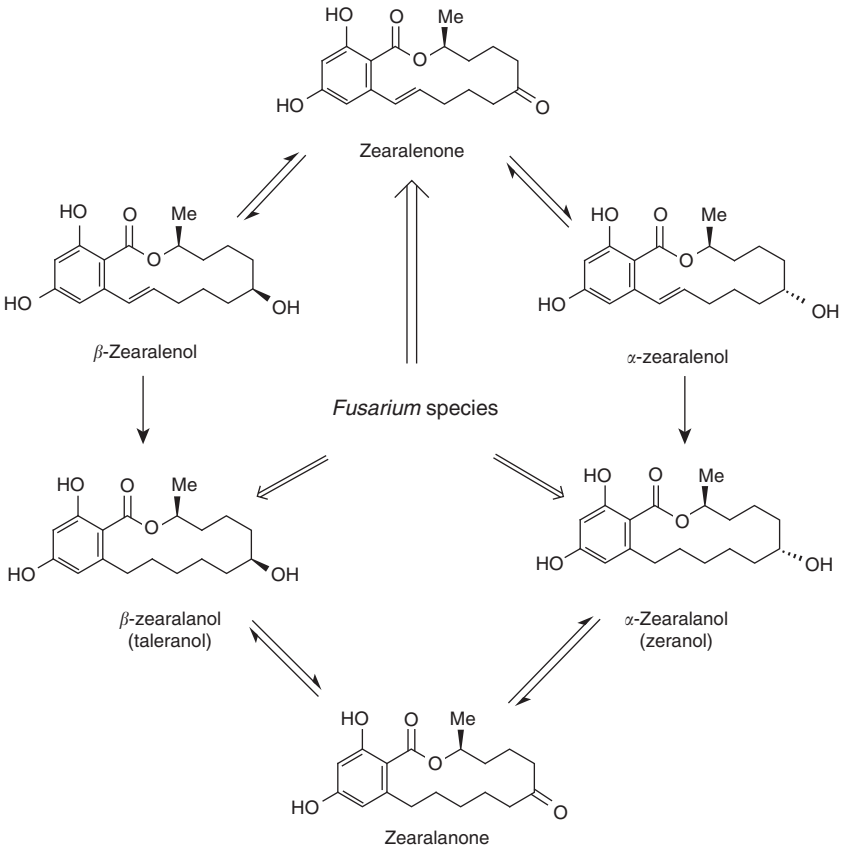


Figure 5 Chemical structures of major members of the zearalenone group.

Trichothecenes

Trichothecenes represent a large family of over 150 secondary metabolites produced worldwide by fungi of different and taxonomically unrelated genera. *Fusarium* species are the most commonly occurring of trichothecene-producing fungi. These species are important plant pathogens that particularly contaminate cereals such as wheat, barley, oats, and maize. They are also responsible for *Fusarium* Head Blight disease, which causes important crop losses worldwide. All trichothecenes are sesquiterpenes, which share a common structural backbone made of a tricyclic nucleus, called trichothecene and, usually, a double bond at C-9,10, and an epoxide at C-12,13 (**Figure 6**). The latter is considered to be very important for toxicity. Based on differences in the position and number of hydroxylations, and the number and complexity of esterifications as well, trichothecenes can be classified in four groups: type A, B, C, and D. Types A and B are the most commonly occurring, and they are generally produced by *Fusarium* species, with *Fusarium sporotrichoides* and *Fusarium poae* producing type A trichothecenes, whereas *F. graminearum* and *F. culmorum* produce type B trichothecenes.

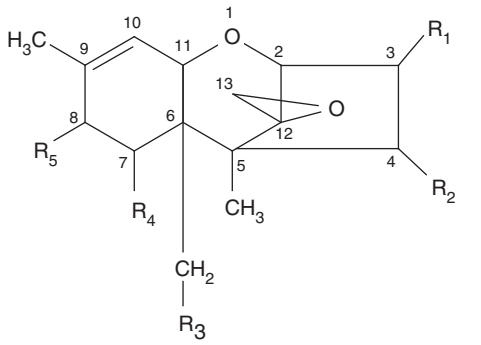
Type A trichothecenes lack a ketide group at C-8 position. The most representative mycotoxins of Type A trichothecene group are T-2 toxin, its hydrolyzed derivate, HT-2, and diacetoxyscirpenol. Type B trichothecenes have a ketide group at C-8 position. Deoxynivalenol (DON), nivalenol (NIV) and their acetylated derivatives (3-acetyldeoxynivalenol, 15-acetyldeoxynivalenol, and fusarenone X, respectively) are the most commonly occurring and the best-characterized mycotoxins of this group.

Occurrence of Mycotoxins in Feedstuffs

Contamination of feedstuffs by toxigenic fungi and their mycotoxins is a worldwide concern, as observed in **Figure 7**. The Food and Agriculture Organization of the United Nations estimated that more than 25% of the worldwide food production is contaminated by some kind of mycotoxin (Benitéz, 2002).

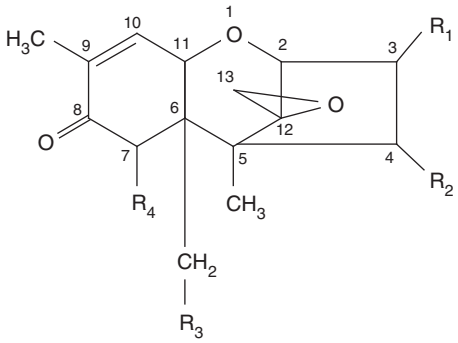
Toxigenic fungi inhabit the most various substrates such as soil, water, vegetables, humans, and animals. From their natural habitat, fungi spread in nature through means like air (the most important mean), water, insects, mites, humans, and animals. They are able to contaminate foods during various production and processing phases, from harvest to transport and storage, especially under favorable conditions of humidity and temperature.

In general, cereals produced in hot and humid regions, where disabled and inappropriate farming techniques and storage conditions, make feedstuffs more susceptible to fungal growth and mycotoxin production. Geographically, within the genus *Aspergillus*, *A. flavus* and *A. parasiticus* species are often



Group A trichothecenes

	R_1	R_2	R_3	R_4	R_5
T-2 toxin	OH	OAc	OAc	H	Isoval-eroxy
HT-2 toxin	OH	OH	OAc	H	Isoval-eroxy
Diacetoxy-scirpenol	OH	OAc	OAc	H	H
Monoacetoxy-scirpenol	OH	OH	OAc	H	H
Trichodermol (Roridin C)	H	OH	H	H	H



Group B trichothecenes

	R_1	R_2	R_3	R_4
Nivalenol	OH	OH	OH	OH
Monoacetylnivalenol (fusarenon-X)	OH	OAc	OH	OH
Diacetylnivalenol	OH	OAc	OAc	OH
Deoxynivalenol (vomitoxin)	OH	H	OH	OH

Figure 6 Chemical structures of trichothecenes types A and B.



Figure 7 Global distribution of main mycotoxins.

isolated in tropical and subtropical regions, are infrequent in temperate regions, and are rarely isolated in cold climates. *Aspergillus ochraceus* and *P. verrucosum* species are frequent in tropical and temperate regions, respectively. In turn, species of the genus *Fusarium* are distinguished by adapting to different environmental conditions. Thus, *F. verticillioides* species (formerly *F. moniliforme*) predominates in humid tropical and temperate regions, but is infrequent in cold-temperate zones;

F. graminearum, in tropical to temperate regions; *F. poae*, in cold-temperate climate, and *Fusarium sporotrichioides* in cold climates.

Table 3 shows the results of some studies on aflatoxin, fumonisin, and ochratoxin levels in feedstuffs and animal feed in countries worldwide. These results indicate that a large percentage of samples show mycotoxin concentrations that may potentially affect animal productivity. Besides, mycotoxins residues may accumulate in animal tissues or be shed in milk or eggs of animals that ingested feed containing mycotoxins. Foods of animal origin contaminated with residues are additional sources of exposure to humans who ingest these products.

Corn is the main cereal used in animal feed that is susceptible to contamination by toxigenic fungi, although other products may also show fungi and mycotoxins, such as sorghum, cotton meal, and soybean meal, as well as prepared feed. It is important to emphasize that the production of mycotoxins is directly related to the growth of the fungi, whereas the presence of the fungi does not necessarily indicate that the mycotoxin is present, because many toxins are thermostable and are not destroyed in feed grinding and pelletizing processes.

Considering the risks posed by mycotoxins to animal-raising activities, several countries have determined tolerance limits for these toxins in ingredients and animal feed, as shown in Table 4.

Toxicological Effects of Mycotoxins

Aflatoxin

After oral ingestion, mycotoxins may be absorbed at different proportions, with some of them being biotransformed before

Table 3 Global mycotoxin occurrence in main feedstuffs samples used in animal nutrition

Region	*Type of mycotoxin*	*Average concentration ($\mu g\ kg^{-1}$) in feedstuffs*			
		Corn	*Soybean meal*	*Wheat/bran*	*Finished feed*
North America	AFLA	17	ND	1	7
	ZEN	74	8	34	157
	DON	857	179	782	1.125
	FUM	533	NA	NA	1.111
	OTA	1	1	ND	NA
South America	AFLA	2	ND	ND	2
	ZEN	75	44	68	115
	DON	37	61	501	33
	FUM	2.966	12	70	1.569
	OTA	16	ND	13	3
Central Europe	AFLA	1	ND	ND	ND
	ZEN	47	2	10	56
	DON	1.028	98	848	533
	FUM	1.308	NA	89	131
	OTA	ND	7	16	2
Southern Europe	AFLA	3	ND	1	3
	ZEN	61	NA	NA	13
	DON	468	101	452	158
	FUM	2.035	291	116	1.505
	OTA	4	ND	ND	1
North Asia	AFLA	13	ND	ND	5
	ZEN	292	22	31	213
	DON	1.062	56	799	741
	FUM	2.111	18	41	1.026
	OTA	ND	1	ND	1
South Asia	AFLA	197	2	ND	91
	ZEN	25	NA	212	25
	DON	60	58	1.463	34
	FUM	626	NA	9	310
	OTA	8	10	2	21
Oceania	AFLA	1	1	ND	ND
	ZEN	173	16	430	74
	DON	50	50	2.407	100
	FUM	1.796	NA	32	179
	OTA	ND	1	ND	2

Abbreviations: AFLA, Aflatoxins (a sum of aflatoxin B_1, aflatoxin B_2, aflatoxin G_1, and aflatoxin G_2 content); DON, deoxynivalenol; FUM, fumonisins (a sum of fumonisin B_1 and fumonisin B_2); ND, not detect; NA, not available; OTA, ochratoxin A; and ZEN, Zearalenone.

Source: Reproduced from Rodrigues, I., Handi, J., Binder, E.M., 2011. Mycotoxin occurrence in commodities, feeds and feed ingredients sourced in the Middle East and Africa. Food Additives and Contaminants B 4, 168–179 and Rodrigues, I., Naehrer, K., 2012. A three-year survey on the worldwide occurrence of mycotoxins in feedstuffs and feed. Toxins 4, 663–675.

Table 4 Worldwide regulation for mycotoxins in animal feeds or feed ingredients

Country	*Products for animal feed*	*Mycotoxin*	*Limit ($\mu g\ kg^{-1}$)*
Austria	Animal feed for swine	Deoxynivalenol (DON)	500
	Animal feed for beef cattle and poultry		1000
	Animal feed for reproduction swine	Zearalenone	50
Brazil	Feed ingredients	Total AF[a]	50
Canada	Feed ingredients	Total AF[a]	20
	Feed ingredients for beef cattle and poultry	DON	5000
		Toxin T-2	100
	Feed ingredients for swine and dairy	DON	1000
		Toxin T-2	25
	Feed ingredients for poultry	Diacetoxyscirpenol	1000
	Feed ingredients for swine		2000
Chile	Animal feed ingredients	AFB_1	20
		Total AF[a]	50
China	Animal feed for poultry	AFB_1	10
	Animal feed for swine		20
	Animal feed ingredients		50
	Complete feed	AFB_1	20
		Ochratoxin A	20
		Fumonisins	500
		Toxin T-2	80
		Zearalenone	100
		Vomitoxin	500
Cuba	Animal feed and feed ingredients	Total AF[a]	5
	All feeds	DON	300
Egypt	Feed ingredients	AFB_1	10
		Total AF[a]	20
European Union[b]	Animal feed	AFB_1	10
	Animal feed for poultry and swine		20
	Feed ingredients		20
	Animal feed for beef cattle		50
	Animal feed for dairy cattle		5
	Animal feed for calves and lambs		10
	Feed ingredients	Rye Ergot	1 000 000
	Feed ingredients	DON	8 000
	Animal feed for piglets and gilts	Zearalenone	100
	Animal feed for ruminants		500
	Grain and coproducts	Ochratoxin A	250
	Maize and maize products	Fumonisins	60 000
	Animal feed for pigs, horses, rabbits, and pet animals		5000
	Animal feed for poultry, calves, and lambs		20 000
	Animal feed for ruminants		50 000
Israel	Grain for animal use	AFB_1	20
		Ochratoxin A	300
		Toxin T-2	100
		Diacetoxyscirpenol	1 000
Japan	Animal feed for beef cattle, swine, and poultry	AFB_1	20
	Animal feed for dairy and broilers	AFB_1	10
	Compound feeds	Zearalenone	1 000
		DON	1 000
Mexico	Animal feed for swine and beef cattle	AFB_1	200
	Animal feed for poultry and dairy		0
Sweden	Animal feed for dairy	AFB_1	1.5
	Animal feed for poultry and swine		20
	Animal feed for beef cattle		50
	Animal feed for swine	Ochratoxin A	100
	Animal feed for poultry		200
United States	Animal feed for finishing beef cattle	Total AF[a]	300
	Animal feed for finishing swine		200
	Animal feed for breeding cattle, swine, and poultry		100
	Animal feed for dairy		20
	Grain and coproducts destined for swine	DON	5 000

(*Continued*)

Table 4 Continued

Country	*Products for animal feed*	*Mycotoxin*	*Limit ($\mu g\ kg^{-1}$)*
	Grain and coproducts destined for beef cattle		10 000
	Corn and by-products destined for equine	Fumonisins	5 000
	Corn and by-products destined for swine and catfish		20 000
	Corn and by-products destined for all other species or classes of livestock and pet animals		10 000

[a]Sum of aflatoxins B_1, B_2, G_1, and G_2.
[b]Relative to a feed ingredients with a moisture content of 12% (w/w).

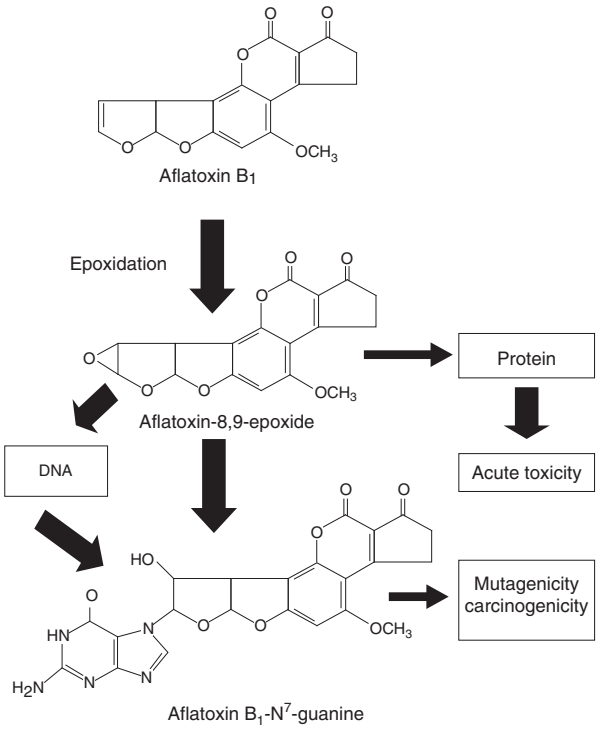


Figure 8 Formation of AFB_1-8,9-epoxide, AFB_1-N_7-guanine and AFB_1-lysine adducts.

urinary or fecal excretion. Aflatoxins are the most studied mycotoxins regarding biotransformation patterns and the biochemical basis of their toxic effects in animal models and in humans. Absorbed AFB_1 and its metabolites are excreted in urine and feces. AFB_1 is concentrated in the liver and, in lesser amounts, in the kidneys. Enzymes of the cytochrome P450 (CYP) family, CYP1A2, CYP3A4, and CYP2A6, are responsible for the biotransformation of absorbed aflatoxins. These enzymes convert AFB_1 into its carcinogenic form, AFB-8,9-epoxide, which bonds covalently to DNA and serum albumin, producing AFB_1-N_7-guanine and lysine adducts, respectively, as shown in Figure 8.

Besides being epoxided, AFB_1 can be also oxidized into several other derivatives. The main hydroxylated metabolites are AFM_1, aflatoxin Q_1 (AFQ_1), a demethylated metabolite, aflatoxin P_1 (AFP_1), and a reduced metabolite, aflatoxicol (Figure 9).

Aflatoxins affect all animal species, although sensitivity to toxic effects is considerably variable among species such as turkeys, quails, ducks, geese, as well as larger domestic animals including cattle, lambs, and pigs. In humans, the most important effect of aflatoxins is the hepatocellular carcinoma. This disease represents more than 80% of primary malignant tumors of the liver, and it is the 7th to 9th most common type of cancer affecting men and women worldwide, respectively.

The particular sensitivity of birds to aflatoxins is related to the quick absorption by their gastrointestinal system. After being absorbed, AFB_1 immediately binds to albumin and spreads to the tissues, mainly the liver, where it is biotransformed by the liver microsomal system. Biotransformed derivatives may bind to intracellular constituents, such as DNA and RNA, and alter protein synthesis functions. In terms of commercial poultry, ducks are the most susceptible species, followed by turkeys, geese, pheasants, and chickens. Dose-response may be different in individuals of the same species, and may vary according to breed, sex, age, and feed composition, among other factors. In many species, males are more susceptible than females, and in general, young animals are more susceptible than adult ones.

Toxic effects of aflatoxins depend on the dose and period of exposure and these factors will determine the occurrence of acute or chronic intoxications. Acute toxic syndrome is related to the ingestion of feedstuffs with high concentrations of aflatoxins, and the following effects may be observed shortly after ingestion: quick deterioration of general condition, loss of appetite, acute hepatitis (Figure 10), jaundice, hemorrhage, and death. The most evident clinical sign of chronic aflatoxicosis is a decrease in the growth rate of young animals due to prolonged, continuous, or intermittent ingestion of feed contaminated with low levels of aflatoxins. Although this is the main form of intoxication in natural conditions, diagnosis is difficult and economic losses may be considerable. Aflatoxicosis in monogastric animals like broilers and pigs is a highly relevant problem because of the economic impact related to mortality, low feed conversion, increased production costs, and negative effects on public health related to human consumption of aflatoxin residues in the viscera of exposed animals.

AFB_1 negatively affects chicken (*Gallus domesticus*) growth, and the effect is more severe during the development of young animals. Serum proteins, succinate dehydrogenase, and glutamate dehydrogenase are sensitive early indicators of this more severe intoxication. Decrease in serum albumin may be used as an early and suitable indicator of the deleterious effects of this mycotoxin in developing chickens. Broilers fed for 35 days with diets containing different levels of AFB_1, had reduced weight gain and histological changes in the liver of birds that received more than 500 $\mu g\ kg^{-1}$ aflatoxin per day. Turkeys submitted to the same treatment showed low weight gain and

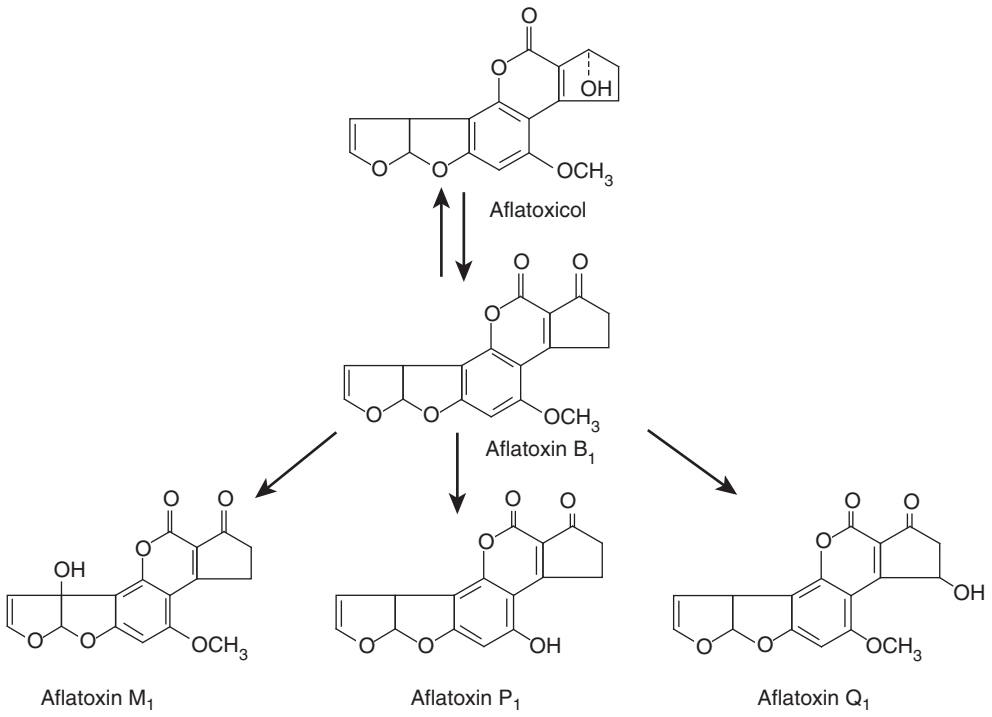


Figure 9 Main metabolites of AFB_1.

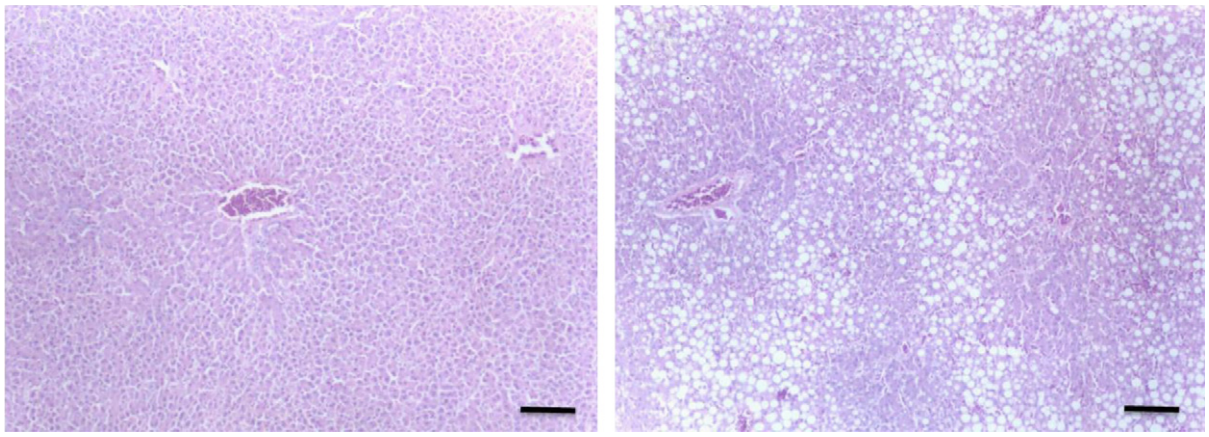


Figure 10 (a) Abdominal overview of a broiler chicken fed 1000 μg kg^{-1} of AFB_1, showing intense liver discoloration. (b) Normal liver of a nonintoxicated broiler.

feed conversion, as well as increased morbidity by different causes, and higher mortality rates, indicating that levels up to 66 μg kg^{-1} AFB_1 in feed were safe for broilers and turkeys.

Jones *et al.* (1982) analyzed five broiler production companies, and selected six growers from each of them. Growers were divided into three categories (good, mediocre, and poor) according to a productivity indicator (mean market weight X 100 per feed conversion). At the end of the study, the authors observed that frequency of feed contamination in good growers was 18% (mean concentration of 6.13 μg kg^{-1}), whereas those classified as mediocre or poor showed contamination frequencies of 22.1 and 31.3% (mean concentrations of 6.5 and 14.0 μg kg^{-1}), respectively. Results demonstrated a significant correlation between mortality rates and carcass condemnation in the groups.

In laying hens, the main symptoms of aflatoxicosis in experimental conditions included reduced egg production and weight; increased hepatic fat, and changes in serum enzyme levels. Ovary atresia in laying hens fed a diet with 8000 μg kg^{-1} AFB_1 for 7 days were also reported. Laying hens fed with 5000 μg kg^{-1} AFB_1 had significant decrease in egg weight, which can be explained by the fact that aflatoxin is primarily metabolized by the liver, the main organ responsible for synthesis and transportation of precursors required for yolk



(a) (b)

Figure 11 Photomicrographs of quail's livers showing (a) normal architecture of parenchyma and (b) intense vacuolar degeneration of hepatic cells and trabecular disorder, after dietary exposure to 100 μg kg^{-1} of AFB_1. Haematoxylin and eosin, bar=60 μm.

production. Toxic effects of aflatoxin in laying hens also include a dose-dependent decrease in egg production and egg quality with increased susceptibility to salmonellosis, candidiasis, and coccidiosis. AFB_1 can have either direct or indirect effects, or both, on the functionality of the gastrointestinal tract of laying hens fed diets containing 0.6, 1.2, or 2.5 mg kg^{-1} AFB_1 for 2 weeks (Applegate *et al.*, 2009).

Aflatoxins are also able to affect the immune system. Immunosuppressing effects demonstrated in domestic birds and other laboratory animals involve aplasia of thymus and bursa of *Fabricius*, reduction in the number and activity of T cells, decrease in antibody response, suppression of phagocytic activity, and reduction in humoral components, such as complement (C4), interferon, and immunoglobulins IgG and IgA. All these changes associated with the exposure of animals to feed contaminated with aflatoxins contribute to the occurrence of concomitant infections caused by viral and bacterial agents.

Concentrations of approximately 300 μg kg^{-1} AFB_1 in the feed of monogastric animals may lead to immunosuppression without any apparent clinical effects. Also, the ingestion of the toxin may be responsible for morbidity or mortality in the flock due to secondary infections. Signs observed in the animals often included significant decrease in T cells, albumins, and globulins.

Aflatoxins poisoning in turkeys cause inappetence, reduced spontaneous activity, unsteady gait, recumbence, anemia, and death. In the postmortem examination, body condition was adequate most of the times, but generalized congestion and edema were observed. Liver and kidneys were congested, enlarged, and firm. Aflatoxins in doses equal or greater than 200 μg kg^{-1} affected turkey performance during a period of 1–42 days. The effect of those toxins on body weight, feed consumption, relative weight of gizzard and liver, mortality, and total protein and cholesterol levels in serum was dependent on the dose. Turkey poults were very sensitive to aflatoxin poisoning, and inadequate mycotoxicological management may cause important economic losses in turkey production.

Chronic exposure of Japanese quails to diets containing AFB_1 adversely affected their performance, especially feed intake, egg weight, and percent eggshell. Intense vacuolar degeneration of hepatic cells and trabecular disorder were also seen after dietary exposure to 100 μg AFB_1 kg^{-1} (Figure 11). Addition of 2.5 and 5 mg kg^{-1} aflatoxin to quail diets led to significant changes in pancreatic alpha and beta cells, and these changes may have a negative effect on carbohydrate metabolism of poultry.

The simultaneous occurrence of aflatoxins and other mycotoxins in feedstuffs has become a greater concern to the animal production, especially in poultry, because of the possibility of interaction effects. The effects of prolonged oral administration of AFB_1 and fumonisin B_1 were evaluated in broilers from 21 to 42 days of age, indicating that either FB_1 or AFB_1, alone or in combination, did not cause marked changes in hematological and serological parameters of broilers, but caused important lesions in liver and kidneys (Del Bianchi *et al.*, 2005).

In swine, clinical signs of acute aflatoxicosis may begin after 6 h of ingestion, leading to severe depression, inappetence, bloody stools, muscle tremors, and motor incoordination with hyperthermia (up to 41 °C). Death may ensue in the following 12–24 h. In subacute intoxication, clinical signs evolve more slowly, and the following symptoms are observed: erect bristles, hyporexia, lethargy, and depression. In parallel, animals may show jaundice, dehydration, and emaciation, with reddish areas on the skin, and progressive weight loss. Chronic intoxication is manifested by decreased weight gain and feed conversion, inappetence, poor general appearance and, sometimes, diarrhea.

In dogs, early signs of aflatoxicosis include depression, loss of appetite, and vomiting. Later stages include orange-colored urine and jaundice. Severely affected dogs produce blood-tinged or blackened stools with difficult vomiting and internal bleeding. Outbreaks of aflatoxicosis in dogs have been reported in several countries, especially in the United States, usually associated with consumption of contaminated feed containing >200 μg kg^{-1} feed.

As the disease advances to the final stages in all animal species, signs of ataxia are frequently seen, besides jaundice and, sometimes, seizures. When high levels of the toxin are ingested, the liver shows fatty degeneration, lobular necrosis with increased number of basophilic cells in the periphery of

the lobule, proliferation of biliary ducts, and cirrhosis. A jaundiced carcass associated with an edematous and yellowish liver, are strong indicators of intoxication. The gall bladder may be edematous, and the liver, friable and hyperemic, mainly in cases of acute intoxication. Blood clotting times are also decreased, and collections of bloody liquid may be observed in the cavities and in mucous membranes, as well as hemorrhage in muscle masses.

Ochratoxin A

Although OT were first isolated from the species *A. ochraceus* (previously known as *Aspergillus alutaceus*), these toxins may be produced by several species in the genera *Aspergillus* and *Penicillium*. The ochratoxin group has 7 components, but only OTA has been found worldwide as a natural contaminant of grains. The kidneys are the target organs of OTA, which interferes in the synthesis of macromolecules in cells of the renal parenchyma, including DNA, RNA, and proteins. Besides, it affects renal carbohydrate metabolism, damaging the epithelium of the proximal tubules (Figure 12) and causing osmotic diuresis by means of decreased absorption of electrolytes and increased excretion of water.

OTA causes a series of adverse effects in most domestic animals. In pigs, it is the causative agent of mycotoxic porcine nephropathy. Similarly, in humans, it is recognized as the etiological agent of the Balkan endemic nephropathy. In poultry, OTA is considered to be the most potent mycotoxin, showing high lethality rates. LD_{50} for broilers is approximately 2.1 mg kg^{-1} of body weight, whereas LD_{50} for AFB_1 is 6.8 mg kg^{-1}. Ochratoxicosis in swine is observed as decreased weight gain, as well as polydipsia, polyuria, and renal lesions. Doses of 200 μg kg^{-1} of OTA in the feed were enough for the animals to present nephropathy, leading to negative impact in feed conversion and weight gain. Mortality may reach 90% in affected lots.

Natural occurrence of outbreaks in turkey breeding facilities due to the presence of OTA in animal feed showed levels ranging from 0.2 to 16.0 mg kg^{-1}, with a mortality rate of 59%, and decrease in feed consumption of 20%. Outbreaks involving laying hens were characterized by decreased egg production, low quality of eggshell, and nephropathy. In broilers, these authors observed low growth rate and feed efficiency, little pigmentation of the carcasses, and nephropathy. In experimental trials, broilers given more than 2.0 mg kg^{-1} OTA in their feed showed decreased weight gain, relative increase in kidney and liver weight, decreased serum levels of total proteins, albumins, globulins, and cholesterol, and increased creatinine and uric acid concentrations.

In broilers fed diets containing 2.0 mg kg^{-1} OTA, a significant reduction in the breaking strength of large intestines was observed, along with increased relative weight of the organ. This finding is important when considering the possible rupture of intestines during poultry processing, which would lead to fecal contamination of the carcass. Male broilers fed diets containing 400 and 800 μg kg^{-1} OTA showed significant decrease in body and thymus weight, feed consumption, feed conversion ratio, and thyroxin concentration. OTA-treated groups developed anemia manifested by a significant decrease in red cell counts (37%), packed cell volume percentage, and hemoglobin concentration. White cell counts, humoral immune response, and cell-mediated immunity were also significantly reduced. The greatest concentrations of OTA (2 and 4 mg kg^{-1}) ever given to broilers produced significant depression in growth rate, reduced feed consumption, and poor feed conversion efficiency and immune response (Verma *et al.*, 2004).

Fumonisins

Fumonisins comprise the latest group of mycotoxins discovered. Since their isolation in 1988, these toxins have been associated with previously known animal diseases, such as

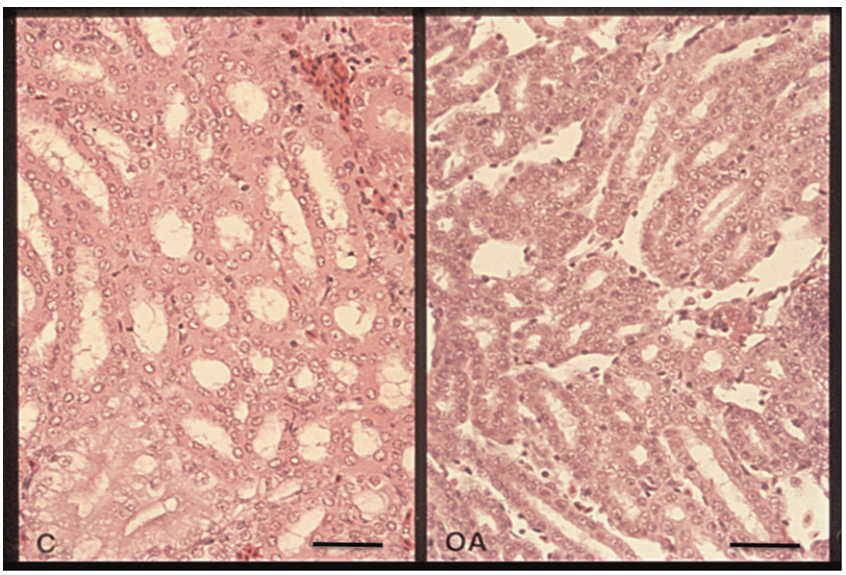


Figure 12 Photomicrographs of broiler's kidneys showing normal architecture of tubular (C) and tubular ephithelium hyperplasia after intoxication with ochratoxin A (OA). Haematoxylin and eosin, bar = 180 μm (Courtesy of Dr. David Ledoux, University of Missouri, USA).

equine leukoencephalomalacia and porcine pulmonary edema. Studies with rodent hepatocytes have shown that fumonisins block sphingolipid production (Figure 13). This evidence corroborates the hypothesis that the interruption of sphingolipid production and the consequent accumulation of sphinganine and sphingosine are the main toxic mechanisms of fumonisin acute toxicity and carcinogenicity. Sphingolipids are important compounds in the maintenance of cell membrane integrity, as well as in the regulation of cell surface receptors, ion pumps, and other vital systems for cell function and survival.

Swine are very sensitive to fumonisin intoxication. This sensitivity has been observed in several natural and experimental outbreaks. The main target organs of fumonisin in swine are the lungs, liver, heart, and pancreas, and the specific syndrome in pigs is called porcine pulmonary edema. The disease has been experimentally reproduced by supplying grains contaminated with *F. verticillioides*, culture material, and intravenous administration of pure FB_1, besides other effects caused by this mycotoxin in these animals, such as hepatic alterations and increased serum cholesterol (Haschek *et al.*, 2001).

Although fumonisins are highly toxic for horses and pigs. However, *F. verticillioides*-contaminated culture material has been shown to induce toxic responses when fed to chickens, ducklings, and turkey poults. Toxicity signs included increased mortality; reduced size of the bursa of *Fabricius*, thymus, and spleen; decreased body weight gain; myocardial degeneration and hemorrhage; changes in hemostatic mechanisms; and necrosis of hepatocytes. Most of the reports on toxic effects of FB_1 in avian species involve chickens and turkeys. High levels of this toxin fed to these species are associated with reduced body weight and feed intake, diarrhea, poor performance, and alterations in hematological and biochemical parameters, with increased activity of the enzymes alanine transaminase and aspartate transaminase (Asrani *et al.*, 2006).

Broilers fed diets of FB_1 had diarrhea, reduction in weight gain, increase in liver weight, histological changes, such as multifocal hepatic necrosis, biliary hyperplasia, muscle necrosis, and rachitism. Broilers receiving 75 mg kg^{-1} FB_1 showed only reduced sphingolipid biosynthesis, indicating that, although clinical signs may not be evident, concentrations as low as 75 mg kg^{-1} FB_1 may be toxic for birds. Immunosuppression is also pointed out as one of the main toxic effects of FB_1, with reports of decreased humoral immunity and lymphocyte suppression.

Fumonisins significantly increased total serum protein and albumin concentrations on 14 and 21 days postfeeding (DPF), serum calcium and cholesterol levels from 14 DPF onward, and creatinine from 21 DPF onward (Asrani *et al.*, 2006). This study revealed that the addition of *F. verticillioides* culture material supplied 300 mg kg^{-1} FB_1 of diet, a highly toxic concentration to quail chicks, resulting in heavy mortality, decreased growth rate, and significant alterations in hematological and biochemical parameters.

When performance is considered, 50 mg kg^{-1} FB_1 were detrimental to turkeys but not to broilers fed to market age. Liver sphingolipid results indicated that 25 and 50 mg kg^{-1} increased the sphinganine/sphingosine (SA:SO) ratio, but no significant toxic effect was observed. The altered SA:SO ratio with no concurrent disease suggested that this ratio is an extremely sensitive biomarker of exposure to FB_1, but may

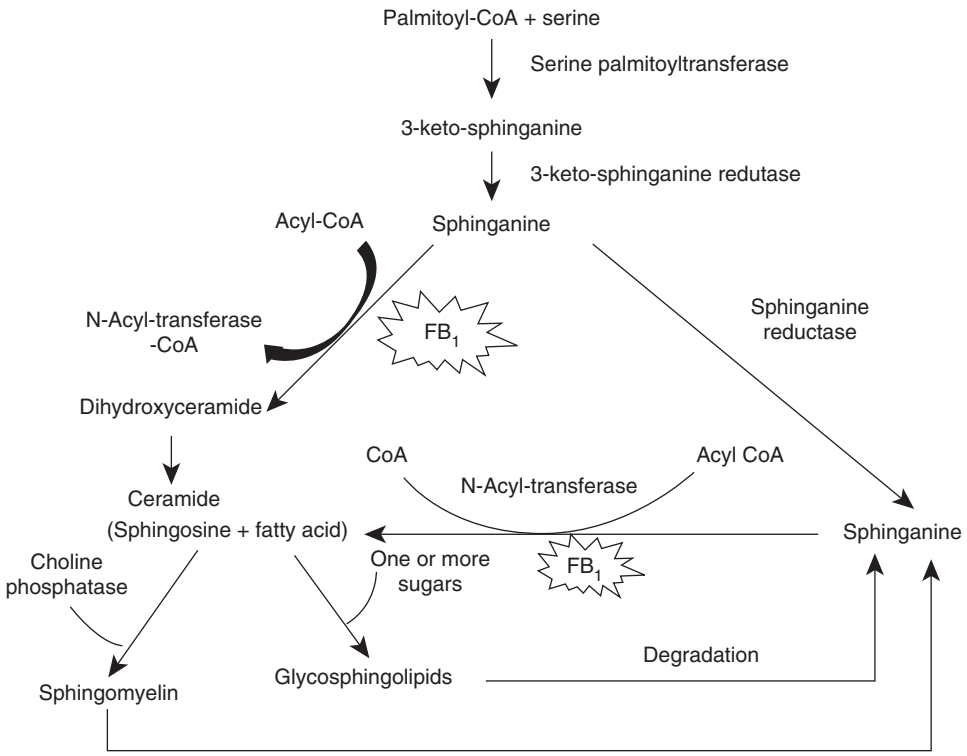


Figure 13 Sphingolipid metabolism disruption by fumonisin B_1.

not be a good indicator of clinically significant disease in poultry.

Interactions between fumonisin and other *Fusarium* toxins in poultry have also been reported. Kubena *et al.* (1999) observed few deleterious effects on the performance and health of adult laying hens given feed containing 100–200 mg kg^{-1} FB_1 and 50–100 μg kg^{-1} moniliformin for a prolonged period of time (420 days). However, Prathapkumar *et al.* (1997) studied natural mycotoxicosis outbreaks in laying poultry, and reported dark and viscous feces, 20% reduction in egg production, and 10% mortality. Flocks showed evident improvement after they stopped receiving the contaminated feed. Analysis of the feed showed contamination levels of 8.5 mg kg^{-1} FB_1 and 100 μg kg^{-1} AFB_1, evidencing the additive effects of the two toxins.

Exposure to FB_1 at concentrations ≥ 50 mg kg^{-1} adversely affected quail performance, causing a reduction in feed intake and lower weight gain. Egg production, weight, and eggshell weight were also affected. Eggshell depigmentation was also observed, and became more marked with increasing concentrations of FB_1 in a dose-dependent relationship (Butkeraitis *et al.*, 2004).

Zearalenone

Zearalenone was first detected after hyperestrogenism symptoms appeared in swine fed moldy maize. These include prolonged estrus, anestrus, changes in libido, infertility, increased incidence of pseudo pregnancy, increased udder or mammary gland development, and abnormal lactation. The toxin is also related to the following secondary complications: stillbirths, abortions, mastitis, vulvovaginitis, and rectal or vaginal prolapses (Figure 14).

Endocrine disruption related to zearalenone is attributed to both genomic and nongenomic effects. First, zearalenone competes effectively with endogenous steroid estrogens, such as 17β-estradiol for the specific binding sites of estrogen receptors, with no preference between the two isomers, estrogen receptor-α, and estrogen receptor-β. Estrogen receptors are found in many different organs, such as the uterus, the mammary glands, the bones, the liver, and the brain, where zearalenone can, therefore, have an impact. Relative binding affinities of the main metabolites are as follows: α-zearalanol > α-zeralenol > β-zearalanol > zearalenone > β-zearalenol. The α-isomers are approximately 10-fold more active than the rest because of the position of the hydroxyl group. Differences in production of α or β isomers explain differences in sensitivity between species. For instance, pigs produce more α-ZEL, whereas poultry species produce more β-zearalenol.

The estrogenic potency of zearalenone shows species-specific differences, and pigs, especially gilts, are considered to be the most susceptible animal species, whereas poultry and ruminants show a higher tolerance to zearalenone-contaminated feeds. Mechanistic studies showed that zearalenone interacts not only with estrogen receptors, but also influences the activity of enzymes involved in the steroidogenesis in the liver and in the reproductive organs. *In vivo* and *ex vivo* experiments show that zearalenone and its metabolites impair oocyte maturation and embryonic development, but do not cause



Figure 14 Hyperestrogenism in a swine female showing vulvovaginitis and vaginal prolapse (Courtesy of Dr. David Ledoux, University of Missouri, USA).

major teratogenic effects. *In vitro* experiments indicated that zearalenone is nonmutagenic, and long-term studies in rodents provided inconclusive evidence for carcinogenicity.

Various studies have addressed the effects of zearalenone in pigs. The source of zearalenone that have been used is either crystalline zearalenone, or highly contaminated zearalenone-containing feedingstuffs. Initial studies suggested that an effective dietary zearalenone concentration producing clear estrogenic effects would be higher than 1 mg kg^{-1} feed. In more recent studies using crystalline zearalenone, estrogenic effects have been reported at concentrations ranging from 0.05 to 0.4 mg zearalenone kg^{-1}. In a study conducted with nonpregnant gilts exposed to 0, 0.04, 0.2, and 0.4 mg kg $b.w.^{-1}$ during days 5–20 of estrus, a no-effect level of 0.04 mg kg b.w. day^{-1} was observed. Several studies have indicated that the female prepubertal pig is particularly sensitive to the estrogenic effects of zearalenone. Using naturally contaminated maize providing dietary concentrations of zearalenone from 0.01 to 0.42 mg kg^{-1} and of DON from 0.2 to 3.9 mg kg^{-1} feed clear estrogenic effect (increased swelling of cervix and increased mean relative uterus weight) was observed at the highest dose level of 0.42 mg kg^{-1} zearalenone in feed. A slight decrease in mean serum follicle-stimulating hormone concentration in the dosed groups was considered influenced by the cooccurrence of DON in the feed. Although only a few studies have been conducted, boars seem to be quite resistant to the effects of zearalenone (EFSA, 2004).

Zearalenone, has also been administrated either orally or intramuscularly, at doses of 50, 200, 400, and 800 mg kg b.w.

day^{-1} for 7 days to broilers. A dose–response related increase of the oviduct weights was found but the potency of zearalenone was estimated to be only 1.37% of that of oestradiol propionate. In turkeys, the oviducts and testes were unaffected at dietary zearalenone concentrations of 10, 25, 50, 100, 200, 400, and 800 mg kg^{-1} diet (week 4–7 of age). Dewlaps and combs showed an increased development and a considerable strutting behavior were observed at 400 and 800 mg kg^{-1} diet. A hyperandrogenic response was observed in male turkeys fed a diet with 800 mg crystalline zearalenone kg^{-1}. Cystic alterations of the lamina epithelialis of the oviduct of female Leghorn chicks, hyperactivity of secreting cells of the oviduct, and atrophy of testes was reported in male chicks exposed to 10 mg kg b.w. day^{-1} for 20 days. The reduced testes weights and the increased weight of the oviducts of ducks to the presence of 0.15 mg kg^{-1}. However, other mycotoxins were also present in the diet in this case (EFSA, 2004). From these experiments poultry can be regarded as quite tolerant to zearalenone as symptoms of hormonal effects were only observed at high zearalenone doses, which will hardly occur under practical feeding conditions.

Deoxynivalenol

DON is also known as vomitoxin due to its emetic effects after acute exposure. In addition to that, symptoms caused by acute exposure are similar to those observed after ionization: abdominal pain, salivation, diarrhea, vomiting, leukocytosis, and gastrointestinal hemorrhage. Chronic exposure to DON causes feed refusal due to alterations of serotogenic activity of both the peripheral and central nervous system. Other effects related to chronic ingestion of DON are weight loss, growth retardation, intestinal irritation, disruption of immune response, and death. Toxicity of DON is caused by the same molecular mechanisms of the other trichothecenes. Immune modulation induced by DON has been extensively studied, and it has been shown that inflammation arises from mitogen-activated kinase activation, followed by activation of the prostaglandin-endoperoxide synthase 2, and a consecutive increase of prostaglandins, which triggers the production of inflammatory cytokines.

Swine and other monogastric animals show the greatest sensitivity to trichotecenes, followed by birds. NIV and DON induce feed refusal and weight loss, show similar toxicities and a combined concentration lower than 0.4 mg kg^{-1} is described as acceptable for swine, which is a relatively susceptible species.

Recently, DON has been shown to maintain inflammation by favoring the Th-17-related immune response, which could be associated with chronic inflammatory intestinal diseases (Cano *et al.*, 2013). The intestine is, in fact, one of the most sensitive organs to DON exposure. Low doses of this toxin can induce morphological and histological impairment of intestinal epithelial cells, and alter intestinal permeability (Pinton *et al.*, 2012). DON toxicity has, thus, repercussions on the neuroendocrine system, the intestinal system, and the immune system. The immune system appears to be the most sensitive to DON concentrations, followed by the neuroendocrine system, and finally, by the intestinal system. Among farm species, swine show the greatest sensitivity to trichotecenes, followed by poultry and ruminants.

Many feeding studies have been done on pigs using either crystalline DON or naturally or artificially infected cereals mixed. The effects of pure DON added to feed and naturally contaminated feed containing similar levels of DON have been compared in at least four feeding studies with pigs. Naturally infected feed had a stronger effect on the feed intake and weight gain than pure toxin in all these studies comparing the difference sources of DON. The difference remains to be explained, but proposed hypotheses include the presence of other toxins in the material, the presence of other compounds (as for example bacterial polysaccharides) or the matrix effect. Complete feed refusal was observed at levels of 12 mg kg^{-1} of crystalline DON and vomiting at 20 mg kg^{-1} feed. The consumption of DON-contaminated feed has been associated also with epithelial lesions in the esophageal region of the stomach when pigs have been given naturally infected feed containing from approximately 3–6 mg DON kg^{-1} feed. The negative effect on feed intake in pigs is generally considered as most sensitive endpoint of toxicity.

Changes in different clinical chemistry parameters (plasma nutrients and plasma enzyme activities) have been reported from several studies whereas in other experiments no changes were observed. Reported alterations are probably due to the reduced feed intake and not a direct effect of the toxin since no changes in these parameters were observed when compared to pair-fed controls.

Effect of DON on the pig immune response has also been investigated. In many experiments, DON increases IgA concentrations in blood serum, generally when DON levels exceed 1 mg kg^{-1} feed (Accensi *et al.*, 2006; Pinton *et al.*, 2008).

Prevention of Mycotoxicoses

Every effort must be made to reduce the occurrence of mycotoxins. This is a complex task that requires an integrated understanding of crop biology, agronomy, fungal ecology, harvesting methods, storage conditions, food and feed processing and technology, and detoxification strategies. There are a number of approaches that can be followed to minimize mycotoxin contamination in the food and feed chains. They involve prevention of fungal growth and therefore mycotoxin formation, as well as strategies to reduce or eliminate mycotoxins from contaminated food commodities.

Preventative Measures to Avoid Grain Contamination

The methods for controlling fungal growth in foods include: physical control, by drying products in safe levels of humidity (water activity and moisture content), cooling under modified or controlled oxygen and carbon dioxide atmosphere and using irradiation process; chemical control, by using organic acids (propionic, sorbic, acetic, and formic), fumigants (phosphine), and compounds isolated from plant extracts; biological control, by using microorganisms competing for space and nutrients, antibiosis and activation of defenses; and genetic control, by using seeds resistant to toxigenic fungi.

Processing may reduce, but not eliminate mycotoxins in cereals, and they become a potential risk for consumers (Lombaert *et al.*, 2002). Therefore, to avoid the presence of mycotoxins, prevention by using good agricultural practices during harvesting and storage of grains is the best option. Biological control may be an ally when the following strategies are used in the agriculture: pulverization of antagonists during the blooming period, treatment of infected seeds, and inhibition of inoculum production by organisms specialized in degradation (Larsen *et al.*, 2004). Therefore, practices that decrease the presence of insects in grain crops, and humidity during storage of raw material and feeds may work well as prevention strategies.

Procedures applied to decrease the moisture in harvested grains and storage under internationally recommended standards are also essential measures to avoid toxigenic fungi and mycotoxins.

Detoxification Methods

Detoxification methods may be the physical removal of contaminated grains, or removal of the toxin by polar solvents, destruction by heat, or degradation by chemical substances or microorganisms. Although these methods may be effective, they are extremely expensive and therefore not economically viable. Heat is one physical method considered as able to decrease FB_1 concentration in corn grains from 87% to 100%. However, temperature has to be approximately 150–220 °C, leading to a possible loss of nutritional content. Simply washing the grains with water and sodium carbonate solution may reduce fumonisin concentration in corn. Initial cleaning of the corn in mills led to a 40% reduction in the concentration of aflatoxins, and 32% in fumonisins (Scudamore and Patel, 2000). However, these techniques have little applicability for large amounts of grain, as used in animal feed plants.

In the animal industry, one of the most used strategies to reduce the exposure to mycotoxins is to decrease their bioavailability by including various mycotoxin adsorbing agents in the compound feed, which leads to a reduction in mycotoxin uptake, as well as in the distribution to the blood and target organs. A diverse variety of substances have also been investigated as potential mycotoxin-detoxyfying agents. Depending on their mode of action, these feed additives may act by reducing the bioavailability of the mycotoxins or by degrading them or transforming them into less toxic metabolites.

Another strategy is the degradation of mycotoxins into nontoxic metabolites by using biotransformation agents, such as bacteria/fungi or enzymes. Substances that do not directly interact with mycotoxins, i.e., antioxidant agents, immunostimulatory agents, are not considered *sensu stricto* as mycotoxin-detoxifying agents. However, such compounds may be very efficient in the reduction of the toxicity of some mycotoxins.

There is a wide variety of chemical products that may be applied to high-moisture stored hay in order to control microbial growth. Among these products, ammonia may be highlighted. Besides acting in the control of fungi by increasing pH, it also affects the fibrous portion of the forage, solubilizing hemicellulose, and increasing the availability of readily fermentable substrates for rumen microorganisms.

Chemical Adsorbents

The use of adsorbent substances is the most common strategy to prevent the toxic effects of mycotoxins that are already formed in foods. Several minerals have been evaluated, probably because of there are easy to incorporate in feeds, without the need for any special equipment. The main mechanism of adsorption of these materials is related to charges exchanged between the adsorbent substance and the mycotoxin. However, as mycotoxin structures are different, the efficacy of chemical adsorbents is not similar for all of them.

One of the most important characteristic of adsorption is the physical structure of the adsorbent, that is, the total charge and total distribution, the size of the pores, and the accessible surface area. However, the property of the adsorbent molecules, the type of mycotoxin, as well as the polarity, solubility, size, shape and, in the case of ionized compounds, charge distribution and dissociation constants also have an important role. Therefore, the efficacy of the whole adsorption process has to be analyzed in relation to the particular properties of the adsorbent (Huwig *et al.*, 2001). The most used chemical adsorbents are activated charcoal, aluminum silicates, and mannan oligosaccharides (MOS).

Activated charcoal

Activated charcoal is an insoluble, very porous powder with large surface in relation to its mass (500–3500 $m^2\,g^{-1}$), formed by the pyrolysis of organic material. It has been used as an antidote against poisoning since the nineteenth century. Therefore, it may also inactivate mycotoxins. In an aqueous solution, it may adsorb most of the mycotoxins efficiently, considering that different activated charcoals have little or no effect against mycotoxins. This may be due to the fact that activated charcoal is a relatively unspecific adsorbent and, therefore, essential nutrients may also be adsorbed, particularly if their concentration in feed is much greater than that of mycotoxins. In studies with goats, however, it was observed that high doses of activated charcoal were beneficial in acute intoxications caused by the ingestion of large amounts of aflatoxin. The adsorption of chemical substances by vegetable charcoal depends on several factors: size of the pores, surface area, chemical nature of the xenobiotic compound, dose of the vegetable charcoal, pH, and gastrointestinal content.

Aluminum silicates (zeolites, hydrated sodium calcium aluminum silicate, and clay)

Most of the studies related to mycotoxin reduction by the use of adsorbents are based on the use of aluminum silicates, mainly zeolites, hydrated sodium calcium aluminum silicate (HSCAS), and aluminum silicate clay. All of them are aluminates, silicates, or some interchangeable ions of alkali metals, mainly alkali metals and alkaline earth metals. Several studies show that phyllosilicates have the ability to chemically adsorb aflatoxins in aqueous solutions. Some aluminum silicates bind

to AFB_1 *in vitro* at variable degrees, and form complexes of different strengths with AFB_1.

HSCAS form a more stable complex with AFB_1 than many other compounds that were tested *in vitro*. It was discovered that HSCAS, bentonite and montmorillonite clays protect laboratory animals from the toxic and teratogenic effects of aflatoxins. HSCAS is a phyllosilicate whose deficiencies in positive charges create a potential to adsorb positive charges or cationic compounds.

Many studies have demonstrated that the addition of adsorbents may effectively reduce aflatoxin toxicity in animals. Determining the mechanism of adsorption of the aflatoxin may make it easier for more efficient adsorbents to be identified or prepared. Phillips *et al.* (1995) analyzed the aflatoxin adsorption mechanism by HSCAS. They suggested that adsorption may involve the β-dicarbonyl system of aflatoxin by means of the chelation of metallic ions on the surface and HSCAS phyllosilicate layers. Aflatoxin is chemically adsorbed in different sites that may include the interlamellar region, borders, and basal surfaces of HSCAS particles. Binding of aflatoxin by HSCAS is so stable that when HSCAS is in animal feed, traditional extraction procedures (methanol-water) for the analysis of aflatoxins have to be modified, and a nonaqueous solvent is necessary.

Zeolites are crystalline, hydrated alkaline aluminum silicates, and alkaline earth cations with infinite possibilities of tridimensional structure. They are characterized by the high capacity of gaining and losing water in a reversible fashion, and to exchange constituent cations without great changes in their structures.

Studies have been carried out to determine if the use of zeolites in the diet of broilers had any beneficial effect. The inclusion of zeolites in broiler feed increased body weight gain and feed efficiency, which favored the feed conversion in mass, increased specific gravity of eggshells, and increased the use of calcium. The inclusion of 5% zeolite or more in the feed of growing and fattening swine significantly increased feed conversion from 35 to 65 kg of body weight. However, there is some evidence that zeolites may interfere with mineral distribution in the tissue, for example, negatively affecting the use of dietary phosphorus by broilers (Moshtaghian *et al.*, 1991).

Bentonite comes from the disaggregation of volcanic ashes *in situ*, and is mainly made up of montmorillonite. Bentonite composition may vary from one deposit to the other, mainly because of interchangeable ions, Na^+, K^+, Ca^{2+}, and Mg^{2+}. These are referred to as sodium, potassium, calcium, and magnesium bentonite. They have a layered (lamellar) crystalline microstructure that enables the adsorption of other molecules, and have the marked ability to swell when water is added. This adsorbent compound has several uses in the industry, engineering, and agriculture, including clarification of beverages and water, and discoloration of oils. Bentonites have demonstrated the ability to improve growth rates and feed efficiency in broilers, such as the use of energy and protein, and increased feed passage time. Supplement in the diet of laying hens with 2.5–5% bentonite improved laying rates, feed efficiency, size of the egg, quality of the eggshell, and decreased mortality and fecal moisture content. Beneficial effects of bentonites were also reported on nutrient retention in turkeys, and egg production and feed efficiency in hens.

Mannan oligosaccharides

MOS are derived from the cell wall of yeasts (*Saccharomyces cerevisiae*) and have a high degree of antigenicity, mainly due to the mannan and glucan components. MOS may be used as aflatoxin adsorbents because they reduce the problems caused by mycotoxins normally found in low-quality maize. MOS have the ability to bind to different pathogens in the gastrointestinal tract and therefore prevent that they colonize it. *In vitro* studies showed that commercial MOS adsorbed AFB_1 and zearalenone (Devegowda *et al.*, 1998), and the addition of esterified glucomannan in the diet of broilers was effective to neutralize the toxic effects of naturally aflatoxin-contaminated diets.

Microbiological Strategies

Microorganisms with ability to bind with mycotoxins

Biological decontamination methods are being widely studied and may be a very promising choice, provided that they are efficient, specific and environmentally correct. Of all kinds of microorganisms available and that may be used for aflatoxin removal from a contaminated medium, yeast and lactic acid bacteria (LAB) are the most studied and promising ones.

Saccharomyces cerevisiae was originally used in animal feeds as growth promoters; however, these organisms have showed to be also useful against aflatoxin contamination because of the ability of its cell wall to bind to the mycotoxin. The adsorbent effect of *S. cerevisiae* is attributed to the esterified glucomannan, which is extracted from the yeast cell wall. Shetty and Jespersen (2006) showed that most of the yeast strains bound to more than 15% of AFB_1, and the bond with toxin was highly strain-specific.

In the poultry industry, *S. cerevisiae* has been used as a general performance promoter in poultry feed, and showed beneficial effects against the exposure to aflatoxin.

Regarding LAB, El-Nezami *et al.* (1998) found some strains of *Lactobacillus* (*Lactobacillus rhamnosus* GG and *Lactobacillus rhamnosus* LC-705) that were able to bind efficiently with large amounts (up to 80%) of AFB_1 in the medium. Peltonen *et al.* (2001) studied 15 types of *Lactobacillus* and five types of *Bifidobacterium*, and found binding with AFB_1 ranging from 5.6% to 59.7%. A minimum concentration of 2×10^9 CFU ml^{-1} of *Lactobacillus* and *Propionibacterium* is required to bind to 50% of the AFB_1, and binding is greater when LAB concentration reaches 10^{10} CFU ml^{-1}. The binding effect is dependent on the temperature, once the efficiency in aflatoxin removal is greater at 37 °C than at 4 °C and 25 °C. Gram-positive bacteria are best sequesters of aflatoxin from the medium than Gram-negative ones, with removal rates of 80–20%, respectively, suggesting that the ability to remove the toxin is dependent on the structure of the cell wall (Bolognani *et al.*, 1997).

Data available today show that bacterial viability is not a requisite for the removal of the toxin, and that the adsorption process occurs rapidly, once nonviable cells were more efficient, and there was no difference in the intervals analyzed. Therefore, it is necessary to study new bacterial cells, to have greater understanding of the mechanism of action of these

bacteria on aflatoxins in order to identify those that are more efficient in the removal of mycotoxins and therefore help to reduce human and animal exposure to these contaminants.

Microbial degradation of mycotoxins

Aflatoxin biodegradation using microorganisms offers an attractive alternative for the control or elimination of aflatoxins in foods and feeds, protecting their quality and safety. Many species of fungi and bacteria, such as *Flavobacterium aurantiacum*, *Corynebacterium rubrum*, *Candida lipolitica*, *A. niger*, *Trichoderma viride*, *Armillariella tabescens*, *Nurospora* spp., *Rhizopus* spp., *Mucor* spp., among others, have shown the ability to enzymatically degrade mycotoxins. However, there are still unanswered questions about the toxicity of enzymatically degraded products and undesirable effects of the fermentation of nonnative microorganisms in the quality of the feed (Shetty and Jespersen, 2006). Microorganisms predominant in fermented cereals are lactic acid bacteria and yeasts, specially *S. cerevisiae* and *Candida krusei* (Jespersen, 2003).

Enzymatic or microbial degradation of mycotoxins ('biotransformation') leading to less- or even nontoxic metabolites is a strategy for the decontamination of crops. Microorganisms including yeast, molds, and bacteria have been screened for their ability to modify or inactivate different mycotoxins. Few microorganisms with respective activity were isolated, the first was *F. aurantiacum* with the ability to detoxify aflatoxins. This organism has since then been studied extensively for possible degradation products. Apart from *F. aurantiacum*, a number of bacterial and especially fungal species have been found to detoxify aflatoxins. *Rhizopus* sp. has been claimed to be particularly suitable for large-scale detoxification of aflatoxin-contaminated feeds by solid-state fermentation. Ochratoxin A is rapidly degraded by microorganisms in the rumen to ochratoxin α (OTα) and phenylalanine. A yeast strain isolated from the hindgut of a termite, *Trichosporon mycotoxinivorans* also showed a potential deactivation of OTA to OTα and a metabolisation of zearalenone. The toxicity of DON is partially attributed to their 12,13-epoxide ring. Reductive deepoxidation could be achieved by ruminal and intestinal flora of pigs, hens, and rats or strain of *Eubacterium* isolated from bovine rumen. Enzymes capable of converting fumonisins to hydrolyzed fumonisin can be used to reduce the toxicity of this toxin (Grenier *et al.*, 2012).

Importantly, all measures aiming to remove or destroy mycotoxins in feeds may only become viable when each feed company considers that monitoring is a fundamental step in a mycotoxin control program. This has to be done by a consistent sampling program in the mass of grains received or to be purchased by the company, with regular analysis of mycotoxins. None of the control practices for toxins that have already been formed are efficient enough to completely reduce the losses caused in the animals; therefore, the implementation of any of these methodologies should be carefully evaluated from an economic standpoint.

See also: Food Microbiology. Food Security: Postharvest Losses. Food Toxicology. Poultry and Avian Diseases

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Animal Health: Tuberculosis

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Glossary

Aerobic Requiring the presence of air or free oxygen for life.
Cell-mediated immunity Immunity dependent on the recognition of antigen by effector T cells.
Granuloma Infiltration of a dense, macrophage-rich mass of cells.
Humoral immune response Antibody-mediated immunity.
Polymerase chain reaction test (PCR) Biotechnology to amplify specific portions of deoxyribonucleic acid (DNA) generating thousands to millions of copies of a particular DNA sequence.
Sensitivity Proportion of infected (diseased) individuals that test positive.
Specificity Proportion of noninfected (nondiseased) individuals that test negative.
Zoonosis Any infectious disease that is naturally transmitted between animals and humans.

The Disease

Bovine tuberculosis (bTB) is a chronic bacterial disease caused by the slow-growing, obligate intracellular bacterium *Mycobacterium bovis*. This pathogen has a worldwide distribution and, in several countries, bTB remains a major health problem in domestic livestock. The disease costs US$3 billion annually in global agricultural losses (Garnier *et al.*, 2003) and it is considered within the four most important cattle diseases globally (Finlay *et al.*, 2012).

Mycobacterium bovis is primarily a pathogen of cattle but it can also infect other mammals including badgers, possums, deer, goats, sheep, and camelids (Pollock and Neill, 2002; Scantlebury *et al.*, 2004; Skuce *et al.*, 2012). The bacterium is also able to affect humans, which makes bTB a relevant zoonosis that can spread through inhalation of infectious droplets and by ingestion of raw milk (Thoen and Barletta, 2006). In developed countries, eradication programs have significantly reduced the prevalence of this disease but, in some cases, reservoirs in wildlife make complete eradication difficult.

bTB primarily involves the respiratory system and associated lymph nodes. Infected individuals shed *M. bovis* in respiratory secretions, feces and milk, and occasionally in urine and vaginal secretions or semen, with large numbers of organisms shed in the late stages of infection. Most of the transmission occurs via aerosol circulation between animals that are in close proximity (Cassidy, 2006; Skuce *et al.*, 2012); however, indirect transmission through ingestion of contaminated feed has also been demonstrated (Neill *et al.*, 1994; Okafor *et al.*, 2011). Interestingly, Collins and Granje (1983) reported that, in experimentally infected calves, the minimum dose required to establish infection by the respiratory tract was up to 1000 times less than via the oral route. However, the oral route is likely most important in calves nursing infected cows (Neill *et al.*, 1994).

At present, *M. bovis* infection in cattle rarely appears as clinical disease. Instead, it is detected in apparently healthy animals, responding to any of the available diagnostic tests (Collins, 2006; Skuce *et al.*, 2012). When clinical signs are present they are nonspecific and, as bTB is a chronic debilitating disease, symptoms generally take months to develop. Loss of body condition, inappetence, and progressive emaciation may occur in advanced cases and respiratory signs may include chronic moist cough (especially during exercise) and thoracic abnormalities at auscultation. Lymph nodes may be enlarged, affecting contiguous blood vessels, airways, or the digestive tract. Mammary and reproductive tract involvement is rare and is usually accompanied by enlargement of associated lymph nodes (Divers and Peek, 2008).

bTB has a significant impact due to the cost of official control programs and represents an obstacle to domestic and international trade. Being a zoonotic pathogen, *M. bovis* has implications in human health, particularly in the developing world, although human disease due to this mycobacterium is now significantly less common than in the past decades (Biet *et al.*, 2005; Robinson *et al.*, 2012).

The Agent: The *Mycobacterium* Genus

Mycobacteria are members of the taxonomic group that includes the genera *Corynebacterium*, *Mycobacterium*, and *Nocardia* (CMN group) and the genus *Rhodococcus* (Cocito *et al.*, 1994). Mycobacteria are nonmotile and nonsporulated rods that are grouped in the suprageneric rank of *Actinobacteria* with a high guanine plus cytosine (G + C) content (61–71%) in the genomic DNA, and high lipid content in the wall; probably the highest among all bacteria. They also present several mycolic acids in the envelope structure that distinguishes the genus (Palomino, 2007).

These organisms include a number of major human and animal pathogens, comprising more than 100 species of obligate parasites, saprophytes, or opportunistic pathogens. Mycobacteria are structurally more closely related to Gram-positive bacteria; however, the genus does not fit into this category as the cell wall molecules are lipids rather than proteins or polysaccharides (Palomino, 2007). Thus, *M. bovis* is neither gram positive nor gram negative but is instead

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described as acid-fast, and as once stained, it resists decolonization with acidified organic solvents (Lawn and Zumla, 2011).

The waxy coat confers the distinctive characteristics of the genus: acid fastness, extreme hydrophobicity, resistance to environmental exposure, and distinctive immunological properties. It also contributes to the slow growth rate of some Mycobacteria by restricting the uptake of nutrients (Palomino, 2007).

On the basis of genomic analysis, this group has been divided into two separate clusters, corresponding to the traditional fast-growing mycobacteria, represented by nonpathogenic environmental isolates, and the slow-growing mycobacteria, containing most of the overt pathogens (Harris and Barleta, 2001). Slow-growing mycobacteria of importance in human and veterinary medicine are found in two major complexes: *Mycobacterium tuberculosis* and *Mycobacterium avium*. The *M. tuberculosis* complex includes *M. tuberculosis*, *M. bovis*, *M. africanum*, and *M. microti*. *Mycobacterium tuberculosis* causes tuberculosis in man, primates, dogs, and other animals. *Mycobacterium bovis* causes tuberculosis in cattle, domestic and wild ruminants, man and other primates, and swine and other animals (Eglund, 2002).

The most relevant member of the slow-growing group, *M. tuberculosis*, is an obligate intracellular pathogen that can infect several animal species, although human beings are the principal hosts. It is an aerobic, acid-fast, nonmotile, nonencapsulated, nonspore-forming bacillus that grows most successfully in tissues with high oxygen content, such as the lungs. Compared with the cell walls of other bacteria, the lipid-rich cell wall is relatively impermeable to basic dyes unless combined with phenol (Lawn and Zumla, 2011).

However, the *M. avium* complex (MAC) consists of genetically similar bacteria including, among others, *M. avium* subsp. *avium* and *M. avium* subsp. *paratuberculosis*, which is the causative agent of Johne's disease in cattle. Microorganisms in this complex are opportunistic pathogens present in multiple locations; although human exposure to MAC is ubiquitous, most individuals rarely develop infection (St. Amand *et al.*, 2005). Relevant to animal health, *Mycobacterium paratuberculosis*, a pathogen for ruminants, is an obligate parasite unable to replicate in the environment (Eglund, 2002).

The unique cell wall in the *Mycobacterium* group enables the organism to persist in the environment and contributes to its resistance to low pH, high temperature, and chemical agents (Manning, 2001). *M. bovis* can survive for several months in the environment, particularly in cold, dark, and moist conditions. At room temperature, the survival time varies from 18 to 330 days, depending on the exposure to sunlight and the organism is infrequently isolated from soil or pastures grazed by infected cattle.

At the molecular level, the genetic configuration of Mycobacteria, in particular *M. tuberculosis*, has been the subject of extensive research. The sequencing of the *M. tuberculosis* genome has been a major advance to better understand the biology of the bacterium. Findings have allowed the subsequent identification of specific antigens for the development of diagnostics tests, multivalent vaccines, and biomarkers for tuberculosis (Lawn and Zumla, 2011). The discovery of genomic diversity help determine the factors involved in cellular growth and metabolism, virulence genes, and antibiotic resistance (Lamrabet and Drancourt, 2012).

Although there are many *M. tuberculosis* strains, studies of the phylogeny and ecology of *M. tuberculosis* have revealed six main strain lineages that are associated with particular geographical regions (Cole *et al.*, 1998; Lawn and Zumla, 2011). However, recent advances in mycobacterial genomics suggest that the amount of sequence variation in the *M. tuberculosis* genome might have been underestimated (Ford *et al.*, 2012) and that some genetic diversity have important phenotypic consequences. Indeed, the use of whole genome sequencing has shown significant heterogeneity in bacterial populations, even between strains with identical MIRU/VNTR, or RFLP patterns (Ford *et al.*, 2012).

As indicated by Rehren *et al.* (2007), the *M. bovis* and *M. tuberculosis* genomes show >99% identity at the nucleotide level. However, distinct phenotypes, virulence, and host range differentiate both pathogens, suggesting that distinctive mechanisms of gene expression might be involved in determining the differences between both bacteria (Rehren *et al.*, 2007; Garnier *et al.*, 2003).

Tuberculosis in Human Beings

Among communicable diseases, tuberculosis is the second leading cause of death worldwide, accounting for 1.7 million deaths each year. At present, the worldwide number of new cases is higher than at any other time in history. Most cases occur in low- and middle-income countries with increasing incidence in Africa and in the former Soviet Union and this trend has been related to the effect of HIV on susceptibility to tuberculosis (Frieden *et al.*, 2003; Lawn and Zumla, 2011).

Human tuberculosis is caused by *Mycobacterium tuberculosis* which is an obligate human parasite; though it can infect most mammals, no animals can reproducibly transmit infection to others. Consequently, the continued existence of *M. tuberculosis* depends on transmission among humans (Hunter, 2011). *Mycobacterium bovis* was responsible for approximately 6% of all human tuberculosis deaths in Europe where the practice of milk pasteurization was not yet implemented (Lawn and Zumla, 2011). However, mandatory pasteurization of milk and advances in public health made the prevalence of human tuberculosis due to *M. bovis* to decline dramatically in developed countries (Granje, 2001). Nevertheless, *M. bovis* is still classified as a risk 3 pathogen for public health (The Center for Food Security and Public Health, 2009; Thoen *et al.*, 2006).

A current concern related to human tuberculosis (TB) is the increased trend of multidrug-resistant tuberculosis that has been documented in a number of countries worldwide (WHO, 2004; Lawn and Zumla, 2011). Treatment for multidrug-resistant TB patients requires the use of second-line drugs for extended periods of time, with the disadvantage of a higher cost and toxicity, together with lower effectiveness compared with first-line drugs used for routine treatment of TB (Shah *et al.*, 2007).

Infection occurring in immunocompetent people when they are first infected is known as primary tuberculosis (Donald *et al.*, 2010). The infection spreads as caseating granulomas to regional lymph nodes and systemically for a

few weeks before regressing as immunity develops. Although the lesions may heal, the bacteria persist (Paige and Bishai, 2010). However, post-primary tuberculosis is typically restricted to the upper lobes of the lungs and a high proportion of cases recover spontaneously. However, those that become ill account for most of the transmission of the infection (Lawn and Acheampong, 1999; Hunter, 2011).

Definitive diagnosis of tuberculosis in human remains based on culture for *M. tuberculosis*, but rapid diagnosis of infectious tuberculosis by sputum smear for acid-fast bacilli is still a common practice (Frieden *et al.*, 2003). In countries with a high tuberculosis incidence the World Health Organization has recommended the use of automated systems based on liquid cultures. However, due to lower cost, traditional culture tests are predominant with some cases of false positives, although differentiation of *M. tuberculosis* from other mycobacteria is attempted on the basis of growth characteristics and specific biochemical reactions (Bekmurzayeva *et al.*, 2013).

The use of serological tests for diagnosis remains a challenge as they do not provide enough sensitivity and specificity to be used as a first-line screening tool. The most commonly used serological tests are immunochromatographic assays (ICAs) based on lateral-flow or flow-through analysis or enzyme-linked immunosorbent assay (ELISA) tests. However, detection of antibodies can lead to false positive results as antibodies against environmental mycobacteria are often present (Bekmurzayeva *et al.*, 2013).

Zoonotic Potential of Bovine Tuberculosis

As stated previously, in addition to its role in livestock disease, *M. bovis* is also responsible for some cases of tuberculosis in human beings. *Mycobacterium bovis* infection in humans was important in the late nineteenth and early twentieth centuries (Granje, 2001; Müller *et al.*, 2013), and accounted for a portion of human tuberculosis in Europe. However, nowadays the relevance of *M. bovis* as the cause of tuberculosis in humans remains and the bovine tuberculosis eradication programs, together with the pasteurization of milk, have been among the most successful campaigns against bacterial disease. In fact, human tuberculosis due to *M. bovis* is now very rare in developed nations and the completion of the bovine tuberculosis eradication programs was accompanied by a significant reduction in the incidence of human tuberculosis due to this bacterium (Cousins and Dawson, 1999; Robert *et al.*, 1999; Granje, 2001).

At present, *M. bovis* accounts for less than 1% of TB cases in humans. For example, in the United States, where differentiation between *Mycobacterium* spp. is routinely done among human patients, *M. tuberculosis* is responsible for approximately 98.6% of human infection and *M. bovis* only relates to 1.4% of the cases (Miller and Olea-Popelka, 2013).

Infection of human beings with *M. bovis* almost always occurs by inhalation of aerosols or consumption of milk containing the bacillus. *Mycobacterium bovis* was historically associated with extra pulmonary tuberculosis in infants, usually occurring due to the consumption of nonpasteurized milk from infected cattle (Thoen *et al.*, 2006). However, aerosols generated during the handling of tuberculous carcasses in slaughterhouses also pose a risk for infection with traumatic inoculation into the skin being a possible, but much less common, route of infection (Granje, 2001).

Currently, the main causes of concern related to human *M. bovis* are migration of individuals from regions where bovine tuberculosis is still prevalent, occurrence of *M. bovis* disease in immunosuppressed HIV-infected patients, epizootics in domesticated and wild mammals, and airborne-acquired *M. bovis* infection in animal keepers and meat industry workers (Thoen *et al.*, 2006). In addition, the number of cases of *M. bovis* in humans and animals may be underestimated or unavailable in some areas of the world, especially in developing countries (Miller and Olea-Popelka, 2013). In a recent study investigating the interphase between domestic cattle and humans, Torres-Gonzalez *et al.* (2013) administered tuberculin skin test and interferon-gamma release assay to 311 dairy farm and abattoir workers and their contacts linked to a dairy production and livestock facility in Mexico. The overall prevalence of latent tuberculosis infection was 76.2% by tuberculin skin test and 58.5% by interferon-gamma release assay, indicating an increased risk among those occupationally exposed to *M. bovis*.

At the present time, there are still questions concerning the relative virulence of *M. bovis* in human beings, the immunological consequences of infection without clinical signs, and the occurrence of human-to-human transmission of *M. bovis* (Lesslie, 1968; Granje, 2001).

Immune Response to Mycobacteria

The immune response to mycobacteria involves a complex sequence of coordinated events, attempting to clear the pathogen, but more likely leads to an adequate control of infection. The loss of control observed in some hosts may be due to genetic factors or may be caused by exogenous stressors such as immunosuppression, malnutrition, or secondary concurrent infections (Tiwari *et al.*, 2006).

After pathogen entry, mainly by the aerosol route, infection is initiated by macrophage phagocytosis where subsequent fusion of a lysosome with a phagosome creates the potential for intracellular destruction of the bacilli by acidification. However, virulent mycobacteria inhibit this fusion, preventing microbe destruction (Robinson *et al.*, 2012), which enables the bacterium to replicate and disseminate (Menin *et al.*, 2013).

The initial immunological response to infection includes the interaction of multiple cell types, leading to the development of a cell-mediated immune (CMI) response, characterized by delayed type hypersensitivity (DTH) and IFN-g production (Palmer and Waters, 2006). Once a CMI response is initiated, a granuloma forms around the infected macrophages by the interaction of immune cells and cytokines. The granuloma is a complex host-protective response to persistent mycobacterial stimuli to localize the infection and to prevent further dissemination (Robinson *et al.*, 2012) and consists of focal accumulation of inflammatory cells, such as multinucleated giant cells and lymphocytes (Menin *et al.*, 2013). The production of connective tissues around the granuloma is also critical for controlling both mycobacterial growth and tissue dissemination (Gil *et al.*, 2010).

Effective immune responses against *M. bovis* may be a result of several factors, such as strain resistance, infection route, and encapsulation of the tuberculous lesions by entrapping bacilli inside the lesions (Pollock and Neill, 2002; Volkman *et al.*, 2004; Gil *et al.*, 2010; Menin *et al.*, 2013). Consequently, progression of mycobacterial disease and survival of the host are dependent on the ability to limit mycobacterial growth by an effective granulomatous response (Menin *et al.*, 2013).

The development of immunity to mycobacteria involves the cooperative action of T lymphocytes as specific inducers and macrophages, but is not restricted to a cell-mediated response; both cellular and humoral responses work reciprocally through T helper type-1 and type-2 cells. In general, specific antibody responses are mostly detected late in the course of infection and correlate with severe progression of disease (Palmer and Waters, 2006). Therefore, as infection progresses with large numbers of bacilli, high antibody levels, and diminished cellular responses to antigens, a shift in the immune response from a proinflammatory and cytotoxic response to an antibody-based response occurs (Chiodini and Davis, 1993; Coussens *et al.*, 2004). Consequently, following the development of the CMI response, immunity develops further with the recruitment of B-lymphocytes (humoral immune response) and the production of antigen-specific antibodies (Pollock *et al.*, 2001). The balance between cell-mediated and humoral immune responses is considered to be a function of the dominant cytokines generated in response to the numbers of the pathogen within the host (Pollock *et al.*, 2006).

Diagnosis

Diagnostic tests for tuberculosis can be divided into two categories: those detecting the organism and those that evaluate the host response to infection. The first category includes, among others, smear and acid-fast stain, bacteriologic culture, and polymerase chain reaction test (PCR), which amplifies one or more specific DNA sequences, generating thousands to millions of copies (Bekmurzayeva *et al.*, 2013). However, indirect diagnostic is based on clinical signs, gross and microscopic pathology, and cellular and humoral immune responses (Maas *et al.*, 2013).

The microscopic demonstration of acid-fast bacilli in direct smears from clinical samples or tissues stained with the Ziehl/Neelsen stain, a fluorescent acid-fast stain, or immunoperoxidase techniques provides a presumptive diagnosis. However, confirmation requires additional testing. Bacteriologic culture remains one of the most important methods for tuberculosis diagnosis, despite the prolonged incubation time and the significant decontamination and biocontainment requirements (Robbe-Austerman *et al.*, 2013). Bacteriologic culture has high specificity and sensitivity and some modified automated mycobacterial radiometric culture devises, including the BACTEC system (Becton Dickinson Laboratories, Sparks, MD, USA), have been designed for human clinical laboratories. Among other advantages, these devises use liquid culture that provides a greater sensitivity. The two automated systems most commonly used are the BACTEC MGIT 960 System, which uses the MGIT 960 media (MGIT), and the BACTEC 460 TB System, which uses BACTEC 12B media (BACTEC). Although these media systems are comparable, the MGIT typically recovered more mycobacteria other than *M. tuberculosis* complex than the BACTEC, but had higher contamination rates (NRC, 2003; Robbe-Austerman *et al.*, 2013).

For more rapid identification, several PCR-based methods have been developed and assays targeting *M. tuberculosis*-specific sequences, including IS*6110* and the MPT64 gene, have been widely applied (Kim *et al.*, 2013). Specific sequences of DNA for diverse mycobacteria have been used as targets for PCR amplification and differentiation of bacteria of the *M. tuberculosis* complex from nontuberculous mycobacteria, as well as for specific differentiation of *M. bovis* from other members of the *M. tuberculosis* complex (Maas *et al.*, 2013). A well-validated probe for the *Mycobacterium* genus that targets the conserved sequence of the *rpo*B gene, which encodes the β subunit of RNA polymerase, is now available. This probe facilitates the identification of all *Mycobacterium* spp. and also distinguishes *Mycobacterium* spp. at the species level by restriction enzyme analysis (Lee *et al.*, 2000; Kim *et al.*, 2013).

As related to host reactions to infection, gross lesions observed postmortem in tissues, organs, and carcasses due to *M. tuberculosis* complex infection are based on the typical granulomatous appearance of tuberculous lesions (Maas *et al.*, 2013). In naturally infected cattle, tuberculous lesions are found most frequently in the dorsocaudal region of the lungs, often close to the pleural surface (Cassidy, 2006). In countries where the disease has been subject to longstanding control, lesions are found with higher frequency in the lymph nodes associated with the respiratory system (tracheobronchial and mediastinal) than in the lung parenchyma (Corner, 1994). However, in disseminated cases, multiple small granulomas may be found in numerous organs.

As cell-mediated immune responses are the first and strongest host response to mycobacterial infections, this category of tests is useful for early detection of MAP infection (Robbe-Austerman *et al.*, 2007). Among others, these include interferon-gamma assay and the tuberculin skin test. The interferon-gamma assay is a test based on production and release of IFN-g by sensitized bovine lymphocytes in response to *in-vitro* stimulation with a series of mycobacterial antigens. As cellular immunity is developed soon after infection, this test is considered the most sensitive during early infection (Collins, 1996; Stabel, 2001). Whole blood or peripheral blood mononuclear cells are incubated in the presence or absence of mycobacterial antigens (avian or bovine purified protein derivative (PPD) or other specific antigens of *Mycobacterium* spp) that induce previously sensitized T cells to produce IFN-g (Bekmurzayeva *et al.*, 2013; Maas *et al.*, 2013). Some studies have questioned the specificity of the IFN-g assay, indicating that the test is subject to cross-reactivity with other mycobacteria (Huda *et al.*, 2003). Although results from some studies suggest that the specificity values are moderate to low (Kalis *et al.*, 2003; de la Rua-Domenech *et al.*, 2006), some field trials have determined specificities as high as 94–100% (Palmer and Waters, 2006).

A widely spread diagnostic test based on the CMI response is the intradermal tuberculin skin test, which measures a DTH to mycobacterial antigens. The swelling formed 3 days after injection of a mycobacterial PPD is measured to determine the increase of skin thickness (Collins, 2006; Kalis *et al.*, 2003;

Maas *et al.*, 2013). The antigen in use is a protein derivative prepared from the heat-treated products of growth and lysis of *M. bovis* or *M. avium*. The derivative elicits a delayed hypersensitivity in an animal sensitized to microorganisms of the same species (Good and Duignan, 2011). The most common tuberculin tests in use today include the caudal fold test and the single intradermal test, which use only bovine tuberculin PPD and the comparative cervical test, which uses bovine and avian tuberculin PPD in combination (Monaghan *et al.*, 1994).

As an example of the use of this test in an official control program, in the United States, accredited veterinarians perform intradermal skin testing using 0.1 ml of PPD tuberculin into either of the caudal tail folds. After 72 h the test is interpreted as negative, suspicious, or positive. Suspicious or positive reactor cattle are retested by regulatory veterinary personnel by a comparative (avian and bovine PPD) cervical skin test (Divers and Peek, 2008).

The tuberculin skin test has long been the standard diagnostic test for tuberculosis in cattle (Welsh *et al.*, 2005), and remains the test of choice as prescribed by the OIE, with the IFN-g assay used as an alternative test (Schiller *et al.*, 2010). However, depending on test interpretation, stage and severity of disease, bTB prevalence, cross-reacting organisms and other factors, sensitivity and specificity are highly variable ranging from 52% to 100% and from 75.5% to 100%, respectively (de la Rua-Domenech *et al.*, 2006; Divers and Peek, 2008; Schiller *et al.*, 2010). In addition, a disadvantage of this test is a poor response in anergic animals, in advanced stages of the disease, in animals with confined infection in the udder or lymphatic nodes that has become latent, and in periparturient cows. Some cases exhibiting reactions to both avian and mammalian tuberculin may also occur (Good and Duignan, 2011).

The sensitivity of the skin test can be improved by increasing the potency of the tuberculin but this tends to raise the frequency of cross-reactions associated with sensitizations from other organisms such as *M. tuberculosis* and *M. avium* and other mycobacteria. As mentioned before, in the description of the United States' control program, in an effort to increase specificity, animals that test positive to the caudal fold test are tested 60 days later using the comparative cervical test that uses PPD bovis and a crude protein derivative from *M. avium* at adjacent sites on the neck. After 3 days, the swelling at each injection site is compared; when the inflammation caused by the PPD bovis injection site is greater than that caused by the PPD avium, the animal is considered *M. bovis* infected (Churbanov and Milligan, 2012). However, as reported by van Dijk (2013), a possible strategy to improve sensitivity is to increase the frequency of the analyses; however, risks of having more false positives together with an increase in the costs of control programs are important considerations.

Tests based on the host humoral immune response detect circulating antibodies against *M. bovis*. A positive test result may indicate the presence of infection, immunity to a previous infection, cross-reactions with antigens from other agents, the presence of maternal antibodies or antibodies present as a result of vaccination (Maas *et al.*, 2013). As progressive disease reduces the level of the cellular immunity and favors the initiation of a humoral response, serological assays are more sensitive after infection has progressed. Serological tests have some advantages in terms of logistics and they include ELISAs targeted to specific antigens and the lateral-flow immunochromatographic test, an animal-side test that uses a combination of multiple antigens (Lyashchenko *et al.*, 2006).

Epidemiology and Risk Factors

In the early twentieth century, bTB was found worldwide in cattle with a high prevalence in many countries. After an association between *M. bovis* infection in humans and the prevalence of tuberculosis in cattle was established, mandatory pasteurization of milk and advances in public health caused the prevalence of human tuberculosis due to *M. bovis* to decline dramatically, especially in developed countries.

Infectious diseases in general arise from an interaction between the infectious agent, the host, and a range of covariables, which may include other infectious diseases and the environment (Cassidy, 2006). Likewise, the transmission of *M. bovis* between cattle is dependent on a number of factors, including frequency of shedding, route of infection, infective dose, and host susceptibility (Griffin and Dolan, 1995).

Diseases transmitted between wildlife and livestock are particularly challenging. When a reservoir of infection exists outside the cattle population eradication becomes difficult (Corner, 2006; Munyeme *et al.*, 2009). In North America, it is estimated that at least 79% of diseases reportable to the World Organization for Animal Health (OIE) have a wildlife component (Miller and Sweeney, 2013). The several animal population interfaces at which *M. bovis* is present are characterized by unique population, climatic, ecologic, behavioral, and political factors (Van Campen and Rhyan, 2010). The test and slaughter policies of tuberculosis control, effectively used with domestic livestock, are insufficient in areas where wildlife reservoirs exist (Palmer, 2007) and disease eradication has been prevented by the presence of a wildlife reservoir of *M. bovis*. An example is provided by free-ranging white-tailed deer (*Odocoileus virginianus*) in Michigan, USA that represents the first known reservoir of *M. bovis* in free-living wildlife in the United States (O'Brien *et al.*, 2006; Palmer, 2007; Conner *et al.*, 2008; Wobeser, 2009). The bacterium persists for a week or longer on feedstuffs used as supplemental feed for deer (Palmer and Whipple, 2006) and deer-to-deer (Palmer *et al.*, 2004b) and deer-to-cattle (Palmer *et al.*, 2004a) transmission by indirect contact via feed has been demonstrated experimentally. In that area, several wildlife species besides white-tailed deer have been found positive for the organism (Bruning-Fann *et al.*, 2001), the most notable being coyotes (Bruning-Fann *et al.*, 1998), although these species are currently considered to be dead-end hosts for the infection.

As reviewed by Wobeser (2009), some other maintenance hosts in which infection persists through intraspecies transmission in the absence of an external source of *M. bovis* include the Eurasian badger (*Meles meles*) in Ireland and the United Kingdom; the brush-tailed possum (*Trichosurus vulpecula*) in New Zealand; African buffalo (*Syncerus caffer*), lechwe (*Kobus lechwe*), warthog (*Phacocoerus africanus*), and kudu (*Tragelaphus strepsiceros*) in Africa; and red deer (*Cervus elaphus*), and European wild boar (*Sus scrofa*) in Spain (Lees *et al.*, 2003; Palmer and Whipple, 2006; Renwick *et al.*, 2007; Naranjo *et al.*, 2008;

Bohm *et al.*, 2009). In these cases, mitigation strategies for TB management usually involve reducing density and exposure of the wildlife reservoir by increased hunting, eliminating supplemental feeding, and preventing contact between infected and at-risk populations. An additional potential strategy is the use of vaccination in wildlife or at-risk cattle, although, developmental work on vaccines is still underway and no effective vaccine exists for bovine TB at this time (Nol *et al.*, 2008; Palmer *et al.*, 2007; Robinson *et al.*, 2012; Menin *et al.*, 2013).

One of the main risk factors identified at the individual level is the age of the animals as life span associates with greater potential exposure time to the pathogen (Humblet *et al.*, 2009). Moreover, animals might get infected at a young age, but only develop a detectable immune response or express clinical disease when they are adults (Griffin *et al.*, 1996).

Differences in genetic resistance and susceptibility to bTB in cattle have been proposed. It is possible that in certain individuals nonspecific immunity could eliminate a low-dose *M. bovis* challenge before infection is established (Humblet *et al.*, 2009). In recent studies, a higher resistance to TB among *Bos indicus* than *Bos taurus* has been reported (Ameni *et al.*, 2007). Moreover, differences in susceptibility to the disease have been indicated for some genetic lines of cattle (Phillips *et al.*, 2002). As reviewed by Humblet *et al.* (2009), breed has been also identified as an individual risk factor for positive skin test. However, it is possible that the difference in susceptibility between breeds may be related to some degree to differences in management between diverse types of animals.

This variation in resistance to infection and disease caused by the *M. tuberculosis* complex seems to be under polygenic control (Allen *et al.*, 2010) and some candidate genes have been identified in the bovine and other species (Morris, 2007). More recently, Sun *et al.* (2012) investigated the role of host genetic factors in susceptibility to bTB in Chinese Holstein cattle and found the G1596A polymorphism in the toll-like receptor 1 (TLR1) gene to be associated with bTB infection status. Subsequently, Finlay *et al.* (2012) reported a genomic region on BTA 22 associated with tuberculosis susceptibility; this region contains the taurine transporter gene SLC6A6, or TauT, which is known to function in the immune system.

However, reported herd-level risk factors comprise a previous history of infection in the herd, presence of human cases, herd size (larger herds related to greater risk), type of production system (level of confinement and design of facilities), and management defining contact between cattle and contaminated environmental sources and wildlife (Humblet *et al.*, 2009). Other significant risk factors include purchasing animals (Gopal *et al.*, 2006; Kaneene *et al.*, 2002), animal movements (Gilbert *et al.*, 2005), and culling rate (Menzies and Neill, 2000).

Disease Control

Eradication of TB from cattle has been successful in several countries including Austria, Belgium, France, Canada, and most of the United States (de la Rua-Domenech, 2006). Traditionally, control efforts have included the removal of tuberculin reactors and suspect cattle (test-and-slaughter), execution of test-and-segregation methods, disinfection of premises, and the implementation of sound hygienic practices, followed by a periodic review of herd disease status using the tuberculin test and meat plant surveillance (Cassidy, 2006; Collins, 2006).

In general terms, there are different strategies and levels for disease detection. From the epidemiological perspective, surveillance aims at demonstrating the absence of disease and involves the systematic, continuous collection, and analysis of data on the health of wild animal species. Surveillance of cattle and wildlife in many developed countries aims to maintain a bTB-free status. Here, diagnostic assays are used to determine the presence of *M. bovis* in a particular area or population, rather than to determine exact prevalence (Maas *et al.*, 2013).

However, monitoring is restricted to known infected populations, and consists of the systematic recording of epidemiological data, with the specific purpose of detecting spatial and temporal trends, such as the spread, interspecies transmission, or the effect of management interventions in wildlife populations (Robinson *et al.*, 2012). Monitoring is often executed on a smaller scale than surveillance and, in general, is more invasive and expensive. Both surveillance and monitoring are used as a screening tool to determine whether the infectious agent is present in a defined population and area (Maas *et al.*, 2013). At another level, when testing individual animals and small populations for bTB, the assays have a short-term true diagnostic application, aiming at confirmation of the *M. bovis* infection status (Maas *et al.*, 2013).

Overall, official programs have focused on the control of animal movements (including the implementation of adequate animal identification and traceability), the detection of infected herds and individual animals, management of affected herds (including compulsory slaughter of reactors and herd depopulation), and the management of wildlife reservoirs (Collins, 2006). Combinations of tuberculin testing to detect infected animals, slaughterhouse monitoring, movement control, and destruction of exposed animals generally have been successful strategies. In the United States, slaughterhouse surveillance and subsequent traceback has been the main large-scale diagnostic strategy. However, a limitation of slaughterhouse inspection at the present time is the reduced

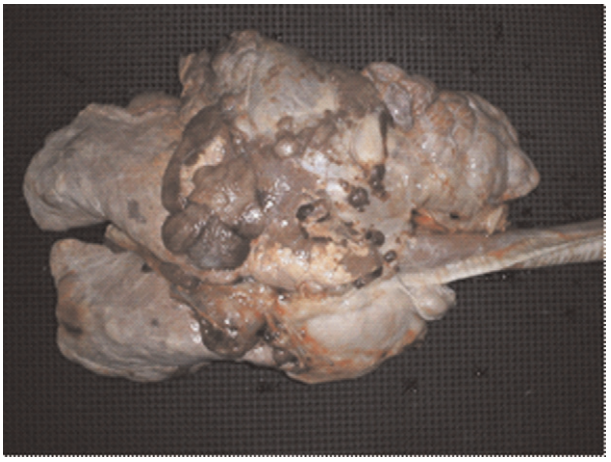


Figure 1 Tuberculosis lesions in the bovine lung. Photo by Dr. Manuel Quezada.

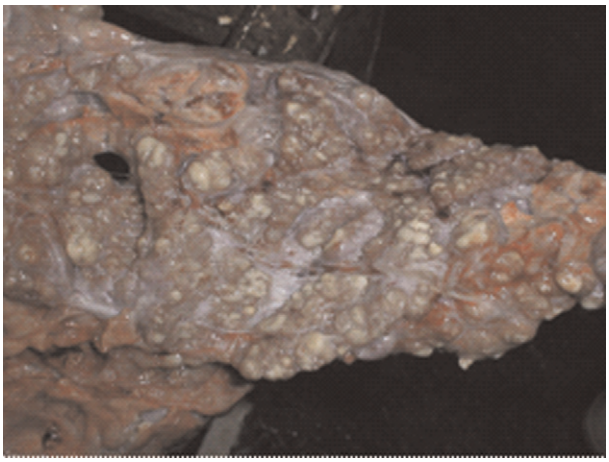


Figure 2 Detailed view of tuberculosis lesions in the bovine lung. Photo by Dr. Manuel Quezada.

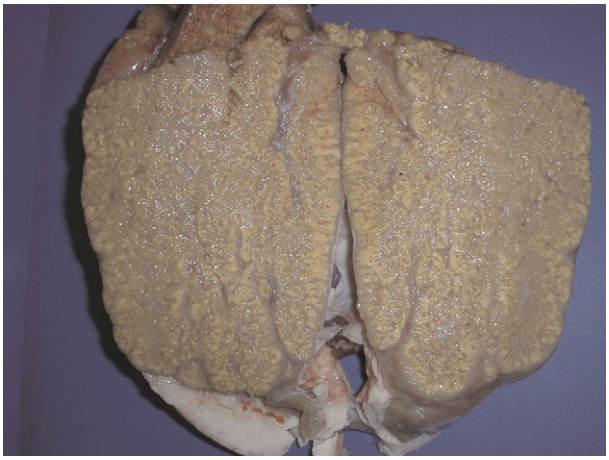


Figure 3 Affected bovine lymph node, showing multiple granulomas. Photo by Dr. Manuel Quezada.



Figure 4 Generalized TB lesions in a bovine (abdominal cavity). Photo by Dr. Manuel Quezada.

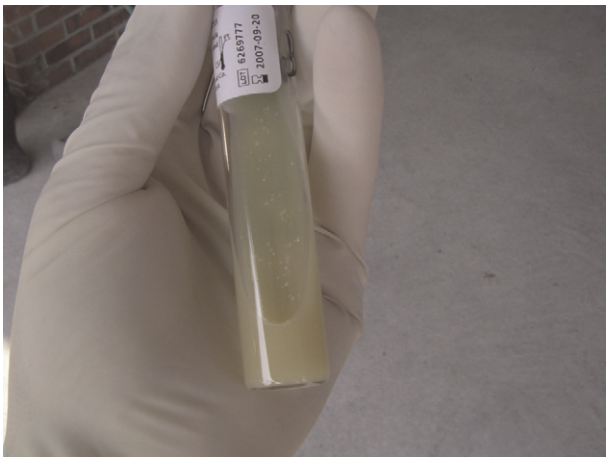


Figure 5 Culture media for Mycobacteria with *M. paratuberculosis* growing colonies.

sensitivity given the small size of lesions (granulomatous tissue lesions primarily from the head and thoracic cavity (Figures 1–5)) in some cattle (Divers and Peek, 2008).

See also: Animal Health: Global Antibiotic Issues. Vaccines and Vaccination Practices: Key to Sustainable Animal Production

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Animal Welfare: Stress, Global Issues, and Perspectives

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Glossary

Allostasis The ability of an animal to cope with physical and mental stress.
Animal welfare The current mental and physical states of an animal.
Distress A state of being when an animal can no longer cope with a stressor in order to maintain homeostasis that takes biological resources away from other biological functions.
Exsanguination An adjunctive method of euthanasia to ensure death in an unconscious animal. An incision is made on the throat and all blood vessels and sensory and motor nerves are transected.
Nonambulatory Weak, debilitated animals that are unable to stand or walk may be referred to as a Downer.
Pain A stressor that serves as a sensory or awareness of potential injury and tissue damage.
Stress A biological response from internal or external events, real or perceived, that disrupt homeostasis.
Stressor Stimulus or threat that elicits a stress response.
Unconsciousness A loss of individual awareness.
Zoonotic disease An infectious disease transmitted from animals to humans and from humans to animals.

Definitions

The term 'animal welfare' has been used by many in society and the media with various intentions of meaning. Much of the disagreement concerning the definition of the term lies in the mixing of the scientific and ethical questions of what animal welfare is. Even though the basis of the concept does have moral implications, this article will focus on the science of animal welfare. As more science on the welfare of animals is acquired, the definition of the term evolves but there are underlining concepts that remain consistent. The Bramble Committee (1965) was one of the first influential writings on animal welfare. It not only had a significant effect on how the world views animal welfare but also had a direct effect on legislative action taken regarding welfare in Europe. The Office International des Epizooties (OIE), commonly known as World Organization for Animal Health, defines an animal's welfare to be good if the animal: "is healthy, comfortable, well nourished, safe, able to express innate behavior and…. Not suffering from unpleasant states such as pain, fear of distress." (OIE, 2010). The Farm Animal Welfare Council (FAWC, 1993) identifies five areas that address the animal's physical and mental well-being when considering welfare. These areas are commonly referred to as the Five Freedoms (**Table 1**).

A more recent concept of animal welfare is based on allostasis, or the ability to cope with stress (McEwen and Wingfield, 2003; Korte *et al.*, 2007). This concept argues that the Five Freedoms are an unrealistic model for an animal's well-being because achieving all five would essentially be a state of 'utopia.' Most animals would naturally experience hunger, which stimulates their hunting/foraging behaviors. Thus, achieving one thing would be in direct conflict with another.

In scientific terms, animal welfare refers to the actual and current state of the animal (Keeling *et al.*, 2011). The scientific community seems to agree that welfare is a "characteristic of the animal, not something that is given to the animal" (Broom, 1996). Thus, individual animals experience varying degrees of welfare from good to bad. Bracke *et al.* (1999) state that the term describes "the quality of an animal's life as it is experienced by an individual animal." Curtis (2007) argued that an animal's state of being, not on how the animal feels, will be its rates of productive and reproductive performance relative to its predicted potential to perform.

The definition of animal welfare is evolving and the methods of how to precisely measure animal welfare as well as interpretations of state of being are likely to be debated for some time.

Stress is a biological response from internal or external events, real or perceived, that disrupt an animal's homeostasis. Threats can be perceived consciously or unconsciously (Carstens and Moberg, 2000). The stressor is the stimulus or threat that elicits a stress response. Stressors can be separated into two categories: by its duration as acute, chronic, or intermittent, and by type as psychological or physiological. Individual animals respond differently to stressors depending on age, health, genetics, and previous life experiences (Hahn and Becker, 1984), and they can easily adapt to stressors (Ladewig, 2000). Pain is a type of stressor that serves as an awareness of potential tissue damage. Noxious stimulus allows an animal to remove itself from or react to the stimulus in order to reduce or avoid the damage (Carstens and Moberg, 2000; Molony and Kent, 1997).

There are four main biological responses to a stressor initiated by an animal: autonomic nervous system, neuroendocrine, immune and behavioral, to cope with a stressor, and elicit a stress response (Moberg, 2000). Animals have adapted mechanisms to cope with stress, similar to humans, so stress is not always a bad thing. Moreover, stress is not always harmful to the body and it helps to maintain homeostasis. For example, the biological response to a stressor can promote memory of the situation in order to avoid it in the future

Table 1 The five freedoms and provisions

Freedom from thirst, hunger, and malnutrition	Free access to freshwater and a diet to maintain full health and vigor
Freedom from discomfort	Providing a suitable environment, including shelter and a comfortable resting area
Freedom from pain, injury, and disease	Prevention or rapid diagnosis and treatment
Freedom to express normal behavior	Providing sufficient space, proper facilities, and company of the animal's own kind
Freedom from fear and distress	Ensuring conditions that avoid mental suffering

Source: Adapted from Webster, A.J.F., 2001. Farm animal welfare: The five freedoms and the free market. Veterinary Journal 161, 229–237.

(McEwen, 2005). However, if the stressor is severe and the animal can no longer sufficiently cope with the stressor to maintain homeostasis, it must then take biological resources from other biological functions and stress becomes distress (Moberg, 2000; Carstens and Moberg, 2000). It is when an animal experiences distress that its well-being becomes compromised. Understanding an animal's physiology, psychology, and behavior can help scientists make educated assessments of the animal's well-being (Broom and Johnson, 1993).

Global Perspective

Attention to animal welfare varies considerably around the world. Generally, the EU has the strongest laws and attention to farm animal welfare among nations. However, individual member countries in the EU have stronger animal welfare rules than the EU as a whole. Some European countries that are not a member of the EU such as Switzerland have strong farm animal welfare laws. As a general rule in Western Europe, the more Northern countries have stricter animal welfare laws than more Southern European countries.

The United States and Canada have some farm animal welfare laws and regulations. Most laws are related to humane slaughter. Transportation of farm animals in the United States must not exceed 28 h. Handling of animals in stockyards are covered by the US Packers and Stockyard Act.

Within the United States, several states have laws to prevent certain production practices. For example, Florida, Arizona, and California have banned gestation crates for pregnant sows. Some state initiatives have also banned cages for laying hens and crates for veal calves.

Asia, Africa, and Latin America have few animal welfare laws or regulations. They may impose international standards (e.g., for the EU) if they export to countries that request for a higher animal welfare standard.

Retail companies that sell animal products include grocery stores, restaurants, and food service companies. Some 'retailers' have animal welfare standards that impact production practices, whereas some have specific requirements for production standards. A search of each retail company's website often yields their animal welfare standards. The retailers often drive change more quickly than through legislation. Activist organizations have learned that pressure on retailers can lead to changes more quickly than through legislation.

One critical question has arisen in recent years about global standards for animal welfare. Most standards are minimum requirements. Some people feel that an animal welfare standard must accomplish a high level of animal welfare. Standards vary around the world based on many factors, including target level (minimum through high); scientific interpretation; geography and unique production methods; cultural differences; and different ethical, moral, or religious standards. The OIE has minimal standards that are accepted by member countries of the World Trade Organization. Otherwise, animal welfare standards vary considerably from no standards through high standards.

Farm Animals

One of the most common issues and concerns with standard agriculture practices is the pain and distress it causes the animal. These practices are performed to improve the overall well-being of the animal, but may have both human and animal implications. Scientists are continually researching improved and more humane methods for standard agricultural procedures. The standard practices of the agriculture industry and the regulations and requirements that must be followed for their use in production and research are discussed immediately below by species, and some recommendations are provided. As stated in the Guide and the Care and Use of Agricultural Animals in Research and Teaching, all basic biological needs should always be met such as food, water, shelter, and even comfort.

Cattle

Castration

Castration has multiple purposes in several male species, primarily to reduce aggression and therefore limit harm to handlers and other animals, satisfy food quality regulations in order to ensure a high-quality eating experience for consumers, and to manage reproductive and genetic control. Several methods of castration in cattle are acceptable in the Ag Guide, for example, surgical or bloodless castration, rubber rings, and tubing bands. When deciding on a method the animal's age and weight should be accounted for, and performed before 2 or 3 months of age or below 230 kg (Farm Animal Welfare Council, 1981) when the procedure is least stressful. At weights greater than 230 kg, local and topical anesthetics should be used to minimize pain.

Castration increases the cortisol response (Robertson *et al.*, 1994), substance-P concentrations (Coetzee *et al.*, 2008), haptoglobin concentrations (Ballou *et al.*, 2013), and abnormal behaviors (Robertson *et al.*, 1994; Currah *et al.*, 2009), whereas it suppresses leukocyte concentrations (Ballou *et al.*, 2013) in calves. The specific castration method used (surgical or bloodless) can cause increased pain. The bloodless castration methods are associated with both acute and chronic pain that can last up to 42 days (Molony *et al.*, 1995; Thüer *et al.*, 2007), and should only be used when surgical castration is not appropriate for research protocols or when

postoperative complications are expected. All ages of castration cause acute pain, but cortisol concentrations were greatest in calves surgically castrated at older ages (Robertson *et al.*, 1994).

Pain relief in the form of a local anesthetic and nonsteroid antiinflammatory drug (NSAID) increased appetite and reduced the cortisol response (Sutherland *et al.*, 2013), and prevented leukocytosis, neutrophilia, and leukocyte suppression (Ballou *et al.*, 2013) in surgically castrated calves. Administering local anesthesia before castration may reduce acute pain; however, it does not eliminate it (Thüer *et al.*, 2007).

Dehorning

Dehorning in cattle is performed to reduce injury to handlers and animals, and reduce bruising of carcasses and damage to hides. Injury to other animals caused by horns is especially high during transportation. The United States currently does not have any regulations for disbudding and dehorning, but the AVMA (2013b) recommends disbudding as the preferred dehorning method in calves with the use of local anesthetics and NSAIDs at the earliest age practicable. Polled breeds eliminate the need for dehorning and disbudding, and should be used when possible.

Disbudding occurs with a heated disbudding iron or chemical paste when the horn buds are 5–10 mm long, approximately 8 weeks of age (Stafford and Mellor, 2005). Amputation dehorning causes a greater cortisol response than cautery or chemical disbudding with cautery having the lowest response and the preferred technique (Stafford and Mellor, 2011). There are no differences in cortisol response between the four different amputation dehorning methods: scoop, guillotine shears, saw, or embryotomy wire (Sylvester *et al.*, 1998a), suggesting that all amputation methods of dehorning are stressful in calves.

The cortisol response using a scoop method of dehorning was elevated for 3–4 h postdehorning (Sylvester *et al.*, 1998b) or as long as 7 h (McMeekan *et al.*, 1998a, 1998b). Local anesthetics reduce the peak cortisol response to scoop dehorning but as soon as the drug wears off, concentrations increase as if no local anesthetic had been applied. More than just local anesthetic is needed for long-term pain from dehorning. Local anesthetic maintains cortisol concentrations 5 h after dehorning, but then it remains elevated for up to 10 h after dehorning (Sutherland *et al.*, 2002a; McMeekan *et al.*, 1998b). Local anesthetic plus cauterizing the wound (Sylvester *et al.*, 1998b; Sutherland *et al.*, 2002b), administering a second treatment of local anesthetics during the period of pain (McMeekan *et al.*, 1998a), or administering both the local anesthetics and a NSAID (McMeekan *et al.*, 1998b) will reduce cortisol concentrations to levels comparable to controls. However, the type of drugs used may not have the appropriate mechanism of action to alleviate the pain caused from dehorning. The NSAID, ketoprofen, worked with local anesthetic, but phenylbutazone did not reduce the cortisol response (Sutherland *et al.*, 2002a).

Abnormal or pain behaviors also increase after dehorning. Head shaking and tail and ear flicking increased after dehorning, but administration of a local anesthetic reduced those behaviors, however, for only 2 h after dehorning (Sylvester *et al.*, 2004). Sutherland *et al.* (2013) also observed that calves dehorned spent more time head shaking and ear flicking, as well as less time eating. Head shaking was reduced and eating increased when local anesthetic and the NSAID banamine were given, but ear flicking behaviors did not change. Calves injected with the NSAID meloxicam and a local anesthetic nerve block showed reduced ear flicking for 44 h, head shaking for 9 h, and displayed less pain sensitivity 4-h postdehorning (Heinrich *et al.*, 2010).

Methods should be used to minimize pain and distress, especially in older animals. The use of both a local anesthetic and an NSAID alleviate the pain for a longer period of time across multiple breeds of cattle.

Identification

Several methods of identification are used in cattle: ear and tail tags, ear notches, back tags, tattoos, electronic identification, branding, and paint marks. Most of these forms of identification are not permanent and the type of identification should be appropriate for the farm and research protocols. However, permanent methods of identification should be used in order to trace the origin of individual production animals in order to protect the agriculture industry and public health (AVMA, 2013c). States in the United States have brand registries and regulations related to branding, but only Montana, Nevada, Oregon, and Idaho require hot-iron branding applied to cattle imported from Canada and Mexico (AVMA, 2011).

The only two methods of permanent identification are hot-iron and freeze branding. Hot-iron branding burns the skin to leave a scar, whereas freeze branding kills pigment-producing cells found in the hair follicles so that the hair is depigmented when it grows back. Cattle that are hot-iron branded have a greater cortisol response (Schwartzkopf-Genswein *et al.*, 1997a), high epinephrine concentrations (Lay Jr. *et al.*, 1992a), show more pain behaviors of tail-flicks, kicks, falls, and vocalizations (Schwartzkopf-Genswein *et al.*, 1997b, 1998), but no differences in sensitivity to touch or in stress-induced analgesia are found between hot-iron and freeze branding (Schwartzkopf-Genswein *et al.*, 1997a). Hot-iron branding causes greater distances and velocities of head movements and forces on the headgate and chute (Schwartzkopf-Genswein *et al.*, 1998). Hot-iron branding also causes more tissue damage than freeze branding, with freeze branding showing more inflammation through infrared thermography early after branding and hot-iron having a prolonged inflammatory response (Schwartzkopf-Genswein and Stookey, 1997). Dairy calves, however, showed a different response with no differences in cortisol, epinephrine, and norepinephrine concentrations between hot-iron and freeze branding, but hot-iron branded cows exhibited a greater escape avoidance reaction and had increased heart rate (Lay Jr. *et al.*, 1992b).

The physiological, behavioral, and inflammatory responses of cattle indicate that hot-iron branding causes more pain or discomfit than freeze branding, and therefore freeze branding is the preferable branding technique regardless of breed. However, other alternatives should be used for branding if possible. No research has studied administered pain relief during branding, but to minimize pain and discomfort this should be considered.

Euthanasia

Humane methods to alleviate or eliminate pain and distress that immediately results in unconsciousness should be carried out during euthanasia. When animals are sick, injured, or suffering for any reason that continued life is not a humane option or is worse than death, then the owner or veterinarian should euthanize the animal. This process is for the sake of the animal's welfare and quality of life. Acceptable methods of euthanasia consistently result in a humane death by (1) direct depression of neurons that are required for life, (2) hypoxia, or (3) physical disruption of brain activity. The AVMA Guidelines on Euthanasia (AVMA, 2013a) lists several methods of euthanasia appropriate for ruminants.

Several criteria have been listed by the AVMA for evaluating humane euthanasia methods: (1) ability to induce loss of consciousness and death with a minimum of pain and distress; (2) time required to induce loss of consciousness; (3) reliability; (4) safety of the personnel; (5) irreversibility; (6) compatibility with intended animal use and purpose; (7) documented emotional effect on observers or operators; (8) compatibility with subsequent evaluation, examination, or use of tissue; (9) drug availability and human abuse potential; (10) compatibility with species, age, and health status; (11) ability to maintain equipment in proper working order; (12) safety for predators or scavengers should the animal's remains be consumed; (13) legal requirements; and (14) environmental impacts of the method or disposition of the animal's remains.

The use of barbiturates is an acceptable method of euthanasia; however, large amounts of drug are required in larger animals so cost may deter its use. Barbiturates must also be administered by a person who is registered with the US Drug Enforcement Agency and under veterinarian supervision. Residues remain in the tissue and animals euthanized with barbiturates; therefore any drug that leaves residues cannot be used for human consumption unless approved by the US Department of Food and Drug Administration. Physical methods of euthanasia using gunshot or penetrating captive bolt (see **Figure 1**) are most commonly used in cattle. Physical methods disrupt and destroy the brain tissue. Additional action after rendering an animal unconscious should be taken to ensure death. Intravenous administration of potassium chloride or magnesium sulfate can be used in animals not to be consumed or exsanguination after physical euthanasia are methods to ensure death, but neither can be used as a sole method of euthanasia. After euthanasia, death must be confirmed by lack of heartbeat, respiration, and corneal reflex along with rigor mortis before rendering the animal.

Tail docking in dairy cattle

Dairy cattle are tail docked in order to increase udder and milk hygiene. However, tail docking is seen as an animal welfare issue because of the pain it causes from performing the procedure, as well as effects on communication between the herd and with caretakers, and because it alters fly avoidance behavior. The United States has no regulations regarding tail docking of cattle; however, the AVMA (2013d) does not support it and state that if amputation is medically necessary then a veterinarian must perform the procedure. Regulations and policies regarding tail docking cattle vary from country to country. It is prohibited in Denmark, Germany, Scotland, Sweden, UK, and some Australian states but a veterinarian can perform the procedure and only for reasons of udder health. In New Zealand, where the practice originated it must be performed by a veterinarian using a rubber ring, and Canada opposes the practice but a trained person can perform the procedure in young calves (Stull *et al.*, 2002).

Two different methods of docking are used, a rubber ring or docking iron (for review of methods and implications see Stull *et al.*, 2002). Banding with a rubber ring makes the tail necrotic and it detaches 3–7 weeks postbanding, or will be manually detached after 7 days, especially in older calves and heifers. Inflammation may be more severe if the band is placed on the vertebra and not over the joint. If the band is placed too close to the base of the tail then the blood vessels in the tail may not constrict, so it is recommended to band distal to the sixth coccygeal vertebrae (Gregory and Matthews, 1998). The docking iron amputates the tail with a heated scissors-like tool.

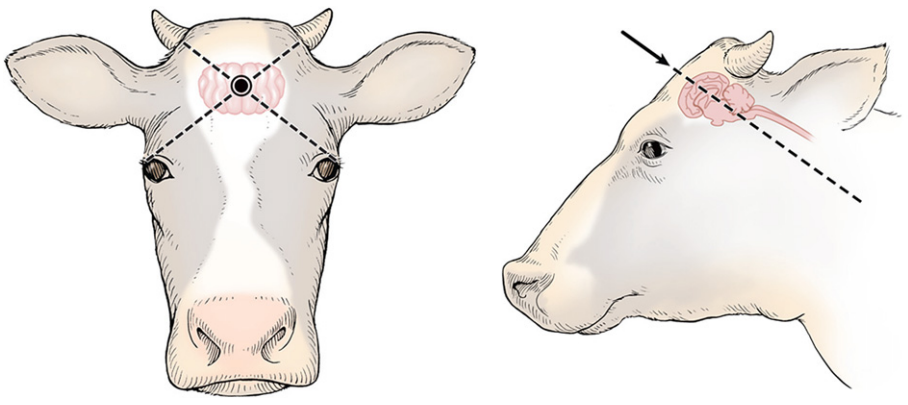


Figure 1 Anatomical landmarks for penetrating captive bolt or gunshot physical methods of euthanasia. The intersection of the dotted lines indicated with a circle in the front view (a) is the proper point of entry. The side view (b) dotted line shows the trajectory through the brain. Reproduced from Shearer, J.K., 2013. Humane Euthanasia of Sick, Injured and/or Debilitated Livestock. Ames, IA: Iowa State University. Available at: http://vetmed.iastate.edu/HumaneEuthanasia (accessed 21.08.13).

The cortisol response (Petrie *et al.*, 1996; Eicher *et al.*, 2000; Schreiner and Ruegg, 2002a) and immune response (Eicher and Dailey, 2002; Eicher *et al.*, 2000, 2001) are not different between docked and control handled dairy heifers and calves. The rubber ring method may be preferred because hemorrhaging can occur when using the docking iron (Petrie *et al.*, 1996), but Tom *et al.* (2002) found that the rubber ring method caused an increase in cortisol concentrations 1 h after banding, but the docking iron did not. So there is some conflict as to which docking method is better and causes the least distress.

Behavioral changes in docked cattle indicate there is some discomfort experienced from tail docking. Increased activity is found 2 h postbanding in docked calves compared with controls (Eicher and Dailey, 2002). Tail grooming increased up to 5 days after docking, and increased frequencies of standing and lying the first day have been seen in rubber ring docked calves with no differences between the docking iron treatment and controls (Tom *et al.*, 2002). Tail docked heifers are also sensitive to heat and cold, showing greater changes in the tail surface temperature and increased stomping activity (Eicher *et al.*, 2006).

Besides the acute stress of removing the tail, the other potential welfare issue from tail docking in dairy calves is the inability to remove flies. More flies are present on docked cows and fly avoidance behaviors increase. Docked calves lick and ear twitch more frequently than control calves that tail swing more frequently (Eicher and Dailey, 2002). Cows that were tail docked had a greater count of flies in the rear legs and foot stomping increased as an alternative fly avoidance behavior (Eicher *et al.*, 2001). Udder cleanliness and contamination to milking equipment and milk is another reason dairy cattle are tail docked. Eicher *et al.* (2001) found docked cows were cleaner, but Schreiner and Ruegg (2002b) found no differences between docked and undocked cows in somatic cell counts, intramammary infection, and udder and leg cleanliness.

No benefits to the animal's welfare have been observed with tail docking. Behavioral changes and sensitivity to hot and cold temperatures suggest that the procedure causes discomfort even if physiological parameters do not indicate stress. Fly avoidance behaviors change with cattle not using their tail as much to remove flies; therefore, more flies are present at the rear of the animal, and little differences are found in the cleanliness of docked and undocked cows. With no consistent and obvious benefit to the animal, it is suggested that tail docking be discouraged.

Hoof care in dairy cows

Dairy cow lameness causes economic loss to the produce because of milk production and fertility losses, and is the primary reason for culling cows. Lameness is painful and increases sensitivity to mechanical noxious stimuli (Whay *et al.*, 1997). The type of diseases causing lameness influences the pain threshold as well. Whay *et al.* (1998) found sole ulcer and white line disease pain thresholds were still reduced 28 days after treatment but acute digital tissue infection did not.

Many producers find it hard to detect lameness at early stages because cows do not show behavioral responses to the pain until the injury is advanced and behavioral changes are obvious (O'Callaghan, 2002). Pain changes the gait of the animal and is the most common system to detect lameness. The FASS (2010) lists the gait changes to look for: (1) arching of the back if rear limb lameness, (2) shortening the stride length of the affected limb as to reduce the time weight bearing on the limb, (3) sinking the dew claws on the unaffected contralateral limb as weight is transferred to the unaffected limb, (4) head bob in a vertical plane because the head raises when the affected limb hits the ground, (5) slower walking speed and more frequent stops, and (6) swinging the affected limb in or out depending on the location of the lesion.

A five-point numerical rating system (NRS) (**Table 2**), with one being sound and five severely lame, is used to assess an animal's gait that producers should be trained on. This lameness system emphasizes posture and gait (Sprecher *et al.*, 1997). The NRS has been found to be a better predictor of ulcers causing lameness than increased lying behavior or walking speed that is also found in lame cows. The NRS was able to predict the appearance of ulcers 4 weeks before diagnosis (Chapinal *et al.*, 2009).

A lameness score greater than two is a risk factor for extended intervals between conception, more service per pregnancy, and increased likelihood of being culled (Sprecher *et al.*, 1997). Milk yield in cows can be reduced 4 months before the cow is diagnosed with lameness and up to 5 months after treatment, with a mean reduction of 360 kg per lactation period (Green *et al.*, 2002). It is important that producers detect lameness as soon as possible in order to treat the cows to improve health and welfare of the animal, but also to reduce economic loss to the producer. Improvements made to the flooring cattle walk on can also improve welfare in lame cows. Flower *et al.* (2007) observed that high-friction composite rubber surfaces provided secure footing and comfort during walking for cattle with and without sole ulcers. Preventative care also helps reduce the prevalence of lameness in dairies. Claw trimming is performed usually once a year in the dry off period, and hooves are trimmed and treated at any point lameness is detected. Foot baths of copper sulfate, zinc sulfate, or formaldehyde are also recommended to control bacteria.

Swine

Housing

Pigs are social animals and should be housed in groups in production systems. Isolation has shown to increase cortisol production and shift leukocyte percentages (Ruis *et al.*, 2001) in pigs. It is common to see group-housed growing pigs in production, typically in groups of 2–30 pigs per pen, but groups of hundreds and thousands are becoming more common (FASS, 2010). Mixing unfamiliar pigs does increase social stress, which affects the physiology and immune system (Morrow-Tesch *et al.*, 1994). Fighting for dominance in larger groups typically lasts 48 h (Meese and Ewbank, 1973) after mixing, then once the hierarchy is established the group remains relatively stable. Hides (structures for animals to put their head in) are one alternative to allow submissive pigs to protect their heads and ears in order to escape aggressive attacks in order to improve their own well-being during mixing

Table 2 The five-point numerical rating system to assess lameness in dairy cows

Score gait	*Description*	*Behavioral criteria*
1. Sound	Smooth and fluid movement	Flat back Steady head carriage Hind hooves track up Joints flex freely Symmetrical gait All legs bear weight equally
2. Imperfect gait	Imperfect locomotion but ability to move freely	Flat or mildly arched back Steady head carriage Hind hooves do not track up perfectly Joints slightly stiff Slightly asymmetric gait All legs bear weight equally
3. Mildly lame	Capable of locomotion but ability to move freely is compromised	Arched back Steady head carriage Hind hooves do not track up Joints show signs of stiffness Asymmetric gait Slight limb
4. Moderately lame	Ability to move freely is diminished	Obvious arched back Head bobs slightly Hind hooves do not track up Joints are stiff and strides are hesitant Asymmetric gait Reluctant to bear weight on hurt limb but still uses it in locomotion
5. Severely lame	Ability to move is severely restricted and must be encouraged to move	Extremely arched back Obvious head bob Poor tracking up with short strides Obvious joint stiffness with no flexion, hesitant and deliberate strides Asymmetric gait Inability to bear weight on one or more limbs

Source: Adapted from Flower, F.C., Weary, D.M., 2006. Effect of hoof pathologies on subjective assessments of dairy cow gait. Journal of Dairy Science 89, 139–146.

or spontaneous fighting outbreaks (McGlone and Curtis, 1985).

Five days before parturition, sows are moved into farrowing stalls. In nature, sows will leave the group 24–48 h before birth to seek isolation and build a nest. Some degree of confinement is therefore necessary in production and preferred by the sow (Phillips *et al.*, 1991). The farrowing system should minimize piglet mortality, provide thermal comfort for both sow and offspring, and accommodate normal behaviors when possible (FASS, 2010). The farrowing crate is designed to reduce piglet injury and protect handlers from aggressive sows, but sow movement is restricted. Sows in farrowing pens are more active, but the piglet suckling duration is longer in the crate, and piglet mortality significantly increases in the farrowing pen (Blackshaw *et al.*, 1994). The farrowing crate is more beneficial to the production and well-being of the piglets.

Individual and group-housed gestation systems are similar in production and animal welfare if the systems are managed properly. Each housing system has its own advantages and disadvantages (McGlone *et al.*, 2004). Each system should minimize aggression and competition during feeding and mixing and allow sows to express normal behaviors (AVMA, 2005). Gestation crates have been banned in the EU and are phasing out in the United States in some states (e.g., Florida, Arizona, and California) after the first 30 days of gestation. The US states with the most pigs have not banned the gestation crate. It is important that good management practices are used in group housing systems as sow welfare will be compromised by social stress and feed competition. Smaller groups (35–40 sows) should be maintained in static groups, whereas larger groups (80–200) in dynamic groups in order to minimize social stress, and different feeding systems: drop-feeding, trickle-feeding, and electronic sow feeding systems, or stalls for individual feeding can be used to minimize feeding competition (FASS, 2010). A review of the recent scientific literature (McGlone, 2013b) essentially agrees with the earlier reviews (McGlone *et al.*, 2004; Rhodes *et al.*, 2005) that sow welfare overall is equivalent based on science in well-managed group pens or gestation crates.

Castration

Pigs are castrated at an early age to reduce boar taint, a foul smelling odor and flavor in meat caused from androstenone and skatole, reduce aggression toward other pigs and handlers, and to control for unwanted pregnancies at market age. Castration causes acute pain-induced distress that can reduce nursing and increase vocalizations and pain-like behaviors making it an animal well-being concern (McGlone *et al.*, 1993). Painful production procedures without the use of

Table 3 Methods of euthanasia approved for different sizes of pigs

Euthanasia method	*Age and size of pig*			
	Suckling pig	*Nursery pig*	*Grower–finisher pig*	*Mature pig*
	Up to 5.5 kg	*Up to 32 kg*	*Up to market weight*	*Sows and boars*
Carbon dioxide	Yes	Yes	Yes but not practical	Yes but not practical
Gunshot	No	Yes	Yes	Yes
Penetrating captive bolt	No	Yes	Yes	Yes
Nonpenetrating captive bolt	Yes	Yes with secondary step	No	No
Electrocution from head to heart	Only for pigs >4.5 kg	Yes	Yes	Yes
Electrocution in head only	Only for pigs >4.5 kg	Yes with secondary step	Yes with secondary step	Yes with secondary step
Anesthetic overdose	Yes	Yes	Yes	Yes
Blunt trauma	Yes	No	No	No

Source: Adapted from National Pork Board, 2008. On-farm Euthanasia of Swine: Recommendations for Producers. Des Moines, IA: National Pork Board.

anesthetics and analgesics are an increasing public concern. Alternatives include slaughtering pigs at younger ages before reaching sexual maturity, immunocastration techniques, and genetic selection for females. Studies using local, general, and topical anesthetics and analgesics have found no reduction in the pain-induced distress of castration as measured by cortisol concentrations, immune function, and substance-P (Sutherland *et al.*, 2010, 2012). The use of anesthetics may temporarily reduce cortisol concentrations from castration but once the drug wears off, typically 30–60 min after the procedure, the cortisol concentrations raise to similar or higher levels than pigs castrated without anesthetics. It has also been found that 3 days after castration, pigs castrated with an analgesic and both anesthetic and analgesic had higher cortisol concentrations than pigs castrated without pain relief (Sutherland *et al.*, 2012).

Immunocastration blocks gonadotropin-releasing hormone thereby reducing luteinizing hormone, follicle-stimulating hormone, testosterone, androstenone, and skatole (Zamaratskaia *et al.*, 2008). Immunocastration occurs later in life so increased lean growth and improved gain: feed of the boar is maintained longer (Dunshea *et al.*, 2001). One concern with immunocastration is the safety of handlers from aggressive boars, but few differences were found between physically and immunologically castrated pigs in a pig–human interaction test although immunocastrated pigs interacted with humans more (Guay *et al.*, 2013). Handling during transportation to slaughter showed significantly less vocalizations and fewer dead and down pigs in immunocastrated pigs compared with physically castrated pigs (Guay *et al.*, 2013). Immunocastration may improve male pig well-being and production economics.

Euthanasia

There are six acceptable methods of euthanasia for pigs of different ages and sizes in 'On-Farm Euthanasia of Swine – Recommendations for the producer' developed by the National Pork Board and American Association of Swine Veterinarians. When a pig is ill or injured a decision based on the best interest of the well-being of the animal should be made for treatment or euthanasia. Euthanasia may be best if the pig has not improved after 2 days of intensive care, it is severely injured or nonambulatory with the inability to recover, or the pig is immobilized. Euthanasia methods either first render the pig permanently insensible and results in death, or renders the pig insensible and requires a secondary step to achieve death (Table 3).

Sheep/Goats

Herd management

Welfare strategies concerning sheep and goats are focused on the typical topics: housing, nutrition, health, and mental well-being. Personnel giving daily care to animals should be familiar with sheep and goat behavior, signs of illness as well as potential health treatments so that they can prevent injury and disease. Sheep and goats should be fed to maintain a body condition score (BCS) of at least a 1.5 on a 1–5 point scale (FASS, 2010). Sheep are particularly sensitive to copper (Cu) toxicity, and therefore, copper should be considered when formulating diets with special consideration to the Cu concentration in available forages. Care should be taken to prevent Johne's disease (paratuberculosis), which can be transmitted from infected ewes on supplementing with raw colostrum from an infected ewe.

Shearing can be stressful as it can not only induce fear by restraint and handling but also from the heat and noise of the shears. In addition, sheep may acquire lacerations during the shearing process; thus, it is suggested that shearing should only be done by trained professionals. Time of shearing should be taken into account and sheep should have access to shelter from severe weather and environmental conditions (freezing temperatures, cold rain, extreme wind, or sun without shade) after shearing if needed. Shearing ewes before lambing can increase birth weights of lambs (Kenyon *et al.*, 2006a,b). Newborn lambs may find it easier to nurse without obstruction when ewes are sheared. If management or weather prevents the shearing of ewes, a common practice of removing wool from the dock and udder (crutching) can be done.

Mulesing is a procedure developed to reduce the incidence of fly strike on particularly wrinkled skin breeds of sheep such as the Merino breed. This procedure involves removing excess skin to prevent flies from laying eggs in soiled folds of skin. However, the procedure is considered painful and is highly criticized. Thus, mulesing is no longer practiced in most countries.

Tail docking and castration

Tail docking and castration are standard husbandry practices that are regularly performed on lambs. It is suggested that these be done as early in life as possible (preferably before 2 weeks of age) considering the lamb is established and healthy. Tail docking is done to prevent fly strike from long tails becoming excessively soiled with manure and urine, attracting flies. Acceptable methods for tail docking and castration include the use of rubber rings, emasculators, surgical removal, and hot iron cautery for tail docking or various combinations of these methods (Battaglia and Mayrose, 1981; Smith *et al.*, 1983; Ross, 1989; ASIA, 2002). Very short tail docking is discouraged due to the increased incidence of rectal prolapse (Thomas *et al.*, 2003). The use of rubber band/rings without corresponding anesthetics or denervation with emasculator has been shown to elicit more behavior indicating pain (Wood *et al.*, 1991; Sutherland *et al.*, 1999). The EU, Australia, and New Zealand consider tail docking and castration after a certain age, a surgical procedure and require the use of anesthetics (Defra, 2013; FASS, 2010).

Behavior

Sheep and goats are very herd oriented. When handling, performing routine herd maintenance and when transporting, animals should be kept in groups to prevent injury to animals and humans by sheep and goats attempting to escape or regroup with the herd. Sheep and goats are trainable to load and can be handled in restraint devices such as a squeeze chute table (Grandin, 1989), head stanchions (Sheldon *et al.*, 2006), manual methods (Battaglia, 1998), and the Panepinto sling (FASS, 2010).

Euthanasia

As in cattle, barbiturates, gunshot, and captive bolt are approved methods of euthanasia followed by exsanguinations, or administration of potassium chloride or magnesium sulfate to ensure death. Electrocution may also be used as a method of euthanasia but restraint and proper placement of the electrodes make electrocution an unlikely option for research and field use (AVMA, 2013a).

Poultry

Housing

There are several housing systems available for poultry: conventional and furnished cages, aviaries, littered floors, and free range. Regardless of the housing system it should allow for the cleaning of equipment and inspection of the birds without handling them, although the birds should be easily accessible (FASS, 2010). No system is stress free. Hens in floor housing have social hierarchies and cannibalistic pecking is a serious welfare concern. In caged hens this seems to be more prominent in extreme crowding when feeding competition is a problem, and in noncaged systems because of the larger group sizes. If group size is too large, hens display escape and fear behaviors (Craig and Adams, 1984).

Systems with similar characteristics have similar welfare problems (Lay Jr. *et al.*, 2011). Conventional cages do not meet behavioral needs of nesting, perching, and dust bathing, and restrict movement, but cannibalism and pecking is less frequent because of the small group sizes. Osteoporosis and claw problems are also more prominent. The EU banned conventional cages in 2012 and the only cages allowed are furnished cages. In complex systems such as furnished cages, or noncaged systems, bone fractures increase because of more movement and expression of behaviors, but bone quality is better (Tactacan *et al.*, 2009). Noncaged and outdoor systems provide litter or soil that meet behavioral needs of the animal but disease and parasites are problematic. An increased repertoire of behaviors does not mean they all benefit the well-being of the animal, as cannibalism and smothering occurs more in larger areas and larger groups. The larger group sizes in these systems also allows for disease to be more easily spread because of the difficulty to clean the system. Prelaying behavior, duration of dust bathing and feather, foot, and claw damage are improved in alternative systems. Perches, however, do lead to keel bone depressions (Appleby *et al.*, 1993). Even with longer periods of dust bathing observed in alternative systems, it does not prevent feather pecking, but resulted in increased foraging behavior (Huber-Eicher and Wechsler, 1997).

Egg quality in laying hens may also be compromised or altered depending on the housing system, which is of economic concern to the producer. Outdoor housing leads to great fluctuations in the external and internal quality of the egg (Van Den Brand *et al.*, 2004). However, Tactacan *et al.* (2009) found no differences in egg production, egg weight, or cracked and soft-shelled eggs between laying hens in conventional and enriched cages, but enriched cages did have 'dirtier' eggs. No one system is completely stress free and each has its own health and welfare advantages and disadvantages.

Forced molting

Natural molting replaces the plumage after sexual maturity in poultry. During this time egg production is paused and can be out of sync with the flock, so commercial production operations force molt in order to synchronize molting, rejuvenate the flock, and extend production by 2 or 3 laying cycles (FASS, 2010). Forced molting is done by reducing day length and withdrawing feed and water from laying hens.

Forced molting increases eosinophils, total white blood cells, monocytes, and packed cell volume (Brake *et al.*, 1982). It also decreases liver, ovary, oviduct, and body weights (Brake and Thaxton, 1979). However, greater amounts of weight loss is associated with more eggs, egg weight, specific gravity, and shell weights (Baker *et al.*, 1983), and nonmolted hens perform poorly in egg quality and production (Zimmermann and Andrews, 1987; Lee, 1982). The practice of forced molting not only benefits the industry by increasing egg production and quality but also reduces the number of male chicks and hens euthanized annually and rejuvenates feathers improving thermoregulation in hens (FASS, 2010).

Beak trimming

Beak trimming is performed in poultry production to reduce cannibalism, aggressive behaviors, and feather pecking (for review see: Cunningham, 1997). This is an economic advantage for the producer, but a welfare concern for the animal. The sensory receptors are cut from the tip of the beak, and sensory

deprivation and pain reduces activity, food intake, preening, and pecking (Hughes and Gentle, 1995; Duncan *et al.*, 1989). Beak trimming should only be performed in young chicks, 1 day old, with proper equipment to minimize pain, excessive bleeding, and infection, and to promote rapid healing (AVMA, 2013e). The earlier the chick at trimming, the less likely the neuromas to form. The beak heals rapidly and grows back but shorter than nontrimmed birds and with no afferent nerves or sensory corpuscles (Gentle *et al.*, 1997).

Several methods of beak trimming exist (AVMA, 2010 Welfare Implications of Beak Trimming). Mechanical techniques use a scissor-like device like secateurs to cut the tip of the beak. The traditional hot blade method cuts and cauterizes the edge of the beak destroying the tissue adjacent to the cut. This blade technique can either be hot or cold. Electric current can be used to damage the beak to shed the tip. The robotic infrared beak-trimming device applies an infrared light beam across the tip of the beak to destroy the living basal tissue. Little or no differences have been found in the welfare of chicks between systems. Henderson *et al.* (2009) did find infrared trimmed chicks were heavier at 11-days old compared with hot blade and nontrimmed chicks, but by 21 days there were no longer differences. Gentle and McKeegan (2007) also found reduced weights compared with nontrimmed chicks, but the hot blade compared with infrared trimmed chicks were smaller and had the least amount of beak regrowth, but no differences have been found between a hot or cold blade in the traditional method (Gentle *et al.*, 1997). When consequences of trimming method performed at an early age was evaluated later in laying hens, no differences were observed in egg production, body weight, or stress physiology. The infrared method did reduce aggression and improve feather condition though suggesting it as a better welfare alternative to the hot blade method (Dennis *et al.*, 2009).

Health and Nutrition

Proper management is paramount to the well-being and health of the herd. An effective health strategy for any type of species can relate to the same basic principles: good biosecurity, trained and perceptive personnel, and good communication among animal caretakers including the veterinarian. When animals, especially breeding stock, are brought to the new production facility they must be quarantined from the existing herd until the health of the incoming animals has been evaluated and found acceptable by the veterinarian. Depending on the species and the types of zoonotic diseases the incoming animals may have been exposed to, quarantine may range from preintroduction testing and simple observation to an extended isolation of new animals under strict observation. Appropriate vaccinations as well as external and internal parasite programs also need to be in place. A list of zoonotic diseases of agricultural animals is listed in the FASS (2010). In addition to an immunization schedule, preventative health also includes routine daily health checks of the animals and facilities, maintaining safe, clean living conditions with appropriate environmental levels.

Good nutrition, in general, encompasses individual animals receiving the nutrients required for the particular classification they fall into as well as proper management of transition from one classification to another (e.g., lactating to nonlactating). Requirements of nutrients, including water, will vary with season, diet, and physiological status (NRC, 2007b). Male animals fed diets of concentrates should be formulated for a calcium to phosphorous ratio of at least 2:1 to help prevent urinary calculi. Osteoporosis in laying hens is common leading to cage layer fatigue, bone fractures, and even paralysis. Hens deficient in calcium, phosphorus, and vitamin D are more susceptible and increased activity can reduce the prevalence of osteoporosis (Webster, 2004). All classes of animals should have as much clean water as they feel the need to drink. Water should be checked daily for contaminants. Dental maintenance is also an important factor in nutrition. Animals that are kept into adulthood such as breeding stock and horses can develop dental problems that make consumption and digestion of feed difficult. Geriatric horses who have worn most of their dental reserve crown are often fed softer, pelleted feed to promote the breakdown and digestion of feed. Some animals are not naturally thrifty and cannot seem to maintain a desirable body condition score. Consideration of these animals should involve the decision to either feed them separately, or with a group of similar animals that need an increased nutritional plan. In extreme cases of inability to assimilate feed, for whatever reasons, euthanasia should be considered to prevent the animal from suffering unnecessarily. A very comprehensive detail of the nutrient requirements of animals can be found in NRC (1996) for beef cattle; NRC (2001) for dairy cattle; NRC (1998) for pigs; NRC (1994) for poultry; NRC (2007b); for horses, and NRC (2007a) for sheep and goats.

Handling and Transport

Handling animals during routine husbandry practices should be performed in a careful, considerate, respectful, and calm manner. This positive interaction with animals will make them calmer and easier to handle (FASS, 2010). It is important when working with animals to know their flight zone (**Figure 2**) as they move more easily when they can see the handler angled from the shoulder (Grandin, 1980, 2011). The flight zone varies by animal and how calm it is, with a larger flight zone in more excited animals and calmer animals having a smaller flight zone. It is best to remain calm and quiet during handling as loud noises can be stressful and cause animals to baulk.

There are several different styles of equipment used to move animals. If the facility is designed well, no equipment may be needed and the natural behaviors of the animal can be used to move them. Flags, paddles, and boards and panels (**Figure 3**) are designed to be used with the natural movement of the animal and to minimize stress to the animal. Electric prods should only be used in specific situations on the hindquarters when all other attempts to move the animal have been made, and less than 10% on ranches or feedlots.

Many US regulatory agencies, such as the US Department of Agriculture (USDA), Department of Transportation, Centers for Disease Control and Prevention, and Food Safety and Inspection, govern animal transportation to ensure the humane transport and prevention of the transmission of communicable

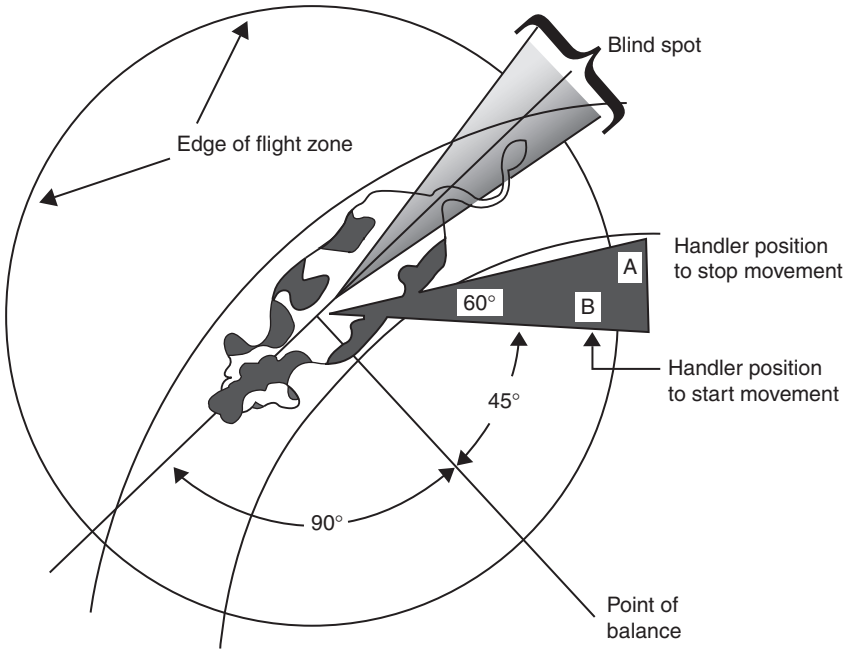


Figure 2 Flight zone showing how to effectively move an animal. Adapted from Figure 1 in FASS, 2010. Chapter 5: Animal handling and transport. In: Guide for the Care and Use of Agricultural Animals in Research and Teaching, third ed., p. 46. Champaign, IL: Federation of Animal Science Societies. Available at: http://www.fass.org/page.asp?pageID=216 (accessed 15.01.14).

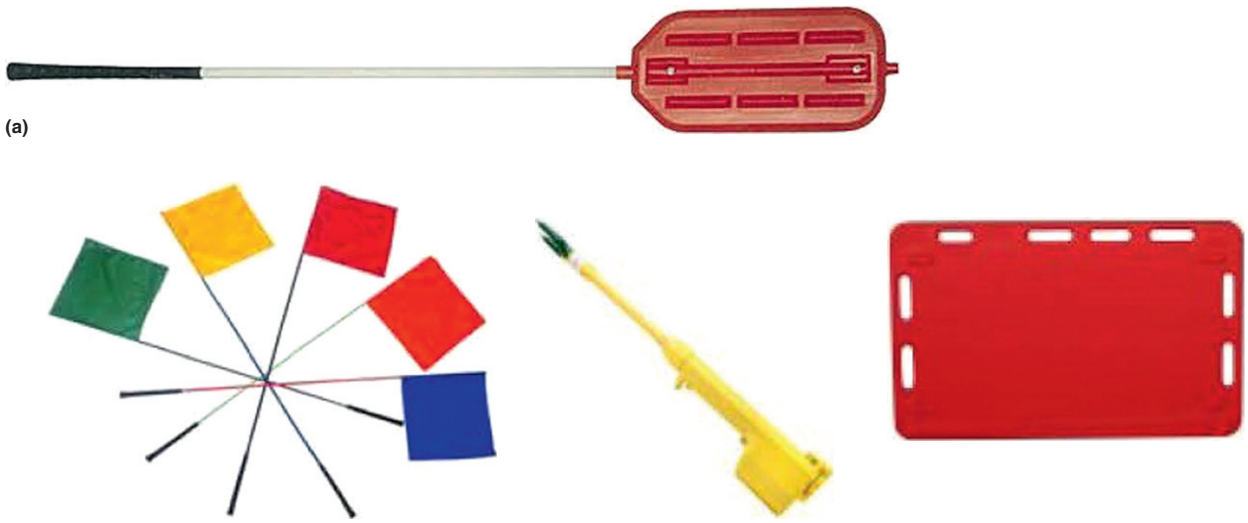


Figure 3 Livestock handling and sorting equipment: (a) rattle paddle, (b) flag, (c) electric prod, and (d) sort board/panel. Products (a) and (b) are provided by Koehn Marketing, Inc. and products (c) and (d) are distributed by QC Supply.

diseases (ILAR, 2011). Transporting livestock is a stressful event because it involves handling, loading, unloading, novelty, mixing or isolation, weaning, inability to maintain balance, motion sickness, feed/water deprivation, and temperature fluctuations, among other factors (FASS, 2010). As so many factors are present during transportation, it is hard to discern the most stressful component, therefore every factor of transportation should be accounted for and overall well-being of the livestock considered, reducing stress from transportation. To do so, calm handling methods should be used, and trailers should be designed to minimize slipping, protect the animal from environmental stressors, and provide adequate space per head (**Table 4**; National Pork Board, 2008).

The 28 h law regulates the maximum time animals are able to be held in trailers without food, water, and rest before being unloaded. After 28 h of transportation, animals must be

Table 4 Minimum space allowances during transportation for different livestock species

Species	*Weight (kg)*	*Space (m^2)*
Cattle	273	0.80
	545	1.40
Swine	5	0.06
	23	0.14
	113	0.40
Sheep	27	0.20
	55	0.30
Horses	113–227	1.75
Foals		1.40

Source: Adapted from FASS, 2010. Guide for the Care and Use of Agricultural Animals in Research and Teaching, third rev. ed. Champaign, IL: Federation of Animal Science Societies and National Pork Board, 2008. Transport Quality Assurance (TQA) Handbook. Des Moines, IA: National Pork Board.

unloaded into pens provided with provisions for at least 5 h (US Code: 49 USC Sec. 80502, 2012). When transporting livestock across state lines or between countries, all federal regulations for vaccinations, veterinary inspections, and health certificates must be in compliance. The Humane Methods of Livestock Slaughter Act (US Code: 21 USC 601, 2012) also states that animals should be minimally excited during loading/unloading, transportation, and handling. Nonambulatory animals should be isolated from ambulatory animals and moved with carts, sleds, canvas tarpaulins, or slide boards. They may not be dragged, hoisted, or dropped. If the animal cannot be moved it should be humanely euthanized on the spot (FASS, 2010). Once animals are unloaded after transportation to a slaughter plant they are moved to lairage pens where water is provided. Animals must have enough room to lie down without being on top of each other, and given a minimum period of rest of 1 h for cattle and 2 h for pigs.

Humane Slaughter

Animals must be killed (also called slaughtering or harvesting) and the carcass processed before human consumption. Animals have been killed for human food since animals were first domesticated more than 10 000 years ago. The method of slaughter in the European and American custom is meant to be humane. EU requires that food animals be "killed in a way that avoids unnecessary suffering." The US legislation that governs animal harvest is the Humane Methods of Slaughter Act of 1958; referred to as the Humane Slaughter Act or HSA). The HSA requires that animals are rendered rapidly insensible before being shackled or cut.

Another method of slaughter is ritual slaughter for Jewish and Muslim faiths. In ritual slaughter, the animal is not rendered insensible before being shackled or cut. Ritual slaughter is considered not humane by some people, but is required by the customs of people of certain religions, and therefore is acceptable.

Transport and handling before stun and exsanguination is also the subject of animal welfare concern. Extensive guidelines are provided by Temple Grandin, the AMI, and others.

Table 5 Recommended minimum space requirements for group-housed small animals (ILAR, 2011)

Animal	*Weight (g)*	*Floor area/animal (cm^2)*	*Height (cm)*
Mice	<10	38.7	12.7
	Up to 15	51.6	12.7
	Up to 25	77.4	12.7
	>25	≥ 96.7	12.7
Female with litter		330	12.7
Rats	<100	109.6	17.8
	Up to 200	148.35	17.8
	Up to 300	187.05	17.8
	Up to 400	258	17.8
	Up to 500	387	17.8
	>500	≥ 451.5	17.8
Female with litter		800	17.8
Hamsters	< 60	64.5	15.2
	Up to 80	83.8	15.2
	Up to 100	103.2	15.2
	>100	≥ 122.5	15.2
Guinea pigs	Up to 350	387	17.8
	>350	≥ 651.5	17.8

Table 6 Recommended minimum space requirements for group-housed larger animals (ILAR, 2011)

Animal	*Weight (kg)*	*Floor area/animal (m^2)*	*Height (cm)*
Rabbits	<2	0.14	40.5
	Up to 400	0.28	40.5
	Up to 5.4	0.37	40.5
	>5.4	≥ 0.46	40.5
Cats	≤ 4	0.28	60.8
	>4	≥ 0.37	60.8
Dogs	<15	0.74	Sufficient to stand
	Up to 300	1.2	with feet on floor
	>30	≥ 2.4	
Pigeons	–	0.07	Sufficient to stand
Quail	–	0.023	with feet on floor
Monkeys			
Group 1	Up to 1.5	0.2	76.2
Group 2	Up to 3	0.28	76.2
Group 3	Up to 10	0.4	76.2
Group 4	Up to 15	0.56	81.3
Group 5	Up to 20	0.74	91.4
Group 6	Up to 25	0.93	116.8
Group 7	Up to 30	1.4	116.8
Group 8	>30	≥ 2.32	152.4
Chimpanzees			
Juveniles	Up to 10	1.4	152.4
Adults	>10	≥ 2.32	213.4

Laboratory Animals

Laboratory animals used for research and teaching should be housed with adequate space (**Tables 5** and **6**) and resources that meet their physiological and behavioral needs (ILAR, 2011). Social animals should be housed in pairs or groups that allow for social interaction unless the research protocol does not allow for social contact. Environmental enrichment should

be utilized in order to improve animal well-being. Types of enrichment vary depending on the species, but it should facilitate exercise, manipulative activities, and cognitive challenges that improve psychological well-being. Animals should be habituated to novel environments and procedures to reduce stress associated with the procedures.

Wildlife

Wildlife mammalian research involves the collection of mammals in the field in order for scientists to understand community and population dynamics, genetics, anatomy and physiology, ecology and diseases (ASM, 1987). Kill traps should have low probability of capturing nontarget animals and kill the animal quickly. Live traps should keep the animal alive and uninjured. Live trapping may be painful or distressful to the animal especially when trying to escape, so padded traps may be more humane (Bekoff, 1995). Pitfalls can be used for both live and dead captures, but should have enough food to sustain the animal until the next trap check or enough liquid to drown the animal quickly. Humane methods should be used during euthanasia. Gases (carbon dioxide and ether), thoracic compression or cervical dislocation, and shooting if it causes instantaneous death are approved methods that should be used when appropriate for the animal.

Taking samples of tissue should be in a way to minimize pain. If it is a short procedure anesthetics may not be used in order to release the animal quickly, but longer more painful procedures should end in euthanasia of the animal. Marking the animal for reidentification should be done with minimal pain and should not restrict the natural movements of the animal, and should be suitable for the length of the study.

When using amphibians and reptiles in research, care must be given to the unique husbandry practices. Thermoregulation is difficult to satisfy because heat uptake and loss is from the environment, and light intensity must match the temperature of the environment. Shallow water containers or daily spraying and hiding places are appropriate for their habitats (Pough, 1992).

Animals in Exhibits and for Recreation

Zoos and Aquariums

Zoos and aquariums are regulated by the Animal Welfare Association (AWA), federal, state, and local laws. In the United States, public animal exhibits must be licensed and inspected by the USDA Animal and Plant Health Inspection Service (APHIS). Inspections are conducted yearly by APHIS as well as when credible complaints are filed. If species of animals housed are listed on the Endangered Species Act (ESA), the facility must also adhere to regulations set by the ESA. The ESA was passed by the Congress in 1973 with the purpose of protecting the species of animals at risk of extinction as well as to protect the ecosystems which they depend on for survival. The US Fish and Wildlife Service is responsible for the regulation of terrestrial and freshwater animals, whereas the National Marine Fisheries Service is responsible for marine wildlife. There are two classifications animals can be listed under within the ESA. Animals listed as endangered are defined as in danger of extinction, and animals listed as threatened are defined as a species that are likely to become endangered in the foreseeable future. All species of animals except pest insects are eligible to be listed in the ESA. North American institutions can volunteer to apply for accreditation with the Association of Zoos and Aquariums to certify that they meet high standards of physical and emotional needs (AZA, 2013). Zoos and aquariums have guidelines for general health and well-being that includes habitat and enrichment requirements, detailed record keeping of all general care, emergency care, custodial care, breeding, staff/human interactions, and a biosafety program to protect all animals and humans from zoonotic diseases. Inspections are performed every 5 years by a subcommittee of three experts in animal care and zoo management, and then reviewed by a panel of 12 before accreditation is awarded. International regulation is overseen by the Convention of International Trade of Endangered Species of Wild Flora and Fauna (CITES), who regulate the trade and movement of approximately 5000 species of animals. Participation in CITES is currently voluntary.

Fairs, Stock Shows, and Rodeos

The AWA requires those who exhibit animals to the public for compensation must obtain a license with USDA and APHIS; however, the AWA exempts certain groups from Federal regulation. Privately owned pets and those who exhibit animals in agricultural events such as fairs, stock shows, and rodeos are exempt from the AWA. These productions are, however, regulated by state and local laws. There are some regulated activities often found at events such as these including exhibition of large/big cats and nonhuman primates, elephant rides, camel rides, and petting zoos. Moreover, exhibitors who train, handle, or own animals used in film or television, or perform in a circus are regulated.

Rodeos are also subject to state and local laws; however, most rodeo associations have rules and regulations for animal welfare written into their bylaws. Both the Professional Rodeo Cowboys Association (PRCA) and the National Intercollegiate Rodeo Association (NIRA) have rules regarding the care and treatment of rodeo animals. Violations of rules can result in disqualification in addition to monetary fines for offenders. Rules are enforced not only by the judges but also officials appointed within organizations to ensure that policies are being followed. Both PRCA and NIRA judges undergo training and certification on specific rules and are familiar with the behavior and physiology of animals used in rodeo events. PRCA judges also communicate with the designated veterinarian regarding any health concerns with the animals. All PRCA rodeos are required to have a veterinarian on-site during the event. All contracted animals are required to be inspected before each event and are required to be withdrawn if they are deemed unfit by the judge or veterinarian. Both the PRCA and the NIRA require animal stock contractors to be approved and in good standing to be allowed to contract their animals to a sanctioned event. Contracted animals, such as the cattle for roping events, have minimal weight requirements. No contracted animal is allowed to perform more than once a day.

Competitors observed by rodeo officials using unnecessary roughness either in the arena or on the grounds can be disqualified or fined. The PRCA has an Animal Welfare Committee that meets regularly to review rules and make recommendations to the Board of Directors concerning animal welfare issues. They are regulated by the AWA but do fall under state and local laws as well as the rules and regulations set forth by the show associations to which the competitor is participating in.

There are many different horse show associations, for example, PRCA and NIRA.

Horse Racing and Dog Racing

Racing is regulated by laws that are set by the state in which the track or meet is located. Owners and trainers of animals are typically required to acquire a license in all states they wish to participate in. Most states require that each racing association have an established racing commission. Racing commissions are typically in charge of maintaining rules and regulations, including the welfare of the animals involved. The presence of an on-site track veterinarian who works under the jurisdiction of the racing commission is required to maintain veterinary reports, monitor use and testing for drugs, and suitability to compete on race day. A Commission veterinarian typically maintains several 'lists': (1) the Veterinarian's List of horses and/or dogs that the veterinarian deems unfit to race due to illness, physical distress, lameness, or another medical condition or (2) a Bleeder's List of horses that have exhibited external signs of exercise-induced pulmonary hemorrhage after a workout or race as observed by the commission veterinarian. Bleeders usually undergo an ineligible, recovery period that progressively lengthens for each incidence, and are often barred from racing after repeated bouts of pulmonary hemorrhage.

Horse Shows

Horses exhibited in a public display, in competition, except events where speed is the prime factor, such as rodeo events, parades, and organized trail rides are regulated by APHIS under the Horse Protection Act (HPA) of 1970. The HPA is focused on the Tennessee Walking Horse industry to prevent the practice of soring, which is stimulating a horse to step higher by intentionally rendering a horse unsound by physical or chemical means. Even though the HPA focuses on soring, it could be applied, or easily amended to include other aspects of the equine industry. It has been proposed to amend the HPA to include the transport of horses for the purpose of slaughter illegal. Larger horse show organizations have implemented their own animal welfare statues as proactive measures in support of the human treatment of horses. Regulations include the testing for controlled substances, altering tail function to minimize tail swishing, appropriate footing, and checkpoints for endurance horses. There are also many tack and equipment rules and regulations among show associations. In 2012, the American Quarter Horse Association received its first report from its newly formed Animal Welfare Commission with regard to identify issues that negatively affect the welfare of horses as well as recommendations to define and prevent inhumane treatment of horses.

Conflicting Societal Issues and Pressures

Many people are interested in improving animal welfare. Some improvements in animal welfare may have negative consequences for other societal issues (McGlone, 2001). For example, when pigs or poultry are outdoors, they may be exposed/inoculated with Salmonella and influenza. These zoonotic exposures would be minimized by use of indoor housing (McGlone, 2013a). Animal welfare changes should be considered in the context of other societal issues such as food safety, environmental pollution (including greenhouse gases), worker health, safety, and community impacts and economics.

See also: Beef Cattle. Biosecurity and Equine Infectious Diseases. Dairy Animals. Swine Diseases and Disorders. Vaccines and Vaccination Practices: Key to Sustainable Animal Production

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www.grandin.com

Asian Aquaculture

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Glossary

Aquaculture The farming of aquatic organisms, including fish, mollusks, crustaceans, and aquatic plants, with some sort of intervention in the rearing process to enhance production, such as regular stocking, feeding, protection from predators, etc. Farming also implies individual or corporate ownership of the stock being cultivated.

Domesticated In a broader sense, animals selected from the wild adapt to a special habitat created for them by humans, bringing a wild species under human management. In a genetic context, process in which changes in gene frequencies and performance arise from a new set of selection pressures exerted on a population.

Feed conversion ratio (FCR) Ratio between the dry weight of feed fed and the weight of yield gain. It is the measure of the efficiency of conversion of feed to fish (e.g., FCR=2.8 means that 2.8 kg of feed is needed to produce 1 kg of fish live weight).

Food and Agriculture Organization (FAO) An agency of the United Nations that leads international efforts to raise levels of nutrition, improve agricultural productivity, better the lives of rural populations, and contribute to the growth of the world economy.

Mariculture Cultivation, management, and harvest of marine organisms in the sea, in specially constructed rearing facilities (e.g., cages, pens, and long lines).

Small-scale aquaculture Aquaculture system with a small annual production (max 1 tonne per unit and 10 t total) made of one or more small production units, run by a family or communally, and requires low to moderate input levels and limited external labor; the motive may be own food supply.

Trash fish/low-value fish Fish that have a low commercial value by virtue of their low quality, small size, or low consumer preference – they are either used for human consumption (often processed or preserved) or used for livestock/fish, either directly or through reduction to fishmeal/fish oil.

Aquaculture – A Brief History

In 2013 more fish ('fish' is a collective term used for mollusks, crustaceans, and any aquatic animal that is harvested (FAO Fisheries Glossary, see 'Relevant Websites' section)) were farmed than beef (Marshall, 2013), which was the outcome of years of steady growth in the production of aquatic animals, aquaculture (Figure 1). The history of aquaculture goes back to thousands of years. Records show that fish farming was first described by Fan Lai in *'The Treatise of Pisciculture,'* in China, around 460 BC. Although the abundance of fish in seas and rivers and the lower population did not justify the intensive farming of fish, as seen for other forms of animal protein production, in recent decades an explosion in aquaculture production has been seen (Figure 2). Since 1950, when the FAO started keeping statistics of aquaculture production 1950, aquaculture has grown 130 times (i.e., 600 thousand metric tons in 1950 to 80 million metric tons in 2011), with a global average annual growth rate of 8.32% since 1950 or 7.72% since 1961 (FAO, 2013a–c). Compared with beef or poultry during the same time (i.e., since 1961), the annual growth over the past 50 years was of 1.64% and 4.98%, respectively (FAO, 2013a–c; Table 1).

But why such incredible growth in the production of farmed fish? There are many reasons for it:

- Although there have been some marked changes in catch trends depending on countries, fishing areas, and species, overall global capture fisheries production continue to remain stable at approximately 90 million metric tons (FAO, 2012), thus creating the need to satisfy the demand for seafood.
- The benefits of eating seafood and its cherished omega-3 became increasingly known for reducing risks of heart disease and supporting brain development of children during gestation and infancy (FAO/WHO, 2011).
- The demand for seafood did not remain constant, but it grew steadily with a growing population and its gross domestic product (GDP) (i.e., people prefer to eat more fish as they get richer). The calculated apparent fish consumption was 123 million metric tons in 2009, where 67.8% of that was consumed in Asia. China accounts for approximately half of Asian seafood consumption and slightly more than one-third of global consumption (Figure 3). Fish consumption significantly varies among countries (Figure 4).
- Technology has made the production of seed (in the form of fingerlings or postlarvae or other earlier life stage used to stock farming units) in captivity; hence, the domestication of many aquatic animals is increasingly possible. Domestication enables better control over quantity and quality of seed for aquaculture without depending on collection of wild seed and hence improves the efficiency and sustainability. Table 2 provides the number of domesticated aquaculture species, illustrating some differences between each phylum, and a total of 37% of all aquacultured species domesticated to date (Benzie *et al.*, 2012).
- Table 3 highlights that fish are also efficient converters of feed. The average feed conversion ratio (FCR) to produce

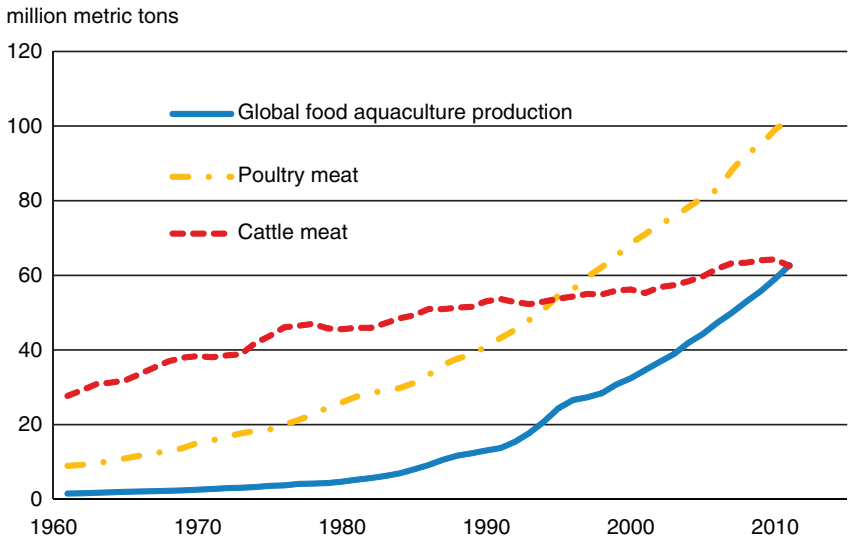


Figure 1 Global production of cattle meat, poultry, and food fish from aquaculture between 1961 and 2011. Reproduced from FAO, 2013a. Aquaculture and Capture Production 1950–2011. Rome: Statistics and Information Service of the Fisheries and Aquaculture Department; FAO, 2013b. Cultured Aquatic Species Information Programme: *Pangasius hypophthalmus* (Sauvage, 1878). Available at: http://www.fao.org/fishery/culturedspecies/Pangasius_hypophthalmus/en (accessed 08.04.14); and FAO, 2013c. FAOSTATS. Available at: http://faostat.fao.org/site/291/default.aspx (accessed 08.04.14).

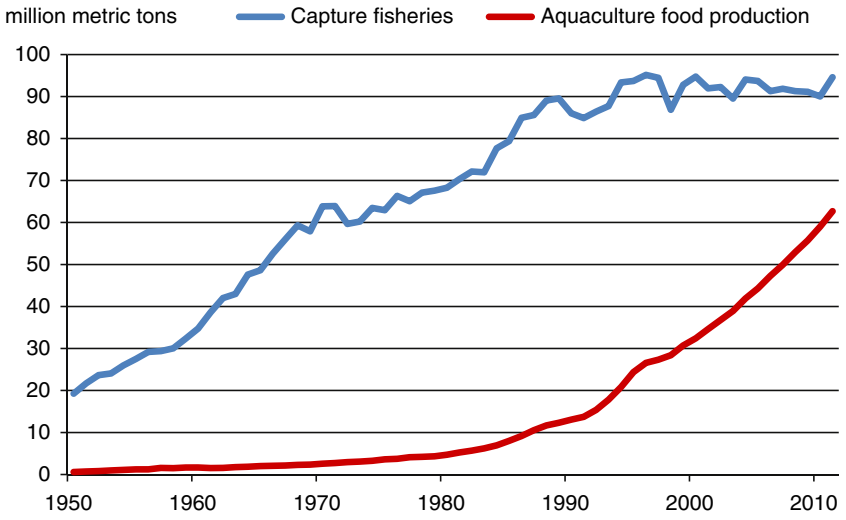


Figure 2 World capture fisheries and aquaculture food fish production during 1950–2011. Reproduced from FAO, 2013a. Aquaculture and Capture Production 1950–2011. Rome: Statistics and Information Service of the Fisheries and Aquaculture Department; FAO, 2013b. Cultured Aquatic Species Information Programme: *Pangasius hypophthalmus* (Sauvage, 1878). Available at: http://www.fao.org/fishery/culturedspecies/Pangasius_hypophthalmus/en (accessed 08.04.14); and FAO, 2013c. FAOSTATS. Available at: http://faostat.fao.org/site/291/default.aspx (accessed 08.04.14).

beef cattle is 12.7, which means that 12.7 kg of feed need to be used to produce 1 kg of beef (the animal, not only the meat). The FCR for poultry is much lower but still averages at 2.3 (Hall, 2011). On the contrary, the FCR for fish like salmon and carp is 1.3 and 1.5, respectively (Tacon *et al.*, 2011), making farming fish a more efficient business. In addition there are number of nonfed aquaculture commodities, such as mollusks, seaweed, and herbivorous fish, which provide valuable proteins and other micronutrients without depending on feed at all.

All this made the farming of fish increasingly needed and possible. There is also an inherent advantage of aquaculture, the number and diversity of species. There are hundreds of domesticated cattle breeds in the world, but all of these are usually classified into two major subspecies, zebu (*Bos indicus*) and European (*Bos taurus*) cattle, and they are believed to descend from the same species, *Bos primigenius* (Cunningham and Syrstad, 1987). However, 90% of aquaculture production is generated by 46 species of fish (FAO, 2013a–c). Although this poses considerable technological challenges, it also

provides opportunities to identify species and production systems that allow great efficiency for the given local conditions.

The production of pangasius (Vietnamese catfish) provides a nice example of the opportunities offered by aquaculture. Pangasius (*Pangasianodon hypophthalmus*), a species indigenous to Southeast Asia (Mekong River, the Chaopraya River and possibly the Mekong basins in Cambodia, Lao People's Democratic Republic, Thailand, and Vietnam, together with the Ayeyawady basin of Myanmar, see 'Relevant Websites' section), especially the Mekong region, used to be farmed in backyard ponds, traditionally cultured since the 1960s using wild-caught seed harvested from the Mekong River (Xuan and Hien, 2010). At that time pangasius was feeding the farmers who were growing it and the overall size of production was probably in the range of thousands of tons. It was not until the drop in cod harvests due to improper management of fisheries resources and the consequent moratorium issued in 1992 by the Canadian government to close cod fisheries (Hamilton *et al.*, 2004) that people started looking at farmed fish as a source of those beautiful white fillets that European and North American consumers cherish so much. The demand for white fillet boosted the production of pangasius, which from backyard ponds 'jumped' to commercial aquaculture operations, with an annual production over the past few years of more than 1 million metric tons from an area estimated to be 6000 ha in 2007 (Xuan and Hien, 2010). This means an average production of 200 ton ha^{-1} $year^{-1}$ (production of 2007 was 1.3 million metric tons), although production of 400–500 ton ha^{-1} have also been common (FAO, 2013a–c).

Seafood is generally thought of as 'food produced in the sea.' However, the industry moved forward with the concept of 'sea' food into considering seafood not only as the wild catches harvested from the seas, and all aquaculture production, but also including freshwater organisms (Wikipedia, 2013). As a matter of fact, although marine farming is responsible for 46.9% of the aquaculture production, 46.6% of farmed fish is generated from inland freshwater environments (FAO, 2013a–c). The remaining 6.6% of aquaculture is produced in brackish water environments, which are environments that lay in coastal areas where freshwater and the sea meet. The large marine production is primarily due to the inclusion in statistics of seaweed and other aquatic plants. When removing aquatic plants from the calculation, as seaweed is often used for uses other than food, the statistics look quite different. In fact 62.1% of the aquatic animals are produced in freshwater, with brackish water and marine environments accounting for 7.8% and 30.2% of the production, respectively (FAO, 2013a–c).

But where are all those rivers and lakes that make the production of 39 million metric tons of freshwater fish possible? Geographically speaking, if the aquaculture could be summarized in a single word, the word would be 'Asia.'

Table 1 Annual average rate of growth for food production between 1961 and 2011

	Cattle	*Poultry*	*Aquaculture*
Production in 1961 (million metric tons)	27.69	8.95	1.52
Production in 2011 (million metric tons)	62.54	101.74	62.70
Annual average rate of growth	1.64%	4.98%	7.72%

Source: Reproduced from FAO, 2013a. Aquaculture and Capture Production 1950–2011. Rome: Statistics and Information Service of the Fisheries and Aquaculture Department; FAO, 2013b. Cultured Aquatic Species Information Programme: *Pangasius* hypophthalmus (Sauvage, 1878). Available at: http://www.fao.org/fishery/culturedspecies/Pangasius_hypophthalmus/en (accessed 08.04.14); and FAO, 2013c. FAOSTATS. Available at: http://faostat.fao.org/site/291/default.aspx (accessed 08.04.14).

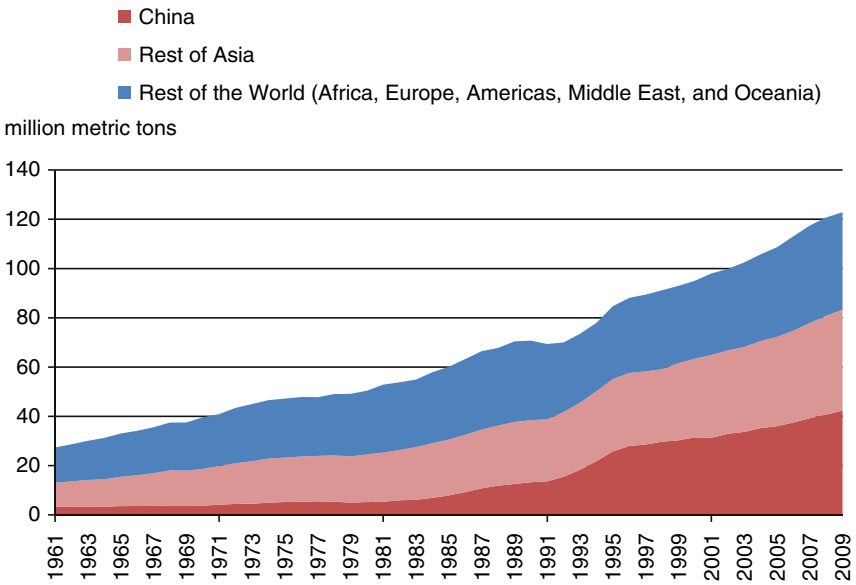


Figure 3 Apparent fish consumption (million metric tons). Reproduced from FAO Food Balance Sheet. Available at: http://faostat3.fao.org/faostat-gateway/go/to/download/FB/*/E (accessed 08.04.14).

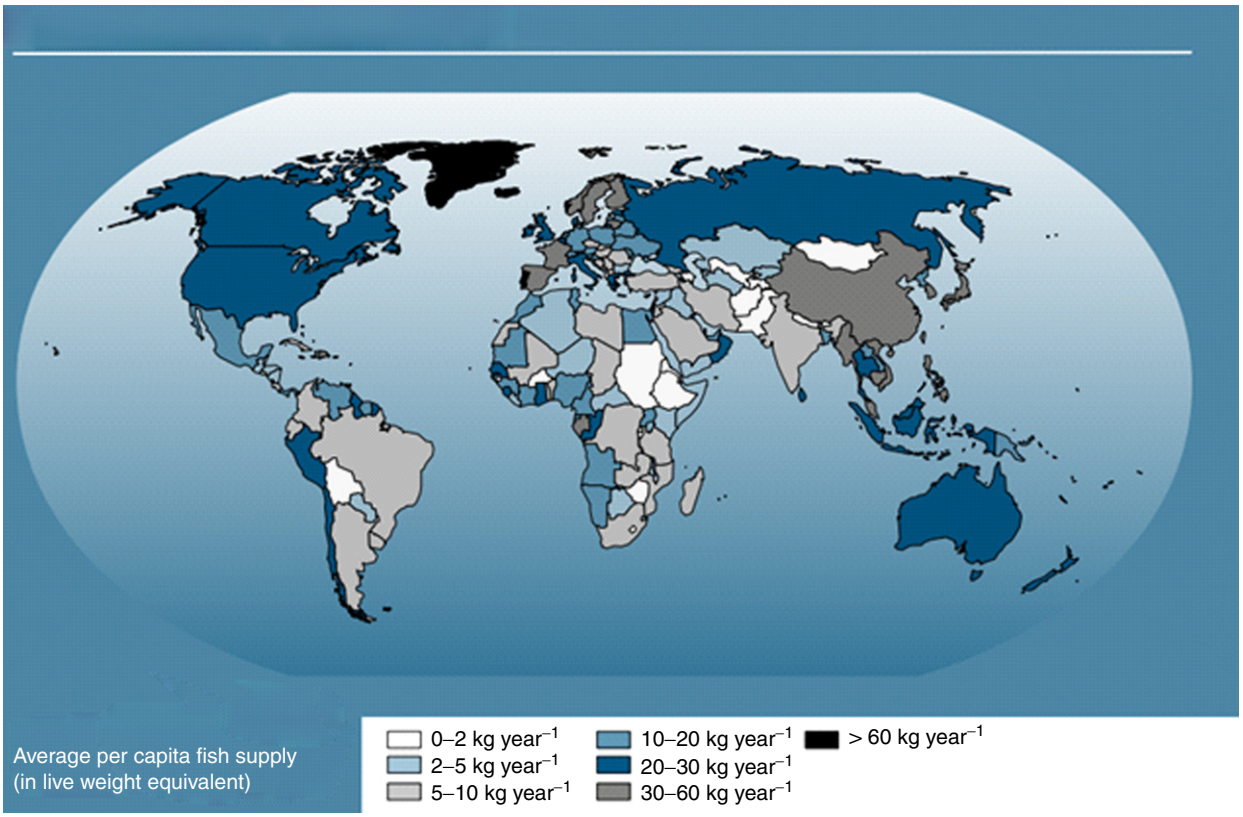


Figure 4 Fish as food: per capita supply (average 2007–09). Reproduced from FAO, 2012. The State of World Fisheries and Aquaculture. Rome: FAO.

Table 2 Number of aquaculture species and number of those aquaculture species that have been domesticated

Phylum	*Aquacultured*	*Domesticated*	*Domestication (%)*
Finfish	227	91	40
Mollusks	77	30	39
Crustaceans	35	19	54
Seaweed	>20	6	30
Total	359	136	37

Source: Reproduced from Benzie, J.A.H., Nguyen, T.T.T., Hulata, G., *et al.*, 2012. Promoting responsible use and conservation of aquatic biodiversity for sustainable aquaculture development. In: Subasinghe, R.P., Arthur, J.R., Bartley, D.M., *et al.* (Eds.), Farming the Waters for People and Food. Proceedings of the Global Conference on Aquaculture 2010, Phuket, Thailand, 22–25 September 2010, pp. 337–383. Rome: FAO and Bangkok: NACA.

Asian Aquaculture: The Champion

Nine out of ten of every kilogram of aquaculture products is produced in Asia (FAO, 2013a–c). A comparison of the production of aquaculture by continents dwarfs the continents like the Americas and Europe, where most of the salmon and trout, for many the emblems of aquaculture, are produced, which is quite obvious as the Americas and Europe account for only 3.5% and 3.2% of the global aquaculture production, respectively (Table 4).

Within Asia, two-thirds of the production comes from China, although other Asian countries such as India, Indonesia, Vietnam, or the Philippines are also major players. As a matter of fact the first non-Asian country to appear on national production statistics is Norway, which takes the eighth position due to its huge production of Atlantic salmon (Table 5).

Table 3 Protein content of major animal foods and feed conversion efficiencies for their production

Commodity	*Milk*	*Carp*	*Eggs*	*Chicken*	*Pork*	*Beef*
Feed conversion (kg of feed/kg live weight)	0.7	1.5	3.8	2.3	5.9	12.7
Feed conversion (kg of feed/kg edible weight)	0.7	2.3	4.2	4.2	10.7	31.7
Protein content (% of edible weight)	3.5	18	13	20	14	15
Protein conversion efficiency (%)	40	30	30	25	13	5

Source: Reproduced from Hall, S.J., Delaporte, A., Phillips, M.J., 2011. Blue Frontiers: Managing the Environmental Costs of Aquaculture. Penang, Malaysia: The WorldFish Center.

Again, just to put things in context, the production of countries like Vietnam and the Philippines, which take the fourth and fifth position in the national production statistics with a production of 3.1 and 2.6 million metric tons, respectively, is comparable to the production of continents like the Americas and Europe, which produce 3 and 2.7 million metric tons, respectively.

Economics of Asian Aquaculture

Aquaculture generated 107 billion USD in Asia in 2011, and many commodities were exported and consumed in other countries. Compared with national gross domestic product (GDP), the contribution of the aquaculture sector is not so significant, but it provides an important source of employment. Table 6 summarizes estimated number of fish farmer in 2010. It was estimated that approximately 16.6 million people were engaged in aquaculture and were concentrated in Asia (97%) (FAO, 2012). In addition, the sector provides numerous jobs in secondary activities, such as processing, packaging, marketing, and distribution. It is estimated that for each person directly engaged in aquaculture production, approximately three to four related jobs are generated in secondary activities (FAO, 2012), making the people directly or indirectly involved in the sector globally comparable with the population of some of the most populated European countries.

Table 4 Global aquaculture production (including nonfood fish (nonfood fish includes pearl oysters and seaweeds))

Continents	*Production in 2011 (million metric tons)*	*%*
Africa	1.5	1.8
Americas	3.0	3.5
Asia	76.3	91.2
Europe	2.7	3.2
Oceania	0.2	0.2

Source: Reproduced from FAO, 2013a. Aquaculture and Capture Production 1950–2011. Rome: Statistics and Information Service of the Fisheries and Aquaculture Department; FAO, 2013b. Cultured Aquatic Species Information Programme: *Pangasius hypophthalmus* (Sauvage, 1878). Available at: http://www.fao.org/fishery/culturedspecies/Pangasius_hypophthalmus/en (accessed 08.04.14); and FAO, 2013c. FAOSTATS. Available at: http://faostat.fao.org/site/291/default.aspx (accessed 08.04.14).

Main Aquaculture Species in Asia

More than 200 species were reported to be farmed in Asia in 2011. Various carp species are important in Asia in terms of

Table 6 World's estimated fish farmers by region in 2010

Continents	*2010*	*Global share (%)*
Asia	16 078 000	97.0
Latin America and the Caribbean	248 000	1.5
Africa	150 000	0.9
Europe	85 000	0.5
Oceania	6 000	0.04
North America	4 000	0.02
World	16 570 000	

Source: Reproduced from FAO, 2012. The State of World Fisheries and Aquaculture. Rome: FAO.

Table 5 Top 20 aquaculture-producing countries in 2011 (including nonfood fish)

Ranking	*Country*	*Continents*	*Production (million metric tons)*	*Global share (%)*
1	China	Asia	50.2	59.9
2	Indonesia	Asia	7.9	9.5
3	India	Asia	4.6	5.5
4	Vietnam	Asia	3.1	3.6
5	Philippines	Asia	2.6	3.1
6	Bangladesh	Asia	1.5	1.8
7	Republic of Korea	Asia	1.5	1.8
8	Norway	Europe	1.1	1.4
9	Thailand	Asia	1.0	1.2
10	Egypt	Africa	1.0	1.2
11	Chile	Americas	1.0	1.2
12	Japan	Asia	0.9	1.1
13	Myanmar	Asia	0.8	1.0
14	Brazil	Americas	0.6	0.8
15	Malaysia	Asia	0.5	0.6
16	Democratic People's Republic of Korea	Asia	0.5	0.6
17	USA	Americas	0.4	0.5
18	Taiwan Province of China	Asia	0.3	0.4
19	Ecuador	Americas	0.3	0.4
20	Spain	Europe	0.3	0.3

Source: Reproduced from FAO, 2013a. Aquaculture and Capture Production 1950–2011. Rome: Statistics and Information Service of the Fisheries and Aquaculture Department; FAO, 2013b. Cultured Aquatic Species Information Programme: *Pangasius hypophthalmus* (Sauvage, 1878). Available at: http://www.fao.org/fishery/culturedspecies/Pangasius_hypophthalmus/en (accessed 08.04.14); and FAO, 2013c. FAOSTATS. Available at: http://faostat.fao.org/site/291/default.aspx (accessed 08.04.14).

both production volume and value. In terms of production, there are 6 species of seaweed and 3 species of mollusks in the top 20 aquaculture species in Asia. However, in terms of value, Crustaceans (e.g., shrimp) are high in the ranking and whiteleg shrimp takes the first position; two other species are in top 10 positions as well (Tables 7 and 8).

Main Environments for Fish

In Asia, almost half of the production volume comes from freshwater (37 million metric tons, 48%), followed by marine environment (35 million metric tons, 46%) and relatively small production comes from brackish water (4 million metric

Table 7 Top 20 aquaculture species in Asia by volume in 2011

Ranking	*Species*	*Categories*	*Production (million metric tons)*	*Share of total Asian aquaculture production (%)*
1	Silver carp	Fish	5.3	7.0
2	Japanese kelp	Seaweed	5.3	6.9
3	Eucheuma seaweeds	Seaweed	4.6	6.0
4	Grass carp	Fish	4.5	6.0
5	Cupped oysters	Mollusks	3.8	4.9
6	Japanese carpet shell	Mollusks	3.6	4.8
7	Common carp	Fish	3.4	4.5
8	Aquatic plants	Seaweed	2.9	3.8
9	Bighead carp	Fish	2.7	3.5
10	Catla	Fish	2.4	3.2
11	Whiteleg shrimp	Crustaceans	2.4	3.1
12	Crucian carp	Fish	2.3	3.0
13	Elkhorn sea moss	Seaweed	2.1	2.7
14	Nile tilapia	Fish	2.0	2.6
15	Wakame	Seaweed	1.8	2.3
16	Warty gracilaria	Seaweed	1.5	2.0
17	Roho labeo	Fish	1.4	1.9
18	Pangas catfishes	Fish	1.4	1.9
19	Scallops	Mollusks	1.3	1.7
20	Freshwater fishes	Fish	1.3	1.7

Source: Reproduced from FAO, 2012. The State of World Fisheries and Aquaculture. Rome: FAO.

Table 8 Top 20 aquaculture species in Asia by value in 2011

Ranking	*Species*	*Categories*	*Value (billion USD)*	*Share of total Asian aquaculture value (%)*
1	Whiteleg shrimp	Crustaceans	9.9	9.2
2	Silver carp	Fish	7.7	7.1
3	Grass carp	Fish	5.8	5.4
4	Catla	Fish	4.7	4.4
5	Common carp	Fish	4.6	4.3
6	Chinese mitten crab	Crustaceans	4.5	4.2
7	Bighead carp	Fish	3.5	3.2
8	Giant tiger prawn	Crustaceans	3.4	3.2
9	Japanese carpet shell	Mollusks	3.3	3.0
10	Nile tilapia	Fish	3.1	2.9
11	Mandarin fish	Fish	2.6	2.4
12	Crucian carp	Fish	2.5	2.3
13	Red swamp crawfish	Crustaceans	2.3	2.2
14	Roho labeo	Fish	2.2	2.1
15	Pangas catfishes nei	Fish	2.2	2.1
16	Cupped oysters nei	Mollusks	2.2	2.1
17	Freshwater fishes nei	Fish	1.9	1.7
18	Scallops nei	Mollusks	1.9	1.7
19	Japanese eel	Fish	1.6	1.5
20	Milkfish	Fish	1.6	1.4

Source: Reproduced from FAO, 2012. The State of World Fisheries and Aquaculture. Rome: FAO.

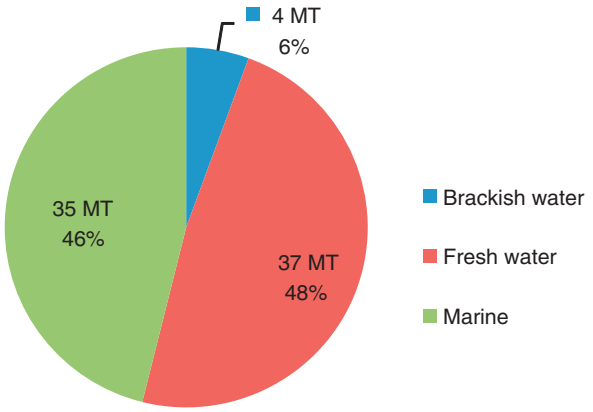


Figure 5 Asian aquaculture production by volume (million metric tons) in 2011.

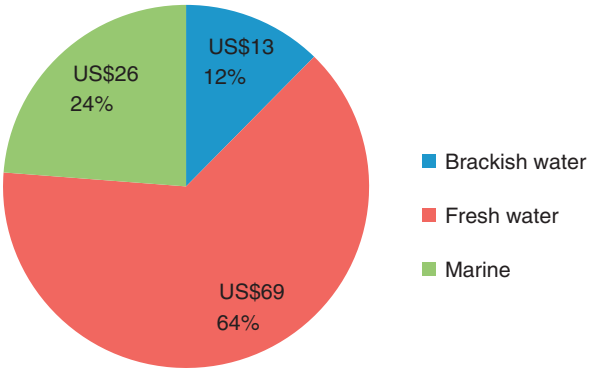


Figure 6 Asian aquaculture production by value (billion USD) in 2011.

tons, 6%). However, considering the value of the production, majority comes from freshwater (69 billion USD, 64%), followed by marine environment (26 billion USD, 24%) and brackish water (13 billion USD, 12%). These differences are shown in Figures 5 and 6 and are caused mainly by (1) large volume of seaweed and mollusks that are produced in marine environment but at relatively low values and (2) smaller quantity of high-value crustaceans produced in brackish water.

Sustainable Aquaculture Production

As described in earlier sections, aquaculture is conducted in various environments, such as inland water, brackish water, and marine environment, as well as being characterized by a large variety of culture species and farming system. This diversity offers both opportunities and challenges for sustainable aquaculture production. Considering the importance of the sector in providing quality nutrients (e.g., proteins and essential fatty acids), such sustainable growth is crucial from a nutritional and socioeconomic perspective and at the same time raises a number of environmental and social challenges.

The long-term development of sustainable fisheries and aquaculture sector is documented in the FAO Code of Conduct for Responsible Fisheries (CCRF) issued in 1995. Aquaculture development is particularly elaborated in Article 9 of this FAO CCRF document and contents are categorized in the following four areas: (1) Responsible development of aquaculture under national jurisdiction; (2) Responsible development within transboundary aquatic ecosystems; (3) Use of aquatic genetic resources; and (4) Responsible aquaculture at the production level (FAO, 1995).

Inland waters are highly competitive resources for many sectors; moreover, demands on freshwater are expected to be doubled by 2050 due to increasing population. Of the estimated available 3800 km^3 of freshwater in the world, it is crucial to promote aquaculture and fisheries into currently dominating sectors, such as agriculture (70%), industries (20%), and domestic use (10%) (FAO, 2012). However, mariculture seems to offer great opportunities in terms of space availability. There are various mariculture cages that are operational in offshore environments; however, the economic viability of these farming system is one of the challenges for further expansion, particularly in Asia.

Regardless of the environment, there is also competition for resources that go into feed. Fed aquaculture productions (e.g., marine shrimps, marine finfishes, and eels) are largely dependent on capture fisheries for the supply of their major dietary source of protein and lipids. For example, on a global basis, it is estimated that the aquaculture sector consumed 3.72 million metric tons of fishmeal (60.8% of global fishmeal production) and 0.78 million metric tons of fish oil (73.8% of global fish oil production) in 2008 (Tacon *et al.*, 2011).

In 2012, FAO/APFIC/NACA Regional Consultation was held in Bangkok, which summarized key challenges to sustainable intensification of aquaculture in the Asia-Pacific region as follows (FAO/APFIC/NACA, 2012):

1. Genetics, improved varieties, and seed quality
2. Strengthen aquaculture biosecurity and health management
3. Availability, cost, and utilization of feeds and feed ingredients
4. Efficient or innovative use of land/water/energy
5. Reduction of environmental impacts of intensified aquaculture
6. Culture-based fisheries is an option to intensify production of open waters
7. Aquaculture as an attractive livelihood
8. Climate change and natural disasters
9. Markets

Although all of the above are issues to be addressed, arguably aquatic animal health management and the control of aquatic diseases is crucial.

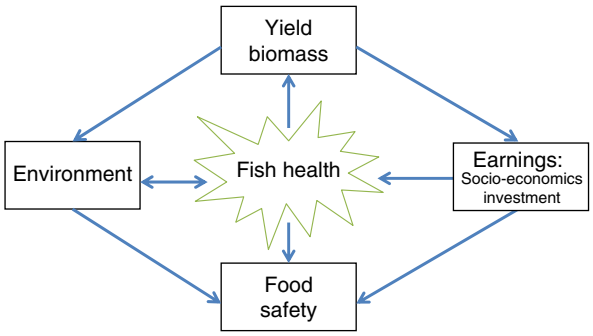
Aquatic Animal Health Management

Aquaculture production systems are notorious for the variability in performance. It is not uncommon for survival in aquaculture operations to fluctuate between crops of several double-digit percentage points, sometime ranging from less than 10% to more than 50% and seldom reaching levels above 90% (authors' personal observation). Such variability offers both challenge and the opportunity for improvement.

Aquatic diseases are central to sustainability for a range of reasons:

- Diseases affect production, hence leading to economic losses for farmers.
- Diseases lead to the use of veterinary medicines, which is a global concern (WHO, 2006). In a context where, for example, crustaceans cannot be vaccinated and the number of commercially available vaccines for Asian finfish is extremely limited, this often leads to the use of antimicrobials, which can affect product quality. This loss of quality also affects prices.
- The use of antimicrobials and other products to reduce disease outbreaks, in addition to the release of pathogens, also affects the environment.
- The reduced earning implies a reduced capacity to invest in improved production practices, hence creating a vicious cycle.

This is exemplified in the figure below, which shows the central role of aquatic animal health management in the path toward aquaculture sustainability.



Asia has taken a proactive role in aquatic animal health management. In spite of the economic challenges associated with disease control in Asian aquaculture, the Fish Health Section of the Asian Fisheries Society has been organizing the Diseases in Asian Aquaculture since 1990. The Network of Aquaculture Centres in Asia-Pacific (NACA), a regional intergovernmental organization, manages the activities of the Asia Regional Advisory Group on Aquatic Animal Health, which, among others, updates regularly a list of diseases of importance to the region. Asia-Pacific countries use such list, which includes also diseases listed by the OIE, to report quarterly on their status with the objective of informing countries in the region on any potential threats while identifying capacity building needs.

Aquaculture Certification

When talking about sustainable development, it is almost impossible to neglect mentioning certification, which for many is synonymous with sustainability. At the earlier time, it is likely that most of the aquaculture production would have been used for local consumption; hence, aquaculture operations were small in nature. However, in the last couple of decades, commercial aquaculture started to flourish, with an increasing amount of fish being produced in larger scale operations and also being traded far and wide. In this regard, food safety standards were issued and international trade regulations were tightened. In addition to this basic requirement for trade, there are environmental and consumer concerns on aquaculture production, which resulted in increasing interest in the certification of aquaculture productions systems, practices, processes, and products from aquaculture. Nowadays, large number of public as well as private aquaculture certification schemes are being developed and implemented at international and country levels.

Although aquaculture certification could potentially serve as a mechanism to shift whole aquaculture industry to more sustainable direction, the implementation of these various schemes has been gradual and a number of issues have risen particularly related to technical barriers to trade for small-scale aquaculture producers. For example, some certification schemes have resulted in higher costs for producers without delivering significant price benefits to small-scale producer. In response to its member countries' requests to address such concerns, the FAO has recently released the technical guidelines on aquaculture certification to provide level playing field for development and implementation of robust and transparent certification schemes (FAO, 2011).

In 2013, the Best Aquaculture Practice (BAP) and the Aquaculture Stewardship Council (ASC) programs, which together with GlobalGAP are arguably the most important aquaculture certification schemes globally, counted a total of 312 and 65 certified farms, respectively, the greatest majority of which was in Asia (Table 9).

Table 9 Number of aquaculture-certified farms

Species	*Total*	*Asia*
ASC certified		
Pangasius	36	36
Tilapi	27	20
Salmon	2	0
Total	65	56
BAP certified		
Salmon	131	0
Shrimp	111	103
Tilapia	49	43
Pangasius	10	10
Mussels	8	0
Catfish	2	0
Jade Perch	1	1
Total	312	157

Abbreviations: ASC, Aquaculture Stewardship Council; BAP, Best Aquaculture Practice.

Future Forecast and Some Final Remarks

Aquaculture is here to stay and is likely to play an increasingly important role in feeding the future generations. FAO Fisheries and Aquaculture Department conducted the future forecast for fish supply and demand up to 2030. The assumptions made to

Table 10 Fish supply – demand projection for 2030

	Estimated supply 2030 (million metric tons)	*Estimated demand 2030 (million metric tons)*	*Supply–demand gap 2030 (million metric tons)*
Africa	11.7	18.7	– 7.0
Asia	156.5	186.3	– 29.8
Europe	18.6	23.4	– 4.8
Latin America and the Caribbean	16.2	18.3	– 2.1
Northern America	6.2	12.9	– 6.6
Oceania	1.5	1.8	– 0.3
World	210.7	261.2	– 50.6

Source: Reproduced from FAO Statistics and Information Service of the Fisheries and Aquaculture Department, 2013. Aquaculture and Capture Production 1950–2011. Rome: Food and Agriculture Organization of the United Nations.

conduct this future forecast were (1) aquaculture follows recent trends and capture fisheries remain stationary and (2) consumers' consumption preference and fish prices unchanged to calculate per capita fish demand using International Monetary Fund (IMF) GDP projection and multiply it by the UN population projection.

The results indicated that there will be 51 million metric tons of fish shortage in the world with most severe insufficiency in Asia, amounting to almost 30 million metric tons (Table 10).

This production increase needs to be driven by expansion of sustainable aquaculture, which can be achieved only through efficient farming systems that operate in harmony with environment while providing social benefits. Asia is both the top producer and top consumer of aquaculture products, which is likely to change for decades to come. For the livelihood and safety of Asian people it is essential that the sustainability challenges of the sector are addressed in a timely manner. This requires a concerted effort that brings together both the public and the private sectors. The experiences from pangasius aquaculture in Vietnam have shown that public–private cooperation can achieve an unprecedented shift toward increased sustainability, with a current production of ASC-certified pangasius of more than 20%, which was achieved within approximately 2 years thanks to a partnership between the Vietnamese government, producers, buyers, and nonprofit organizations (authors' personal observation). Public–Private Partnerships are increasingly becoming key instruments to achieve similar sustainability shifts and, with a growing competition for resources, are likely to become essential for the aquaculture of the future.

See also: Food Chain: Farm to Market. Food Labeling. Food Security: Food Defense and Biosecurity. International Trade. Invasive Aquatic Animals. Critical Tracking Events Approach to Food Traceability

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ENCYCLOPEDIA OF AGRICULTURE AND FOOD SYSTEMS

VOLUME 2

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The alphabetical contents list, which appears at the front of each volume, lists the entries in the order that they appear in the encyclopedia. It includes both the volume number and the page number of each entry.

2 Cross-References

Most of the entries in the encyclopedia have been cross-referenced. The cross-references, which appear at the end of an entry as a See also list, serve four different functions:

i. To draw the reader's attention to related material in other entries.
ii. To indicate material that broadens and extends the scope of the article.
iii. To indicate material that covers a topic in more depth.
iv. To direct readers to other articles by the same author(s).

Example

The following list of cross-references appears at the end of the entry Critical Tracking Events Approach to Food Traceability.

> *See also*: Agribusiness Organization and Management. Food Chain: Farm to Market. Food Labeling. Food Law. Food Packaging. Food Security: Development Strategies. Food Security: Food Defense and Biosecurity. Food Security, Market Processes, and the Role of Government Policy. Food Security: Postharvest Losses. Global Food Supply Chains. Government Agricultural Policy, United States. Regulatory Conventions and Institutions that Govern Global Agricultural Trade

3 Index

The index includes page numbers for quick reference to the information you're looking for. The index entries differentiate between references to a whole entry, a part of an entry, and a table or figure.

4 Contributors

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PREFACE

Food is absolutely necessary for human existence, yet for most in wealthy nations it is largely taken for granted because of its abundance. Sufficient food is a concern, however, for about 1 billion of the earth's inhabitants today who often go to bed hungry. Food security in a broad sense is becoming a worry of the future for those who understand the limitations of our earth's ecosystems. Malthusian prophecies have so far been wrong, but there is growing concern that we are rapidly reaching the point where feeding the world's growing and richer population will be at the cost to our environment that is unacceptable. In the next few decades we face the challenge of growing more food, with less water, with less fertilizer on less land – because of the growth of urban areas on prime agriculture land. We also face the largely unknown consequences that global warming will have on agricultural production. During the last century agricultural scientists were able to bring cutting-edge science into traditional agricultural practices and increase food production sufficiently to prevent global food shortages. The hope that new scientific discoveries will provide the means to keep ahead of world food demand is complicated by a growing public discomfort with biotechnology being applied to food production.

The concept of services being provided by the ecosystems of the earth is a fairly recent attempt to understand and place value on functions of natural lands that have historically been assumed to have few limits. In the past, if more food was needed, new lands were converted from forests or steppe lands into farm land and new water systems developed to provide the water needed for agriculture. When human populations were low our activities were largely buffered by the abundance of forest and steppe, but too late, we are beginning to understand that these provisioning services of our ecosystems are being overused and are no longer buffered by the abundance of wild lands and waters. We are rapidly losing our planet's biodiversity, irreplaceable ground water is being unsustainably consumed, and major river systems are being overused and polluted. Our oceans, the last place on the planet that still support our hunter and gathering traditions may not be able to sustain these activities into the future. And, food production and processing activities contribute to the greenhouse gas emissions that are rapidly warming our planet. Agriculture is the single greatest user of the earth's land and water resources. In the concept of ecosystem services, provisioning or providing food for all organisms is one of the services provided by ecosystems. Human population growth has and will continue to overtax the ecosystems we inhabit. The ultimate outcome of this major diversion of nature's resources into provisioning the human species is unknown, but it is critically important for us to understand what we must do to sustain our planet.

The breakthrough discovery about 10 000 years ago that plants and animals could be bred to provide a more abundant and secure food source was the foundation upon which all other human activities were able to flourish. Activities other than finding food now became possible and our diverse cultures were able to develop because of agriculture. Until fairly recently, however, the majority of the population of most nations was still directly involved in producing food. Mechanization of agriculture and continued improvements in genetics, fertilizers, and pesticides made food production very efficient in developed nations. In the United States, the leading nation in value of agricultural exports, less than 2% of the workforce is currently employed in producing food. The United States, however, is alone among the most populous nations of the world in having such a small population employed as farmers. In countries such as China, India, Indonesia, and Nigeria the majority of people are rural and involved in agriculture either directly or indirectly. But, as food production becomes more efficient in these countries, and as wages increase in other sectors, a major shift is occurring from rural to urban occupations. This revolution is potentially as important in affecting our cultures and community structures as was the development of agriculture. Many nations are currently experiencing a very rapid transition from rural to urban living with all of the social and logistic problems associated with such rapid structural changes. While this transition in our social and cultural structures is a broad subject, it does have significant impacts on agriculture and our food systems. To mention just a few, agriculture labor, food transport, food safety, and access to healthy food.

There is genuine concern among agricultural scientists that human populations and changing diets are outpacing our ability to meet the increasing food needs of the planet. In the first iteration by Academic Press in 1994 of the *Encyclopedia of Agricultural Science*, Noble Prize Winner Normal Borlaug wrote in its forward:

> Had the world's 1990 food production been distributed evenly, it would have provided an adequate diet (2350 calories, principally from grains) for 6.2 billion people – nearly one billion more than the actual population. However, had the people in Third World countries attempted to obtain 30% of their calories from animal products – as in the United States, Canada, or European Economic Community countries – a world population of only 2.5 billion people could have been sustained – less than half of the present world population.

The issue raised by Dr. Borlaug is probably the most important challenge we face. Human behavior and the food choices of consumers will determine the outcome of the race between food supply and population. Population control has been advocated for decades, and in some cases has become part of national policy, but the world's population continues to grow. Science breakthroughs cannot solve our food security and environmental quality challenges if consumers reject food that is not traditionally produced. Likewise, if meat products and other inefficiently produced food continue to be in high demand by consumers, there will be increased pressure on our food production systems. As supplies become short, prices rise. While this may be good for farmers, high food prices and food shortages will probably undermine our efforts to preserve the

world's remaining arable land as natural lands. We must change human behavior to solve the problems we face.

Food choices, nutrition, diets, food cultures, water and air quality, GMOs, global warming, food security, and similar topics are daily in the news throughout the world. We are all concerned about these issues, yet with all of the information easily available in the popular media about food there seems to be too little informed discussion on these various topics. In planning the *Encyclopedia of Agriculture and Food Systems* the editorial committee chose to organize the topics primarily by issues, rather than to focus on a traditional topic approach. We organized the issues that would be discussed in the chapters around the broad topics of Agriculture and People, Agriculture and the Environment, Agricultural Products, Plant Health Management, Animal Health Management, and Agriculture and Science. The issues raised in this preface are the ones that we felt needed to be addressed in this encyclopedia.

The associate editors joined me in the development of topics for the encyclopedia and were responsible for working with the authors – they deserve particular recognition. I was fortunate to be joined by a very distinguished group of colleagues who, I hope, are still friends. They spent much more time and effort in bringing this project to completion than any of us anticipated. I want to thank our authors who while overly committed and overworked, fulfilled their commitments to contribute to this work. I have been impressed with the quality of their contributions. The editorial staff of Elsevier have had the professionalism and patience to work with scientists who do not work under the same time and budget constraints that the staff work. I want to particularly thank Kristi Gomez, Donna de Weerd-Wilson, and Simon Holt who, each in succession, oversaw this effort, and I especially thank the project managers, who worked directly with me, and the associate editors, Kate Miklaszewka-Gorczyca, Will Bowden-Green, and Sam Mahfoudh.

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B

Beef Cattle

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Glossary

Beef The meat from cattle carcasses.
Bos indicus Distinct subspecies of cattle that are descendants of domestication in South Central Asia (India); these cattle generally have a hump over the shoulder and are known for extreme tropical adaptation.
Bos taurus Distinct subspecies of cattle that are descendants of domestication in the Near/Middle East and comprise the historical breeds of Europe; these cattle are nonhumped.
Bull An intact (uncastrated) male bovine.
Calf A young bovine, generally less than 12 months of age.
Cow A female bovine that has reproduced. The word cow is not a general descriptor of cattle.
Criollo A group of cattle that trace origins to Spain and Portugal and are known for tropical adaptation, especially in South America.
Heifer A female bovine that has not yet reproduced, or just recently has given birth to her first calf.
Sanga A group of cattle native to Eastern and Southern Africa that have a neck hump and are known for tropical adaptation.
Steer A male bovine that has been castrated before reaching puberty.

Beef Cattle Operations and Production Systems

In the broadest sense, cattle producers can be classified as cow-calf, stocker/grower, or finisher producer (Table 1). Some operations may comprise combinations of these. At the cow-calf level, operations (or herds) are seedstock or commercial. The systems concept of beef production (production philosophy that includes considerations of potential genetic–environment–market interactions (see BIF, 2010)) presents challenges both to seedstock producers (producers of predominantly purebred breeding animals) and to commercial cow-calf producers (those that produce market beef animals) as well as to producers of growers and finishers. The more reliant the cattle producers are on 'natural' production environments, the more critical the understanding and utilization of systems-based approaches become.

Animals sold for breeding purpose have higher animal values (prices) than commercial animals. Many beef cattle breed societies or associations that record pedigree information and issue official certificates of registration exist. Utilization of registered purebred cattle for typical market uses is undesirable as they do not have higher value carcasses, may have less desirable growth or cost of gain compared with crossbred cattle, and have a higher animal initial cost. Growing and finishing phases may be stand-alone operations or may be additional components to a cow-calf operation as part of an overall production system. It may also be possible that some systems include ownership at least in part further into the supply chain, such as sales through butcher shops or through specific beef programs. The overall impact of various production systems have been evaluated by several groups regarding productivity and environmental impact.

A recent report (Gerber *et al.*, 2013) from the FAO has estimated potential livestock contribution to climate change. This report has stated that 14.5% of the human-induced global greenhouse gas emissions are attributed to farm animals. This report further stated that meat and milk production from cattle accounted for 41% and 20%, respectively, of farm animal contributions and that pig meat and poultry (meat and eggs) contributed 9% and 8%, respectively. Table 2 shows the estimated emissions from global dairy and cattle meat production.

There is a high degree of variability for both total emissions and categories of emissions across geographical region and production system in both milk and beef production. It may not be obvious why dairy systems are being discussed in a beef production article, but there are many areas of the world where the vast majority of beef production comes as a by-product of milk production systems. The regions of the world Gerber *et al.* (2013) identified as being the lowest for greenhouse emissions from beef production were North America, Europe, the

Table 1 Types of beef cattle production systems

Name	*Description*
Seedstock	Seedstock herds are mainly purebred herds with animals registered in breed society herd books that produce animals for breeding purposes. They can be classified as elite and multiplier operations. Elite operations produce the highest valued breeding animals in the breed and sell animals to other seedstock operators; multiplier operations sell primarily bulls to commercial cow-calf operations
Cow-calf, production of weaner calves	Cow-calf operations are driven by cow reproductive performance and overall productivity evaluated through calf production to weaning. Commercial cow-calf operations may sell calves close to weaning or may also/instead sell animals from grower and finishing phases. Different combinations of traits will receive emphasis relative to what age/stage of development animals are sold
Stocker, grower, and developer	These operations purchase or obtain young animals for growth. This can be grazing based on rangeland, forage crops, row crop residues, or may be feedlot based. Cattle are grown for some time, but not to completion of market size, weight, or fatness. These may utilize calves destined for beef, or replacement heifers or males for breeding purposes
Finisher	These operations produce cattle that go directly to slaughter. These can be grazing entirely, grain-assisted with grazing, confined feeding of green crops (such as cut-and-carry), or confined feeding of high-grain/concentrate diets. These operations can obtain cattle from cow–calf operations or from grower operations
Combination seedstock and commercial	A commercial herd as component of a seedstock operation adds flexibility for progeny testing, production of recipient females for embryo transfer; it is common that some seedstock operations also have a commercial herd rather than a primarily commercial herd developing a seedstock portion

Table 2 Estimated global production, emissions, and emission intensity from cattle milk and meat production

System	*Production (million tons)*		*Emissions (million tons CO_2 eqivalent)*		*Emission intensity (kg CO_2 eqivalent per kg product)*	
	Milk	*Meat*	*Milk*	*Meat*	*Milk*	*Meat*
Dairy	508.6	26.8	1331.1	486.2	2.6	18.2
Beef	–	34.6	–	2338.4	–	67.6

Source: Reproduced from Gerber, P.J., Steinfeld, H., Henderson, B., *et al*., 2013. Tackling Climate Change Through Livestock – A Global Assessment of Emissions and Mitigation Opportunities. Rome: Food and Agriculture Organization of the United Nations (FAO).

Russian Federation, the Near East and Northern Africa, and Oceania (Australia and New Zealand). Other areas that were identified with highest greenhouse emissions rely mostly on grass-finishing production of beef and produce animals for harvest at later relative ages. An encouraging recommendation from this report was that management techniques that increase efficiency of production (such as increased digestibility of feeds, improved animal husbandry, etc.) also appear to reduce carbon footprints. In most instances the optimal production practices that increase efficiency can also increase profitability for beef cattle producers.

Successful beef cattle management relies on knowledge of many disciplines, such as breeding and genetics, nutrition, reproductive physiology, health, behavior, and meat science as well as marketing options and market expectations. However, it cannot be overemphasized that familiarity with beef cattle from regular live animal evaluation is crucial for success in all of these discipline areas and provides important insight into meeting most production goals. Figure 1 illustrates some general physical areas that are important to evaluate in beef cattle.

Breeding and Genetics

Discussion of cattle breeding and genetics begins with their classification into evolutionary groups (Table 3). Animals of the genus *Bos* are known as the true cattle and include yak, banteng, gaur, kouprey, and domesticated cattle. Yak, banteng, and gaur have domesticated populations as well as wild populations. The autosomes of cattle (*Bos* spp.) are acrocentric and the X chromosome is submetacentric; however, in *Bos taurus* the Y chromosome is submetacentric, whereas in *Bos indicus* it is acrocentric.

Domesticated cattle (*B. taurus* and *B. indicus*) were developed from the ancient wild ox (aurochs, aurochsen plural, and *Bos primigenius*) that existed from the European (present-day Britain) Atlantic coasts to the Asian Pacific coasts. Several cave paintings in Western Europe show artists interpretations of the appearance of these animals. They had long horns, were lean, apparently light muscled in hindquarters, and had medium-length hair with large skeletal size, perhaps 2 m (6 ft) tall at the shoulder (Porter, 1991). *Bos indicus* and *B. taurus* are believed to have arisen from two distinct domestication events, and the common ancestors of these two groups may have separated 100 000 years ago or more (well before domestication).

Breeds

There are approximately 1000 different breeds of cattle globally. Most breeds have been developed purposely or have evolved from local cattle types. In the past 100 years, several

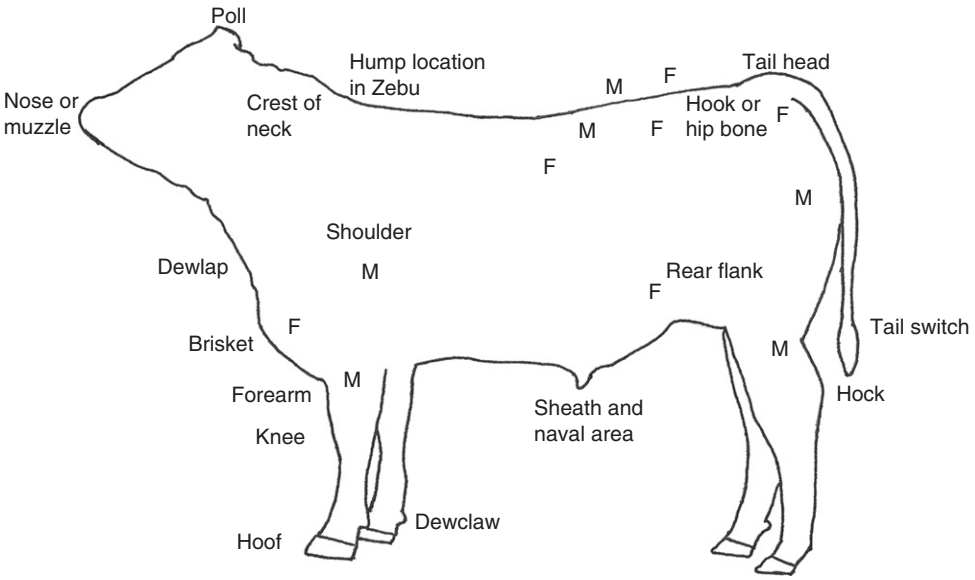


Figure 1 Identification of some general beef cattle body areas and locations to evaluate fat (F) and muscle (M).

Table 3 Classification groups of cattle

Name	*Description*
Class – Mammalia	Have hair and mammary glands that secrete milk
Subclass – Theria	Marsupials and placental animals with nipples on mammary glands
Infraclass – Eutheria	Fetus develops entirely by means of placenta
Order – Cetartiodactyla	Even-toed ungulates (grazing animals) and whales
Suborder – Ruminatia	Stomach with three or four chambers and no upper incisors
Infraorder – Pecora	Stomach with four chambers, the true ruminants
Family – Bovidae	Hollow horned; in general cattle-, antelope-, and goat-like species
Subfamily – Bovinae	Cattle, spiral-horned antelope, and nilgai
Tribe – Bovini	Bison, buffalo, and cattle
Genus – *Bos*	Yak, gaur, banteng, kouprey, and domesticated cattle
Species – *Bos indicus* or *Bos taurus*, or hybrids	Domesticated cattle arose from the ancient Aurochs (*Bos primigenius*) in two separate events

'new' breeds have been developed by crossing two or more existing breeds into what has been called a composite breed, but this is not a new phenomenon.

Breeds within a biological type share many similar production characteristics, and the proper choice of biological type or types should be the genetic basis for a beef cattle production system. If a breed type is used in a production environment that does not suit it, the input costs will be very high in order to obtain a desired level of production or the level of production will be quite disappointing relative to the lower level of inputs. The concept that breeds (or biological types) do not have consistent performance advantages (or disadvantages) across all environments is referred to as genotype × environment interaction. There is obviously no single breed of cattle that is superior for all traits of importance across all production environments.

Not all of the terms used in Table 4 to describe cattle groups are exclusive of others. In fact, combinations of these terms may many times provide the most useful descriptions for several breeds or types, such as *Bos indicus* dairy, British beef, criollo dual purpose, etc. Many breeds have been taken from their area of origin and been further developed or changed for local conditions. Further, the same breed at an earlier point in time may not be the same type of animal later, particularly if the group is responding to some form of selection (natural or artificial) (Table 5).

Genetic Improvement Strategies

The ability to genetically alter traits is a function of the degree of genetic influence on those traits. The term heritability (historically denoted by h^2) describes the percentage of the phenotype differences that are attributed to breeding value (gene content) differences. This is an important concept because the h^2 value is directly related to how quickly a trait may be changed due to selection, and the value can vary substantially across traits. Table 6 shows the heritability values for several traits important for beef cattle production (Figure 2).

Many people may assume that if the heritability of a trait is low then there is little genetic influence; however, this is typically not the case. Heritability is a function of the individual genes or alleles that affect traits without regard to their potential interactions. Many traits are affected by interactions

Table 4 General classifications and descriptions of some fundamental biological types of domesticated cattle that relate to production and adaptation aspects

Term	*Description and background*
Subspecies	
Bos taurus	Nonhumped breeds of the world, originally from the Middle East
Bos indicus	Shoulder-humped breeds of the world, also known as zebu (cebu) originally from Indian subcontinent of Asia and generally viewed as highly tropically adapted
Purpose	
Beef	Cattle produced for the primary purpose of meat production
Dairy	Cattle produced for the primary purpose of milk production
Draft	Cattle used primarily for farm-related work and transportation
Dual purpose	Cattle intended for two major purposes, such as milk and beef, milk and work, etc.
All purpose	Cattle used for all (general use) purposes as historically with subsistence agriculture
Geography	
British	Breeds from British Islands off European continent developed for meat production
Caucasian	Short-horned ancient-type of *B. taurus* cattle from Mediterranean, the Middle East, Eastern and Southeastern Europe, and Northern Africa
Chinese yellow cattle	Indigenous domestic cattle of China, not a reference to coat color. Common yellow cattle are typically nonhumped; yellow cattle further south have some evidence of a hump
Continental European	Breeds from Western and Central Europe used for meat production, but many had ancestors also used for draft; several are dual purpose meat and milk
Criollo	Tropically adapted *B. taurus* cattle of North and South America whose ancestors originally came from the Iberian peninsula of Spain and Portugal
Gray Steppe	Long-horned, light haired, and dark-pigmented *B. taurus* cattle of Eastern Europe considered an ancient type
Podolian	Breeds of Central Europe, primarily Italy, which were derived from eastern steppe cattle origin and include Apulian, Chianina, Maremmana, Marchigiana, Piedmontese, and Romagnola
Sanga	Cattle native to Africa that possess a neck hump, originally in Eastern and Southern African continent, some have classified Sanga as *B. taurus* because these breed possess a submetacentric Y chromosome
Western African humpless	Nonhumped breeds that are indigenous and survive in the tsetse fly region of West Africa and include Baoulé, N'Dama, Kuri, and Lobi
Japan/Korea	Wagyu/Hanwoo East Asian breeds known for extremely high levels of intramuscular fat deposition ability

of genes/alleles (such as when an allele is dominant over another or when the genotypes at different spots of the genome interact to influence the phenotypic expression). These potential nonadditive genetic interactions typically influence many traits through the phenomenon of heterosis (hybrid vigor). This phenomenon occurs when the crosses of parental stocks perform more favorably than expected, which is based simply on the amount of parental stock in the crossbred animals. Table 7 provides general guidelines of heterosis expectations relative to heritability for types of traits in beef cattle. Consideration of both of these genetic influences is quite important for beef cattle production systems but can have varying relative importance in specific production components. In the vast majority of situations, some type of crossbreeding system where crossbred cows are utilized allows improved productivity when production of market beef animals is the goal (Figure 3).

Nutrition

Beef cattle as ruminants have the ability to convert forage into meat production that cannot directly occur in nonruminant species. Consequently, cattle and other grazing livestock can commonly utilize lands that are not functional for other agricultural uses, such as farming. Depending on the geographical region, the ability to match the nutritional requirements of cattle to environmental resources is highly related to beef cattle productivity and profitability. More intensive beef cattle production systems will likely use more detailed nutritional information than total digestible nutrients (TDN) and crude protein (CP) in nutritional management; however, for general beef cow herd nutritional management these values present useful tools.

The nutritional requirements of cattle fluctuate with their phase of life cycle and stage of production. The general considerations associated with energy (represented by TDN) and protein (represented by CP) are provided in Tables 8 and 9. Both energy and protein in diets of cattle need to be adequate so that body condition score (estimate of percent body fat) is not too low, which will hinder reproduction and growth. Considerations of all important nutrients, including minerals, vitamins and water, are vital for optimal beef cattle management.

In grazing situations, supplemental nutrients may be offered to complement existing forage resources. Supplements may be minerals or vitamins or may be energy or protein. In other situations complete diets may be fed to cattle as with intensive production systems (Figure 4).

Feeding Cattle under Intensive or Confinement Conditions

In many situations cattle are fed a complete mixed diet (or may be called a total mixed ration), where everything they

Table 5 Examples of some breeds (excluding recent composites) with regard to biological groupings

British beef		*Sanga*	
Angus/Red Angus	Hereford	Africander (Afrikaner)	Mashona
Belted Galloway	Highland	Ankole	Nguni
British White	Shorthorn	Barotese	Nkone
Devon	South Devon	Bapedi	Tuli
Dexter	Sussex	Dinka	Tswana
Galloway	Welsh Black		
Zebu[a]		*Continental European beef*	
American Brahman	Indu-Brazil	Belgian Blue	Marchigiana
Boran	Kankrej (Guzerá)	Blonde d' Aquitaine	Piedmontese
Fulani	Ongole (Nelore)	Charolais	Romagnola
Gir	Red Sindi	Chianina	
Hariana	Sahiwal	Limousin	
Criollo[b]		*European dairy*	
Blanco Orejinegro	Mexican Corriente	Ayrshire	Milking Shorthorn
Caracú	Romosinuano	Guernsey	Norwegian Red
Chaqueño	San Martinero	Holstein-Friesian	Swedish Red and White
Chusco	Texas Longhorn	Jersey	Swiss Brown
Continental European dual purpose		*Eastern European Gray Steppe*	
Braunvieh	Pinzgauer	Hungarian Gray	Turkish Gray
Gelbvieh	Salers	Mursi	Ukranian Gray
Maine Anjou	Simmental	Romanian Steppe	
Normande	Tarentaise		
Caucasian		*Common Chinese yellow*	
Anatolian Black	Buša	Jinnan	Nanyang
Baladi	Greek Shorthorn	Kazakh	Qinchuan
Brown Atlas	Kurdi	Luxi	Tibetan
		Mongolian	Yanbian

[a]Some of these would be considered dual purpose or dairy type.
[b]Although the term criollo (or crioulo) generally refers to cattle developed in the New World from imported Spanish and Portuguese cattle, several breeds in present-day Spain and Portugal, such as Barrosã, Morucha, and Retinta, etc., would also be in this category.

consume is provided to them as in a feedlot. In some situations there may be conditions that warrant intensive feeding of cattle for a particular stage of production or environmental situation (such as drought, etc.). **Tables 10** and **11** provide some examples of diets to feed growing cattle. Adequate daily supply of clean water is crucial; cattle are expected to consume approximately 1 l of water per every 12 kg of live weight (1 gal per 100 lb) daily under nonextreme conditions.

The diets, mentioned in **Table 10**, which are appropriate for growing cattle can also be used for mature cows or feedlot fattening (finishing) of growing or older cattle. The rate of weight gain associated with any diet fed to cattle depends on their current weight (and stage of production) and the rate of intake of the diet. Usually, with intensive feeding of cattle there is a balance desired between increased production potential and increased costs. This same concept holds true for grazing situations but may not be obvious to managers if they do not know the forage cost or consumption. Any ration that is formulated to meet nutritional requirements must be fed at the recommended rate for it to be effective as it was designed.

Proper feeding of cattle is essentially proper feeding of the rumen microbes. Thus, it is obvious that rapid transitions from drastically different diets could cause digestive problems when the rumen microbial population has its nutrient inputs severely changed; hence, transition of cattle across drastically different diets needs to occur in incremental steps (**Figure 5**).

The ability to 'step up' cattle from a low-concentrate to a high-concentrate diet should be of concern to anyone providing feed to cattle, but it is of critical concern to feedlot managers and personnel. Feeding cattle much grain alters the rumen digestion processes and can lead to acidosis and potentially death but can also cause general digestive upset and bloat. Most feedlots utilize a 3–6 diet step-up plan that transitions cattle from low-concentrate, high-roughage diet to a high-concentrate, low-roughage diet for finishing, which avoids potential digestive problems. **Table 12** provides example of some feedlot diets with varying amounts of concentrate. There are both science and art needed in effective cattle feeding.

Manure Production

It is appropriate that the last topic discussed under nutritional concepts is manure production. The amount and nutritional composition of manure vary directly as a function of the diet according to digestibility and specific feedstuffs consumed. Manure is the waste produced from digestion and

Table 6 Heritability estimates for some traits in cattle

Trait	*Estimate*
Reproductive traits	
Age at first calving	0.10–0.25
Age at puberty	0.20–0.40
Calf survival	0.10
Calving interval	0.10
Calving date	0.10–0.20
Calving rate	0.10
Calving to first insemination	<0.10
Days to calving	<0.10
Dystocia	0.30
First service conception rate	0.05–0.20
Heifer pregnancy rate	0.15–0.20
Pregnancy rate	0.05–0.10
Ovulation rate	0.10–0.40
Twinning rate	0.10
Scrotal circumference	0.30–0.50
Growth and size traits	
Birth weight	0.40
Preweaning weight gain (birth to weaning)	0.30
Weaning weight	0.35
Weaning shoulder height	0.80
Weaning hip height	0.80
Feedlot gain	0.35
Pasture gain	0.30
Final feedlot weight	0.45
Final yearling pasture weight	0.45
Carcass and end product traits	
Carcass weight	0.42
Dressing (%)	0.28
External fat thickness	0.39
Longissimus muscle area	0.41
Kidney, pelvic, and heart fat	0.48
Marbling score	0.45
Estimated retail product (%)	0.28
Retail product weight	0.51
Fat weight	0.52
Bone weight	0.51
Actual retail product (%)	0.54
Fat (%)	0.51
Bone (%)	0.45

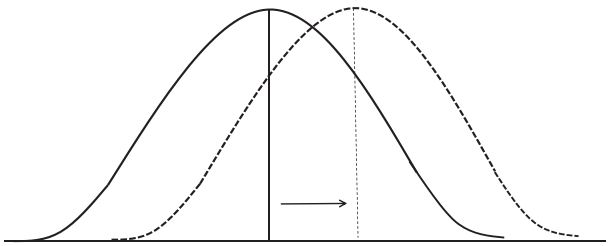


Figure 2 Concept of selection response. Selection response for a quantitatively inherited trait has implied shifting the mean of a population over time as a reflection of which animals are allowed to become parents.

is composed of both urine (the liquid waste removed from the blood by the kidneys) and feces (the semisolid waste that comes from the large intestine). The manure of cattle is composed of water, undigested feedstuffs, living and dead microbes, plant nutrients, and salts. Manure can be used to improve soil fertility but can also be a contaminant for water sources or can add excessive nutrients to soil or water sources. Manure management can be a formidable environmental issue for feedlots or other areas where cattle are intensively fed. Table 13 provides general guidelines that can be followed to predict manure production from different sizes of cattle.

Reproduction

Reproduction in beef cattle herds is the primary limitation for beef production systems, and the amount of beef that can be produced is a direct function of animal numbers. Some reproductive considerations specific to beef cattle are addressed here regarding female, male, and herd concepts.

Female Considerations

The estrous cycle in cattle is defined as the time between two consecutive estrus periods (time between heat periods) of a female. In cattle the estrous cycle is 21 days long on average. The length of the heat or estrus period itself is approximately 12–18 h, and ovulation typically occurs 24–30 h after the onset of estrus (beginning of heat period), so this typically corresponds to approximately 12 h after heat (and is the basis of the old recommendation that if a cow is in heat in the morning, breed it in the evening that day, and if it is in heat in the evening, breed it the following morning, otherwise known as the am–pm rule).

Heifers must reach puberty at an early enough age where herd fertility is not impeded, and this is critical when there are defined breeding and calving seasons. In many environments and with most *B. taurus* breeds and their crosses, age of puberty is not a limiting factor of reproductive success, provided that adequate nutrition is available. Puberty in heifers can be defined in different ways, such as time of first ovulation, time of first estrus, or time of first pregnancy carried to full term; here it means the time when a heifer can first become pregnant and produce a calf. Breeds that are known for high levels of milk production are known to have earlier age of puberty than breeds with lower milk production potential. Within the same level of milk production, breeds that are larger in size may reach puberty later than those of smaller mature size, but this relationship is less precise than with milk production.

Heifers of most *B. taurus* breeds reach puberty at 10–13 months of age when nutrition is not limiting; however, in many dual-purpose breeds this can be as low as 6 months or even earlier. In those cases puberty may be so early that some of the bull calves may breed some of their heifer mates before they are weaned, which presents other reproductive management challenges. This is the exception rather than the rule in most situations. In many environments, a target calving age of approximately 24 months is realistic with *B. taurus* breeds and most *B. indicus–B. taurus* crosses. With limited feed resources, a more realistic age of first calving is approximately 36 months

Table 7 Summary of heritability and heterosis levels for beef cattle production traits

Type of trait	*Heritability*	*Heterosis*
Female fertility and calf survivability	Low	High
Male fertility, growth, early life body size, and intramuscular fat (i.e., marbling)	Moderate	Moderate
Product-type traits, loin eye area, fat depth, mature size, and linear body measurements	High	Low

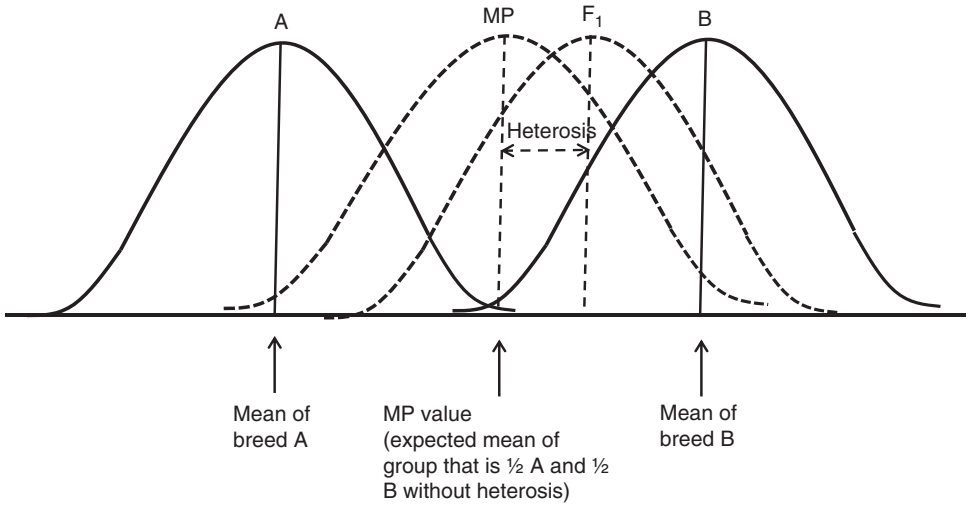


Figure 3 When crossing two breeds (A and B), the mid-parent(MP) value is halfway between the purebred means. The amount of deviation of the crossbred population mean from the MP value is the amount of heterosis. F_1 – Refers to the first cross progeny resulting from mating purebred parents of different breeds such as A sires with B dams, and, B sires with A dams.

Table 8 General guidelines for total digestible nutrients (TDN) and crude protein (CP) requirements for cattle

Class of cattle	*TDN (%)*	*CP (%)*
Growing animals	60–65	12–13
Lactating mature cows	55–60	10
Dry mature cows	50–55	7–8

Table 9 Production cycle/calendar of the cow herd thought of in 3-month increments relative to energy and protein requirements

Stage	*Total digestible nutrients (%)*	*Crude protein (%)*
Early lactation	Highest	Highest
Mid-lactation–early pregnancy	Intermediate	Intermediate
Late lactation–mid-gestation	Lowest	Lowest
Late gestation	Intermediate	Intermediate

because the heifers may be of 18–24 months before they reach puberty. Increase in nutritional plane and percent body fat reduces age of puberty in all breeds and crosses, and heterosis exist for age of puberty and will cause crossbred heifers to start cycling before the purebred average. The first estrus (heat) period may not have as high chance of conception as other estrus periods, so ideally heifers would have multiple estrous cycles before they have to get bred.

Weight management is important from the time heifers are born until the time they leave the herd as cows. It is important to have a good idea of what the mature size and weight of heifers will be because it is recommended that 50–60% of the mature weight at body condition score of 5 (moderate fat cover on a 1–9 scale, approximately 5 mm of fat cover over last two ribs, and approximately 18–20% body fat) is the target breeding weight for heifers, and 85–90% of their mature weight is the recommended target calving weight. Both of these targets ensure that heifers will be in the proper body condition at these critical production time points. Cows that can maintain body condition score close to 5 following calving have the highest chances of breeding back annually (Figure 6).

Artificial Insemination

Artificial insemination (AI) is a reproductive tool that can greatly aid in breeding programs and is widely available for beef cattle producers. Semen is commonly collected on highly prized bulls and available for purchase. In general, bulls are kept at facilities specialized in semen collection and processing. The semen is collected by means of an artificial vagina when the bull mounts a fixed 'dummy' structure or another animal. After collection, the semen is evaluated for its quality (abnormalities, motility, etc.), has some type of extender solution added to it, and is placed into plastic straws that are labeled with the facility code, breed, and individual ID of the bull. The straws are then

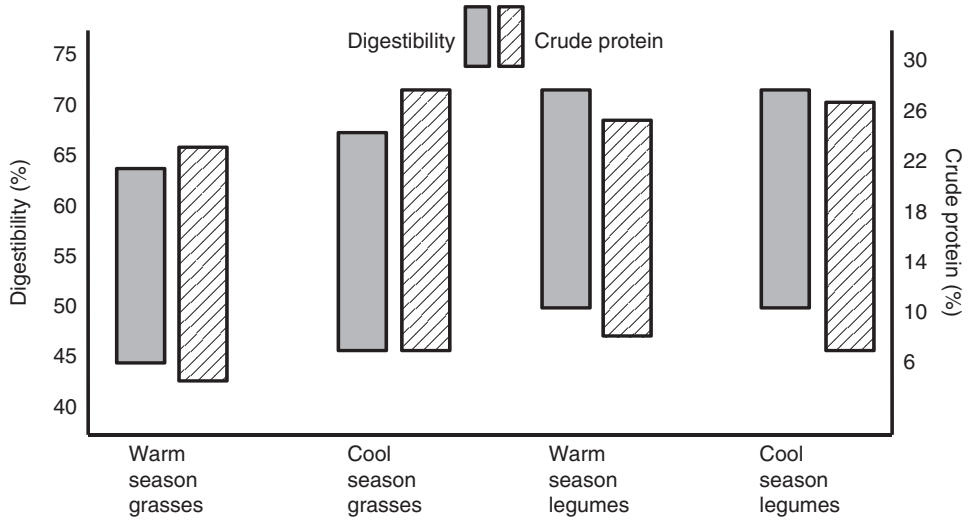


Figure 4 General guidelines for energy (digestibility as TDN) and CP content of different classes of forage for meeting cattle nutritional requirements. All forage species are highly variable within and across time and location. Annuals may be slightly higher in digestibility than perennials.

Table 10 Example of growing diets than can be fed to weaned cattle

Example 1	*Proportion (%)*	*Example 4*	*Proportion (%)*
Sudan hay	55.7	Grass hay	54.7
Wheat	20.0	Wheat	20.0
Maize	18.0	Grain sorghum	19.0
Soybean meal	5.0	Soybean meal	5.5
Dicalcium phosphate	0.5	Dicalcium phosphate	0.5
Limestone	0.5	Limestone	0.5
Salt	0.3	Salt	0.3
Example 2	*Proportion (%)*	*Example 5*	*Proportion (%)*
Grass hay	52.2	Sudan hay	57.2
Grain sorghum	40.0	Maize	35.0
Soybean meal	7.0	Soybean meal	7.0
Dicalcium phosphate	0.5	Dicalcium phosphate	0.5
Limestone	0.5	Limestone	0.5
Salt	0.3	Salt	0.3
Example 3	*Proportion (%)*	*Example 6*	*Proportion (%)*
Alfalfa hay	67.7	Alfalfa hay	59.2
Maize	31.5	Grain sorgum	40.0
Dicalcium phosphate	0.5	Dicalcium phosphate	0.5
Salt	0.3	Salt	0.3

Note: It is recommended that hays be ground and grains be rolled or ground. Components of these examples may be used as supplements for cattle grazing forage if relative nutritional values of forage are known.

Source: Adapted from Lusby, K.S., Gill, D., 1982. Formulating Complete Rations. Fact Sheet 3013. Stillwater, OK, USA: Oklahoma State University (OSU) Cooperative Extension Service.

sealed and frozen in liquid nitrogen. Semen that is processed and stored properly can be kept almost indefinitely. Many examples exist where calves have been sired through AI by bulls that died many years back. AI in cattle is physically convenient because the size of the rectum easily allows a person's arm to be inserted and physically guide the insemination syringe to and through the cervix (which is a landmark structure used in cattle AI). Many fixed-time AI protocols have been developed in recent years where cows or heifers are inseminated at a set time following estrus synchronization as opposed to visual observation for estrus.

Male Considerations

Several research trials have been conducted that show semen quality and scrotal circumference increase dramatically for 4–6 months following puberty. As a result, it should not be assumed that a bull is fully fertile because it has reached puberty.

Table 11 Sample rations for growing cattle

Ration 1		*Ration 2*		*Ration 3*		*Ration 4*		*Ration 5*	
Item	*Kg day*$^{-1}$	*Item*	*Kg day*$^{-1}$	*Item*	*Kg day*$^{-1}$	*Item*	*Kg day*$^{-1}$	*Item*	*Kg day*$^{-1}$
Dry hay – 12% protein	5.5	Dry hay – 15% protein	5.2	Dry hay – 15% protein	2.5	Dry hay – 15% protein	0.5	Dry hay – 15% protein	0.5
Grain corn	2.8	Mixed grain	3.5	Corn silage	8.5	Corn silage	7.5	Corn silage	10.0
Supplement	0.5	Supplement	0	Corn screenings	2.5	Haylage	7.5	High moisture corn (HMC) and cob meal	2.5
Premix	0.03	Premix	0.06	Supplement	0.5	Corn	1.4	Corn gluten feed	2.4
				Premix	0.03	Supplement	0.2	Premix	0.09
						Premix	0.03		
Would require approximately 1100 kg of hay and 560 kg of grain corn per calf		Would require approximately 1040 kg of hay and 700 kg of mixed grain per calf		Would require approximately 500 kg of hay, 1700 kg of corn silage and 500 kg of corn screenings per calf		Would require approximately 100 kg of hay, 1500 kg of corn silage and 1500 kg of haylage per calf		Would require 100 kg of hay, 2000 kg of corn silage, 500 kg of high moisture corn and cob meal and 480 kg of corn gluten per calf	
Total feed (kg) per calf for feeding period:									
1766		1752		2806		3426		3098	

Note: Diets such as these should result in average daily gain of 0.9 kg day^{-1} over 200 days for cattle growing from 227 to 408 kg of weight with an expected daily dry matter intake of 2.5% of body weight; all are expected to provide approximately 8.6–8.7 feed to gain ratio.

Source: Reproduced from Martin, D., 2006. Typical beef feedlot and background diets. Fact Sheet Agdex# 425/60. Ontario Ministry of Agriculture and Food. Available at: http://www.omafra.gov.on.ca/english/livestock/beef/facts/06-017.htm (accessed 03.09.13) as for Ontario, Canada.



Figure 5 Nellore bulls in Brazil fed corn plant-based diet. The picture on the right shows the ration in the feed bunk (trough) that consisted mainly of maize (corn) plants (stalk and leaves and cobs with grain) that had been ground.

Puberty is the ability to impregnate heifers or cows, not the ability to be a herd sire. It is also recognized that puberty in bulls occurs close to when the bull has 26–28 cm of scrotal circumference, and the age at which this happens can vary widely across breed types. Table 14 shows scrotal circumference in bulls across ages in several breeds.

Some indication of the bulls' potential to impregnate females is needed before the breeding season and is typically accomplished through a breeding soundness examination or breeding soundness evaluation, which considers scrotal circumference but includes more detailed information (Table 15).

Controlled Breeding and Calving Seasons

Farm and ranch managers make decisions, plan activities, and pay bills on a regular repeating time schedule. The challenge from cow-calf production is to make the animals reproduce annually in a timely manner. As a result, a target annual calving interval of 365 days is the goal for beef cows. The closer the calving interval is to 365 days, the easier it is to keep the cows on a repeating annual production cycle. Reproductive management for beef cows revolves around having a short and controlled calving season. It is typical that beef cows will not return to estrous activity until approximately 30 days or more

Table 12 Example of feedlot rations with varying amounts of grain and associated nutritional analyses from a study evaluating feed transition time

Item	*Proportion of concentrate (grain plus supplement) in diet (%)*[a]						
	40.0	*48.3*	*56.7*	*65.0*	*73.3*	*81.7*	*90.0*
Ingredients (% of DM)							
Barley silage	45.0	41.7	38.3	35.0	26.7	18.3	10.0
Grass hay	15.0	10.0	5.0	0	0	0	0
Concentrate							
Barley grain[b]	35.0	43.3	51.7	60.0	68.3	76.7	85.0
Supplement[c]	5.0	5.0	5.0	5.0	5.0	5.0	5.0
Chemical composition (%)[d]							
DM	56.7	58.6	61.6	63.7	67.9	76.3	83.2
Organic matter	93.6	93.5	94.0	93.6	93.8	95.7	95.2
Crude protein	14.1	14.0	15.6	15.0	15.4	15.5	15.3
Neutral detergent fiber	38.2	37.9	32.6	32.9	31.2	31.5	31.3
Acid detergent fiber	17.7	17.4	14.2	13.0	11.0	8.5	7.7

Proportion of concentrate (% DM basis) fed during two feeding adaptation strategies

Treatment[e]	*Days on which adaptation diet was fed (inclusive)*						
	≤ 0	*1–3*	*4–6*	*7–9*	*10–12*	*13–15*	*16–19*
Rapid adaptation	40.0	65.0	90.0	90.0	90.0	90.0	90.0
Gradual adaptation	40.0	48.3	56.7	65.0	73.3	81.7	90.0

[a]On the rapid adaptation protocol, only the 40%, 65%, and 90% concentrate diets were fed. All diets were used in the gradual adaptation protocol (shown above).

[b]The barley grain was dry-rolled as a single lot to a processing index of 84.6%: [(volume weight after processing/volume weight before processing) × 100%].

[c]Supplement contained urea as a N source, as well as Ca, 10.9%; Na, 1.4%; Zn, 1150 ppm; Mn, 530 ppm; Cu, 290 ppm; I, 13.0 ppm; Se, 5.7 ppm; Co, 4.7 ppm; vitamin A, 96 000 IU kg^{-1}; vitamin D, 9500 IU kg^{-1}; vitamin E, 630 IU kg^{-1}; and monensin sodium, 684 ppm.

[d]Values determined from analysis. All values except DM, %, are expressed on a DM basis.

[e]All cattle were on 40% diet, but beginning on day 1 half were switched to 65% diet and half were switched to 48.3% diet. On day 4 the rapid adaptation heifers were switched to 90% diet, but the gradual adaptation heifers were switched to the 56.7% diet, etc.

Abbreviation: DM, dry matter.

Source: Reproduced from Bevans, D.W., Beauchemin, K.A., Schwartzkopf-Genswein, K.S., McKinnon, J.J., McAllister, T.A., 2005. Effect of rapid or gradual grain adaptation on subacute acidosis and feed intake by feedlot cattle. Journal of Animal Science 83, 1116–1132.

Table 13 Daily manure production expected from cattle of different size classes

Rate excreted per 454 kg (1000) lb live weight[a]					*Examples*[b]		
Component	*Grazing cow*	*Grazing 200 to 340 kg calf*	*340 to 454 kg Yearling on high-forage diet*	*340 to 454 kg Yearling on high-energy diet*	*550 kg Cow grazing pasture*	*400 kg Steer grazing*	*400 kg Feedlot steer*
Quantity							
Weight (kg day^{-1})	28.57	26.39	26.80	23.22	34.6	23.6	20.5
Volume (m^3 day^{-1})	0.028 3	0.026 319	0.026 885	0.023 206	0.034 3	0.023 7	0.020 4
Total solids (kg day^{-1})	3.31	3.42	3.07	2.68	4.0	2.7	2.4
Organic matter							
Volatile solids (kg day^{-1})	2.81	2.91	2.74	2.47	3.406	2.413	2.174
COD (kg day^{-1})	2.72	2.72	2.77	2.54	3.296	2.441	2.242
C:N ratio	10	12	11	10			
Plant nutrients							
N (kg day^{-1})	0.15	0.14	0.14	0.14	0.18	0.12	0.12
P (kg day^{-1})	0.05	0.05	0.05	0.04	0.07	0.04	0.04
K (kg day^{-1})	0.12	0.09	0.11	0.10	0.14	0.10	0.08

[a]Values from Hamilton (2004). Weight is total mass of urine and feces excreted; volatile solids refer to mass percentage of total solids that will ignite when heated to 550 °C; Chemical oxygen demand (COD) is related to amount of oxygen required to digest manure; carbon to nitrogen ratio (C:N) is related to stability.
[b]The calculation for daily manure production in the examples comes from taking the appropriate rate for the size class in accordance with the animal's weight (for instance daily manure solids from a 550 kg cow takes the rate of 3.31 kg day^{-1}/454 kg of weight and multiplies this value by the ratio of the animal's weight of 550 kg as compared with the standard rate, or 3.31 kg is expected from a 454 kg cow, but a 550 kg cow is expected to produce 550/454 = 1.21 times as much, or 4.0 kg, etc.).

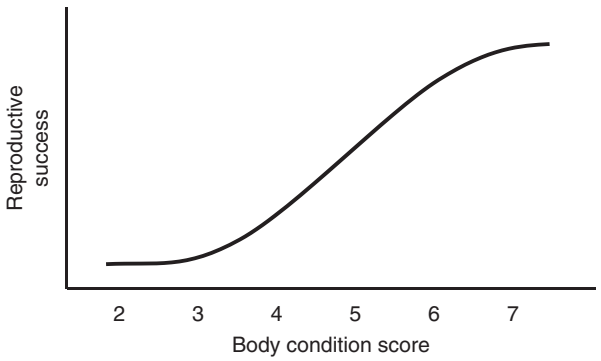


Figure 6 General relationship of body condition score (1–9 scale) of beef females and fertility.

after calving. Gestation length in beef cattle is approximately 283 days among many *B. taurus* breeds, 285 days among *B. indicus–B. taurus* crosses, and approximately 290 days in *Bos indicus* (Zebu). As a result of maintaining a 365-day calving interval, there will only be 365 − 285 − 30 = 50 days in which cows can breed back. The time of the year when calves are born should be based on the forage reserves in pastures (or feed costs) in order to coordinate the times of greatest nutritional requirements with the times of most available/cheapest feed costs to minimize annual cow maintenance cost. If feed resources are not adequate, cows will lose body condition after calving, and this will lengthen the postpartum anestrous period. In many harsh environments, particularly when supplemental feed cannot be offered, a very low percentage of cows may calve annually (Figure 7).

The length of time for the calving season is also important. Many production records for contemporary groups are based on individuals that are born within a 90-day period (individuals within this age range can be fairly compared with one another for performance traits). As a result, if all individuals within a herd (and there could be multiple herds within a ranch) are born within this 90-day window, they can be classified as a single contemporary group, provided they are all managed the same. Many people assume that the length of the breeding season will be exactly the same as the length of the calving season, but the length of the calving season will usually be 10–14 days longer because there is individual variability in gestation length. So, if a 90-day calving season is the target, then a 75-day breeding season is recommended. A 60-day breeding season should result in a 75-day calving season, etc.

Early Weaning

In many geographical areas it is common to wean calves at an average age of approximately 7 months. There is nothing magical about this calf age for weaning, but many breed societies or associations adjust weaning weight to a standardized calf age (200 days, 205 days, etc.). Some producers weigh calves around this age to submit weights to breed societies, but keep calves on the cows until 9 or 10 months of age. Many

Table 14 Reported mean scrotal circumference (cm) across ages in beef breeds

Breed	*Age (in months)*							
	< 14	*14–17*	*18–20*	*21–23*	*24–26*	*27–30*	*31–36*	*> 36*
Angus	34.8	35.9	36.6	36.9	36.7	36.3	36.6	38.2
Charolais	32.6	35.4	34.5	34.9	34.6	36.2	37.1	38.1
Horned Hereford	33.0	32.2	34.1	36.2	33.4	33.8	35.2	34.0
Polled Hereford	34.8	34.2	34.9	34.9	34.8	35.0	35.6	36.4
Simmental	33.4	36.5	–	–	36.0	–	–	37.2
Limousin	30.6	31.7	32.0	33.9	–	–	–	35.5
Santa Gertrudis	34.0	35.3	35.5	36.7	36.5	36.4	38.3	40.5
Brahman	21.9	27.4	29.4	31.4	31.7	33.5	34.7	36.7

Source: Reproduced from Sprott, L.R., Thrift, T.A., Carpenter, B.B., 1998. Breeding Soundness of Bulls. Pub # L-5051. College Station, TX: Texas A&M AgriLife Extension Service.

Table 15 Components of bull breeding soundness exams

General physical health	*Reproductive tract*	*Semen evaluation*
Assessment of overall health – evaluation of the eyes, structural soundness, knee and hock joints, body condition score, and parasite infestation	Physical palpation and visual evaluation of reproductive organs – penis, prepuce or foreskin, sheath, scrotum and testicles, and secondary sex glands such as prostate and seminal vesicles	Evaluation of actual ejaculate – semen color, number of live cells, live to dead cell ratio, motility of cells, and abnormalities

Note: Although only semen evaluation traits are given a score, the failure in any category can result in failure of the overall breeding soundness exam. Libido or serving capacity is not evaluated as a component of breeding soundness exams under the Society of Theriogenology (USA) but is included under the Australian Association of Cattle Veterinarians (McGowan *et al*., 1995) evaluation. The Western Canadian Association of Bovine Practitioners (Barth, 2000) has a spot on the form for libido assessment but states the producer of the bull should evaluate this.

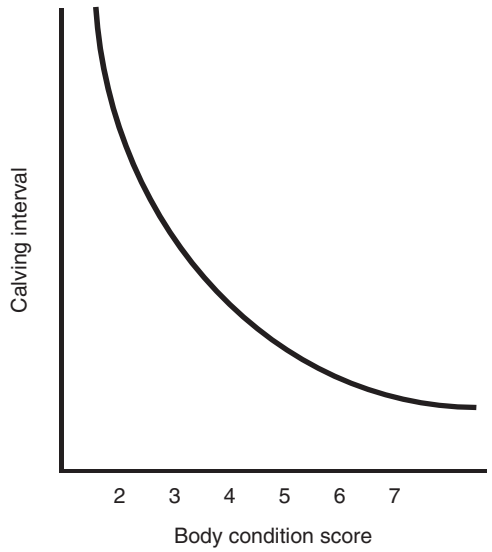


Figure 7 General relationship of body condition score (1–9 scale) of beef females and time between birth of calves (calving interval).

commercial producers wean calves when they are approximately 6–8-month old on average. Some producers may let cows wean the calves on their own; under extensive conditions a cow will usually stop nursing its calf when it is getting closer to having another calf, but not always. Other commercial producers may wean calves early at approximately 60–90 days of age. Weaning at this young age has widely reported reproductive advantages for the cows. There is a direct neural feedback mechanism triggered when a cow has its calf weaned, which typically instigates estrous activity and shortens postpartum anestrous.

Reproductive measures can be monitored at (1) the herd level, (2) the individual cow level, and (3) the individual bull level. All producers have the ability to measure herd level reproductive measures if they have adequate inventory numbers, and these herd level measures provide benchmark values to monitor herd performance over time. Many cow- and bull-level reproductive measures require individual animal identification and represent a higher level order of data collection and decision making. No strategies to improve reproduction will be able to compensate for inadequate nutrition. Recording of important performance measures in herds will set benchmark values to monitor reproductive success within and across years. There are many reproductive technologies that may be of varying benefit under different circumstances, but these need to be evaluated relative to cost versus benefit on a case-by-case basis.

Health

There are many diseases in cattle that need to be considered. Some are specific to regions and some are global in their occurrence. The readers may refer to local sources for specific diseases that may limit production in their area(s), as this is beyond the scope of this article. The basis for monitoring and maintaining the health of cattle begins with understanding typical normal and abnormal signs of animals (Table 16) and understanding that proper nutrition and sanitation are key

Table 16 Expected signs and values of healthy cattle

Sign	*Expected normal value*	*Abnormal indications*
Rectal temperature	38.5 °C (101.5 F)	Many antimicrobial products are administered when higher than 40 °C
Breaths per minute	30	Rapid, shallow breaths; long pauses between breaths
Heart beats per minute	60–70	Slow and rapid heart rates can result from a variety of causes
Nose	Beads of perspiration, shiny, and even skin	Dry, very warm to touch, and cracked or scaly surface
Eyes	Moist, smooth and shiny, and brown iris	Dull and nonreflective, unusual color or presence of growths
Demeanor[a]	Alert, but at ease; attentive but not combative	Actions that substantially deviate from 'normal' behavior
Feces	Greenish color, not extremely dry or watery; makes a plop sound and forms patties/pads	Color may be dark, light, grayish; consistency too firm or too loose; appearance of blood
Movement[a]	Even and smooth actions of walking, moving neck, standing, and no trembling	Limping, shaky in movements such as walking, holding head at unusual angle, and wobbly or jerky
Hair appearance	Shiny and evenly distributed	Dull without luster, patchy areas of thin or lost hair, and unusual color

[a]What is 'normal' behavior as well as other traits can vary drastically across individuals and circumstances (such as with a newborn calf), and abnormal is a marked deviation from what is typical. History of observation provides useful information. Documentation of these signs that are suspected to be abnormal will aid veterinarians in diagnoses.

Table 17 Summary statistics for hair coat characteristics and sweating rate for Braford cows in Mato Grosso do Sul (Brazil)

Trait	*Mean*	*SD*	*CV (%)*	*Minimum*	*Maximum*
Coat thickness (mm)	3.73	1.72	46.1	1.00	13.00
Hair number (hair cm^{-2})	993	504	50.8	319	4852
Hair length (mm)	10.41	3.91	37.6	4.13	26.50
Hair diameter (μm)	30.98	8.13	26.2	11.00	69.00
Coat reflectance (%)	18	13	72.2	1	63
Sweating rate ($gm^{-2}\ h^{-1}$)	319.97	83.02	25.9	89.20	591.48

Note: Based on 1607 observations across heifers and cows through 5-year-olds in a single commercial herd. Females were generated from 33 sires and varied in breed composition from 25% Hereford–75% Nelore to 75% Hereford–25% Nelore.

Source: Reproduced from Bertipaglia, E.C.A., da Silva, R.G., Cardoso, V., Fries, L.A., 2007. Hair coat characteristics and sweating rate of Braford cows in Brazil. Livestock Science 112, 99–108.

elements for all cattle health programs. Health problems of beef cattle may originate from infectious microbial pathogens, internal and external parasites, digestive disorders, ingestion of toxic substances, and genetic lines.

The World Organisation for Animal Health (OIE) is a valuable resource for information on major livestock diseases, and there is much useful information at its web site. Efforts to control animal diseases at the global level led to creation of the Office International des Epizooties (hence OIE) in 1924. In 2003 the name became the World Organisation for Animal Health but kept its historical acronym of OIE. It is responsible for improving animal health worldwide, is recognized as a reference organization by the World Trade Organization, and as of 2013 had a total of 178 member countries. Another valuable resource free of charge for both animal health professionals and the general public is the Merck Veterinary Manual online with searchable databases.

Adaptation

Cattle as a species are quite remarkable in that they can exist in very extreme climatic conditions. However, this does not mean that all types of cattle can equally exist in all conditions. Cattle can adapt to harsh cold climates as well as tropical environments. Two terms that should be discussed here are acclimatization and adaptation. Acclimatization refers to an animal's ability to adjust to or cope with a new environment, and this can happen over a few days, weeks, or months. Acclimatization deals with the concepts of the processes in an animal operating differently to achieve homeostasis under new conditions. Adaptation, however, is a genetic concept and means a group of animals changing genetically so that they are better genetically suited to a particular environment; it is more of an evolutionary development concept (Table 17).

Behavior and Welfare

There is no substitute for regular observation of cattle behavior to help understand components of beef cattle production. Understanding of 'normal' and 'abnormal' behaviors in general as well as observation and recognition of individual animal differences for what are 'normal' and abnormal' are also very important. Cattle, as most animals, can and will respond to a wide variety of stimuli, including training. Training with regard to proper handling techniques can reduce stress levels for both animals as well as personnel. Design of cattle handling equipment and facilities can complement (or inhibit) animal experiences and the effectiveness of training

Table 18 Recommendations about space and rest for cattle hauled long distances and small calves

Cattle size 500 kg	*Travel duration (h) Up to 12 h*	*Floor space allowance (m^2) 1.35*	*Travel duration (h) More than 12 h*	*Floor space allowance (m^2) 2.03*
	First travel period (h)	*First rest (h)*	*Second travel period (h)*	*Second rest (h)*
Calves less than 6 months	8	6	8	24
Cattle more than 6 months	12	6	12	24
	Floor space for young calves of different sizes			
Weight	Up to 55 kg	55–110 kg	110–250 kg	
Space allowance	0.3–0.4 sq m	0.4–0.7 sq m	0.7–0.8 sq m	

Source: Values taken and adapted from European Commission (2002). The welfare of animals during transport (details for horses, pigs, sheep and cattle). Report of the Scientific Committee on Animal Health and Animal Welfare. Brussels: European Commission.

Table 19 Recommended loading densities of cattle to be transported by truck

Mean live weight (kg, lb)	*Floor area per animal (m^2, sq ft)*	*Number animals per 12.2 m single-deck trailer*
250, 551	0.77, 8.3	38
300, 662	0.86, 9.3	34
350, 772	0.98, 10.5	30
400, 882	1.05, 11.3	28
450, 992	1.13, 12.2	26
500, 1103	1.23, 13.2	24
550, 1213	1.34, 14.4	22
600, 1323	1.47, 15.8	20
650, 1433	1.63, 17.5	18

Source: Taken from Australian standards and guidelines for the welfare of animals-land transport of livestock.

effort. Behavior of cattle is as important when they are not under the influence of managers as when they are being processed through facilities or being transported. Cattle modify their behavior in response to conditions that are deemed unfavorable to alleviate stress, such as seeking shade to reduce heat stress or seeking cover and separation from the herd before giving birth. Overall, welfare and well-being of cattle is very important to their production efficiency and longevity, and documentation of proper cattle welfare management techniques is likely to become more important for some consumers and regulatory agencies (Tables 18 and 19).

There are many behaviors that are inherent to cattle, such as how they use their tongue and mouth during grazing, how females stand to be mounted or mount other females as they are in heat, etc., and many of these types of behaviors have been discussed in the preceding section. However, there are also aspects of behavior referred to as temperament or disposition that describe inherent differences about how cattle respond to certain handling or stressful situations.

It is widely recognized that cattle may be trained to perform many different tasks or activities. What producers may not recognize is that animals have to be trained in many aspects related to production, such as how to drink out of a water trough or eat out of a feed bunk when calves go from a ranch to a feedlot, but they can also be trained for things such as how to utilize pastures and how to proceed through working facilities. Providing supplemental feeding, placement of salt and mineral licks, addition of watering sources, etc. can be very useful to influence how animals utilize large pastures. Likewise, handling cattle calmly and quietly as they are moved from pasture to pasture or through alleys and chutes of working facilities will make the same task much easier in the future because the animals are not stressed by this manner of handling, and they will be less adverse to similar situations in the future. Proper cattle-handling and transportation guidelines are now viewed as important aspects of beef quality assurance programs, and it is important for cattle producers to think about the impacts of how they handle their cattle, not just for their own future interactions with the same animals, but also that even though cattle are being sold from their operation, other people as well in the industry will interact with these animals. Previous handling and treatment of animals affect their perception of humans, working pens, and transportation and can impact production responses, such as health and meat quality.

Carcass and End Products

The ultimate value of beef cattle production in most settings is utilization of their various body components primarily for food and secondarily for other aspects, such as clothing. In dairies, milk production (quantity and quality) takes on a primary purpose; in other scenarios, ceremonial uses may be a primary use. No matter which of these primary uses exist, the conversion of cattle into food and other useful components is important. Where cattle are converted into end products for human consumption, sanitation is critical for protecting human health and minimizing risks of illness from potential pathogens. It is important to have inspection systems in order to ensure safety and wholesomeness of beef and associated end products and by-products. Grading or classification of beef carcasses and associated products based on specific standards that relate to consumer satisfaction are needed for trade as well as consumer confidence (Figure 8).

Several factors have been shown to impact beef carcass yield and composition. A general range for the dressing percentage (ratio of carcass weight to live weight) of cattle is 52–68%, depending on degree of body condition and muscle expression. In discussing factors that impact beef carcass composition, it must be emphasized that there is considerable variability within and across all factors, and stereotypes cannot be accurate predictors in many cases.

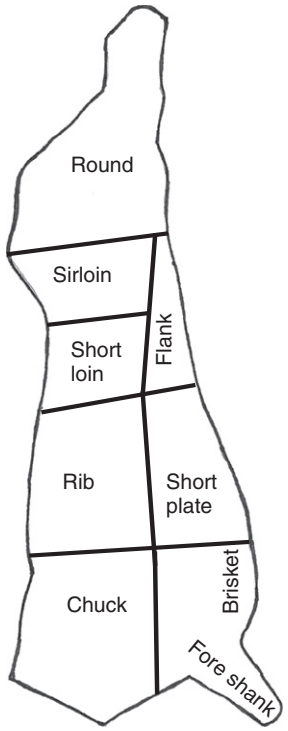


Figure 8 General descriptors for wholesale cuts from beef carcasses. Exact locations of distinction between these cuts may vary across countries or markets. Wholesale cuts are further fabricated into retail cuts, the names of which may vary drastically across countries.

Genetics

Within *B. taurus*, biological type of British-based versus Continental European-based differences exist with regard to tenderness, marbling, and muscle deposition that correspond to differences in growth rate, weight at the time of slaughter, and fatness at slaughter. British types seem to have slight advantages in tenderness when other composition factors are held constant, but increase in tenderness in several cases when differences in other factors, such as fat thickness, time on feed, etc., are not equal. Continental European cattle tend to be taller, have heavier and more muscular carcasses at a constant fat thickness, and require a longer time on high-energy diets to reach a constant fat endpoint. The two main differences (related to genetics) between *B. taurus* and *B. indicus* cattle relate to tenderness associated and degree of marbling, where *B. taurus* (particularly British type) has advantages in both traits. Certain genetic types, such as Japanese Black (Wagyu) and Korean Hanwoo, have extremely high marbling potential, particularly when fed for long times; other genetic types, such as double-muscled breeds like Belgian Blue, Piedmontese, etc., have very little marbling.

Physiological Age

Age is associated with palatability, which is usually assessed by skeletal ossification and dentition but may also be indicated by lean muscle color. Increased age is associated with reduced palatability, particularly in cattle more than 42-month old. Contractile state of muscle and the amount of connective tissue affect tenderness but are not significantly different between breeds and differ due to animal age and sex.

Table 20 General compositional aspects of market weight beef, pork, and lamb

Trait	*Beef*	*Pork*	*Lamb*
Average live animal weight (kg)	454–544	95–104	45
Age (months)	36	6	8–12
Dressing percentage (ratio carcass/live weight)	60	70	50
Carcass weight (kg)	272–318	68–73	23
	Carcass composition (%)		
Lean	52	50	55
Fat	32	32	28
Bone	16	18	17

Source: Reproduced from FAO, 2012. Meat cutting and utilization of meat cuts. Rome, Italy: Food and Agriculture Organisation of the United Nations. Available at: http://www.fao.org/docrep/004/t0279e/t0279e05.htm (accessed 22.10.13).

Nutrition

Higher planes of nutrition will speed up growth rate as well as fat deposition. Type of diet, such as grass-fed versus concentrate-fed diet, and even type of forage and grain can impact color, flavor, and fatty acid profile. Differences in marbling are thought to be driven primarily in differences in external fat thickness. Differences in tenderness appear to be a function of differences in age.

Growth-Promoting Hormones and Hormone-Like Compounds

Testosterone, estrogen, progesterone, and synthetic derivatives found in growth-promoting implants as well as beta-agonists administered through feeds increase rate of gain, efficiency of gain, and red meat yield by increasing muscle deposition at the expense of fat deposition. Extremely intense use of growth-promoting hormone products may reduce tenderness. Marbling may be reduced as a function of reduced external fat.

Environmental Stresses

How animals handle stress can affect energy metabolism. This may be due to illness as severity of bovine respiratory disease has been shown to reduce carcass marbling; impacts on tenderness do not seem to be obviously impacted but have not been intensely studied. Energy used to conserve and dissipate body heat can affect efficiency of gain and carcass composition when conditions are drastically different from the thermoneutral zone. Long-term stress is thought to increase risk of producing 'dark cutting' beef (color of the lean muscle is much

Table 21 Expected percentages of live weight and weights for various by-products from cattle of different biological type (550 kg live weight basis at external fat of 10–12 mm)

	Percentage (%) of live weight			*Weight of by-product (kg)*		
	English	*Holstein*	*≥50% Indicus*	*English*	*Holstein*	*≥50% Indicus*
Green hide	8.2	6.5	9.2	45.1	35.8	50.6
Trimmed hide	7.7	6.0	8.7	42.4	33.0	47.9
Fleshed hide	6.7	5.7	7.4	36.9	31.4	40.7
Cured hide	5.9	5.0	6.3	32.5	27.5	34.7
Liver	1.45	1.96	1.26	8.0	10.8	6.9
Heart	0.48	0.50	0.39	2.6	2.8	2.1
Tunic tissue	0.026	0.02	0.024	0.1	0.1	0.1
Green tripe	2.04	2.15	2.00	11.2	11.8	11.0
Scalded tripe	1.24	1.13	1.04	6.8	6.2	5.7
Oxtail	0.26	0.21	0.28	1.4	1.2	1.5
Weasand meat	0.030	0.034	0.032	0.2	0.2	0.2
Pancreas	0.084	0.093	0.086	0.5	0.5	0.5
Sweetbread	0.091	0.104	0.062	0.5	0.6	0.3
Kidney	0.223	0.255	0.215	1.2	1.4	1.2
Whole head	2.35	2.56	2.13	12.9	14.1	11.7
Cheek meat	0.45	0.47	0.35	2.5	2.6	1.9
Head meat	0.20	0.20	0.15	1.1	1.1	0.8
Oxlips	0.097	0.110	0.089	0.5	0.6	0.5
Salivary glands	0.098	0.063	0.083	0.5	0.3	0.5
Skull	1.51	1.77	1.47	8.3	9.7	8.1
Whole tongue	0.78	0.75	0.71	4.3	4.1	3.9
Trimmed tongue	0.39	0.36	0.35	2.1	2.0	1.9
Tongue trim	0.21	0.19	0.23	1.2	1.0	1.3
Tongue meat	0.026	0.051	0.012	0.14	0.28	0.07
Gullet	0.096	0.105	0.078	0.5	0.6	0.4
Tongue bone	0.018	0.018	0.015	0.10	0.10	0.08
Tongue root muscle	0.042	0.029	0.027	0.23	0.16	0.15
Blood	2.48	2.93	2.62	13.6	16.1	14.4
Hooves	1.76	1.78	1.79	9.7	9.8	9.8
Lungs	0.85	1.1	0.92	4.7	6.1	5.1
Small intestine	2.29	2.71	1.99	12.6	14.9	10.9
Spleen	0.20	0.24	0.20	1.1	1.3	1.1
Ear and lip trim	0.24	0.23	0.24	1.3	1.3	1.3
Large intestine	4.31	5.15	4.09	23.7	28.3	22.5
Trachea	0.12	0.28	0.13	0.7	1.5	0.7
Ruffle fat	0.95	1.3	0.85	5.2	7.2	4.7
Final rail trim	0.95	0.24	0.52	5.2	1.3	2.9
Heart bone	0.006	0.005	0.007	0.03	0.03	0.04
Bile	0.066	0.096	0.075	0.4	0.5	0.4

Source: Percentages taken from Terry, C.A., Knapp, R.H., Edwards, J.W., *et al*., 1990. Yields of by-products from different cattle types. Journal of Animal Science 68, 4200–4205.

darker than typical and is not the color that consumers are accustomed to).

Animal Sex Class

Differences exist in bulls versus steers versus heifers for muscle, fat, and bone growth patterns and percentages. In general, the ranking from bulls to steers to heifers are: (1) leanest to fattest, (2) most muscular to least muscular, (3) longest time to shortest time to reach a fat constant endpoint, and (4) lowest marbling to highest marbling (Table 20).

Cattle By-Products

Parts of the animal's body that do not remain with the carcass are collectively referred to as offal, and most of these items can be useful by-products, some edible, others not. Hooves may be used for dog treats and horns may be used as containers (such as for gun powder, historically) or for decorations. Some items that are made in part with inedible cattle by-products include cosmetics, explosives, and numerous leather products. Edible by-products include the heart, liver, pancreas, kidneys, stomach, tail, head, and several other components. Since recent bovine spongiform encephalopathy (BSE, or mad cow disease)

Table 22 Uses of edible by-products obtained from cattle

Raw by-product	*Principle use*
Brains	Variety meat
Heart	Variety meat
Kidneys	Variety meat
Liver	Variety meat
Spleen (melt)	Variety meat
Sweetbreads (pancreas)	Variety meat
Tongue	Variety meat
Oxtails	Soup stock
Cheek and trimmings	Sausage ingredient
Beef extract	Soups and bouillon
Blood	Sausage component
Fats from cattle and calves	Shortening, candies, and chewing gum
Stomach	
Suckling calves	Rennet for cheese making
Beef (reticulum and rumen)	Sausage ingredient, variety meat (tripe)
Intestines, small	Sausage casings
Intestines, large (beef and pork)	Sausage casings
Esophagus (weasand)	Sausage ingredient
Bones	Gelatin for confectioneries, ice cream, and jellied food products
Calf skin trimmings	Gelatin for confectioneries, ice cream, and jellied food products

Source: Aberle, E.D., Forrest, J.C., Gerrard, D.E., Mills, E.W., 2001. Principles of Meat Science, fourth ed. Dubuque, IA: Kendall/Hunt Publishing Company.

Table 23 Nutritional aspects for 100 g of cooked meat from veal calf

Variety meat	*Protein (g)*	*Fat (g)*	*Calories*
Brain	10.5	7.4	111
Heart	26.3	4.5	153
Kidney	26.3	5.9	165
Liver	21.5	7.6	160
Lung	18.8	2.6	104
Pancreas	29.1	14.6	256
Spleen	23.9	2.6	125
Thymus	18.4	2.9	105
Tongue	26.2	8.3	187

Source: Adapted from Romans, J.R., Costello, W.J., Carlson, C.W., Greaser, M.L., Jones, K.W., 2001. The Meat We Eat, fourteenth ed. Danville, IL: Interstate Publishers, Inc.

outbreaks, it is not recommended to consume brain of other mammals by humans because the organism that causes BSE is found in the central nervous system of the infected cattle. As a result, the brain, spinal cord, and major nerves close to the spinal column are not consumed. This is also why feeding of ruminant-derived meat and bone meal to ruminants has been banned in most countries. The one thing of the animal that has little value associated with its weight is feed in the stomach, and animals are generally withheld from feed for several hours before harvest as this simply adds lost weight to the viscera. Animals are not withheld from water before harvest as dehydration could add to stress and impede exsanguination and hide removal.

The single most valuable by-product in most instances is the hide for the leather industry. In many countries during the industrialization age, the majority of the leather was used for draft livestock harnesses and associated accessories, but with the advent of increased mechanization for farming and transportation, the demand for this purpose was transferred to manufacturing and use of leather belts. As this trend passed, the footwear industry became the main use of leather from cattle. Romans *et al.* (2001) summarized this trend for North America. **Table 21** shows some expected percentages and weights of various by-products than can be expected from cattle.

In some markets, the variety meats may be a less valuable source of income than the carcass, but in other markets that collective value of the variety meats may be equal to or even exceed the value of the carcass. When there are regional or cultural differences in demand for these different types of products, this provides much trade potential and the possibility of added value for new markets. **Table 22** provides a summary of some different uses of edible by-products from cattle, and **Table 23** provides some nutritional values for some variety meat examples.

Use of inedible by-products

Numerous uses for various inedible by-products from cattle exist. Many organs and glands have compounds that can be extracted for human medicine and biomedical uses, several of which are summarized in **Table 24**. Also, several products or compounds can be used in a variety of industrial and manufacturing processes and uses, and many of these are provided in **Table 25**.

Table 24 Uses of organs and glands from cattle

Lungs – heparin (blood thinner), pet food
Heart – pericardium patches
Trachea – chondroitin sulfate (arthritis treatment)
Tendons – elastin and peptone
Gall bladder – cleaning agent for leather, paints, and dyes
Intestines – glycosaminoglycans (for cartilage and joint treatment), sutures, musical strings, and sport racquet strings
Liver – catalase, used in contact lens care products
Pancreas – insulin, chromotrypsin, and glucagons
Placenta – glycosaminoglycans, alkaline phosphatases, and fetal bovine (calf) serum
Testicles – hyaluronidase (cartilage and joint treatment)
Umbilical cord – hyaluronic acid
Uterus – glycosaminoglycans
Spinal cord – historically pharmaceuticals, laboratory reagents, source of neural lipids, and cholesterol
Bile – bile acids used to make industrial detergents and bilirubin to measure liver function
Nasal septum – chondroitin sulfate
Nasal mucosa – heparin
Bone – charcoal ash (for refining products such as sugar), ceramics, cleaning and polishing compounds, and bone and dental implants

Source: Reproduced from Klinkenborg, V., 2001. Cow Parts. Discover Magazine (online). Available at: http://discovermagazine.com/2001/aug/featcow (accessed 14.01.12).

Table 25 Summary of some uses of inedible by-products from cattle

Blood

Cell culture laboratories: Bovine serum albumin provides a wide variety of macromolecular proteins, low molecular weight nutrients, carrier proteins for water-insoluble components, and other compounds necessary for *in vitro* growth of cells, such as hormones and attachment factors. Serum adds buffering capacity to the medium and binds or neutralizes toxic components in the growth milieu.

Home and industrial uses: Plywood adhesives, fertilizer, foam fire extinguisher, and chemical fixer for dyes

Fatty acids (derived from tallows)

General uses: Plastics, tires, candles, crayons, cosmetics, lubricants, soaps, fabric softeners, asphalt emulsifiers, synthetic rubber, linoleum (metallic stearate), PVC (calcium stearate), jet engine lubricants, carrier for pesticides and herbicides, wetting agents, dispersing agents, defoamers, solubilizers, and viscosity modifiers

Many specific examples (oleic acid, stearic acid, etc.) are used for specific purposes or products

Tallow (fats and oils derived from meat, bone, hooves, and horns)

Various industrial tallows used as lubricants and greases: Top White Tallow, All-Beef Packer Tallow, Extra Fancy Tallow, Fancy Tallow, Bleachable Fancy Tallow, Prime Tallow, Special Tallow, No. 2 Tallow, A Tallow, Choice White Grease, and Yellow Grease

Collagen (derived from connective tissues and beef hides)

Numerous uses: Hemostats, vascular sealants, tissue sealants, orthopedic implant coatings, vascular implant coatings, artificial skin, bone graft substitutes, corneal shields, injectable collagen for plastic surgery, injectable collagen for incontinence treatment, meat casings, food additives, artificial dura maters, dental implants, wound dressings, antiadhesion barriers, platelet analyzer reagents, research reagents, antibiotic wound dressing, and lacrimal plugs

Glycerin products (derived from tallows)

Glycerin derivatives: A wide range of pharmaceuticals, including cough syrups and lozenges, tranquilizers, eyewashes, contraceptive jellies and creams, ear drops, poison ivy solutions, solvent for digitalis and intramuscular injection, sclerosing solutions for treatment of varicose veins and hemorrhoids, suppositories, and gel capsules

Glycerol: Solvent, sweetener, dynamite, cosmetics, liquid soaps, candy, liqueurs, inks, lubricants, antifreeze mixtures, and culture nutrients for antibiotics

Gelatin (derived from collagen)

Nonfood uses include cosmetics, industrial uses, photographic paper, and photograph development as an aid in binding for glues, adhesives, and emulsion and as a binder in pills and suppositories

Source: Reproduced from Klinkenborg, V., 2001. Cow Parts. Discover Magazine (online). Available at: http://discovermagazine.com/2001/aug/featcow (accessed 14.01.12).

Table 26 Top 10 rankings for cattle numbers by country for year 2012

Rank	*Total cattle*		*Calf crop*		*Imports*		*Exports*	
	Country	*Number*[a]	*Country*	*Number*[a]	*Country*	*Number*[b]	*Country*	*Number*[b]
1	India	323.7	India	63.4	USA	2256	Mexico	1539
2	Brazil	197.6	Brazil	49.7	Venezuela	616	Canada	825
3	China	104.3	China	41.0	Russia	138	EU-27	769
4	USA	90.8	USA	34.3	China	115	Australia	620
5	EU-27	86.2	EU-27	29.3	Egypt	95	Brazil	512
6	Argentina	49.6	Argentina	13.8	Canada	56	Colombia	299
7	Colombia	30.9	Australia	10.0	Japan	14	USA	191
8	Australia	28.5	Russia	6.9	Mexico	10	Uruguay	75
9	Mexico	20.1	Mexico	6.8	Ukraine	3	New Zealand	42
10	Russia	19.7	Colombia	5.1	Belarus	2	China	28
	World	1019.3	World	280.8	World	3112	World	4878

[a]Numbers for total cattle and calf crop are reported in millions.

[b]Numbers for imports and exports are reported in thousands.

Source: Taken from USDA Foreign Agricultural Service Production, Supply and Distribution (PSD) online database. Available at: http://www.fas.usda.gov/psdonline/psdHome.aspx (23.04.13).

Global Cattle and Beef Comparisons

Finally, some discussion is provided regarding beef production across regions of the world. Differences in these values occur due to combinations of production resources, genetic types of cattle, management practices, cultural preferences, and various political issues. Table 26 provides numbers of cattle (number of head), whereas Table 27 provides values for production, consumption, and trade (in kg of beef on a carcass weight, or bone-in, basis). For both of these tables, countries (or region

Table 27 Top 10 rankings for beef production and trade amounts by country for year 2012

Rank	Total production		Domestic consumption		Imports		Exports	
	Country	Amount	Country	Amount	Country	Amount	Country	Amount
1	USA	11 855	USA	11 744	Russia	1023	Brazil	1524
2	Brazil	9 307	Brazil	7 845	USA	1007	India	1411
3	EU-27	7 765	EU-27	7 806	Japan	737	Australia	1407
4	China	5 540	China	5 597	South Korea	370	USA	1114
5	India	3 460	Argentina	2 458	EU-27	348	New Zealand	517
6	Argentina	2 620	Russia	2 395	Canada	301	Uruguay	355
7	Australia	2 152	India	2 049	Egypt	250	Canada	335
8	Mexico	1 820	Mexico	1 835	Hong Kong	241	EU-27	307
9	Pakistan	1 400	Pakistan	1 367	Venezuela	220	Paraguay	251
10	Russia	1 380	Japan	1 255	Mexico	215	Mexico	200
	World	57 170	World	55 513	World	6683	World	8324

Note: Values are reported in millions of kg and are on carcass weight equivalent basis.
Source: Taken from the USDA Foreign Agricultural Service Production, Supply and Distribution (PSD) online database. Available at: http://www.fas.usda.gov/psdonline/psdHome.aspx (accessed 23.04.13).

for EU-27) are listed from 1 to 10 in ranking within each category along with their respective values.

New and Emerging Technologies

There are numerous technologies available to assist in beef cattle production. Reproductive tools such as nonsurgical embryo transfer, *in vitro* fertilization (IVF), and sexed semen are available and used to varying degree (and in combinations) among seedstock and commercial cow-calf producers. Sequencing of the bovine genome and numerous research efforts in beef cattle genomics have allowed the development of numerous genetic tests for a variety of beef cattle traits, and the field of genomic selection is being explored by many beef cattle groups. An increased focus on individual animal efficiency for feed utilization and many other traits has led to improved animal identification and evaluation systems that rely on automated data capture. There are more tools available to beef cattle producers worldwide than many thought ever possible just a few years ago. Beef cattle producers must prioritize and evaluate their financial information in conjunction with production information in whole systems considerations in all cases and weigh costs versus benefits for use of any technology.

Summary

Beef cattle are very useful in a wide range of production environments globally to supply a wide array of products. The weight and amount of muscle in beef cattle are important in many cultures. In some cases, it is the older animals that are utilized for beef after they have been utilized for draft purposes; however, it has been the assumption throughout this article that production of cattle for beef carcass markets is a primary goal. This article has not discussed many specific considerations involved in beef cattle production but has attempted to point out unique aspects of beef cattle production that might be different in other livestock species. General principles for breeding, genetics, nutrition, reproduction, health, and welfare are similar across livestock species, but specific knowledge and management within each species (as well as within combinations of animal resources, production environment, and local markets) are crucial for short-term as well as long-term economic success.

See also: Air: Confined Animal Facilities and Air Quality Issues. Animal Health: Ectoparasites. Animal Health: Global Antibiotic Issues. Animal Welfare: Stress, Global Issues, and Perspectives. Breeding: Animals. Climate Change: Animal Systems. Critical Tracking Events Approach to Food Traceability. Domestication of Animals. Food Chain: Farm to Market. Forage Crops. Genomics of Food Animals. International Trade. Production Economics. Vaccines and Vaccination Practices: Key to Sustainable Animal Production. Zoonotic Helminths of Livestock

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Biodiversity and Ecosystem Services in Agroecosystems

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Glossary

Agroecology The application of ecological concepts and principles to the design and management of sustainable agroecosystems.
Agroecosystems Agricultural ecosystems including biophysical and human components and their interactions.
Biodiversity The variation of life in all forms from genes, to species, to communities, to whole ecosystems.
Ecosystem service providers Organisms, guilds, and ecological communities that are biological mediators of ecosystem services, providing services through their functions and interactions.
Ecosystem services Functions of ecosystems – including agroecosystems – that are useful to humans or support human well-being: (1) provisioning services include the production of food, fuel, fiber, and other harvestable goods; (2) regulating services include climate regulation, flood control, disease control, waste decomposition, and water quality regulation; (3) supporting services include the foundational processes necessary for production of other services, including soil formation, nutrient cycling, and photosynthesis (primary production); and (4) cultural services provide recreational, esthetic, spiritual, and other nonmaterial benefits.
Human well-being A context- and situation-dependent state that comprises basic material for a good life, freedom and choice, health, good social relations, and security.
Millennium Ecosystem Assessment An international synthesis released in 2005, created by more than 1000 of the world's leading scientists, that analyzed the state of the Earth's ecosystems.
Payment for ecosystem services Market-based instruments used to channel investment in ecosystem services.
Resilience The capacity of a system to absorb disturbance and retain structure and function; this includes the human capacity to anticipate and plan for the future (e.g., in managing agricultural systems).
Scale Geographical extent; relevant scales for agroecosystems often include units commonly used in management and decision making, such as field (local and on-farm cultivated area), farm (including cultivated and noncultivated areas), landscape, regional, and global.

Introduction

Historically, agricultural systems have been managed, above all, for the production of food and fiber; however, agricultural landscapes can provide a wide range of goods and services to society. 'Ecosystem services' are those functions of ecosystems – including agroecosystems – that are useful to humans or support human well-being (Daily, 1997; Kremen, 2005). The ecosystem services concept is remarkably longstanding. Mooney and Ehrlich (1997) noted that in approximately 400 BC, Plato observed how forests provided important services to Attica and forest loss resulted in drying springs and soil erosion. Plato's work highlights that people have been aware of these critical services long before the dawn of industrial agriculture (Rapidel *et al.*, 2011).

In the past two decades, work at the interface of ecology and economics to characterize, value, and manage ecosystem services has supported a paradigm shift in how society thinks about ecosystems and human relationships to them. As both major providers and major beneficiaries of ecosystem services, agricultural landscapes and the people within them are at the center of this shift. Growing calls for agriculture landscapes to be managed as 'multifunctional' systems create new mandates, as well as opportunities, to maintain and enhance ecosystem services as part of productive agroecosystems.

Work on multifunctional ecosystems draws on the Millennium Ecosystem Assessment (2005) and other recent evaluations of ecosystem services (e.g., The Economics of Ecosystems and Biodiversity and The Common International Classification of Ecosystem Services). The Millennium Ecosystem Assessment provides a globally recognized classification that emphasizes relationships between ecosystem services and human well-being and describes four types of services (The authors draw on the classification of ecosystems services used in Millennium Ecosystem Assessment throughout the article (MEA, 2005), recognizing that more recent classifications have minimized or eliminated supporting services in favor of specific, operational descriptions designed for environmental accounting (Haines-Young and Potschin, 2012) and economic valuation (TEEB, 2010)). Provisioning services include the production of food, fuel, fiber, and other harvestable goods. Regulating services include climate regulation, flood control, disease control, waste decomposition, and water quality regulation. Supporting services include the foundational processes necessary for production of other services, including soil formation, nutrient cycling, and photosynthesis (primary production). Cultural services provide recreational, esthetic, spiritual, and other nonmaterial benefits. Most classifications, despite their variations, consider interdependence between ecosystem services and human well-being as well as variation in ecosystem

services across spatial scales ranging from local to global (Figure 1).

Biodiversity – the variation of life in all forms from genes, to species, to communities, to whole ecosystems – is a significant determinant of ecosystem function and provision of ecosystem services. Although relationships between biodiversity and ecosystem services are complex and vary widely across different types of ecosystems, at the broadest level, increased native biodiversity is generally associated with higher levels of ecosystem services within a given system (Balvanera *et al.*, 2006; Cardinale *et al.*, 2012). Plant diversity, for example, has been found to enhance belowground plant and microbial biomass, which is associated with the ecosystem service of erosion control through the effects of large root and mycorrhizal networks holding soil in place (Balvanera *et al.*, 2006). It is also important to note that some ecosystem services are provided in part by the abiotic (nonliving) components of ecosystems, such as aquifers and inorganic portions of soils. Biodiversity can be considered a form of 'biological insurance' that helps to assure ecosystem performance, including providing ecosystem services, as diversity increases the chances that one or more species will be able to perform critical functions, even in the event of disturbance or species loss (e.g., natural disaster and human-induced land use change) (Naeem and Li, 1997).

Agroecosystems both provide and rely on ecosystem services to sustain production of food, fiber, and other

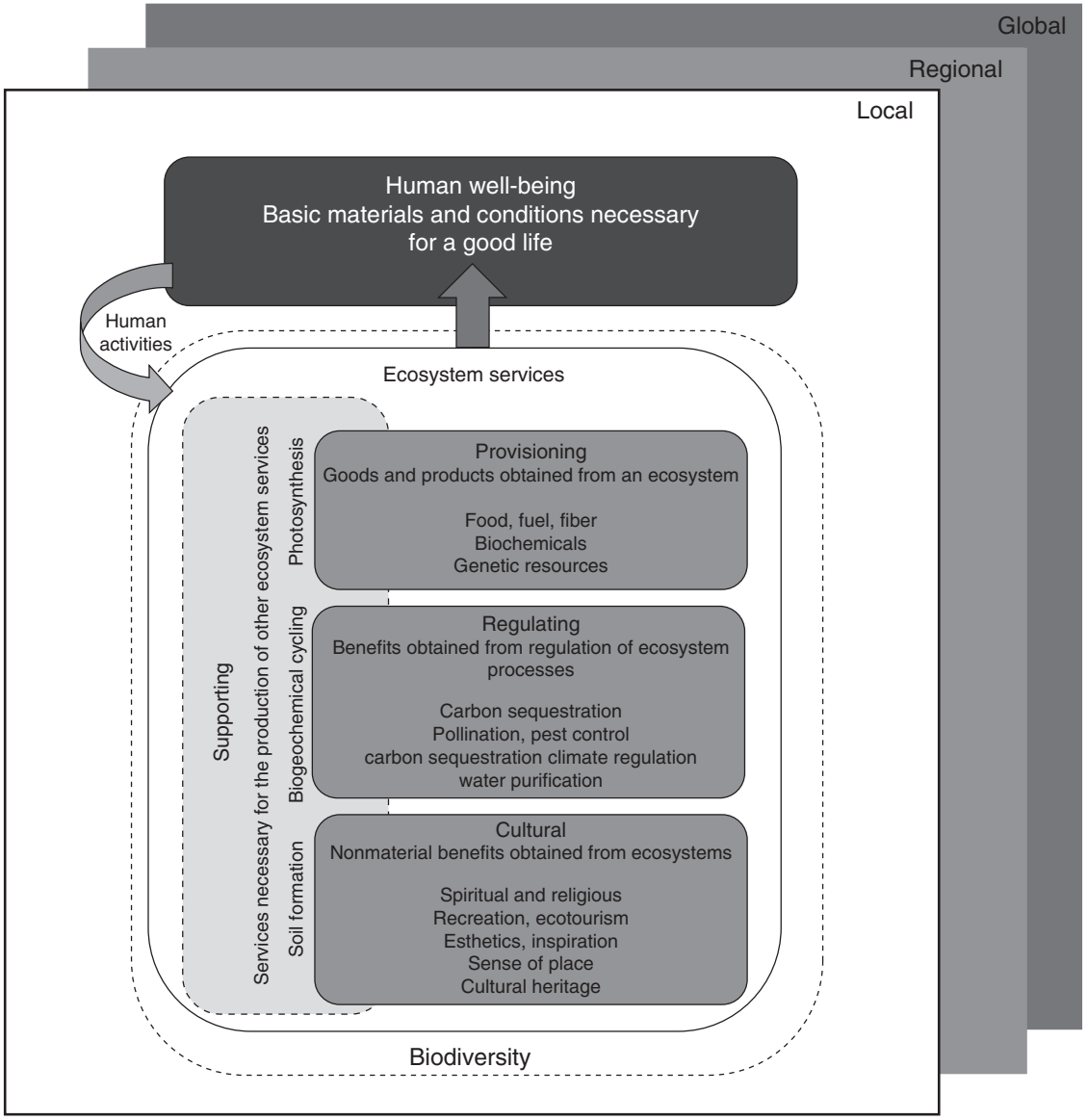


Figure 1 Typology of ecosystem services. This ecosystem service typology, adapted from the Millennium Ecosystem Assessment (MEA, 2005), considers biodiversity as a foundation for all ecosystem services (represented with a dotted line framing ecosystem services). Ecosystem services include provisioning, regulating, and cultural services (dark gray boxes, solid outline), as well as supporting services (light gray box, dashed outline). Ecosystem services support human well-being (charcoal gray box, white text), and, in turn, are influenced by human activities and land-use management decisions. Both ecosystem services and human well-being can be considered at nested spatial scales from local, to regional, to global.

harvestable goods. Many services have on-farm benefits (e.g., for farmers, plantation managers, and other people on-site), whereas others have broader public benefits to off-farm users; some benefit both groups (Table 1).

The evaluation and management of ecosystem services in agricultural landscapes has emerged as a top priority for several reasons. First, agricultural ecosystems – including croplands and pastures – are among the largest terrestrial

Table 1 Ecosystem service descriptions and related on-farm benefits and public, off-farm benefits

Ecosystem service	*Description*	*On-farm benefits*	*Public, off-farm benefits*
Provision of food, fuel, fiber, and biochemicals	Harvestable goods from agroecosystems	Food and other goods for on-farm consumption or sale	Goods for agricultural markets
Soil structure and fertility enhancement	Soil structure and processes of nutrient cycling and delivery of nutrients to plants; processing organic matter and transforming detritus and wastes	Support for crop growth; can limit need for chemical fertilizers	May limit need to mine or manufacture chemical fertilizer
Erosion protection	Soil retention; limiting soil loss through wind and water erosion	Maintain soil, and the nutrients it contains, to support production	Potential reduction of sediment transfer to downstream systems & users
Hydrologic services: Water flow regulation	Buffering and moderation of the hydrologic cycle, including water infiltration into soils and aquifers, moderation of runoff, and plants transpiration	Water in soils, aquifers, and surface bodies available to support plant growth	Stabilize stream base flow and mitigate flooding to downstream areas; recharge into aquifers and bodies of water; plant transpiration may support precipitation patterns
Hydrologic services: Water purification	Filtration and absorption of particles and contaminants by soil and living organisms in the water and soil	Clean water available for human consumption, irrigation, and other on-farm uses	Clean water available to downstream users
Pollination	Transfer of pollen grains to fertilize flowers	Necessary for seed set and fruit production in flowering plants and crops	Necessary for outcrossing in noncultivated flowering plants
Pest control	Control of animal and insect pests by their natural enemies – predators, parasites, and pathogens	Minimize crop damage and limit competition with crops	May limit need for pesticides that threaten environmental and human health
Weed control	Botanical component of pest control; suppressing weeds, fungi, and other potential competitors through physical and chemical properties of cover crops, intercrops, and other planted elements	Minimize weed competition with crops	May limit need for herbicides that threaten environmental and human health
Carbon sequestration	Atmospheric carbon dioxide is taken up by trees, grasses, and other plants through photosynthesis and stored as carbon in biomass and soils	Few demonstrable on-farm benefits[a]	Regulation of the carbon cycle; mitigation of greenhouse gas contributions to atmospheric change
Genetic resources	Pool of genetic diversity needed to support both natural and artificial selection	Distinct genotypes (cultivars) allow fruit set in orchards and hybrid seed production; trait diversity (from landraces and wild relatives) supports disease resistance, new hybrids, and climate adaptations	Prevention against large-scale crop failure
Cultural and esthetic services	Maintaining landscapes that support: esthetics and inspiration; spiritual and religious values; sense of place; cultural heritage; recreation and ecotourism	Esthetics and inspiration; spiritual and religious values; sense of place; cultural heritage; recreation and ecotourism	Esthetics and inspiration; spiritual and religious values; sense of place; cultural heritage; recreation and ecotourism

[a]On-farm carbon sequestration can be associated with on-farm benefits in closely related ecosystem services, such as increased soil organic matter and microclimate regulation (e.g., shade provided by trees).

biomes and account for approximately 40% of the Earth's surface (Foley *et al.*, 2005). Second, increases in food and fiber production have often been achieved at the cost of other critical services. The Millennium Ecosystem Assessment (2005) reported that approximately 60% (15 out of 24) of services measured in the assessment were being degraded or unsustainably used as a consequence of agricultural management and other human activities. Finally, evaluations of 'planetary boundaries,' which describe the safe operating space for human activities with respect to the planet's biophysical systems and processes, indicate that modern, industrial agriculture is among the activities that have most significantly undermined the Earth's life-support systems (Rockström *et al.*, 2009). Major negative impacts have occurred through converting natural habitat to agriculture and infrastructure, environmental pollution, and environmental change induced by shifts in nitrogen and phosphorus use.

Recent work highlights the need for better understanding the ecological processes that underpin critical ecosystem services (Kremen, 2005). Provision of ecosystem services in farmlands is directly determined by their design and management (Zhang *et al.*, 2007) and strongly influenced by the function and diversity of the surrounding landscape (Kremen and Ostfeld, 2005; Tscharntke *et al.*, 2005). Yet, there is an outstanding need for field studies that describe the mechanisms, which control how ecosystem services vary across both space and time. Building understanding of the mechanisms underlying ecosystem services is also essential to developing the ability to predict how management activities will affect the single ecosystem services, and suites of services, needed to support both productive farmlands and human well-being.

Ecosystem Services and Disservices in Agricultural Landscapes

Ecosystem Services and Disservices

Agroecosystems both provide and rely on ecosystem services. Services that help to support production of harvestable goods can be considered services to agriculture (Zhang *et al.*, 2007). These services include soil structure and fertility enhancement, nutrient cycling, water provision, erosion control, pollination, and pest control, among others (**Figure 2**). Ecological

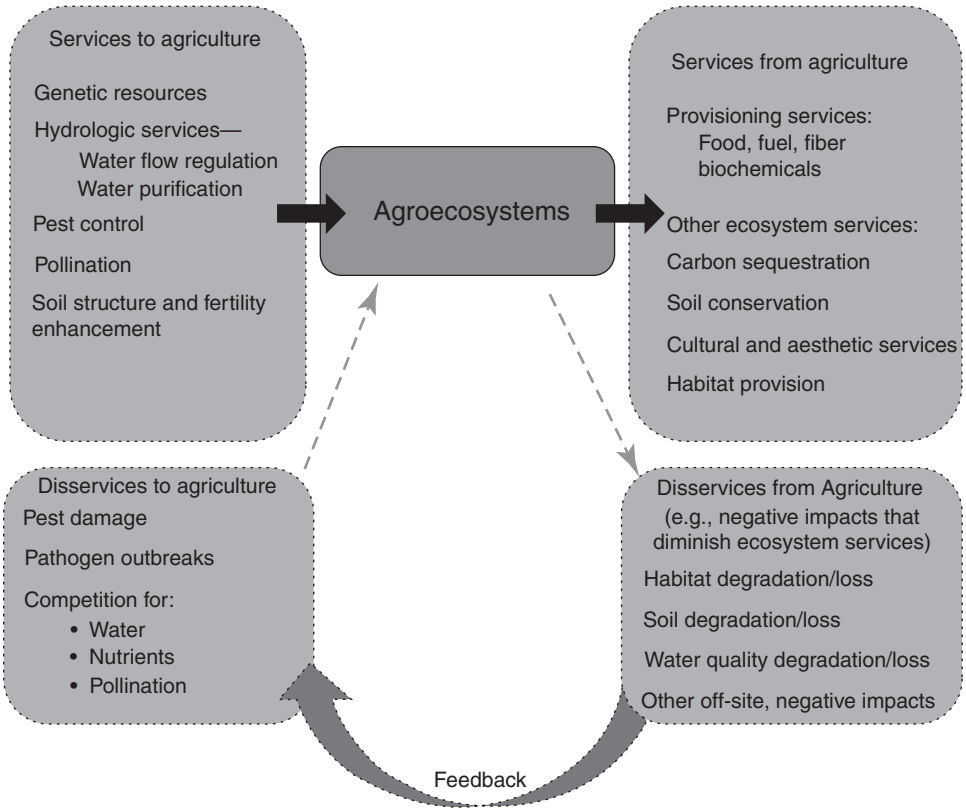


Figure 2 Ecosystem services and disservices to and from agriculture Farming systems can be both producers and beneficiaries of ecosystem services, and in many cases these relationships are deliberately managed by farmers. Such ecosystem services are represented by two gray boxes in the diagram. Production systems can also suffer from various disservices or contribute to disservices or loss of services. These negative relationships are usually the unintentional result of management action, represented by the two lower gray boxes and the dashed arrows. Disservices from agriculture can also lead to agricultural inputs and result in detrimental on-farm impacts, such as when habitat for natural enemies is removed and pest outbreaks increase, represented by the feedback arrow at the bottom of the diagram. Adapted from Zhang, W., Ricketts, T., Kremen C., *et al.*, 2007. Ecosystem services and dis-services to agriculture. Ecological Economics 64, 253–260 and Swinton, S., Lupi, F., Robertson, G., Hamilton, S., 2007. Ecosystem services and agriculture: Cultivating agricultural ecosystems for diverse benefits. Ecological Economics 64, 245–252.

processes that detract from agricultural production can be considered disservices to agriculture (Zhang *et al.*, 2007) and include pest damage, competition for water, and competition for pollination. Management of agricultural ecosystems also affects flows of ecosystem services and disservices (or diminution of naturally occurring services) from production landscape to surrounding areas. Services from agriculture include provisioning services (food, fuel, fiber, and biochemicals) as well as carbon sequestration, soil conservation, cultural and esthetic services, and habitat provision (e.g., providing habitat for endemic organisms). Disservices from agriculture can include degradation or loss of habitat, soil, water quality, and other off-site, negative impacts. Both services and disservices are typically a result of management practices within agricultural fields and landscapes. The remainder of this section describes some of the key ecosystem services that support agricultural productivity (summarized in **Table 1**) and disservices detract from it (see Swinton *et al.*, 2007 for detailed discussion of services and disservices from agriculture).

Services to Agriculture Help to Sustain Agricultural Productivity

Soil structure and fertility enhancement services include the processes of soil formation, structural development (including physical, chemical, and biological properties of soil), and nutrient cycling mediated by biotic and abiotic factors to support plant growth. These soil characteristics are important determinants of the quantity and quality of farming outputs (Zhang *et al.*, 2007). As soil organisms process dead organic matter, and their waste replenishes nutrients required for primary production, the fertility needed to support primary production is maintained (Daily *et al.*, 1997).

Soil structure is enhanced through the activities of macrofauna – such as earthworms, centipedes, millipedes, and isopods – that aerate soil by creating pores as they burrow through the soil profile, mixing organic and mineral particles, redistributing organic matter and microorganisms, and enriching soil with castings (Hendrix *et al.*, 1990; Edwards, 2004). A host of microfauna also act as biological mediators of soil fertility and structure. Their activities support soil fertility as they break down plant detritus and other organic matter, and incorporate nutrients into their biomass, which may otherwise move through the system or be lost downstream (Paul and Clark, 1996). Micro- and macrofauna (e.g., acarina and collembola) influence nutrient cycling by regulating bacterial and fungal populations, release energy by breaking down large molecules into smaller units (catabolizing organic matter), and mineralizing and immobilizing nutrients. Their activities influence soil structure by producing organic compounds that bind soil aggregates. Bacteria and fungi are also part of an important cadre of microflora that mediates nitrogen fixation from the atmosphere, transforming it into plant-available forms (Hendrix *et al.*, 1990).

Soil processes in agroecosystems are subject to removal of nutrient-rich biomass during harvest, plus elevated decomposition rates that increase with frequency of tillage and irrigation. In some systems, organic matter is also lost when fields are burned (e.g., to clear biomass for the next planting). Nutrient losses in agroecosystems contrast with unmanaged, undisturbed ecosystems in which nutrient cycles tend to be more nearly closed, with inputs approximately matching outputs (Daily *et al.*, 1997). Many high-intensity farming systems do not retain soil structure and fertility through biological processes, they are rather maintained through tillage and additions of chemical and organic fertilizers (Daily *et al.*, 1997; Matson *et al.*, 1997).

Pollination

Animal pollinators are essential for approximately 35% of global crop production, and 60–90% of all plant species are pollinator-dependent (Klein *et al.*, 2007). Bees are recognized as the taxon providing most pollination services, yet other taxa – including birds, bats, thrips, butterflies and moths, flies, wasps, and beetles – also pollinate some of the world's most important food crops (Nabhan and Buchmann, 1997). Pollination is necessary for sexual reproduction in many crops, including fruits, vegetables, nuts, and seeds (Klein *et al.*, 2007) as well as many wild plants known to contribute calories and micronutrients to human diets (Sundriyal and Sundriyal, 2004). There are also many globally important crops that are pollinated passively or by wind, including cereals, sugarcane, and grasses (Klein *et al.*, 2007).

Overall, pollinators play a significant role in the world's food systems and agricultural economies. The estimated value of insect-pollinated crops in the United States ranged from US $18–27 billion in 2003. If calculations include secondary products, such as beef and milk from cattle fed alfalfa, the estimated value more than doubles (Mader *et al.*, 2011). Although honey bees (*Apis* spp.) are the most important commercially managed pollinator, native and wild bee species also make significant contributions. Approximately 15% of the value associated with pollination services comes from native bees and other animals living in farmlands and adjacent natural habitat (Mader *et al.*, 2011). Both agricultural management and landscape configuration are important in determining availability and distribution of pollination services. Some wild (native) pollinators nest within fields, including ground-nesting bees, or disperse from nearby unmanaged habitats to pollinate crops (Ricketts *et al.*, 2004). Conserving wild pollinators in unmanaged or restored natural habitats adjacent to agricultural fields can improve pollination levels and stability, which can support increases in agricultural yields (Klein *et al.*, 2003).

The potential contributions of native pollinators have received a great deal of recent attention due to global declines in managed honey bee colonies (National Academies, 2006). Declines in honey bee abundance, driven by establishment of parasitic mites (e.g., *Varroa destructor)*, hive pests, and social factors such as aging beekeeper populations, have resulted in pollination shortages in some areas (Klein *et al.*, 2007). This has caused increased prices for honey bee rental and created concern about pollination shortfalls, such as those seen in California almonds (National Academies, 2006). These factors have heightened interest in the role of native pollinators to help assure availability and stability of crop pollination services. Recommendations for managing pollinator-friendly landscapes include maintaining areas of natural and semi-natural perennial habitat (e.g., grass and woodlands, forests,

old fields, and hedgerows) to provide ample floral and nesting resources available throughout the year (Kremen *et al.*, 2007; Mader *et al.*, 2011).

Pest control

Pest damage is a major limiting factor for global food production. Animal pests destroy 8–15% of global wheat, rice, maize, potato, soybean, and cotton production (Oerke, 2005) and cause more than US$30 billion in damage in the United States each year (Pimentel *et al.*, 2005). However, despite dramatic increases in pesticide application, damage levels remained roughly unchanged during the four decades following the escalation of pesticide use after World War II (Pimentel *et al.*, 1992; Oerke, 2005). Pesticides have even precipitated pest outbreaks. For instance, Southeast Asian rice fields were devastated by the brown planthopper (*Nilaparvata lugens*) after excessive pesticide application caused the pest to evolve resistance while its predators continued to suffer high mortality (Kenmore *et al.*, 1984). In Indonesia, planthopper outbreaks abated once many pesticides were banned (Naylor and Ehrlich, 1997). Instead, farmers adopted an integrated pest management approach in which natural pest predators were fostered, and pesticides were used only after damage exceeded critical economic thresholds.

The idea that farmers can harness nature to provide pest control benefits is not new. As early as AD 304, Chinese farmers created and maintained citrus ant (*Oecophylla smaragdina*) nests in their orchards to control pest outbreaks (Huang and Pei, 1987). Centuries later, in 1888, the modern concept of classic biological control emerged, again in citrus orchards, when introduced vedalia beetles (*Rodolia cardinalis*) caused the near complete collapse of cottony-cushion scale (*Icerya purchasi*) pests in California (Caltagirone and Doutt, 1989). Since then it has become widely recognized that adjusting agricultural practices to benefit pest predators can provide a valuable pest control strategy with significant benefit to farmers.

Strategies for enhancing pest control services to agriculture may require understanding predator ecology to ensure that pest predators have suitable food and habitat resources throughout their life cycles (Landis *et al.*, 2000). Plants that provide floral or nectar resources can be used to sustain predators and parasitoids. Sweet alyssum (*Lobularia maritima*) has proven especially effective for bolstering syrphid fly abundances in California (Tillman *et al.*, 2012). Predator populations can also be enhanced indirectly through agricultural practices that increase nonpest prey, for example, by applying mulch or intercropping (Riechert and Bishop, 1990; Bugg *et al.*, 1991). Small patches of native vegetation on and around farms can provide these species with food resources and overwintering habitat (Landis *et al.*, 2000; Tillman *et al.*, 2012). Emerging evidence suggests that conservation activities at a landscape scale can also benefit farmers. For example, conserving natural habitat surrounding farms increases predators and often enhances pest control services (Thies and Tscharntke, 1999; Bianchi *et al.*, 2006; Chaplin-Kramer *et al.*, 2011b; Karp *et al.*, 2013). These examples represent but a few of many techniques that have emerged for controlling crop pests with native predators, many of which are readily accessible to farmers through government, university, and agency extension programs.

Hydrologic services – water flow regulation and water purification

Agricultural production relies on a host of water-related ecosystem services, ranging from water supply (quantity), to purification (quality), and flood protection (Brauman *et al.*, 2007). Globally, agroecosystems are a major consumer of groundwater and surface water, accounting for approximately 70% of freshwater use worldwide (UN Water, 2013). Agricultural water use may be as high as 90% of total withdraws in fast-growing economies (UN Water, 2013) or arid environments (USDA ERS, 2013). Irrigation is considered a consumptive water use, in that water is not directly returned to rivers and streams. Much of this water eventually returns to the atmosphere through evaporation and plant transpiration (e.g., the process of water moving through plant tissues and evaporating through leaves, stems, and flowers), particularly in thirsty crops, such as alfalfa and cotton.

The majority of prime land for rainfed cultivation is already in use and development of irrigated land has contributed substantially to production gains. A prime example is in India, where the growth of irrigated rice and wheat on the semiarid plains of Punjab has substantially boosted food production over the past several decades (Matson *et al.*, 1997). Globally, approximately 40% of crop production is supported by irrigated agricultural lands, which account for 20% of all agricultural areas (UN Water, 2013). Scientists project that continued increases in agricultural production would require sustained or increased supply of irrigation water (Matson *et al.*, 1997).

Ecosystems do not create water; however, they can modify the amount of water moving through the landscape. These modifications result from ecosystem influence on the hydrologic cycle, including local climate, water use by plants, and modification of ground surfaces that alter infiltration and flow patterns (Brauman *et al.*, 2007). The amount of water stored in watersheds, or discharged above and below ground, influences water supply and availability to downstream users. The understanding of how water availability changes with land use and land cover change is elementary (Brauman *et al.*, 2007). Planting of forests and trees – native or introduced – can either increase or decrease evapotranspiration and downstream water availability, depending on the context. In one study, analysis of paired catchment experiments found that stream flows were reduced 45% on an average when grasslands were converted to forests (Farley *et al.*, 2005). Other studies from the Amazon basin illustrate that evapotranspiration from a pasture can be up to 24% less than a nearby forest (Von Randow *et al.*, 2004). Vegetation can also be selected to support management goals based on water requirements. For example, Australian studies describe use of plants such as lucerne (*Medicago sativa*), eucalyptus trees (*Eucalyptus* spp.), and saltbush (*Atriplex* spp.), which are thought to mitigate potential crop damages in areas where rising water tables bring saline water into root zones by lowering water tables through high transpiration rates (Heuperman *et al.*, 2002).

Water purification depends on filtration and absorption of particles and contaminants by clay, silt, and sand particles in soil as well as living organisms in soil and water. Agricultural production depends on water quality to maintain productive capacity, but there are a number of threats and challenges the

continued provision of clean water. Irrigated farmlands in arid and semiarid regions are experiencing degradation due to salinization and waterlogging (Matson *et al.*, 1997).

Maintaining water quality for agriculture and other uses is increasingly thought to require maintaining buffers of vegetation with intact groundcover and root systems throughout the watershed. Vegetation, microbes, and stabilized soils can remove pollutants from overland flow and from groundwater by physically trapping water and sediments, by adhering to contaminants, by reducing water speed to enhance infiltration, by biochemical transformation of nutrients and contaminants, and by absorbing water and nutrients from the root zone (Naiman and Décamps, 1997). Vegetated riparian buffer zones in particular perform critical functions to support water quality.

Genetic resources provide a pool of raw material necessary to support the process of natural selection and produce evolutionary adaptations in unmanaged ecosystems. In agroecosystems, crop and animal breeders draw on genetic diversity using traditional breeding and biotechnology to artificially select and perpetuate desirable traits (Zhang *et al.*, 2007). A broad portfolio of genetic resources increases the likelihood of maintaining production, particularly as environmental pressures such as climate, pests, and disease fluctuate. Production stability comes through an array of genotypes, each with different characteristics of disease resistance, tolerance for environmental extremes, and nutrient use (Esquinas-Alcázar, 2005). Different genotypes, or cultivars, are required for plants in orchard systems and hybrid seed production to set fruit or seed (Free, 1993; Delaplane and Mayer, 2000). The benefits of genetic variation at the species level include enhanced biomass production, reduced loss to pests and diseases, and more efficient use of available nutrients (Tilman, 1999).

Crop production is supported by genetic resources from two important sources. First are 'landraces,' the varieties of crops and livestock that have been cultivated and selected by farmers over many generations practicing traditional agriculture (Shand, 1997). Second are closely related species that survive in the wild, known as crop 'wild relatives.' Areas with high concentrations of landraces and wild relatives are considered centers of crop genetic diversity (Shand, 1997). These centers are critical, as many important crops could not maintain commercial production without periodic infusions of genetic resources from wild relatives (de Groot *et al.*, 2002).

The consequences of losing genetic resources in a crop system can be severe. The Irish potato famine in the 1830s is one such example. The crop failure can be attributed in part to a very limited number of genetic strains of potatoes in Ireland, which made the crop particularly susceptible to potato blight fungus (Hawtin, 2000). Reintroducing disease-resistant varieties from Latin America, where the potato originated, helped to resolve the problem. Recent reviews of crop genetic resources highlight that increases in human population size, ecological degradation in farmlands, and globalization have contributed to a dramatic reduction of crop diversity worldwide. Approximately 150 species now comprise the world's most important food crops and most human diets are dominated by no more than 12 plant species (Esquinas-Alcázar, 2005). Loss of crop genetic diversity is of great concern because it reduces the pool of genetic material available for natural selection and artificial selection by farmers and plant breeders, thereby increasing the vulnerability of crops to sudden environmental changes (Esquinas-Alcázar, 2005).

Disservices to Agriculture Detract from Agricultural Productivity

Disservices to agriculture result from the ecological processes or relationships that detract from agricultural productivity. Crop pests, including seed eaters, herbivores, frugivores, and pathogens (e.g., insects, fungi, bacteria, and viruses), can result in reduced productivity, or total crop loss in worst case scenarios (Zhang *et al.*, 2007). Weeds and other noncrop plants can reduce agricultural productivity through competition for resources. At the field scale, weeds compete with crops for sunlight, water, and soil nutrients and may limit crop growth and productivity by limiting access to these critical resources (Welbank, 1963). Within fields, plants may exhibit allelopathy (biochemical inhibition of competitors), such as the toxins exuded by some plant roots that can decrease crop growth (Weston and Duke, 2003).

Resource competition that potentially detracts from agricultural yields can also take place at larger scales. Competition for pollination from flowering weeds and other noncrop plants beyond agricultural fields can reduce crop yields (Free, 1993). Water used by other plants, such as trees that reduce aquifer recharge, can reduce water available to support agricultural production by diminishing an important source of irrigation water (Zhang *et al.*, 2007).

Food safety concerns related to pathogen outbreaks are other potential detractors from agricultural productivity. Since the 1990s these concerns have gained some prominence in highly productive regions, such as the Salinas Valley of California (the 'salad bowl of America'), which experienced *Escherichia coli* contamination of leafy greens. The unfortunate consequence has been broad-scale removal of riparian habitat to minimize wildlife intrusion into crop fields. Wildlife was posited to spread harmful bacteria, although whether it constitutes a significant food safety risk remains unclear. Nevertheless, over a 5-year period following an *E. coli* O157:H7 outbreak in spinach, 13.3% of remaining riparian habitat was removed from the Salinas Valley (Gennet *et al.*, 2013). This habitat removal may result in degradation or loss of the ecosystem services typically provided by riparian areas.

It is important to note that disservices from agriculture can also affect the productivity and environmental impacts of farming systems through multiple feedbacks. For instance, when habitat for natural enemies is removed, pest outbreaks can result in crop damage or loss, resulting in reduced productivity and potentially increased use of pesticides, which may be accompanied by further detrimental effects. Similarly, when riparian habitat is degraded or removed, the hydrologic services of water flow regulation and water purification services can be diminished or lost (**Figure 2**).

Managing Ecosystem Services in Agricultural Landscapes

Different ecosystem services are mediated and delivered at different scales, ranging from individual farm plots to entire

watersheds or regions (Zhang *et al.*, 2007). Accordingly, efforts to maintain or enhance ecosystem services in farming landscapes may require deliberate management of different areas and scales, including cultivated areas within farms, noncultivated areas within farms, and broader landscapes (well beyond farm boundaries) that comprise both cultivated and noncultivated areas.

Management of cultivated fields often focuses on ecosystem services that have a direct influence on farm productivity; farmers have a direct interest in managing services, including pollination, pest control, soil fertility and nutrient cycling, soil retention, water purification, and water flow regulation. On-farm practices that target water conservation, including moisture from rainfall that is stored in the soil profile, may help to offset water shortages during dry seasons or droughts (Rost *et al.*, 2009). Mulching or modification of field tillage practices can reduce evaporation of soil water by 30–50%. In addition, farmers can harvest rainwater by installing microtopographic features in their fields (e.g., small bunds or pits) as well as ponds, dykes, or other infrastructure, enabling recovery of up to 50% of water normally lost in the system (Rost *et al.*, 2009; Power, 2010).

Management of noncultivated areas of farms may support both ecosystem services of benefit both to farmers themselves and to the broader public. Studies of smallholder farms have documented the benefits of planting trees in noncultivated areas, in both temperate and tropical regions, including Nepal (Carter and Gilmour, 1989) and Costa Rica (Casasola *et al.*, 2007). Increasing tree cover is associated with enhanced diversity and richness of mobile organisms – such as birds, bats, and butterflies (Harvey *et al.*, 2006) – soil retention (Carter and Gilmour, 1989), and carbon sequestration (Montagnini and Nair, 2004). In the case of management that supports ecosystem services, which provide public benefits but does not directly support farm productivity (e.g., carbon sequestration needed to support climate regulation), farmers may have less incentive to implement management practices. To stimulate provision of public benefits, policies and programs may be needed to offset the costs of management investments or create financial incentives for using new management practices (Garbach *et al.*, 2012).

Broader landscape management to support ecosystem services requires to understand the ways in which ecosystem processes take place across multiple parcels of land (including movement of biotic and abiotic components, such as organisms, water, and nutrients). Pollination illustrates the importance of broader landscape management, highlighting that mobile organisms respond to resources both within and beyond cultivated fields. Studies in California suggest that pollination by native bees was higher in farms near greater proportions of natural habitat (no significant relationship was found between pollination and farm type, insecticide usage, field size, or honeybee abundance) (Kremen *et al.*, 2004). There is some evidence that multiple farmers practicing diversified farming – using practices focused on maintaining and enhancing biodiversity of flora and fauna within and across fields – across a region can result in greater provision of ecosystem services than simply the sum of their individual management actions (Gabriel *et al.*, 2010).

Considerations for Managing Ecosystem Services

Managing ecosystem services requires building an in-depth understanding of the species, functional groups, and ecological processes through which services are provided (Kremen, 2005). **Table 2** highlights some of the key organisms, guilds, and communities that are the biological mediators of ecosystem services and disservices to agriculture. Their biological activities affect the provision of ecosystem services at the field, farm, landscape, and regional-to-global scales. For example, at the field scale, services of soil structure and fertility enhancement (including the processes of soil formation, development of structure, and nutrient cycling) are provided by microbes, invertebrates, and nitrogen-fixing plants. Thus, field-scale management may focus on practices such as incorporating nitrogen-fixing plants into crop rotations and planning the timing and depth of tillage to minimize impacts on beneficial invertebrates. At the farm scale, soil-related ecosystem services may also be influenced by levels and types of vegetative cover; thus, farm-scale management may focus on the total area, type, and timing of harvest (if any) of vegetation, including both cultivated and noncultivated areas (**Table 2**).

Measuring Ecosystem Services and Evaluating Service Providers

There is a great deal of interest in methods used to measure provision of ecosystem services. One method is to evaluate the presence or abundance of organisms believed to provide ecosystem services. A second method is to measure the delivery of the service themselves (Kremen and Ostfeld, 2005). For instance, in order to measure pollination in a California squash field, the first method would focus on the abundance and distribution of key pollinators, such as native squash bees (*Peponapis pruinosa*) and other insects. Alternatively, the second method would evaluate whether a squash crop was sufficiently pollinated. These two methods are complementary and may be used together to build a comprehensive understanding of ecosystem service delivery. Counting ecosystem service providers can provide insight into the likelihood of an ecosystem service being available. In contrast, measuring the outcomes (e.g., pollination metrics, such as seed set or pollination deficit) can help to verify delivery of a service but does not provide much information about the organisms providing the service. A comprehensive approach to understanding and measuring ecosystem services includes understanding key ecosystem service providers (e.g., organisms, guilds, and communities), factors influencing the ability of providers to deliver services of interest, and measuring spatial and temporal scales over which providers operate and ecosystem services are available (Kremen and Ostfeld, 2005).

The relationships between biodiversity and ecosystem function are also important for understanding provision of ecosystem services (Altieri, 1995; Hooper *et al.*, 2005; Tscharntke *et al.*, 2005). In general, species richness – measured as the number of species in a given area – is associated with enhanced ecosystem services (Balvanera *et al.*, 2006). Similarly, biodiversity loss is associated with diminished

Table 2 Ecosystem services and disservices to agriculture, the scales over which they are typically provided, and organism, guilds, and communities that provide them

	Organisms, guilds, and communities that provide services at the following scales:			
	Field	*Farm*	*Landscape*	*Region/globe*
Services to agriculture				
Genetic resources	Diversity within a single crop; genotypes help to provide pest and disease resistance	Diversity across multiple crops; rotations help to provide pest and disease resistance	Landrace varieties, wild relatives of crops; can be used to infuse crops with genetic diversity	Landrace varieties, wild relatives of crops; can be used to infuse crops with genetic diversity
Hydrologic services: Water flow regulation, water purification	Vegetation within cultivated areas	Vegetation around water sources, drains, and ponds	Vegetation cover in watershed; riparian communities	Vegetation cover in watersheds; riparian communities
Pest control	Predators, parasites (animals and insects, including vertebrates, invertebrates, and parasitoids)	Predators, parasites (animals and insects, including vertebrates, invertebrates, and parasitoids)	Predators, parasites (animals and insects including vertebrates, invertebrates, and parasitoids)	–
Weed control	Predators, competitors (herbivores, seed predators, and other competitors that limit plants and fungi)	Predators, competitors (herbivores, seed predators, and other competitors that limit plants and fungi)	Predators, competitors (herbivores, seed predators, and other competitors that limit plants and fungi)	–
Pollination	Pollinators: primarily bees but also bats, thrips, butterflies and moths, flies, wasps, beetles, and birds (note: some crops are wind-pollinated)	Pollinators: primarily bees but also bats, thrips, butterflies, and moths, flies, wasps, beetles, and birds (note: some crops are wind-pollinated)	Pollinators: primarily bees but also bats, thrips, butterflies and moths, flies, wasps, beetles, and birds (note: some crops are wind-pollinated)	–
Soil structure and fertility (including processes of soil formation, development of structure, nutrient cycling supporting fertility)	Microbes, micro and macro invertebrates, nitrogen-fixing plants	Vegetative cover	Vegetative cover	–
Erosion protection	Cover crops and perennial crops	Cover crops and perennial crops	Riparian vegetation; vegetative cover on steep areas, thin soils; floodplains	Riparian vegetation; vegetative cover on steep areas, thin soils; floodplains
Disservices to agriculture				
Pest damage and pathogen outbreaks	Insects, snails, birds, mammals, fungi, bacteria, viruses, and weeds	Insects, snails, birds, mammals, fungi, bacteria, viruses, and weeds	Insects, snails, birds, mammals, fungi, bacteria, viruses, and rangeland weeds	–
Competition for water	Weeds	Vegetation near drainage ditches	Vegetation in watersheds	Vegetation in watersheds
Competition for pollination	Flowering weeds	Flowering weeds	Flowering plants in watershed	

Source: Adapted from Zhang, W., Ricketts, T., Kremen, C., *et al*., 2007. Ecosystem services and dis-services to agriculture. Ecological Economics 64, 253–260.

provision of ecosystem services, often due to reduced efficiency of resource capture and use in ecological communities, diminished biomass production, and diminished rates of nutrient decomposition and recycling (Cardinale *et al*., 2012). In addition to biodiversity, ecosystem function is influenced by the identity, density, biomass, and interactions of species within a community (Kremen and Ostfeld, 2005). These attributes can aggregate at different levels (e.g., field, farm, and landscape scales). Thus, it is important to consider how ecological attributes may vary over space and time, as this can influence when and where ecosystem services are available.

Many ecological studies aim to understand which populations, species, functional groups, guilds, food webs, and habitat types produce key services. One method to do so is a functional inventory, which includes identifying and describing the focal ecosystem service providers in a landscape and quantifying their contributions (Kremen and Ostfeld, 2005). A functional inventory is most relevant at the scale of the focal ecosystem service. Thus, evaluating disease resistance in crops may require a functional inventory at the genetic level, (Zhu *et al*., 2000) whereas evaluating biological control of pests may require an inventory at the

level of a population or food web (Kruess and Tscharntke, 1994).

Functional Differences

A second method to build understanding of ecosystem service providers is evaluating functional attribute diversity (Kremen and Ostfeld, 2005). This method describes differences within the guild, functional group, or community that provides each service. A commonly used metric is ecological distance, which describes differences in morphology, ecology, or behavior of the organisms (Laliberté and Legendre, 2010; Walker *et al.*, 1999) that provide ecosystem services. Characteristics that determine how an organism performs key functions are often used for measuring ecological distance, such as root depth of plants (potential determinant of water flow regulation), timing of emergence and senescence (primary production and nutrient cycling), or pollinator's tongue length (pollination).

Response to Disturbance

Comprehensive evaluation of the abundance of ecosystem services providers, and broader patterns of ecosystem services availability, can build a solid foundation for investigating potential influence of disturbance. For example, what happens when species that provide key services are lost? Sometimes ecosystem services are resilient to disturbance and loss. If remaining species can compensate for the species that are removed or have become extinct, ecosystem services may also be maintained rather than diminished. This compensation effect can happen in several ways.

First, compensation can occur through response diversity, described as the diversity of responses to change shown among species contributing to the same ecosystem functions and services disturbance (Elmqvist *et al.*, 2003). Second, it can occur through functional compensation, which occurs when efficiencies of individual ecosystem service providers shift in response to changing community composition. Third, compensation may also happen through the portfolio effect. Just as having a diverse investment portfolio may buffer an investor against fluctuations in individual investments, a diverse biological community is more likely to contain some species that can persist through disturbances (Tilman *et al.*, 1998).

Promoting Synergies between Yield and Ecosystem Services

Recent global estimates project the need to double world food production by 2050 (World Bank, 2008a; The Royal Society, 2009; Godfray *et al.*, 2010). At the same time, there is a growing consensus that increased food production must not come at the expense of diminishing key ecosystem services, such as carbon sequestration, water flow regulation, and water purification. Additionally, the prospect of clearing additional land for agriculture is unappealing, as most of the remaining potentially arable land on the Earth is covered by tropical rainforest; agricultural expansion in these areas would come at a steep cost to biodiversity and the delivery of services from biodiversity-rich rainforests (Ramankutty and Rhemtulla, 2012). Therefore, existing farmlands are being called on to simultaneously increase crop yields and provision of ecosystem services. This call for multifunctional agricultural landscapes can be summarized as agroecosystems in which productivity and ecological integrity are complementary outcomes, rather than opposing objectives.

Agroecology is a scientific subdiscipline and farming approach intended to do precisely this by applying ecological concepts and principles to the design and management of sustainable farming systems (Altieri, 1995). Agroecology emphasizes understanding the ecology of crop, livestock, and other species in a farming system as well as the mechanisms that govern their functions. It highlights the role of human managers in maintaining and enhancing desirable functions and related ecosystem services to optimize use of water, energy, nutrients, and genetic resources (Altieri, 1995; Gliessman *et al.*, 1998). In doing so, the practice of agroecology often seeks to intensify production systems – that is, to deliver greater yields per unit of land, water, or other inputs used – in a way that is based on and, in turn, maintains healthy systems of soil, water, and biodiversity.

There is considerable evidence that systems of agroecological intensification can increase yields relative to prevailing farmer practices in many parts of the world (e.g., Pretty *et al.*, 2006). A recent quantitative review investigated whether agroecological intensification systems tend to deliver yield and ecosystem service benefits simultaneously (Garbach *et al.*, in press). Here the authors summarize results for two illustrative systems of agroecological intensification: conservation agriculture and the system of rice intensification.

Conservation agriculture is an agroecological intensification system that aims to increase productivity and sustainability of soil resources through three main practices: (1) minimal soil disturbance, (2) permanent soil cover, and (3) crop rotations (Kassam *et al.*, 2009). Development agencies, such as the Food and Agriculture Organization of the United Nations, have promoted this system due to its potential applications in farms of diverse sizes and crop systems (FAO, 2011).

Field studies of conservation agriculture report benefits in soil structure, nutrient cycling, erosion protection, and animal biodiversity relative to conventional soil tillage (Milder *et al.*, 2012). However, inconsistent results have been reported for key services, such as pest control, which was found to be diminished in some field studies due to increased pests harbored by crop residues (Van den Putte *et al.*, 2010). Other field studies have reported increased pest control associated with maintaining soil cover (e.g., mulching and retaining plant residues on soil surfaces) and increased species richness and population density of beneficial insects, such as predatory crickets, beetles, bugs, ants, and spiders (Jaipal *et al.*, 2005).

Synergistic outcomes in conservation agriculture – enhanced yield and ecosystem services – were reported in approximately 40% of comparisons (17 of 43 total quantitative comparisons with conventional cultivation, reported in 16 studies, Garbach *et al.*, in press) (**Figure 3**). However, conservation agriculture studies have also reported trade-offs, such as enhanced yield despite diminished weed control services (Haggblade and Tembo, 2003) and diminished yield but

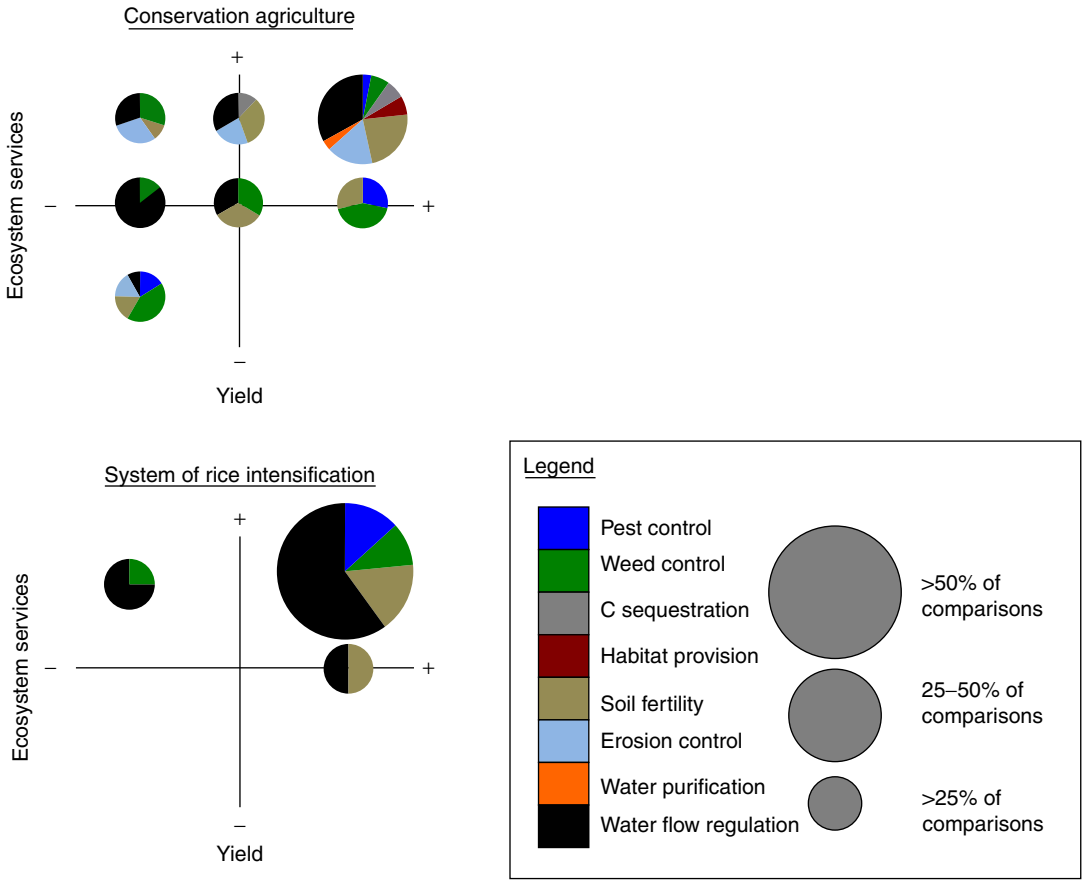


Figure 3 Synergies and trade-offs between ecosystem services and yield in conservation agriculture and system of rice intensification. Bubble location indicates the specific combination of outcomes for ecosystem services (Y-axis: enhanced, upper quadrants; diminished, lower quadrants) and yield (X-axis: enhanced, right quadrants; diminished, left quadrants) relative to comparison systems. Bubbles located on the axis indicate no significant difference from the comparison system. Bubble size indicates the percent of reviewed comparisons reporting each combination of yield and AEI outcomes: large bubbles indicate >50% of comparisons; medium bubbles indicate 25–50% of comparisons; and small bubbles indicate <25% of comparisons. The ecosystem services evaluated are represented by colored charts in each bubble and represented as the percentage of comparisons in which the ecosystem service was measured. Adapted from Garbach, K., Milder, J.C., DeClerck, F., *et al.*, in press. Closing yield gaps and nature gaps: Multi-functionality in five systems of agroecological intensification. Proceedings of the National Academy of Sciences-Plus.

enhanced soil structure and erosion control (Araya *et al.*, 2011) (7% of comparisons, **Figure 3**). A small number of studies have reported both diminished yield and ecosystem service (6% of comparisons, **Figure 3**). Diminished yield in conservation agriculture was often associated with a decrease in weed control (Narain and Kumar, 2005) and pest control services (Van den Putte *et al.*, 2010).

The system of rice intensification has received a great deal of recent attention as an agroecological intensification system developed specifically for a staple grain. This approach to irrigated rice cultivation includes six key practices: transplanting young seedlings; low seedling density with shallow root placement; wide plant spacing; intermittent application of water (vs. continuous flooding); frequent weeding; and incorporation of organic matter into the soil, possibly complemented by synthetic fertilizer (Africare, Oxfam America, WWF-ICRISAT, 2010).

Field studies report considerable evidence for synergies between yield and ecosystem services in the system of rice intensification, particularly water flow regulation. Enhancement of both yield and ecosystem services were reported in 87% of comparisons (39 of 45 quantitative comparisons reported in 15 studies, Garbach *et al.*, in press) (**Figure 3**). Most studies compared the system of rice intensification to the predominant unintensified farmer practices in the study area. Thus, the results suggest that the system of rice intensification can significantly improve productivity and ecosystem service delivery relative to current practices in many regions. However, the relative benefits of the system of rice intensification compared with regionally specific best management practices in conventional rice farming are less clear (McDonald *et al.*, 2006).

Landscape Context

From above, agricultural landscapes often resemble a patchwork of rural villages, natural and seminatural habitat, and farms cultivating a diverse array of crops. 'Natural habitat' in this context describes the full range of natural, seminatural, and weedy vegetation types that tend to be present in

agricultural areas. However, over the past decades in many parts of the world, remnants of natural habitat have begun disappearing, replaced by vast fields of industrial agriculture (Perfecto *et al.*, 2009). This physical restructuring of agricultural landscapes has resulted in dramatic changes in many critical ecosystem services.

Ecological processes often occur at scales larger than individual farms, making the composition of the broader agricultural landscape an essential determinant of ecosystem service provision. Natural habitat can provide many benefits to farmers and the public (Kremen and Miles, 2012). Benefits include harvestable goods, such as fuelwood, medicinal plants, and bushmeat, as well as genetic resources provided by crop wild relatives. Natural habitat can provide recreational opportunities and has been found to support mental health in some case studies (Bratman *et al.*, 2012).

Ensuring that agricultural systems realize diverse benefits requires looking beyond on-farm practices and managing the broader landscape. Here the authors focus on examples of landscape management for two animal-mediated ecosystem services: pollination and pest control. Many other ecosystem services, including water purification, genetic resources, and soil structure and fertility enhancement, also require landscape management. Animal-mediated services, however, are among the most severely affected by landscape simplification, and landscape-level effects have been well documented.

When natural habitat is removed for agriculture, beneficial pollinators and predators of insect pests often decline in abundance, whereas pests increase, which may precipitate lower yields for farmers (Philpott *et al.*, 2008; Karp *et al.*, 2011; Melo *et al.*, 2013). The amount of natural habitat required to sustain pest control and pollination services is often a product of the home range sizes of the predator and pollinator species that provide these services, an attribute that can vary considerably among species. The relevant management scale for farmers depends on both the focal ecosystem service and on the attributes of its animal providers. Fortunately, the past decades have seen a surge of research documenting the role of landscape structure and composition in sustaining pollinators and pest control providers.

Pollination

Although managed honey bees (*Apis mellifera*) provide most pollination globally, native insects are often more effective pollinators and provide complementary pollination benefits (Garibaldi *et al.*, 2013). Further, native insects enhance pollination resilience, especially as honey bee colonies continue to collapse (Winfree and Kremen, 2009). Retaining a diverse pollinator community is thus increasingly recognized as an essential component of any sustainable food system.

Unsurprisingly, native pollinators rely on native habitat. Many species center their foraging activity around the nest, often located in patches of habitat embedded in agricultural landscapes (Lonsdorf *et al.*, 2009; Jha and Kremen, 2013). Pollinator activity matches pollinator foraging ranges, and pollination is thus consistently higher at the edges of crop fields near native habitat than in the interior of large crop monocultures (Kremen *et al.*, 2004; Ricketts *et al.*, 2004, 2008; Klein *et al.*, 2012). As large fields of a single crop variety replace more diversified farms, the total length of time during which crop species are flowering becomes shorter. As a result, pollinators may become increasingly dependent on the wild plants that flower throughout the year in noncropped areas (Mandelik *et al.*, 2012). Pollination services are thus not only higher but also more stable at field edges than in the interior (Garibaldi *et al.*, 2011).

Although pollination services may vary from crop to crop, pollinator to pollinator, and region to region, the positive influence of natural habitat on pollinator activity has proven remarkably consistent across many studies (Ricketts *et al.*, 2008). This consistency has allowed researchers to create spatial pollination models that estimate pollination provision on the farm based on the composition of the surrounding landscape (Lonsdorf *et al.*, 2009). For instance, the InVEST, the ecosystem service modeling platform operated by the Natural Capital Project, allows land managers to predict the pollination consequences of their land-use decisions and manage land assets accordingly.

Pest Control

Not all crops are animal pollinated, but every crop suffers pest damage. The shift from diversified, agricultural landscapes with patches of natural habitat to large monocultures that lack natural habitat has likely brought with it more severe pest outbreaks. High vegetation diversity ensures that specialist pests do not enjoy vast food resources (Matson *et al.*, 1997). Further, because not all crops and vegetation in natural habitat is palatable to pests, complex landscapes may inhibit pest movements and cause more localized outbreaks (Avelino *et al.*, 2012). However, natural habitat can sometimes provide pests with resources vital for completing their lifecycles and thus facilitate outbreaks (Chaplin-Kramer *et al.*, 2011b). For example, because aphids sequester chemicals in wild mustards (*Brassica nigra*) as antipredator defenses, the proximity of natural habitat with high mustard density may function to increase the density of aphids in nearby crop fields (Chaplin-Kramer *et al.*, 2011a).

Another critical consideration, however, is the predators of crop pests. Predators rely on natural habitat for essential activities, including breeding, roosting, foraging, and hibernating (Landis *et al.*, 2000; Jirinec *et al.*, 2011). Predator abundance and diversity thus regularly decline as agricultural landscapes shift from complex mosaics of natural habitat and cropland to simplified monocultures (Bianchi *et al.*, 2006; Chaplin-Kramer *et al.*, 2011b). Although diverse predator communities are not always more effective at providing pest control because predators sometimes consume each other (Vance-Chalcraft *et al.*, 2007), most studies report that more predator diversity translates to more effective pest control (Bianchi *et al.*, 2006; Letourneau *et al.*, 2009; Chaplin-Kramer *et al.*, 2011b).

An increasing number of studies have documented increased pest consumption in complex versus simple landscapes (Thies and Tscharntke, 1999; Gardiner *et al.*, 2009; Chaplin-Kramer and Kremen, 2013; Karp *et al.*, 2013). Fewer studies, however, have traced the benefit of maintaining natural habitat

all the way to crop yields and profits, but some have reported positive effects (Thies and Tscharntke, 1999; Karp *et al.*, 2013). Like pollination, the relevant scale for pest management can vary from predator to predator and from pest to pest, such that distant areas may determine the abundance of highly mobile animals (Werling and Gratton, 2010). Simply focusing on local agricultural practices may be ineffective. Because predator communities often collapse after harvest, a stream of colonizers from adjacent natural habitat may be required to replenish the predator community in the following year.

Landscape Effects on Agriculture: A Costa Rican Case Study

Tropical rainforest provides an array of ecosystem services, including water purification, water flow regulation (e.g., supporting hydropower production), carbon sequestration, and cultural services such as ecotourism. Recognizing this, in the mid-1990s the Costa Rican government created the first national payment for ecosystem services (PES) scheme, in which landowners were paid to maintain rainforest on their private lands (Sánchez-Azofeifa *et al.*, 2007). For farmers, the program provided the dual benefit of monetary compensation for uncultivated lands and continued provision of critical ecosystem services.

The canton of Coto Brus in Southern Costa Rica has been studied as a model system for how strategic conservation efforts influence agricultural production. Unlike many other parts of the country that now host vast expanses of pineapple, oil palm, or banana, Coto Brus still exists as a patchwork of coffee plantations, pasture, small rural villages, and tropical wet forest, perhaps a result of its hilly terrain (Mendenhall *et al.*, 2011). This complex configuration supports a remarkable concentration of biodiversity, often at par with native forest (Daily *et al.*, 2001; Mendenhall *et al.*, 2013). Coffee, the most extensively cultivated crop in the region, benefits from this biodiversity. Although coffee can self-pollinate, animal pollination increases yields, sometimes by more than 50% (Ricketts *et al.*, 2004). Because wild bees rely on rainforest habitat, coffee plants located near rainforest enjoy significantly higher pollination than sites in the middle of extensive plantations. Higher pollination translates to higher yields, better coffee quality, and increased profits. One study found that yields increased by 20% and misshaped 'peaberries' decreased by 27% within 1 km distance of two forest patches (Ricketts *et al.*, 2004). These benefits translated into a significant economic gain, approximately US$60 000 per year for a single coffee plantation.

Costa Rican coffee plantations also enjoy pest control benefits from forest patches. The coffee berry borer beetle (*Hypothenemus hampeii*), coffee's most damaging insect pest, arrived in Costa Rica in 2000 and the canton of Coto Brus in 2005 (Staver *et al.*, 2001). Not more than 5 years later, native birds had already expanded their diets to include the pest and began reducing infestation severity by half (Karp *et al.*, 2013). Like wild bees, many of the pest-eating birds rely on forest habitat, and pest control provision is higher on farms with more forest cover (Karp *et al.*, 2013). Small, unprotected forest patches embedded in coffee plantations provided the most benefits. Forest patches smaller than 1 ha area secured approximately 50% of the total pest control benefits across the Coto Brus valley (Figure 4).

Policies and Programs to Conserve and Enhance Ecosystem Services in Agricultural Landscapes

Growing interest in the management of ecosystem services has been matched, in recent years, by a proliferation of policy and programmatic strategies to promote the conservation or enhancement of these services in agricultural landscapes. Traditionally, environmental management policies were often described in terms of a dichotomy between regulatory instruments ('command and control' requirements put forth by governments) and market-based instruments focused on shifting incentives and price signals for farmers, businesses, and other market actors. However, this dichotomy is now understood to be too simplistic: not only have the boundaries

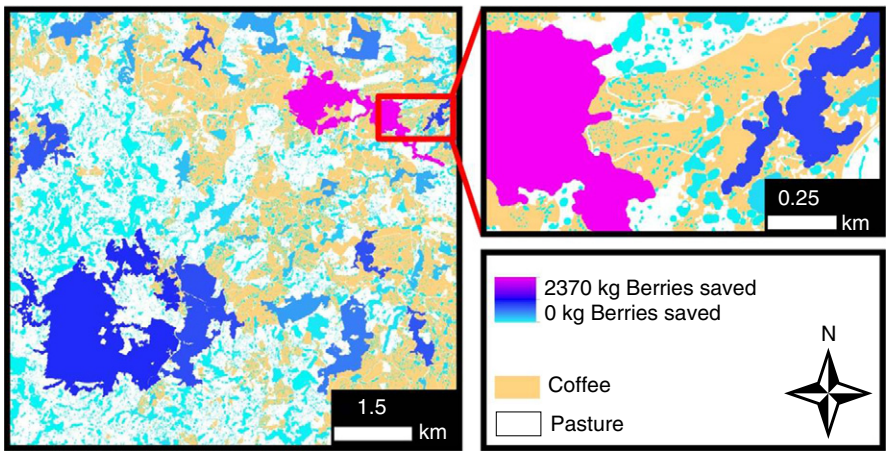


Figure 4 Pest control value of forest patches to coffee plantations in Southern Costa Rica forest provides habitat for the insectivorous birds that consume the coffee berry borer beetle (*Hypothenemus hampei*), coffee's most economically damaging insect pest. Maps show the estimated kilograms of coffee berries saved from infestation by each patch of forest across the Coto Brus Valley. Integrated together, the small, unprotected forest patches embedded within or adjacent to coffee plantations provided the majority of pest control value to coffee farmers.

between regulatory and market-based approaches blurred in many cases, but the range of market-based approaches has also proliferated to the point where further categorization is necessary (Lemos and Agrawal, 2006). This situation reflects a broader shift from the primacy of state institutions in environmental governance to the inclusion – and sometimes dominance – of other groups, including corporations, consumers, civil society organizations, and multinational organizations (Liverman, 2004).

Before describing the range of policy and programmatic strategies used to conserve and manage ecosystem services from agricultural landscapes, it is worth noting some challenges endemic to the governance of agricultural systems, which have limited the effectiveness of most if not all these strategies to varying degrees. First, in contrast to other ecosystem types that are major providers of ecosystem services (e.g., forests, wetlands, and water bodies), agricultural lands are predominately owned or managed by private individuals and companies, or in some instances collectively by rural communities. This means that government authorities generally cannot influence the use of these lands simply by adjusting management plans and policies for lands and water over which they have substantial control, as they might for a state-owned protected area or water body. Second, the historically private nature of agricultural enterprises means that there is little tradition of public sector regulation of agricultural activities, at least with regard to major agronomic decisions affecting ecosystem services, such as rural land use, tillage, planting, and soil fertility management.

Third, agricultural management systems are highly context-dependent (based on climate, soils, hydrology, and other factors), making it inappropriate to devise 'one size fits all' regulations and frequently inefficient to incentivize specific management practices, which may not be appropriate in all contexts. Fourth, most of the major ecosystem services and disservices from agriculture are 'nonpoint' in nature, meaning that they flow from the land itself, in heterogeneous patterns, and are, therefore, difficult to quantify, monitor, or regulate (Ribaudo *et al.*, 2010). In contrast, point source impacts, such as water withdrawals and factory emissions from a smokestack or effluent pipe, are much easier to monitor and regulate and have been the subject of many effective environmental regulations. Fifth, monitoring and enforcement in agricultural settings is always a challenge, given the dispersed, private nature of agricultural activities and the nonpoint nature of key ecosystem service outcomes. This is particularly so on the world's approximately 350 million small farms, where the transaction and administrative costs of policies and programs can become proportionately quite high.

Table 3 provides a basic typology of policies, programs, and instruments that may be used to conserve and enhance ecosystem services from agricultural landscapes. Each of these is described further below.

Government Regulation

Agriculture in most countries is a relatively lightly regulated enterprise when compared with other land uses, such as industrial facilities, mines, urban development, and even forestry. Land-use regulations restrict or prohibit agriculture in certain locales (e.g., protected areas, watershed conservation areas, and multiuse management zones) and in some instances aim to reduce the degree to which agriculture conflicts with the provision of important ecosystem services. On a broader scale, both Brazil and Indonesia have enacted temporary moratoria on deforestation for agricultural expansion, which have been credited with reducing the loss of ecosystem services associated with soybean and oil palm expansion, respectively (Macedo *et al.*, 2012). A limited number of regulation require on-farm protection of remaining natural ecosystems (e.g., remnant forest patches), or riparian buffers, recognizing their capacity to provide ecosystem services both within and beyond cultivated areas. Nonetheless, these regulations are quite limited overall, and, in many places where they exist, have been poorly enforced and widely ignored. A notable example is Brazil's Forest Code, which on paper requires farmers to establish mosaics of natural habitat within agricultural landscapes but in practice has been generally flaunted.

Regulation of certain farm inputs – particularly pesticides – is robust in many countries and may help to mitigate certain negative impacts of agriculture, including the negative off-site impacts on water quality. However, even where the most toxic pesticides are effectively regulated, use of other legal, but still toxic, pesticides may contribute to large aggregate impacts that diminish both water quality and habitat provision (Schiesari *et al.*, 2013). In particular, pesticide contamination can negatively affect the ecological communities in waterways, resulting in degradation or loss of the important services these communities provide (e.g., pest control services provided by mosquito fish in small channels near populated areas; fishing and other cultural services supported by rivers and streams).

Agriculture (and the ecosystem services it provides) may also be governed by broader regulations that apply across many sectors. However, these laws are not always applied fully in the context of farms and ranches. For instance, in the United States, agricultural operations enjoy a variety of statutory or de facto exemptions from otherwise strong environmental laws including the federal Clean Water Act, federal Endangered Species Act, and certain state endangered species acts. These exemptions highlight both the privileged political status that the agriculture sector enjoys in many countries and the difficulty in enforcing these types of laws in an agricultural context. They also underscore the need for interventions focused on ecosystem services that support rather than compromise production functions.

Market-Based Instruments

In the context of policy options, the term 'market-based' is used broadly to refer to strategies that seek to influence behavior by adjusting the price signals to various market actors, including farmers, corporations, and consumers. Such instruments are often intended to remedy 'market failures' that can occur when the providers of ecosystem services do not reap the full benefit of delivering these services, or when they avoid bearing the full cost when they diminish these services. For instance, farmers usually receive little or no monetary benefit from protecting wildlife habitat, although this is an important

Table 3 Typology of policies, programs, and instruments that may be used to conserve and enhance ecosystem services from agricultural landscapes

Type of policy, program, or instrument	*Level of state involvement*	*Role of farmers*	*Examples*
Government regulation ('command and control')			
Land use regulations	High (set and enforce regulations)	Subject of regulations	Land-use zoning; temporary moratoria; riparian buffer zone requirements
Regulation of agricultural inputs			Bans and restrictions on use of certain pesticides; prohibition on planting genetically modified organisms
Regulation of other agricultural practices			Good agricultural practices regulations focused on food safety
Other regulations affecting agricultural lands			Regulations on water, wetlands, and endangered species
Market-based instruments (*influencing price signals or incentive structures*)			
Taxes and subsidies	High (establish tax and subsidy policies)	Payer of taxes or recipient of subsidies	Earning tax credits for best management practices (e.g., Resource Enhancement and Protection Program in PA, USA) subsidies for no-till planters
Markets formed through regulation (e.g., cap-and-trade), leading to PES	Moderate to high (set regulations and oversee market)	Buyers or sellers of ecosystem services, where required or eligible to participate	Water quality trading, regulated carbon markets
Public sector PES	High (deploy funds and administer PES program)	Sellers of ecosystem services	Agri-environment payments (Europe), Farm Bill environmental programs (USA)
Private and voluntary PES	None or low	Buyers or sellers of ecosystem services	Various watershed, biodiversity, and carbon PES involving farmers
Eco-standards and certification	None to moderate	Sellers of agricultural goods produced in accordance with eco-standards	IFC Performance Standards, Rainforest Alliance, and Roundtable on Sustainable Palm Oil
Rural development and farmer assistance programs			
Technical assistance and cost-share programs	None to high (some programs are funded or run by the public sector, others by private or civil society entities)	Program participants and beneficiaries	Farm Bill programs for conservation measures on US farms
Education and training programs			Conservation Farming Unit (Zambia)
Rural development projects and programs			Sustainable Land Management investments (Global Environmental Facility/World Bank)

Note: Some of these instruments also serve additional aims or are not always used to manage ecosystem services in agricultural landscapes. The abbreviation PES stands for payment for ecosystem services.

public benefit. Conversely, when fertilizer runoff from farms contributes to downstream eutrophication and its attendant environmental and economic harms, the farmers responsible for these harms usually bear no economic consequences. Market-based instruments can address such environmental 'externalities,' which would otherwise result in suboptimal delivery of or investment in the provision of ecosystem services.

The most long-standing types of market-based instruments are various forms of taxes and subsidies, which are deployed across many different economic sectors, including agriculture. Historically, agricultural subsidies (e.g., for fertilizer inputs) played a significant role in promoting both the expansion and intensification of agriculture to the significant detriment of ecosystem services. However, taxes and subsidies can also promote conservation-friendly agriculture that may deliver increased levels of ecosystem services. For instance, in Kazakhstan, the government in 2008 began subsidizing farmers to adopt conservation agriculture technologies – including continuous soil cover, direct seeding, and no-till management – that are credited with helping to increase farmer yields and profitability while reducing soil erosion.

PES are abroad set of market-based instruments that have proliferated since the mid-1990s to channel new investment in ecosystem services. Formally, PES has been defined as voluntary transactions between ecosystem service seller(s) (such as farmers or other land managers) and ecosystem service buyer (s) (such as water users or conservation organizations) that provide cash or other payment in exchange for the provision of specific defined ecosystem services (Engel *et al.*, 2008). In practice, however, many PES schemes do not conform to this definition, for instance, because they do not target specific

ecosystem services or make payments contingent on actual delivery of these services (Muradian *et al.*, 2010). For instance, many publicly administered PES schemes – including those in Costa Rica, Mexico, Europe, and the United States – function more like environmentally focused farmer subsidy programs than true conditional payments targeted to deliver the largest quantity of ecosystem services for the least cost.

Ecosystem service payments that involve the creation of open markets (as opposed to government payments) are likely to more closely resemble market-based instruments in the classic sense of the term. In the United States and other countries, such markets have been established through regulations that cap total levels of pollution or degradation to a given ecosystem or ecosystem type but enable landowners to trade the limited allocated rights to pollute or degrade. Such 'cap-and-trade' mechanisms are intended to reduce the overall cost of achieving specific environmental goals and have resulted in robust markets for wetland mitigation, wildlife habitat, and agricultural runoff, among other ecosystem services and disservices. Truly voluntary private markets for ecosystem services involving farmers as ecosystem service sellers have also developed in places, although on a smaller scale. These markets have formed around carbon sequestration, watershed conservation, and biodiversity protection, with buyers ranging from private companies (e.g., water bottling businesses), to individuals and corporations wishing to offset their carbon emissions, to conservation organizations.

On a global scale, PES makes only a modest contribution to incentivizing increased ecosystem service delivery from agricultural landscapes. However, this contribution is proportionately much larger in the United States, Europe, and China, where large government PES programs – totaling perhaps US$20 billion per year – exist to support watershed protection, biodiversity conservation, and esthetic protection ('landscape beauty') services (Milder *et al.*, 2010). The future size of ecosystem service markets affecting farmers remains uncertain: although it is clear that farmers deliver critical ecosystem services to a wide range of stakeholders, it is not clear whether these beneficiaries will actually be willing to pay for such services on a large scale, or whether markets will be formed that support the cost-effective procurement and management of these services. The future regulation of greenhouse gas emissions (or lack thereof) at national or global level is a critical factor, as farmers stand to participate heavily in carbon markets if they coalesce at full scale.

Experience from a wide range of contexts suggests that PES in agricultural landscapes is likely to be most effective and scalable where management practices that sustain or increase ecosystem service delivery also support agricultural productivity or profitability. In these situations, PES can provide farmers with supplemental revenue that helps them to overcome initial investment barriers or other constraints to adopting more conservation-friendly management practices (FAO, 2007; Majanen *et al.*, 2011). However, where there is a high opportunity cost to manage agricultural landscapes for increased levels of ecosystem services, PES schemes are unlikely to be able to compete with the profitability of environmentally destructive farming and will find few willing sellers of ecosystem services. A prime example is at the agricultural frontiers of major commodity crops, such as palm oil (Southeast Asia), where levels of carbon payments supported by ecosystem service markets may provide insufficient incentive to prevent deforestation and the significant loss of ecosystem services (Fisher *et al.*, 2011).

A final market-based instrument is the adoption and use of voluntary sustainability standards – often called 'eco-standards' – and associated 'eco-certification' labels for agricultural products and investments. Agricultural sustainability standards are sets of social and environmental criteria put forth to define and encourage sustainable farming by providing market recognition for sustainable producers. These include standards developed and managed by nonprofit organizations (e.g., Fairtade, Rainforest Alliance, and UTZ Certified), multi-stakeholder 'roundtables' for various commodities (e.g., for soybeans, palm oil, sugar, beef, and cotton), individual food companies (e.g., Unilever, Nestlé, Mars, and others), and the finance sector (e.g., IFC Performance Standards and the Equator Principles). By participating in such schemes, farmers, traders, and food companies that produce and sell certified products may benefit from improved market access or market share, price premiums, or improved legitimacy and reputation in the eyes of consumers and regulators. Most, if not all, agricultural sustainability standards include provisions intended to help conserve biodiversity, including sensitive habitat that supports organisms of conservation concern, and ecosystem services (e.g., water purification and water flow regulation and soil fertility and erosion control) (UNEP-WCMC, 2011). Thus, e co-certification may provide monetary incentives for farmers to maintain or enhance ecosystem services, although such incentives are not necessarily explicit or direct with respect to specific ecosystem services.

Rural Development and Farmer Assistance Programs

Governments, international donors, civil society organizations, and others have been involved for decades in supporting agricultural development around the world. In the past 10–15 years, an increasing proportion of these efforts have begun to orient program objectives and activities toward maintaining or increasing flows of ecosystem services in concert with increased yields and farmer profitability. Some initiatives, particularly in developed countries, provide technical assistance, farmer training, or cost sharing of on-farm investments to reduce the negative environmental impacts of agriculture. For instance, a variety of programs funded under the US Farm Bill provide technical assistance and cost sharing for practices such as improved water management structures, erosion control practices, integrated pest management, and transitioning to organic practices.

In the developing world, agricultural development efforts that strongly integrate ecosystem management have been advanced under a variety of names and approaches. A 2006 review surveyed 286 such interventions covering a total of 37 million hectares and found evidence of substantial increases in crop yields together with water-use efficiency gains and potential gains for carbon sequestration and other ecosystem services (Pretty *et al.*, 2006). More recently, the World Bank and other multilateral institutions have supported 'sustainable land management' programs in dryland regions of dozens of countries to enable farmers and pastoralists to increase

productivity while conserving water, forests, and other natural resources on which rural livelihoods depend (World Bank, 2008b). The recent dialog around 'climate-smart agriculture' prioritizes the conservation of ecosystem services that help to build resilience in agroecosystems (e.g., water flow regulation, flood control, water storage, and erosion protection) and allow farmers to maintain food production in changing or extreme weather conditions as well as access other livelihood resources if crops fail. In addition, climate-smart agriculture promotes climate change mitigation through carbon sequestration in farm soils and vegetation as well as reduction of greenhouse gas emissions from sources such as livestock, rice paddies, and soil denitrification.

Knowledge Gaps

Although scientific understanding of ecosystem services and their biological mediators in agricultural landscapes has grown dramatically in the past couple of decades, several critical knowledge gaps remain.

First, there is a need to develop mechanistic understanding of the organisms, guilds, and ecological communities that provide ecosystem services (Kremen and Ostfeld, 2005; Kremen, 2005). Identifying key ecosystem service providers and understanding their requirements for performing the biological functions that underpin service delivery are essential for effective management of agroecosystems that deliver both sustained crop yield and ecosystem services. However, to date, these biological requirements are known for only a small subset of key ecosystem service providers (e.g., area requirements for pollination by native bees; Kremen *et al.*, 2004). Second, there are relatively few studies that examine quantitative measures of yield and ecosystem services in the same system (Milder *et al.*, 2012). For instance, although recent metareviews have included 300 or more comparisons of yield effects relative to conventional systems (e.g., Seufert *et al.*, 2012), relatively few studies provide rigorous data on paired outcomes for yield as well as ecosystem services. A third knowledge gap is the lack of studies that link management practices to ecosystem service outcomes at multiple scales. Measuring the spatial and temporal scales over which ecosystem service providers deliver key services is imperative to addressing this gap (Kremen and Ostfeld, 2005). Specifically, building understanding of how ecosystem functions are influenced by the species and communities within an area is needed to understand how their attributes and services can aggregate at different scales from cultivated fields to broader regions, including cultivated and noncultivated areas.

Addressing these knowledge gaps is essential to designing and managing multifunctional agroecosystems. Continued work on this front is needed to answer the growing call for agricultural landscapes that can simultaneously meet production and conservation goals.

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Biodiversity: Conserving Biodiversity in Agroecosystems

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Glossary

Biochory Passive, unintentional transport of spores, eggs, microbial cells, or small animals by organisms that move in the litter and soil, thereby promoting the dispersal of almost immobile organisms.

Bioturbation Soil mixing carried out by organisms in soils, mainly earthworms, termites, and ants, plus a few Coleoptera, nymphal Cicadidae, Isopoda, or Grylotalpidae ('mole crickets'). Bioturbation may be effected by ingesting the soil and passing it through the animal gut (earthworms and humivorous termites), or by constructing mounds, digging galleries and chambers to accommodate colonies and food reserves (ants and foraging and fungus-growing termites). Roots also affect some degree of bioturbation through creating holes that are further used by other organisms as habitats and passageways for movement once the root has died and disappeared.

Catena of soils A succession of soils arrayed down a slope, with profiles changing according to their topographic position. The low-lying parts of the catena generally have a higher moisture status and receive elements eluviated, detached, and transported from the higher parts. The upper parts of the catena may become depleted in clay and nutrients by these processes.

Chemolithotrophy The ability to use energy obtained by the oxidation of inorganic compounds.

Comminution The physical transformation of leaf and root litter with limited chemical (digestive) decomposition. This is an essential process in litter recycling whereby large plant-derived structures, such as leaves, are progressively fragmented into increasingly smaller pieces, thereby increasing the surface area exposed to microbial attack.

Drilosphere A word coined by Bouché (1972) that describes the 'functional domain' created within soil by earthworms ('drilos' in Greek) and is analogous to the well-recognized 'rhizosphere,' the sphere of influence of roots. The drilosphere is thus the sum of earthworms and the structures that they create in soil as casts, galleries, and pores of different sizes and shapes, together with the communities of smaller organisms, invertebrates, and microorganisms that inhabit the habitats thus constructed. The earthworm gut is the critical component of the drilosphere in which earthworm digestion in conjunction with microorganism activity provides the energy necessary to maintain this structure.

Geophagous An organism that ingests soil. Endogeic earthworms and humivorous termites are the main groups using this feeding regime. They actually digest the organic part of the soil, in a mutualistic association with the ingested microflora. The activity of the microflora is greatly enhanced during gut transit and makes part (usually some 10%) of the ingested organic matter available to the earthworm as a product of microbial digestions. A further fraction, as yet unevaluated, is converted into microbial biomass.

Inoculation (with microorganisms, invertebrates, or plants) Addition to the soil of an organism that is absent or present in such low quantities that its effect on, for example, soil structural formation or plant protection is no longer observed. Inoculations are possible only if suitable conditions are present. Re-inoculating an organism that has disappeared from the environment due to impairment of its natural living conditions requires restoration of these conditions. Inoculation of exotic species of microorganisms or invertebrates is often rendered impossible through competition or other effects of local species, an important point to consider when trying to improve plant growth by using microbial supplements and inoculates.

Mineralization/immobilization When microorganisms use a substrate to meet their maintenance and growth needs, they secrete enzymes that degrade the substrate and absorb the metabolites thus made assimilable. Nutrients are absorbed according to the needs of the organism in proportions that can be fixed or variable. When nutrients are assimilated in excess, they are secreted into the external medium in mineral forms as, for example, NH_4 or NO'_3 for nitrogen. When the element is deficient in the substrate used, microorganisms use whatever source of the element that occurs in the soil in mineral form. The result is a decrease in concentration of this mineral element and is referred to as immobilization within the microbial biomass.

Protocooperation An association between microbial and other communities that allows the degradation of a substrate which they would not be capable of degrading alone.

Stoichiometric imbalances Occur when the composition of assimilable nutrients in a food source is so different from their relative tissue concentrations that growth of organisms using this resource becomes dependent on the concentration of the most limiting nutrient.

Theca The external skeleton of some Protoctists of the thecamaebian group and formed from silica. This often sub-spherical envelope protects the organism from predators and drought.

Introduction

The Green Revolution boosted agricultural production approximately 2.5 times and was associated with an approximately 40% price reduction in the cost of food (MA, 2005). Following on the euphoria of this success there has been increasing pressure to diversify production and to improve the planet's environment (Hubert *et al.*, 2010). Successful realization of this pressure will require better soil management. However, current conditions are very different from what they were 50 years ago. The success of the Green Revolution came at the expense of the natural capital, such that 18 of the 24 currently acknowledged ecosystem services have been impaired. Although soils have aided climate regulation by sequestering an estimated 2 Gt carbon (C) per annum from fossil fuel burning, they have lost part of their capacity to regulate hydrological fluxes and nutrient cycles and therefore to support plant production.

The soils of the earth are now being asked to produce 70% more food over the next 35 years, while also producing biofuels, regulating climate through further C sequestration, and helping to conserve biodiversity. However, the other side of this coin is the declining amount of land remaining available for conversion to agroecosystems and the increased cost of energy, which has led to a substantial increase in the price of fertilizers. Further, world sources of phosphorus (P) are being rapidly depleted and the toxic effects of pesticides are now forcing the replacement of these former pillars of intensive agriculture with new technical options.

Agriculture now needs to sustain high levels of production while preserving or restoring the natural capital of the soil. Maintenance of an appropriate level of soil biodiversity is critical to achieving this goal, but in order to protect the soil resource and optimize its long-term use, new land use practices are needed to be developed, based on much greater understanding of the factors controlling its functioning.

This article summarizes the current knowledge of the composition and taxonomic richness of the soil biota. It then examines the participation of the soil biota in the major soil functions and discusses ways to reconcile the conservation and/or improvement of this natural capital with the production of critical ecosystem goods and services.

Components of Soil Biodiversity

Soils were the first terrestrial biotope to be colonized from the marine environment. Hence, they have retained a large component of aquatic organisms in their water-filled pore spaces while evolution has progressively added aerial organisms adapted to living within the soil air spaces. Several hundred millions of years of continuous evolution in this confined environment has conserved some of the most primitive forms of life. It has also created novel associations among organisms with no equivalents in less-constraining parts of the ecosystem.

General Constraints to Life in the Soil Habitat

Life in soil is constrained by three major soil features (Lavelle and Spain, 2001; Lavelle, 2012):

1. A compact soil matrix that possesses few open pores as habitat and limited systems of connected pores, thereby constraining internal flows of air and water;
2. Low-quality food, composed of dead leaves and roots rich in decomposition-resistant polyphenolic compounds, humified and stabilized organic matter, living roots, and other organisms; and
3. Variable moisture conditions that result in the alternation of flooding and drought at the scale of a soil pore, with increasing incidence of saturated anaerobic conditions as pore size decreases.

No single group of soil organisms has been able to adapt optimally to living with all these constraints. Although the smallest microorganisms find relatively constant conditions in the water-filled pores, they have a very limited ability to remain active in aerial conditions. Consequently, once they have exhausted their existing substrate they enter a resting stage – most commonly as a spore or a small dormant bacterial colony. Thus, soil-based microorganisms frequently exist in dormant stages; however, fungi are more active and may be more readily transported by biotic or abiotic agents than bacteria (Lavelle and Spain, 2001). Fungal hyphae, able to cross between pores without water, are generally better adapted to higher water potentials than bacteria, which makes them more tolerant of water deficit. They often rely on invertebrates for the dispersion of their spores (Lavelle and Spain, 2001).

Dormant microorganisms can resume activity when such physical or biological agents as water flows and disturbance caused by mixing, bioturbation, or biochory by roots and invertebrates move microorganisms toward a new source of food. For example, spores of mycorrhizal fungi may be activated when they come into contact with root exudates, leading to the initiation of a mutualistic symbiosis with the host plant. Through this association, a continuous supply of plant-derived carbon substrates is supplied to the fungus, which provides the energy for it to actively colonize the soil and so provide its host plant with soil-derived nutrients (Smith and Read, 2008).

In contrast to microorganisms, large soil invertebrates of the 'soil ecosystem engineer' group, which are principally termites, earthworms, ants, and some Coleoptera and Isopoda, have developed the ability to move and work the soil (bioturbation). This is achieved either by digging with strong legs or mandibles or, as in the case of earthworms, by ingesting the soil and compacting it with their hydrostatic skeleton. These invertebrates, however, have very limited abilities to digest litter and soil resources on their own and consequently interact with microorganisms to take advantage of their outstanding capacities for digestion.

Adaptive Strategies of Soil Fauna

The primary indicator of general adaptive strategy is size (**Figure 1**: Decaëns, 2010 after Swift *et al.*, 1979).

The smallest animals – micro-fauna – are invertebrates smaller than 0.2 mm. They are the predators of the microorganisms and principally comprise proctoctists, nematodes, and a number of groups of lesser importance, such as tardigrades and rotifers. Most of the micro-fauna consume fungi or bacteria and are, therefore, referred to as 'microbial grazers.'

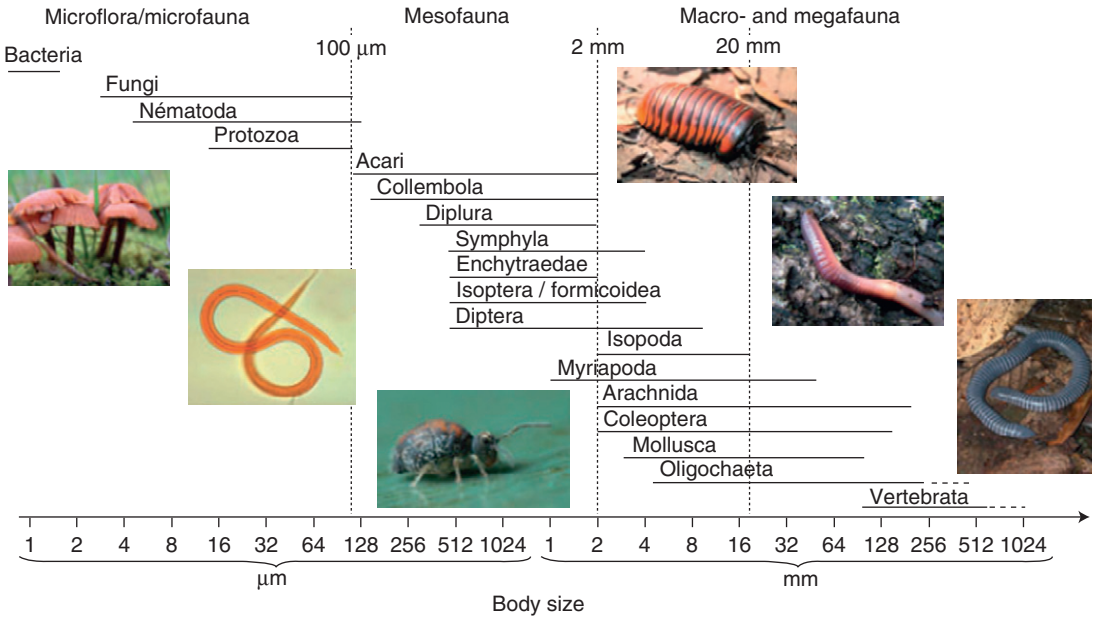


Figure 1 Representation of the main taxonomic groups of soil organisms on a body size basis. Reproduced from Decaëns, T., 2010. Macroecological patterns in soil communities. Global Ecology and Biogeography 19, 287–302 after Swift, M.J., Heal, O.W., Anderson, J.M., 1979. Decomposition in Terrestrial Ecosystems. Oxford: Blackwell Scientific.

They exert the primary control of microbial populations and communities. As a result of stoichiometric imbalances, they excrete available forms of mineral nitrogen (N) and other nutrients into the soil solution. Consequently, the complex foodwebs that they form are of great importance to the biological control of microbes and to soil organic matter (SOM) dynamics and the cycling of nutrients (Moore *et al.*, 2004). This is especially true in ecosystems where arid conditions, deep disturbance, or agrichemical stress restrains the activities of larger invertebrates. Such foodwebs based on microbial grazing are of lesser relative importance in natural ecosystems where ecosystem engineers have large populations (Wardle and Lavelle, 1997; Lavelle *et al.*, 2006).

The next group, the meso-fauna, and some large litter-dwelling invertebrates feed on above- and below-ground dead plant material. The comminution and limited digestive processes that they carry out allow some degree of composting. They have been called 'litter transformers' and they accelerate nutrient release on short time scales. Commonly, their fecal pellets are subjected to microbial incubation, thereby releasing assimilable compounds, which will then be consumed by themselves or other invertebrates. This is known as 'external rumen digestion' (Swift *et al.*, 1979; Hassall and Rushton, 1985). Alternatively, the released nutrients may be utilized by microorganisms, thus increasing the microbial biomass.

The largest invertebrates are the 'soil ecosystem engineers.' Members of this group have developed the most efficient interaction with microorganisms and have a sophisticated mutualistic digestion system contained within their own gut (Lavelle *et al.*, 1995). Efficient digestion allows the capture of the large amounts of energy required to ingest several times their own weight of soil daily or to dig dense gallery networks (Lavelle *et al.*, 1997). Where ecosystem engineers are active, the entire upper 10–15 cm of soil may be ingested over the course of a couple of years. This creates a macro-aggregated structure that has highly favorable physical properties, providing resistance to erosion and the promotion of water infiltration and storage. Many ants are, however, predators and are clearly an exception to the above. The 'leaf cutter ants' in particular, and some termites, enter into 'external rumen' relationships with microorganisms; some termites also produce an efficient suite of enzymes in their mid guts.

The correspondence between invertebrate size and function tends to spread their activities across a number of well-separated and discrete scales. The proximate control of microbial communities and their activities by micro-foodwebs occurs mainly within pores and aggregates 50–100 µm in size (Hattori and Hattori, 1976). Litter transformers, however, vary in size from mm to cm and operate at larger scales in the leaf or root litter. The ecosystem engineers operate at even larger scales (from cm to >m), creating structures such as ant or termite colonies, or patches where earthworm populations dominate (Ettema and Wardle, 2002; Rossi, 2003; **Table 1**).

Different Groups and Their Respective Species Richnesses at Local and Global Scales

Although soil biodiversity comprises a large part of global diversity, no precise data are available (**Figure 2**). Recent estimates of total diversity suggest that both bacteria and fungi may each comprise as many as 1.5 million species.

Generally, many of the larger organisms represented in the soil biodiversity have been described, but estimates suggest that only 0.1% of species in the micro-fauna and micro-organisms have been described so far (Decaëns, 2010; Wurst *et al.*, 2012).

Another interesting feature of soil organisms is the relative rate of endemism – measured by the local α, to regional β, or

Table 1 Main parameters of the adaptive strategies of organisms in soils

Functional group	*Microorganisms*	*Micro-fauna*	*Meso-fauna*	*Macrofauna*
Body width	0.3–20 mm	$<$0.2 mm	0.2–10 mm	$>$10 mm
Taxa	Bacteria and fungi	Proctoctists nematodes	Microarthropods Enchytraeidae	Termites earthworms myriapoda, ants, etc.
Water relationships	Hydrobiont	Hydrobiont	Hygrobiont	Hygrobiont
Interactions with microorganisms	Antibiosis mutualism competition	Predation	Predation	Mutualism (external rumen and facultative/obligate internal mutualism)
Ability to change the physical environment	Very limited	None	Limited (fecal pellets)	High (galleries, burrows, and macro-aggregates)
Resistance to environmental stresses	High (cysts, spores, etc.)	High (cysts, spores, etc.)	Intermediate	Low but possible behavioral compensation
Intrinsic digestive capabilities	High	Intermediate	Low	Low

Source: Reproduced from Lavelle, P., Spain, A.V., 2001. Soil Ecology. Amsterdam: Kluwer Scientific Publications.

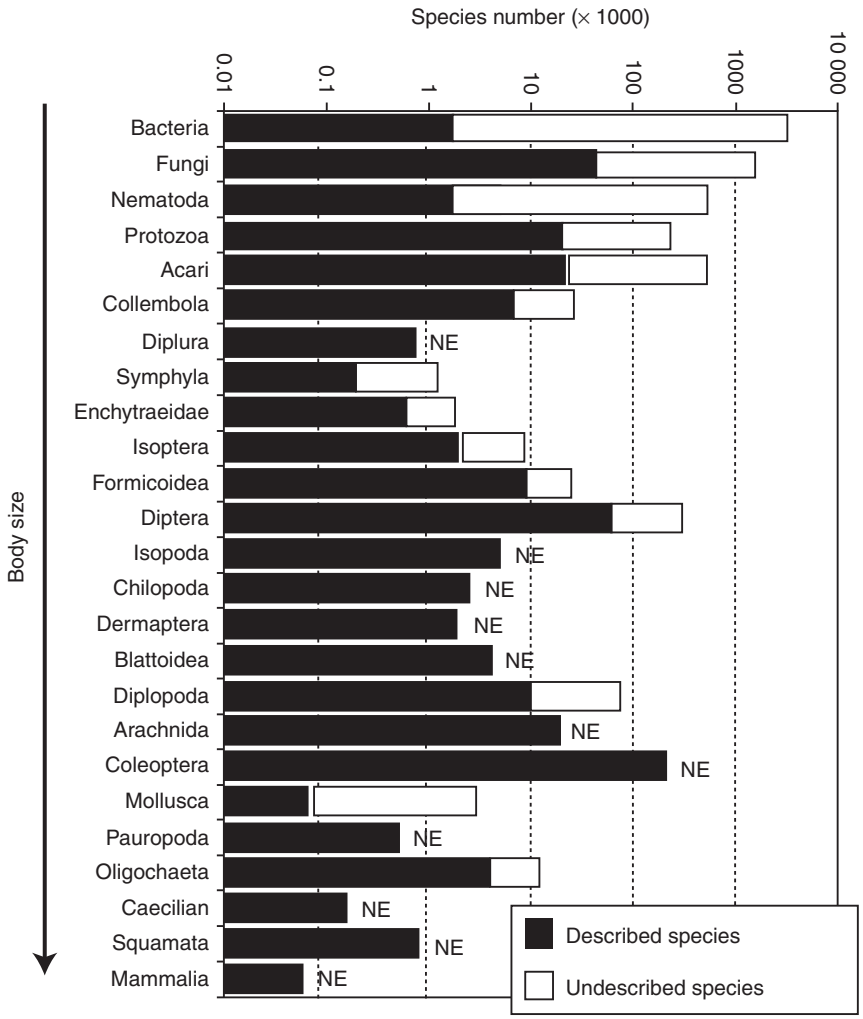


Figure 2 Biodiversity range in dominant soil-dwelling organisms. NE, not estimated. Reproduced from Decaëns, T., 2010. Macroecological patterns in soil communities. Global Ecology and Biogeography 19, 287–302.

global γ diversity. Generally the smallest microorganisms/microflora have the largest worldwide distributions. The arbuscular mycorrhizal fungi, for example, are relatively ubiquitous, and a significant proportion of the known species may be found at a single site (e.g., 33% in Amazonia) (Stürmer and Siqueira, 2011). Earthworms, however, have very high rates of endemism and two points separated by 500–1000 km have little chance of sharing common species; nonetheless, a small set of populous species may be found almost everywhere (Lavelle and Lapied, 2003).

Organization of Soil Biodiversity

Species of the same taxonomical group (families or orders) can adapt to soil conditions in different ways and so belong to different functional groups; the number and relative importance of which represent their functional diversity. To avoid competition, communities typically adapt during the course of evolution with limited niche overlap among species.

However, adaptation to soil conditions has led organisms to develop interactions with other organisms of different taxonomic groups at the same site. For example, earthworms depend on interactions with microflora for their digestion, whereas microorganisms are dependent on bioturbation and the habitats created by earthworms to resume activity after periods of dormancy in microsites where organic substrates were exhausted or out of reach. Similarly, small invertebrates, microorganisms, and the roots of plants occupy these nutrient-rich habitats created by earthworms and other ecosystem engineers. Roots usually follow earthworm galleries and fine roots tend to concentrate in fresh casts, which sometimes have high concentrations of easily absorbed nutrients and even growth hormones

As a result, the presence and abundance of populations of a given species may be as dependent on its relationships with species of the same functional group within a community of species of the same family or order ('horizontal biodiversity'), as with soil organisms of other functional groups (the 'vertical biodiversity').

Within-group diversity: Functional groups

Communities of a given functional group of soil-dwelling organisms are comprised of populations with well-developed functional differences. In each group, functional classifications have been produced to describe niche partitioning among different species and the diversity of functions that they fulfill (Table 2).

Microorganisms, such as fungi, bacteria, and archaea, are responsible for more than 90% of the chemical transformations associated with organic matter decomposition and nutrient cycling. They can be classified according to the range of their abilities to digest and degrade specific chemical substrates ranging from easily assimilated glucids and proteins to complex humic and phenolic molecules that require very specific metabolic abilities. Simple molecules, like glucose, may be metabolized by most microorganisms, whereas the most complex ones, including cellulose and starch, are used by fewer species, usually fungi and actinobacteria. Finally, the phenol–protein complexes that comprise 85% of dead leaf and root nitrogen may only be decomposed by a few basidiomycetes of the 'white-rot' fungal group (Lavelle and Spain, 2001; Kadimaliev *et al.*, 2010). Methanotrophs and methylobacteria use substrates with only one molecule of carbon, whereas cellulolytic bacteria are able to decompose cellulose polymers that have thousands of carbon molecules. Only a few soil arthropods and earthworms have efficient cellulolytic enzymes and are able to digest cellulose because of symbiotic interactions with microorganisms in their guts. Complex substrates are usually degraded by consortiums of diverse microorganisms (Zanaroli *et al.*, 2010) in protocooperative interactions. The nutrient composition of organic matter, specifically expressed by the C:N, C:P, and C:S ratios, also plays an important role in the processes of mineralization or immobilization in organic molecules of nutrients within the soil. Mineralization requires high relative concentrations of nutrients (e.g., C:N ratio < 20) and is inhibited when nutrient deficiencies limit the growth and activities of the decomposers.

Another functional classification of microorganisms is based on their mode of respiration: aerobic, anaerobic, or microaerophilic. This reflects their capacities to be active in different oxygen environments.

Finally, the decomposition of organic matter is associated with numerous biochemical reactions linked to the nutrient cycles mediated by microorganisms, principally bacteria. For example, chemolithotrophy is the ability to use the energy obtained by the oxidation of inorganic compounds; thus chemolithotrophs mediate reactions that are important steps in nutrient cycles, such as nitrification, denitrification, methanogenesis, and the use of reduced sulfur, copper, iron, and other

Table 2 Major functional groups in some groups of soil-dwelling organisms

Taxa	*Functional groups*					*References*
Bacteria	Bacteria	Carbon cycle: e.g., photosynthetic, methanogenic, methylotrophs, and celulolitic	N cycle: e.g., N2 fixers, nitrifiers, amonifiers, and denitrifiers	P, K, Ca, and Mg: Solubilizers	S: Oxidation of sulfur, thiosulphate, tetrathionate or sulphides Reduction of sulfate ions to hydrogen sulfide	Moreira and Cassia (2013)
Fungi	Antagonists	Saprophytes	Symbiotic	Pathogenic		Wainwright (1988)
Nematodes	Bacterivores	Fungivores	Root feeders	Carnivores	Mixed feeders	Banage (1966)
Collembola	Epiedaphic	Hemiedaphic	Euedaphic			Gisin (1943)
Acari	12 groups based on: Occurrence of phoresy, feeding habits, demography, and type of reproduction					Siepel (1994)
Earthworms	Epigeic	Anecic	Endogeic			Bouché (1977)
Termites	Wood feeders	Fungus growers	Humivores	Litter feeders		Waller and LaFage (1987)
Ants	Omnivorous	Predators	Fungus growers	Homoptera breeders		Korasaki *et al.* (2013)

minerals. As an example, biological nitrogen fixation and the reduction of N_2 to NH_3 is mediated by some specialist bacteria.

Invertebrate functional classifications reflect their responses to the three main constraints they face in the soil.

Micro-fauna (protoctists, nematodes, and a few other groups generally of a size $<200\ \mu m$) are mainly predators of microbes and other smaller invertebrates or herbivores. They are aquatic organisms that have no ability to create habitats in soil by digging, or bioturbation. They survive dry periods with a large variety of extraordinarily efficient mechanisms involving dormancy in different forms (spores, cysts, and desiccated individuals) (Lavelle and Spain, 2001).

Protoctists comprise three main taxonomic groups: ciliates, amoebae, and flagellates. Each group is characterized by different capacities to resist drought: amoebae, for example, can be more active than other proctoctists, because they can enter very small pores and shelter in theca that they secrete.

Nematodes are classified according to their feeding regimes (trophic groups): plant parasites, bacterivores (bacterial feeders), fungivores (fungal feeders), predators, and omnivores (Bongers, 1990). The relative proportion of 'persisters,' with relatively slow population turnover (k strategists), to 'colonizers,' with highly active turnover (r strategists), has been used to calculate the 'maturity index' of soils. It is considered a reliable indicator of the state of a soil and includes all soil nematodes except the plant parasites. A high maturity value indicates a low level of soil general stress due to drought, or nutrient deficiency, whereas a low value denotes high soil disturbance and difficult conditions for life, such as those generally found in soils subject to intensive agriculture (Bongers, 1990).

Ecosystem Engineers

Earthworms have been classified into three groups (epigeics, endogeics, and anecics) according to their main feeding habits and habitats. A suite of biological traits (morphology, anatomy, feeding regime, and demographic profile) is associated with these basic adaptive strategies. Epigeics are very active, small, and thoroughly pigmented earthworms that feed on fresh leaf litter and live within the surface litter itself. Their small size and use of a relatively rich food allow fast growth and active reproduction, a necessary demographic strategy in the face of high mortality from predators and the unstable moisture conditions that occur within their habitat. In contrast, Endogeics live in the soil and feed on it, having a purely geophagous regime based on the consumption of soils of high (polyhumic), medium (mesohumics), or low (oligohumics) organic matter contents (Lavelle, 1983). Anecics are very large earthworms ($>$ 20 cm in length) with an anterodorsal pigmentation. They live in vertical galleries that open at the soil surface and feed on a mixture of partly decomposed leaves and soil. The conditions of the humid tropics favor communities of large dominant mesohumic and oligohumic endogeic populations, whereas with the declining temperature the proportion of epigeics and polyhumics increases. The decrease in the efficiency at lower temperatures of the mutualistic digestion based on interactions with ingested soil bacteria (Barois and Lavelle, 1986; Lavelle, 1983) forces earthworms to rely on higher quality resources, thus favoring litter feeders rather than geophagous organisms.

In cropped agroecosystems, earthworm populations often decline as survival, growth, and reproduction are severely affected by the general decrease in organic resources or the unfavorable temperature and moisture conditions during the frequent periods when tilled soil is bare or treated with pesticides. Thus, in intensive European cropping systems, endogeics may become dominant, as long as the intensification does not exceed a still to be identified degree. Permanent pastures are often the habitat of large communities of anecics (Lavelle and Spain, 2001).

Ants have been classified according to several criteria: feeding regime (herbivores feeding on grains or cultivated fungi, aphid growers, and carnivores (Korasaki *et al.*, 2013); behavior (dominant or submissive); habitat (soil 'cryptic' or tree dwelling); or whether they are specialists or generalists (Andersen, 1995). For practical field work, ants can be classified into six main categories: subterranean carnivores (specialists or generalists); litter-based carnivores (specialists or generalists); arboreal/epigeic carnivores (specialists or generalists); subterranean herbivores; litter-based herbivores; or arboreal/epigeic herbivores (Bignell *et al.*, 2008).

Termites have been classified according to their feeding behaviors with additional subdivisions based on the nature and location of the nest.

Self-organization between groups across five-size scales

Self-organization that creates interactions among organisms of different types, with complementary functions, results in the concentration of biological activities at different scales, nested into one another (Lavelle *et al.*, 2006). Five relevant scales of physical structure have thus been identified with regard to soil physical organization (**Figure 3**). At each scale, interactions among organisms of one or more groups develop within the boundaries of structures, such as biofilms, meso-aggregates, or the accumulations of biogenic structures of invertebrate ecosystem engineers (Lavelle *et al.*, 2006). Structures at Scale 1 are generally embedded into larger scale structures made or inhabited by larger organisms that organize space on larger scales. For example, the rhizosphere, at Scale 3, hosts structures of Scale 1 (the bacterial colonies that develop at the surface of the root) and Scale 2 with communities of micropredators and the microenvironment in which they live.

Although these scales are implicitly acknowledged, based on empirical observations, such a discrete organization of the soil environment is still not proven. Although discrete patterns of physical organization have been observed in both porosity and aggregate size distribution across a limited range of scales (Menendez *et al.*, 2005; Globus, 2006; Fedotov *et al.*, 2007), data are still rather scarce and fragmentary.

Scale 1: Microbial biofilms and colonies. The smallest habitat in soils is represented by assemblages of mineral and organic particles approximately 20 μm in size, called micro-aggregates (**Figure 3**, Scale 1). Microorganisms in these microsites are involved in most chemical transformations that result in organic matter cycling and improved soil nutrient fertility. Guts of invertebrate ecosystem engineers or fecal

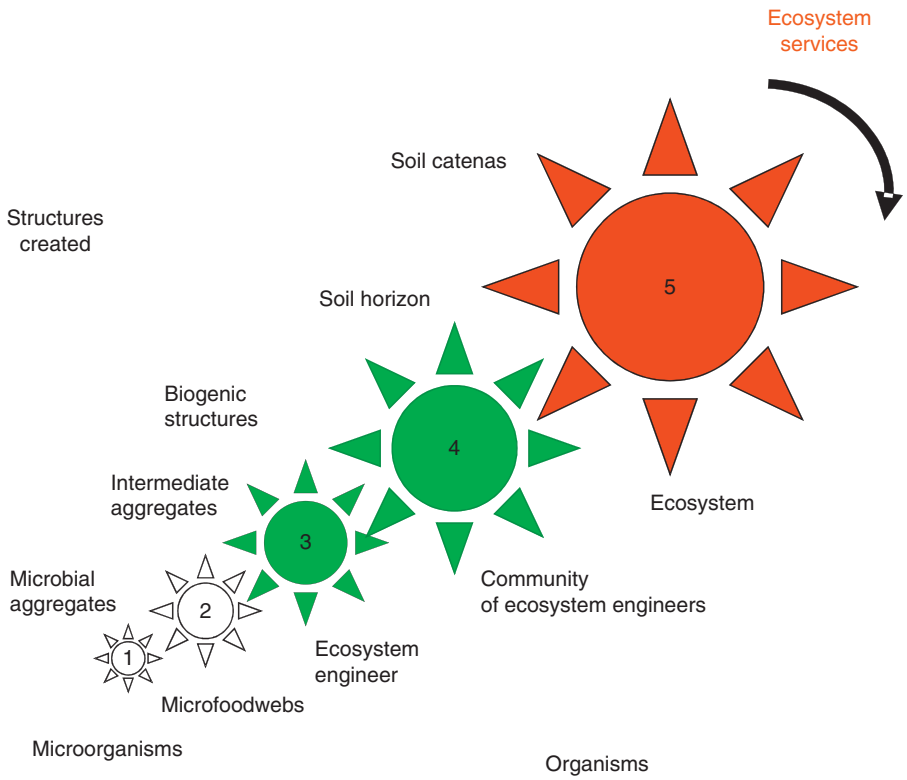


Figure 3 Self-organizing systems in soils at different scales from microbial biofilms and aggregates (1) to intermediate aggregates, (2) individual ecosystem engineer functional domains, (3) mosaics of functional domains in an ecosystem, (4) landscape, (5) and the biosphere (6, not represented), where ecosystem services are delivered along soil catenas. A community of interacting organisms, a set of physical structures that they inhabit and, in some cases, have created themselves, and the processes that operate at this scale of time and space define each scale. Modified from Lavelle, P., Decaens, T., Aubert, M., *et al.*, 2006. Soil invertebrates and ecosystem services. European Journal of Soil Biology 42, S3–S15.

pellets of litter transformers (Scale 3) are typical microsites where these Scale 1 structures are to be found.

Scale 2: Micropredator foodwebs in meso-aggregates. At a scale of approximately 100–500 μm, micro-aggregates form assemblages that leave spaces among them where micropredators, such as nematodes and protoctists, can feed on microbial biomass, thus controlling their populations and activities. Specific assemblages of microorganisms in the rhizosphere, such as mycorrhizal fungi, also operate within pores of this size scale representing an autotrophic option for meso-aggregate interactions (Högberg and Read, 2006; Grayston *et al.*, 1998).

Scale 3: At the scale of decimeters to decameters, ecosystem engineers and abiotic factors determine the architecture of soils through the accumulation of aggregates and pores of different sizes: micro-aggregates of Scale 1; meso-aggregates of Scale 2; and the macro-aggregates that they produce (Lavelle, 2002). These spheres of influence (or functional domains) extend horizontally over areas ranging from decimeters (e.g., the rhizosphere of a grass tussock) to 20–30 m (drilosphere of a given earthworm population) or more and from a few centimetres up to a few meters in depth, depending on the organism (Decaëns and Rossi, 2001; Jimenez *et al.*, 2006).

Scale 4: Functional domains are distributed in patches that may have discrete or nested distributions and form a mosaic of patches (Scale 4). Such a mosaic has been described, for example, by Rossi (2003), who observed the distribution of two groups of earthworms with opposing effects on soil aggregation. One group, called 'compacting' earthworms, stimulates soil macro-aggregation through the accumulation of large ($\sim$1 cm) compact casts, which reduce soil macroporosity (Blanchart *et al.*, 1997). 'Decompacting' earthworms, however, have the opposite effect by breaking large aggregates into smaller pieces. This reduces the bulk density of the soil and allows an increased density of rootlets in this more favorable environment. More complex spatial domains of ecosystem engineer communities probably mix the structures of termites, ants, earthworms, and plant roots, although their structure and the relationships between their different constituents have very seldom been described or understood (**Figure 4**).

Scale 5: Ecosystem and landscape. At the landscape level, different ecosystems coexist in mosaics with often clearly visible patterns. The occurrence and distribution of land cover types in landscapes may result from natural variations in the environment or human land management. Soil formation processes, for example, are very sensitive to topography, which is reflected in the formation of catenas of related soils from upper to lower lying areas. Significant differences in soil type at this scale often determine different vegetation types and hence the ecosystem (Sabatier *et al.*, 1997). Conversely, there is growing evidence that the composition and structure of artificial mosaics created through different land management

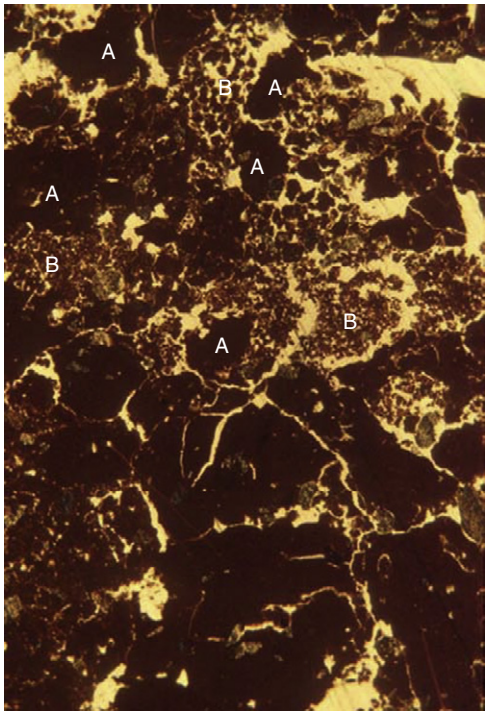


Figure 4 Thin section of a forested oxisol from Central Amazonia (X 0.5) showing accumulation of biogenic structures made by different ecosystem engineers. (a) compact earthworm casts and (b) dispersed pellets of soil deposited in a soil cavity by ants or termites.

practices have effects on biodiversity and the distribution of soil habitats.

Above these five scales there is, of course, the biosphere where all ecosystem services merge. At this global scale, atmospheric composition, temperature conditions, and the dynamics of the ozone layer are determined.

Examples of vertical organizations in soils

Climatic conditions determine the production of biomass by different ecosystems and so may significantly influence the amount and quality of organic matter produced. This, in turn, affects the populations of ecosystem engineers (**Figure 5**).

For example, dry or cold desert soils have no earthworms and the common ecosystem engineers are mainly ants (which have little influence on SOM dynamics) and termites. In such conditions, microbial communities tend to be dominated by fungal components and a discontinuous and relatively modest contribution of soil ecosystem engineers to soil processes (Scales 3 and 4). This gives foodweb control (Scale 2) a predominant role in these systems (Moore *et al.*, 2004).

Following soil and climate natural variations, the set of embedded processes that represent soil function may have different importance and composition. In the same region, different soils – or different types of natural or managed vegetation on a similar soil type – may have rather different species communities. Plant communities typically have a strong effect on the community of soil organisms (De Deyn and Van der Putten, 2005). Forest ecosystems tend to produce litter of a rather low quality and decomposition processes generally rely on communities dominated by fungi and arthropods that decompose the litter *in situ*. Earthworms that bury leaves in soil to stimulate decomposition by bacteria and open the soil structure to allow deeper rooting are often in very low densities in such environments. In contrast, grasslands and pastures are generally more favorable for earthworms, so the overall system shifts from fungi/micro-foodweb/arthropod to earthworm/bacteria-dominated litter decomposition systems. In agriculture, data from many different environments indicate a general depletion of macro-faunal communities when natural vegetation is replaced by managed systems (Lavelle and Spain, 2001).

Communities of ecosystem engineers (plants and invertebrates) organize their functional domains in ecosystem mosaics, which create a diversity of habitats for smaller organism communities in the rhizospheres of different plants (Marschner *et al.*, 1986). The continuous release of readily available substrates into the rhizosphere stimulates a high diversity and abundance of soil biota, especially heterotrophic microorganisms. However, Blackwood and Paul (2003) suggested that this activation selects only fast-growing microorganisms which take advantage of the release of easily decomposed C sources for growth, extract nutrients from the surrounding soil, and release them when they are preyed upon by small predators (Clarholm, 1985). Once completed, this flush of activity diminishes as root tips move away and fine roots die, allowing a different microflora to form in the root litter. Plants are also associated with specific communities of mycorrhizal fungi, which substantially enhance the ability of plants to forage for nutrients and water and protect them from diseases (van der Heijden *et al.*, 1998; Hedlund and Harris, 2012).

Similarly, collembola and acari may have rather different communities inside or outside of patches dominated by a given earthworm population (Loranger *et al.*, 1998). They thereby exert different effects on fungal communities by selectively feeding on their hyphae, or by dispersing their spores.

There is also abundant evidence in the literature that invertebrate ecosystem engineers (earthworms and termites) have similar specific effects within their respective functional domains. For example, intestinal mucus of earthworms, or the saliva of termites, has analogous effects as root exudates in stimulating a specific microflora that digests the ingested organic matter. They then continue their activities for a while in the excreta of these animals and thus become part of the macro-aggregated fraction of soils (Barois and Lavelle, 1986).

Response of Soil Communities to Agricultural Practices and Other Disturbances

Agricultural soil management strongly affects the whole ecosystem as it can change the dominant type of vegetation (forest to grassland or annual crops), the quality and amount of organic inputs (often reduced when plant cover is not continuous and chemical fertilizers are used), and affect some basic soil characteristics, such as pH.

In contrast, it has been shown that changing from tillage to 'no till' agriculture can increase the microbial biomass as well as the ratio of fungal to bacterial biomass (Beare *et al.*, 1997). In this way, it is clear that there can be a significant decrease in

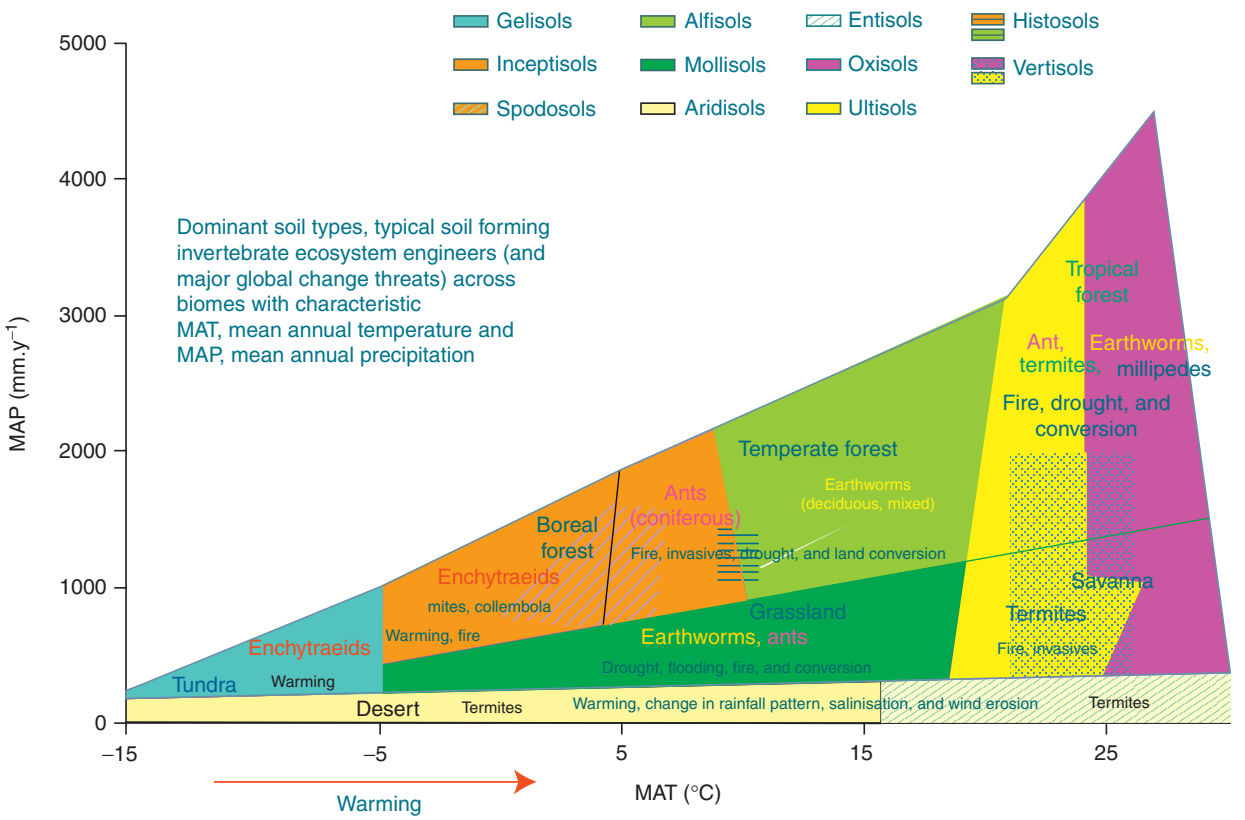


Figure 5 Dominant groups in soil faunal communities across a climate gradient. Reproduced from Brussaard, L., 2012. Ecosystem services provided by the soil biota. In: Wall, D.H., Bardgett, R.D., Behan-Pelletier, V., *et al.* (Eds.), Soil Ecology and Ecosystem Services. Oxford, UK: OUP, pp. 45–58.

functional diversity of microbial communities along a gradient of increasing agricultural intensification (Degens *et al.*, 2000) (**Figure 6**).

T-RFLP and cloning data obtained in representative land use systems in Western Amazonia have shown that diversities of total bacteria, symbiotic nitrogen-fixing bacteria, and arbuscular mycorrhizal fungi are not affected by land use systems (Jesus *et al.*, 2009; Lima *et al.*, 2009; Stürmer and Siqueira, 2011; Leal *et al.*, 2013). However, the relative abundance of these functional groups is affected, probably due to the different rhizosphere characteristics of the various plant communities. However, diversity and density of macro-fauna, like beetles, decrease with land use intensification from forest to pasture (Korasaki *et al.*, 2013). A significant relationship between ecological functions (seed dispersion, dung removal, soil excavation, and abundance of fly larvae/biological control) and the density and diversity of dung beetles was also found, in which the highest diversity of dung beetles was related to an increase in all these functions *in situ* (Braga *et al.*, 2013). Traditional management by local human communities, i.e., shifting cultivation, can even restore diversity to levels larger than those characteristic of the nearby natural vegetation.

Invertebrate communities are all significantly affected by agricultural practices, although to different degrees and in different directions. Some practices, like the establishment of improved pastures with better-performing African grasses, legumes, and liming, enhance their communities, whereas

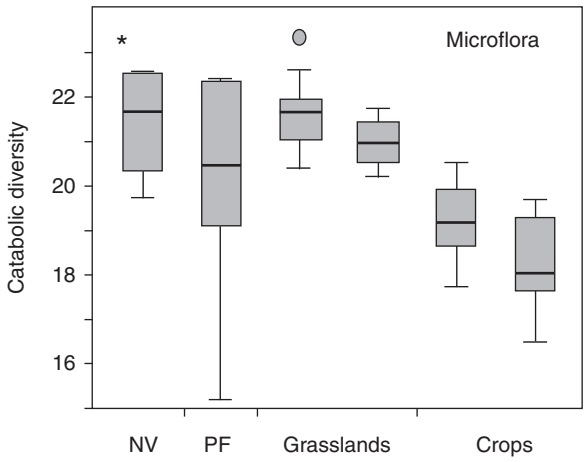


Figure 6 Effects of land use on the functional diversity of soil microflora in New Zealand. NV, native vegetation and PF, pine forest; in the box plot representation, horizontal line = median, limits of the gray rectangle = confidence interval, error bars = interquartile range, and isolated points = outliers. Reproduced from Degens, B.P., Schipper, L.A., Sparling, G.P., Vojvodic Vukovic, M., 2000. Decreases in organic C reserves in soils can reduce the catabolic diversity of soil microbial communities. Soil Biology and Biochemistry 32 (2), 189–196.

others, like traditional annual crops, severely deplete their density and diversity (Lavelle and Pashanasi, 1989; Decaens *et al.*, 1994; **Figure 7**).

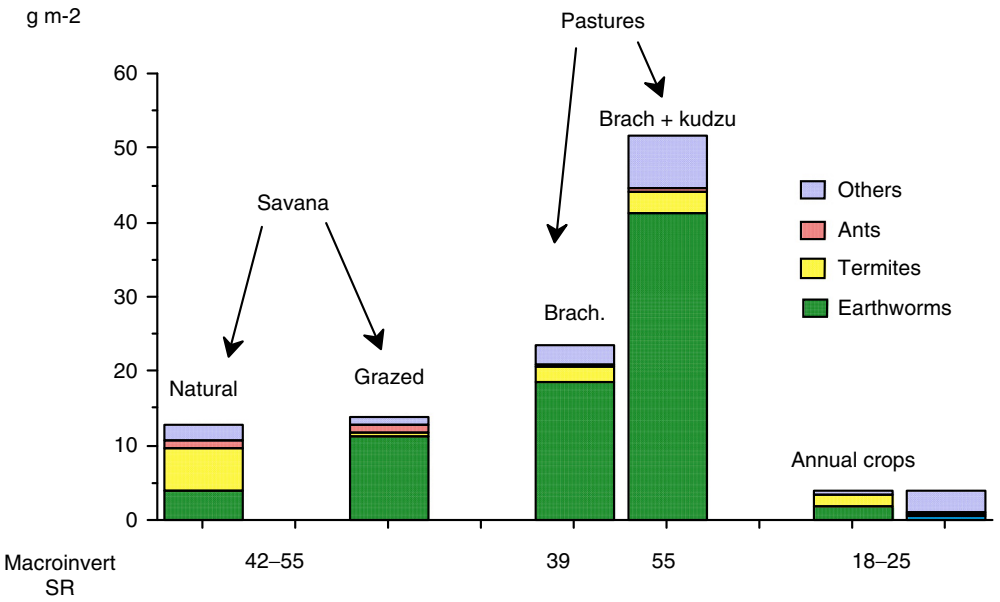


Figure 7 Density per m² of soil ecosystem engineers and other components of the macrofauna in soils from the Llanos Orientales de Colombia under six different plant covers. Reproduced from Decaens, T., Lavelle, P., Jaen, J.J.J., Escobar, G., Rippstein, G., 1994. Impact of land management on soil macrofauna in the oriental Llanos of Colombia. European Journal of Soil Biology 30 (4), 157–168.

Biodiversity and Soil Function: Why Maintaining Abundant and Diverse Communities Is Beneficial?

Ecosystem services provided by soils directly depend on the diversity and intensity of biological activities. Although microorganisms mediate more than 90% of all chemical transformations involved in nutrient cycling and the chemical protection of organic matter, the large ecosystem engineers create habitats for the smaller organisms and thus determine soil hydraulic properties. All organisms play important and sometimes very specific roles in sustaining plant production and protecting them from pests and diseases.

Ecosystem Engineers: Soil Structure and Hydraulic Properties

When water infiltrates into the soil, it is either stored for later use by plants or released to recharge aquifers. Soil water status and the balance among these important functions are made possible by soil porosity and the effect of gravity. Porosity is a very complex and dynamic soil attribute that has both a textural and a structural component. Textural porosity is a function of mineral particle size, whereas structural porosity is formed by either physical (e.g., creation of cracks in drying soil) or biological processes, such as bioturbation and burrowing. The latter is what allows vertical and horizontal water flows and plant provisioning.

The literature provides ample illustration of the importance of soil invertebrates and plant roots for the formation of macro- and meso-porosities (Lavelle and Spain, 2001). Subtle balances among soil-dwelling invertebrates that compact and aggregate soil particles and those that decompact and disaggregate these structures determines the size, shape, and organization of the pore space. This balance, which is strongly

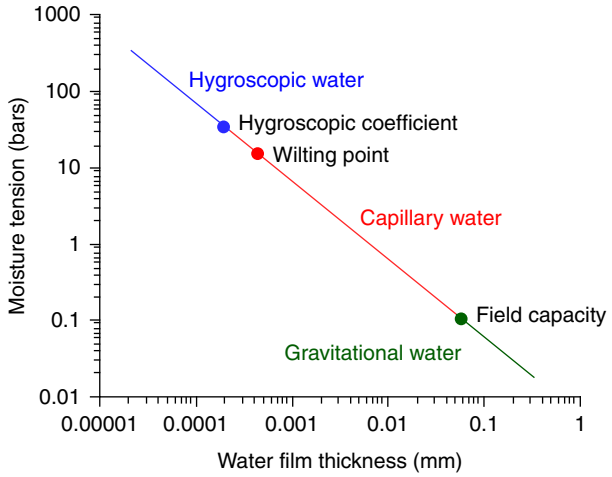


Figure 8 Different kinds of water according to the size of pores within which it is retained.

influenced by plant roots, seems to optimize the permeation of water into the soil by infiltration (in pores > 100 μm), plant provisioning from pores of a size between 0.02 and 6 μm, whereas the transfer of water to deep aquifers and rivers occurs through the largest macropores (Figure 8).

Soil aeration and water dynamics, therefore, largely depend on the activities of ecosystem engineers, which themselves are dependent on a biodiverse ecosystem. Losses of biodiversity may lead to imbalances in the dynamics of pore formation, including, for example, by invasive compacting earthworms (*Pontoscolex corethrurus*) causing severe soil compaction (Chauvel *et al.*, 1999) or the uncontrolled multiplication of surface structures by ants *Camponotus punctulatus*, as in abandoned rice fields in Northeast Argentina (Folgarait, 1998;



Figure 9 Uncontrolled multiplication of mounds created by *Camponotus punctulatus* in Northeast Argentina.

Figure 9). It is evident, therefore, that the diverse activities of soil invertebrate ecosystem engineers are of the utmost importance in agricultural ecosystems, especially those that do not use mechanical tillage.

Decomposition and SOM Dynamics

Decomposition of SOM is the result of two contrasting processes: mineralization and humification. Mineralization allows the release of nutrients contained in dead organic matter into inorganic forms and is important in their uptake by growing organisms, especially plants. Humification is the opposite process and leads to the conservation of organic matter in the ecosystem in protected forms. Protection may occur through chemical processes (by condensation of large-weight molecules or accumulation of undigested compounds) or through physical processes, in which organic elements are protected from microbial attacks within compact aggregates. An important attribute of mineralization is the synchrony in time and space between nutrient release and its uptake by plants and microbial biomass. Synchrony is best achieved in natural ecosystems, within which the combined diversity of decomposing material and decomposer communities allows a fine tuning of the process (Swift and Anderson, 1994; Myers *et al.*, 1994). Agroecosystems most often lose large amounts of nutrients to aquifers and the atmosphere because synchrony is no longer achieved, as in systems that receive excessive chemical fertilizer inputs (Lavelle *et al.*, 2005). Regarding humification, it has recently been argued that the addition of small amounts of easily assimilated organic compounds, like glucose, can allow microorganisms to further assimilate more complex substrates, like cellulose or lignin, and that this can relatively easily release chemical protection (Martin *et al.*, 1992; Fontaine and Barot, 2009). Thus, it would appear that the putative chemical resistance is nothing other than a physical separation of decomposers from their feeding resources. If this assumption is proven it would actually reduce the cases of chemical protection to a very few specific components.

Plant Growth Stimulation and Plant Protection

Sustaining plant production is the third major ecosystem service provided by soils through biological activities. During the course of million of years of coevolution, plants have developed mutualistic relationships with microbes and invertebrates that allow sustained growth and protection from pests and diseases.

Mutualisms with microorganisms

Nitrogen-fixing prokaryotes

Nitrogen is the element required in the largest quantities by plants. The sources of N in soil are: organic matter, usually very low, especially in tropical ecosystems; artificial nitrogen fertilizers, quite expensive and potential pollutants; and biological nitrogen fixation. Biological nitrogen fixation, the conversion of gaseous N_2 into ammonium, is one of the most important functions for the sustainability of life on the planet. Only some groups of bacteria and archaea are able to fix N_2 symbiotically. These prokaryotes can live freely in soil and water or in mutualistic relationships with fungi, lichens, and certain plants. The most important among these relationships are those of rhizobial bacteria with some legumes (Leguminosae). This is due to the economic relevance of many nitrogen-fixing legumes as crops, as well as their widespread occurrence in natural ecosystems. Development of molecular techniques in the last three decades has allowed a significant increase in the knowledge of rhizobial diversity: from the 6 species in a single genus known in 1984 to approximately two hundred species in 12 genera today. The mutualistic relationships between legumes and rhizobial species range from very specific to rather promiscuous. This diversity must be considered in the selection of specific bacterial strains to produce effective inoculum for a given plant species.

Mycorrhizal fungi

Although not required in such large quantities as nitrogen, phosphorus is usually the nutrient element mostly limiting plant growth in tropical ecosystems. The low availability of phosphorus is due to its immobilization through strong chemical fixation on components of weathered soils to form insoluble inorganic calcium, aluminum, and iron phosphates. Phosphorus also has a very low mobility in soil, which further limits its availability.

Mycorrizal fungi can establish mutualistic relationships with the majority of plant species (Read, 1991). Hyphae infect the roots of plants and spread through the soil exploring a soil volume much larger than that which could be explored by the roots alone. They thereby scavenge nutrients such as phosphorus and zinc from sources very distant from the root system. There are seven types of mycorrhizal fungi, but the most important ones are arbuscular or endomycorrhizas and ectomycorrhizas. They also enhance plant resistance to various stresses, such as heavy metal contamination and drought, as well as provide some protection against pathogens.

The use of rhizobial nitrogen fixation by legumes to replace artificial nitrogen fertilizers is an outstanding example of the contribution of biological processes within sustainable agriculture (Sileshi *et al.*, 2008). For example, the inoculation of soybeans in Brazil with selected *Bradyrhizobium* strains completely replaces nitrogen fertilizers, saving billions of US dollars annually. Unfortunately, this practice is virtually restricted to soybean (99%) and only 1% is applied to the bean *Phaseolus vulgaris*.

Plant interactions with invertebrates

Soil invertebrates have well-identified and measured effects on plant growth, some directly through physical conditioning of the soil and others indirectly through protection against pests and diseases or the selection and activation of mutualistic microbial populations. Pot experiments, with or without almost any type of non-pest micro- to macro-fauna, have typically found significant increases in growth/biomass (Setälä and Huhta, 1991; Brown *et al.*, 1999; Scheu, 2003), especially above ground. In addition, below-ground biomass can sometimes be reduced, even under conditions of high nutrient fertility (Lavelle and Spain, 2001).

In the case of earthworms, five mechanisms have been identified that promote a better growth and protection of plants (Brown *et al.*, 2000). They are:

- Enhanced nutrient release in fresh casts that are then subsequently colonized by plant fine roots (Lavelle *et al.*, 1992; Chapuis-Lardy *et al.*, 1998; Decaëns *et al.*, 1999);
- Improved soil physical conditions, which enhance plant water supply;
- Enhanced root mycorrhizal colonization;
- Direct control of plant parasites;
- Production of hormone-like compounds (Blouin *et al.*, 2005).

Conserving Soil Biodiversity in Agroecosystems through Management Options at Different Scales

Soil biodiversity is highly sensitive to human intervention at five scales (**Figure 3**), so good soil and vegetation management is important for its conservation. Large organisms are more sensitive to disturbance than smaller ones, and changes in communities of large organisms can have cascading effects on the communities of smaller organisms.

The organization of the agricultural landscapes (Scale 5) influences the regional pool of biodiversity (β diversity) and possible recolonization of degraded farm land. At the plot/farm scale (Scale 4), soil tillage, irrigation, the use of chemical fertilizers and pesticides, and the configuration of the plant communities all have strong effects on above- and below-ground biodiversities. At the scale of individual plants (Scale 3) and their associated ecosystem engineers, introduction of plants with specific ecological or environmental properties (such as, e.g., those with high N contents in N fixing plants, allelopathic properties for other plants and microbes, strongly anchoring or fine and dense root systems) may be used to manipulate the biodiversity of the meso- and micro-fauna, and the microflora. For example, plant parasitic nematodes can be controlled/regulated by earthworms that create assemblages of soil aggregates and soil pores that are favorable/unfavorable habitats for nematodes (Scale 2). Likewise, microbial supplements can be inoculated into soils to directly modify and enrich microsites with favorable microorganisms (Scale 1).

Scale 5: Landscape

The organization of eco-efficient landscapes that combine satisfactory economic performance with equitable and adequate social development and the conservation or improvement of their natural capital is slowly becoming a priority in rural development (Jackson *et al.*, 2012; Leakey, 2012). This awareness comes from the understanding that most ecosystem services are delivered at the landscape scale rather than at smaller scales. Pollination is a clear example that shows that if natural areas are not conserved close to intensively managed plots, dramatic deficits in pollination will occur (MA, 2005). Conversely, when landscape intensification is associated with a decrease in biodiversity, soil ecosystem services, such as hydrological functions, carbon storage, and nutrient cycling (Lavelle *et al.*, 2014), may be impaired or lost.

Ways to manage landscape composition and structure are still poorly studied and understood (Nelson *et al.*, 2009). However, the total number of patches of different types of land use (e.g., natural forest vs. annual crops) seems to be a determining feature affecting biodiversity and ecosystem services. In a study of deforested areas in Amazonia, the crucial tipping point in the relationship between landscape intensification and biodiversity maintenance corresponded to landscapes with at least 50% of tree cover, 20% of which was natural forest. This ratio may serve as an indicator for restoration projects in degraded landscapes. Landscape structure, however, is also important as exemplified by the creation of biodiversity corridors (Rantalainen *et al.*, 2006). However, such relationships may not be immediate and simple as it now seems that the biodiversity of plants is not necessarily linked with biodiversity of other groups. However, delay may occur between the reconstitution of a desired plant community and the expected levels of soil ecosystem services during the early steps of an adaptive cycle *sensu* (Holling, 2001).

Scale 4: Manipulation at Ecosystem Level in a Crop Plot: Tillage, Rotations

Processes of ecosystem reconstruction at the plot scale are much better understood as this is the scale that has frequently been considered, often almost exclusively, by farmers and agronomists.

At this scale the following four major technical elements should be considered to allow an appropriate management of biodiversity (Cavigelli *et al.*, 2012).

- The nature and diversity of plant cover;
- The need for tillage and soil mechanical preparation;
- Fertilization and protection of plants from pests and diseases;
- Application of organic materials as a way of promoting biological activities.

Plant cover: Structure, composition, and diversity

Although plant diversity in cropped land has considerably decreased since the advent of the Green Revolution (Cavigelli *et al.*, 2012), a large number of studies suggest that appropriate levels of plant diversity may be a prerequisite to conserving the diversity of other organisms and the provision of ecosystem services (ES), even within areas of primary production being the first one to respond to this increased diversity. Relationships among plant diversity, the diversity of other organisms, and the provision of ES, however, are not always clear and the

impacts may not be visible for many years (Hector *et al.*, 1999; Hector, 2002).

In general, agroecosystems that mimic the original system – for example, agroforestry systems in a forest area or an improved pasture in a savanna area – are better at conserving biodiversity than those based on monocultures of annual crops. For example, in the savannas of the Colombian Orinoco, macro-invertebrate communities are greatly enhanced, both in total density and species richness in improved pastures with African grasses (Decaens *et al.*, 1994; **Figure 6**). Under such conditions, annual crops have highly deleterious effects, whereas perennial tree crops do not differ significantly from the original savanna. Similar patterns are observed in rainforest areas where agroforestry systems generally have larger communities of invertebrates than annual crops (Barros *et al.*, 2002).

Some plants directly stimulate organisms (e.g., legumes for biological N fixation), whereas others have more systemic effects at keeping soil covered with their stolons and litter production, upper tree canopy shade, or by sustaining generalist predators that will control pests and make applications of toxic agrochemicals unnecessary (Velasquez *et al.*, 2012; Settle *et al.*, 1996; Leakey, 2014).

Plants affect soil biodiversity through the amount and quality of organic material they contribute to the soil as dead leaves and roots (Vohland and Schroth, 1999; Lavelle *et al.*, 2001). They also have a direct effect on soils through the deposition of root exudates, exfoliation of tip cells, and death of fine roots. In some cases, the addition of particular plant species may greatly enhance, or decrease, specific elements of the soil community. This is the case in the approximately 20 000 species within the family Leguminosae, which produce grains, wood, gums, and green manure and which establish symbioses with N-fixing rhizobial bacteria. These legumes have high N contents ($>3\%$) that can be released during organic matter decomposition, or be transferred to other species by the hyphae of mycorrhizal fungi that form root connections and supply N to other plants. Legumes also enhance earthworm activities, with subsequent effects on soil aggregation and physical properties. For example, in Amazonian pastures that contain *Brachiaria brizantha*, the partial or total substitution by the legume fodder plant *Arachis pintoi* allows earthworm density to significantly increase from 217 to 365 individuals per square meter (68%), with a subsequent 87% increase in the fraction of biogenic aggregates to 25.3% and a 15% decrease in non-macro-aggregated soil. Plant-available water in these soils increased 20%, from 79 to 95 g kg^{-1} (Velasquez *et al.*, 2012).

In contrast, some plants may have intrinsic detrimental effects on soil biota. Particular attention has recently been brought to new cultivars of soybean that no longer favor rhizobial associations and to rice cultivars that do not respond favorably to earthworm or organic matter additions (McCouch, 2004; Noguera *et al.*, 2011).

Polycultures (e.g., agroforestry) with diverse plant community composition have greater rhizosphere diversity than monocultures, as significantly greater amounts of carbon substrates are released by roots. This stimulates greater biodiversity among the invertebrate litter decomposers (Vohland and Schroth, 1999) and primary consumers living close to the root systems. They attract predators and other organisms vital to foodweb functioning. In Africa, the ratio of organism densities in agroforestry systems to conventional farming systems varied from 1 (parasitic nematodes) to 2–3 (nonparasitic nematodes, acari, collembola, ants, and coleoptera), and other ratios were as follows: earthworms (3.1), chilopoda (5.6), and diplopoda (6.1) (Barrios *et al.*, 2012).

Tillage

Tillage and other soil mechanical preparations are a further critical element of agroecosystems that may profoundly influence soil-living communities. The recurrent destruction of soil structure by plowing maintains soils at an early successional stage, according to Holling's (2002) adaptive cycle paradigm. Under such conditions, species that require stable environmental conditions and mutualistic relationships with other organisms for their development are progressively eliminated as negative interactions (competition and predation) prevail. Tillage affects soil biota both directly by killing them and indirectly by decreasing the food resource base and destroying their habitat. This is illustrated by the mortality of large invertebrates and the destruction of fungal networks (Cavigelli *et al.*, 2012) and the significant reduction of earthworm numbers and diversity with its consequent negative impacts on soil physical properties (Wardle, 1995; **Figure 10**).

Similar results have been reported for a variety of soil invertebrates (Marchao *et al.*, 2009) in cropping systems derived from the Cerrado vegetation of Brazil, where, with the exception of termites and ants, most groups benefit from a shift from tillage to 'no-till' systems. Nevertheless, Dominguez *et al.* (2009) reported that no-till systems had a lower population density than the natural grassland (70 individuals per square meter as compared to 297 in the original ecosystem).

Systems with reduced tillage can have higher microbial biomass and higher fungi:bacteria (F:B) ratios (Beare *et al.*, 1997), but recent studies suggest that this is not the general situation. In Laos, for example, in no-till and cover crops systems in tropical grasslands, Lienhard *et al.* (2012) did not find a change in the F:B ratio, although a clear relationship was observed between the density and the quantity of microbial groups and diversity of crop residues (**Figure 11**). Overall genetic diversity of the microbial community showed a different pattern linked to soil chemical parameters, such as soil acidity (exchangeable Al, pH, and CEC) and C:N ratio. Similarly, Strickland and Rousk (2009) had indicated that these results were far from general. However, Helgason *et al.* (2009) did not find that effect of tillage in intensive tilled versus untilled soils of the Great North plains (Beare *et al.*, 2009).

Fertilizers and plant protection

Agrochemicals are yet another element of agroecosystems that impact strongly on soil biodiversity. Some chemicals usually have positive (e.g., liming) or neutral effects (chemical fertilizers), whereas others (most pesticides) are detrimental (**Figure 12**).

Liming reduces soil acidity and generally increases overall biological activity, and there is a trend for the F:B ratio to decline (Rousk *et al.*, 2010). Earthworms respond to this by significantly increasing their biomass (Edwards and Bohlen, 1996; Davidson *et al.*, 2004; Potthoff *et al.*, 2008). In the

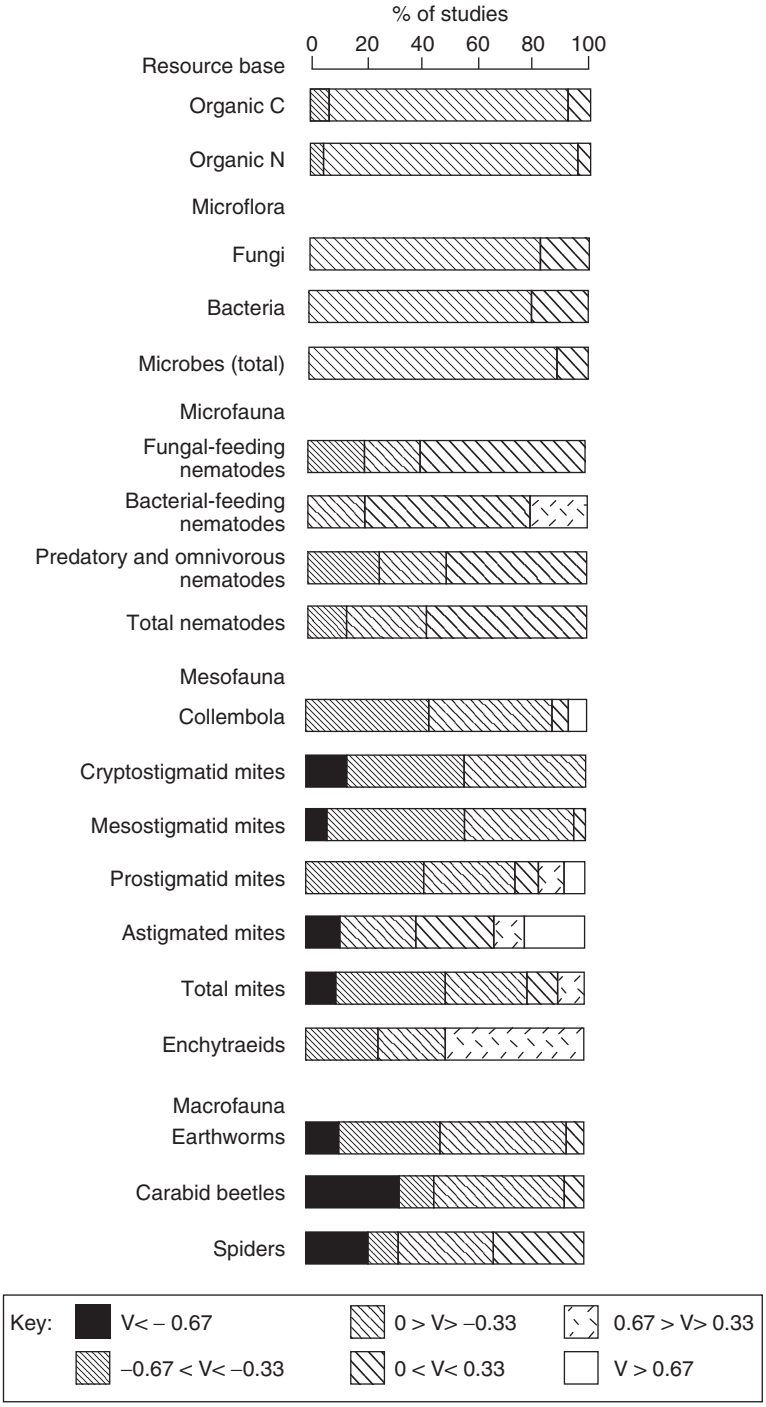


Figure 10 Effect of tillage on abundance or biomass of soil organism populations. V is the ratio of no-till to control tilled systems. Reproduced from Kladivko, E.J., 2001. Tillage systems and soil ecology. Soil and Tillage Research 61, 61–76.

Colombian savannas, the positive effect of exotic pastures (Figure 7) is also a system response to liming and changes in the vegetation cover. However, liming aimed at counteracting the effects of atmospheric acid deposition in forests in Europe did not affect species richness but did significantly decrease macro-invertebrate densities, with contrasting effects on different groups. Although some coleoptera were favoured, the majority of Araneae families (Lithobiidae) and Coleoptera (Staphylinidae) had larger densities in nontreated plots (Auclerc *et al.*, 2012). Part of the observed detrimental effect was related to the increased aluminum toxicity that occurs in some soils when pH is increased (Larssen *et al.*, 1999).

Industrial chemical fertilizers usually do not directly affect soil organisms (Beauregard *et al.*, 2010) but increase plant production. However, the production of certain soil enzymes that are involved in nutrient cycles (e.g., amidase in the

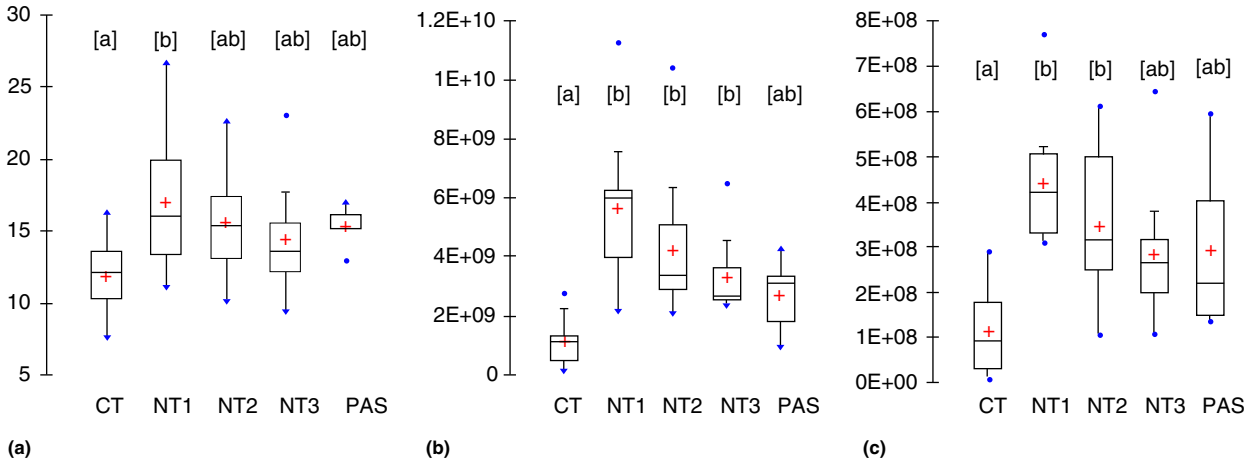


Figure 11 Effect of tillage on microbial diversity in crops from Laos (Lienhardt *et al.*, 2010). Box and whisker representation of (a) molecular biomass (micrograms and per gram of soil), (b) bacterial density (copy of 16S rDNA per gram of soil), and (c) fungal density (copy of 18S rDNA per gram of soil) recorded in natural pasture land (PAS), conventional tillage (CT), and no-till systems (NT (1, 2, and 3)). Letters in brackets indicate significant differences (Kruskal–Wallis test ($P < 0.05$, Bonferroni corrections).



Figure 12 Adult cicada from a gallery forest killed by aerial applications of *Beauveria* in nearby industrial crop fields in the Llanos Orientales region of Colombia (Photo Patrick Lavelle).

nitrogen cycle), which normally releases mineral nutrients, may be significantly depleted (Dick, 1992). Loss of such functions may explain, at least in part, the decrease in production generally observed when shifting from conventional to organic agriculture.

Pesticides are by far the most detrimental agrochemicals with regard to biological activity and biodiversity. However, their wide chemical diversity, the large variation in frequency and quantity of applications, and the resulting soil reactions make generalizations difficult. This is exacerbated by poor assessment methodologies. The literature is also limited and generally focused on one type of pesticide, although it suggests that one-time applications have only small effects in the medium term, because the product is biodegraded, allowing microbial or invertebrate communities to return to pre-application levels within a few weeks (Cavigelli *et al.*, 2012). Repeated applications, however, may lead to more serious and durable changes in soil biology (Stromberger *et al.*, 2005; Larink, 1997; Edwards and Bohlen, 1996). Studies with the herbicide glyphosate indicate few long-term effects on microbial communities and their activities (Kremer and Means, 2009). However, increased susceptibility to fungal diseases (*Fusarium*, *Phytophthora*, and *Pythium* spp.) has been detected. Selection of the most aggressive parasitic nematodes in the presence of pesticides has been also observed (Lavelle *et al.*, 2004). This may perhaps explain why the need for pesticide applications is growing in highly intensive crop systems, especially in the tropics. A special mention should finally be made here of biological insect-control agents (such as the fungus *Beauveria* or *Bacillus thurigiensis*) that have less contaminating effects but still have undesired nontarget effects on non-pest insect populations.

Organic amendments

As a generalization, organic inputs increase the species richness and abundance of soil organisms as compared with conventional cropping systems (Bengtsson *et al.*, 2005; Hole *et al.*, 2005), although in some cases no response has been observed (Cavigelli *et al.*, 2012). This may result from the absence of species that would have benefited from the improved conditions.

A large part of the detrimental effects of intensive agriculture on soil organisms is due to starvation. Although residue inputs are severely decreased by weeding and the exportation of large part of the above-ground plant biomass, the use of chemical fertilizers reduces food sources even more (Lavelle *et al.*, 2004). In contrast, organic agriculture based on diverse materials, such as animal and green manures,

biosolids, biochar, compost, decomposing plant lixiviates, small branches, and other wood residues, provides organisms with beneficial substrates while it increases biomass and plant species diversity, with a wide range of organic inputs (Cavigelli *et al.*, 2012). All this diversity leads to great variation in decomposition, mineralization, and humification, which is further varied by the effects of climate and soil differences at large scales and by invertebrate and microbial communities at smaller scales (Lavelle *et al.*, 1993).

An early consequence of depositing organic matter on the soil surface is the enhancement of communities associated with litter, such as micro-arthropoda, myriapoda, isopoda, and a large number of insects (Ruiz-Camacho *et al.*, 2011). This community participates in the composting of organic residues and their further mineralization by soil microorganisms in the casts of endogeic or anecic earthworms. A common situation following organic inputs is an increase in aggregation and aeration leading to improved soil physical structure through the enhanced activities of ecosystem engineers (Lavelle *et al.*, 1997).

Another interesting function of organic inputs is the maintenance of dense invertebrate populations that provide food for generalist predators which can switch to any invertebrate pests emerging on crops, thereby providing an element of biological control (Settle *et al.*, 1996). However, there are significantly different effects of different types of organic materials on soil macro-fauna. In a study involving 13 cereal crops, 4 pastures, and 5 forests conducted on similar soils of the Bassin Parisien region of France, Ruiz *et al.* (2011) found significant differences in the biodiversity, abundance, and species composition of macro-invertebrate communities depending on the quality of the organic inputs. A mixed compost of sewage sludge, green manure, and urban solid waste compost did not greatly increase either the total density or biodiversity over that of conventional cropping plots. However, a mixture of farm yard manure, liquid compost of green waste, and the organic fraction of municipal solid waste compost increased the total abundance of macro-invertebrates up to fourfold. However, total species richness per sample did not vary much except in one direct-drilled system with a winter cover crop in which species richness more than doubled and reached similar values to those of nearby forest sites.

Scale 3: Manipulation of Populations of Ecosystem Engineers: Plants and Invertebrates

Increases in the density of beneficial organisms are often sought through the direct inoculation of plants, invertebrates, or microorganisms. The aim is to enhance ecosystem engineering in its physical, chemical, and biological dimensions.

However, these inoculated organisms will survive only if suitable conditions for their activities occur. These include adequate moisture and temperature, appropriate soil pH and nutrient status, and sufficient organic matter quality and quantity (Lavelle *et al.*, 1993).

As is the case in agroecosystems managed by tillage or the use of agrochemicals, plant communities are relatively easy to manipulate, so long as natural competing communities are suppressed or eliminated. The use of other plants integrated into farming systems as companion crops to provide ecological/environmental goods and services is also widely implemented to enhance production. Some introduced species have physical roles, forming erosion-control barriers or windbreaks, whereas others may be N-fixing legumes included for soil fertility management. Such plants may be so effective that N fixed in these artificial systems is equal to 1.5 times N fixed in natural ecosystems (Lavelle *et al.*, 2005; MA, 2005). Other plants may be used as traps for pests, especially phytoparasitic nematodes, parasitic weeds like *Striga*, and cereal stem borers (Khan *et al.*, 2007; Cook *et al.*, 2007).

Inoculation of earthworms has been widely practiced to improve exotic grass pastures in New Zealand (Edwards and Bohlen, 1996). Likewise, earthworm inoculation has been used as part of the FBO (Fertilization Bio Organique) patented technology (Senapati *et al.*, 1999) in which earthworms are inoculated into trenches where the highly organic conditions create small islands of favorable soil functionality (Brown *et al.*, 1999). Interestingly, in addition to occasional spectacular increases in production, this technology also improved the organoleptic quality of tea from plantations in India and China by 15–30%.

Scale 1: Manipulation of Microbial Communities

Microorganisms, such as N-fixing bacteria, plant growth promoters that release growth phytohormones in soil, bacteria that protect plants from fungal (*Fusarium* and *Phytophthora*) diseases (*Pseudomonas* spp. and *Trichoderma*), and fungi that feed on phytoparasitic nematodes, are by far the most frequently used organisms for agroecological manipulations. Soil microbial communities, however, occupy specific microsites in soil, built by ecosystem engineers (macro-invertebrates and roots). They are, furthermore, subject to predation from micropredators and to competition with other microbial colonies (Lavelle and Spain, 2001). This particular ecological circumstance is a substantial obstacle to microorganism inoculation in soils because before they reach the expected target (e.g., a root) they may be preyed upon by any element of the predator micro-fauna, be lost in a micropore where no root will penetrate for months, or be eliminated by more competitive microorganisms even if they arrive at the right site.

Because these conditions are not taken into consideration or, as often so, not really understood, inoculation may only be effective when careful inoculation techniques are implemented.

In a survey of 62 preparations available in SSA Africa, Jefwa *et al.* (2013) found no effect at all in 95% of cases. Of the 31 products tested, only 42% of those claimed to contain Rhizobia actually contained the expected strain, with no contaminant, whereas 34% only had contaminants. In total, for the 62 preparations, 54 strains of bacterial nonrhizobial products of the 147 announced and 26 of 73 mycorrhizal products had the expected strain. Of 13 preparations referred to as mycorrhizal inoculants, only three had a substantial effect under laboratory conditions, although seven had smaller than expected; the remaining three preparations produced no colonization at all. Of 37 bacterial strains not supposed to be present in these preparations, eight had potentially severely

harmful effects for human health and one for plants. Out of 18 nonbacterial preparations, only 33% increased maize growth, whereas in soybean only 22% of tested products were effective (Jefwa *et al.*, 2013).

However, many countries have developed legislative frameworks to control the quality and efficiency of inoculants and a large proportion of the products are delivered with detailed instructions for an efficient use.

Future Research in Soil Biodiversity

A large number of studies have shown the importance of conserving and managing biological activities within agriculture and at the same time have indicated that the soil biota is a vulnerable resource. To better use and protect this essential resource, research efforts must continue, with special emphasis on (1) the determination of effective indicators and (2) development of techniques for conserving and using soil biodiversity.

Indicators

The need for indicators: Synthesis of existing approaches and a proposal for establishing a unique set of tools with ISO labeling

A large and diverse number of biological, chemical, physical, and synthetic indicators of soil quality and ecosystem services have been proposed in the literature (Turbé *et al.*, 2010). However, a comparative analysis of the respective advantages and disadvantages of these indicators is needed before testing.

Conservation of biodiversity and manipulation of communities to improve the provision of soil ecosystem services must be considered across all scales simultaneously

This article has shown the vulnerability of soil biological components and the difficulty of managing them properly. This follows directly from the inherent complexity of biological interactions in soils and the imperfect understanding. To improve this understanding and enhance the potential for ecological manipulations at different scales, research should focus on the following:

Scale 1: Microbial inoculants

In situ field tests of survival and development of the inoculated populations are necessary to determine the range of conditions for the use of these microbial inoculants and to provide quantitative estimates of the benefits obtained in the short and longer term.

Scale 2: Control of plant-parasitic nematodes

Determine how to enhance the biodiversity of parasite communities for ecosystem level control through earthworm activities. Of particular importance is assessment of the density and distribution of microsites in which micro-foodweb processes occur and analysis of their impacts on microbial communities.

Scale 3: Earthworm inoculation, service plants, and ants and termites

There is a need to better understand the internal mechanisms affecting the specific interactions that operate between plants and invertebrate ecosystem engineers. This is especially so of the interactions among the different functional domains derived from the activities of different groups of ecosystem engineers, their precise geography in soil, and their successional processes. In addition, the potential to modify the expression of resistance genes in plants should be further explored.

Together, the outputs of such research could lead to better disease control and an enhanced delivery of ecological services from soil biodiversity.

Scale 4: OM applications and biological control

With regard to the determination of appropriate sources of OM for nutrient release, plant protection, C sequestration, biodiversity enhancement, and on-farm production of OM inputs, there is a need to investigate the effects of soil OM quality on nutrient availability, water retention, and carbon sequestration, especially with regard to the activity of soil engineers.

Scale 5: Ecoefficient landscapes

There is now growing evidence that biodiversity conservation and critical ecosystem services, such as pollination, pest and disease control, decontamination, water infiltration, and supply to plants, need to be delivered at landscape scale. There is consequently a need to improve the design of landscapes for enhanced function through such means as biodiversity corridors and the creation of more natural ecosystems within which natural resource capital, such as trees and conserved water bodies, meets the needs of humanity and the environment. Further natural principles to be included are recycling and composting of organic waste using vermiculture and related techniques.

Conclusion

The conservation and management of soil biodiversity is central to the attainment of agriculture that is productive and sustainable over long periods. From this, it follows that greater effort is now needed to maximize the benefits flowing from a wise and conservative use of natural capital. This particularly applies to the soil taht has become seriously degraded both in fertility and agroecological function and is responsible for the declining productivity that is the main cause of the nutritional insecurity and poverty prevalent in many developing countries (Leakey, 2012). Urgent tasks are, therefore, to prevent further resource degradation by maintaining diverse soil covers and adding organic inputs to the soils. Ultimately, a better understanding of ecological processes is required, including the improved, naturally based management of pests and diseases. This, together with a reduction in pollution, is necessary to reverse declining fertility and improve crop yields in ways that have much improved environmental and social consequences for local people, as well as the global community. Once understood, these mechanisms should be urgently

integrated and enhanced in the next generation of agricultural systems to promote greater agricultural productivity and ecosystem conservation.

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Biosecurity and Equine Infectious Diseases

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Glossary

Biosecurity All hygienic practices (measures) designed to prevent the occurrence of infectious disease.

Equine herpesvirus 1 neurological disease (Equine herpes myeloencephalopathy, EHM) It is rare in the horse population but apparently increasing in incidence now occurring as outbreaks rather than as individual cases.

Infectious disease Pathogens spread easily from subject to subject either directly or indirectly; in general the index subject has the disease but may be a carrier.

Methicillin-resistant *Staphylococcus aureus* (MRSA) An emerging pathogen of the horse particularly associated with wounds and surgical site infections.

Neurological disease A condition affecting the nervous system control over motor and sensory functions producing a deficit.

Strangles A condition caused by *Streptococcus equi* subspecies *equi*, an unusual inhabitant of the horse's upper respiratory tract, can occur as outbreaks or affect individuals in closed herds through contact with carriers.

Zoonotic disease A disease that can be spread directly from animals to humans or from humans to animals.

Introduction

Infectious diseases are a constant threat to the health and welfare of horses. Several diseases have assumed greater importance as the performance and pleasure horse populations and equine activities have increased and there are new owners who do not understand the implications of equine infectious disease outbreaks to their animals. In addition, emerging diseases have beset the equine species in recent years in North America. Firstly, the introduction of the Old World West Nile virus to a susceptible population has made the the virus to be considered as endemic. Secondly, the change in the antigenicity of equine herpesvirus-1 (EHV-1) to induce a more aggressive form of neurological disease may affect clusters of horses than the field strain encountered previously. Fortunately, North America has been spared the infection caused by the paramyxovirus responsible for Hendra virus infection spread by flying foxes (bats), which is a zoonotic disease and a deadly infection of horses in Australia. However, other infectious diseases are more likely to emerge among horses in North America in the next decade as pathogens and vectors move into and become accustomed to new climate zones. The threat of emergent diseases is apparent in the UK, where a warming climate could precipitate a northward spread of those *Culicoides* spp. responsible for African horse sickness among a highly susceptible population.

Vaccination and preventive management procedures are critical to disease prevention, but these need to be more widely adopted, complied with, and promulgated. The National Animal Health Monitoring System (1998) survey raised the specter that a significant number of horses throughout the United States do not receive regular vaccinations and preventive health is not part of the owners' protocol. Therefore, much work remains to be done in communicating the message before a devastating outbreak of infectious disease among horses takes hold. Unfortunately, vaccines are unavailable or are inefficient for several infectious diseases in the United States. Successful vaccines to protect against equine herpes myeloencephalopathy (EHM) and equine strangles are awaited.

The list of infectious diseases, and the pathogens involved, considered as real or potential threats or concerns in the United States by veterinarians, technicians, and horse owners continues to expand. Some are emerging or emergent diseases (E). Other infectious diseases are potential zoonotic diseases (Z), spread from horses to humans or vice versa (Table 1).

This article provides an overview of biosecurity measures that apply to all potential pathogens with an emphasis on the principles learned from the threat of EHV-1 myeloencephalopathy (an emergent disease), MRSA (a zoonotic disease), and strangles, an infectious disease of historical record that remains a scourge to susceptible horses. The emphasis is on examples from the United States, although the principles of biosecurity are applicable elsewhere.

Much has been written in the veterinary, equine, and lay press on biosecurity matters and the threat of equine infectious diseases getting out of hand. The threat is still real. The human race lurches from one crisis to the next having eluded the bullet without learning from its errors. Biosecurity is much cheaper than dealing with actual infectious disease in any species. The importance of hand washing, the preeminent biosecurity measure, is a major factor why nosocomial infections with MRSA and *C. difficile* are such hazards to patients in human hospitals. The healthcare workers do not routinely wash their hands between patients. What has one learned?

Biosecurity

Biosecurity represents an important part of the veterinarian's responsibilities in the clinic or practice facility, at farms, stables, barns, and at shows and events, where horses commingle from multiple locations. Technicians, owners, and caretakers must understand the implications, share the responsibilities, and implement specific management procedures. Communication with and education of all personnel

Table 1 List of infectious diseases of horses

Viral

- Equine coronavirus
- EHV-1 respiratory disease
- EHV-1 neurological disease (EHM) (E)
- EHV-4 respiratory disease
- Equine influenza
- West Nile virus (Z not by horses) (E)
- Vesicular stomatitis virus (multiple species)
- Equine viral arteritis
- Rabies (Z)
- Eastern/Western equine encephalitis (Z not by horse)
- Equine infectious anemia

Foreign animal diseases (viral)

- Venezuelan equine encephalitis (Z)
- Japanese encephalitis (Z not by horse)
- African horse sickness
- Hendra virus (Z)

Bacterial

- *Salmonella* sp. (Z)
- Strangles (*Streptococcus equi* var *equi*)
- Contagious equine metritis (*Taylorella equigenitalis)*
- Methicillin-resistant *Staphylococcus aureus* (MRSA) (Z) (E)
- *Leptospira* sp. (some serovars are Z)
- *Clostridium difficile* (Z)
- *Clostridium perfringens*
- *Lawsonia intracellularis*
- *Rhodococcus equi*

Foreign animal disease (bacterial)

- Glanders (*Pseudomonas mallei*) (Z)

Protozoal (Tick borne)

- Equine piroplasmosis (babesioisis)
- Potomac horse fever (*Neorickettsia risticii*)
- Lyme Disease (*Borrelia burgdorferi*)

on infectious disease control measures is vital. This is before an outbreak happens and subsequently at regular intervals. Technicians must be empowered to enforce the codes of practice. They are a constant presence at the facility and integral to sustaining biosecurity procedures.

Biosecurity includes all hygienic practices designed to prevent the occurrence of infectious diseases, for example, preventing the introduction of infectious agents, controlling the spread within populations or facilities, and the containment or disinfection of infectious materials. Biosecurity is affected by the ecology of animal and human populations, the biological nature of infectious agents, and the management actions affecting interaction between host and agent. Rigorous hand hygiene is an important part of effective biosecurity and is emphaisized throughout this article.

Preparedness is the Key to Biosecurity

A plan of action to manage equine infectious disease outbreaks should be in place before the onset of clinical disease based on the evaluations of risk assessment, resource management, and horse management. All personnel must be familiar with and preferably certified on the infectious disease protocol for the premises. Risk assessment is the knowledge of ongoing disease outbreaks elsewhere and the potential for their spread. Resource management includes devising and establishing a chain of command with defined responsibilities, for example, to identify isolation and biosecurity capabilities both on- and off-site; to insure the availability of diagnostic sampling materials, disinfectants, and biocontainment materials; and to inspect facilities recently vacated after another equine or livestock event for adequate sanitation (decontamination) and waste removal before animals are readmitted (this includes transport vehicles and trailers/vans). Horse management involves publicizing and enforcing health requirements for access to the facility and implementing an equine identification and tracking system.

If an infectious disease is suspected, the veterinarian must make decisions and assume responsibilities according to the devised plan. The clinician should communicate to all individuals (key personnel, technicians, and owners at the premises) the established plan and indicate that diagnostic testing is valuable but can take time. The clinician must think biosecurity by not making the situation worse, for example, avoid rushing into a barn/stall without having a plan to leave it and must respond to the 'worst-case scenario' until a diagnosis is made.

In the case of a positive (suspect) diagnosis, management procedures based on disease-specific guidelines must be adopted. If there is no diagnosis, biosecurity measures must be maintained for a minimum of 21–28 days after the last case had developed, the differential diagnosis list must be expanded, and infectious disease experts and state health officials must be contacted.

Biosecurity measures have assumed a much greater level of significance based on the experiences gained by many veterinarians and support personnel engaged in managing outbreaks of life-threatening equine salmonellosis mainly in referral hospitals and, more recently, neurological disease associated with EHM at racetracks, showgrounds with large horse populations, and tertiary referral hospitals. Most tertiary referral hospitals, particularly those at universities, have infectious disease control policies and procedures for horses and other species that are updated regularly. Infectious disease control strategies (policies and procedures) should be developed for private practices (and individual equine operations) to cover on-site horse health admissions, accommodation, patterns of personnel and animal traffic on-site, disinfection, waste management, and off-site farm/stable/barn precautions by veterinarians and other personnel.

Biosecurity is only as effective as the acceptance of and compliance with regulations by all personnel, for example, the equine influenza outbreak that emanated from a quarantine center in Australia. Moreover, biosecurity measures however well developed and accepted cannot be taken for granted, for example, spread of foot-and-mouth disease virus from Pirbright, England (foot-and-mouth disease virus World Reference Laboratory) on the tires of contractors' vehicles.

Biosecurity Measures to Limit Infectious Disease Spread

Biosecuity for the technician at a veterinary practice and for the horse owner or caretaker is critical to managing the introduction of an infectious agent. The most common means of spread is through the introduction of a new horse, particularly a horse that is returned from a hospital to a property. New horses should be isolated from the resident population for a minimum of 14 days, ideally for 30 days. Clinical condition and temperature should be monitored daily. Supplies should be separated. The recent arrival should be attended to last. Manure and bedding should not be spread on the fields. Hand washing in running water with soap after handling horses (waterless hand foams or gels if no running water) should be mandatory even if gloves have been worn.

Vaccination is not 100% preventive but is critical to control an infectious disease as exposure is unlikely to be prevented. Vaccination decreases the severity of clinical disease and serves to increase resistance against certain diseases in individual horses and in horse populations.

Quarantine is an important aspect of implementing biosecurity measures. Ideally, there should be a separate facility used for any horse that has left the premises for showing or breeding (commingling) and not just for sick or new horses.

Technicians and handlers should initiate a traffic pattern, wear disposable gloves, booties, and barrier clothing with at-risk and sick horses, and practice the procedure for removing protective gear (without further contamination). Cleaning and disinfection frequency should be enhanced during an outbreak and hand hygiene is crucial.

Visitors should be restricted to one entrance and exit. Vehicle tires and visitor's shoes should be disinfected and footbaths and overboots must be provided. Records of visitors and their horse contact must be kept.

It is critical to be vigilant away from the horse premises (e.g., avoid direct contact with a diseased horse at an event or activity and do not touch horses' noses going down the line from stall to stall) and follow a specific biosecurity procedure on returning.

Biosecurity requires common sense and the ability to communicate clearly. The mantra is to adopt precautionary measures to include waste management, cleaning and disinfection, environmental control, and storage and use of equipment and supplies. Biosecurity plans for any horse facility are never completed. They may be patterned by a particular outbreak and should be reevaluated and updated regularly.

Equine Herpesvirus-1 Neurological Disease

EHV-1, a ubiquitous virus among horses, was occasionally responsible for neurological disease. However, when groups of horses became affected by a neurological disease at the same time, diagnostic results showed the agent to be a variant of EHV-1, prompting the adoption of strict biosecurity measures. Much was learned in a short time frame. Increased risk for exposure in recent US outbreaks included commercial shipping with horses collected from multiple sites and venues, such as quarantine stations, rest farms and stops, veterinary clinics, race tracks, polo events, and hunter/jumper dressage shows, and movement of animals before the disease is recognized. Other important risk factors involved recent exposure to sick horses, including those having increased rectal temperature without evidence of recent surgery, vaccination, or other medical condition associated with fever, and recent exposure to horses that have acute neurological signs, especially if a noninfectious cause has been ruled out.

EHVs are major equine pathogens. There are nine EHVs, not all are associated with overt clinical problems. EHV-1 and EHV-4 are α-herpes viruses transmitted by the respiratory route, infect the upper respiratory tract epithelium, and are the most common.

EHV-1 myeloencephalopathy (EHM) is not a new disease; however, neurological disease associated with EHV-1 (causing EHM) appears to be increasing in incidence in the United States and Europe, although it remains a relatively rare disease in the horse population. Outbreaks of EHM have occurred among pleasure horses and racehorses, show jumpers, horses referred to tertiary clinics, and quarter horses at a cutting horse show. This disease has had significant economic and equine activity impacts. Some racetracks ordered quarantine for several weeks for thousands of horses sent to compete after multiple cases of EHV-1 causing neurological disease occurred, resulting in deaths of several horses. Shows were canceled in many Western states and interstate movement of horses was restricted after the cutting horse event. Some tertiary referral centers have imposed strict quarantine protocols after clinical cases of EHM were confirmed at their facilities.

EHV-1 is highly contagious and is a serious concern and threat to those involved with horse shows, events, farms, auctions, and clinics with a high volume of horse traffic. Certain strains of EHV-1 that affect the central nervous system have resulted in outbreaks of EHM with high morbidity and case fatality. Horses with neurological signs have large viral loads in their blood and nasal secretions. The incubation period is highly variable depending on the host, pathogen, and the environment (including stress) and ranges from 1 to 12 days but often 1 to 3 days. Once sick, the horse can shed the virus and be a source of infection for 7–10 days and for up to 28 days in some instances. Horses can be clinically normal and still shed the virus.

The virus may be disseminated by nasal and respiratory secretions for up to 11 m (35 feet) (animals should be separated by 300 feet) and can survive a wide temperature range (surviving 3–4 weeks in the environment without a host). Transmission can occur directly by nose-to-nose contact and indirectly by vectors, contaminated hands, shoes, clothing and equipment, inanimate objects, such as water buckets, brushes, bits, clippers, etc., and aborted placenta and fetal tissues.

Clinical signs of EHV-1 infection vary from mild respiratory disease to severe EHM. Neurological signs are generally, although not exclusively associated with a recent history of pyrexia, respiratory disease, or abortion in the affected animal or more likely a herd mate. Respiratory signs may be minimal and of short duration. Increased rectal temperature may be the only clinical sign. There may be two fever spikes – an initial temperature rise that is usually mild (101.5–102.5), and transient for up to 4–5 days, and may be missed; the horse may remain clinically normal or develop respiratory disease

with signs of nasal discharge, an increased temperature (>102.5), and coughing. The second wave starts between days 5 and 7 and can continue until day 10 coinciding with the viremia. Infected pregnant mares may spontaneously abort within a week to several months of being exposed, although the mares may have shown only limited initial signs. Other signs include scrotal edema and loss of libido in stallions, uveitis, dependent and facial edema in adults, nasal discharge, and pneumonia in young foals.

Neurological Signs

Expression of clinical signs in the relatively small number of EHM cases is a consequence of vasculitis followed by hemorrhage, thrombosis, hypoxia, and secondary ischemic degeneration in the central nervous system.

Signs include progressive or acute onset ataxia (incoordination) or recumbency approximately 1 week after viral exposure that affects a single animal or group of at least 2 years of age. Signs may progress rapidly over 24–48 h. Pyrexia and depression are usually noted 3–4 days before the onset of neurological signs, which include pelvic limb ataxia, paresis, or paralysis and may affect all four limbs. Signs are usually more severe in the pelvic limbs than in the thoracic limbs and may lateralize. There may be signs consistent with lower motor neuron dysfunction, urinary incontinence, reduced tail tone, penile or vulval flaccidity, and loss of perineal sensation. Tetraplegia and death may supervene. Paralysis and recumbency carry an increasingly poor prognosis. Horses rarely show abnormal mentation or develop cranial nerve signs. Most horses exhibit mild to moderate neurological signs and stabilize rapidly becoming normal 3–6 months after onset of clinical signs, although residual deficits may persist.

EHV infections are ubiquitous. Most animals are infected during the first year of life. The pathogen is latent. Up to 80% of horses (possibly more) are purported to be latently infected with EHV-1 or EHV-4, cannot easily be identified, and serve as important reservoirs.

EHM outbreaks have occurred in late fall through late spring, possibly coinciding with pregnancy and lactation associated with abortigenic EHV-1 in mares and respiratory EHV-4 transmission among foals. EHM outbreaks may be dependent on the reactivation of latent EHV-1, EHV-4, or both viruses on introducing a new animal into a population and associated stress. EHV-1 (and possibly EHV-4) can remain latent for the horse's entire life. Under stress conditions, the virus may replicate and is shed in nasal secretions. Other horses can be exposed and infected without necessarily the shedder becoming ill. Outbreaks may represent new infections with a virulent strain that occurs in a large number of horses over a short period of time.

Immunology

High virus-neutralizing titers (humoral immune response) are detected within a few days of the onset of neurological signs. However, there is no correlation between the level of serum antibody titers and virus protection. Viremia occurs in the presence of neutralizing antibodies, as apparent in vaccinated or naturally immune horses. Cellular immunity is critical and complex and plays an important role in clearing EHV-1 leukocyte-associated viremia. EHV-1 exhibits similarities with many herpes viruses and may be capable of modulating (evading) the horse's immune response.

Therapy

Supportive therapy may be needed for several weeks to months and includes slinging the horse if it is weak in the pelvic limbs or is recumbent. Ataxic horses that remain standing may be better on a (firm) ground surface than in a stall. Use of nonsteroidal anti-inflammatory drugs), such as flunixin meglumine, makes the patient feel better, and the antiherpesvirus drugs widely used in human patients, acyclovir and valocyclovir, may be beneficial early in the course of the disease or prophylactically.

Prognosis

Many horses stabilize and recover completely in weeks to months. Some retain residual neurological deficits. The prognosis is worse if the horse is recumbent in the first 24 h.

Prevention

Efficacy of EHV-1 vaccines is questionable and randomized controlled studies are lacking. Vaccine products provide varying levels of protection against respiratory disease (modified live virus (MLV) and killed) and abortion (killed and some MLV). Anecdotal evidence suggests that vaccination may offer reasonable protection against a flare up of respiratory disease (although few data exist). Protection against abortion is less clear as the prevalence is extremely low. Current EHV-1, EHV-4, or EHV-1/4 vaccines are not effective against the neurological disease. At best the vaccinated horse that develops neurological disease will shed fewer virus particles and be less likely to spread the disease to other horses. There is evidence of an association between neurological disease and recent and regular vaccinations with mono- or bivalent killed vaccines.

On premises with confirmed EHM, exposed horses should not receive booster vaccinations. However, the immune status of nonexposed horses and those that must enter the premises if not vaccinated against EHV-1 within the past 60 days should be enhanced by booster vaccination. The reduced nasal shedding of infectious EHV-1 by recently vaccinated horses may indirectly help to protect other horses by reducing the dose of exposed virus.

Regulations

State animal health officials provide information on enhanced requirements in the face of an outbreak.

Several states require reporting of EHV-1 (known as EHM) and quarantine of affected and in-contact horses.

Clinical Outcomes

Clinical outcomes in EHM outbreaks are modulated by many risk factors, including the host immune system (vaccination,

cytotoxic T-lymphocytes, and major histocompatability complex), stress (lactation, double infections, and racing), and the genetic characteristics of virus isolates. The proportion of animals showing neurological signs when infected with the neuropathic strain varies with each outbreak. Neurological diseases outbreaks are relatively rare compared with non-neurological disease outbreaks, suggesting that the majority of EHV-1 strains encode the nonneuropathic strain.

Diagnostic Testing

Identification of the pathogen requires nasal swab (shedding may be of short duration) and whole blood sample (for buffy coat) at the onset of clinical signs (temperature). Polymerase chain reaction provides the most rapid testing. Real-time polymerase chain reaction (RT-PCR) assays are used to detect and differentiate neuropathic from nonneuropathic EHV-1 strains.

RT-PCR assays detect only viral genomic deoxyribonucleic acid in the specimens tested and are unable to distinguish between lytic, dead, or latent virus and do not predict clinical outcome. Interpretation of PCR viral detection for EHV-1 should be done only in the context of the presenting signs for disease in the horse being tested. The significance of a positive PCR in an asymptomatic horse is unknown.

Horses with high fevers and signs of coughing or mild nasal discharge, with or without neurological deficits, should be tested for EHV-1 by PCR diagnostics if there are no other explanations for their signs of disease. Detection of a positive PCR for EHV-1 in such instances should warrant isolation and limited movement of exposed horses.

Management of Outbreaks of Neurological Disease Associated with EHV-1

If the horse is at high risk for exposure, primary security measures must be implemented to include stopping any horse movement at the event or hospital, confining the horse to a stall or moving immediately to a separate facility and placing all horses with clinical signs in this area. Disease surveillance must be introduced by taking and recording rectal temperature twice daily, having the owner/caretaker/technician contact the veterinarian immediately if findings are abnormal, and having the veterinarian perform a physical examination on suspect horses and initiating clinical and diagnostic testing. Access must be limited to essential personnel, veterinarians, technicians, and caretakers who should receive training in and follow biosecurity protocols.

Once a positive horse is identified, either state or voluntary quarantine must be imposed for 21 days after the last clinical sign (usually the temperature rise), although quarantine may last at least 28 days. Recommended exit (discharge) requirements include testing negative for EHV-1 shedding from the nasal cavity and no virus detected in blood.

It is vital to identify and implement a secondary perimeter to allow horses to be exercised and enable limited continuation of internal organized activities. This could be the entire facility, venue, or township. All animals within the secondary perimeter are considered free of infection but at increased risk of exposure and development of disease. Enhanced surveillance is critical. Horses can travel only from outside of this facility and are under the regulation of the veterinarian in charge. Arrival and departure of any horse must be recorded. Every horse should have its temperature taken twice daily and be physically inspected for disease daily. All horses admitted must have a current health certificate and should be vaccinated at the recommendation of the veterinarian in charge. To exit, a horse must have a health certificate endorsed 'free of EHV-1' signed by the veterinarian in charge and with vaccination requirements specified by the receiving venue. Of particular note, the PCR test does not provide a diagnosis in the absence of clinical disease and should not be used as a screening tool in clinically normal nonexposed animals.

Methicillin-Resistant *Staphylococcus aureus*

Staphylococcus aureus is a common bacterium that colonizes the skin and is associated with disease in many species. MRSA is one of the most important nosocomial pathogens and is associated with increased morbidity, mortality, duration of hospitalization, and treatment costs in humans. MRSA is an important emerging pathogen of the horse. MRSA is typically resistant to all β-lactam antibiotics (penicillin and cephalosporin families) and to many other antibiotics. *Staphylococcusx intermedius*, another coagulase-positive *Staphylococcus* spp., occurs in horses and can be methicillin resistant. MRSA in horses is associated with wound and surgical site infections, cellulitis, catheter site infections, pneumonia, septic arthritis, skin infections, endometritis, and peritonitis.

Humans can transmit MRSA to horses. Approximately 25% healthy children and adults can carry the organism in their nose or on the skin. Bacterial carriage causes no ill effects. However, a wound or an illness requiring hospitalization can result in an active infection. Approximately 0–5% horses carry MRSA in their nasal passages with a far lower percentage on the skin or in the intestinal tract. Carrier rates of up to 50% were found on some farms with a history of MRSA in horses. Carrier horses can transmit MRSA to other horses and may develop active infections under certain conditions. Carrier horses can transmit MRSA to humans. There is an equine-adapted strain that is uncommon in humans unless they have contact with horses. Studies of equine veterinarians have reported colonization rates of 10–14% with the equine strain of the bacterium.

Eighty percent of horses with MRSA infections survived in a multicenter study. Specific complication included prolonged hospital stays and additional surgeries, particularly if pneumonia or wound infections supervened. Adequate antibiotic options (topical and systemic) exist in most cases and culture and sensitivity will guide selection. The antimicrobial resistance pattern from many studies shows that MRSA isolates are frequently resistant to gentamicin, tetracycline, and trimethoprim-sulfa. Early detection of the pathogen and treatment are crucial to the outcome. Drugs, such as vancomycin, used in stubborn human multiple-drug-resistant pathogens, such as MRSA cases, should be avoided in horses and other animals.

Control of Methicillin-Resistant *Staphylococcus aureus*

Control involves implementation of all the elements of the aforementioned biosecurity measures. Ideally, horses infected or colonized with MRSA should be isolated. This may be difficult to achieve on farms. However, prevention of nose-to-nose contact and transmission by people and to people is of paramount importance. Hand hygiene is crucial even after wearing disposable gloves to touch a horse. Tissues can be quickly contaminated. Bleach solution (1:10) or quaternary ammonium compounds can be used to decontaminate the treatment area or stall. Stringent cleaning protocols must be effected for common equipment items, such as an ultrasound unit and treatment carts. MRSA organisms survive well in dust.

Standard operating procedures should be adopted for wounds, for example, at this teaching hospital, all surgical wound infections must have a sample obtained for culture and sensitivity before specific therapy is started. Furthermore, a patient who has received previous antibiotic therapy for a wound or infection that remains unresolved must have a sample obtained for culture and sensitivity at the initial examination.

Strangles in Horses

This is not an emerging disease of horses, although it remains an important infectious disease for susceptible individuals or populations. The causative agent is *S. equi* subspecies *equi*, (Lancefield Group C, Gram positive β-hemolytic bacterium). There is a close genetic relationship between *Streptococcus equi* subspecies *equi* and *Streptococcus zooepidemicus*, the former being a clone of the more genetically diverse *S. zooepidemicus* and isolates of these two organisms show at least 92% homology. Immunity is species specific; immunization with *S. zooepidemicus* does not protect against challenge by *S. equi equi*. *Streptococcus equi* (as subsequently described) is not a normal inhabitant of the equine upper respiratory tract. PCR may aid in confirming *S. equi* isolates but not active infection.

Epidemiology

Infection occurs primarily in horses 1–5 years of age and in geriatric and immune-compromised horses. In susceptible populations, morbidity is high (up to 100%) and mortality low (10%) with appropriate treatment.

Approximately 75% horses are immune for 5 years or longer if infected and not treated. Immunity is not lifelong. Most animals recover from the disease and eliminate *S. equi* over a 4–6-week period. Up to 10% affected animals continue to shed *S. equi* intermittently for prolonged periods after resolution of clinical signs.

The organism is transmitted by direct contact with nasal secretions or lymph node discharges from infected horses or by exposure to fomites. Highly concentrated or transient populations are at greater risk of contracting the disease. A strangles outbreak suggests a recent addition to a stable (premise) and a recovering horse may shed *S. equi* for several weeks. In a closed herd there is most likely to be exposure to an asymptomatic chronic carrier of the organism in the guttural pouch and paranasal sinuses. The organism survives for long periods in the environment depending on temperature and substrate.

Pathogenesis

Streptococcus zooepidemicus usually infects young horses through the nose or the mouth and colonizes the mucosal surface and tonsillar tissues of the nasopharynx. By contrast, *S. equi* is a poor colonizer. Rather than colonizing the epithelial surface, *S. equi* quickly invades tonsillar tissues of the oro- and nasopharynx and multiplies rapidly producing many extracellular microcolonies. Virulence factors contribute to pathogenicity. At the onset of fever, tonsillar tissues and one or more mandibular and retropharyngeal lymph nodes are heavily infiltrated by neutrophils and long chains of extracellular *S. equi* organisms. Mutant *S. equi* lacking virulence factors are not seen in draining lymph nodes.

Clinical Signs

The incubation period is 2–6 days, typically with fever (>103 F), lethargy, depression, and serous nasal discharge that becomes mucopurulent. Submandibular and retropharyngeal lymph nodes initially firm become fluctuant and rupture after 7–10 days (retropharyngeal lymph node abscesses may rupture internally into a guttural pouch).

Lymphadenopathy, if severe, may lead to dysphagia and respiratory distress, hence the term 'strangles.'

Pus in the guttural pouches may become inspissated, leading to chondroid formation enabling *S. equi* to persist for up to several years and be transmitted to naïve horses. There is a soft moist cough occasionally. The average course of the disease is 3 weeks. Atypical infection is associated with mild signs and minimal lymph node abscess development.

Pyrexia is the consequence of the acute phase inappropriate immune response generated by *S. equi* and can be monitored and detected in the absence of bacterial shedding. Once a strangles outbreak is confirmed, presumptively infected pyrexic horses may be identified and isolated before the organism is passed on to in contacts.

Diagnosis

Strangles diagnosis is based on clinical signs and identification (culture) or detection (PCR) of *S. equi* from a lymph node, nasopharyngeal swab, or lavage fluid from a guttural pouch. Chronic asymptomatic carriers pose the greatest difficulty in identification. Culture of lavage samples collected endoscopically is considered the gold standard for carrier detection. Serology is becoming widely used. The enzyme-linked immunosorbent assay (ELISA) for SeM protein is useful to detect recent but not current infection, assess the need for vaccination, identify horses predisposed to purpura hemorrhagica (PH), and to diagnose *S. equi*-associated PH and metastatic abscessation.

Treatment

Treatment is contentious and is a function of the stage of the disease. Penicillin is the drug of choice, although the organism is sensitive to many antimicrobials. Treatment plans have been developed, for example, (1) Horse exposed: penicillin helps to prevent seeding of the pharyngeal lymph nodes. It should be

continued for as long as the horse is exposed to the organism. Once stopped, there is a risk of the horse developing strangles. (2) Horse exhibiting signs without abscessation: penicillin may arrest disease progression. The horse should be isolated. (3) Horse exhibiting signs of lymph node abscessation: penicillin slows progression of lymph node abscessation; thus, the abscess should be hot packed, lanced, and flushed. The horse should be treated in isolation, and (4) horse systemically ill or developed complications: supportive care and penicillin should be provided.

Complications

The major complications are:

1. 'Bastard strangles,' in which metastatic (internal) abscesses occur in the mesentery or parenchymatous organs and even in the brain promulgated by inadequate antimicrobial therapy, although abscesses can occur naturally at those sites following infection. Clinical signs include intermittent colic, periodic pyrexia, anorexia, depression, weight loss, and neurological dysfunction.
2. PH – an aseptic vasculitis following reexposure to *S. equi* by natural infection or vaccination. Affected animals have higher IgA titers to SeM and to nonspecific proteins in the *S. equi* culture supernatant and immune complexes of IgA and M-like proteins. There is an association with the attenuated live intranasal *S. equi* vaccine. Clinical signs include a mild transient reaction to a severe and fatal form, with pitting edema of limbs, trunk, and head; petechiation and ecchymoses of mucosae; and colic. Vasculitis may lead to skin sloughing and infarcts of skeletal muscle. Death can result from pneumonia, cardiac arrhythmias, renal failure, or gastrointestinal disorders.

Other complications of strangles include guttural pouch empyemia and chondroid formation; septicemia, development of infectious arthritis, pneumonia, and encephalitis; retropharyngeal abscesses; laryngeal hemiplegia; tracheal compression following abscesses in the cranial mediastinal lymph nodes; endocarditis or myocarditis following abscess formation; suppurative necrotic bronchopneumonia; and two types of myopathies (myositis) – one a vasculitis with infarction of skeletal muscle and pulmonary and gastrointestinal tissues characterized by unrelenting pain; the second affecting quarter horses showing malaise, significant muscle atrophy, and chronic active rhabdomyolysis.

Control During an Outbreak

Control follows the detailed biosecurity measures that are integral to the sensible management of an infectious disease. Specifically, prevent the spread of infection to horses on other premises and to new arrivals. Ideally, all movement of horses on and off the premises must be stopped and new horses should be isolated for 3 weeks. Identify symptomatic and asymptomatic carriers by sampling nasopharyngeal or guttural pouch regions at weekly intervals and test for *S. equi* by culture and PCR. Infectious horses should be isolated from those screened negative for *S. equi*. Rectal temperature should be taken twice daily. The isolation area should be cordoned off and staff should be dedicated to this area with protective clothing and footwear. The area and contents should be disinfected. After clinical signs disappear, perform at least three consecutive nasopharyngeal swabs or lavage for *S. equi* at approximately weekly intervals and test by culture and PCR to detect carriers.

Prevention

Less immunity is provided following vaccination than that following recovery from natural disease.

The intramuscular killed (*S. equi* extract) vaccine with an adjuvant is used more widely than the intranasal attenuated *S. equi* live culture, which should not be administered with parenteral injections or at the time of invasive procedures. No current vaccine guarantees prevention of strangles in vaccinated horses.

Vaccination of infected animals during an outbreak may be associated with PH, and vaccination during an outbreak is controversial.

The 2005 American College of Veterinary Internal Medicine Consensus Statement recommends measuring SeM-specific antibody titers by ELISA before vaccination and to not vaccinate if titers $\geq$1:3200. Horses previously given the intranasal vaccine, nonthoroughbreds and nonwarmbloods, are significantly more likely to have higher titers ($>$1:1600).

Generation of an immune response to multiple protective epitopes may be required to achieve the greatest protection. Development of a strangles vaccine (ideally with differential diagnostic potential) benefitting from an improved immunogenicity and safety profile is a priority to achieve widespread protection against strangles.

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Biotechnology Crop Adoption: Potential and Challenges of Genetically Improved Crops

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Introduction

The ultimate grand challenge of our times is nothing less than the sustainability of the Biosphere and our place in it. Can we learn how to meet our needs today without compromising the ability of future generations to meet theirs? With the 7 billionth member of humanity having joined the planet, achieving global food security sustainably is the single most important issue facing civilization and, by implication, the planet in the next 30 years. Over the coming decades, food and agricultural production systems must be significantly enhanced to respond to a number of transformative changes, such as a growing world population; increasing international competition; globalization; shifts to increased meat consumption in developing countries; and diet-related disease and rising consumer demands for improved food quality, safety, health enhancement, and convenience. New and innovative techniques will be required to ensure an ample supply of healthy food by improving the efficiency of the global agriculture sector. To confound this situation the inequity between the affluent and the developing countries will continue to grow and only a handful of technologies are sufficiently scale neutral to help with redressing this imbalance. Of even greater concern is the very immediate need of global food security. In 2012, the United Nations issued an unprecedented warning about the state of global food supplies. They noted that global food reserves have reached their lowest level in almost 40 years and that failing harvests in the United States, Ukraine, and other countries in 2012 have eroded reserves to their lowest level since 1974 when the global population was much lower. They warned that world grain reserves are so dangerously low that another year of severe weather in the United States or other food-exporting countries could trigger a major hunger crisis by 2013. Clearly, unprecedented needs require effective solutions (Eliasson, 2012).

Over the millennia many technologies have been developed and used to enhance productivity of the original coterie of cultivated crops and to bring more into the domestic fold. In the latter half of the twentieth century, major improvements in agricultural productivity were largely based on selective breeding programs for plants and animals, intensive use of chemical fertilizers, pesticides and herbicides, advanced equipment developments, and widespread irrigation programs. This has been a very successful model for raising productivity; yet, these improvements have brought the corresponding problems of an increasing narrow genetic base of crop plants and domestic animals, pests resistant against chemical pesticides, adverse impacts on environmental quality, and capital-intensive production. In addition, from a global perspective, these advances have been the prerogative of more affluent regions. Farmers in developing countries have not had access to many of these technologies and capital-intensive methods of production. During the coming decades, food and agricultural production systems must be significantly enhanced to respond to a number of wide-ranging and far-reaching transformations, including a changing climate, growing world population, increasing international competition, globalization, shifts to increased meat consumption in developing countries, and rising consumer demands for improved food quality, safety, health enhancement, and convenience. New and innovative techniques will be required to ensure an ample supply of healthy food against competing interests and this can only be achieved by improving the effectiveness of all components of the global agriculture sector. Innovation is essential for sustaining and enhancing agricultural productivity and this involves new, science-based products and processes that contribute reliable methods for improving quality, productivity, and environmental sustainability.

At its most basic level food is the source of nutrition to meet daily requirements but is now taking on an ever greater role in the quest for health optimization. The latter focus is a luxury that is primarily the purview of an affluent society and has little relevance in many areas where mere survival is the driving force. From the basic nutrition perspective, there is a clear dichotomy in demonstrated need between different regions and socioeconomic groups, the starkest being addressing injudicious consumption in the developed world and undernourishment in less developed countries (LDCs). Both extremes suffer from forms of malnourishment: one through inadequate supply and the other, in many but not all instances, through inappropriate choices; the latter often influenced by economic considerations. From the food deserts of inner cities to the real barren wastelands of many regions, access to a healthy diet is a challenge. Dramatic increases in the occurrence of obesity, cardiovascular disease, diabetes, cancer, and related ailments in developed countries are in sharp contrast to chronic undernutrition and genuine malnutrition in many LDCs. Both problems require a modified food supply, and the tools of biotechnology, although not the sole solution, do have a significant part to play.

Worldwide plant-based products comprise the vast majority of human food intake, irrespective of location or financial status (Mathers, 2006). In some cultures, either by design or default, plant-based nutrition comprises almost 100% of the diet. Given this one can deduce that significant nutritional improvement can be achieved via modifications of staple crops. New and innovative techniques will be required to improve the efficiency of the global agriculture sector to ensure an ample supply of high quality food. To confound this situation the inequity between the affluent and developing countries will continue to grow and only a handful of

technologies are sufficiently scale-neutral to help with redressing this imbalance. In October 2009, the United Nations' Food and Agriculture Organization (FAO) determined that farming in developing countries needs US$83 billion of annual investment for production to feed the world in 2050. The 2008 World Bank Development Report emphasized, "Agriculture is a vital development tool for achieving the Millennium Development Goals that calls for halving by 2015 the share of people suffering from extreme poverty and hunger" (World Bank, 2008). The Report notes that three out of every four people in developing countries live in rural areas and most of them depend directly or indirectly on agriculture for their livelihoods. It recognizes that overcoming abject poverty cannot be achieved in sub-Saharan Africa (SSA) without a revolution in agricultural productivity for resource-poor farmers in Africa, many of whom are women. Likewise the FAO publication, the State of Food Insecurity in the World 2011, highlights the differential impacts that the world food crisis of 2006–08 had on different countries, with the poorest being most affected. Although some large countries were able to deal with the worst of the crisis, people in many small import-dependent countries experienced large price increases that, even when only temporary, can have permanent effects on their future earnings capacity and ability to escape poverty. African smallholder farmers are some of the most impoverished people in the world (43% are women) and they account for 80% of food production in SSA. Some people argue that their future will be driven by the private sector – the UK's Department for International Development has been working to link up businesses with smallholder farmers. Giant food retailers are also starting to realize that they need to look after African smallholders to safeguard their future. Although not the only answer, the technological advances of biotechnology can help to assist with providing food sufficiency and economic independence for such resource-poor regions.

Most of the innovative technologies that have been applied to production agriculture have come into common usage without much controversy or even knowledge by the average consumer. If asked, the majority of respondents would no doubt agree that this involves at some level new, science-based products and processes that contribute reliable methods for improving quality, productivity, and environmental sustainability. In the past we have not regulated changes in agriculture based on unpredictable socioeconomic consequences. However, some recent innovative technologies, namely biotechnology and more specifically recombinant deoxyribonucleic acid (DNA) technology, have inspired debate in a manner unlike any other previous technological development. Although biotechnology has introduced a new dimension to such innovation, offering efficient and cost-effective means to produce a diverse array of novel, value-added products and tools is not viewed with unmitigated optimism by all existing and potential stakeholders. The stakeholders involved in this debate are many and diverse, ranging from academic and industrial scientists to conventional and organic producers, to international, national, federal, state, and local government and nongovernmental organizations (NGOs) and agencies, to activist groups and, of course, consumers. How this technology is viewed depends very much on the perspective from which it is viewed and the goals and objectives of the different players involved. And this perspective is formed by the complexity of the prism through which it is viewed. Each individual's prism is built of our cumulative life experiences, educational background, innate prejudices, world view, and, of course, personal objectives. To most producers, and academic and industrial researchers, biotechnology is seen as offering a new dimension to innovation, providing efficient and cost-effective means to produce a diverse array of value-added products and tools. To some of our national and international markets it is seen as a trading barrier or chip, depending on which side of the fence one is standing. To others it represents an unnecessary, and for some, unnatural risk at a broad level to our food system and environment and at a very fundamental level to a way of life or code of beliefs. Unfortunately, as in every walk of life, there are some who seize on these many nuances of perception, and indeed fear, to propagate their own, covert or otherwise, agenda. Although on the surface scientific facts may appear immutable, how those facts are presented within a socioeconomic context makes for an interesting study of the stratagems used by the diverse stakeholders to advance their own agenda for any given target demographic. These tactics are played out on local and world stages and often by the same players who customize their approach depending on the context.

The vast majority of biotechnology products approved to date are in the area of agronomic traits most specifically to protect against biotic stress. The principal focus in the immediate future will remain on agronomic traits, especially the area of pest control but with an increasing interest in abiotic stress tolerance, which is gaining prominence as external pressures from climate change to land use is challenging productivity. In 2013, 175.2 million hectares of biotech crops were grown globally, at an annual growth rate of 3%, up 5 million from 170 million hectares in 2012. Of the 18 million farmers who grew biotechnology crops in 2013, more than 16.5 million (90%) were in developing countries, which produced more global biotechnology crops than industrial countries (52% vs. 48%), and considerable more emerging economies (19% vs. 8%) grew these crops (James, 2014). More than 7.5 million small farmers in China and another 7.3 million small farmers in India collectively planted a record 14.5 million hectares of biotechnology crops (**Figure 1**; James, 2014). In 2013, Bangladesh approved their first genetically modified (GM) crop Bt eggplant. The Sudan became the fourth country in Africa, after South Africa, Burkina Faso, and Egypt, to commercialize a biotechnology crop – Bt cotton – in 2012. Iran and Cuba also planted GM crops, but it is challenging to document numbers for these countries. In 2010, Pakistan planted Bt cotton, as did Myanmar, and notably Sweden, the first Scandinavian country to plant a biotechnology crop, planted 'Amflora,' a potato with high amylose starch for industrial applications. Germany briefly resumed adoption of biotechnology crops by planting Amflora in 2010. However, both ceased after Amflora was pulled from the market in 2012. BASF cited opposition to the technology as their reason for withdrawing the potato. Currently, only one GMO crop is grown commercially in Europe – an insect-resistant variety of maize developed by Monsanto. It is sown on approximately 100 000 ha (247 000 acres) of farmland, mainly in Spain.

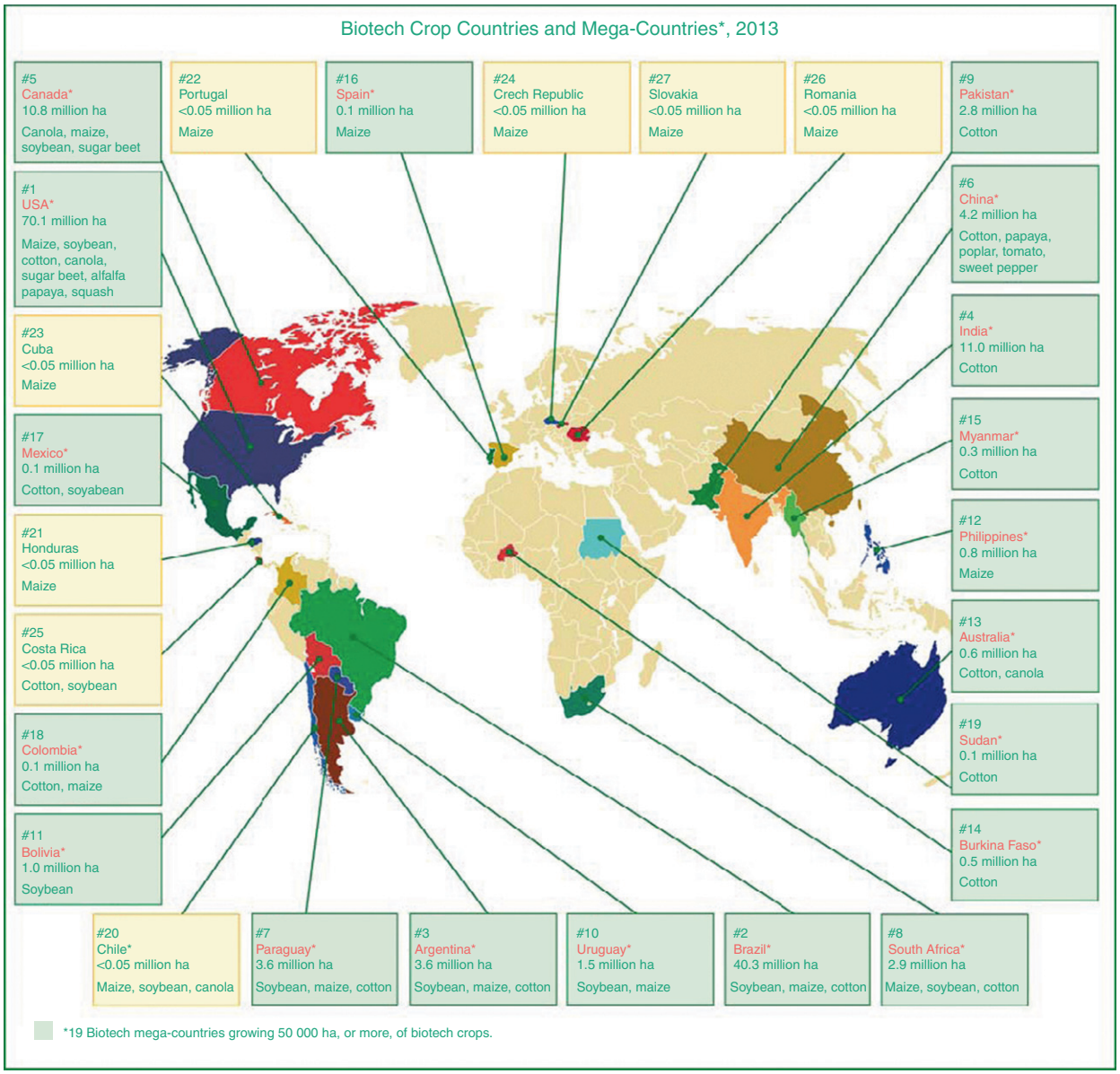


Figure 1 Adapted from James, C., 2013. Global Status of Commercialized Biotech/GM Crops: 2012. ISAAA Brief No.44. Ithaca, NY: International Service for the Acquisition of Agri-biotech Applications. Available at: http://www.isaaa.org/ (accessed 24.02.13).

Agronomic Traits and Sustainability

Agricultural biotechnology already has helped farmers around the world boost their productivity and grow crops in more ecologically healthy fields while allowing much more efficient use of resources. This technology allows reduced tillage, which cuts down on greenhouse gas emissions, water runoff, soil erosion, and fuel consumption. Improved pest control increases yields on existing acreage and reduces the pressure to convert forests and wildlands into farmland. Research by Brookes and Barfoot shows that, in the first 15 years of GM crop cultivation, pesticide use (which includes both insecticides and herbicides) fell by more than 448 million kg worldwide, or a decline of 9% (see Section 'Relevant Websites'). In addition to the obvious direct benefits, less spraying means fewer tractor passes, contributing to lower carbon dioxide emissions. The technology has reduced pesticide spraying by 443 million kg (approximately 9.1%) and, as a result, decreased the environmental impact associated with herbicide and insecticide use on these crops, as measured by the indicator the Environmental Impact Quotient, by 17.9%. In addition, insect-resistant maize has a collateral effect – less insect damage results in much less infection by fungal spores, which reduces mycotoxins that are known health risks resulting in diseases such as liver cancer in humans and animals. Bt corn resulted in a 90% reduction in mycotoxin fungal fumonisins. In addition to the obvious health benefits, the total US economic benefit is estimated to be approximately

US$23 million annually (Wu, 2006). The only 'natural' way to control those fungi is the use of copper sulfate, which has one of the highest toxic hazard ratings of acceptable pesticides and selects for antibiotic-resistant bacteria in the soil (Berg *et al.*, 2005).

Meanwhile, the economic benefits experienced by large- and small-scale farmers in both industrialized nations and lesser developed countries have been significant. The Brookes and Barfoot (2014) analysis shows that there have been very significant net economic benefits at the farm level amounting to US$116.9 billion during the 17-year period, 1996–2012, of which 58% were due to reduced production costs (less plowing, fewer pesticide sprays, and less labor) and 42% due to substantial yield gains of 377 million tonnes. The corresponding figure for 2012 alone was 83% of the total US$18.7 billion gain due to increased yield (equivalent to 47 million tonnes) and 17% due to lower cost of production (Brookes and Barfoot, 2014). The majority (51.2%) of these gains went to farmers in developing countries. GM technology has also made important contributions to increasing global production levels of the four main crops, having added 110 million tonnes and 195 million tonnes, respectively, to the global production of soybeans and maize since the introduction of the technology in the mid-1990s. In addition, the environmental footprint associated with pesticide use was reduced by 18.5%, and there was a reduction in carbon dioxide emissions in 2012 alone by 26.7 billion kg, equivalent to taking 11.8 million cars off the road for 1 year (Brookes and Barfoot, 2014).

Phelan in 2007 argued that there are two major threats to food production: farm subsidies for biodiversity-friendly farmingand expansion of protected areas to protect biodiversity (approximately 15% of arable land). He maintains that neither work is intended and both can damage biodiversity. But, in each case, there is much at stake for vested interest groups. Coming from what arguably may be considered an alternative perspective, a 2005 paper from the Royal Society suggested that intensive high-yield farming on less land is better for wildlife than 'wildlife friendly' less-efficient farming (Green *et al.*, 2005). They provide convincing evidence that without yield increase land use will double by 2050 and that this effect will be especially significant in developing countries, such as China and India, where without greater productivity four times the land area will be needed to support their expanding populations. They show that in Latin America where increased productivity was achieved there was a significant decrease in deforestation; those producers with greatest yield increase had lower land use. This proposition was supported by the demonstration of biotechnology's contribution to conserving biodiversity by saving 108.7 million hectares of land from being converted to agricultural production (James, 2013).

An earlier study by researchers at Denmark's National Environmental Research Institute (NERI) monitored fields of conventional and glyphosate-tolerant sugar beet. They found that the GM plots supported more plant species and insects than the conventional plots, thus providing more food for birds, and other types of wildlife use of transgenic crops increased biodiversity compared with traditional herbicide treatments (Elmegaard, 2001). Proper measurements in the United Kingdom indicate that no-till, (directly compared with plowed organic fields on the same farm and using the same farmer) uses only one-third fossil fuel, uses land much more efficiently, reduces nitrate (and pesticide) runoff by at least half, and increases soil carbon that is lost when plowed. In addition, bird territories are orders of magnitude greater, soil erosion almost vanishes, and soil invertebrates such as earthworms soar in numbers, as do predatory arthropods to keep pests down. Organic fields in the United Kingdom see a threefold rise in weeds on conversion that necessitates use of the plow (Trewavas, 2008).

Therefore, reduced-till agriculture means healthier soil, with reduced erosion and far less carbon dioxide release. Soil carbon sequestration will be an important part of any international strategy to mitigate the increase in atmospheric CO_2 concentrations. By adopting more sustainable management practices, agriculture may play a large part in enhancing soil carbon sequestration across the globe. One way is by reducing the amount of conventional tillage; after long-term tillage soil carbon stocks are depleted. Through reduced-till production, this technology allowed significant reduction in the release of CO_2 emissions in 2011 alone of 23.1 billion kg, which is equivalent to taking 10.2 million cars off the road (Brookes and Barfoot, 2012). In general, cultivation is not a sustainable practice. It is energy intensive, exposes soil to wind and water erosion. It allows rain to compact the soil and increases the oxygen content, thus allowing organic matter to oxidize away. In turn, lower organic matter in the soil allows more compaction and more nutrient loss. Additionally, in warmer and drier climates evaporative water loss may be reduced as residue remains on the soil surface creating a wetter and cooler soil microclimate.

Although North America remains the epicenter for cutting-edge GM research, other regions, namely China, are emerging as contenders on the global stage. Agricultural science is now China's fastest-growing research field with China's share of global publications in agricultural science growing from 1.5% to 5% in 1999 and 2008 respectively (James, 2011). China's early experience with Bt cotton demonstrated the direct and indirect benefits of its investment in plant biotechnology research and product development. In 2002, Bt cotton was grown in 2.1 million hectares by around 5 million farmers. At that time the average Bt cotton farmer had reduced pesticide sprayings for the Asian bollworm from 20 to 6 times per year, applications were reduced by 59–80% compared with conventional cotton (assessed in 3 years of use) and produced a kilogram of cotton for 28% less cost than the farmer using non-Bt varieties. Net revenues increased by US$357–549 ha^{-1} compared with conventional cotton (assessed in 3 years of use). Ultimately, however, it is the social benefits from reducing exposure to insecticides and saving lives that is the real payoff.

The demand for productivity-enhancing technologies by farmers and for cost savings by consumers, the rate of increase in research investments, and success with Bt cotton suggest that products from China's research program will one day become widespread inside China. Indeed, China is emerging as one of the trend setters in the adoption of novel traits as more recently it is setting the pace for new approvals with Bt rice and phytase maize approved on 27 November 2009. Rice

is the principal staple for much of the world and maize is the largest animal feed source. Bt rice has the potential to increase yields up to 8%, decrease pesticide use by 80% (17 kg ha^{-1}), and generate US$4 billion in benefits annually (James, 2011). The phytase approval is a major step forward in approvals as it is the first transgenic since the FLAVR SAVR tomato focusing on a 'quality' trait. However, it is far more than this, both literally and figuratively, as this single trait addresses several issues from nutritional to environmental ones as expanded on later. Two further 'quality' traits are under consideration for deregulation: the Arctic apple, which has been modified to resist oxidation when the apple is cut and the injured cells are exposed to oxygen activating the polyphenol oxidase (PPO) gene. To achieve this effect Okangan have co-expressed PPO genes and have effectively achieved reduced oxidation by silencing the endogenous PPO gene (Carter, 2012). The second is JR Simplot's reduced acrylamide potato, described below.

The first GM crop to be released for commercial cultivation in India was Bt cotton, developed by the Maharashtra Seed Company (Mahyco) in partnership with Monsanto. The approval, which was given in 2002, came after several years of field trials following the biosafety procedures laid down by the government. Three cotton hybrids were granted permission for field sowing in six states for 3 years. For the first season, farmer demand for Bt cotton seed was very high; it is estimated that 44 500 ha of certified Bt cotton were planted by nearly 55 000 farmers (Choudhary and Gaur, 2008). However, the initial events thrived in regions that resembled the area in which they were originally developed but did not perform very well in growing regions with disparate climate challenges. It was not until the trait was introgressed into locally adapted varieties that Bt cotton thrived in all growing regions. Between 2005 and 2006 the biggest impact of this approach was realized. From 3 Bt cotton hybrids in 2002 to 62 in 2006, the rapid deployment of Bt cotton hybrids based on different agroclimatic conditions resulted in decreased insecticide sprays by 39% and increased yields 31%, resulting in increased profit per hectare of 88% or US$250. Over this period of rapid deployment, the average cotton yields increased from 308 kg ha^{-1} to 450 kg ha^{-1} of lint (of this increase, 50% could be attributed to Bt technology). Over this period raw cotton exports also rose from 0.9 million bales in 2005 to 4.7 million by 2006 and 5.9 by 2007. By 2009, 5.6 million resource-poor farmers in India planted 8.4 million hectares of Bt cotton, equivalent to 87% of the 9.6 million hectare national cotton crop. The increase from 50 000 ha when Bt cotton was first commercialized in 2002 to 8.4 million hectares in 2009 represents an unprecedented 168-fold increase in 8 years (Choudhary and Gaur, 2010). Between 2002 and 2008, Bt cotton generated economic benefits valued at US$5.1 billion for farmers, halved insecticide requirements, contributed to the doubling of yield, and transformed India from a cotton importer to a major exporter. Choudhary and Gaur (2010) contended that the deployment of Bt cotton over the years has resulted in India becoming the number one exporter of cotton globally as well as the second largest cotton producer in the world.

However, despite the success of Bt cotton, the expected successful commercialization of Bt eggplant never materialized as an effective opposition managed to scupper its approval. Bt eggplant, or brinjal as it is referred to in India, was found to be effective against fruit and shoot borer (FSB), with 98% insect mortality in shoots and 100% in fruits compared with less than 30% mortality in non-Bt counterparts. The multilocation research trials confirmed that Bt brinjal required, on average, 77% less insecticides than non-Bt counterparts for control of FSB and 42% less for the control of all insect pests of brinjal. The benefits of Bt brinjal translate to an average increase of 116% in marketable fruits over conventional hybrids and 166% increase over popular open-pollinated varieties. Furthermore, the significant decrease in insecticide usage reduced the farmers' exposure to insecticides and results in a substantial decline in pesticide residues on brinjal fruits (Bricknel, 2010). Scientists have estimated that Bt brinjal will deliver farmers a net economic benefit ranging from US$330–397 per acre with national benefits to India exceeding US$400 million per year. However, in February 2010 the environmental minister announced a 6-month moratorium citing, "There is no overriding food security argument for Bt brinjal. Our objective is to restore public confidence and trust in Bt brinjal," clearly articulating the fact that the decision was not based on scientific analysis or risk assessment.

A number of other multi-institutional projects have also been launched in India, including the development of transgenics for resistance to geminiviruses in cotton, mungbean, and tomato; resistance to rice tungro disease; development of a nutritionally enhanced potato with a balanced amino acid composition; and development of molecular methods for heterosis breeding. Other transgenic crops that are awaiting approval for commercial cultivation include transgenic herbicide-tolerant mustard hybrids and nutritionally enhanced potato varieties. However, despite the resounding success of Bt cotton, given the experience with Bt brinjal, it is difficult to be optimistic about the prospects for commercialization of food crops. To reinforce this notion in 2012 an interim report of the technical expert committee (TEC) appointed by the Supreme Court of India recommended a ban on open field trials, including any ongoing trials, for 10 years, which will result in a serious impact on the application of biotechnology to Indian agriculture. However, in October 2012 the Supreme Court decided that before considering this interim recommendation they would seek the views of all stakeholders, including the agriculture ministry and the GM crop industry, on the issue (Times of India, 2012).

A similar context applies to another potentially valuable disease resistance system. Late potato blight is one of the most devastating plant diseases. It is caused by the oomycete *Phytophtera infestans*, a pathogen of the potato and, to a lesser degree, the tomato. No potato has been bred to date that has any measure of resistance to the pathogen. Approximately 15–20% of annual global crop yields of approximately 330 million tonnes fall victim to the disease (and up to 75% in many LDCs) that was introduced to Europe in the mid-nineteenth century and was responsible for the Irish potato famine. The International Potato Center (Lima, Peru) estimates the annual value of these losses to be US$3–5 billion, excluding losses from tomato infestations. In the potato, *Solanum tuberosum*, there are four main dominant genes for resistance to blight infection, *R1* through *R4*. An additional 7 genes were identified, 5 of which are alleles of the complex *R3* locus (for a total of 11 dominant *R* genes). Hybridization with wild Mexican

species began in 1909 and continues to the present. However, in spite of constant effort, *P. infestans* strains have rapidly developed that overcome genetic disease resistance. Chemical fungicides have been developed to control blight but these also succumb to the versatility of the organism. The only acceptable organic control system is copper sulfate, which has a hazard rating of one and is neither desirable nor sustainable as a chemical control system.

The oomycete has two mating types (A1 and A2), both of which appeared first in Mexico; however, only the A1 mating type was present in European potatoes until 1978 when the A2 mating type appeared in Britain and Ireland. The presence of the two mating types greatly enhances gene exchange, leading to accelerated loss of genetic resistance and fungicide control. Potato has a narrow breeding base, is highly heterozygous, and suffers from acute inbreeding depression, making introduction of resistant traits to market-adapted genotypes difficult. Attempts to introduce various resistance genes from wild *Solanum* species have been undertaken in the past century, but *P. infestans* has evolved much faster, enabling it to counteract these breeding efforts. Early resistant potatoes were obtained using true sexual hybridization with wild Mexican species, but these resistant hybrids soon succumbed to mutant strains of the blight. A wild Mexican plant, *Solanum bulbocastanum*, is stably resistant to blight but could not be sexually crossed with potatoes. Transgenic breeding lines have many advantages over other methods to introduce resistance, especially speed and robust resistance. The blight pathogen suppresses the potato defense genes in susceptible plants but is thwarted by successful defense genes in resistance plants. The NBS-LRR (nucleotide-binding site leucine-rich repeat) resistance genes in plants are predominantly localized in the cell cytoplasm, although many move to the nucleus after infection and do not span the cell membrane but are activated by pathogen signals that penetrate the cell. The German company BASF transformed the potato using two plasmids, each containing copies of the wild Mexican *S. bulbocastanum* NBS-LRR resistance genes *Rpiblb1* and *Rpi-blb2*. They confer robust resistance and are a much preferred and more sustainable system than the use of topical fungicides, natural or otherwise. In October 2011 the company requested cultivation and marketing approval as a feed and food from the EU Food Safety Authority (EFSA) for their GM 'Fortuna' potato with a notion of commercializing it by 2015 (BASF, 2011). However, in March 2012 BASF announced the discontinuation of its breeding efforts for all GM crops adapted to European conditions (Dixelius, 2012). It will close its agricultural branch in Europe and is choosing instead to focus on the American and Asian markets.

The vast majority of products approved to date are in the area of agronomic traits, most specifically biotic stress. The principal focus in the immediate future will remain on agronomic traits, especially the area of pest control, but with an increasing interest in abiotic stress tolerance, which is gaining prominence as external pressures from climate change to land use change. On the biotic stress tolerance side the focus is expanding to multitiered control systems. This in theory serves a double advantage, primarily expanding the effectiveness of the broad-based resistance events but also allowing more effective management of the resistance trait as there is less selective pressure when genes are stacked. SmartStax, an eight-trait event developed through collaboration between Monsanto and Dow, takes advantage of multiple modes of insect protection and herbicide tolerance against above- and below-ground insects and provides broad herbicide tolerance, including Yieldgard VT Triple (Monsanto), Herculex Xtra (Dow), RoundUp Ready 2 (Monsanto), and Liberty Link (Dow). It is currently available for corn, but cotton, soybean, and specialty crop variations are in the pipeline. It is estimated that this should require only 5% refuge acres as opposed to the 20% required of older technologies to militate against pest tolerance (Choudhary and Gaur, 2010).

On the second area of agronomic traits, namely abiotic stress, there is a meta issue that overlays much of the individual efforts, that is, climate change. This poses a real challenge in terms of available agricultural land and fresh water use. Apart from the obvious effects of climate change, the decline of crop yields, ocean acidification, poor plant nutrition and abiotic stress, population displacement, and threatened ecosystems are effects underlined by the Stern Report (2006) as potential consequences of climate change. In addition, there are also broader, more systemic effects of drought beyond food insecurity, such as decreased household income, the loss of assets due to slaughter of livestock, health threats due to the lack of water for hygiene and household uses, environmental degradation, and less sustainable land management. These effects must be considered in the light of growing population levels. In order to feed the overall population, the world will have to double its rate of agricultural production over the next 25 years, despite having already quadrupled it in the last 50 years. It is estimated that merely 10% of world's arable land may be categorized as free from stress. The rapid change in environmental conditions is likely to override the adaptive potential of plants. Such abnormal environmental parameters include drought, salinity, cold, freezing, high temperature, waterlogging, high light intensity, ultraviolet (UV) radiation, nutrient imbalances, metal toxicities, and nutrient deficiencies, which are collectively termed as abiotic stress. Severe drought accounts for half the world's food emergencies annually. In 2003, the World Food Program spent US$565 million in response to drought in SSA (Anderson, 2005). In this context, solutions must be developed to adapt crops to existing but also evolving conditions, such as deteriorating soils or harsher conditions, such as cold, heat, drought, and salinity.

The agriculture sector is both a contributor to and provider of potential solutions to this phenomenon. It impacts two of the principal components of climate change – greenhouse gases and water. Agriculture is a major source of the former emissions. Practices such as deforestation, cattle feedlots, and fertilizer used currently account for approximately 25% of greenhouse gas emissions. When broken down in total, this amounts to 14% of carbon dioxide emissions, 48% of methane, and 52% of nitrous oxide emissions (Stern, 2006). In addition, this sector uses a significant amount of available fresh water; approximately 70% of the water currently consumed by humans is used in agriculture, and this is likely to increase as temperatures rise. The impact between resource-poor LDCs and developed countries is likely to be asymmetrical with much greater impacts on resource-poor farmers.

Given the potential impacts of climate change on the range and extent of agricultural productivity and the impact of

agricultural practice itself on global warming, effective technology should play a substantial part in militating against climate change. This is especially relevant in emerging countries where producers and consumers are more subject to the mercy of the vagaries of climate fluctuations than in the west where there is greater capability of responding to the effects and managing resources. Green biotechnology offers a set of tools that can help producers to limit greenhouse gas emissions as well as adapting their agricultural techniques to shifting climates. The three major contributions of green biotechnology to the mitigation of the impact of climate change are greenhouse gas reduction, crop adaptation (environmental stress and changing niches) crop protection, and yield increase in less desirable and marginal soils.

On the first of these issues, greenhouse gas reduction in addition to carbon dioxide, agriculture contributes two of the other major greenhouse gases, indeed one of them, nitrous oxide, has a global warming potential of approximately 300 times that of carbon dioxide. In addition, nitrous oxides stay in the atmosphere for a considerable period. Nitrous oxide is produced through bacterial degradation of applied nitrogen fertilizer, which can also contribute to eutrophication at ground level, so its reduction is desirable on several levels. However, nitrogen is essential for crop production because it is quantitatively the most essential nutrient for plants and a major factor limiting crop productivity. One of the critical steps limiting the efficient use of nitrogen is the ability of plants to acquire it from applied fertilizer. Therefore, the development of crop plants that absorb and use nitrogen more efficiently can serve both the plant and the environment. Arcadia Biosciences of Davis, CA developed nitrogen-efficient crops by introducing barley AlaAT (alanine aminotransferase) into both rice and canola. In a report, Arcadia's Nitrogen Use Efficiency (NUE) technology produces plants with yields that are equivalent to conventional varieties but which require significantly less nitrogen fertilizer because the AlaAT gene allows more efficient use. Compared with controls, transgenic plants also demonstrated significant changes in key metabolites and total nitrogen content, confirming increased nitrogen uptake efficiency. This technology has the potential to reduce the amount of nitrogen fertilizer that is lost by farmers every year due to leaching into the air, soil, and waterways (Omanya *et al.*, 2008). In addition to environmental pressures, nitrogen costs can represent a significant portion of a farmer's input costs and can significantly impact farmer profitability. Farmers spend US$60 billion annually for 150 million tonnes of fertilizer (Svoboda, 2008). The technology has been licensed to DuPont for maize and to Monsanto for application in canola.

The second area where green technology can help in a changing climate is crop adaptation to environmental stress and changing niches. Under stress, plants divert energy into survival instead of producing biomass and reproduction, so addressing this impact should have substantial effect on yield. In addition, improved stress tolerance allows an expanded growing season, especially earlier planting, and further reduces yield variability and grower financial risk. The most critical of these stresses is water. One of the most effective methods of addressing water limitation problems, namely irrigation, unfortunately is also one of the major causes of arable land degradation. It is estimated that 24.7 million acres of farmland worldwide is lost each year due to salinity buildup resulting from over irrigation. In fact, salinity limits crops on 40% of the world's irrigated land (25% of the United States). To address the extreme end of irrigation impact, Sottosanto *et al.* (2007) used AtNHX1, the most abundant vacuolar Na^+/H^+ antiporter in *Arabidopsis thaliana*, which mediates the transport of Na^+ and K^+ into the vacuole. By overexpressing this vacuolar Na^+/H^+ antiporter transgenic tomatoes were able to grow, flower, and produce fruit in the presence of 200 mM sodium chloride (Sottosanto *et al.*, 2007).

It is estimated that water stress is the most important variable in determining crop yield and can explain approximately 80% variance in yields (Shin *et al.*, 2009). Even at a more moderate level of impact it is estimated that approximately 70–80 million acres in the United States suffer yield losses due to moderate water stress (Kramer, 1980). The most critical time for water stress is near pollination and flowering where yields with or without irrigation can vary by up to 100%. This effect is clearly demonstrable in dry land production where yields can be cut in half in the absence of irrigation. At this time approximately 15% of US maize acres are irrigated. Given the negative effective and cost of irrigation, it is estimated that 20 million acres in the United States would benefit from a drought tolerance gene that gives a 10% yield increase. It would also allow shifting of high-value crops into production on more marginal land.

One of the first commercialized products to have included a 'yield gene' was Monsanto's second generation Roundup Ready 2 Yield® Soybeans, which not only include the glyphosate-tolerant trait but also were developed using extensive gene mapping to identify specific DNA regions that segregate with yield increase (Monsanto, 2010). First-generation Roundup Ready varieties had demonstrated yield drag due to the unfortunate insertion close to a gene that influenced seed size and co-segregated with the transgene. The second generation is a good example of the power of combining recombinant DNA technology with genomics tools. The company claims that following 4 years of field trials across six US states showed 7–11% higher yields, compared with the first generation of Roundup Ready soybeans. However, there have been some problems with fungal (white mold) susceptibility in certain regions. At the National Technical Biosafety Committee (CTNBio) meeting in Brazil in August 2010, the committee approved the Bt-enhanced version of this product for planting in Brazil.

As noted, transcription factors are some of the most versatile tools being employed in developing stress-tolerant plants. One of the most versatile classes of transcription factors in so far as environmental response is concerned is the dehydration-responsive element-binding protein (DREB) transcription factors that are involved in the biotic stress signaling pathway and can activate as many as 12 resistant functional genes relying on DRE members of *cis* regulation under adverse conditions, for instance, *rd29*, *cor15*, and *rd17* cause proline content to rise so as to enable plants to improve in many resistances, such as drought, freezing, and salt tolerance (Agarwal, 2006). It has been possible to engineer stress tolerance in transgenic plants by manipulating the expression of DREBs. One isolated from *Arabidopsis* has improved drought tolerance, increasing productivity by at least twofold during

severe water stress. DroughtGard™ maize is the first commercially available transgenic drought-tolerant crop. Hybrid seed sold under this trademark combines a novel transgenic trait (based on the bacterial cspB gene, an ribonucleic acid (RNA) chaperone, which helps to maintain normal physiological performance under stress by binding and unfolding RNA molecules so that they can function normally) with Monsanto's optimized conventional breeding program. In field trials using this approach, maize yields have increased under water stress by up to 30%. The yield gain of this variety under drought appears to occur due to slowing of growth, specifically under drought stress such that existing soil moisture is saved for the critical period surrounding flowering, resulting in less kernel abortion, higher harvest index, and greater yield (Castiglioni *et al.*, 2008).

Other approaches include modification of individual genes involved in stress response and cell signaling. For example, drought-tolerant canola engineered to reduce the levels poly (ADP-ribose) polymerase, a key stress-related protein in many organisms, shows relative yield increases of up to +44% compared with control varieties. A subset of the transcription factors, homeodomain leucine zipper proteins (HDZip), plays a role in regulating adaptation responses, including developmental adjustment to environmental cues, such as water stress in plants (Deng *et al.*, 2006). One of these effectors is abscisic acid (ABA), an important plant regulator controlling many environmental responses, including stomata movement that is itself modulated by the DREB elements. Some work is being done on modifying HDZip directly, whereas other works aim to modify it indirectly, for example, downregulating farnesyltransferase, a signaling system in the production of ABA and stomata control, which results in stomata closure and water retention.

Eduardo Blumwald is also working on modifying basic acid to enhance the tolerance of plants to water deficit by delaying the drought-induced leaf senescence and abscission during the stress episode. Using tobacco plants expressing an IPT gene under the control of a stress- and maturation-induced promoter they showed that delayed drought-induced leaf senescence resulted in remarkable drought-tolerant phenotypes as well as minimal yield loss when plants were watered with only 30% of the water used under controlled conditions (Zhang, 2010). This is now being introduced into rice, among other crops. This work is being done in conjunction with Arcadia Biosciences. In addition, Bayer CropScience, Pioneer Hi-Bred, BASF, and Dow, among others, are conducting research on maize, cotton, canola, and rice to develop a new generation of stress-tolerant, high-performance crop varieties. Clearly, stress-tolerant traits are of paramount importance in LDCs, especially sub-Saharan Africa and Asia. Major efforts are already underway on this front. The partnership, known as Water Efficient Maize for Africa (WEMA), was formed in response to a growing call by African farmers, leaders, and scientists to address the devastating effects of drought on small-scale farmers (Foundation, 2007). Frequent drought leads to crop failure, hunger, and poverty, which climate change can only aggravate.

At the other end of the spectrum of climate change impact is flooding due to changing rain patterns and rising sea levels. This is already a major cause of rice crop loss. It is estimated that 4 million tonnes of rice are lost every year because of flooding, which is sufficient to feed 30 million people. Rice is not grown in flooded fields through necessity but rather to control weeds; however, most rice varieties die after more than 3 days of complete submergence. Researchers know of at least one rice variety FR13A that can tolerate flooding for longer periods, but conventional breeding failed to create an event that was acceptable to farmers. The Ronald laboratory at UC Davis cloned the submergence tolerance (*Sub1*) locus from this resistance variety using a map-based cloning approach (Jung, 2010). The *Sub1* locus encodes three putative transcription regulators, one of which (*Sub 1A-1*) increases dramatically in response to oxygen deprivation in *sub1* seedlings, whereas *Sub1C* levels decrease. Transgenic lines overexpressing the *Sub1A-1* gene have been introgressed into a submergence-intolerant line and display enhanced submergence tolerance.

There is also some research in the final abiotic stress focus area, namely expansion of crops into and increased yield in less desirable and marginal soils. For example, a gene that produces citric acid in roots can protect plants from soils contaminated with aluminum, as it binds to the contaminant preventing uptake by the root system (Lopez-Bucio, 2000). Genes such as these can allow crops to be cultivated in hostile soils and temperatures, increasing geographic range while reducing potential impact on fragile ecosystems.

Increased Nutrient Content

The first generation of the products commercialized from biotechnology were crops focusing largely on input agronomic traits primarily in response to biotic stress. The coming generations of crop plants can be generally grouped into four broad areas. The present and future focus is on continuing improvement of agronomic traits such as yield and abiotic stress resistance, in addition to the biotic stress tolerance of the present generation; crop plants as biomass feedstocks for biofuels and 'bio-synthetics;' value-added output traits such as improved nutrition and food functionality; and plants as production factories for therapeutics and industrial products. Developing and commercializing plants with these improved traits involve overcoming a variety of technical, regulatory, and perception challenges inherent in perceived and real challenges of complex modifications. Both the panoply of traditional plant-breeding tools and modern biotechnology-based techniques will be required to produce plants with the desired quality traits. **Table 1** presents examples of crops that have already been GM with macro- and micronutrient traits which may provide nutritional benefits.

Although the correlative link between food and health, beyond meeting basic nutrition requirements, has only been unequivocally proven in a number of cases, a growing body of evidence indicates that food components can influence physiological processes at all stages of life. Nutrition intervention from a functionality perspective has a personal dimension. Determining individual response is at least as complex a challenge as the task of increasing or decreasing the amount of a specific protein, fatty acid, or other component of the plant itself (Brigelius-Flohe and Joost, 2006). There is also

Table 1 Examples of crops in research and development with nutritionally improved traits intended to provide health benefits for consumers and animals[a]

Trait	*Crop (trait detail)*	*References*
Proteins and amino acids		
Protein quality and level	Bahiagrass (protein↑)	Luciani *et al.*, 2005
	Canola (amino acid composition)	Roesler *et al.*, 1997
	Maize (amino acid composition and protein↑)	Cromwell, 1967, 1969; Yang *et al.*, 2002; O'Quinn *et al.*, 2000; Young *et al.*, 2004
	Potato (amino acid composition and protein↑)	Chakraborty *et al.*, 2000; Li *et al.*, 2001; Yu and Ao, 1997; Atanassov *et al.*, 2004
	Rice (protein↑ and amino acid)	Katsube *et al.*, 1999
	Soybean (amino acid balance)	Rapp, 2002; Dinkins *et al.*, 2001
	Sweet Potato (protein↑)	Prakash *et al.*, 2000
	Wheat (protein↑)	Uauy *et al.*, 2006
Essential amino acids	Canola (lysine↑)	Falco *et al.*, 1995
	Lupin (methionine↑)	White *et al.*, 2001
	Maize (lysine↑ and methionine↑)	Agbios, 2006; Lai and Messing, 2002
	Potato (methionine↑)	Zeh *et al.*, 2001
	Sorghum (lysine↑)	Zhao *et al.*, 2003
	Soybean (lysine↑ and tryptophan↑)	Falco *et al.*, 1995; Galili *et al.*, 2002
Oils and fatty acids		
	Canola (lauric acid↑, γ-linolenic acid↑, $+\omega$-3 fatty acids, 8:0 and 10:0 fatty acids↑, lauric + myristic acid↑, and oleic acid↑)	Del Vecchio, 1996; Froman and Ursin, 2002; James *et al.*, 2003; Ursin, 2003, Dehesh *et al.*, 1996; Agbios, 2006; Roesler *et al.*, 1997
	Cotton (oleic acid↑ and oleic acid + stearic acid↑)	Chapman *et al.*, 2001; Liu *et al.*, 2002
	Linseed ($+\omega$-3 and $-$6 fatty acids)	Abbadi *et al.*, 2004
	Maize (oil↑)	Young *et al.*, 2004
	Oil Palm (oleic acid↑ or stearic acid↑ and oleic acid↑ + palmitic acid↓)	Parveez, 2003; Jalani *et al.*, 1997
	Rice (α-linolenic acid↑)	Anai *et al.*, 2003
	Soybean (oleic acid↑ and γ-linolenic acid↑)	Kinney and Knowlton, 1998; Reddy and Thomas, 1996
	Safflower (γ linoleic acid (GLA↑))	Arcadia, 2008
Carbohydrates		
Fructans	Chicory, (fructan↑ and fructan modification)	Smeekens, 1997; Sprenger *et al.*, 1997; Sévenier *et al.*, 1998
	Maize (fructan↑)	Caimi *et al.*, 1996
	Potato (fructan↑)	Hellwege *et al.*, 1997
	Sugar beet (fructan↑)	Smeekens, 1997
Frustose, raffinose, and stachyose	Soybean	Hartwig *et al.*, 1997
Inulin	Potato (inulin↑)	Hellwege *et al.*, 2000
Starch	Rice (amylase↑)	Chiang *et al.*, 2005; Schwall, 2000
Micronutrients and functional metabolites		
Vitamins and carotenoids	Canola (vitamin E↑)	Shintani and DellaPenna, 1998
	Maize (vitamin E↑, vitamin C↑, folate↑, and lycopene)	Rocheford *et al.*, 2002; Cahoon *et al.*, 2003; Chen *et al.*, 2003; Bekaert, 2008; Naqvi *et al.*, 2009; Harjes, 2010
	Cassava ($+\beta$-carotene)	Welsch *et al.*, 2010
	Mustard ($+\beta$-carotene)	Shewmaker *et al.*, 1999
	Potato (β-carotene and lutein↑)	Ducreux *et al.*, 2005; Diretto *et al.*, 2010
	Rice ($+\ \beta$-carotene and folate↑)	Ye *et al.*, 2000; Storozhenko *et al.*, 2007
	Strawberry (vitamin C↑)	Agius *et al.*, 2003
	Tomato (folate↑, phytoene and β-carotene↑, lycopene↑, and provitamin A↑)	Della Penna, 2007; Díaz de la Garza *et al.*, 2004; Enfissi *et al.*, 2005; Mehta *et al.*, 2002; Fraser *et al.*, 2001; Rosati, 2000; Sun *et al.*, 2012; Klee *et al.*, 2012
Functional secondary metabolites	Apple (+ stilbenes)	Szanowski *et al.*, 2003
	Alfalfa (+ resveratrol)	Hipskind and Paiva, 2000
	Kiwi (+ resveratrol)	Kobayashi *et al.*, 2000
	Maize (flavonoids↑)	Yu *et al.*, 2000
	Potato (anthocyanin and alkaloid glycoside↓, and solanin↓)	Lukaszewicz *et al.*, 2004
	Rice (flavonoids↑ and + resveratrol)	Shin *et al.*, 2006; Stark-Lorenzen, 1997

(*Continued*)

Table 1 Continued

Trait	*Crop (trait detail)*	*References*
	Soybean (flavonoids↑)	Yu *et al.*, 2003
	Tomato (+resveratrol, chlorogenic acid↑,flavonoids↑, and stilbene↑anthocynanins↑)	Giovinazzo *et al.*, 2005; Niggeweg *et al.*, 2004; Muir *et al.*, 2001; Rosati, 2000; Gonzali *et al.*, 2009
	Wheat (caffeic and ferulic acids↑ and +resveratrol)	UPI, 2002
Mineral availabilities	Alfalfa (phytase↑)	Austin-Phillips *et al.*, 1999
	Lettuce (iron↑)	Goto *et al.*, 2000
	Rice (iron↑)	Lucca *et al.*, 2002
	Maize (phytase↑ and ferritin↑)	Drakakaki, 2005; Han, 2009
	Soybean (phytase↑)	Denbow *et al.*, 1998
	Wheat (phytase↑)	Brinch-Pedersen *et al.*, 2000, 2006

[a]Excludes protein/starch functionality, shelf life, taste/aesthetics, fiber quality, and allergen/toxin reduction traits.

Source: Modified from ILSI (International Life Sciences Institute), 2004a. Nutritional and safety assessments of foods and feeds nutritionally improved through biotechnology. Comprehensive Reviews in Food Science and Food Safety 3, 35–104. Available at: http://members.ift.org/NR/rdonlyres/27BE106D-B616-4348-AE3A-091D0E536F40/0/crfsfsv3n2p00350104ms20040106.pdf (accessed 03.05.14); ILSI (International Life Sciences Institute), 2004b. Nutritional and safety assessments of foods and feeds nutritionally improved through biotechnology: An executive summary. Journal of Food Science 69, CRH62–CRH68; ILSI (International Life Sciences Institute), 2008. Nutritional and safety assessments of foods and feeds nutritionally improved through biotechnology: Case studies. Comprehensive Reviews in Food Science and Food Safety 7, 50–99. Reviewed in Newell-McGloughlin, M., 2010. Modifying agricultural crops for improved nutrition. New Biotechnology 27 (5), 494–504.

evidence that early food regimes can affect health in later life, for example, some children that survived famine conditions in certain regions of Africa grew into adults battling obesity and related problems presumably due to the selective advantage of the thrifty gene in their early food-stressed environment becoming a hazard during more abundant times, especially if later diets are calorie dense.

Functional food components are of increasing interest in the prevention and/or treatment of a number of the leading causes of death, including but not limited to cancer, diabetes, cardiovascular disease, and hypertension. Many food components are known to influence the expression of both structural genes and transcription factors in humans (Go *et al.*, 2005; Mazzatti *et al.*, 2008). Examples of these phytochemicals are listed in **Table 2** (reviewed in Newell-McGloughlin, 2010). The large diversity of phytochemicals suggests that the potential impact of phytochemicals and functional foods on human and animal health is worth examining as targets of biotechnology efforts. From a health perspective, plant components of dietary interest can be broadly divided into four main categories, which can be further broken down into positive and negative attributions for human nutrition, macronutrients (proteins, carbohydrates, lipids (oils), and fiber), micronutrients (vitamins, minerals, and phytochemicals), anti-nutrients (substances such as phytate that limit bioavailability of nutrients), allergens, intolerances, and toxins.

There are approximately 25 000 metabolites (phytochemicals), of the 200 000 or so produced by plants, with known effect in the human diet (Go *et al.*, 2005). Analysis of these metabolites (most specifically metabolomic analysis) is a valuable tool in better understanding of what has occurred during crop domestication (lost and silenced traits) and in designing new paradigms for more targeted crop improvement that is better tailored to current needs (Hall *et al.*, 2008). In addition, with modern techniques, we have the potential to seek out, analyze, and introgress traits of value that were limited in previous breeding strategies. Research to improve the nutritional quality of plants has historically been limited by a lack of basic knowledge of plant metabolism and the challenge of resolving the complex interactions of thousands of metabolic pathways. Complementary techniques, both traditional and novel, are needed to metabolically engineer plants to produce desired quality traits. Metabolic engineering is generally defined as the redirection of one or more reactions (enzymatic or otherwise) to improve the production of existing compounds to produce new compounds or mediate the degradation of undesirable compounds. It involves the redirection of cellular activities by the modification of the enzymatic, transport, and regulatory functions of the cell. Significant progress has been made in recent years in the molecular dissection of many plant pathways and in the use of cloned genes to engineer plant metabolism.

Although progress in dissecting metabolic pathways and our ability to manipulate gene expression in GM plants has progressed apace, attempts to use these tools to engineer plant metabolism have not. As the success of this approach hinges on the ability to change host metabolism, its continued development depends critically on a far more sophisticated knowledge of plant metabolism, especially the nuances of interconnected cellular networks, than what currently exists. This complex interconnectivity is regularly demonstrated. Relatively, minor genomic changes (point mutations and single-gene insertions) are regularly observed following metabolomic analysis, to lead to significant changes in biochemical composition (Bino *et al.*, 2005; Davidovich-Rikanati *et al.*, 2007; Long *et al.*, 2006). Giliberto *et al.* (2005) used a genetic modification approach to study the mechanism of light influence on antioxidant content (anthocyanin and lycopene) in the tomato cultivar Moneymaker. However, other than what on the surface would appear to be more significant, genetic changes unexpectedly yield little phenotypical effect (Schauer and Fernie, 2006).

Likewise, unexpected outcomes are often observed, for example, significant modifications made to primary Calvin cycle enzymes (fructose1,6-bisphosphatase, and phosphoribulokinase) have little effect, whereas modifications to minor enzymes (e.g., aldase, which catalyzes a reversible reaction),

Table 2 Examples of plant components with suggested functionality[a]

Class/components	*Source*[b]	*Potential health benefits*
Carotenoids		
Alpha-carotene	Carrots	Neutralizes free radicals that may cause damage to cells
Beta-carotene	Various fruits and vegetables	Neutralizes free radicals
Lutein	Green vegetables	Contributes to maintenance of healthy vision
Lycopene	Tomatoes and tomato products (ketchup and sauces)	May reduce risk of prostate cancer
Zeaxanthin	Eggs, citrus, and maize	Contributes to maintenance of healthy vision
Dietary fiber		
Insoluble fiber	Wheat bran	May reduce risk of breast and/or colon cancer
Beta glucan[c]	Oats	May reduce risk of cardiovascular disease (CVD)
Soluble fiber[c]	Psyllium	May reduce risk of CVD
Whole grains[c]	Cereal grains	May reduce risk of CVD
Collagen hydrolysate	Gelatin	May help to improve some symptoms associated with osteoarthritis
Fatty acids		
Omega-3 fatty acids – docosahexaenoic acid/ eicosapentaenoic acid	Tuna; fish and marine oils	May reduce risk of CVD and improve mental and visual functions
Conjugated linoleic acid	Cheese and meat products	May improve body composition and may decrease risk of certain cancers
Gamma linolenic acid	Borage and evening primrose	May reduce inflammation risk of cancer, CVD disease, and improve body composition
Flavonoids		
Anthocyanidins: cyanidin	Berries	Neutralize free radicals and may reduce risk of cancer
Hydroxycinnamates	Wheat	Antioxidant-like activities and may reduce risk of degenerative diseases
Flavanols: catechins, and tannins	Tea (green and catechins), (black and tannins)	Neutralize free radicals and may reduce risk of cancer
Flavanones	Citrus	Neutralize free radicals and may reduce risk of cancer
Flavones: quercetin	Fruits/vegetables	Neutralize free radicals and may reduce risk of cancer
Glucosinolates, Indoles, and Isothiocyanates		
Sulphoraphane	Cruciferous vegetables (broccoli and kale) and horseradish	Neutralizes free radicals and may reduce risk of cancer
Phenolics		
Stilbenes – Resveratrol	Grapes	May reduce risk of degenerative diseases, heart disease, and cancer; may have longevity effect
Caffeic acid and Ferulic acid	Fruits, vegetables, and citrus	Antioxidant-like activities; may reduce risk of degenerative diseases, heart disease, and eye disease
Epicatechin	Cacao	Antioxidant-like activities; may reduce risk of degenerative diseases and heart disease
Plant Stanols/sterols		
Stanol/sterol ester[c]	Maize, soy, wheat, and wood oils	May reduce risk of coronary heart disease (CHD) by lowering blood cholesterol levels
Prebiotic/probiotics		
Fructans, Inulins, and Fructooligosaccharides (FOS)	Jerusalem artichokes, shallots, and onion powder	May improve gastrointestinal health
Lactobacillus	Yogurt and other dairy	May improve gastrointestinal health
Saponins	Soybeans, soy foods, and soy protein-containing foods	May lower LDL cholesterol; contains anticancer enzymes
Soybean Protein	Soybeans and soy-based foods	25 g day^{-1} may reduce risk of heart disease

(*Continued*)

Table 2 Continued

Class/components	*Source*[b]	*Potential health benefits*
Phytoestrogens		
Isoflavones – Daidzein and Genistein	Soybeans and soy-based foods	May reduce menopause symptoms, such as hot flashes, reduce osteoporosis, and CVD
Lignans	Flax, rye, and vegetables	May protect against heart disease and some cancers; may lower LDL cholesterol, total cholesterol, and triglycerides
Sulfides/thiols		
Diallyl sulfide	Onions, garlic, olives, leeks, and scallions	May lower LDL cholesterol, helps to maintain healthy immune system
Allyl methyl trisulfide and Dithiolthiones	Cruciferous vegetables	May lower LDL cholesterol and helps to maintain healthy immune system
Tannins		
Proanthocyanidins	Cranberries, cranberry products, cocoa, chocolate, and black tea	May improve urinary tract health May reduce risk of CVD and high blood pressure

[a]Examples are not an all-inclusive list.

[b]US Food and Drug Administration approved health claim established for component.

Source: Modified from ILSI (International Life Sciences Institute), 2004a. Nutritional and safety assessments of foods and feeds nutritionally improved through biotechnology. Comprehensive Reviews in Food Science and Food Safety 3, 35–104. Available at: http://members.ift.org/NR/rdonlyres/27BE106D-B616-4348-AE3A-091D0E536F40/0/crfsfsv3n2p00350104ms20040106.pdf (accessed 03.05.14) and ILSI (International Life Sciences Institute), 2004b. Nutritional and safety assessments of foods and feeds nutritionally improved through biotechnology: An executive summary. Journal of Food Science 69, CRH62–CRH68.

seemingly irrelevant to pathway flux, have major effects (Hajirezaei *et al.*, 1994; Paul *et al.*, 1995). These observations demonstrate that caution must be exercised when extrapolating individual enzyme kinetics to the control of flux in complex metabolic pathways. With evolving 'omics' tools, a better understanding of the global effects of metabolic engineering on metabolites, enzyme activities, and fluxes is beginning to be developed. Attempts to modify storage proteins or secondary metabolic pathways have also been more successful than have alterations of primary and intermediary metabolism (Della Penna, 2006). Although offering many opportunities, this plasticity in metabolism complicates potential routes to the design of new, improved crop varieties. Regulatory oversight of engineered products has been designed to detect such unexpected outcomes in biotechnology crops and, as demonstrated by Chassy *et al.* (ILSI, 2004a,b, 2008) existing analytical and regulatory systems are adequate to address novel metabolic modifications in nutritionally improved crops.

A number of new approaches are being developed to counter some of the complex problems in metabolic engineering of pathways. Such approaches include use of RNA interference (RNAi) to modulate endogenous gene expression or the manipulation of transcription factors (Tfs) that control networks of metabolism (Kinney, 1998; Bruce *et al.*, 2000; Butelli *et al.*, 2008; Gonzali *et al.*, 2009). For example, expression in tomato of two selected Tfs involved in anthocyanin production in snapdragon (*Antirrhinum majus* L.) led to high levels of these flavonoids throughout the fruit tissues, which, as a consequence, were purple. They also stimulated genes involved in the side-chain modification of the anthocyanin pigments and genes possibly related to the final transport of these molecules into the vacuole processes that are both necessary for the accumulation of anthocyanin (Gonzali *et al.*, 2009). Such expression experiments hold promise as an effective tool for the determination of transcriptional regulatory networks for important biochemical pathways. Gene expression can be modulated by numerous transcriptional and posttranscriptional processes. Correctly choreographing the many variables is the factor that makes metabolic engineering in plants so challenging.

In addition, there are several new technologies that can overcome the limitation of single-gene transfers and facilitate the concomitant transfer of multiple components of metabolic pathways. One example is multiple-transgene direct DNA transfer, which simultaneously introduces all the components required for the expression of complex recombinant macromolecules into the plant genome as demonstrated by a number of studies, including Nicholson *et al.* (2005), who successfully delivered four transgenes that represent the components of a secretory antibody into rice. Carlson *et al.* (2007) constructed a minichromosome vector that remains autonomous from the plant's chromosomes and stably replicates when introduced into maize cells. This work makes it possible to design minichromosomes that carry cassettes of genes, enhancing the ability to engineer plant processes, such as the production of complex biochemicals. Naqvi *et al.* (2009) demonstrated that gene transfer using minimal cassettes is an efficient and rapid method for the production of transgenic plants stably expressing several different transgenes. As no vector backbones are required, this prevents the integration of potentially recombinogenic sequences, insuring stability across generations. They used combinatorial direct DNA transformation to introduce multi-complex metabolic pathways coding for beta-carotene, vitamin C, and folate. They achieved this by transferring five constructs controlled by different endosperm-specific promoters into white maize. Different enzyme combinations show distinct metabolic

phenotypes resulting in 169 fold beta-carotene increase, six times the amount of vitamin C, and doubling folate production effectively, creating a multivitamin maize cultivar (Naqvi *et al.*, 2009). This system has an added advantage from a commercial perspective in that these methods circumvent problems with traditional approaches that not only limit the amount of sequences transferred but may also disrupt native genes or lead to poor expression of the transgene, thus reducing both the numbers of transgenic plants that must be screened and the subsequent breeding and introgression steps required to select a suitable commercial candidate.

As demonstrated, 'omics'-based strategies for gene and metabolite discovery, coupled with high-throughput transformation processes and automated analytical and functionality assays, have accelerated the identification of product candidates. Identifying rate-limiting steps in synthesis could provide targets for modifying pathways for novel or customized traits. Targeted expression are used to channel metabolic flow into new pathways, whereas gene-silencing tools reduce or eliminate undesirable compounds or traits or switch off genes to increase desirable products (Davies, 2007; Liu, 2002; Herman, 2003). In addition, molecular marker-based breeding strategies have already been used to accelerate the process of introgressing trait genes into high-yielding germplasm for commercialization. **Table 1** summarizes the work being undertaken to date on specific applications in the categories listed above. The following sections briefly review some examples under those categories.

Macronutrients: Protein

The FAO estimates that 850 million people worldwide suffer from undernutrition, of which insufficient protein in the diet is a significant contributing factor (FAO, 2004, 2011). Protein–energy malnutrition is the most lethal form of malnutrition and affects every fourth child worldwide according to the WHO (2006). Most plants have a poor balance of essential amino acids relative to the needs of animals and humans. The cereals (maize, wheat, rice, etc.) tend to be low in lysine, whereas legumes (soybean and peas) are often deficient in the sulfur-rich amino acids, methionine and cysteine. Successful examples of improving amino acid balance to date include high-lysine maize (Eggeling *et al.*, 1998; O'Quinn *et al.*, 2000) canola, and soybeans (Falco *et al.*, 1995). Free lysine is significantly increased in high-lysine maize by the introduction of the *dapA* gene (*cordapA*) from *Corynebacterium glutamicum*, which encodes a form of dihydrodipicolinate synthase that is insensitive to lysine feedback inhibition. Consumption of foods made from these crops potentially can help to prevent malnutrition in developing countries, especially among children.

Another method of modifying storage protein composition is to introduce hetero- or homologous genes that code for proteins containing elevated levels of the desired amino acid, such as the sulfur-containing amino acids (methionine and cysteine) or lysine. An interesting solution to this is to create a completely artificial protein containing the optimum number of the essential amino acids methionine, threonine, lysine, and leucine in a stable, helical conformation designed to resist proteases to prevent degradation. This was achieved by a number of investigations, including sweet potato modified with an artificial storage protein (*ASP-1*) gene (Prakash *et al.*, 2000). These transgenic plants exhibited a two- and fivefold increase in the total protein content in leaves and roots, respectively, over that of control plants. A significant increase in the level of essential amino acids, such as methionine, threonine, tryptophan, isoleucine, and lysine, was also observed (Prakash *et al.*, 2000; ILSI, 2008). A key issue is to insure that the total amount and composition of storage proteins is not altered to the detriment of the development of the crop plant when attempting to improve amino acid ratios (Rapp *et al.*, 2002).

Some novel indirect approaches have also been taken to improve protein content. Uauy *et al.* (2006) 'rescued' an ancestral wheat allele that encodes a transcription factor (*NAM-B1*) which accelerates senescence and increases nutrient remobilization from leaves to developing grains (modern wheat varieties carry a nonfunctional allele.) Reduction in RNA levels of the multiple *NAM* homologs by RNAi delayed senescence by more than 3 weeks and reduced wheat grain protein, zinc, and iron content by more than 30%. Young *et al.* (2004) used yet another approach to indirectly increase protein and oil content. They used a bacterial cytokinin-synthesizing isopentenyl transferase (IPT) enzyme, under the control of a self-limiting senescence-inducible promoter, to block the loss of the lower floret resulting in the production of just one kernel composed of a fused endosperm with two viable embryos. The presence of two embryos in a normal-sized kernel leads to displacement of endosperm growth, resulting in kernels with an increased ratio of embryo to endosperm content. The end result is maize with more protein and oil and less carbohydrate (Young *et al.*, 2004; ILSI, 2008).

Macronutrients: Fiber and Carbohydrates

Fiber is a group of substances chemically similar to carbohydrates that nonruminant animals, including humans, poorly metabolize for energy or other nutritional uses. Fiber provides bulk in the diet such that foods rich in fiber offer satiety without contributing significant calories. Current controversies aside, there is ample scientific evidence to show that prolonged intake of dietary fiber has various positive health benefits, especially the potential for reduced risk of colon and other types of cancer.

Recent microbiome twin studies addressing the interrelationships between diet and gut microbial community structure/function indicated that differences in our gut microbial ecology affect our predisposition to obesity or malnutrition and that diet rather than applied probiotics was the single most important characterization of gut health (Turnbaugh, 2009). These studies involved characterization of the gut microbiota/microbiome of twins, concordant or discordant for malnutrition, living in several developing countries, who are sampled just before, during, and after treatment.

When such colonic bacteria (especially Bifidobacteria) ferment dietary fiber or other unabsorbed carbohydrates, the products are short-chain saturated fatty acids. These short-chain fatty acids may enhance absorption of minerals such as

iron, calcium, and zinc; induce apoptosis preventing colon cancer; and inhibit 3-hydroxy-3-methylglutaryl coenzyme-A reductase (HMG-CoAR), thus lowering low-density lipoprotein (LDL) production (German, 2005). Plants are effective at making both polymeric carbohydrates (e.g., starches and fructans) and individual sugars (e.g., sucrose and fructose). The biosynthesis of these compounds is sufficiently understood to allow the bioengineering of their properties and to engineer crops to produce polysaccharides not normally present. Polymeric carbohydrates such as fructans have been produced in sugar beet and inulins and amylase (resistant starch) in potato (Hellwege *et al.*, 2000) without adverse effects on growth or phenotype. A similar approach is being used to derive soybean varieties that contain some oligofructan components that selectively increase the populations of beneficial bacterial species in the intestines of humans and certain animals while inhibiting the growth of harmful ones (Bouhnik, 1999).

Macronutrients: Novel Lipids

Genomics-based approaches, specifically marker-assisted plant breeding, combined with recombinant DNA technology provide powerful means for modifying the composition of oilseeds to improve their nutritional value and provide the functional properties required for various food oil applications. Genetic modification of oilseed crops can provide an abundant, relatively inexpensive source of dietary fatty acids with wide ranging health benefits. The production of such lipids in vegetable oil provides a convenient mechanism to deliver healthier products to consumers without the requirement for significant dietary changes. Major alterations in the proportions of individual fatty acids have been achieved in a range of oilseeds using conventional selection, induced mutation, and, more recently, posttranscriptional gene silencing (PTGS). Examples of such modified oils include: low- and zero-saturated fat soybean and canola oils; canola oil containing medium-chain fatty acids whose ergogenic potential may have application in LDCs; high stearic acid canola oil (for trans fatty acid-free products); high oleic acid (monounsaturated) soybean oil; canola oil containing the polyunsaturated fatty acids (PUFA) and gamma-linolenic acid (GLA; 18:3 n-6); and soybean oils containing stearidonic acids (SDA; C18:4 n-3) (SDA, 2011), very long-chain fatty acids (Zou *et al.*, 1997), and omega-3 fatty acids (Yuan and Knauf, 1997; SDA, 2011). These modified oils are being marketed and many countries have a regulatory system in place for the premarket safety review of novel foods produced through conventional technology.

Edible oils rich in monounsaturated fatty acids provide improved oil stability, flavor, and nutrition for human and animal consumption. High-oleic soybean oil is naturally more resistant to degradation by heat and oxidation, and so requires little or no post-refining processing (hydrogenation), depending on the intended vegetable oil application. Oleic acid (18:1), a monounsaturate, can provide more stability than the polyunsaturates, linoleic (18:2) and linolenic (18:3) acids. Antisense inhibition of oleate desaturase expression in soybean resulted in oil that contained >80% oleic acid (23% is normal) and had a significant decrease in PUFA (Kinney and Knowlton, 1998). DuPont has introduced soybean oil composed of at least 80% oleic acid, approximately 3% linolenic acid, and more than 20% less-saturated fatty acids than commodity soybean oil. Monsanto's Vistive contains less than 3% linolenic acid, compared with 8% for traditional soybeans, which results in more stable soybean oil and less need for hydrogenation.

A key function of α-linolenic acid is as a substrate for the synthesis of longer chain ω-3 fatty acids, found in fish, eicosapentaenoic acid (EPA; C20:5n-3), and docosahexaenoic acid (DHA; C22:6n-3), which play an important role in the regulation of inflammatory immune reactions and blood pressure, brain development *in utero*, and, in early postnatal life, the development of cognitive function. Stearidonic acid (SDA, C18:4n-3), EPA, and DHA also possess anticancer properties (Reiffel and McDonald, 2006; Christensen JH *et al.*, 1999; Smuts, 2003). Research indicates that the ratio of n-3 to n-6 fatty acids may be as important to health and nutrition as the absolute amounts present in the diet or in body tissues. Current Western diets tend to be relatively high in n-6 fatty acids and relatively low in n-3 fatty acids. Production of a readily available source of long-chain PUFA, specifically ω-3 fatty acids, delivered in widely consumed prepared foods could deliver much needed ω-3-fatty acids to large sectors of the population with skewed n-6:n-3 ratios. In plants, the microsomal ω-6 desaturase-catalyzed pathway is the primary route of production of polyunsaturated lipids. Ursin *et al.* (2000, 2003) had introduced the delta-6 desaturase gene from a fungus (*Mortierella* sp.), succeeding in producing omega-3 in canola. In subsequent work the same gene was added to soybean and transgenic soybean oil was obtained that contained >23% SDA, with an overall n-6: n-3 ratio of 0.5, which the body converts to heart-healthy eicosapentaenoic acid (EPA), one of three omega-3 fatty acids used by the body. This product is now being developed for commercialization by Monsanto (SDA, 2011).

However, not all omega-6 fatty acids are created equal. GLA, C18:3n-6 is an omega-6 fatty acid with health benefits that are similar and complementary to the benefits of omega-3 fatty acids, including anti-inflammatory effects, improved skin health, and weight loss maintenance (Schirmer *et al.*, 2007). Davis, CA company, Arcadia has engineered GLA safflower oil, with up to 40% GLA, essentially quadrupling the levels obtained in source plants such as evening primrose and borage (Arcadia Biosciences, 2008). Structural lipids also have positive health benefits; for example, in addition to their effect in lowering cholesterol, membrane lipid phytosterols have been found to inhibit the proliferation of cancer cells by inducing apoptosis and G1/S cell cycle arrest through the HMG-CoAR as noted above (Awad, 2000). In addition, specialty oils may also be developed with further pharmaceutical and chemical feedstock applications in mind.

Micronutrients: Vitamins and Minerals

Micronutrient malnutrition, the so-called hidden hunger, affects more than one-half of the world's population, especially women and preschool children in developing countries (UN

SCN, 2004). Even mild levels of micronutrient malnutrition may damage cognitive development and lower disease resistance in children and increase incidences of childbirth mortality. The costs of these deficiencies, in terms of diminished quality of life and lives lost, are large (Pfeiffera and McClafferty, 2007). Such deficiencies prevent children from reaching their full potential as adults; malnutrition, especially during the 1000 days between pregnancy and age 2 years, can lead to irreversible physical stunting and cognitive impairment. However, children who are well nourished are able to grow, learn, and prosper. They achieve more in school, are better able to survive illnesses, and tend to earn more as adults (Kraemer, 2012). The clinical and epidemiological evidence is clear that select minerals (iron, calcium, selenium, and iodine) and a limited number of vitamins (folate, vitamins E, B_6, and A) play a significant role in maintenance of optimal health and are limiting in diets (Asensi-Fabado, 2010).

As with macronutrients, one way to ensure an adequate dietary intake of nutritionally beneficial phytochemicals is to adjust their levels in plant foods. Using various approaches, including genomics, vitamin E levels are being increased in several crops, including soybean, maize, and canola, whereas rice varieties are being developed with the enhanced vitamin A precursor, beta-carotene, to address vitamin A deficiency that leads to macular degeneration and impacts development. Golden Rice II accumulates up to 37 μg of beta-carotene per gram of rice (23-fold more than the original). This beta-carotene has been shown to be bioavailable in sufficient amounts that 100–200 g per day can provide adequate pro-vitamin A to ameliorate against deficiency (Tang *et al.*, 2009). It is estimated that Golden rice will finally be approved for commercialization in the Philippines by 2014. A number of other staple crops on which many depend almost exclusively for calories have been produced enriched in beta-carotene, including maize, cassava, millet, and sorghum (Harjes *et al.*, 2008; Welsch *et al.*, 2010; Yan *et al.*, 2010). Cassava is being field tested in Nigeria. Ameliorating another major deficiency in LDCs, namely minerals such as iron and zinc, has also been addressed. Iron is the most commonly deficient micronutrient in the human diet, and iron deficiency affects an estimated 1 to 2 billion people. Anemia, characterized by low hemoglobin, is the most widely recognized symptom of iron deficiency, but there are other serious problems, such as impaired learning ability in children, increased susceptibility to infection, and reduced work capacity. Drakakaki *et al.* (2005) demonstrated endosperm-specific co-expression of recombinant soybean ferritin and *Aspergillus fumigatus* phytase in maize, which resulted in significant increases in the levels of bioavailable iron. A similar end was also achieved with lettuce (Goto *et al.*, 2000). The Africa Biofortified Sorghum (ABS) Project developed the world's first sorghum transformation system as well as the first 'golden' sorghum that had elevated provitamin A levels, reduced phytate, raised grain protein profile, and raised absorbability of zinc and iron (Blaine, 2011).

A rather interesting approach was taken by Connolly *et al.* (2008) to increase the levels of calcium in crop plants by using a modified calcium (Ca)/proton antiporter (known as short cation exchanger 1 (sCAX1) to increase Ca transport into vacuoles. They also demonstrated that consumption of such Ca-fortified carrots results in enhanced Ca absorption. This demonstrates the potential of increasing plant nutrient content through expression of a high-capacity transporter and illustrates the importance of demonstrating that the fortified nutrient is bioavailable. Other targets include folate-enriched tomatoes and isoflavonoids (Yonekura-Sakakibara and Saito, 2007; DellaPenna, 2007).

Micronutrients: Phytochemicals

Unlike for vitamins and minerals, the primary evidence for the health-promoting roles of phytochemicals comes from epidemiological studies, and the exact chemical identity of many active compounds has yet to be determined. However, for select groups of phytochemicals, such as non-provitamin A carotenoids, glucosinolates, and phytoestrogens, the active compound or compounds have been identified and rigorously studied. Epidemiologic studies have suggested a potential benefit of the carotenoid lycopene in reducing the risk of prostate cancer, particularly the more lethal forms of this cancer. Five studies support a 30–40% reduction in risk associated with high tomato or lycopene consumption in the processed form in conjunction with lipid consumption, although other studies with raw tomatoes were not conclusive (Giovannucci, 2002). As carotenoids are lipid soluble and cooking breaks down carotenoid-binding proteins, this is not an unexpected outcome. In a study by Mehta *et al.* (2002) to modify polyamines to retard tomato ripening they found an unanticipated enrichment in lycopene with levels up by 2- to 3.5-fold compared with conventional tomatoes. This is a substantial enrichment, exceeding that so far achieved by conventional means. This approach may work in other fruits and vegetables. Flavonoids meanwhile are soluble in water, and foods containing both water-soluble and fat-dissolved antioxidants are considered to offer the best protection against disease. Anthocyanins offer protection against certain cancers, cardiovascular disease, and age-related degenerative diseases. There is evidence that anthocyanins also have anti-inflammatory activity, promote visual acuity, and hinder obesity and diabetes. Both Gonzali *et al.* (2009) and Butelli *et al.* (2008) used snapdragon transcription factors to achieve high levels of the reactive oxygen scavengers, anthocyanins expression in tomatoes. In a pilot test, the lifespan of cancer-susceptible mice was significantly extended when their diet was supplemented with the purple tomatoes compared with supplementation with normal red tomatoes.

Other phytochemicals of interest include related polyphenolics such as resveratrol, which has been demonstrated to inhibit platelet aggregation and eicosanoid synthesis in addition to protecting the sirtuins, genes implicated in DNA modification and life extension; flavonoids, such as tomatoes expressing chalcone isomerase that show increased contents of the flavanols rutin and kaempferol glycoside; glucosinolates and their related products, such as indole-3 carbinol (I3C); catechin and catechol; isoflavones, such as genistein and daidzein; anthocyanins; and some phytoalexins. **Table 1** summarizes activities in improving nutritional characteristics of various crops worldwide. A comprehensive list of phytochemicals are outlined in **Table 2** (reviewed in Newell-McGloughlin, 2010). To reiterate, although there is a growing

knowledge base indicating that elevated intakes of specific phytochemicals may reduce the risk of diseases, such as certain cancers, cardiovascular diseases, and chronic degenerative diseases associated with aging, further research and epidemiological studies are still required to prove definitive relationships.

Protecting Plants

Plants produce many defense strategies to protect themselves from predators. Many, such as resveratrol and glucosinate, which are primarily pathogen-protective chemicals, also have demonstrated beneficial effects for human and animal health. Many, however, have the opposite effect. For example, phytate, a plant phosphate storage compound, is considered an anti-nutrient as it strongly chelates iron, calcium, zinc, and other divalent mineral ions, making them unavailable for uptake. Nonruminant animals generally lack the phytase enzyme needed for digestion of phytate. Poultry and swine producers add processed phosphate to their feed rations to counter this. Excess phosphate is excreted into the environment, resulting in water pollution. When low-phytate soybean meal is utilized along with low-phytate maize for animal feeds the phosphate excretion in swine and poultry manure is halved. A number of groups have added heat- and acid-stable phytase from *A. fumigatus* inter alia to make the phosphate and liberated ions bioavailable in several crops (Potrykus, 1999). To promote the reabsorption of iron, a gene for a metallothionein-like protein has also been engineered. Low-phytate maize was commercialized in the United States in 1999 (Wehrspann, 1998).

In November 2009, the Chinese company Origin Agritech announced the final approval of the world's first GM phytase-expressing maize (Han, 2009). Research indicates that the protein in low-phytate soybeans is also slightly more digestible than the protein in traditional soybeans. In a poultry-feeding trial, better results were obtained using transgenic plant material than with the commercially produced phytase supplement (Keshavarz, 2003). Poultry grew well on an engineered alfalfa diet without any inorganic phosphorus supplement, which shows that plants can be tailored to increase the bioavailability of this essential mineral. A similar effect was achieved in wheat by a Danish group where temperature-tolerant phytase resisted boiling (Brinch-Pedersen *et al.*, 2006).

One of the first products modified for safety was submitted for petition for determination of nonregulated status in 2013. The submission was by JR Simplot for a potato that has three specific modifications for quality improvement. They use what they term 'Innate' technology, basically utilizing RNAi (to silence genes related to expression of black spot bruise, asparagine, and reducing sugars in tubers).

The three traits modified are important from a commercial perspective as they greatly improve the quality of the potato, making them more appealing to both producers and consumers. The first of those traits, reduced black spot from bruising and browning, is achieved through RNAi suppression of PPO effectively reducing oxidation by silencing the endogenous PPO gene. Not alone is this more appealing for the consumer, it will help to reduce waste for growers as fewer potatoes will be discarded.

The second is a reduction in reducing sugars through downregulation of phosphorylase and starch-associated genes slowing the conversion to sucrose and fructose, which provides potatoes with a consistent golden color resulting in improved taste and texture qualities.

The third is suppression of asparagine through expression of asparagine synthetase-1, which reduces the potential for the formation of acrylamide by 80%. The latter is created when potatoes are cooked at high temperatures. In addition, the reducing sugars react with amino acids, such as asparagine, to produce Maillard products, including acrylamide. So by reducing the levels of these sugars and asparagine in stored potatoes, they can significantly reduce the levels of acrylamide in the food. Accordingly, this modification improves not only the quality but also the safety of the potato by reducing the levels of this toxic chemical.

Expression of the first cassette lowers transcript levels for the asparagine synthetase-1 (Asn1) and polyphenol oxidase-5 (Ppo5) genes and, consequently, limits the formation of the acrylamide precursor asparagine and the formation of impact-induced black spot bruise that occurs when the enzyme PPO oxidizes phenols to produce dark pigments. The presence of black spot bruise results in lower quality and subsequent production losses during processing into fries or chips.

A reduction in the formation of reducing sugars is accomplished by the downregulated transcript levels for the PhL (phosphorylase-L) and R1 (starch associated) genes resulting from expression of the second cassette. These traits function by slowing the conversion of starch to reducing sugars (glucose and fructose). Benefits include improved quality, especially relating to color control, and thus contributing to the desired golden brown colors required by most French fry or chip customers. Also, the reducing sugars react with amino acids, such as asparagine, to produce Maillard products, including acrylamide. So by reducing the levels of these sugars in stored potatoes, we can significantly reduce the levels of toxic acrylamide in the food.

Other anti-nutrients that are being examined as possible targets for reduction are trypsin inhibitors, lectins, and several heat-stable components found in soybeans and other crops. Likewise, strategies are being employed to reduce or limit food allergens (albumins, globulins, etc.), malabsorption, and food intolerances (gluten) and toxins (glycoalkaloids, cyanogenic glucosides, and phytohemagglutinins) in crop plants and aesthetic undesirables, such as caffeine (Ogita, 2003). Examples include changing the levels of expression of the thioredoxin gene to reduce the intolerance effects of wheat and other cereals (Buchanan, 1997) and using RNAi to silence the major allergen in soybeans (P34 a member of the papain superfamily of cysteine proteases) and rice (14–16 kDa allergenic proteins). Blood serum tests indicate that p34-specific IgE antibodies could not be detected after consumption of gene-silenced beans (Helm, 2000; Herman, 2003).

Modern biotechnology approaches can be employed to downregulate or even eliminate the genes involved in the metabolic pathways for the production, accumulation, and activation of these toxins in plants. For example, the solanine content of potato has already been reduced substantially using an antisense approach, and efforts are underway to reduce the level of the other major potato glycoalkaloid, chaconine

(McCue *et al.*, 2003). Work has also been done to reduce cyanogenic glycosides in cassava through expression of the cassava enzyme hydroxynitrile lyase in the roots (Siritunga and Sayre, 2003). When 'disarming' plants' natural defenses in this way one must be aware of potentially increased susceptibility to pests, diseases, and other stressors, so that the recipient germplasm should have input traits to counter this.

Improvement of crop nutritional quality is a technical challenge hampered by a lack of basic knowledge of plant metabolism and the need to resolve the complexity of intersecting networks of thousands of metabolic pathways. With the tools now available through the field of genomics, proteomics, lipomics, glycobiomics, metabolomics, and bioinformatics, we have the potential to study and manipulate genes and pathways at the metalevel while simultaneously studying the expression and interaction of transgenes on tens of thousands of endogenous genes. With these newly evolving tools we are beginning to dissect the global effects of metabolic engineering on metabolites, enzyme activities, and fluxes. For essential macro- and micronutrients that are limiting in various regional diets, the strategies for improvement are clear and the concerns, such as pleiotropic effects and safe upper limits, are easily addressed. However, for many putative health-promoting phytochemicals, clear links with health benefits are yet to be demonstrated. In addition, one must be careful when extrapolating attributes from an individual substance acting independently to that substance acting within a complex milieu. However, if such links can be established it will make it possible to identify the precise compound or compounds to target and which crops to modify to achieve the greatest nutritional impact and health benefit. With rapidly emerging technologies the increase in our understanding and ability to manipulate plant metabolism during the coming decades should place plant researchers in the position of being able to modify the nutritional content of major and minor crops to improve many aspects of human and animal health and well-being.

Barriers to Introduction

Commercialization of the first generation of products of recombinant DNA technology was another facet in a long history of human intervention in nature for agricultural and food production purposes. Hence, the same parameters of risk-based assessment should apply. Commercialization of products must be undertaken within a regulatory framework that ensures adequate protection of the consumer, the environment, and alternate production systems while not stymieing innovation. The first generation of such crops focused largely on input agronomic traits; the next generation will focus more on value-added output traits.

There is almost universal agreement that innovation is essential for sustaining and enhancing agricultural quality and productivity. There also would be general concurrence that this involves at some level new, science-based products and processes that contribute reliable methods for improving quality, productivity, and environmental sustainability. Most of the innovative technologies that have been applied to production agriculture have come into common usage without much controversy or even knowledge by the average consumer. However, thanks to the globalization and democratization of knowledge afforded by the internet, the cult of the amateur as noted by Trewavas (2008) is in danger of giving equal weight to uninformed opinions and blatant fearmongering when it comes to applying the tools of modern technology to improving agricultural efficiencies and enhancing food security.

In the past we have not regulated changes in agriculture based on unpredictable socioeconomic consequences. However, some recent innovative technologies, namely biotechnology and more specifically recombinant DNA technology, have inspired debate in a manner unlike any other previous technological development. Although biotechnology has introduced a new dimension to such innovation, offering efficient and cost-effective means to produce a diverse array of novel, value-added products and tools is not viewed with unmitigated beneficence by all existing and potential stakeholders. The stakeholders involved in this debate are many and diverse, ranging from academic and industrial scientists to conventional and organic producers, to international, national, federal, state, and local government organizations, NGOs and agencies, to activist groups, and ultimately consumers. How this technology is viewed depends very much on the perspective from which it is viewed and the goals and objectives of the different players involved. Individual perspectives are formed by the complexity of the prism through which the world is viewed. Each individual's prism is built of our cumulative life experiences, educational background, innate prejudices, world view, and personal objectives. Although on the surface, scientific facts may appear immutable, how those facts are presented within a socioeconomic context makes for an interesting study of the stratagems used by the diverse stakeholders to advance their own agenda for any given target demographic. These tactics are played out on local and world stages and often by the same players who customize their approach depending on the context.

To most producers, and academic and industrial researchers, biotechnology is seen as offering a new dimension to innovation, providing an efficient and cost-effective means to produce a diverse array of value-added products and tools. To some of our national and international markets it is seen as a trading barrier or chip, depending on which side of the fence one is standing. To others it represents an unnecessary, and for some, unnatural risk at a broad level to our food system and environment and at a very fundamental level to a way of life or code of beliefs. Unfortunately, as in every walk of life, there are some who seize on these many nuances of perception, and indeed fear, to propagate their own, covert or otherwise, agenda.

There is a need to address the issue of barriers that exist to commercialization. Most of the crops approved to date support the notion that the deregulation process is prohibitive for any but well-financed companies whose focus are primarily the large commodity crops as just discussed. Worldwide, there is clear asymmetry and lack of consensus in regulatory systems. Non-hypothesis-based evaluations have become the standard around the world, and these are being enshrined in the Cartagena Protocol's Roadmap, with the result that cost of safety assessment has sky rocketed without any discernible gain in safety. Given the current regulatory climate, it is difficult to

imagine many of the traits described ever reaching the marketplace. This discourages research on anything but the most mundane of crops and traits and is a real disincentive to creative research. For all intent and purposes there is just one trait from a public institution that has successfully traversed the regulatory minefields and been translated into a commercially viable commodity and that is the viral coat protein protection system initially developed for the papaya ringspot virus (PRSV) pandemic in Hawaii. Papaya is a major tropical fruit crop in the Asian region. However, production in many countries is set back by the prevalence of the PRSV disease as well as postharvest losses. The PRSV-resistant papaya, based on RNAi suppression of the coat protein expression, literally saved the US$17 million economy in Hawaii and although the disease is of significant importance in Taiwan and other SE Asian countries, it has yet to be approved. Coat protein-based resistance is a demonstration of what is known as PTGS later determined to be RNAi, as described earlier. A 20-year effort to combat plum pox virus (PPV) disease through PTGS resistance paid off. In 1990, the USDA/Agricultural Research Service (ARS) scientists began their efforts with a papaya ringspot virus coat protein gene obtained from Dennis Gonsalves. This gene shows 70% homology to the plum pox gene and has been used to control other viruses similarly related to papaya ringspot. Based on this, the USDA developed a transgenic plum line C5, which contains multiple copies of the PPV-CP transgene and is stably resistant to the virus (Scorza *et al.*, 2009) This has been deregulated by Animal and Plant Health Inspection Service (APHIS) and rather incongruously the construct within the trees is registered as a pesticide under EPA FIFRA (Federal Insecticide, Fungicide, and Rodenticide Act) and nurseries that produce them are designated 'pesticide producing establishments' (U.S. Environmental Protection Agency, 2010). However, irrespective of the mechanism, it is important that resistance based on a single gene is managed well and alternate control mechanisms are introduced to reduce pressure on the development of viral resistance. Other approaches include expression of the genes for RNA-replicating enzymes of the virus, expression of satellite RNA, replicating RNA molecules that are molecular parasites of the virus, or the use of protease inhibitors to interfere with processing of the viral proteins.

Rather interestingly, Gonsalves (2003) reported that the transgenic papaya has helped growers to raise nontransgenic papaya in Puna by reducing the overall virus pressure in Puna and serving as buffer zones, suggesting that virus-resistant transgenic crops can directly control the virus and also serve as a tool to minimize infection to nontransgenic crops that are grown in the area. It has been reported that organic papaya growers now surround their plots with the transgenic rainbow variety as the PTGS system proves to be a most effective method to reduce the viral reservoir, thus protecting susceptible varieties through a mechanism that is similar to herd immunity in mammalian systems (Summers, 2014). The late blight resistant potatoes discussed above could feasibly provide the same cooperative resistance for organic potato farmers in Europe, but as BASF has pulled its production in the European Union, this cannot now be demonstrated. Research by Hutchison *et al.* (2010) demonstrates a variation of this halo effect for Bt maize. As noted to militate against the evolution of resistance, growers are required to maintain a 20% refugium of non-Bt maize. Despite predictions that this single-gene protection may select the development of resistant in corn borer larvae on maize or bollworm in cotton, it has proven to be remarkably resilient. Although some resistance has arisen most specifically in the latter where a mutation in the cadherin receptor has led to localized resistance, it is much lower than what might be expected given the extent of usage of the Bt phenotype. Actually, although mutations providing small decreases in susceptibility to Bt proteins are relatively common, those conferring sufficient resistance to enable survival on some types of Bt corn are exceedingly rare. Hutchison (2010) had demonstrated that this had led to cumulative benefits over 14 years of between US$3.2 and US$3.6 billion with US$1.9–2.4 billion of this total accruing to non-Bt maize growers. They postulated that these results affirmed theoretical predictions of pest population suppression and highlighted economic incentives for growers to maintain non-Bt maize refugia for sustainable insect resistance management. Although initially these refugia were required to be in specified plots, it has been put forward that mixing Bt and non-Bt maize grain during planting may be an equally effective management strategy. However, this effect is disputed by some entomologists. Again, enforcement of these requirements had been relatively easy in the developed world, whereas doing so in some regions may prove more challenging.

The obdurate attitude of the European Union has consequences beyond the obvious economic. A case in point is the BASF's decision to pull the Fortuna potato as cited above. Now instead of adopting the GM Fortuna cultivar and the subsequent reduction of the use of harmful chemicals, European farmers must rely on the continued use of fungicides, which are some of the least friendly biocontrol chemicals. Ironically, as noted, this choice obstructs further expansion of organically produced potatoes and tomatoes because adopting the GM Fortuna cultivar in 'conventional' agriculture could have led to reduced disease pressures benefitting alternative farming systems (Dixelius, 2012). In addition, as a major consumer of potatoes, the European Union will now become increasingly dependent on import from other regions, as they inevitably lose the battle against *P. infestans*. Over time these imported potatoes are likely to be GM Fortuna, so Europe is still left with the problem of tackling political resistance against it or any other GM crop.

Although translation of biotechnology research into value added products for producers and consumers is a challenge in the European Union and even in the United States, it is exponentially more difficult in LDCs. A problem facing Africa in particular is the lack of a dynamic private sector to take technologies to the farmer. It has also been estimated that regulatory costs exceed the costs of research and experimentation needed to develop a given GM crop, which is a major problem in releasing such crops to the market. A way to reduce the costs of generating food and environmental safety data is to develop regional 'centers of excellence' with complementary facilities for biosecurity compliance. If this can be done reliably, then regulatory costs could be reduced. The economic gains from using GM crop technology in SSA are potentially large according to the World Bank Group (Anderson, 2005). The results suggest that the welfare gains are potentially very large,

especially from golden rice (beta-carotene-enhanced rice) and nutritionally enhanced GM wheat and that those benefits are diminished only slightly by the presence of the European Union's current ban on imports of GM foods.

Using the global economy-wide computable general equilibrium model, known as Global Trade Analysis Project (GTAP), Anderson *et al.* (2005) specifically noted that if SSA countries impose bans on GM crop imports in deference to EU market demand for non-GM products, the domestic consumer net loss from that protectionism would be more than the small gain derived from greater market access to the European Union.

In December 2012 the FAO's Director-General, José Graziano da Silva, noted that food insecurity in Africa's Sahel region is closely linked to peace and stability, and he stressed that short-term humanitarian efforts in the Sahel needed to be replaced with longer term development (da Silva, 2012). Apart from the suggested implication of food and agricultural markets as being one of the trigger factors in catalyzing the 'Arab Spring,' the most recent global food crisis was in 2008 and, as noted, we may be facing an even greater one in coming years. During this crisis, which was erroneously laid disproportionately on the shoulders of biofuel production, most especially grain ethanol, the Gates Foundation announced US$306 million in grants to boost agricultural yields in the developing world, with nearly US$165 million to replenish depleted soils in Africa. As noted by US News and World reports these efforts are not without controversy as they charge that critics consider that western philanthropists are violating African 'food sovereignty' and promoting American at the expense of peasant farmers knowledgeable about local practices (Lavelle *et al.*, 2008). But local practices have yielded scarcity. A farmer in India grows three to four times as much food on the same amount of land as a farmer in Africa; a farmer in China, roughly seven times as much. Biotechnology crops can contribute to a 'sustainable intensification' strategy favored by many science academies worldwide, which allows productivity to be increased only on the current 1.5 billion hectares of global crop land, thereby saving sensitive land and biodiversity.

Problems cited for the slow passage of GM crops from experimental, to trial, to commercial stage include the lack of capacity to negotiate licenses to use genes and research techniques patented by others, especially for crops with export potential. In addition, there are difficulties in meeting regulatory requirements and a lack of effective public commercialization modalities and working extension networks. Biosafety and Intellectual Property Rights (IPR) regulations still have to be enforced in many countries for an effective and purportedly 'safe' use of genetically engineered crops, especially if their production is intended for the export market.

As noted, intellectual property constraints continue to be a significant barrier in some regions and for some technologies. If the public sector is going to contribute in tangible ways to technological approaches for food security, the public research system needs to be optimized for translation in this arena. At the research level, this is usually not of major importance in developing regions, but at the commercialization stage this has the potential to be a significant barrier to initial adoption, but most specifically to enforcement of regulations. An additional impediment that public sector researchers often encounter is that the constructs for which they have Freedom to Operate in research applications are patent protected and must be licensed at some cost before a product can be considered for commercialization. Benchmarking standards and best of breed should be created to facilitate this type of translation. There are some entities, such as CAMBIA in Australia and the Public-Sector Intellectual Property Resource for Agriculture (PIPRA) at the University of California, Davis, which seek to assist both public and private sector crop developers to assess the IP terrain, to develop licensing and other types of agreements, and to formulate a commercialization or product release strategy for resource-poor regions (Bennett, 2010).

But what of the context in which these crops are grown? Can all cropping systems coexist in harmony? According to Brookes and Barfoot (2008), it is important to determine the relative importance of different crop production systems based on planted area, production, and economic value to the region in question. The issue is what, if any, are the economic consequences of adventitious presence of material from one crop system within another based on the notion that farmers should be able to cultivate freely the crops of their choice using whichever production system works best in any given context (GM, conventional, or organic). It is never a food or environmental safety issue but rather a production and marketing matter. The heart of the issue is assessing the likelihood of the adventitious presence of material from one production system affecting another and the potential impacts. This requires consistency when dealing with the adventitious presence of any unwanted material, including, but most definitely not limited to, biotechnology-derived material. Adventitious presence is simply the unintended incidence of something other than the desired crop, such as small quantities of weed seeds, seeds from other crops, dirt, insects, or foreign material (e.g., stones). It is unrealistic to expect 100% purity for any crops, or products derived therefrom, so thresholds that are consistent across all materials should be set and should not discriminate (e.g., thresholds for adventitious presence of biotechnology material should be the same as applied to thresholds for other unwanted material and vice versa). All measures should be proportionate, nondiscriminatory, and science based.

The issue of economic liability provisions that compensate growers for adventitious presence of biotechnology material is often raised and is hotly contested. Historically, legal systems have placed the burden of preventing adventitious presence of unwanted material in an agricultural crop on the grower of that crop. For example, seed breeders bear the legal burden of isolating certified seed crops from undesired pollination by a neighbor's crop of the same species. Breeders, not their neighbors, must use geographic isolation, physical barriers such as trees or hedgerows, and buffer zones to separate seed and non-seed crops. By extension, many biotechnology advocates have suggested that the onus of preventing unwanted cross pollination by biotechnology plants should fall on growers of any specialty crops, such as organic grains, fruits, and vegetables.

Many organic growers and others who wish to preserve the non-biotechnology identity of their crops counter that biotechnology and biotechnology crops are sufficiently different

from historical forms of 'contamination' and that the burden of preventing cross-pollination should fall on the growers of biotechnology varieties. Although, in the United States, organic products cannot be (legally) downgraded or the producer decertified by unintentional presence when all required measures and best practices are adhered to and no producer has been so impacted to date, there is a perception that these production systems have been negatively impacted. Indeed, as noted by Bradford (2011), among others, given that certain production systems, as noted organic, seek to prevent all the presence of GE products in organic commodities (although not required for certification), the implications on production agriculture in general that implementation of those extreme requirements would have is profound. In essence, in an effort to address the concerns that 'onerous measures carried out in an attempt to prevent contamination will similarly burden Plaintiffs Family Farmers,' as noted in the alfalfa lawsuit cited above, the onerous burden on conventional agricultural growers is discounted. In essence this means that an agricultural system that accounts for $<1\%$ of production agriculture in the United States can potentially dictate growing terms to the majority production system when their growing areas are contiguous. This is not only onerous but also disproportionate and potentially devastating for production agriculture in the United States.

Virtually all EU member states have transcribed EU Directive 2001/18 and implement EU regulations on traceability and labeling. Within the European Union, provision has been made for a *de minimis* threshold for the unavoidable presence of GMOs, but no actual threshold has been set. Therefore, the default state of the 0.9% on labeling and traceability is the one enforced. Indeed, there have been at least two occasions to date in which the presence of minute levels of transgenes in non-biotechnology crops has given rise to legal concerns. The transgene from Bayer Crop Sciences' unapproved LLRICE 604 were found in Clearfield 131 (CL131) rice seed in 2007, and the transgene from Mycogen's unapproved event '32' was discovered in maize in 2008. US regulatory agencies were able to move quickly and determine that these events did not prove any risk because they carried similar constructs to those already having achieved nonregulated status. The problem nevertheless rendered the 'contaminated' rice and corn unapproved for export, causing financial losses of millions of dollars for growers. In those cases, involving as yet unapproved biotechnology varieties, US courts determined that the developers did, in fact, have an obligation to ensure isolation from non-biotechnology and approved biotechnology crops.

For fully approved varieties, however, growers of specialty crops who have themselves chosen a more stringent standard than that established by the market for basic commodity products should not expect their neighbors to bear the special management costs of meeting that self-imposed standard. To do so would reverse fundamental freedom of economic activity and would establish a dangerous precedent. It would allow specialty operators to formulate unrealistic standards for biotechnology production, would impose impossibly high standards on neighbors, and would effectively impose a ban on the choice of other producers. Specialty crop growers usually are rewarded by higher prices and niche markets for taking such actions. Their neighbors enjoy no such advantage. Furthermore, because organic certification is process based, not content based, accidental cross-pollination of an organic crop by biotechnology plants does not, in fact, affect the organic status of the resulting food or feed.

If new regulations were adopted to address economic liability provisions for any negative economic consequences of adventitious presence of unwanted material, one might argue that the same principle should apply to all farmers regardless of their chosen production methods. On equity grounds, biotechnology growers should have equal access to compensation for adventitious presence of material from conventional or organic crops (such as fungal contamination) as conventional and organic producers have from biotechnology growers. All coexistence measures should be based on legal, practical, and scientific realities and not on commercial or niche marketing objectives.

According to Brookes and Barfoot (2008), fully approved biotechnology crops do generally coexist successfully with conventional and organic crops in North America (where, as noted, biotechnology crops account for the majority of acreage of important arable crops, like soybeans, cotton, and maize), Spain, and more recently the Czech Republic. The market has developed practical, proportionate, and workable coexistence measures without new regulations or indeed any government intervention. Where isolated instances of adventitious presence of biotechnology material have been found in conventional or organic crops, these have usually been caused by inadequate implementation of good coexistence practices (e.g., inefficient segregation of crops in storage and transport and nonuse of tested, certified seed).

Under civil liability (i.e., tort damages) and for intellectual property infringement (except for the unauthorized StarLink corn, which had received split approval only for animal consumption but was found in human food), there have been no lawsuits brought by any parties for adventitious presence. Every case brought by a seed company for infringement has involved a claim that the farmer charged with infringement was an intentional infringer (i.e., adventitious presence was not the issue). Moreover, to date each of these cases was upheld by the courts. Indeed, all except one notable exception in North America has conceded to this claim.

Therefore, the actual commercialization of biotechnology products may have little to do with technical limitations and more to do with external constraints, primarily the process of regulatory approval. The flagship of improved nutritional varieties, namely beta-carotene-enhanced rice (commonly referred to as golden rice), despite being under consideration since the late nineties and subject to a barrage of risk assessments has yet to receive approval. By incorporation of beta-carotene into rice cultivars and widespread distribution of this 'packaged technology in the seed,' it is estimated that it could prevent one to two million deaths each year. Ingo Potrykus, the developer, says an unreasonable amount of testing was required, without scientific justification. In a 2011 Nature article, he laid the blame solely at the door of the regulatory process that he considered excessive, stating "I therefore hold the regulation of genetic engineering responsible for the death and blindness of thousands of children and young mothers," (Potrykus, 2010).

Scientific, civic, and religious opinion leaders from all over the world have expressed support for the value of this

technology. Noted African scientist Florence Wambugu (1999) of Kenya stated that the great potential of biotechnology to increase agriculture in Africa lies in its 'packaged technology in the seed,' which ensures technology benefits without the need to change local cultural practices. Golden rice is a seminal example of this contention. Florence Wambugu observed that in the past, many foreign donors funded high-input projects, which had not been sustainable because they had failed to address social and economic issues, such as changes in cultural practice. In concurrence with this, Ismail Serageldin, former Chairman of the Consultative Group on International Agricultural Research (CGIAR), noted that a priori biotechnology could contribute to food security by helping to promote sustainable agriculture centered on smallholder farmers in developing countries. Harvard's developing economies expert Juma (2012) noted that Africa's precautionary approaches to biotechnology not only are misguided, but they also expose the continent to long-term political risks. He maintained that the issue is no longer a simplistic argument about becoming an importer of GM foods; it is about building up the requisite capacity to diversify the technological options needed for long-term agricultural adaptation. There are others that hold opposing positions, but their views, on the whole, are based on uninformed opinions unsupported by scientific data.

Future Directions

As agriculture must adapt to rapidly changing needs and growing conditions, we must become more effective at producing more or less with limited resources and only the tools of biotechnology will allow us to bypass physiological and environmental limitations to produce sufficient food, feed, fuels, and fiber on ever-diminishing arable land to meet ever-increasing demand. The challenges going forward are foremost technical as we strive to modify qualitative as opposed to quantitative traits and intricate metabolic pathways and networks as opposed to single genes; the scientific hurdles to achieve these aims are not trivial. However, with the tools now coming on line in the fields of genomics, proteomics, metabolomics, and bioinformatics, we have the potential to make major modifications to introgress desirable traits. For example, tools such as genome editing (using artificial nucleases such as Zn fingers, transcription activator-like effector nucleases, and clustered regularly interspaced short palindromic repeats), next-generation sequencing, RNAi, Tfs, minichromosomes, non-integrating vectors, combinatorial transformation, epigenetic modification, network engineering, synthetic biology, and systems biology will allow us to apply both reductive and holistic approaches to identify, modify, introgress, and subsequently simultaneously study the expression and interaction of transgenes on tens of thousands of endogenous genes in elite germplasm backgrounds. With rapidly emerging technologies, the increase in our understanding of, and ability to, manipulate plant metabolism during the coming decades should place plant researchers in the position of being able to modify crop traits to respond to the diverse needs from minimizing environmental impact to optimizing productivity and quality output.

Nontechnical limitations to adoption of this technology include intellectual property restrictions that may limit translation of public research if not managed judiciously; second, liability concerns over use, abuse, or misuse of constructs; third, prohibitive and asymmetric biosafety regimes; and finally public acceptance. The latter two in many ways are the most insidious of limitations as they have little basis in rational process and thus are difficult to redress effectively – the last in particular is often predicated on how much of the former is perceived to be of concern, and how positions are presented by the opposing factions. It is often easier to appeal to emotion and sell fear than it is to present reasoned and judicious scientific rational for basing risk analysis. Indeed, the actual commercialization of biotechnology products may have little to do with technical limitations and more to do with these external constraints, primarily the process of regulatory approval. As a noted case in point, 'golden' rice is only now at the point of finally being approved for commercialization, (Potrykus, 2010), where the blame has been laid on the regulatory process for the delay in approval. As noted by Juma (2012), biotechnology is not simply a matter of rhetorical debate guided by short-term interests; it is central to how countries define their place in the global knowledge ecology.

Given that resources are finite, we must be pragmatic in our assessment of agricultural methodologies and insure that we deploy approaches that make the most sense in any given circumstance. Genuine sustainability can only be attained by promoting the development of resource-enhancing technologies. The only sure way to protect the planet's resources is not to settle into the complacency of maintaining the status quo but to engage in continual, constructive change based on scientific knowledge. If we are to be accountable to posterity, it is not just our choice but our duty to promote and apply responsible science and technology in all endeavors.

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Biotechnology: Herbicide-Resistant Crops

SO Duke, USDA, ARS, Oxford, MS, USA

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Glossary

Auxinic herbicide A herbicide such as 2,4-dichlorophenoxyacetic acid that acts as a synthetic form of the plant hormone indoleacetic acid (auxin).
Deregulation The approval of a transgenic crop by regulatory agencies for its commercialization.
Dicotyledonous A flowering plant with two cotyledons in the seed.
Gene stacking The process of inserting more than one functional transgene into an organism by genetic engineering.
Monocotyledonous A flowering plant with a single cotyledon in the seed, for example, grasses, lilies, and orchids.
Photosystem II The first protein complex of the light-dependent processes of photosynthesis in which water is split.
Shikimate pathway The biochemical pathway that leads to the synthesis of the aromatic amino acids phenylalanine, tryptophan, and tyrosine and their derivatives.
Transgene A gene that has been inserted into the genome of an organism by genetic engineering.

Introduction

In the developed world, weeds have been managed primarily with herbicides since the middle of the past century. The first highly successful herbicide – 2,4-dichlorophenoxyacetic acid (2,4-D) – killed most dicotyledonous weeds, but at the same time it did not injure monocotyledonous crops or turf. Subsequently, companies involved in herbicide discovery screened for selective compounds that kill important weeds without significantly injuring crops. Such products usually killed only a fraction of the important weeds in a crop, so that another selective herbicide with a different weed species spectrum also had to be used in the crop if the farmer was to rely on herbicides for weed management. Minor crop injury commonly occurred with selective herbicides, but farmers were willing to accept this risk in return for good weed management, as weeds can devastate a crop if not controlled. Nonselective herbicides that kill all plants, like paraquat or glyphosate, were usually used with crops only before planting or after harvesting.

Except for auxinic herbicides such as 2,4-D and grass-killing herbicides inhibiting acetyl-CoA carboxylase (ACCase), the mechanism of crop selectivity did not involve resistance at the molecular target site of the herbicide. Most selective herbicides did little harm to the crop because the crop metabolically degraded the active ingredient much more rapidly than the weed. For example, triazine herbicides are quickly degraded by maize (Esser *et al.*, 1975), the crop of their primary use, even though these herbicides are active at the D-1 site of photosystem II (PSII) of all plants. For most selective herbicides, phytotoxicity to a crop is variable, depending on factors that might influence metabolic degradation of the herbicide, such as climatic conditions. A concern of herbicide manufacturers was that the 'selective' herbicide might cause unacceptable problems in cultivars for which it had not been tested. Use of compounds that induce increased metabolism of the herbicide by the crop (herbicide safeners) to provide protection has been one approach to protect the crop from unacceptable herbicide damage (Rosinger *et al.*, 2012). This approach further complicates weed management and adds another chemical to the environment.

Thus, finding a genetic approach to manipulate the crop in order to make it resistant to the herbicide was an attractive alternative to manipulation of the chemical or the crop's response to a herbicide with a safener. Attempts were made to find crop cultivars with resistance to existing commercial herbicides. For example, the Tracy-M cultivar of soybeans was resistant to metribuzin, an inhibitor of PSII, to which other varieties of soybean were significantly more sensitive (Barrentine *et al.*, 1982; Klein and He, 1992), thus indicating that germplasm for herbicide resistance exists in some crops. This approach was not successful in expanding the use of any herbicide with any crop. Another approach was to introgress evolved resistance genes from weedy relatives into crops. The only success with this approach was the use of the evolved triazine-resistant bird's turnip rape (*Brassica campestris*) germplasm to produce triazine-resistant canola (Hall *et al.*, 1996). Commercial triazine-resistant canola was produced with this method and was introduced into the market in 1984, gaining a small amount of market share in Canada first and much later in Australia. However, the resistance gene produces a modified D1 protein that, although resistant to triazines, is not quite as efficient in PSII, resulting in reduced yield under some environmental conditions (Hall *et al.*, 1996).

The real success in altering crops to resist herbicides has come from gene selection in tissue culture and transgene technology. The former method has produced crops resistant to two major classes of herbicides. They are the sulfonylurea and imidazolinone inhibitors of acetolactate synthase (ALS) and the cyclohexanedione and aryloxyphenoxypropionate (AOPP) inhibitors of ACCase. These nontransgenic herbicide-resistant (HR) crops will be discussed, but most of this article will deal with transgenic HR crops, particularly glyphosate-resistant (GR) crops, as these crops have had the most impact on weed management and agriculture. Several books and reviews are available that deal with the topic of transgenic HR crops in general (e.g., CaJacob *et al.*, 2004; Duke, 1996; Duke and Cerdeira, 2005, 2010; Martino-Catt *et al.*, 2012; Nandula,

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2010) and on GR crops in particular (e.g., Dill *et al.*, 2008; Green, 2009). Special issues of the journal *Pest Management Science* have dealt with HR crops from biotechnology in March 2005 and with GR weeds and crops in April 2008. This article will try to cover the more important information from these sources, while updating the information in this rapidly moving field of science and agriculture.

Nontransgenic Herbicide-Resistant Crops

HR crops can be generated for some herbicides by selecting for target site mutations in plant populations or tissue culture or by mutation breeding. Green and Castle (2010) and Green and Owen (2011) have reviewed this topic. This approach to produce HR crops has worked for herbicides with relatively plastic molecular targets to which resistance evolves easily, such ALS and ACCase inhibitors. This plasticity is proven by the fact that there are 129 and 42 weed species, respectively, that have evolved resistance to herbicides that target these two enzymatic sites, almost exclusively due to target site mutations (Heap, 2013). Crops made resistant to grass-killing ACCase-inhibitor herbicides, such as aryloxyphenoxypropionates and cyclohexanediones, by selection for resistance in tissue culture have not gained large market shares, although there were substantial efforts to develop such crops (Somers, 1996). These crops were all resistant by means of a HR ACCase. Maize made resistant to the cyclohexanedione herbicide sethoxydim was commercialized in 1996 (Green and Owen, 2011). Adoption of sethoxydim-resistant maize never rose to more than 1%, and it is no longer available (Martino-Catt *et al.*, 2012). The reason(s) for the failure of these nontransgenic crops to gain wider market share is unclear. This question is intriguing in that transgenic ACCase-inhibitor HR crops requiring much more regulatory data for approval are now being developed (see below).

Crops have been made resistant to sulfonylurea herbicides by selection for ALS mutations (Saari and Mauvais, 1996). Nontransgenic sulfonylurea-resistant soybeans (STS™) were commercialized in 1993, 3 years before the first transgenic HR soybeans. Before 2005, this product accounted for 2–4% of the soybean market, but its market share declined thereafter (Martino-Catt *et al.*, 2012), largely due the success of GR crops. The number of active ingredients used on at least 10% of the US soybean area dropped from 11 in 1995 to only 1 (glyphosate) in 2002 (Green and Owen, 2011).

Crops made resistant by selection of ALS mutations to impart resistance to imidazolinone herbicides, another chemical class of ALS inhibitors, have been relatively successful. Imidazolinone-resistant rice, wheat, sunflower, lentils, canola, and maize are commercially available. The first of these crops, maize, was launched in 1992. Single-codon mutation-based ALS resistance was selected in mutagenized seed (rice and wheat) and microspores (canola), as well as simple selection in tissue culture (maize) or in the field (sunflower) (Shaner *et al.*, 1996; Tan *et al.*, 2005). In the case of wheat, which has three genomes, each apparently with its own ALS, two resistant ALS genes provide optimal resistance, especially in spring wheat (Tan *et al.*, 2005). These crops have been the most successful of the nontransgenic HR crops, perhaps in part because no other HR rice, wheat, sunflower, or lentils are available. Where GR maize and canola are available, imidazolinone-resistant crops have not been very competitive, primarily because of the superior characteristics of glyphosate compared with any imidazolinone herbicide (Duke and Powles, 2008). As GR maize was adopted, the market share of imidazolinone-resistant maize decreased from a maximum of approximately 5% during 1999–2002 to less than 1% in 2009 (Martino-Catt *et al.*, 2012). Imidazolinone-resistant canola was introduced in 1995 and rose to approximately 10–20% adoption rates, depending on the year, from 1997 to 2004 (Martino-Catt *et al.*, 2012).

Clearly, imidazolinone-resistant crops have been the most successful nontransgenic HR crops. As mentioned earlier, evolution of weeds resistant to ALS-inhibiting herbicides occurs relatively quickly. Thus, one might expect a problem with imidazolinone-resistant weeds in these crops after only a few years. Stewardship programs have been instituted to avoid or delay this problem.

Because the mutated genes only generate isoforms of enzymes that are already in the crop, and there is no insertion of new DNA into the genome, unintended consequences of the mutation are considered highly unlikely, and regulatory approval of the genetics of such crops is not needed. One of the weed management advantages of imidazolinone-resistant crops is that closely related weed species, such as red rice (a feral *Oryza sativa*) in rice, can be controlled by a herbicide that was previously active on both the crop and weed. But, gene flow from the crop to the close relative is much more likely in the presence of the selection pressure of the herbicide. In fact, imidazolinone-resistant red rice has appeared in imidazolinone-resistant rice in several countries (Kaloumenos *et al.*, 2013; Scarabel *et al.*, 2012; Valverde, 2007). The majority of appearance of resistant red rice is apparently due to gene flow, but some of it is due to evolved resistance (Dos Reis Goulart *et al.*, 2012; Rajguru *et al.*, 2005; Shivrain *et al.*, 2007). Although the outcrossing rate is low, spraying the selected herbicide enforces introgression of the resistance gene into the feral population of red rice. Strategies to mitigate gene flow in rice have been devised and called for in order to retain the utility of imidazolinone-resistant rice (Gressel and Valverde, 2009). There has also been concern about flow of the resistance gene from imidazolinone-resistant wheat to jointed goatgrass (*Aegilops cylindrica*), as the two species can interbreed under field conditions (Seefeldt *et al.*, 1998; Gaines *et al.*, 2008).

Many weed species have evolved resistance to ALS-inhibitor herbicides (Heap, 2013), and there is sometimes cross-resistance to imidazolinones for resistant weeds selected by nonimidazolinone ALS-inhibitor herbicides (e.g., Hashem and Dhammu, 2002). Widespread use of all types of ALS-inhibitor herbicides and the ease with which weeds evolve target-site resistance to all ALS inhibitors make resistance management problematic.

Imidazolinone-resistant crops can be used to control parasitic weeds, in that imidazolinones translocate to metabolic sinks, such as infecting parasitic weeds (e.g., *Striga* spp.). Thus, seeds of resistant maize can be coated with herbicide in order to provide *Striga* control (De Groote *et al.*, 2007; Kanampiu *et al.*, 2009). This method can provide season-long

control of these highly destructive weeds (Ransom *et al.*, 2012). However, the rapid evolution of resistance to ALS inhibitors indicates that any weed that survives this treatment should be destroyed before they produce seed.

Some imidazolinones have long soil residual properties, disallowing the planting of a nonresistant crop the next year, for example, planting barley after imidazolinone-resistant wheat. To deal with this problem, the development of imidazolinone-resistant barley by mutation breeding was proposed (Lee *et al.*, 2011). In this case, imidazolinone herbicides would not be used with barley.

Transgenic Herbicide-Resistant Crops

Bromoxynil-Resistant Crops

One of the first commercially available HR transgenic crops, in 1995, was bromoxynil-resistant cotton (**Table 1**). It was followed, in 2000, with bromoxynil-resistant canola. Bromoxynil (3,5-dibromo-4-hydroxybenzonitrile) is a selective PSII-inhibitor herbicide (Fedtke and Duke, 2005) that kills only certain weeds at recommended doses. It also kills dicotyledonous crops at these doses and can be used on some grass crops, such as maize, that are much less sensitive. Thus, making crops resistant to bromoxynil gave farmers another tool for managing certain weed species in sensitive crops.

Only three weed species have evolved resistance to bromoxynil (Heap, 2013). The first case was common groundsel (*Senecio vulgaris*), in 1995 in Oregon, in a peppermint field in which bromoxynil was used for weed management (Park and Mallory-Smith, 2006). The other cases were for maize in Canada in 2004 (smooth pigweed, *Amaranthus hybridus*) and 2005 (redroot pigweed, *Amaranthus retroflexus*) (Heap, 2013). Thus, the selection pressure in bromoxynil-resistant cotton and canola was apparently too weak in geographic scope and duration for bromoxynil-resistant weeds to evolve in these crops.

The transgene for bromoxynil resistance was derived from an isolate of the soil microbe *Klebsiella ozaenae* collected in bromoxynil-contaminated soil (reviewed by Stalker *et al.*, 1996). This isolate could use bromoxynil as a sole source of nitrogen. This gene encodes a nitrilase that converts bromoxynil into a nonphytotoxic derivative, 3,5-dibromo-4-methoxybenzoic acid. The enzyme has substrate specificity for bromoxynil over other nitrile compounds (McBride *et al.*, 1986). In initial studies, the gene provided crops a 10-fold level of resistance to the herbicide (Stalker *et al.*, 1988). In the field, 20-fold field rates caused no sustained damage to bromoxynil-resistant cotton (Stalker *et al.*, 1996).

The market share for these two GR crops was small. This may be partly because the weed species spectrum killed by bromoxynil was limited, giving it little advantage over other nonselective herbicides used in cotton and canola. Also, GR crops that were introduced in canola in 1996 and cotton in 1997 (**Table 1**) had great advantages over bromoxynil-resistant crops (discussed below), although there were a few weed situations in which a farmer might find the bromoxynil-resistant crop cost effective. In the only published assessment comparing a bromoxynil-resistant crop with a GR crop, Clewis and Wilcut (2007) estimated a higher net economic return in GR cotton than in bromoxynil-resistant cotton. Both bromoxynil-resistant crops were discontinued for economic reasons (cotton in 2004 and canola in 2001). Interestingly, volunteer bromoxynil-resistant canola was collected in Canadian fields as late as in 2007, 6 years after it was discontinued (Beckie and Warwick, 2010). Another phenomenon that occurred with bromoxynil-resistant canola was unintentional gene stacking of the bromoxynil resistance gene with genes from other HR canola cultivars through gene flow between glufosinate and GR canola varieties (Beckie *et al.*, 2004). The abandonment of the bromoxynil-resistant crops is perhaps unfortunate, as this option would have been useful in creating the weed management diversity needed to mitigate or slow the evolution of glyphosate resistance, especially because most of the weeds that have evolved resistance to glyphosate in North America are broadleaf species that are sensitive to bromoxynil.

Table 1 Transgenic herbicide-resistant crops that have been or are now available for planting in the US

Herbicide	*Crop*	*Year of introduction*
Bromoxynil[a]	Cotton	1995
	Canola	2000
Glufosinate	Canola	1995
	Maize	1997
	Cotton	2004
	Soybean	2011
Glyphosate	Soybean	1996
	Canola	1996
	Cotton	1997
	Maize	1998
	Sugar beet	2008
	Alfalfa[b]	2005

[a]All bromoxynil resistant crops have been withdrawn from the market.
[b]Removed from market by court order in 2007 but returned to the market by a US Supreme Court ruling and after further USDA/Animal and Plant Health Inspection Service examination in 2011.

Glufosinate-Resistant Crops

Glufosinate-resistant crops also were first introduced for commercial production in 1995 (**Table 1**). Glufosinate (DL-2-amino-4-(hydroxy(methyl)phosphonoyl)butanoic acid) is the chemically synthesized racemic mixture of the D and L stereoisomers of the natural compound L-phosphinothricin, which is produced by several taxa of *Streptomyces* (Copping and Duke, 2007; Lydon and Duke, 1999). Only the natural form, the L-isomer, is herbicidally active. Glufosinate is a nonselective herbicide that kills many weed species, but not as many as glyphosate (Feng *et al.*, 2010).

Glufosinate kills plants by inhibition of glutamine synthetase (GS) (reviewed by Lydon and Duke, 1999). Inhibition of chloroplast GS by glufosinate is essentially irreversible and causes rapid accumulation of one of its substrates, ammonia, which is highly toxic (Lydon and Duke, 1999; Sellers *et al.*, 2004). Loss of glutamine, and subsequently glutamate, leads to inhibition of photorespiration due to missing amino acid donors (Wild and Wendler, 1993). Inhibition of photorespiration in sunlight results in oxidative damage to the

chloroplast. Glufosinate is a fairly fast-acting herbicide and is more like bromoxynil than glyphosate. Like glyphosate, glufosinate is a nonselective, foliar-applied herbicide; however, glufosinate does not have all of the desirable attributes of glyphosate (see below). For example, it translocates relatively poorly in some species (Everman *et al.*, 2009), although this is not true for all species (e.g., Grangeot *et al.*, 2006). The relatively fast action of glufosinate may reduce its movement from strongly affected sites of herbicide deposition after spraying.

Phosphinothricin-producing *Streptomyces* spp. also have an enzyme that detoxifies L-phosphinothricin by acylating it. This enzyme is encoded by the *bar* gene. *Bar* is the abbreviation of bialaphos resistance. Bialaphos is a GS-inactive tripeptide produced by the same microbe. It is degraded by plants to form L-phosphinothricin. The *bar* gene is used in glufosinate-resistant cotton. A very similar gene (the *pat* gene; phosphinothricin acyl transferase) from a different *Streptomyces* species will also generate glufosinate-resistant plants (Wehrmann *et al.*, 1996). It is used in glufosinate-resistant maize and soybean. Both genes have been used extensively as selectable markers for selection of transformants (Jones and Sparks, 2009). Use of the *bar* and *pat* genes in commercial glufosinate-resistant crops produces a very high level of resistance all the way to flowering and beyond (Áy *et al.*, 2012; Thomas *et al.*, 2004). A concentration of 64 times the lethal dose for nonresistant wheat was reported to have no effect on yield of glufosinate-resistant wheat transformed with the *bar* gene (Áy *et al.*, 2012). *Pat* genes from *Nocardia* sp. have also been used as transgenes to experimentally produce glufosinate-resistant crops (Kita *et al.*, 2009; Yun *et al.*, 2009).

Four glufosinate-resistant crops (canola, maize, cotton, and soybean) are available in the US (**Table 1**). Glufosinate-resistant rice was deregulated (approved for sale) but never commercialized, perhaps partly because of the potential problem of gene flow to weedy rice and nontransgenic rice (Oard *et al.*, 2000; Olofsdotter *et al.*, 2000; Sanchez-Olguin *et al.*, 2009; Song *et al.*, 2011). The adoption of glufosinate-resistant crops has been only a small fraction of the HR crop market, primarily because glyphosate is a more effective herbicide than glufosinate on many weed species. However, the growing evolution of GR weeds is increasing the adoption of glufosinate-resistant crops. Glufosinate is effective on some GR weeds such as palmer amaranth (*Amaranthus palmeri*) (Hoffner *et al.*, 2012), perhaps the most problematic GR weed (see Section Glyphosate-Resistant Crops). Resistance to glufosinate has not yet evolved in glufosinate-resistant crops, but it has evolved in *Eleusine indica* and *Lolium multiflorum* in orchards where glufosinate was used year after year (Avila-Garcia and Mallory-Smith, 2011; Heap, 2013). The mechanism of evolved resistance in one glufosinate-resistant Italian ryegrass (*Lolium perenne* L. ssp. *multiflorum*) biotype is a one-codon change in chloroplast GS, making it less sensitive to glufosinate (Avila-Garcia *et al.*, 2012). Other biotypes apparently have a different mode of resistance (Avila-Garcia and Mallory-Smith, 2011). Again, the absence of evolved resistance to glufosinate in glufosinate-resistant crops is probably due to low selection pressure, as defined by limited use of these crops in space and time.

Glufosinate-resistant canola can outcross with other canola varieties, as well as weedy relatives. In Canada, both glufosinate and GR canola (both transgenic) and imidazolinone-resistant canola (nontransgenic) are grown from commercial seeds that have only one of these resistances. Yet, all combinations of these resistances have been found in individual volunteer canola plants, both outside and within canola fields (Knispel *et al.*, 2008; Schafer *et al.*, 2012b). Gene flow can also occur between glufosinate-resistant canola and weedy relatives (Song *et al.*, 2010). Fully introgressed *bar* genes into weeds have not been documented. This scenario requires that the F1 and subsequent backcrosses be fit in the absence of glufosinate or that each cross be subjected to glufosinate. F1 hybrids of some canola/weedy relative combinations are not very fit (e.g., Scheffler and Dale, 1994), yet there are reports of introgression of the *cp4* glyphosate-resistance gene from commercial canola into a weed relative *Brassica rapa* (Warwick *et al.*, 2008). The gene was persistent in the population more than a 6-year period, despite the fitness cost of hybridization and absence of glyphosate use (with the exception of one possible exposure). Nevertheless, gene flow from HR canola to weedy relatives has not created a major weed problem.

There are potential benefits of glufosinate-resistant crops in addition to weed management. Glufosinate is fungitoxic (Liu *et al.*, 1998) and bactericidal (Pline *et al.*, 2001) and provides some level of protection from plant diseases in glufosinate-resistant crops. For example, glufosinate reduced the severity of rice blast and brown leaf spot in glufosinate-resistant rice (Ahn, 2008). The herbicide also provides some degree of protection to glufosinate-resistant soybean from *Pseudomonas syringae* pv. *glycinea* at field rates (Pline *et al.*, 2001). Glufosinate also reduces fungal diseases in glufosinate-resistant bentgrass (*Agrostis* spp.) (Liu *et al.*, 1998; Wang *et al.*, 2003). There may be similar benefits of glyphosate in GR crops with some plant pathogens.

As mentioned earlier, the *bar* gene is used extensively as a selectable marker in transgenic plant production. Therefore, any crop could be made glufosinate resistant (e.g., peppermint – Li *et al.*, 2001 and wheat – Áy *et al.*, 2012). However, the current costs in gaining approval for commercialization of transgenic crops, as well as variety development costs, preclude the introduction of many more glufosinate-resistant crop species. At least in the foreseeable future, new glufosinate-resistant crops will more likely be existing glufosinate-resistant crops (canola, cotton, maize, and soybean) with genes for resistance to other herbicides stacked with them.

Glyphosate-Resistant Crops

Glyphosate: The herbicide

Glyphosate (*N*-(phosphonomethyl)glycine) is the most successful herbicide in history in terms of market share and customer satisfaction (Duke and Powles, 2008). Before GR crops were available, glyphosate was a successful herbicide, but its use grew substantially due to its use in glyphosate-resistant (GR) crops. Because glyphosate is a very good nonselective herbicide, it could only be used with agronomic crops before planting, after crop maturity or harvest, or with devices that did not allow the herbicide to reach the foliage of the crop (e.g., shielded sprayers and rope-wick applicators). It was also heavily used in perennial horticultural crops (e.g., grapes and

tree crops) when foliage had not appeared in the crop or with ground spraying below the crop foliage. It was also used in many noncrop situations. It is considered a very safe herbicide, as its acute toxicity is lower than that of aspirin or NaCl. The vast majority of toxicological studies have found glyphosate to be very safe to mammals from both an acute and a chronic standpoint (Mink *et al.*, 2012; Williams *et al.*, 2000, 2012).

Glyphosate is the only herbicide that kills plants by inhibition of the enzyme 5-enolpyruvylshikimate-3-phosphate synthase (EPSPS). The fact that there is no secondary mode of action at doses of glyphosate used in the field is clear from the finding that plants with a transgene that encodes a resistant form of EPSPS are approximately 50-fold more resistant to glyphosate than untransformed plants (Nandula *et al.*, 2007). EPSPS is a critical enzyme of the shikimate pathway, from which the three aromatic amino acids (phenylalanine, tyrosine, and tryptophan) are derived. The sequence of events causing death of the plant after inhibition of EPSPS is not entirely clear. The most rapid effect is the accumulation of shikimate acid and benzoates in affected plant tissues (Amrhein *et al.*, 1980; Lydon and Duke, 1988). Inhibition of carbon fixation can also be very rapid in some species (e.g., Servaites *et al.*, 1987), apparently due to the loss of carbon intermediates, which, in turn, is caused by the loss of regulation of carbon flow into the shikimate pathway (Siehl, 1997). Certainly, levels of aromatic amino acid are reduced, so is the synthesis of auxin from tryptophan and many secondary products that are derived from aromatic amino acids. Thus, many physiological functions are compromised by this herbicide. Glyphosate is perhaps the most slow-acting herbicide that is sold. Its slow action allows it to translocate throughout the plant, like sucrose, to metabolic sinks (Gougler and Geiger, 1981), such as meristems, where it concentrates. Thus, all growing points of the plant are killed, eliminating regrowth. This makes it very effective on perennial weeds with subterranean rhizomes or stolons that make these species less vulnerable to other herbicides.

Transgenes for glyphosate-resistant crops

Three transgenes for glyphosate resistance have been used in commercially available GR crops. The predominantly used gene has been the *cp4* gene from *Agrobacterium* sp., which encodes a GR EPSPS (Green, 2009). In some maize varieties, a maize EPSPS gene (*TIPS-EPSPS*) modified by site-directed mutagenesis of two codons was used for G21 varieties (Dill, 2005; Feng *et al.*, 2010; Pollegioni *et al.*, 2011). TIPS-EPSPS is kinetically inferior to CP4 EPSPS in the presence of glyphosate. This gene was used only for the first generation of GR maize and was replaced by the *cp4* transgene in the second generation of GR maize (Feng *et al.*, 2012). Until now, all GR canola has contained both *cp4* and a gene (*goxv247*) from the soil bacterium *Ochrobactrum anthropi*, which encodes glyphosate oxidoreductase (GOX), an enzyme that degrades glyphosate to glyoxylate and aminomethylphosphonic acid (AMPA) (reviewed by Duke, 2011a). The microbial GOX gene was modified by mutagenesis and selection for variants with better enzymatic efficiency, as well as some codon modification for better expression in plants (Pollegioni *et al.*, 2011). The GOX transgene alone does not provide sufficient resistance for commercialization (Feng *et al.*, 2012), but why *cp4* alone was not sufficient for commercial resistance in canola has not been divulged. Second generation GR canola with a different promoter for *cp4* will not include a gene for GOX. An uncharacterized plant GOX can occur in some crops and weeds, but not in sufficient amounts to provide natural resistance to glyphosate (Duke, 2011a; Reddy *et al.*, 2008). Some soil microbes contain C-P lyase that will degrade glyphosate to sarcosine and inorganic phosphate (e.g., some *Arthrobacter* spp., *Rhizobium* spp., and *Pseudomonas* spp.) (Kishore and Jacob, 1987; Liu *et al.*, 1991; Dick and Quinn, 1995). However, there are no reports of using the gene for this enzyme to render plants resistant to glyphosate.

Overexpression of glyphosate-sensitive EPSPS was proposed early during the quest for GR crops, but greater than 20-fold-increased expression did not produce plants that were completely resistant to field rates of glyphosate (Shah *et al.*, 1986). This is interesting because biotypes of Palmer amaranth (*A. palmeri*) have evolved up to 160-fold more copies of the natural EPSPS gene by gene amplification, resulting in more EPSPS protein and extractable EPSPS activity, and are highly resistant to glyphosate (Gaines *et al.*, 2010). These resistant biotypes do not seem to pay any fitness penalty and may even have an advantage under drought stress (Chandi *et al.*, 2013). If crops could be manipulated this way, GR crops without transgenes might be possible.

Other transgenes encoding GR EPSPS have been proposed for generating GR crops. For example, a gene ($aroA_{1398}$) for GR EPSPS was selected with glyphosate in an unidentified soil microbe and used as a transgene in maize, producing plants that were highly resistant to glyphosate (Vande Berg *et al.*, 2008). Five rounds of gene shuffling and screening were used to produce a GR EPSPS from apple with two amino acid changes that provided a high level of resistance (Tian *et al.*, 2013). This transgene imparted glyphosate resistance to rice, although the level of resistance was unclear. An artificial transgene was produced by gene shuffling of a gene from *Bacillus licheniformis*, which had a weak ability to acetylate glyphosate (Castle *et al.*, 2004; Siehl *et al.*, 2005). After 11 iterations of gene shuffling, the final version of the glyphosate acetyl transferase (GAT) had enzymatic activity roughly four orders of magnitude greater than the native enzyme. This transgene provides good levels of resistance to glyphosate in crops (Green *et al.*, 2008, 2009). A fungal glyphosate decarboxylase confers resistance to glyphosate (Hammer *et al.*, 2007), but there is no indication at this time of it being commercialized.

Adoption of glyphosate-resistant crops

Commercial GR crops have been rapidly adopted. Crops with transgenic *Bt* toxin for insect resistance, glyphosate resistance, or a combination of these two traits represent almost 100% of all transgenic crops grown on 160 million ha of land worldwide, as of 2012 (James, 2012). GR crops with (in maize and cotton) or without *Bt* toxin represent more than 80% of all transgenic crops sold worldwide, and their market share continues to grow globally (Duke, 2011b). The GR trait is by far the most predominant transgenic trait worldwide. This technology has had more influence on weed management than any other since the advent of synthetic herbicides.

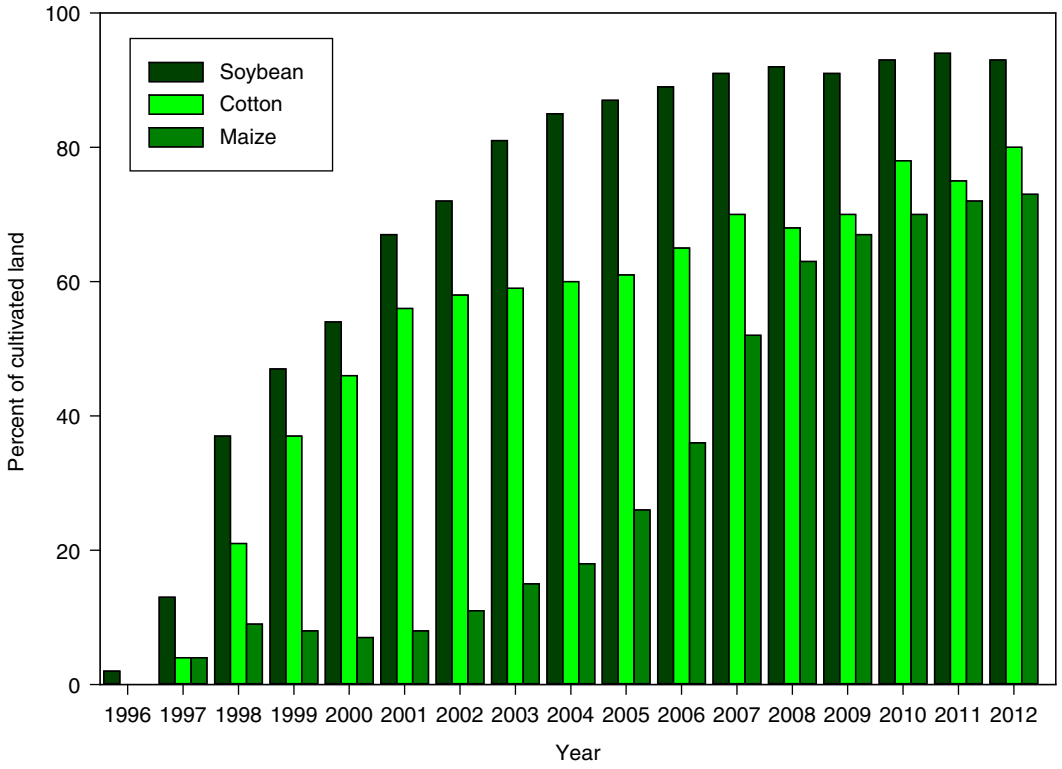


Figure 1 Adoption of GR crops in the US by year. Data from http://www.ers.usda.gov/data-products/adoption-of-genetically-engineered-crops-in-the-us.aspx

In the US, adoption of GR soybeans rose to approximately 90% within 10 years after its introduction (**Figure 1**). Adoption of GR soybeans was even more rapid in Argentina, reaching 90% within 4 years (Penna and Lema, 2003), and adoption in other parts of South America has also been very rapid (Cerdeira *et al.*, 2011). Adoption of GR cotton was also rapid, reaching almost 70% within 10 years and now at approximately 80%. The GR trait was slower to be used in maize, but after a lag period of approximately 5 years, its adoption rose rapidly to reach that of cotton (**Figure 1**). The slower adoption of maize was in part related to trade restrictions on transgenic maize (Martino-Catt *et al.*, 2012) and in part due to inexpensive and adequate weed management with existing selective herbicides. Adoption of GR sugar beet in the US was almost 100% after only 2 years of its commercial release. Canola is the only GR crop in which adoption has not been very rapid. Within 4 years of introduction of GR canola to North America (95% of the canola in North America is in Canada), adoption leveled off at approximately 40% and has remained at that level (Martino-Catt *et al.*, 2012). In 2009, most of the rest of the canola market was glufosinate resistant, with a few percent being resistant to imidazolinone through nontransgene technology (see Section Nontransgenic Herbicide-Resistant Crops).

Adoption of GR crops also led to reduced use of other herbicides in these crops. For example, glyphosate replaced almost all of the herbicides used in soybeans in the US by 2006 (**Figure 2**). This loss of market share for other herbicides in major agronomic crops led to devaluation of the herbicide market, leading to reduced prices of herbicides competing with glyphosate (Nelson and Bullock, 2003) and reduced herbicide discovery efforts by major agrochemical companies (Duke, 2012). These economic impacts were exacerbated by the loss of patent protection on glyphosate in 2000 and the consequent dramatic decreases in the price of glyphosate.

Perhaps the most obvious driving force for this rapid adoption has been economics. For example, since its introduction, GR soybeans have boosted farm income globally by $32.2 billion (Brookes and Barfoot, 2013). In addition to economic drivers, surveys of the US farmers who grow GR soybeans, maize, and cotton found that other important factors promoting adoption were perceived reduced adverse effects on family health, better weed management efficacy, improved safety to the crop, consistency, and good yields (Hurley *et al.*, 2009). All of these factors were rated above cost benefits among factors influencing herbicide choices. Despite the claims by some that the transgene, glyphosate, or both adversely affect yields of GR crops (e.g., Johal and Huber, 2009; Zobiole *et al.*, 2010c; 2011b), trends in yield increases in GR cotton, soybean, and maize after they were introduced have remained the same as before their introduction (**Figure 3**). Analysis of the available literature on yield of HR crops led Darmency (2013) to the conclusion that there are no significant effects of the transgenes for GR or any other HR crops on yield. The flexibility and time-saving aspects of GR crops have allowed small farmers to increase household incomes by having time for off-farm employment (Fernandez-Cornejo *et al.*, 2005, 2007; Gardner *et al.*,

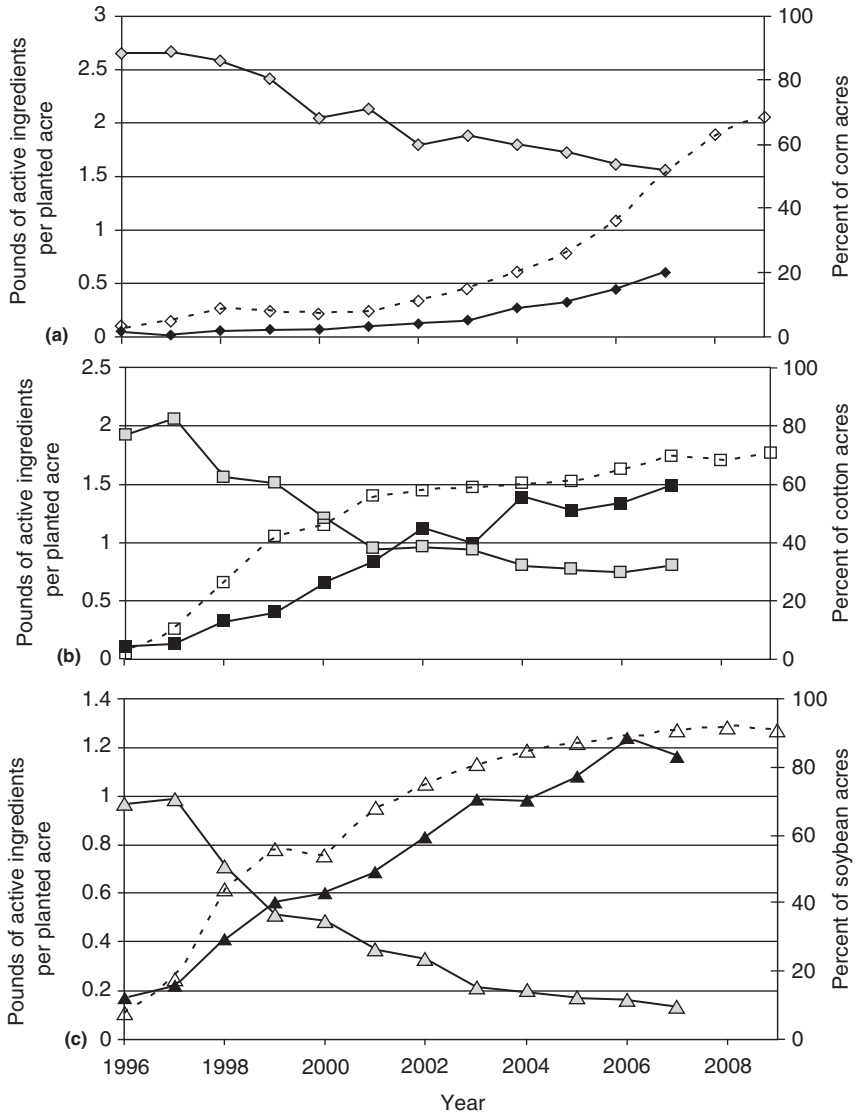


Figure 2 Quantity of glyphosate (dark symbols) and all other herbicides (gray symbols) used on the US crop areas (A, maize; B, cotton; and C, soybean). Open symbols are percent adoption of GR crop. Reproduced with permission of the National Academies Press from Ervin, D.E., Carrière, Y., Cox, W.J., *et al.*, 2010. The Impact of Genetically Engineered Crops on Farm Sustainability in the United States. Washington, DC: National Research Council, The National Academies Press, 250 pp.

2009). Thus, this technology has been as or more beneficial to farmers of small holdings as or than to big agribusiness operations.

How much additional growth will occur in the adoption of GR technology is dependent on several factors. GR soybeans are already 81% of the global market and a substantial portion of the global cotton market (James, 2012), so there is not much room for growth in these crops. However, GR crops represent a much lower fraction of the global area planted to maize and canola crops. There is no GR rice or wheat. GR wheat was almost introduced in North America but was not commercialized largely because of concern about foreign market acceptance. Rapid increases in the evolution of GR weeds and weed shifts to naturally resistant weed species is causing farmers to diversify weed management tools. One approach to diversification is to not use glyphosate in the same field year after year. Also, this impending diversification is not reflected in the data from **Figure 1**, but it may influence GR crop adoption in the future.

Environmental impact of glyphosate-resistant crops

HR crops in general and GR crops in particular have received high-profile bad press from the time before their introduction (e.g., Goldberg *et al.*, 1990) to the present (e.g., see Benbrook, 2012; Mortensen *et al.*, 2012). However, unknown to most of the public, the environment has generally benefited from the adoption of GR crops (Bonny, 2011; Duke and Cerdeira, 2005; Cerdeira and Duke, 2006; Green, 2012; Shiptalo *et al.*, 2008). A study of all available data by a US National Research Council committee concluded that HR crops (which during the period of the studies were more than 95% GR crops) generally have fewer adverse effects on the environment than

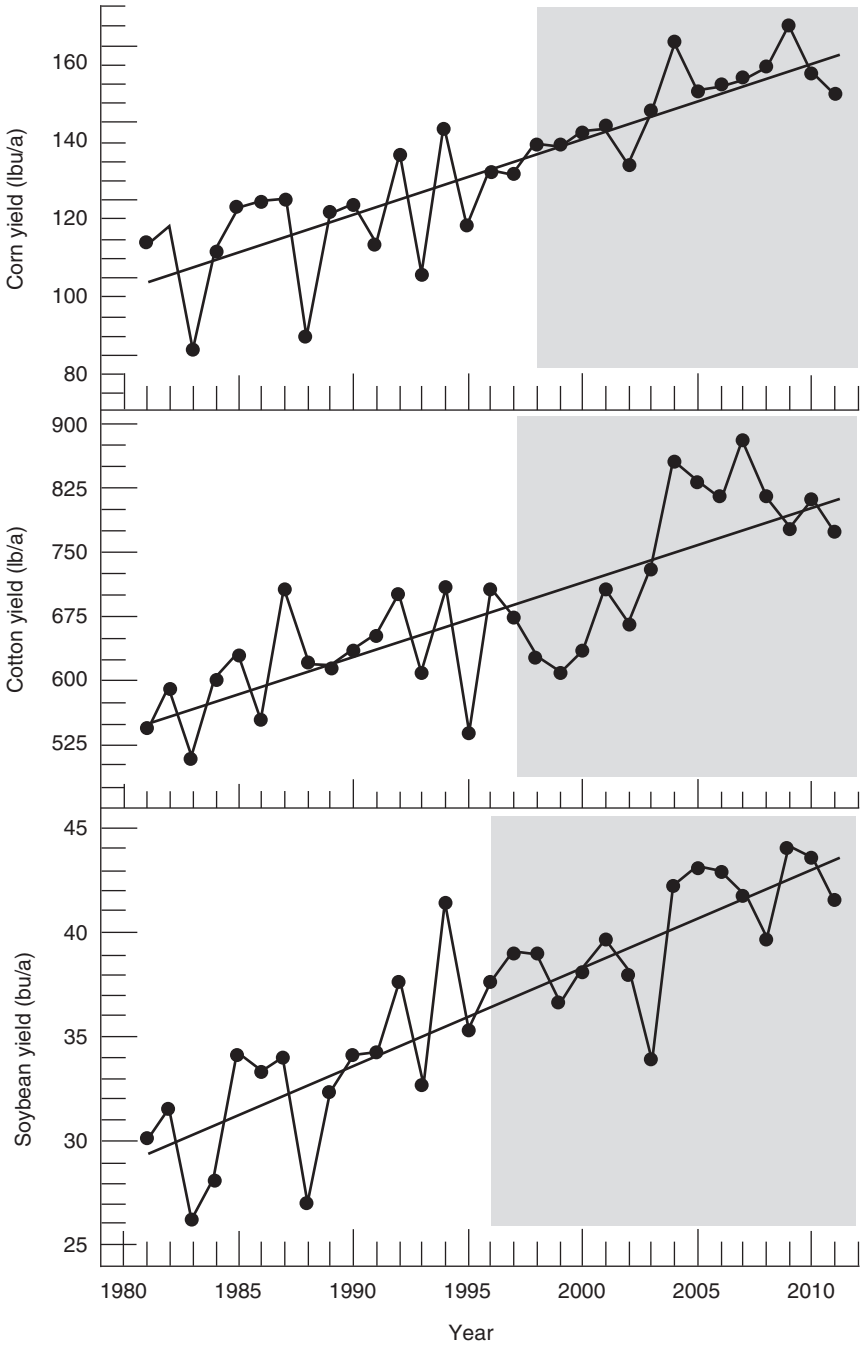


Figure 3 The US yields of the three crops over the past 30 years that are now grown mostly as GR cultivars. The shaded represents the years since the introduction of each GR crop. Reproduced with permission from Duke, S.O., Lydon, J., Koskinen, W.C., *et al.*, 2012b. Glyphosate effects on plant mineral nutrition, crop rhizosphere microbiota, and plant disease in glyphosate-resistant crops. Journal of Agricultural and Food Chemistry 60, 10375–10397. Copyright 2012 American Chemical Society.

non-HR crops (Ervin *et al.*, 2010). Adoption of GR crops has resulted in reductions in soil loss, fossil fuel use, and use of less toxicologically benign herbicides.

The primary reason for tillage is weed management. Other than removing land from its natural state, the most destructive practice in agriculture has been soil loss by wind and water after tillage. Pollution due to loss of applied fertilizers is also exacerbated by tillage, as is loss of soil microbial life and soil organic matter. Postemergence herbicides facilitate reduced- or no-tillage agriculture. Thus, GR crops are ideal for reduced- or no-tillage agriculture, as glyphosate is used only as a post-emergence herbicide that kills almost all weed species. After GR crops were introduced in the Americas, adoption of reduced tillage in those crops greatly increased, especially in cotton and soybean (Bonny, 2011; Derpsch *et al.*, 2010; Dill *et al.*, 2008; Fernandez-Cornejo *et al.*, 2012; Givens *et al.*, 2009;

Locke *et al.*, 2008; Penna and Lema, 2003; Powles, 2008a). Furthermore, the use of complete no-tillage agriculture was twice as high with GR soybean as with conventional soybean (Fernandez-Cornejo and McBride, 2002). In Argentina, there was a one-to-one ratio between adoption of GR soybeans and no-tillage soybeans between 1996 and 2005 (Trigo and Cap, 2006). As long as the glyphosate/GR weed management system was robust, tillage was less valuable, but the advent of evolved GR weeds and shifts of naturally tolerant weed species in GR crop fields has made tillage more desirable as a component of a diversified weed management system, although it is recommended that farmers not abandon conservation tillage systems when GR weeds become a significant problem (Shaw *et al.*, 2012). Nevertheless, the use of reduced- or no-tillage methods in GR crops may wane somewhat in coming years unless other postemergence herbicides can substitute for tillage to control GR weeds.

Another aspect of reduced tillage with GR crops is reductions in fossil fuel use. Tillage requires considerable use of fuel, as do multiple trips across a field to spray the several herbicides that glyphosate replaced. GR crop use in 2005 was estimated to reduce carbon emissions approximately the same as the removal of four million family automobiles from the road (Brookes and Barfoot, 2006). Indirectly, yet another environmental benefit of reduced tillage in parts of South America is a shortening of the production cycle, enabling farmers to plant a crop of soybeans immediately after a wheat crop in the same growing season (Brookes and Barfoot, 2012). The resulting additional crop production on the same unit of land reduces the amount of land that must be converted from the natural state to farmland in order to feed the world.

Although the effects of GR crops on the volume of herbicides used per unit area of land has been debated (Benbrook, 2012; Brookes and Barfoot, 2006), it is clear that adoption of these crops resulted, at least in part, in a large decrease in the use of other herbicides where GR crops were adopted (**Figure 2**). This is particularly apparent with soybeans (**Figure 2(c)**). As mentioned earlier, glyphosate is considered a low-toxicity pesticide with a relatively high LD_{50}. Gardner and Nelson (2008) calculated the reduction in LD_{50} doses per unit area that were caused by transition from conventional to GR crops in the US. The reductions averaged 720 and 248 LD_{50} doses per ha with maize and cotton, respectively. More recently, Bonny (2011) determined the changes in environmental impact quotient (EIQ), a function based on several factors other than LD_{50} values (Kovach *et al.*, 1992), in the US soybean before and after the adoption of GR soybeans (**Figure 4**) and found that EIQ values of herbicide use decreased significantly after adoption. The EIQ levels began to increase somewhat during the past few years, due to increases in quantities of glyphosate sprayed. A detailed analysis of the adoption of GR crops (canola, cotton, maize, and soybean) on the environmental impact (total, farm worker impact, consumer impact, and ecology impact) found reductions of 7–62%, depending on the crop and environmental factor (Kleter and Kuiper, 2003). A more recent analysis of changes in herbicide use associated with GR soybeans in the US found reductions in the use of herbicides that were more toxicologically and environmentally hazardous (Fernandez-Cornejo *et al.*, 2012). Analyses of potential environmental benefits of adoption of GR crops in Europe have also estimated significant environmental and toxicological benefits (Devos *et al.*, 2008; Kleter *et al.*, 2004). Another component of environmental toxicity that favors glyphosate is the relatively short half-life and low leaching capability in soil of glyphosate compared with many of the herbicides that it has replaced (reviewed by Borggaard and Gimsing, 2008; Cerdeira and Duke, 2006; Duke and Cerdeira, 2005).

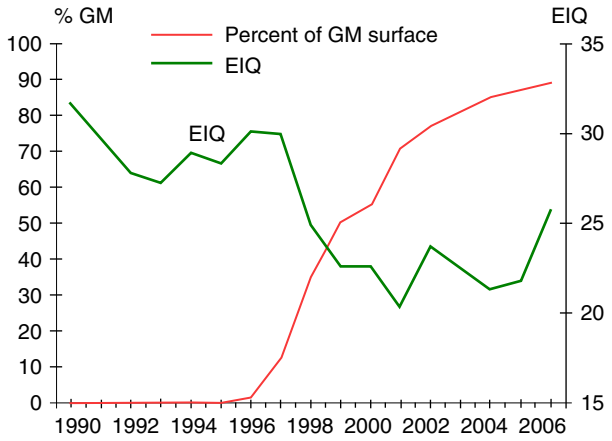


Figure 4 Changes in the EIQ of soybean from 1990 to 2006 (field value per ha). EIQ is a composite pesticide-risk indicator: The higher the EIQ, the higher the environmental and toxicological impact. Reproduced with permission from Bonny, S., 2011. Herbicide-tolerant transgenic soybean over 15 years of cultivation: Pesticide use, weed resistance, and some economic issues. The case of the USA. Sustainability 3, 1302–1322.

Glyphosate-resistant crops and mineral nutrition

Several years after induction of GR crops, several studies indicated that glyphosate causes reduced levels of certain minerals, especially Mn and Ni, in GR crops (e.g., Zobiole *et al.*, 2010 a,b,c, 2011a, 2012; Bellaloui *et al.*, 2009; Bott *et al.*, 2008). Most of these studies were conducted in greenhouse and have been used as support for claims of decreased yields and other adverse effects of glyphosate on GR crops (e.g., Huber, 2007; Johal and Huber, 2009). Other research groups have found no effects of glyphosate on mineral nutrition in GR crops (e.g., Bailey *et al.*, 2002; de Andrade and Rosolem, 2011; Duke *et al.*, 2012a; Henry *et al.*, 2011; Loecker *et al.*, 2010; Rosolem *et al.*, 2010; Serra *et al.*, 2011). A thorough analysis of this topic was made by Duke *et al.* (2012b). They concluded that although there is conflicting literature on this topic, most of the literature indicates that there is no effect and that yield data on GR crops (**Figure 3**) do not support the view that there are significant effects of the transgenes for glyphosate resistance or glyphosate on GR crop mineral nutrition.

Glyphosate-resistant crops and crop disease

Various claims have been made about plant disease in GR crops (reviewed by Duke *et al.*, 2007, 2012b). There is no evidence that the genes used to produce GR crops have any influence on susceptibility of GR crops to disease. Claims of

Table 2 Glyphosate influences and lack of influence on plant disease in glyphosate-resistant crops

Crop	*Disease organism*	*Effect*	*Reference*
Soybean	*Phakopsora pachyrhizi*	Decreased	Feng *et al.* (2005, 2008)
		Decreased	Dill *et al.* (2010)
		Decreased	Rosa *et al.* (2010)
	Myrothecium roridum	Decreased	Rosa *et al.* (2010)
	Erysiphe diffusa	Decreased	Rosa *et al.* (2010)
	Fusarium spp.	Increased	Zobiole *et al.* (2011b)
		Increased	Kremer and Means (2009)
	Fusarium virguliforme	No effect	Sanogo *et al.* (2000)
		No effect	Sanogo *et al.* (2001)
		No effect	Njiti *et al.* (2003)
	Schlerotinia sclerotiorum	No effect	Lee *et al.* (2000)
		No effect	Nelson *et al.* (2002)
	Rhizoctonia solani	No effect	Harikrishnan and Yang (2002)
Cotton	*Rhizoctonia solani*	Decreased	Pankey *et al.* (2005)
Wheat	*Puccinia triticina*	Decreased	Feng *et al.* (2005)
		Decreased	Anderson and Kolmer (2005)
	Puccinia striiformis	Decreased	Feng *et al.* (2005, 2008)
	Rhizoctonia solani	No effect	Baleyii *et al.* (2009)
	Rhizopus oryzae	No effect	Baley *et al.* (2009)
	Pythium ultimum	No effect	Baley *et al.* (2009)
	Gaeumannomyces graminis	No effect	Baley *et al.* (2009)
Alfalfa	*Uromyces striatus*	Decreased	Samac and Foster-Hartnett (2012)
	Phoma medicaginis	Decreased	Samac and Foster-Hartnett (2012)
	Colletotrichum trifolii	Decreased	Samac and Foster-Hartnett (2012)
Sugar beet	*Rhizoctonia solani*	No effect	Larson *et al.* (2006)
		No effect	Barnett *et al.* (2011)
		No effect	Barnett *et al.* (2012)
	Fusarium oxysporum	Mixed results[a]	Larson *et al.* (2006)
		No effect	Barnett *et al.* (2011)

[a]No effect or increased, depending on the variety.

increases in disease of these crops is due in part to the fact that glyphosate makes non-GR plants more susceptible to plant pathogens, due to inhibited production of compounds from the shikimate pathway that are used by the plant for protection from pathogens (Duke *et al.*, 2007). Because of this effect, non-GR plants are more susceptible to glyphosate in soil with pathogens than in sterilized soil (e.g., Schafer *et al.*, 2012a). This phenomenon has been proposed as an important contributor to the mode of action of glyphosate.

However, glyphosate does not alter the levels of disease-fighting shikimate derivatives in GR crops, and glyphosate acts as a fungicide, albeit a weak one, on some plant pathogens (Duke *et al.*, 2007; Dill *et al.*, 2010). Fungi across several taxa of plant pathogenic fungi have EPSPS enzymes that are similar to those of plants, and the EPSPS of Asian soybean rust (ASR) is sensitive to glyphosate (Dill *et al.*, 2010). Thus, there is reason to hypothesize that GR crops sprayed with glyphosate would have less of some diseases than the same crops without herbicide treatment. There are more papers supporting this hypothesis than those that do not (**Table 2**). Of special interest are the papers showing that glyphosate used on GR crops can have preventative and curative effects on rust diseases in GR maize, soybean, and alfalfa (Anderson and Kolmer, 2005; Dill *et al.*, 2010; Feng *et al.*, 2005, 2008; Samac and Foster-Hartnett, 2012). Glyphosate also protected GR alfalfa from foliar diseases caused by *Colletotrichum trifolii* and *Phoma medicaginis* (Samac and Foster-Hartnett, 2012).

Proof of a direct effect of glyphosate on ASR was obtained by measuring shikimate levels in ASR-infected soybeans with and without glyphosate treatment (Dill *et al.*, 2010). No shikimate accumulated in noninfected plants treated with glyphosate or in non-ASR-inoculated plants without glyphosate, but high levels did accumulate in inoculated plants treated with glyphosate. These results are most clearly interpreted as the shikimate being derived from inhibition of fungal EPSPS.

Johal and Huber (2009) and Kremer and Means (2009) had suggested that glyphosate treatment of GR soybeans increases fungal root diseases (e.g., *Fusarium* spp.). However, several studies reported no effects of glyphosate on *Fusarium virguliforme* (formerly known as *F. solani*) in GR soybeans (**Table 2**). Powell and Swanton (2008) concluded that there was insufficient evidence to conclude that glyphosate promotes infection of GR soybeans by *Fusarium* spp.

An extensive analysis of the published data concluded that the baseline disease resistance or susceptibility of the host plant variety is the major contributor to disease susceptibility in GR crops regardless of the presence of the glyphosate resistance gene or treatment with glyphosate (Duke *et al.*, 2012b). In fact, the reports listed in **Table 2** would suggest that glyphosate treatment can reduce the effects of many plant pathogens on GR crops, whereas having no effect on most others.

Weed shifts, volunteer glyphosate-resistant crops and evolution of glyphosate-resistant weeds

GR crops were initially extremely successful in managing the problematic weed species in those crops. Farmers used this economical and highly effective weed management system year after year. This behavior may have been reinforced by the mistaken view that evolution of resistance would occur very slowly, if at all (Bradshaw *et al.*, 1997). But nature abhors a vacuum, so weeds that could exist in the vacuum caused by year after year use of glyphosate/GR crop cropping systems moved into the ecological niches vacated by those species that were effectively controlled (weed shifts). Weed species shifts involved perennial weeds that were less sensitive to glyphosate, such as nutsedges (*Cyperus* spp.), shifts to weeds with more natural resistance (tolerance) to glyphosate, such as morning glory species (*Ipomoea* spp.), and shifts to weeds that germinate after glyphosate is normally sprayed, such as *Solanum ptychanthum* (Reddy and Norsworthy, 2010). Some weed species fit into more than one of these categories. Analysis of surveys of prevalent weeds in agronomic crops before and more than 10 years after adoption of GR cultivars of the same crops in the southern US concluded that major changes in weed species were primarily due to use of glyphosate, via both weed shifts and evolution of resistance (Webster and Nichols, 2012). The changes were less drastic in maize, for which adoption was slower (**Figure 1**).

Glyphosate had been used for 22 years before the introduction of GR crops. It was used intensively year after year for weed management before or after harvest and with woody crops such as grapes and fruit tree orchards. Ironically, the first case of evolved resistance to glyphosate (*Lolium rigidum* in Australia – Powles *et al.*, 1998; Pratley *et al.*, 1999) was reported soon after the paper claiming that evolved resistance was highly improbable (Bradshaw *et al.*, 1997). At present, there are 24 weed species that have evolved resistance to glyphosate (**Figure 5**; **Table 3**). During first few years of this increase, evolution of resistance did not occur in GR crops, but most of the cases of evolved resistance in the past decade have been in GR crop fields where farmers have used glyphosate year after year in the same crop or in alternating GR crops in the same field.

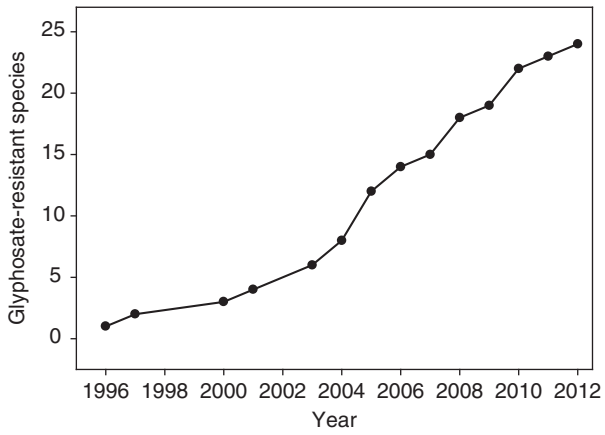


Figure 5 Cumulative number of weed species that have evolved resistance to glyphosate worldwide. Data from Heap, I., 2013. International Survey of Herbicide Resistant Weeds. Available at: www.weedscience.org (accessed 30.05.13).

Bradshaw *et al.* (1997) were correct in that a one base pair change in a codon of the EPSPS gene would not impart the robust level of resistance reported on herbicide classes targeting more resistance-prone enzymes. The odds that the two codon mutations needed for a robust but resistant form of EPSPS to occur in nature are indeed extremely remote, and none of the 24 species of evolved GR weeds has been documented to be resistant via such a mechanism. The confirmed mechanisms of evolved resistance to glyphosate are: (1) single-codon changes in the gene for EPSPS, (2) gene amplification of the gene for EPSPS, and (3) reduced translocation due to sequestration of glyphosate into the vacuoles of treated leaves (Shaner *et al.*, 2012).

There are several cases of single base pair mutations of the EPSPS gene providing a low level of glyphosate resistance. For example, resistance to glyphosate in *E. indica* L. is caused by a single-codon change (Pro_{106} to Ser) in the EPSPS gene, providing a 5-fold decrease in sensitivity to glyphosate (Baerson *et al.*, 2002). The same amino acid change in EPSPS was found in a GR *L. rigidum* biotype (Simarmata and Penner, 2008) and a GR *Amaranthus tuberculatus* (Nandula *et al.*, 2013). A Pro_{106} to Thr substitution in EPSPS was identified in another GR *L. rigidum* biotype (Wakelin and Preston, 2006), and this change was also reported in another *E. indica* biotype (Ng *et al.*, 2003). None of these one-codon changes provides a high level of resistance.

Another mechanism that involved the glyphosate target is that of greatly increased amounts of EPSPS enzyme due to gene amplification, so that field rates of glyphosate cannot inhibit enough of the *in vivo* enzyme activity to inhibit the shikimate pathway. The first case of this was in *A. palmeri* in GR crops in the US, where this weed evolved a high level (up to 8-fold in the laboratory and more than 12-fold in the field) of resistance to glyphosate (Culpepper *et al.*, 2006). Another GR biotype of *A. palmeri* was at least 20-fold less sensitive to glyphosate than the wild type (Whitaker *et al.*, 2007). Gaines *et al.* (2010) found that individual plants of the resistant biotype populations had a range of extra copies of the EPSPS gene, from 5 to 160 additional copies. The extra genes were scattered throughout the genome with copies on every chromosome. The extra gene copies (gene amplification) correlated positively with additional EPSPS mRNA, enzyme protein, and enzyme activity, thus requiring significantly more glyphosate to effectively shut down the shikimate pathway. More recently, amplification of the copy number of EPSPS has helped to evolve GR *L. perenne* spp. *multiflorum* (Salas *et al.*, 2012) and *Kochia scoparia* (Wiersma, 2012), with up to 25 and 9, respectively, extra copies of the gene. In both cases, the extra gene copies resulted in additional EPSPS enzyme activity. Preliminary data indicate that at least one mechanism of glyphosate resistance in an evolved *A. tuberculatus* biotype is due to gene amplification of EPSPS (Tranel *et al.*, 2011).

Reduced translocation of glyphosate to meristems and young, developing tissues occurs in some species that have evolved resistance to glyphosate; for example, *Conyza bonariensis* (Dinelli *et al.*, 2008), *Conyza canadensis* (Feng *et al.*, 2004 and others), and *L. multiflorum* (Lorraine-Colwill *et al.*, 2003;

Table 3 Weed species that have evolved resistance to glyphosate

Weed species	*Location (countries)*	*Year*
Amaranthus palmeri	USA	2005
Amaranthus spinosus	USA	2012
Amarnathus tuberculatus (syn *rudis*)	USA	2005
Ambrosia artemisiifolia	USA and Canada	2004
Ambrosia trifida	USA and Canada	2004
Bromus diandrus	Australia	2011
Chloris truncata	Australia	2010
Conyza bonariensis	South Africa, Spain, Brazil, Israel, Columbia, USA, Australia, Greece, and Portugal	2003
Conyza canadensis	USA, Brazil, China, Spain, Czech Republic, Poland, Canada, Italy, and Greece	2000
Conyza sumatrensis	Spain, Brazil, and Greece	2009
Cynodon hirsutus	Argentina	2009
Digitaria insularis	Paraguay and Brazil	2008
Echinochloa colona	Australia, USA, and Agentina	2007
Eleusine indica	Malaysia, Colombia, China, USA, and Argentina	1997
Kochia scoparia	USA and Canada	2007
Leptochloa virgata	Mexico	2010
Lolium multiflorum	Chile, Brazil, USA, Spain, and Argentina	2001
Lolium perenne	Argentina	2008
Lolium rigidum	Australia, USA, South Africa, France, Spain, Israel, and Italy	1996
Parthenium hysterophorus	Columbia	2004
Plantago lanceolata	South Africa	2003
Poa annua	USA	2010
Sorghum halepense	Argentina and USA	2005
Urochloa panicoides	Australia	2008

Source: Data from Heap, I., 2103. International Survey of Herbicide Resistant Weeds. Available at: www.weedsci.org (accessed 30.05.13).

Wakelin *et al.*, 2004). Reduced translocation in both GR *Lolium* spp. and *C. canadensis* may be associated with sequestration of glyphosate into the vacuoles of cells of the treated leaves (Ge *et al.*, 2010, 2011, 2012). Much less or no vacuolar sequestration of glyphosate is seen in susceptible biotypes. In *C. canadensis*, low temperatures reduce the sequestration of glyphosate, causing loss of resistance (Ge *et al.*, 2011). Vacuolar sequestration is probably due to a membrane transporter, similar to the case of a GR *Escherichia coli* with overexpression of a gene for a glyphosate membrane transporter (Staub *et al.*, 2012).

Some plants can slowly metabolize glyphosate to relatively much less toxic or completely nontoxic metabolites (Duke, 2011a). Thus, genes encoding enzymes that will detoxify glyphosate exist in some plant species, although neither the genes nor enzymes have been characterized. Enhanced metabolic degradation of glyphosate has been looked for but has not been found to be a mechanism of evolved resistance to date (Duke, 2012; Perez-Jones and Mallory-Smith, 2010). One laboratory has claimed that enhanced resistance has been involved in resistance of two different weed (*Digitaria insularis* – de Carvalho *et al.*, 2011; *C. canadensis* – Gonzalez-Torralva *et al.*, 2012) and one crop species (*Mucuna pruriens* – Rojano-Delgado *et al.*, 2012), although conclusive proof of the metabolites was not provided in these papers. In each of these cases, metabolism of glyphosate was reported to occur by both a GOX enzyme to produce AMPA and a C-P lyase enzyme that produced sarcosine, something that had not been identified in previous studies with other species, including studies with *C. canadensis* (Feng *et al.*, 2004). If the results of these papers can be corroborated, metabolism of glyphosate can be added to the mechanisms of evolved resistance. Metabolism-based herbicide resistance is very common for most other herbicide resistances, and many of these are based on cytochrome P450 monooxygenases (Powles and Yu, 2010).

In some biotypes of *Ambrosia trifida* L. that have evolved resistance to glyphosate, this normally slow-acting herbicide causes rapid necrosis of the foliage to which it is applied (Robertson, 2010). This limits translocation of the herbicide to meristems and developing tissues, allowing a phoenix-like regrowth from the mostly desiccated plant. The physiological/biochemical basis of the very rapid effect of glyphosate in treated tissues of this biotype is unknown. Very few plant species, such as sugar beet (*Beta vulgaris* L.), have a similar rapid response to glyphosate (Madsen *et al.*, 1995).

Volunteers of GR crops can be significant problems in GR crops of a different species the next year (Reddy and Norsworthy, 2010). Problems with volunteer GR maize in GR sugar beet (Kniss *et al.*, 2012), volunteer GR maize in GR soybean (Marquardt *et al.*, 2012), volunteer GR soybean in GR cotton (Lee *et al.*, 2009b), and with volunteer GR cotton in GR soybeans (Lee *et al.*, 2009a) have been documented. GR crops in non-GR crops, such as GR soybean in non-GR rice (Bond and Walker, 2009) and GR canola in non-GR wheat (Lawson *et al.*, 2006), can also be a problem. Volunteer crops seldom persist for more than a year. But, in some climates, some HR crop species could become weeds that persist for several seasons, due to persistence of seeds in the seed bank, as has been the experience with GR canola in California (Munier *et al.*, 2012). One could assume that this has nothing to do with the transgenic trait, other than making it impossible to control the volunteer crop with the herbicide to which it has been made resistant.

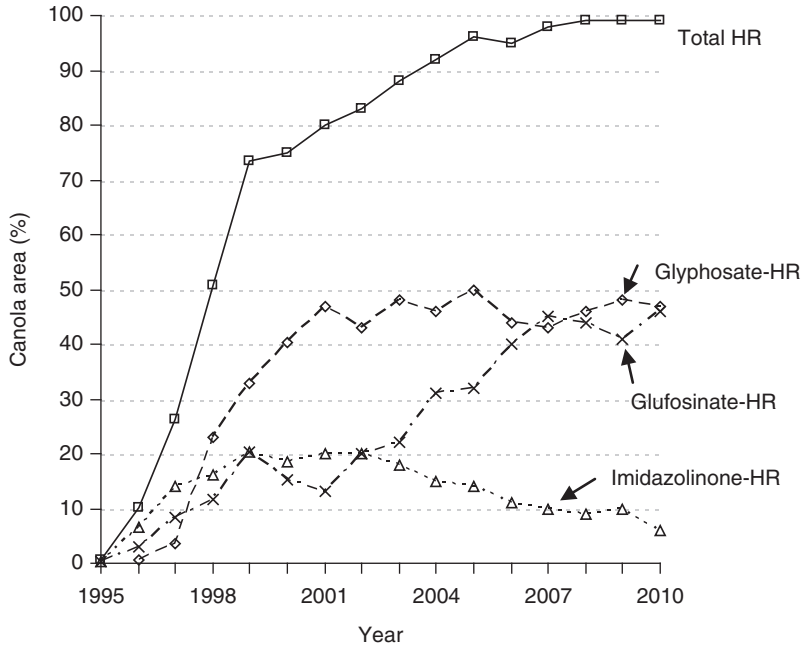


Figure 6 Adoption of herbicide-resistant oilseed rape (*Brassica napus* L.) in Canada: Mainly grown in Alberta, Saskatchewan, and Manitoba. Reproduced from Beckie, H.J., 2011. Herbicide-resistant weed management: Focus on glyphosate. Pest Management Science 67, 1037–1048, with permission from Wiley Press, Chichester, UK.

Using the same weed management technology year after year is not feasible in the long run, due to weed shifts and evolutionary processes. The clear initial superiority of weed management with GR crops is being compromised by the long-term use of one or more GR crops, with little or no weed management diversity (Powles, 2008a, b). The economic and environmental advantages of this technology are being diminished due to these developments (Carpenter and Gianessi, 2010; Shaw *et al.*, 2012). Additional weed management costs can be more than $70/ha with some GR weeds (e.g., *A. palmeri*) in some crops (e.g., cotton). Clearly, strong emphasis will have to be made on instituting more diverse weed management strategies in order to preserve the high value of GR crops in weed management technology. For example, canola farmers of Canada have had access to herbicide resistant canola since 1996 but have never planted more than 50% GR canola (**Figure 6**), instead they have planted a significant amount of imidazolinone- and glufosinate-resistant canola. Also, there was a small amount (never more than 1%) of bromoxynil-resistant canola grown in 2000 and 2001 (Beckie *et al.*, 2006). The more diversified weed management used in Canadian canola, using other HR canola varieties and crop rotation, has probably been the reason that no GR weeds have evolved from selection in Canadian canola (Beckie, 2011, Hugh Beckie, personal communication, May, 2013). Strategies involving use of herbicides for which evolution of resistance is less likely are needed (Beckie and Tardif, 2012). Both the need for diversity and the increases in GR weeds and weed species shifts are causing farmers to supplement GR crop-based weed management with older technologies such as selective herbicides and tillage. A recent survey of 1299 US farmers who grow GR crops reported that they perceived tillage to be a more effective management method for GR weeds than it actually is (Prince *et al.*, 2012). Some of these strategies will also include new HR crops with new herbicide resistance traits that can be used with or instead of glyphosate alone with GR crops. The new HR crop technologies that will soon be available are described in the next main section, and HR crop technologies that might follow them are discussed.

Gene flow from glyphosate-resistant crops

A possible means of production of GR weeds is gene flow of the resistance transgene from the crop to a weedy relative and subsequent introgression of the transgene from the cross into the weed population. The only GR crop in which flow of a transgene to a weedy relative has been documented in the field is canola (Warwick *et al.*, 2008), although this has not created a significant weed problem. No gene flow has been reported in cotton or soybeans. In maize, there were disputed cases of gene flow to teosinte and land races of maize in Mexico (e.g., Ortiz-García *et al.*, 2005); however, if this occurred, it has not created a GR weed problem. The biggest problem with canola and maize is gene flow from the GR crop to non-GR varieties (Gealy *et al.*, 2007), which causes trade problems when the adventitious presence of the transgene in harvested non-GR crops exceeds allowable limits. There are feasible 'fail-safe' approaches utilizing multiple technologies to stop gene flow (Gressel and Al-Ahmad, 2005), but the seed industry has yet to adopt such methods. One can speculate that the greater potential for gene flow to weedy relatives in rice and wheat (see Section Nontransgenic Herbicide-Resistant Crops) may have played a part in the decision to not commercialize GR varieties of these crops.

Presumably, a herbicide resistance transgene will not cause ecological disruption in a natural setting where the herbicide is not used; however, where the herbicide is used, it can facilitate

introgression of all transgenes in a crop to a wild species. If there is a benefit in a natural setting of a nonherbicide resistance transgene, such as insect resistance, the herbicide can provide the temporary protection needed for even relatively unfit crosses to persist (Londo *et al.*, 2011). Herbicide resistance genes can flow not only from HR crops but also from resistant weeds to other weed species. For example, Zelaya *et al.* (2007) found gene flow between GR *C. canadensis* to *Cylindropuntia ramosissima* could occur, followed by introgression of resistance into *C. ramosissina*.

The case of unintended gene flow from experimental plots of GR creeping bentgrass (*Agrostis stolonifera* L.) being developed for its use in turf to wild bentgrass (Snow, 2012; Watrud *et al.*, 2004) illustrates that, once genes escape to wild populations, they can spread in unexpected ways and cannot be called back. Not only the *cp4* gene for glyphosate resistance is prevalent in some feral populations of bentgrass after escape of the gene in 2002 (Reichman *et al.*, 2006), but also a GR hybrid between feral bentgrass (pollen receptor) and rabbitfoot grass (*Polypogon monspeliensis*) (pollen donor) has occurred (Zapiola and Mallory-Smith, 2012). Such gene flow events portend significant weed management problems in GR crops due to gene flow if care is not taken.

Crops Made Resistant to Auxinic Herbicides

Auxinic herbicides are those that act in some ways like the endogenous plant hormone indoleacetic acid, which is also called auxin (Fedtke and Duke, 2005). There are several types of auxinic herbicides, and crops are being made resistant to two of these, namely dicamba and 2,4-D, with transgenes that encode enzymes that inactivate the herbicide. Target site resistance is an unlikely option for these crops, as auxinic herbicides bind several F-box proteins that are regulatory in nature (Gleason *et al.*, 2011; Walsh and Schmitzer, 2012). Which of these receptors are bound varies between herbicides. Making sufficient binding sites resistant to the herbicide would probably require several transgenes.

Dicamba-resistant crops

Dicamba (3,6-dichloro-2-methoxybenzoic acid) is an older auxinic herbicide, killing mainly broadleaf weed species in monocot grain crops. It is too phytotoxic for its use as a postemergence herbicide in maize, in which it can only be used as a preplant herbicide with a delayed planting to avoid injury to the crop. It controls more weed species than most other auxinic herbicides, such as 2,4-D, and even controls more species than glufosinate (Feng *et al.*, 2010). Dicamba-resistant crops have been generated by inserting a transgene from a soil microbe (*Stenotrophomonas maltophilia*) that encodes dicamba monooxygenase (DMO) (Behrens *et al.*, 2007). This enzyme demethylates dicamba to form nonphytotoxic 3,6-dichlorosalicylic acid. The gene provides a high level of resistance to dicamba in both dicots (cotton and soybean) and monocots including maize (Cao *et al.*, 2011). Dicamba resistance will be stacked with glyphosate and/or glufosinate resistance in cotton and soybeans in the first introductions.

Dicamba provides excellent control of some of the weed species that have evolved resistance to glyphosate, for example, *C. canadensis* (Kruger *et al.*, 2010) and *A. trifida* (Vink *et al.*, 2012). There are relatively few cases of evolved resistance to dicamba: *Sinapis arvensis* (Yajima *et al.*, 2004); *K. scoparia* (Goss and Dyer, 2003; Nandula and Manthey, 2002; Preston *et al.*, 2009); *Galeopsis tetrahit* (Weinberg *et al.*, 2006); *Chenopodium album* (Rahman *et al.*, 2008); and *Lactuca serriola* (Burke *et al.*, 2009). However, one of these species (*K. scoparia*) has also evolved resistance to glyphosate (**Table 3**). Dicamba resistance will provide a useful tool in diversification of weed management, but the cases of evolved dicamba resistance already reported indicate that overuse of this new tool will eventually bring about problems with evolved dicamba resistance.

Another concern is that aerial drift of dicamba to dicamba-sensitive crops and other nontarget vegetation will pose economic and environmental problems (Egan and Mortensen, 2012). Some plant species are very sensitive to very low exposures to auxinic herbicides as can be experienced by vapor drift. However, dicamba has been used for more than 40 years as a postemergence spray, and it is still used extensively (USGS, 2013) without overwhelming problems. Vapor drift can be reduced significantly with a diglycolamine formulation (Egan and Mortensen, 2012). Low-volatility formulations may be required for use with dicamba-resistant crops.

2,4-Dichlorophenoxyacetic acid-resistant crops

Crops are also being made resistant to one of the oldest herbicides, 2,4-D. Like dicamba, resistance is provided by the use of a transgene derived from a microbe that encodes an enzyme that detoxifies the herbicide. Several microbes (*Ralstonia eutropha*, *Sphingobium herbicidivorans*, and *Delfiia acidovorans*) have genes encoding an aryloxyalkanoate dioxygenase (AAD) that converts 2,4-D into dichlorophenol, a nonphytotoxic compound (Llewellyn and Last, 1996; Wright *et al.*, 2010). Variants of this enzyme also detoxify other auxinic herbicides, such as triclopyr and fluroxypyr, as well as AOPP grass-killing, ACCase-inhibiting herbicides such as quizalofop. The first 2,4-D-resistant crops will be maize and soybeans with an AAD transgene for 2,4-D resistance stacked with genes for glyphosate and/or glufosinate resistance (**Table 4**). AAD from different microbes vary in their efficiency in detoxifying 2,4-D and AOPP herbicides. The AAD from *S. herbicidivorans* provides the best 2,4-D resistance in crops, but it is not sufficiently active against the herbicidal enantiomers of AOPP herbicides to provide resistance (Wright *et al.*, 2010).

Plans have been made for marketing 2,4-D-resistant maize, soybean, and cotton (Robinson *et al.*, 2012). AOPP- and 2,4-D-resistant maize and glufosinate- and 2,4-D-resistant soybeans have been approved by Canadian authorities but will not be sold until after 2013. Crops with three herbicide resistances (2,4-D, glufosinate, and glyphosate) are under development (**Table 4**). The possibility of unacceptable herbicide drift problems with 2,4-D- and dicamba-resistant crops has slowed the deregulation (approval) process for these crops due to the United States Department of Agriculture (USDA) Animal and Plant Health Inspection Service's recent (as of early 2013) requirement that both products undergo an environmental impact study. So, the earliest introduction of 2,4-D-resistant crops in the US will probably be in 2015.

As with dicamba, drift of 2,4-D to nontarget natural vegetation and other crops has been a problem since 2,4-D was

Table 4 Herbicide-resistant crops for which petitions for deregulated status (approval for commercialization) have been filed but not yet granted (APHIS, 2013)

Year of application	*Herbicides*
Maize	
2009	2,4-Dichlorophenoxyacetic acid (2,4-D) and acetyl-CoA carboxylase inhibitors
2011	Glufosinate
2011	Glyphosate
Soybean	
2009	Glyphosate and isoxaflutole (hydroxyphenylpyruvate dioxygenase (HPPD) inhibitor)
2009	2,4-D and glufosinate
2009	Imdazolinone (acetolactate synthase inhibitor)
2010	Dicamba
2011	2,4-D, glyphosate, and glufosinate
2012	HPPD inhibitor and glufosinate
Cotton	
2012	Dicamba and glufosinate
Canola	
2011	Glyphosate

introduced in the mid-1940s and sold as amine or ester formulations. These formulations of 2,4-D are still used in large amounts for weed management. 2,4-D choline, a quaternary ammonium salt with much lower volatility than previous 2,4-D products, is planned to be the only formulation allowed with 2,4-D-resistant crops. Thus, introduction of this low-volatility formulation of 2,4-D could even decrease the 2,4-D drift problem with non-GRC uses.

As pointed out by Egan *et al.* (2011), there are almost 20 weed species that have evolved resistance to 2,4-D. In fact, the first two reported cases of evolved herbicide resistance were of 2,4-D in 1957 (Heap, 2013). Beckie and Tardif (2012) considered 2,4-D and other auxinic herbicides to have a lower risk for evolution of resistance than some other herbicide classes. In at least some cases, a single, dominant gene confers resistance to more than one auxinic herbicide (Jugulam *et al.*, 2005). Considering that auxinic herbicides appear to have multiple binding sites (Walsh and Schmitzer, 2012), single-gene-based resistance may be due to an enzyme that degrades the herbicide (Harrington and Wooley, 2006), but other mechanisms of resistance have apparently evolved (Kelley and Riechers, 2007). Weeds have had more than 60 years to evolve resistance to this still heavily used herbicide. Clearly, 2,4-D resistance neither does not evolve as readily as resistance to ACCase or ALS inhibitor herbicides does nor perhaps as slowly as to glyphosate.

Other Transgenic Herbicide-Resistant Crops

There are patents and publications on many genes for resistance to almost all herbicide classes. Only a few of these are likely to be developed and commercialized. Crops made resistant to hydroxyphenylpyruvate dioxygenase (HPPD)-, ACCase-, and ALS-inhibitor herbicides will probably be commercialized, so these are dealt with separately in this section; others are discussed in the last section.

Hydroxyphenylpyruvate dioxygenase inhibitor-resistant crops

More than 20 years ago, the last group of herbicides with a new mode of action was commercialized. They were inhibitors of HPPD, an enzyme that produces homogentisic acid, a precursor for plastoquinone (PQ) and vitamin E (Duke, 2012). PQ is needed as a cofactor for phytoene desaturase (PD), a key enzyme in carotenoid synthesis, and as an electron transport component of PSII. The symptoms of complete bleaching of leaves are much like those of PD inhibitors (Arias *et al.*, 2005). Several transgenic approaches to make crops resistant to these herbicide have been successful, including overexpression of a bacterial HPPD, use of a mutant plant enzyme that is resistant through bypassing HPPD in the synthesis of homogentisic acid with three bacterial genes, and, finally, overexpression of HPPD plus enhancing HPPD substrate (*p*-hydroxyphenylpyruvate) levels with a transgene for yeast prephenate dehydrogenase (Matringe *et al.*, 2005). HPPD HR crops for which petitions of deregulation have been filed are soybean with stacked glyphosate resistance and another with stacked glufosinate resistance (**Table 4**). Maize is naturally resistant to some HPPD inhibitor herbicides through rapid detoxification of the herbicide and a less sensitive form of HPPD than most weeds (Grossmann and Ehrhardt, 2007). Only two weed species have evolved resistance to HPPD-inhibitor herbicides (*A. palmeri* and *A. tuberculatus* (syn. *rudis*) (Heap, 2013). Unfortunately, there are HPPD-resistant biotypes of *A. tuberculatus* with multiple resistances with up to four additional resistances, including resistance to glyphosate, in all combinations (Hausman *et al.*, 2011; Tranel *et al.*, 2011).

Acetyl-CoA carboxylase inhibitor-resistant crops

As mentioned in the Section 2,4-Dichlorophenoxyacetic acid-resistant crops, the same genes that encode the degradation enzyme ADD can provide resistance to AOPP herbicides that inhibit ACCase (Wright *et al.*, 2010). The company developing crops using these genes has chosen to introduce 2,4-D-resistant crops first, although one of their petitions for deregulation is for 2,4-D- and ACCase inhibitor-resistant maize (**Table 4**). Nontransgenic crops made resistant to ACCase inhibitors via mutation of ACCase were never very successful (Martino-Catt *et al.*, 2012), and weeds evolve target-site resistance to AOPP herbicides relatively rapidly (Beckie and Tardif, 2012; Heap, 2013). Some plant species (e.g., *L. rigidum*) have evolved rapid degradation of AOPP herbicides (Yu *et al.*, 2013).

Transgenic crops resistant to acetolactate synthase inhibitors

HR crops with resistance to ALS inhibitors have been developed (Green *et al.*, 2008) and brought to the deregulation stage. These HR crops have the *hra* transgene that encodes a form of ALS with two amino acid substitutions that is highly resistant to sulfonylureas, providing more than 10 000-fold resistance to chlorimuron in maize and very high levels of resistance to nicosulfuron and tribenuron in soybean (Lee *et al.*, 1988; Green *et al.*, 2008). Maize with both glyphosate

and ALS-inhibitor resistance has been deregulated (APHIS, 2013) but not commercialized yet. A petition for deregulation of transgenic imidazolinone-resistant soybean has been filed (Table 4). Genes for mutated, ALS inhibitor-resistant crops have been introduced into the chloroplast genome (the plastome) (Shimizu *et al.*, 2008). The resulting transformants were resistant to a variety of ALS-inhibiting herbicides. This approach greatly lowers the possibility of transgene flow through pollen, as the plastome is rarely transmitted via pollen.

Unfortunately, the ALS gene is very plastic, with a number of mutations yielding resistant plants that are quite fit in a field situation (Gutteridge and Thompson, 2012). Thus, many weed species have evolved resistance to these herbicides, with an array of cross-resistances (Heap, 2013). Introduction of ALS inhibitor-resistant crops in many cases will increase the selection for weed resistance to these herbicides.

Resistance to other herbicides

There are numerous papers on potential genes for HR crops, such as that of Zhang *et al.* (2012), which describes the microbial gene for an arylamidase that can degrade a number of herbicides with amide groups (e.g., propanil). A few such genes have been used to transform plants in order to successfully impart herbicide resistance. Some examples that are unlikely to result in commercial HR crops in the near future are summarized in Table 5.

Of these, the crops made resistant to protoporphyrinogen oxidase (PPO) herbicides came closest to development and commercialization. PPO inhibitor-resistant maize and rice were generated with a double mutant (two codons) of *Arabidopsis* PPO and were field tested successfully (Li and Nicholl, 2005). Plants with this double mutant were cross-resistant to a range of commercial PPO inhibitors sold by several companies. The developing company proceeded to give these crops a trade name before shelving this technology. The reasons for stopping development have not been made public.

The inability to connect HR crops to a single herbicide may have been a factor that has made some of these possible HR crops too economically risky for introduction. Glyphosate- and glufosinate-resistant crops can only be used with the one herbicide to which the crop is engineered to be resistant, and in each case, the company that sells the seed also produces the herbicide. This was also true with bromoxynil-resistant crops. Thus, the economic equation for HR crops like the PPO inhibitor-resistant crops may be weakened by cross-resistances that allow farmers to buy and use the herbicide that is most economical to them for that crop. This is even more problematic for transgenic HR crops with inactivation genes such as gene for human cytochrome P450 monooxygenases that confer resistance to many herbicides with different chemical structures and modes of action (Inui *et al.*, 2001). In the case of dicamba- and 2,4-D-resistant crops, tying the use of the HR crops to proprietary, low-volatility formulations of the herbicides can improve both the stewardship and economic viability of the product for the producing companies.

The Future – Where This Technology May Be in the Next Decade and Beyond

Transgenic crops with resistance to each of three different herbicides (bromoxynil, glufosinate, and glyphosate) have been commercialized. Bromoxynil-resistant crops were discontinued for economic reasons. GR crops have completely dominated the HR crops market, for the reasons discussed above and in Duke and Powles (2008). Most of the worldwide soybean crop is GR, and most of the canola, maize, and cotton crops in the US are GR. The utility of GR crops is waning somewhat due to the increasing numbers of weeds, both evolved and species shifts, that can no longer be adequately managed with glyphosate. There is no product on the horizon that will bring back the combination of simplicity, low cost, excellent efficacy, and reduced environmental impact that was available to farmers by the use of GR crops during the first decade of their use. There is currently no stream of new herbicides with new modes of actions to save the day, as occurred every few years until approximately 20 years ago (Duke, 2012). However, most of the pending petitions for deregulation of transgenic crops in the US are for HR crops (APHIS, 2013).

The next generation of HR crops, with different combinations of stacked genes for resistance to glyphosate, will provide farmers with more flexibility and diversity for weed management, but weed management will become more like the approaches used before the introduction of GR crops. In

Table 5 Some transgenes that have been used to generate herbicide-resistant plants that are unlikely to be commercialized in the near future

Gene/enzyme[a]	*Herbicide(s)*	*Gene source*[b]	*Reference*
Cytochrome P450 (D)	Phenylureas	*Helianthus tuberosus* (P)	Didierjean *et al.* (2002)
	Multiple	*Homo sapiens* (A)	Inui *et al.* (2001)
Dehalogenase (D)	Dalapon	*Pseudomonas putida* (M)	Buchanan-Wollaston *et al.* (1992)
Dihydropteroate synthase (T)	Asulam	*Escherichia coli* plasmid (M)	Joel *et al.* (1995); Surov *et al.* (1998)
Esterase (D)	Pyrimidines	Rabbit liver (A)	Feng *et al.* (1997)
Glutathione *S*-transferase	Alachlor, EPTC, and Dimethenamid	*Zea mays* (P)	Milligan *et al.* (2000)
Hydrolase (D)	Phenmedipham	*Arthrobacter oxydans* (M)	Streber *et al.* (1994)
Phytoene desaturase (T)	Fluridone and norflurazon	*Hydrilla verticillata* (P)	Arias *et al.* (2005)
Protoporphyrinogen oxidase (T)	Acifluorfen	*Arabidopsis thaliana* (P)	Li and Nicholl (2005)
Superoxide dismutase (D)	Paraquat	*Pisum sativum* (P)	Sen Gupta *et al.* (1993)
α-Tubulin (T)	Dinitroanilines	*Eleusine indica* (P)	Anthony *et al.* (1999)

[a]D, detoxification; T, target site.
[b]A, animal; M, microbe; P, plant.

those days, farmers had to use combinations of selective herbicides to control a wide range of weeds on which none of the herbicides was effective alone. All of the herbicides to which the new HR crops are resistant are selective herbicides to which some weeds have already evolved resistance. Multiple resistance of weeds to different combinations of herbicides (Tranel *et al.*, 2011) will make choosing the proper HR crop–herbicide combinations more problematic than selection of the proper selective herbicides for a crop before the introduction of HR crops and the wide-spread evolution of herbicide resistance. Thus, weed management will grow even more complicated than before the advent of GR crops. This problem would have occurred without the introduction of HR crops because most evolution of herbicide resistance would have occurred without HR crops. One can theorize that GR crops have slowed the resistance to other herbicide classes because of the negative impact they have had on their use.

Despite the remarkable success of GR crops, the number of HR crops that have pending petitions for deregulation is not large (**Table 4**). Devine (2005) discussed reasons for the lack of more transgenic HR crops almost 10 years ago. His reasons included the high costs of research and development and regulatory approval, both for the HR crop and the use of the herbicide with that crop. International trade issues were also considered a barrier. An issue that was not mentioned was the incredible success of GR crops, compared with other HR crops. Potential market share in competition with GR crops was also a factor that inhibited introduction of other HR crops, just as the success of GR crops slowed herbicide discovery and development research (Duke, 2012). All of these hindrances still exist, but the rapid evolution of GR weeds is changing the economic equation in favor of development of new HR crops, just as it has for renewed herbicide discovery efforts. It is hard to foresee how weeds will be managed past the next decade, but GR crops will almost certainly still play a major role. Without another major new technology with a success like GR crops, weed management will surely utilize more diverse tools and strategies and become more complex.

See also: Agbiotechnology: Costs and Benefits of Genetically Modified Papaya. Biotechnology: Plant Protection. Breeding: Plants, Modern. Genomics: Plant Genetic Improvement. Plant Biotic Stress: Weeds. Plant Health Management: Herbicides. Regulatory Challenges to Commercializing the Products of Ag Biotech. Soil: Conservation Practices

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Biotechnology: Pharming

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Glossary

Adventitious agent A foreign entity that is introduced inadvertently or accidentally. It often refers to viruses, bacteria, or other organisms.
Biopharmaceuticals Drugs based on large biological molecules.
Bioreactor A closed device or system for the culture of cells in an aseptic manner.
Good manufacturing practice (GMP) A system for ensuring that products are consistently produced and controlled according to quality standards.
Monoclonal antibody Single-cell-originated proteins that bind foreign target molecules with high specificity to elicit various immune responses.
***N*-linked glycosylation** Sugar chains added to a secretory protein at the consensus sequence *N*-X-(S/T), where X is any amino acid but proline; it is important for protein stability, activity, trafficking, and targeting as well as pharmacokinetic properties of protein therapeutics.
***O*-glycosylation** Addition of complex sugar residues to the hydroxyl group of serine or threonine on proteins that have completed their folding in the Golgi apparatus.
Plant-made pharmaceuticals (PMPs) Production of biopharmaceuticals in plants.
Vaccines Biological compounds that elicit immunogenic responses to diseases, primarily caused by microorganisms.
Validation The documented act of demonstrating that a procedure, process, and activity will consistently lead to the expected results.

Introduction

Drugs based on large biological molecules, known as biologics or biopharmaceuticals, have been produced in genetically engineered animal and bacterial and yeast cells for more than two decades and the current market for these products exceeds US$149 billion. The growing global demand for biopharmaceuticals is fueling the development of platforms that increase safety, capacity, and flexibility and decrease production costs. The tools of modern plant biotechnology now enable a spectrum of recombinant protein products to be produced in plants, including biopharmaceuticals, and it is widely accepted that plant-made pharmaceuticals (PMPs), or molecular pharming, will help to meet the rising demand. Indeed, plants can now be considered alongside traditional production platforms and may provide numerous potential advantages over microbial and mammalian production systems. These include cost and scale of production, target flexibility, intrinsic safety, and quality of the products. Some of these factors are contrasted in Table 1. By some estimates, PMPs could be produced at 10% of the cost of microbial systems and 0.1% of the cost of mammalian cell culture (Maxmen, 2012). In many cases, production in plants can allow large-scale production that can be adapted to the changing demands of the market. Plants also lack the health risks that can arise from contamination by human pathogens, toxins, or oncogenes that can be harbored in mammalian expression systems.

Plants, like any host system for protein expression, are not a suitable host for production of every class of protein therapeutic, and there are a multitude of factors that can influence the success of PMP production. The key factors influencing protein accumulation include choice of a suitable host species, design and optimization of the protein-coding sequence, selection and optimization of the expression system, the transformation system, plant production and containment, and purification and characterization of the recombinant protein. The spectrum of products in various stages of development in plant production systems, a review of the key factors for successful production of biopharmaceuticals, and a discussion of biosafety considerations will form the subject matter of the following sections. The authors also present a case study to exemplify this process.

Products

Pharmaceutical products engineered for production in transgenic plants are primarily comprised of protein and lipid molecules. In contrast, bioactive small molecules and other plant chemical entities are isolated from the so-called medicinal crops. As eukaryotes, plants have protein-processing machinery similar to mammals and are consequently a good choice to synthesize complex or novel therapeutic proteins. Here the authors discuss the main classes derived from these recombinant protein production systems: therapeutic proteins, vaccines, and antibodies, all with uses that span veterinary and human pharmaceutical applications.

Therapeutic Proteins

Therapeutic proteins refer to pharmacologics used to treat a clinical issue derived from a biochemical deficiency. Examples include enzymes, hormones, structural proteins, antimicrobial agents, etc. (Nagels *et al.*, 2012; Thomas *et al.*, 2011).

The first demonstration that production of a relevant therapeutic protein was possible in a variety of plant species

Table 1 Comparison of different production systems for expression of pharmaceutical compounds

	Production costs[a]	*Scale-up capacity*	*Humanization*	*Safety risk*	*Hurdles*	*Other considerations*
Bacteria	Low	High	None	Endotoxins		Currently in use for commercial production
Yeast	Medium	High	Incorrect			Currently in use for commercial production
Mammalian cell culture	High	Medium	Correct	Viruses; oncogenes		Currently in use for commercial production
Transgenic animals	High	High	Correct	Viruses/prions		Currently in use for commercial production
Plant cell cultures	Medium	Medium	Correct[b]	Low	Acceptance; regulatory	Single product in commercial production
Transgenic Plants	Low	Very high	Correct[b]	Low/ mycotoxins	Acceptance; regulatory framework	No products in commercial production

[a]Not including regulatory costs.
[b]Requires transgenic alteration of host plant. Without minor differences in glycosylation.

was the expression of human growth hormone in tobacco and sunflower callus tissue (Barta *et al.*, 1986). In this milestone example, human growth hormone messenger ribonucleic acid (mRNA) was correctly transcribed when expressed in the plant but not processed. Clearly, this was early in the demonstration of this technology, and active human growth hormone has since been produced from plants using a transient expression approach (Rabindran *et al.*, 2009).

Today, plant systems have been used to produce many types of therapeutic proteins, including collagen, interferon, and other replacement enzymes. As of this article, the farthest commercially advanced therapeutic, with Food and Drug Administration (FDA) approval, is manufactured by Protolix Biotherapeutics in a carrot cell culture system. The enzyme taliglucerase (Eleyso) is a therapeutic for treatment of Gaucher's disease, a lysozomal storage disorder, and has recently completed a phase-III trial (van Dussen *et al.*, 2012). Another therapeutic in late-stage development is a collagen product called Collage™, which has medical (wound healing) and possibly cosmetic applications. Produced by CollPlant in *Nicotiana tabacum*, production requires coexpression of five genes that are targeted to the plant vacuole (Stein *et al.*, 2009).

Vaccines

Vaccines are biological compounds that elicit immunogenic responses to diseases, primarily caused by microorganisms. In the context of PMPs, targeting second-generation vaccine products (subunits of a microorganism) have been attractive because the cell biology of plants is well suited for production of the glycoproteins or lipoproteins that typically constitute these antigenic molecules. Most interestingly, the plant tissue itself has been promoted as the delivery vehicle for vaccines by mucosal immunity (oral delivery) and this consideration drove initial development in the field of vaccine production.

An early example of vaccine production in plants is found in the patent literature (Curtiss and Cardineau, 1997), where the main claims concern immunity against pathogenic bacteria after oral delivery of transgenic tobacco leaves expressing bacterial antigens. A landmark paper establishing the utility of plants to express antigens involves expression of hepatitis B surface antigen (HBsAg) in tobacco plants (Mason *et al.*, 1992). Although shown to be biochemically equivalent to the human serum-derived HBsAg, demonstration of oral obtained immunity, knowledge of protein glycoslylation patterns, and increased total protein levels were demonstrated in subsequent studies.

A benefit touted in the early development of plant-produced vaccines was that production material, indeed the edible parts of plants, could be used as a delivery vehicle. This has an obvious public health advantage in developing countries where routine vaccinations can be difficult. However, as the technology has developed, problems with variable protein expression levels in the host plant and controlling the release kinetics of the vaccine result in an unpredictable dose, and these problems have guided the development of vaccines toward purification strategies and routes of administration that are parenteral (Obembe *et al.*, 2011). Additionally, although advances are being made in the understanding of the immunology of mucosally delivered vaccines, delivery of vaccines through injection is easier to test and better understood (Neutra and Kozlowski, 2006). Nevertheless, there is a recent example where reproducible and quantifiable levels of expressed protein are obtained from leaves that are dried and packaged into capsules. This is a promising approach to deliver a predictable dose (Lakshmi *et al.*, 2013).

A key milestone in the production of vaccines from plants occurred in 2006 with the first regulatory approval of a vaccine produced in plant cell culture; Newcastle disease vaccine is manufactured by Dow Agrosciences, LLC and is for veterinary use. The fact that it was produced in plants was the main advantage to this regulatory approval because contamination from animal proteins was not a concern (Vermij, 2006). Nevertheless, it has not been commercialized, as Dow had intended the approval as a case study in regulatory approval, rather than a step in establishing a platform. There are some industry examples of plant-produced vaccines currently in late-stage development. iBio, Inc. uses transient expression

technology of viral epitopes against H1N1 and H5N1 and has vaccines currently in Phase-I trials. Medicago uses a different technology, producing virus-like particles in leaf tissue, and has conducted clinical trials for H5N1 vaccine (Phase II) and H1N1 (Phase III) as well. Production of this vaccine is highlighted in the Section 'Case Study.' Clearly, production of second-generation-type vaccines today is feasible from both a technical and business perspective and vaccines for diseases such as cholera, rabies, and influenza are currently in efficacy trials.

Monoclonal Antibodies

As therapeutic proteins, monoclonal antibodies (MABs) are single-cell-originated proteins that bind foreign target molecules with high specificity to elicit various immune responses. Owing to their specificity, antibodies are used to treat diseases such as arthritis, immune and inflammatory diseases, or target-specific cancers for immune system recognition. Additionally, MABs are used for diagnostic purposes, disease prevention, and transplant rejection treatments (Fischer *et al.*, 2004). There are five types of antibody (immunoglobulin (Ig)) molecules produced by mammals (IgG, IgM, IgA, IgD, and IgE). Antibodies of the IgG, IgM, and IgA types are the most commonly expressed in plant pharmaceuticals, although other classes such as Fab genes (the variable, epitope-recognizing region of the antibody molecule) have also been successfully expressed. IgGs and IgMs are general classes of antibodies that play important roles in protecting the body from pathogenic infection (Knoll *et al.*, 2012).

Because glycosylation pathways and subcellular protein targeting and assembly are similar (but with important differences, see Section Purification) between plants and mammals, recombinant production of complex immunoglobulin molecules was predicted to be feasible. Indeed, the first report of antibody production in plants showed that a functional multimeric IgG could be isolated from a cross from separate *N. tabacum* plants stably transformed for the subunit chain components (Hiatt *et al.*, 1989). Importantly, assembly of this functional molecule required a secretion signal on both chains, highlighting the importance of correct subcellular targeting. Production of antibodies has now been demonstrated in plant species including Arabidopsis, carrot, potatoes, soybean, maize, alfalfa, and various tobacco species, among others. There are a variety of strategies for expression of these complex molecules that include a single transformation event (either stable or transient) from one transfer deoxyribonucleic acid (T-DNA) as well as utilization of specific subcellular targeting technologies to achieve efficacious glycosylation of the antibody (De Muynck *et al.*, 2010).

Several plant-produced antibody products have reached clinical testing stage. A product that prevents tooth decay, CaroRx™, has been tested by Planet Biotechnology. By binding to the bacteria *Streptococcus mutans*, this antibody keeps the bacteria from remaining on the teeth, preventing decay. Another example where pharmaceutical production in plants provides an advantage is the development of antibody microbicide directed at human immunodeficiency virus infection/acquired immunodeficiency syndrome (Lotter-Stark *et al.*, 2012). This promising therapy is closer to reality as Fraunhofer, IME, has successfully completed phase-I trials of an iteration of this therapy.

Production Systems

Plant biotechnology has successfully enabled the development of crops with new or improved attributes through ectopic expression (or suppression) of recombinant proteins, many of which have achieved commercial success. These include crops with quantitative changes in intrinsic properties, such as yield, tolerance to abiotic or biotic stresses, or qualitative changes in composition, such as accumulation of oils or with altered lipid profiles. The optimal expression of the recombinant protein is generally determined empirically by conducting phenotypic analysis, and often very low levels of the recombinant protein are needed to produce the desired trait without undesired off-types. In contrast, successful PMP production is largely a function of maximizing the protein yield, stability, and where necessary, posttranslational processing of the target protein. It is generally accepted that there is no reliable way of predicting a successful plant host, protein expression level, stability and assembly, and in the case of vaccines, whether the protein will be antigenic. Therefore, each of these aspects must be determined empirically. Although the range of available plant expression hosts for molecular farming is impressive, the choice becomes even more varied when the different expression systems are considered **Figure 1**. In this article, an expression host, an expression system, and production system are considered as separate entities: an expression host is defined as a particular species, whereas an expression system is defined as transformation and expression methods, including posttranslational strategies that address protein stability and efficacy. Production system describes the propagation and growth to harvest of the expression host. The combination of host and expression system results in an expression platform, for example, stably transformed rice seeds, transiently transformed alfalfa leaves, stably transformed tobacco suspension cells, virus-infected spinach leaves, etc. Factors that must be considered to guide the selection of the expression host and the assembly of the appropriate expression platform include the intrinsic properties of the protein; yield and scale-up requirements to meet expected market demands; speed of development of a new product; product quality criteria, such as correct protein folding and glycosylation, to 'humanize' the therapeutic; downstream processing and purity needs; delivery route; containment issues; and biosafety and regulatory considerations. For each of these factors, there are specific elements of the production platform that can be optimized (**Figure 2**). These elements will be discussed in the following paragraphs.

Expression Host

A broad range of plant species have been used for the production of therapeutics, including alfalfa, Arabidopsis, banana, barley, carrot, false flax, flax, lettuce, maize, pea, potato, safflower, spinach, soybean, tobacco, and tomato (Twyman *et al.*, 2013). Advantages of leafy crops, such as alfalfa and tobacco, include high biomass yield, multiple growth cycles per year,

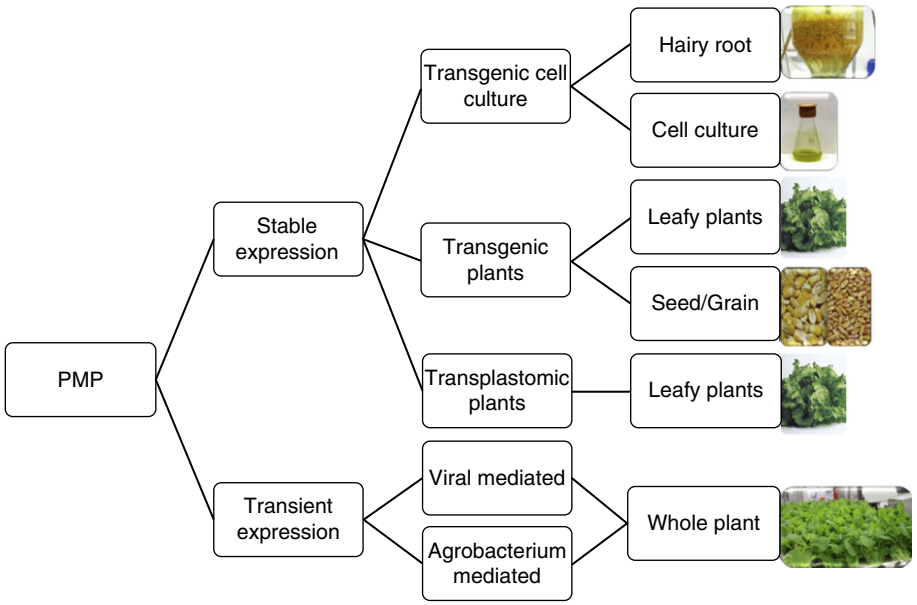


Figure 1 Representation of expression and production platforms for plant-produced pharmaceuticals.

	Host production system		
	Whole plants		Plant cell culture
Criteria	Stable transformation	Transient expression	Stable transformation
Speed of development	Long development time	Short development and production time	Short development and production time
Glycosylation	Similar to mammalian	Similar to mammalian	Similar to mammalian
Scalability	Highly scalable	Moderately scalable	Limited, costly
Processing/GMP	Complex, costly	Complex, costly	Varies, potentially less complex
Biosafety	Field grown to partial containment	Partial containment	Aseptic culture
Examples Company Production system Compound Stage of development	Ventria bioscience Stably transformed rice VEN100 rh-lactoferrin Phase II	Medicago Transient expression in tobacco Influenza vaccine Phase II	Protalix Carrot soot suspension cells Elelyso (taliglicerase alfa) FDA cleared

Figure 2 Comparison of key factors associated with different PMP production systems.

and established agricultural production practices. Tobacco has been the leading leaf-based system for commercial production of recombinant proteins since the first report of MAB-expressing tobacco (Hiatt *et al.*, 1989). The major advantages of tobacco are the well-established technology for gene transfer and expression, the high biomass yield (more than 100 000 kg ha^{-1} for close cropped tobacco because it can be harvested up to nine times a year), and the existence of large-scale infrastructure for processing that does not come into contact with the human or animal food chains. Nevertheless, because leaf tissue has high water content, proteins are expressed and accumulated in an aqueous environment where they are subject to degradation. Consequently, leaves must be processed soon after harvest, adding significantly to production costs. Although not as prolific as tobacco, alfalfa also produces large amounts of leaf biomass and has a high leaf protein content. Other leafy crops, such as lettuce, are being explored for PMPs. Because lettuce is edible, it may be possible to decrease or eliminate purification costs, if the leaf tissue is directly consumed.

The problem of protein instability in leaf tissue can be overcome by expressing proteins in the dry seeds of cereals and

grain legumes. Several different species have been investigated, including the cereals maize, rice, wheat, and barley and the legumes soybean and pea. Accumulation of protein in seeds and grain allows long-term storage of target proteins at ambient temperatures (Ramessar *et al.*, 2008). Scale-up capacity is high as seed yields can exceed hundreds of kilograms per hectare. Disadvantages of seed crops include the lower overall grain yields that are generally obtained relative to leaf biomass. Although there are specific examples where grain yields have exceeded that of tobacco (Stoger *et al.*, 2002), the biomass per hectare from a tobacco crop generally outweighs grain and seed.

Fruit and vegetable crops, like potato, carrot, tomato, and banana, have also been explored for PMPs and have the unique advantage of protein accumulation in edible storage organs; however, dosage from direct ingestion is not consistent, limiting their commercial development. Recombinant antibodies have been produced in potato (*Solanum tuberosum* L.) and tomato (*Solanum lycopersicum* L.), which also offer certain advantages over other crops. Proteins accumulating in potato tubers are generally stable because, like the cereal seed endosperm, these are storage organs that are adapted for high-level protein accumulation. The potential of potato tubers for antibody production was first demonstrated in 1998 (Artsaenko *et al.*, 1998) and have since been developed as a general production host for antibodies as well as other biopharmaceuticals based on antibodies (Schünmann *et al.*, 2002).

Production in plant tissues in cell-based culture systems has also been established and offers a higher degree of control for protein production than whole plant systems (Huang and McDonald, 2012). These plant cell culture-based bioreactor systems include suspended dedifferentiated plant cells, moss, and hairy roots. Compared with the use of whole plants or plant organs as a production platform, plant cell cultures offer several advantages for economical, sustained foreign protein production (Hellwig *et al.*, 2004), such as shorter production cycles (days or weeks); more consistency in batch-to-batch product yield, quality, and homogeneity of the target protein *N*-glycan pattern (De Muynck *et al.*, 2010; Liénard *et al.*, 2007); potentially cheaper and simpler downstream recovery and purification, particularly for products secreted into the extracellular medium (Rawel *et al.*, 2007); the elimination of the need for intensive labor for cultivation of greenhouse or field-grown plants; and the ease of compliance with cyclic good manufacturing practice (cGMP) requirements and product registration process, etc. (Huang and McDonald, 2012). Cell cultures have been derived from tobacco, rice, soybean, potato, and carrot that have successfully expressed therapeutic proteins and MABs, including enzyme taliglucerase (Eleyso) manufactured by Protolix Biotherapeutics in a carrot cell culture system. The scalability of bioreactor systems is limited relative to greenhouse or field production; however, the advantages can outweigh this for high-value compounds.

Expression Systems

The expression system encompasses the transformation system and the expression strategy, including posttranslational modifications (PTMs) of PMPs.

Transformation

Transformation refers to the process of delivering a recombinant DNA or RNA molecule to cells from which protein is produced, and the transformation system utilized will impact the outcome to at least as great an extent as host species. Transformation can be stable or transient. Stable transformation delivers DNA to either the nuclear or the plastid genomes, where the genetic material becomes integrated into the genome and becomes a stable part it. Efficient nuclear transformation systems have been developed for a broad range of crop plants. In brief, a DNA cassette containing the genetic code for the desired protein and instructions for the required spatial and temporal expression levels and patterns is introduced into the plant tissue either by direct means, for example, using biolistics, or via cocultivation of plant cells with transgenic *Agrobacterium* engineered to deliver the DNA expression cassette to the plant cells. Cells in which the transgenic material has successfully integrated into the nucleus are selectively cultured away from the surrounding nontransgenic cells, and using specific hormone regimes, transgenic plants are regenerated and sampled for protein expression. Plants containing the desired levels of the target protein can be grown to maturity and assessed for genetic quality and stability. Transgenic plant lines produced through stable transformation typically exhibit genetic stability over many generations, and accordingly, this plant production system is highly scalable. Nevertheless, there are disadvantages to stable transformation. Stable transformation is a time-consuming and costly process. The recovery of a single line with the required attributes can take several years. Low protein yield is the most common problem encountered using stable nuclear transformation, although optimization strategies exist to maximize protein yields.

An alternative to stable nuclear transformation is insertion of the coding material into the chloroplast genome, creating a so-called transplastomic plant. The presence of up to 100 chloroplasts in a leaf cell and up to 100 genomes per chloroplast allows very high protein accumulation. In one case, it was reported that levels of proinsulin accumulated between 47% and 53% of total leaf protein of transplastomic plants. With these protein yields, it is estimated that one acre of transplastomic tobacco could produce up to 20 million doses of insulin per day (Boyhan and Daniell, 2011). In another case, the human papillomavirus antigen was fused with an adjuvant and successfully expressed in transplastomic tobacco. This outcome paves the way for the development of low-cost adjuvant-coupled vaccines that may eventually obviate the need for cold chain and sterile needs (Waheed *et al.*, 2011). A summary of vaccine antigens against different human diseases expressed in plastids is presented in Lössl and Waheed (2011). This transformation system has some drawbacks. Because plastids lack glycosylation, this production system is suited only for non-glycosylated proteins, and the number of species for which efficient plastid transformation technology exists is very limited. Currently, tobacco and lettuce represent the higher plant species that have robust chloroplast transformation systems.

An alternative to stable transformation that overcomes many of the aforementioned limitations is transient expression. Transient expression enables rapid transgene expression and massive protein accumulation, often within days. For example, at the conclusion of a 30-day manufacturing

campaign, Medicago produced greater than 10 million doses of vaccine (see Section Case Study). Transient expression does not depend on chromosomal integration and is instantly scalable by increasing the number of host plants. There are two transient expressions systems in use: one based on plant viruses and the other uses the T-DNA from the bacterium *Agrobacterium*. For both, *Agrobacterium* is widely used as a delivery system. Viral vectors have attracted interest because in plants viral infections can be rapid and systemic and infected cells yield large amounts of virus and viral gene products (Streatfield, 2006). There are two major plant RNA virus expression vector systems engineered to express immunogenic peptides and proteins in plants. The first includes epitope presentation systems: short peptides fused to the viral coat protein and are displayed on the surface of assembled virus particles (virus lipid particles (VLPs)). The second class includes polypeptide expression systems where the proteins are not encapsulated after synthesis (Yusibov *et al.*, 2011). Plant viruses engineered to produce vaccines and therapeutic proteins include tobacco mosaic virus, potato virus X, cucumber mosaic virus, cowpea mosaic virus, and alfalfa mosaic virus. DNA viruses, specifically geminiviruses, have also been under exploration as protein expression platforms (Chen *et al.*, 2011).

In the agroinfiltration method, a suspension of recombinant *Agrobacterium tumefaciens* encoding the proteins that form VLPs or the therapeutic polypeptides on the T-DNA plasmid is infiltrated into leaf tissue. This initiates the transfer of the T-DNA to a very high percentage of cells, where the gene is expressed at high level for approximately 2–5 days without genome integration. Agroinfiltration allows for the routine production of 50–150 mg of protein per kilogram of leaf tissue in a timescale of weeks, and hundreds of kilogram of tobacco leaves can be processed in a single run.

Expression Methods

Although the intrinsic production capacity of the chosen production platform cannot be modified easily as it is dependent on the overall biomass yield of the crop, the specific yield of recombinant protein per unit of plant biomass can be influenced by the optimization of transgene expression, which is achieved through expression construct design. Gene expression is regulated at multiple levels in plants. In play are regulatory processes for transcription, translation, PTM, import and export, stability, and ultimately the degradation of proteins encoded by the nuclear or organellar genomes. Successful production of PMPs requires manipulating the regulatory machinery through the strategic use of endogenous and exogenous genetic and regulatory elements introduced into plant cells to orchestrate these processes to the desired ends (**Figure 3**). Perhaps the most important component of the expression construct is the promoter used to control transcription of the transgene. For dicotyledonous species, such as tobacco, potato, and tomato, the strong and constitutive cauliflower mosaic virus 35S promoter (CaMV 35S) is often chosen to drive transgene expression (Ma *et al.*, 2005). In cereals, other promoters have been tested, such as the maize ubiquitin-1 (ubi-1) promoter (Chiera *et al.*, 2007). Tissue-specific promoters are an alternative to constitutive promoters and can provide numerous advantages. For example, although constitutive promoters allow high-level accumulation of recombinant proteins in virtually all tissues, including meristems, leaves, pollen, seeds and roots, a seed-specific promoter largely restricts recombinant protein accumulation in the seeds, reducing or eliminating foreign protein accumulation in vegetative organs. In one case, yields in excess of 30% total soluble protein (TSP) of a single-chain antibody in *Arabidopsis thaliana* were obtained with the seed-specific promoter, arc5-I promoter from the common bean (*Phaseolus vulgaris* L.), and the antibody retained its antigen-binding affinity (De Jaeger *et al.*, 2002). There are other reasons to have an alternative strategy for promoter-driven localization of PMPs to different tissues. Although a high transcription level is desirable for maximal protein production, highly expressed transcripts and proteins may lead to growth and developmental defects in the plant or cell culture. Use of promoters that are conditionally induced may ameliorate this issue. A recent example is use of a CaMV 35S promoter that is engineered with control elements from the *Escherichia coli* tetracycline operon. This promoter is derepressed by the application of tetracycline and was shown to induce the expression of an antiinflammatory viral interleukin-10 (vIL-10) 3.5 times higher than with the standard CaMV 35S promoter (Bortesi *et al.*, 2012).

An appropriate polyadenylation site must be paired with any specific promoter and is inserted at the 3′ end of the coding region in the expression cassette (Ma *et al.*, 2003). With

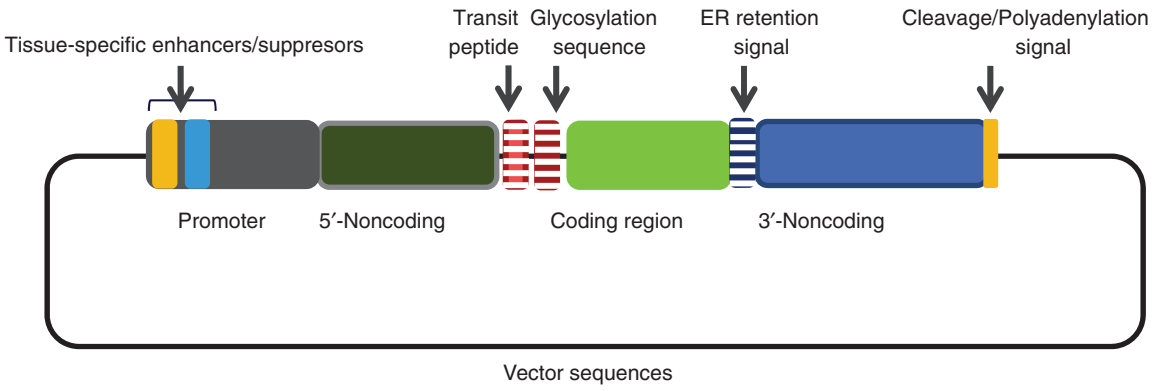


Figure 3 Representation of a plant expression vector, containing coding and noncoding elements necessary for protein production and posttranslational modifications.

the high expressing constitutive CaMV 35S or the maize ubiquitin-1 promoter, the polyadenylation sites of the CaMV 35S transcript, the *A. tumefaciens* nos gene, or the pea ssu gene are often used (Ma *et al.*, 2003; **Table 2**).

Posttranscriptionally, translational efficiency of the mRNA transcript can also have a profound impact on protein accumulation. One of the approaches to increase the translation efficiency in a given host is to optimize the codon usage in the mRNA, by changing the nucleotide (DNA) sequence without changing the amino acid sequence, to suit the respective host (Gustafsson *et al.*, 2004; Desai *et al.*, 2010). Preferred codon usage differs between monocots and dicots, and it is greatly different even between nucleus and plastid of the same plants (Desai *et al.*, 2010). Cryptic splice sites and sequences with the potential to form hairpins can also be removed from the construct (Gisby *et al.*, 2011).

There are many modifications a protein can undergo post-translationally, and early consideration of these in a PMP project is necessary to guide the strategy of expression and purification. PTMs include disulfide bond formation, hydroxylation, lipidation, and importantly, *N*-linked glycosylation. Disulfide bond formation improves protein stability in the cell, and during purification, hydroxylation and lipidation are frequently considered for product delivery, whereas appropriate *N*-linked glycosylation of PMPs is important for protein stability. These modifications are determined by subcellular targeting.

Therefore, after promoter choice and codon optimization, the next most important aspect of construct design is the inclusion of sequences that control subcellular targeting of the protein. This is another general method to increase the yield of recombinant proteins because the compartment in which a recombinant protein accumulates influences its folding, assembly, and PTM (Ma *et al.*, 2003; Schillberg *et al.*, 2005). Comparative targeting experiments have shown that the secretory pathway is a more suitable compartment for folding and assembly than the cytosol and is, therefore, advantageous for high-level protein accumulation (Schillberg *et al.*, 1999). Following the transcription and translation of a target gene, the recombinant proteins are directed to the secretory pathway using either a heterologous (part of the construct design) or an endogenous signal peptide located at the *N*-terminus of the nascent protein. Proteins containing these targeting signals are cotranslationally imported into the endoplasmic reticulum (ER) and are eventually secreted into the apoplast, a supracellular network of interlinked compartments underlying the cell wall. Depending on its size, a protein can be retained in the cell wall matrix or can leach from the cell. This 'default' pathway for proteins in the secretory pathway allows apoplastic localization of a PMP and can be a useful approach for protein purification from root cultures or in single-cell systems such as algae (Nagels *et al.*, 2012).

Some peptide signals required for targeting through the endomembrane system and to specific organelles are well known, such as ER retention peptide, whereas others, such as vacuole-targeting signals, have not been shown to have a canonical sequence and need to be empirically determined (Vitale and Pedrazzini, 2005). Once known, these signals are easily engineered onto the protein. Because the majority of recombinant proteins are most stable in the ER lumen, an effective strategy in increasing protein expression levels is to confine the protein to the ER using an H/KDEL C-terminal tetrapeptide 'tag,' in addition to the signal sequence. Accumulation levels can be increased up to 100 fold by adding the KDEL signal (Schillberg *et al.*, 2002). A further advantage of ER accumulation is that these proteins will not be modified in the Golgi apparatus (GA), preventing modification with plant-specific xylose and fucose residues (Sriraman *et al.*, 2004). In addition, the ER provides an oxidizing environment and an abundance of molecular chaperones; however, the number of proteases is only a few.

Table 2 Examples of Promoter and Tissue Localization of plant-made pharmaceuticals (PMPs) in development

Protein	*Tissue*	*Plant species*	*Promoter*	*Subcellular localization*	*Production level*
Cytokinin viral interleukin-10	Cell culture	Tobacco	Inducible: Tetracycline derepressed		9.3±1.4 μg g^{-1} fresh weight
Taliglucerase	Cell culture	Carrot			
B-subunit of the heat-labile toxin	Hairy root	*Nicotiana tabacum*	NtQPT2: wound-inducible root localized		330 μg g^{-1} fresh weight
H1N1	Leaf	*Nicotiana benthemenia*	CaMV 35S	Lipid rafts of plasma membrane	200 μg g^{-1} fresh weight
HBsAg	Tuber	Potato	CaMV 35S+PB33 (patatin)		1 μg g^{-1}
Human transferrin	Seed	Rice	rice seed storage protein glutelin 1 gene promoter	Endomembrane system	8–10 mg g^{-1} seed weight
Human insulin-like growth factor 1 (hIGF-1)	Seed	Arabidopsis	Oleosin promoter	Oil bodies	0.17% of the TSP
Human immunodeficiency virus protein Nef	Leaf	Tobacco	cauliflower mosaic virus 35S (CaMV 35S)	Endoplasmic reticulum stacks	0.7% TSP
a1-Antichymotrypsin protein	Leaf	Potato	CaMV 35S with coexpressed protease inhibitor	Cytosol	Threefold higher than without inhibitor

Protein storage vacuoles are important organelles of the endomembrane in the seed, and targeting recombinant proteins to these organelles permits seed localization, resulting in the aforementioned advantages of high stability and storage capability.

In addition to the secretion pathway, there are other ways to utilize the endomembrane system for enhanced protein stability. For example, because the first step in protein glycosylation occurs in the ER in some cases, adding sugar moieties to a PMP may not be desired. Glycosylation can be avoided at this step by targeting oil bodies. These organelles derive from the ER membrane; although the localization signal is embedded in the membrane, the C and N termini of the protein are exposed to the cytosol. This strategy was used for both the thrombin inhibitor hirudin in oilseed rape (Obembe *et al.*, 2011) and insulin in *Arabidopsis* seed (Li *et al.*, 2011). Another novel approach to avoid glycosylation in the ER lumen yet retain stability in the cytosol leverages the C-terminal of tail-anchored membrane proteins on the ER. As an example of this system, the human immunodeficiency virus protein Nef was anchored to the cytosolic face of the ER membrane by fusing to the C-terminal domain of mammalian ER cytochrome b5, a tail-anchored (TA) protein. This resulted in a stacked ER structure that protected the protein in the cytosol. The recombinant protein Nef could be removed *in vitro* from its TA because a thrombin cleavage site had been engineered between the protein and the anchor (Barbante *et al.*, 2008).

To avoid unwanted PTM on a PMP, expression outside of the endomembrane system in the cytosol can still be a viable option. Stable protein expression can be achieved but generally requires the presence of recombinant protease inhibitors. The PMP can be coexpressed with a cytosolic protease inhibitor, such as tomato cathepsin D inhibitor (Goulet *et al.*, 2012). In this example, the authors show not only the increased protein levels in leaf tissue but also increased stability of a human a1-antichymotrypsin protein in the presence of this inhibitor.

Humanization via posttranslational modification

Humanization of therapeutics refers to the PTMs of a PMP to closely resemble the same protein had it been produced in human cells. The primary modification of concern is *N*-linked glycosylation and is important because of the roles that glycan structures play in immune recognition.

The process of *N*-linked glycosylation involves sequential addition and trimming of sugar chains (glycans) onto a nascent secretory protein as it moves through that pathway. These sugar modifications on the resulting glycoprotein are important for protein stability, activity, trafficking, and targeting, as well as pharmacokinetic properties of protein therapeutics. For example, protein stability is driven by the high mannose glycan structures that initially decorate proteins because these are ligands for the ER-based calnexin/calreticulin protein-folding checkpoint. Beyond roles in protein stability, glycans can also be key efficacious aspects of a therapeutic. For example, a well-characterized mammalian-targeting signal glycan is phosphorylated $Man_8GlcNAc_2$ structures found on protein hydrolases; the mannose-6-phosphate receptor in the *trans*-Golgi-network (TGN) recognizes that structure on the hydrolases to import them into the lysosomes. Loss of these protein hydrolases is the basis of many lysosomal storage diseases, so these proteins are key pharmaceutical targets. From a pharmacologic perspective, glycoproteins also serve as potent recognition ligands for macrophage-located receptors in order to elicit an efficient immune response (Nagels *et al.*, 2012).

The *N*-linked glycosylation pathway is an active area of study in plants and excellent detailed reviews on the topic are available (e.g., Ruiz-May *et al.*, 2012; Gomord *et al.*, 2010). A brief summary is useful to illustrate some important differences between plant and animal glycosylation pathways. The first step in protein glycosylation is the attachment of a cytosolic and ER lumen-generated high mannose sugar ($Glc_3Man_9GlcNAc_2$) oligosaccharide core structure select asparagine (Asn) residues. The Asn residue is embedded in the consensus sequence *N*-X-(S/T), where X is any amino acid but proline. This step occurs in the ER lumen and is conserved among eukaryotes. Additional saccharide trimming and important glycoprotein-folding checkpoints (e.g., the calnexin/calreticulin pathway) occur in the ER before the glycoprotein moves to the GA. *N*-acetylglucosamine molecules are added to the sugar chain and the mannose core is trimmed in the initial part of the GA. The trimming and subsequent glycan additions occurring beyond the ER result in moieties referred to as complex *N*-glycans. The pathways between plants and humans then diverge as the glycosylated protein sequentially moves past the *cis*-Golgi further into the GA (**Figure 4**). Past the *cis*-Golgi, the plant-specific β1,2-xylose and core α1,3-fucose sugar molecules are added to the core $Man_3GlcNAc_2$ molecule. Additional maturation to these plant glycan structures in some tissues include the so-called Lewis (Le^a) epitope, where one or two β 1,3-Galactose, α 1,4-fructose moieties are added onto the last GlcNAc residue. This antennae structure is thought to elicit an IgE-mediated immune response. Indeed, generation of complex glycans can be different even between plant species and organs. For example, in monocot seeds, Le^a-antennae are not added. Hence, consideration of glycosylation differences between species can also drive species decisions for PMP development. Subsequent to processing in the GA, glycosylated proteins are sorted in the TGN to their final destination at the plant cell wall, apoplast, vacuole, or chloroplast.

Owing to the importance of glycan structures for therapeutic efficacy and the potential for immune reactions to plant glycan structures, platforms for the 'humanization' of PMPs have been developed. In one such platform, the Golgi additions can be avoided by targeting the PMP to remain in the ER by means of the ER retention signal (C-terminal K/HDEL). An interesting additional use of this platform is primarily the exploitation of the oligomannose glycan structures decorating the protein in this compartment. The mannose glycan structure on proteins is detected by mannose receptors on macrophages, and this approach has been used to target therapeutics that address lysosomal storage disorders. In another humanization platform, the plant-specific β1,2-xylose and core α1,3-fucose glycosyl transferase genes can be knocked out using RNAi technology, minimizing the glycan elaboration with these plant-specific structures. In a third approach, human glycosyl transferases are engineered into the host plant. In this platform, the recombinant transferases are preferentially used in Golgi-located galactosyl additions (Webster and

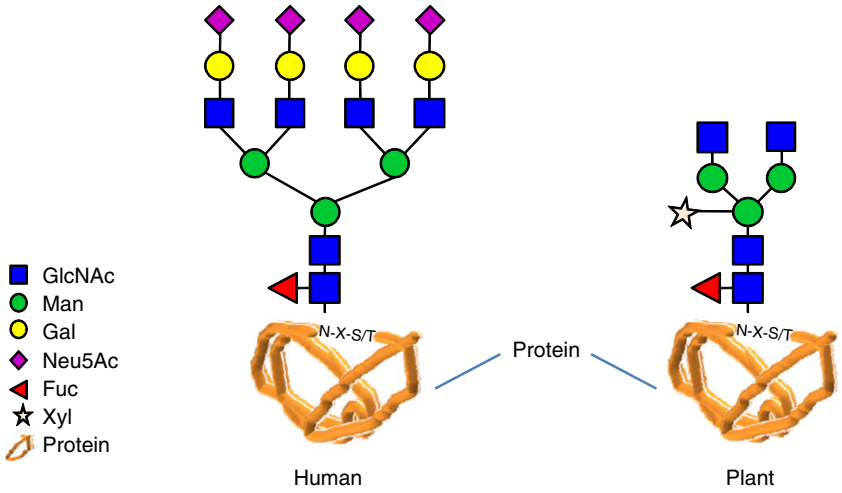


Figure 4 Some key similarities and differences of complex human and plant glycosylation. Note the xylose present on the plant structure, not present in human structure, and the sialic acid structure at the terminal of the human structure. Structures are elaborated according to Consortium of Functional Glycomics essential symbols nomenclature: http://www.functionalglycomics.org/static/consortium/Nomenclature.shtml

Thomas, 2012). Finally, a recent report highlights the successful addition of terminal sialic acid residues onto plant-produced glycoproteins by introducing the human pathway into *Nicotiana benthamiana* (Castilho *et al.*, 2010).

Another PTM with therapeutic consequences is O-glycosylation. In O-glycosylation, fucose, xylose, mannose, GlcNAc, galactose, glucose, or *N*-acetylgalactosamine (GalNAc) residues are added to the hydroxyl group of serine or threonine on proteins that have completed their folding in the GA. In mucin-type O-glycosylation, additional sugars are then added to these structures. The resultant modification affects biological activity of proteins involved in inflammation response, coagulation, cancer, and viral infection pathways. Unlike *N*-linked glycosylation, the O-linked pathway in plants is not as well described as in mammalian systems; although monosaccharides are added to proline, hydroxyproline, and serine in plants, mammalian-like additions (e.g., GlcNac) have just recently been described (Gomord *et al.*, 2010). In biopharming, O-glycosylation has primarily been used to stabilize proteins to increase their shelf life by adding an O-glycosylation consensus sequence to the C-terminus of the protein (Webster and Thomas, 2012).

Hydroxylation of proline on proteins is a PTM that affects stability in some proteins; collagen is an example. The hydroxyproline modification has been characterized in plants at only low levels; consequently, a humanization approach has been used to recapitulate this modification in plants. Coexpression of collagen and recombinant prolyl 4-hydroxylase in transgenic maize seeds has been shown to produce effective levels of hydroxyproline-stabilized collagen (Xu *et al.*, 2011). This modification has been used more to improve stability and shelf life of the protein rather than address its immunological effect (Webster and Thomas, 2012).

The addition of lipid molecules onto proteins (e.g., palmitoylation and myristoylation) is a PTM that has been considered in PMP design. Lipidation serves primarily to target the protein on the plasma membrane or other intracellular lipid location and also has been shown to have roles in signal transduction. Correct subcellular targeting of PMPs that require lipidation is important; lipidation of the OspA vaccine against Lyme disease or the Nef12 protein that addresses the immune response to HIV indicates that chloroplast targeting is a key to developing efficacious proteins (Webster and Thomas, 2012).

Production System

Production refers to the method of propagating, growing, or producing plant, organs, or cells from which the PMP will be purified. To a great extent, the host organism and expression strategy will dictate the production method. For example, expression of a recombinant protein in seeds requires field production of stably transformed whole plants. Leaf expression can be achieved in field or protected culture and be the product of stable, transient, or plastid transformation methods. Because the production method has significant implications for cost, scale-up, and risk management, it needs to be factored early in the process. The regulatory framework for genetically modified organism crops is presented elsewhere in this volume, and regulatory considerations for PMP are discussed in the Section Regulatory Considerations; hence, they will not be addressed in this section. Where production method as it factors into the key decisions for PMP production will be reviewed.

There are essentially five options for PMP production. These are: growth of whole stably transformed plants in open fields; growth of whole stably or transiently transformed plants in a greenhouse; growth of whole stably or transiently transformed plants in an artificially lit growth chamber; production of lower or aquatic plants in a semiclosed system; and production of plant cells in a sterile, closed bioreactor (**Table 3**). Growth in open fields theoretically allows infinite scale-up, limited only by the amount of seed produced to establish the crop. Indeed, perennial crops, such as alfalfa, can even allow multiyear production. Field production provides the greatest flexibility for production platforms, as it encompasses the

Table 3 Comparison of production systems for plant-made pharmaceuticals (PMP)

Production system	*Type of plant*	*Advantages/challenges*	*Example*
Closed system	Single-cell suspension, hairy roots, or anchorage dependent cells	• High level of containment • High level of control • Cell seed stock well characterized • Bioreactor based • Expensive to implement	Protalix Biotherapeutics Carrot cell culture Taliglucerase alfa
Semiclosed system	Small aquatic plants that can be grown in sterile cell culture	• High level of containment • High level of control • Single-use systems with overhead lighting • Expensive to implement	Biolex/synthon Lemna Interferon alpha 2b
Enclosed artificially lit chambers	Tobacco, lettuce, tomatoes, alfalfa, etc.	• Light cycle, temperature, humidity, and CO_2 control • Automatable • Expensive utilities • Transient expression possible	Fraunhofer Nicotiana Flu HA protein
Greenhouse	Tobacco, lettuce, tomatoes, alfalfa, etc.	• Sun supplies energy • Supplemental light required to supplement seasonal affects • Transient expression possible • Automatable • Inexpensive	Medicago Nicotiana Flu virus-like particles
Field	Tobacco, lettuce, tomatoes, alfalfa, potatoes, bananas, etc.	• Sun supplies energy • Containment difficult • No barrier to pests • Transmission through animals and birds	Prodigene Corn Trypsin

broadest number of host species and expression systems. Field-based production also does not require a capital-intensive infrastructure. Nevertheless, there are significant drawbacks that have to date limited the number of PMPs produced in open fields. As mentioned in the Section Transformation, the development of stably transformed transgenic or transplastomic crop lines for commercial production requires many years and millions of dollars in development costs, making this potentially the highest cost production method. In addition, regulatory agencies, such as the United States Department of Agriculture (USDA), impose more stringent regulations than what is required for transgenic plants expressing nontherapeutic proteins. The primary difference for PMPs over the so-called input traits for genetically engineered crops entails the level of containment required when a crop expressing an output trait, such as PMP, is in the field. For example, fields are subject to multiple inspections, the field must be surrounded by a 50-foot fallow zone, isolation distance from similar crops is strictly enforced with wind-pollinated crops at a larger distance than self-pollinated crops, and equipment must be dedicated to the field trial for the entire field season and then cleaned using the USDA-approved Standard Operating Procedures. No crop can be planted on the plot the following year, so that volunteers can be destroyed. These requirements increase production costs over other types of transgenic crops (Breyer, 2009). For a list of crops for which field trial permits have been obtained and case studies for field release of PMP, see Breyer *et al.* (2012). A recent survey of farmer's perceptions of biopharming showed that the greater the number and cost of production changes, the fewer the farmers were willing to adopt the technology, even if profits increased (Hayes and Kostandini, 2013). An evolving, but yet not finalized, process for GMP for field-based production increases substantially the uncertainties of field production.

Growth in enclosed or protected environments, such as greenhouses and growth chambers, has been widely adopted for PMP, including vaccines, monoclonal antibodies (MABs), and therapeutic proteins, for a variety of reasons, such as providing physical containment and confinement. Scale-up is limited by facility size, whereas production can continue year-round with multiple production runs possible annually. Potato and a number of leafy crops, such as tobacco, alfalfa, lettuce, and spinach, are examples of plants that can be grown successfully in contained facilities. All can be stably transformed and for lettuce and tobacco, plastid transformation systems have been developed. For a stably transformed line, a master stock of transgenic seed (or asexually propagated tubers in the case of potato) is produced that is planted to initiate a 'run.' Maximum flexibility is achieved when transient expression is used as the expression system. Although transient expression systems exist for multiple plant species, *N. benthamiana* is used almost exclusively for commercial scale transient production, having the most well-developed system, including multiple vectors (Hellens *et al.*, 2005) and silencing suppressors (Voinnet *et al.*, 2003).

Plant cell culture techniques have been in existence since the 1950s and have been utilized successfully to synthesize a wide variety of natural compounds with therapeutic value, including paclitaxel (Taxol). Recombinant therapeutic protein was produced in tobacco cells in 1990, and since then, a number of antibodies, enzymes, hormones, and growth factors have been produced (Hellwig *et al.*, 2004; Paul and Ma, 2011). Plant cell cultures combine the advantages of whole plant

production with those of microbial cultures (Huang and McDonald, 2012). Growth in a bioreactor allows precise control and batch-to-batch consistency and enables GMP production practices. Several approaches can be used for the *in vitro* production of plant cells, but the two systems widely used for PMP are cell suspensions and hairy root cultures. (Bioreactors can also be used to culture aquatic plants, moss, and some algae, for PMP production, and that will not be covered here.) Recombinant suspension cultures have been derived from several species, including *Arabidopsis*, tobacco, rice, soybean, tomato, and carrot. To establish a cell culture for PMP, a transgenic plant or transgenic cell line is produced and selected for stable, high-performing cell lines. These master lines are then scaled up for production. Hairy roots are generated by infection of plants with *Agrobacterium rhizogenes* that contains the 'root-inducing' (Ri) plasmid. Integration of the plasmid into the plant genome results in differentiation and growth of neoplastic root structures called hairy roots. Once established, hairy root cultures grow rapidly and can be propagated indefinitely in liquid medium. The number of species reported to have successfully produced therapeutics via hairy roots is limited and includes potato and tobacco (Huang and McDonald, 2012). The morphology and culture characteristics of hairy root cultures are different than suspension cultures and can create unique challenges that have to be taken into account (Huang and McDonald, 2012).

Purification

Biotherapeutics are typically administered by injection, although oral administration of plant-produced vaccines has been suggested and studied. In the case of injection, the product typically is of a higher purity than a product that is administered orally. Removal of host cell proteins, DNA, vector (virus or *Agrobacterium*), and other plant-based compounds such as chlorophyll and nicotine during processing is a necessity in injected products, whereas in an oral pharmaceutical, the presence of some of these compounds would be fully acceptable.

Production of an injectable product requires an extensive amount of purification. A purification process may be divided into three general stages: product recovery, clarification, and purification. Plant-based therapeutics use purification strategies common to other biologics (Li and Qiu, 2013). These include chromatographic operations as well as multiple types of filtration operations. These types of operations are well documented in many reviews (Li and Qiu, 2013) and any number of commercial suppliers of chromatography resins and filtration media and equipment are willing to aid in development of these purification operations. An example of techniques used in downstream purification of a plant-derived vaccine is given in the 'Case Study' at the end of this article.

However, plants, when used as hosts for protein production, present unique challenges to bioprocessing recovery and clarification operations. Plants contain a large amount of fibrous, solid material that is a barrier to recovery of therapeutic molecules, especially protein. Thus, recovery operations for plant-based products often include a milling, grinding, pressing, or digestion step that is more severe than steps used in some microbial or mammalian cell culture operations. If the product of interest is prone to physical degradation, these operations may have a detrimental effect on product quality. Elimination of these solids in the food and beverage industry is often part of production processes and thus methods of production may be adapted from these industries. However, the standards for equipment design and cleaning are often more strict in the pharmaceutical industry as compared with the food industry and thus specialized equipment may need to be designed.

Some plants contain low molecular weight compounds that are subject to rapid oxidation and are capable of impacting coexisting proteins in the early-process stream. The time required to separate these compounds from the target protein and the methods used to prevent oxidation have a major impact on product quality. Attention must be given early in a plant-based process to a wide variety of compounds, such as chlorophyll, phenolics, and alkaloids, that are not present in microbial and mammalian cell-based processes.

Colored components, such as chlorophyll, are easily visible as process residues in equipment used in plant-based processes and present a challenge in removal from the process stream as well as in equipment cleaning. The presence of pectins, cellulose fibers, and other viscous, slime-like residues are a challenge to clean from processing equipment, such as centrifuges, filter housings, and mixing vessels. The selection of proper cleaning agents is critical in validation of cleaning operations in plant-based processes. The presence of these viscous components in a process stream also creates challenges in mixing, fluid movement, and product recovery in the production process.

Production of an orally available biotherapeutic may require minimal or no purification. A transgenic plant that is edible is in itself a potential product if the biotherapeutic can survive the transport to the site of interaction (typically the gut). However, use of a system such as cell culture or a transiently infected plant that is not typically part of the food chain would require at least partial processing and formulation to make the product not distasteful to the patient. Removal of objectionable species in some production systems, such as very high bioburden levels in *Agrobacterium*-infiltrated systems, may be required and would depend on the production system. Orally available biotherapeutic products may be viewed as more akin to food than drugs from a safety perspective; therefore, many process controls that exist in the pharmaceutical industry would likely be relaxed and the manufacturer could argue that compliance with the food industry's regulations was sufficient. However, the burden of proof of product stability, process reproducibility, and efficacy would still fall on the manufacturer and adherence to pharmaceutical requirements in these areas would more likely apply.

Regulatory Considerations

The use of plants as the 'biofactories' for making a protein-based pharmaceutical requires a new level of consideration of the risks associated with the plant and production process as compared with those used for food or even medicinal small-molecule products. Consideration and ranking of the risks will

initially depend on the route of administration of the product produced, the population that will receive the treatment, and existing therapies for the disease target (e.g., does the new product provide a solution for an unmet clinical need?). As always, there are no templates one can use that guarantee success in regulatory acceptance, and each country's regulatory agency has unique concerns about the production of biopharmaceuticals. The sponsor of a new entity produced in plants will more likely have their product considered by the regulators on a 'case-by-case' situation.

The regulatory considerations begin with the choice of the plant host system that will be used to produce the protein therapeutic. The increased genetic knowledge and ability to manipulate protein expression of many systems has led to opportunities to use single-cell systems as well as whole plants or fungi. If an edible plant is chosen as the production system, it will be important for the manufacturer to assure regulatory agencies that there are tight controls around the biomass that would prevent its unwanted entry into the food chain. If the system is edible and also transgenic, cross-pollination with other food source plants in the surrounding area is of concern, so the containment used to grow transgenic plants that produce a biotherapeutic protein must also be considered and demonstrated. Examples of the many plant types that have been considered and containment considerations are shown in **Tables 2** and **3**.

One factor that requires attention and greatly affects the process and facility design is containment of the plant during its growth. A diverse range of options are available to consider here. ELELYSO™ or taliglucerase alfa (Protalix Biotherapeutics), an approved drug for Gaucher's disease, is produced using a carrot cell culture system that can be tightly controlled and operated as a closed system. In contrast, consider the other extreme case of a crop grown in a field in a developing nation in order to provide low-cost injectable vaccines to a large population. The level of control around plants is completely different in these two cases and must be considered in the manufacturing process.

A case where product from a genetically modified corn crop was mixed with a soybean crop harvested for food after use of the same field for growth led to large fines and even larger cleanup costs in 2002 in the US. This led to a major setback in the consideration of using a field-based crop system in the US. **Table 3** lists some of the considerations for containment of the production system chosen.

In theory, it is possible to use field-grown plants for manufacture of a product for injection. However, at the current time, the lack of regulatory experience with plant-based pharmaceuticals in the USA, Canada, and Europe may result in a barrier to entry that is too high to attempt to push this system through toward product licensure.

The theoretical risk of adventitious agent (AA) entry into the product in an open processing system (plant growth through extraction of the protein of interest) will always be present and there is no way to effectively argue against a theoretical risk. Therefore, a large burden will be placed on the production process to provide assurance that any potential threat would be eliminated. For the first generations of plant-produced biotherapeutics, the use of a contained environment, such as a greenhouse or growth chamber, is more likely to be the minimal requirement for use in the growth of plants and will be considered in the following sections. However, a recent draft Health Canada Guidance, human-use biologic drugs derived from plant molecular farming (PMF), proposes that it is acceptable to use a field-based crop to manufacture PMP if the proper controls are in place. The FDA has published a Guidance for Industry, "Drugs, biologics and medical devices derived from bioengineered plants for use in humans and animals," which is useful in developing strategies in navigating the regulatory pathway in the US. Based on these guidance, the case can be made that plants used in the production process are a critical raw material that can be produced under controlled 'GMP-like' conditions as opposed to more traditional organisms grown in fermentors or bioreactors that are considered as a part of the manufacturing process from the moment they are used to establish a master cell bank.

After the plant and growth system are selected, the next level of critical decisions must be made by the manufacturer. If a whole plant system is chosen, a selection must be made on the substrate to support the plant. A synthetic system, such as rock wool or Pillowtex, may be chosen or a natural substrate, such as soil or peat, may be used. The design of the facility will depend on this choice as the robotics to manipulate the different systems must be considered. In addition, the substrate chosen impacts the control required around feeding, control of microorganisms, and waste management. The value of the product (e.g., a flu vaccine that sells for US$30 or a cancer treatment that may sell for thousands of dollars a dose) and the process yields, production costs, and development costs will impact some decisions in the choices made. For instance, a greenhouse that uses the sun's energy to provide light may have lower operating costs as compared with a closed system lit entirely by artificial lights. However, the process control and biomass productivity may be more consistent in an artificially lit system (Wirz *et al.*, 2012). Consideration on how the plants will be manipulated must also be made early in the process design phase. Robotics has great potential to minimize human–plant interaction and is operationally efficient but requires high capital investment. Manufacturing personnel can be used in the process of growing and moving plants and are very adaptable but create a concern for introducing AAs in the process as will be discussed further in the Section Case Study. The choice of the system will more likely depend on what product is being produced and labor costs figure into the location of the production plant.

In the past, plant-based systems used for production of biotherapeutics were often described as extremely safe in the literature and hence it had been suggested that there is no AA risk in products produced in plants (Fischer *et al.*, 2012). Although it is true that the risk of AA derived from a plant cell is much less than that in a product derived from a mammalian cell, regulatory agencies do not consider the risk zero. Concern that an AA which could jump species from plants to humans may appear in the future or that an AA which had not been detected (i.e., porcine circovirus in Merck's and GSK's rotavirus vaccine (Victoria *et al.*, 2010)) may emerge in a product is of regulatory concern in all countries. Therefore, any plant-based manufacturer can be certain that they will be asked to show at least some viral inactivation or clearance in their process. The main concern will be introduction of AA from human sources,

for example, people interacting with process intermediates; rodents in the facility or in contact with raw materials; especially hard to control in field-grown crops; or insect- and animal-derived raw materials used in the process. Knowing this, a manufacturer can choose production methods to mitigate risks, provide viral clearance in their production process, and choose raw materials that carry a low risk of introducing any AA into the process. A detailed guidance on AA considerations may be found on the FDA website in document ICH Q5A (R1).

Control of bioburden, including mycoplasma and spiroplasma, is also important in production processes. Bioburden can often be removed early in purification operations by the use of a sterilizing grade filter. However, bioburden alone is not the only agent that may contribute to safety concerns in a biopharmaceutical. Contaminants, such as mycotoxin (from fungi) and endotoxin (from Gram-negative bacteria), must also be excluded or removed from process intermediates before producing drug product. Exclusion of endotoxin becomes a challenge when *Agrobacterium* is used as the transfer vector for genetic elements in a process, because it is a Gram-negative bacterium that releases endotoxin into the production stream. Control of bioburden and other contaminants in raw materials must also be considered and critical raw materials must be tested and limits set as to the appropriate level of contaminants that a raw material may contain and that the production process can tolerate.

As with the production of any biopharmaceutical, the production process must adhere to current GMP practices. It is up to the manufacturer to design a facility and production process and use materials that comply with the Code of Federal Regulations, Title 21. The interpretation of what constitutes the production process, where it begins, and how plants can be considered a critical raw material in the process is the manufacturer's case to make. Reference to the Guidance for Industry Q7A, Good Manufacturing Practice Guidance for Active Pharmaceutical Ingredients, is useful in this respect. Nevertheless, the regulatory agencies must concur with the proposal if regulatory approval for the product is to be granted and control over the growth and acceptability of plants as the 'bioreactor' for a biotherapeutic is mandatory. Thus, even a plant-based production process must comply with industry standards in terms of facility and process validation, including cleaning and changeover between production campaigns; people, material, and waste flow in the facility; segregation of raw materials, process intermediate, and product; and adequate documentation, including testing, production records, and change of control management.

In summary, there are many considerations to be made in the selection of a host plant, process, and facility to be used in the manufacture of a biotherapeutic. The best decisions are made by assembling a diverse team of scientists, engineers, and quality and regulatory subject matter experts, so that many aspects of the product and its manufacture are considered. Failure to adequately consider many factors can result in product failure, as the product development evolves and much money has been committed to development. This topic has been considered by many academic and industrial subject matter experts and reviews (Sparrow *et al.*, 2007) are available for those wishing to explore this topic in greater detail.

Case Study

Case Study: Rapid Production of Vaccine in Plants to Address Pandemic Threats

In 2010, Medicago was contacted by the Defense Advanced Research Projects Agency (DARPA) to partner in a program sponsored by the US government to prevent strategic surprise from negatively impacting the US national security and create strategic surprise for the US adversaries by maintaining the technological superiority of the US military (DARPA Website). Medicago was asked to demonstrate the potential of a plant-based biopharmaceutical vaccine to mitigate risks associated with a pandemic threat because of the speed and flexibility with which a new vaccine could be produced by Medicago. This request was also made because Medicago had clinical experience with plant-based, highly immunogenic vaccines that contained flu hemagglutinin (HA) proteins in virus-like particles. To accomplish the key milestones of the project, Medicago had to build a facility, scale up, and transfer a vaccine production process in approximately 1 year and then produce 10 000 000 doses of a flu vaccine in 30 calendar days. The following case study highlights the process used to produce the vaccine.

The production of the vaccine can be divided into three main sections: (1) transient protein expression after *Agrobacterium* delivery to leaf tissue, (2) protein separation from plant biomass via tissue digestion, and (3) protein purification via standard industrial filtration and chromatographic techniques.

Production: Host Plants

Nicotiana benthamiana was selected as the host system because it had been demonstrated to be efficient at transient expression of a variety of proteins, it was an efficient system for infiltration and, its natural protease profile was lower than many other species. The growth environment chosen for *N. benthamiana* was a greenhouse. This system was selected on the basis of a number of factors, including cost of greenhouse construction, cost of producing plants in this environment, energy use, simplicity, and previous experience with growth and protein expression in *N. benthamiana*. Each production lot was initiated with seeding to paper pots and seedling germination within a growth chamber. After germination, plug trays containing seedlings were moved into the greenhouse. Once the seedlings reached the appropriate stage of growth, they were transplanted into pots containing peat-based substrate and automatically moved back into the greenhouse via a rail and drive system for further growth. Pots were rearranged from a high- to low-density configuration after growth in the greenhouse for a predefined period. This respacing was accomplished using robotics to pick and replace the pots onto greenhouse tables. The robot is shown in Figure 5. The plants were monitored for stage of growth, physical characteristics, absence of disease, insect contact, and soil chemistry throughout the growth cycle. Watering and fertilization were accomplished automatically with a flood and drain type system that was able to deliver fertilizer of desired nutrient content depending on stage of growth of the plants. The greenhouse area required for



Figure 5 The pick and place robot used for plant arrangement for greenhouse operations.



Figure 6 Infiltration robot used to introduce *Agrobacterium* into the leaf tissue of plants.

expansion of biomass was determined on the basis of the number of plants required to meet the production objectives, the level of protein expression in the plants, the process recovery, and the dose to be administered. Given the objective of the DARPA project to produce 10 000 000 doses in 30 days, the greenhouse- and plant-handling operations occupied approximately one third of the total production facility space. After the manufacturing campaign was completed, the data generated from growth of plants indicated that the greenhouse system was of sufficient size, was efficient, and resulted in production of healthy plants that were of a consistent growth stage and target weight (±13%). A video clip of the greenhouse operations is available at LLL.

Production: Expression System

The expression system used for the H1 protein and VLP production was based on *Agrobacterium* transfer of genetic material to plant cells in the leaf tissue of plants. Medicago used a binary plasmid to develop its genetic construct. A binary plasmid is a plasmid that can multiply (replicate) in two hosts. For the molecular work involved in the assembly of genetic constructs, the host used was *E. coli*. The binary plasmid consisted of regions responsible for replication in the two hosts (*E. coli* and *A. tumefaciens*) and of regions located within T-DNA borders. Expression cassettes consisted of assemblies of DNA transcription and translation elements, one of which was the gene encoding the H1 protein. When genetic constructs were completed, the resulting plasmid was transferred to *Agrobacterium*. *Agrobacterium* was the 'transfer' vector used to pass the genetic information into plant cells. Medicago's expression system required the use of a suppressor of silencing as a helper protein. The gene for the helper protein was also included on the transfer vector along with the H1 gene. As two proteins were thus required for efficient expression of H1, Medicago's technology used for the production of H1–VLPs is described as a 'coexpression' technology.

Large-scale production of the *Agrobacterium* culture required two phases: a small-scale propagation phase and a larger expansion phase. In the first phase, *Agrobacterium* was propagated from a working cell bank through shake flasks until transfer into a 125-l fermentor to achieve the bacterial mass required for the infiltration process. The fermentation was accomplished in a batch mode, and substrate utilization, optical density, oxygen, pH, and agitation speed were monitored throughout the fermentation cycle. Once a fermentation batch of *Agrobacterium* was obtained, the *Agrobacterium* was diluted in a suitable diluent in a stirred stainless-steel process vessel. This solution was fed to the infiltration unit during the infiltration operation. A constant solution level was maintained in the unit during the infiltration period.

Once plants and *Agrobacterium* were confirmed to meet specifications for process use, vacuum infiltration was used to introduce the *Agrobacterium* into the interstitial space in the leaves. This operation required a contained environment due to the number of organisms used and required plants that were contained in a substrate/container system that was amenable to movement into the area and then infiltration; hence, field-grown plants are not a good choice for transient expression that is infiltration driven. Plants were placed by robotics into trays and transported via conveyors into a containment suite for infiltration. All materials and solutions, including process intermediate, used in production in these process areas were treated to kill or remove any *Agrobacterium* before release from the containment area. Vacuum infiltration was performed batch wise with a specified number of plants infiltrated per cycle. Infiltration cycle parameters were monitored and controlled to provide a robust process. Figure 6 contains a picture of the infiltration unit used during operations.

Production: Processing

Once infiltrated, plants were placed in an environmentally controlled chamber under strict conditions for temperature, light intensity, and light exposure cycle for a specified period of time to allow protein expression and VLP accumulation in the leaves of the plant. After incubation, leaves of the plants were harvested manually and placed on a conveyor. The biomass was transported via conveyor to a dicer and the leaves were cut into small squares. Diced leaves were transported via conveyor to a stainless steel, mechanically agitated digestion

vessel that contained an enzymatic solution. The enzymatic solution allowed digestion of the structural components of the diced leaves and released the VLP from the plant biomass. Reaction conditions, such as agitation, pH, time, and temperature, were controlled during the release of VLP.

Once digested, VLP were recovered and residual solids and some host cell impurities were removed by clarification operations in the process. Clarification operations consist of a number of unit operations, such as centrifugation and filtration that are designed to reduce particulates and *Agrobacterium* in the process stream. After completion of digestion, the in-process solution was passed through stainless steel strainers and then transferred into a single-use 1000-l mixing vessel that fed a disk stack centrifuge. After centrifugation, the solution was filtered through a glass fiber filter and a 0.2-μm filter. The last filtration operation assured that all *Agrobacterium* were removed from the solution.

The clarified material was concentrated using a tangential flow filtration (TFF) membrane system. After concentration, the material was diafiltered to allow removal of process impurities, such as host cell proteins and small molecules. This process step was important for purification of the VLP and also for preparing the process intermediate for further purification by chromatography. Retentate from the TFF system was loaded to an ion exchange column and process impurities, such as DNA, endotoxin, and host cell proteins, were separated from the VLP. VLP were bound to the column and eluted with a step gradient to high salt content. The eluate from the ion exchange column was loaded to a second ion exchange column as a polish step. VLP were passed through the column under the loading conditions, and residual DNA and some host cell proteins were bound to the column. The material that flowed through the second ion exchange column was diafiltered on a TFF skid in order to suspend the VLP in an excipient matrix suitable for injection. The VLP solution was filtered through a 0.22-μm filter that was part of a sterile manifold containing single-use bioprocess containers. The VLP solution, drug substance, was loaded to the sterile bags, sealed with a heat sealer, and stored at 2–8 °C until use for testing purposes.

Vaccine release specifications for the drug substance were set based on previous results from analysis of clinical material produced at pilot scale. A number of release and characterization assays were performed on the drug substance. Determination of protein concentration, HA identity, residual DNA, nicotine, anabasine, RuBisCo, pH, appearance, and sterility were some of the assays performed to assure product quality. Additional characterization assays, such as mass spectrometry, dynamic light scattering, nanotracking analysis, and cryoelectron microscopy, were performed on drug substance to assess purity and structure.

Conclusions

The project was deemed successful because the facility construction was completed in approximately 1 year and the production process was transferred and scaled up 30-fold. After a series of development and engineering runs, the process was demonstrated to be ready to support manufacturing operations. At the conclusion of a 30-day manufacturing campaign, greater than 10 000 000 doses of vaccine had been produced. The vaccine met the quality attributes that had been prespecified for the vaccine and the vaccine was shown to be immunogenic in mice.

See also: Biotechnology: Regulatory Issues. Genomics: Plant Genetic Improvement. Medicinal Crops. Regulatory Challenges to Commercializing the Products of Ag Biotech. Transgenic Methodologies – Plants

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US Food and Drug Administration.

Biotechnology: Plant Protection

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Glossary

Avirulence (Avr) factor A pathogen/pest effector recognized either directly or indirectly by the corresponding functional plant resistance (R) protein.

Effector A secreted protein or other molecule used by plant-associated organisms to modulate plant metabolism, suppress, activate, and reprogram plant defenses and thereby enable successful colonization of plant tissues.

Host-induced gene silencing (HIGS) This technique is used for silencing genes in plant-associated organisms. In HIGS, silencing is triggered directly within the plant and targets genes in plant pathogens or plant pests. Silencing induces the production of short double-stranded RNA (dsRNAs) in the host plant cells following one of the two delivery methods: (1) microprojectile particle bombardment of RNAi constructs into plant leaves or (2) stable plant transformation with RNAi constructs. It is used primarily to silence genes in obligate biotrophic species, which are not transformable via stable transformation methods.

Leucine-rich repeat (LRR) A structural motif found in many resistance (R) proteins that mediate effector-triggered immunity and also in some pattern-recognition receptors (PRRs). This type of motif contains leucines or other hydrophobic amino acids at regular intervals over a stretch of 23 or 24 amino acids. The LRR is reiterated numerous times in most plant PRR and R proteins and can occur extracellularly or intracellularly. The LRR forms a parallel β sheet structure within the protein. Within this structure, the hydrophobic leucines are in the protein interior whereas the other residues are surface exposed and form a surface capable of interacting with other proteins. Different interacting surfaces can be generated via single amino acid changes, and this permits the evolution of specific interactions. LRR motifs mediate protein–protein and receptor–ligand interactions in many organisms. The LRR motifs in plant R proteins probably participate in effector perception and PAMP perception.

Pathogen- or microbial-associated molecular patterns (PAMPs/MAMPs) Molecules associated with groups of pathogens that are recognized by host cells, via PRRs and activate the innate immune system resulting in PAMP triggered immunity (PTI). The PAMP/MAMP molecules recognized are typically small molecular motifs that are conserved within a class of microbes such as bacterial flagellin or fungal chitin.

Pathogenicity factor This is a qualitative term used to describe a gene, protein, or metabolite from a pathogenic species that is absolutely required for disease formation on at least one plant host species. In the absence of this pathogenicity factor the pathogen is unable to cause plant disease on a susceptible host plant species, but is still able to grow and develop normally on a range of *in vitro* conditions.

Programmed cell death (PCD) Death of a cell mediated by an intracellular program. PCD is carried out in a regulated process. Apoptosis and autophagy are both forms of PCD, whereas necrosis is not.

***R* gene stacking** The deliberate accumulation in an elite or semielite plant line of more than one *R* gene that effectively controls a single pathogen or pest species. *R* gene stacking is achieved though plant breeding over several generations, in a single generation via plant transformation or via a combination of the two methods.

'Stacked *R* – anti-*S* gene' T-DNA cassette The tightly linked pairing of a disease resistance gene and another type of gene that prevents /minimizes disease susceptibility. Both have been placed under the control of different promoters between the right and the left border of the transfer DNA construct used for plant transformation with *Agrobacterium tumefaciens*. Once within the transgenic plant, the desirable gene pair cannot be separated by genetic recombination.

Virulence factor This is a quantitative term used to describe the degree to which a gene, protein, or metabolite from a pathogenic species contributes to disease formation on at least one plant host species. In the absence of this virulence factor, the pathogen species is only able to cause reduced plant disease on a susceptible host plant species. Without the virulence factor, the pathogen is still able to grow and develop normally on a range of *in vitro* conditions.

Introduction

To fulfill the future demands for food, feed, and fiber of the ever-growing human population, novel crop protection strategies are required to minimize potential losses to agricultural crops from the myriads of pathogenic microbes and invertebrate pests that cause diseases and damage. These plant-infecting organisms include phytopathogenic bacteria, fungi, oomycetes (water molds), viruses, insects, and nematodes. The resulting biotic stresses cause major losses to crop yield and product quality, and when severe disease epidemics occur this can result in the complete loss of the harvest (Agrios, 2005). Globally, an estimated 20–40% reduction in agricultural production occurs each year due to pathogens and pests (Strange and Scott, 2005; Oerke, 2006). In addition, over the past few decades a steady increase in the virulence of plant-infecting organisms has been observed, making the task of pathogen and pest control even more difficult. This increase in pathogen virulence is, at least partially, caused by globalization and the increased genetic exchange between previously geographically separated pathogen and pest populations. This genetic exchange accelerates the emergence of new pathogen genotypes. In particular, increases in worldwide trade and international travel are considered to be the major routes

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underlying the macroevolutionary genesis of plant pathogens and pests (Fisher *et al.*, 2012).

To protect crops, farmers, crop advisers/consultants and crop protection companies can deploy a range of options. These include cultural practices, for example, deep plowing of infested or infected crop residues and the rotation of different crop species, the use of conventionally bred resistant germplasm, and the application of pesticides. Pesticides can be applied as seed dressing, soil drenches, soil fumigants, or directly to the growing crop within guided spraying regimes. In many situations, an integrated pest and disease management system is deployed that combines several crop protection approaches in a single growing season.

Over the past 25 years, plant biotechnology has emerged as an additional control option, which can be used either alone or in conjunction with the other crop protection options. The use of plant biotechnology has for a long time been considered the best route to enhance the performance of an already high-yielding elite plant genotype. The plant biotechnology approach is used to try to eliminate the elite cultivars susceptibility to a major pest or pathogen prevalent in a particularly important geographical region or country (Stuiver and Custers, 2001; Hammond-Kosack and Jones, 2000; Hammond-Kosack and Parker, 2003).

In this article, innovative genetic engineering approaches devised to improve crop protection by providing a novel form of resistance that may also be more durable will be described alongside the original underpinning basic science discoveries. In a few instances genetically engineered plant solutions are now fully adopted by farmers and are in commercial use. These successfully adopted examples have already been described in detail in two earlier articles of this Encyclopedia. Enhanced insect resistance in many crop plant species based on the overexpression of different *Bacillus thuringiensis* (*Bt*) endotoxins (BT toxins) is the second most widely used trait (after herbicide resistance) present in commercial genetically modified crops. The global adoption of BT crops has been recently reviewed by Tabashnik *et al.* (2013) and Chen *et al.* (2011).

The focus of this article is the novel plant biotechnology solutions already available which could, in the future, be used to enhance the repertoire of crop protection strategies available against one or more pathogen or pest species. The most promising solutions have been successfully tested in replicated field trials done in one or more geographical locations. However, for the majority of the novel plant biotechnology solutions described in this article the only data available have so far been generated exclusively in glasshouses or in other controlled environments. The most recent comprehensive reviews on this topic are provided by Dangl *et al.* (2013), Atkinson *et al.* (2012), Collinge *et al.* (2010), Dodds and Rathjen (2010) and Gust *et al.* (2010).

Breakthrough Scientific Discoveries and New Scientific Resources Available for Exploitation

Fundamental research done over the past 25 years has led to an increasingly clear conceptual understanding of the two-tiered plant defense system. Within this new knowledge framework exciting opportunities have emerged to improve crop disease resistance via plant biotechnology. At the same time, the underlying pathogen and pest processes recognized as absolutely required for different types of infection, colonization, and disease development have emerged. These fundamental new insights have also been targeted to provide novel plant-specified inhibitory mechanisms via plant biotechnology.

Plant Detection of Nonself

For a plant to respond to attack by a potential pathogen or pest, each plant cell must recognize the threat of nonself. This is now known to be based on the recognition of conserved pathogen- or microbial-associated molecular patterns (termed PAMPs or MAMPs) or damage-associated molecular patterns (DAMPs), such as plant cell wall fragments released via wounding or pathogen attack, by PAMP recognition receptors (PRRs) (reviewed by Zipfel and Robatzek, 2010). The best known true PAMP is the major constituent of the fungal cell wall, chitin. Chitin is released from the fungal cell wall by the action of plant chitinases. Chitin-binding PRR lysine motif (LysM) receptors have been described in *Arabidopsis*, rice, and wheat (reviewed by Lee *et al.*, 2014). Chitin-binding PRR proteins present at the plant cell surface in the plasma membrane recognize the presence of a fungal invader and thereby rapidly activate several plant defenses that result in PAMP-triggered immunity (PTI) (**Figure 1**). Other PAMPs detected by plants include bacterial flagellin and bacterial elongation factor EF-Tu. Defense responses activated following PAMP recognition include the production of reactive oxygen species (ROS), such as superoxide anions ($\bullet O_2^-$) and hydrogen peroxide (H_2O_2), which damage pathogen membranes and act as additional plant signaling molecules. The rapid thickening of plant cell walls at the penetration sites via callose deposition also occurs. Upstream of these defense responses, there is a rapid and coordinated induction of specific ion fluxes as well as the activation of plant protein kinases, regulatory proteins such as the redox sensitive signaling protein NPR (see Section Systemic Plant Defense Responses) and transcription factors. These responses increase the signaling complexity and further enhance the local plant defense response. Often a range of toxic metabolites accumulate at the infection site, thereby further inhibiting pathogen growth or pest feeding. This highly localized response immediately restricts nutrient acquisition by the pathogen or pest and this minimizes their further progress.

PTI places selective pressures on all potential pathogenic species to produce proteins or other compounds known as effector molecules, which interfere with and suppress these defense mechanisms or their activation. This is known as effector-triggered susceptibility (ETS) (**Figure 1**). Successful plant pathogens, nematodes, and insects secrete a plethora of effectors to circumvent or suppress plant defenses (de Wit *et al.*, 2009; Dodds and Rathjen, 2010). The induction of ETS is a common prerequisite to a successful host–pathogen or host–pest interaction that requires the presence of living plant cells through all or just the early phase of the infection (see Section Different Pathogen and Pest Lifestyles). Pathogen and pest effectors can be divided into those that function extracellularly, termed apoplastic effectors, and those that function

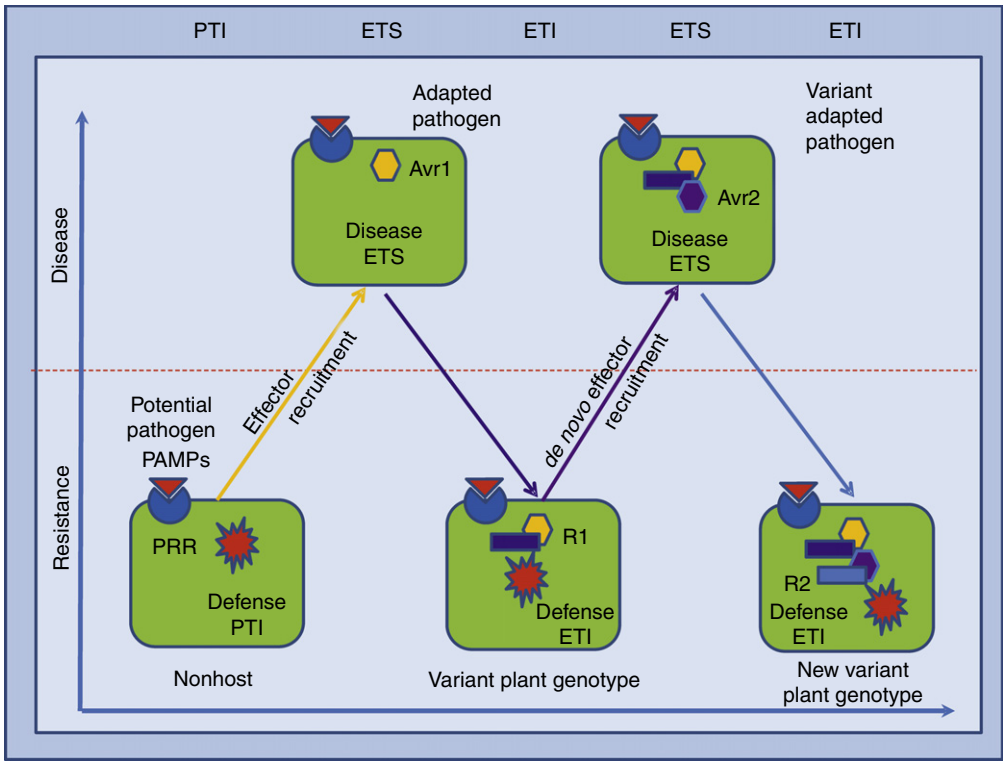


Figure 1 The zig-zag-zig model. The evolutionary arms race between pathogen and host is represented by the sequential activation of layers of plant defense and by the acquisition of novel effectors, resulting in either disease resistance or disease susceptibility (disease). Phase 1: PAMP recognition and PAMP-triggered immunity (PTI). Phase 2: The adapted pathogen evolves or acquires an effector (Avr1) that circumvents PAMP recognition, resulting in effector-triggered susceptibility (ETS). Phase 3: A variant plant with the ability to express the resistance protein (R1) that is capable of directly or indirectly detecting the presence of Avr1, resulting in effector-triggered immunity (ETI). Phase 4: A variant adapted pathogen evolves or acquires an additional effector, Avr2, resulting in ETS. Phase 5: A new variant plant with the resistance protein (R2) capable of directly or indirectly detecting Avr2, resulting in ETI.

from within the host cell, termed cytoplasmic effectors. To increase protein stability, secreted apoplastically accumulating effectors tend to be cysteine rich whereas those translocated and subsequently functioning in the plant cytoplasm are rarely cysteine rich.

Successful plant colonization is achieved through the production and delivery of specialist pathogen- and pest-effector molecules. This places selective pressure on the plant population to recognize these effectors and the consequence is the activation of defense responses. These variant plants found in natural populations, germplasm collections, or created during plant breeding have alleles of resistance (*R*) genes that recognize either a subset of the effector molecules (direct recognition) or the effects of these effectors on other 'guarded' host proteins (indirect recognition). This form of defense is known as *R* gene-mediated defense, or effector-triggered immunity (ETI) (**Figure 1**). The receptors that lead to the direct or indirect recognition of pathogen effectors and then trigger ETI can either be intracellular, as is the case for nucleotide binding site–leucine-rich repeat (NBS-LRR) receptors, or extracellular such as LysM and LRR receptors that possess short transmembrane domains with or without a cytoplasmically located kinase domain (reviewed by Jones and Dangl, 2006). The local defense responses triggered during ETI include rapid synthesis and release of various ROS, activation of specific ion fluxes, protein kinase cascades and transcription factors, papillae formation, single host cell death termed the hypersensitive response (HR), accumulation of defense-related/pathogenicity-related (PR) proteins, and various antimicrobial proteins. The local defense reactions triggered by ETI are usually, but not always, stronger than those triggered by PTI (Jones and Dangl, 2006). For historical reasons, many effector-encoding genes were first called Avirulence (Avr) genes because their presence in the pathogen is recognized by a corresponding plant *R* gene.

Resistance protein-mediated activation of ETI places a selective pressure on the pathogen to evolve and recruit new effectors to provide the same function as the now defeated effectors (**Figure 1**). Once a suitable effector is successfully selected or evolved, the adapted pathogen is able to cause disease once again on the host plant species via ETS. This ETI-ETS-ETI cycle can be reiterated numerous times and the eventual outcome is now known to be influenced by the activities of plant breeders, local and global climatic conditions, as well as by the presence of other pathogenic species.

In summary, in the interaction between a successful pathogen and its plant host, on the pathogen side there is a constant acquisition or loss of effectors, whereas on the host side there is a constant recruitment or loss of proteins that detect these effectors. This is described by the 'zig-zag-zig' model (Jones and Dangl, 2006, **Figure 1**). Others have since

invoked an evolutionary framework to the original 'zig-zag-zig' model, and describe this series of molecular changes to both the pathogen and the host as an evolutionary arms race (Chisholm *et al.*, 2006; Dangl *et al.*, 2013). The molecular interactions that mediate ETI are predominantly represented by small proteinaceous effectors and exclude the broader-acting secreted secondary metabolites, toxins, and plant substrate-degrading enzymes. Although examples that conform to the 'zig-zag-zig' model are now well documented for many plant-infecting fungi, bacteria, viruses, and nematodes, currently this fundamental information is far more fragmentary for insect pests (Hogenhout *et al.*, 2009).

For plant-pathogenic fungi and bacterial species that deploy host-selective toxins for successful infection and tissue colonization, a different interaction model is proposed. This is most frequently referred to as the 'inverse gene-for-gene' model (Oliver and Solomon, 2010). Pathogen virulence must be dominant because of the need to produce a functional toxin or enzyme to cause disease; whereas, plant resistance is predominantly inherited as a recessive trait and resistance is achieved via the loss or alteration of the toxin target.

Systemic Plant Defense Responses

In some plant–pathogen interactions, the formation of localized necrosis at the point of initial infection during ETI leads to the activation of a subset of defense responses in distal plant tissues. The type of systemic response induced is determined by the identity of the initial attacking organism. Systemic responses induced to fungi, bacteria, and viruses are distinct from those of insects. Nematodes induce a blend of the two response types. For all plant species, the adaptive advantage of orchestrating systemic responses is enormous because this ensures that the distant plant tissues can deal more effectively with subsequent attacks. Fungi, bacteria, and viruses activate a phenomenon known as systemic acquired resistance (SAR) (reviewed by Spoel and Dong, 2012). SAR requires at least four plant-derived signaling molecules and four plant-derived signaling proteins that operate either locally or distally or are transported through the vasculature. Studies done on tobacco and *Arabidopsis* have identified the key molecules to be (1) salicylic acid (SA), (2) methylsalicylic acid and the vasculature mobile signals, (3) azelaic acid, and (4) glycerol-3-phosphate. The key proteins required locally to initiate SAR are the (1) low-affinity SA receptor protein NPR3 and (2) the redox-sensitive signaling protein NPR1, which shuttles between the cytoplasm and the nucleus. The NPR1 protein binds to TGA (TGACG motif-binding) transcription factors, thereby enhancing their binding to SA-responsive plant promoters. Post the arrival of the signaling molecules in the distal tissues, (3) the high-affinity SA receptor NPR4 functions in conjunction with the NPR1 protein, and (4) the apoplastic lipid-transfer protein DIR1 to promote defense-gene induction without causing host cell death. SAR leads rapidly to the transcriptional activation of a wide repertoire of defense responses and considerable pathogen resistance. Another type of systemic plant response is called induced systemic resistance (ISR) or 'priming', which can be activated by either non-pathogenic root-colonizing bacteria or the application of synthetic chemistry, including β-aminobutyric acid (BABA) (reviewed by Conrath *et al.*, 2006).

Herbivorous insects mechanically wound the plant tissue while feeding and induce the rapid accumulation of proteinase inhibitors (PIs) and defense proteins throughout the plant. This systemic response is often referred to as the wound response. An 18-amino acid polypeptide called systemin is the mobile systemic signal. In tomato, once systemin reaches the target tissue, a lipid-based signaling cascade is activated, which is reliant on jasmonic acid (JA) production and ethylene biosynthesis. This in turn induces the expression of PI and other defense genes (Reymond *et al.*, 2000; Schilmiller and Howe, 2005).

Of the three systemic responses described, SAR is the phenomenon that has most frequently been exploited by plant biotechnology (see section Use of Defense-Signaling Components).

Different Pathogen and Pest Lifestyles

Among the pathogenic species that cause disease on plants, huge variation exists in their modes of infection and the methods subsequently deployed to sustain the acquisition of sufficient nutrients from extracellular and intracellular sources that are needed to complete each pathogen's *in planta* lifecycle. Plant-pathogenic fungal, oomycete, and bacterial species are generally subdivided according to their *in planta* nutritional strategy. Biotrophs acquire sustenance for extended periods only from live plant cells, whereas necrotrophs rapidly kill the host plant cells and live on the released nutrients. However, not all plant pathogens clearly fit into these two distinct categories. Many plant pathogenic species are now recognized to have an initial transient phase reminiscent of a biotroph, followed by a later necrotrophic phase. These pathogens are classified as either hemibiotrophs or latent necrotrophs and the duration of the biotrophic phase can be very short (1–2 days) or extend over several weeks (Agrios, 2005; Oliver and Solomon, 2010). Some fungal and oomycete species, in addition to using filamentous hyphae to colonize plant tissue, also form specialist feeding structures inside plant cells called haustoria to facilitate the acquisition of nutrients. When devising novel crop protection strategies through plant biotechnology, the lifestyle of the pathogenic species and its intracellular versus extracellular location in the plant tissue needs to be considered carefully. Likewise, the potential to cause undesirable outcomes needs to be evaluated. For example, would a strategy devised to control a biotrophic species lead to enhanced susceptibility of the transgenic crop to necrotrophic species?

A multitude of insect species feed, reproduce and shelter on plants. Two main insect categories are recognized: those that chew and those that suck sap. Chewing insects cause the greater plant tissue damage. For example, species of locusts and Colorado potato beetle as well as the larvae of many insect species can defoliate an entire crop within a couple of days. Other chewing insects feed only on roots or seeds. Crop protection by the ingestion of BT toxin takes advantage of the chewing habit of these insect species (Vaeck *et al.*, 1987). The sap-sucking insects, such as adult aphids, trips, or leafhoppers,

cause minimal direct tissue destruction. Instead, feeding occurs via a specialized mouth part, the stylet. The phloem sieve elements in the plant's vascular tissue are located, penetrated, and the sap removed. When present in high numbers, sap-sucking insects cause chronic shortages of photosynthates and lead to a severe reduction in plant growth. Many of these insect species also transmit plant viruses.

When insects feed, specific plant volatiles are released from the feeding sites and these can act as both attractants and deterrents to further colonization by the same or other insect species. Considerable insight into the complexity of insect–plant volatile communication events is beginning to be gained by analyzing the changes to air composition during insect-feeding events and exploring insect-neural stimulations in response to specific plant volatiles. The largest group of plant volatiles discovered to date is the terpenes, a diverse class of secondary metabolites, which includes monoterpenes (C_{10}) and sesquiterpenes (C_{15}). One of the best characterized plant-produced sesquiterpene volatiles is (*E*)-*β*-farnesene (EBF). For many aphid species, EBF is the principal constituent of the aphid alarm pheromone (Beale *et al.*, 2006). The constitutive production of EBF by plants could hold promise in the control of specific aphid pests (see Section Enhancing Resistance Against Insect Pests).

Soil-dwelling plant parasitic nematodes – tiny roundworms approximately 1 mm long – feed on plant roots and more than 20 genera of nematodes are known to cause plant disease. Nematode infections are nearly always confined to the plant root system. However, the plant's entire metabolism can be drastically altered, the roots become swollen and distorted and, as a consequence, the crop's yield and quality can be dramatically reduced. Sedentary endoparasitic nematodes, which are obligate biotrophs, are by far the most crop-damaging ones globally. These include root-knot nematodes (genus *Meloidogyne*) and cyst nematodes (genera *Heterodera* and *Globodera*) species. These species possess a hollow feeding stylet that penetrates plant cell walls and eventually permits a feeding sedentary female nematode to spend 30–40 days gaining sustenance from highly modified xylem parenchyma cells. Ectoparasitic nematodes feed exclusively at the root surface (Agrios, 2005).

In recent years, a number of key scientific breakthroughs made in plant-nematode research are potentially exploitable through plant biotechnology (reviewed by Atkinson *et al.*, 2012). These include the identification of plant-specific chemical signals released by healthy roots that induce the hatching of the juvenile nematode from the dormant egg. For the potato and soybean cyst nematodes the hatching factors identified are solanoeclepin A and glycinoeclepin A, respectively. The nematodes then invade the roots in the zone of elongation, migrate inwards to the vasculature, and then activate at a selected site in the xylem parenchyma the expression of specific plant genes. Once feeding commences, the nematode become sedentary (nonmotile). The feeding of each sedentary female nematode over the next 30–40 days induces the formation of either highly modified giant cells or syncytial structures. The plant promoters recovered from these induced genes are particularly valuable for targeting the expression of different types of anti-nematode proteins directly to the feeding sites (see Section Engineering Nematode Resistance). Furthermore, some of the candidate effectors secreted by nematodes through the stylet, which are hypothesized either to facilitate feeding or to suppress plant defenses, have been identified through proteomics analysis of nematode gland secretions (Bellafiore *et al.*, 2008).

The Availability of Fully Sequenced Plant, Pathogen, and Pest Genomes

The sequencing of entire plant genomes and the systematic profiling of changes to the plant transcriptome in the presence or absence of specific pests and pathogens is already underway across the 'tree of plant life.' This sudden influx of new comparative data on an unparalleled scale, initially significantly enhanced our understanding of the plant-immune system in the diploid model plant *Arabidopsis thaliana* and the diploid crop species, rice. Since the mid-2000s, there has been an ongoing reduction in sequencing costs, improvements in sequencing technology, and a refinement of the bioinformatics tools available to assemble genomes and transcriptomes, to predict the gene repertoire of each species and assign other key genomic features, for example, transposons, repeat-rich regions, gene clusters, and the sequences potentially coding for regulatory microRNAs and gene promoters. As a consequence of these large community endeavors, extensive genome and transcriptome information has rapidly become available for most agriculturally important crop plant species, which have much larger and often polyploid genomes. Major new resources are now available in the public domain for all the major cereal species, i.e., maize, barley, wheat, sorghum, foxtail millet, and many key vegetable, fruit, and commodity crop species, including coffee, tomato, potato, cassava, and banana. With this abundance of new information on plant genomes, the potential *R* gene repertoire for many plant species has now been defined and is available for immediate exploitation (see Section Relevant Websites).

Sequencing the entire genomes of important pathogens and pests has been ongoing since the mid-1990s. By defining the complete repertoire of predicted genes for a given plant-pathogenic or pest species, and by comparing the content and layout of each genome, this is beginning to provide researchers with a wealth of new information to better understand pathogen and pest biology. In this context, intercomparing the genomes and gene content of free-living and plant-associated species is very informative. This genomic information also provides clues to the range of intercellular and extracellular molecules (proteins and metabolites) produced by pathogens and pests that may be detected by plant cells. The genomic era for plant-infecting pathogens began with the sequencing of plant viruses and viroids, then plant-pathogenic bacteria, and recently has embraced a full range of plant-pathogenic fungi, oomycetes, plant parasitic nematodes, and insect pests.

By comparing the whole genomes of many different strains or isolates of the same pathogenic species, the candidate effector gene sets that may be responsible for key biological differences can be pinpointed and then experimentally assessed for function. In many studies, the transcribed portion (transcriptome) of the pathogen or pest genome specifically expressed *in planta* has also been characterized in detail, in an

attempt to identify the putative effector sequences and induced metabolic pathways. Today, fully sequenced genomes for hundreds of agriculturally important pathogenic species are now available (Raeffaele and Kamoun, 2012; The International Aphid Genomics Consortium, 2010). Major breakthroughs include sequencing the complex genomes of the oomycete *Phytophthora infestans*, which causes late blight of potatoes and tomatoes, the barley powdery mildew *Blumeria graminis* f. sp. *hordei* and the pea aphid *Acyrthosiphon pisum* (see Section Relevant Websites). Within the next 5 years, the number of species with full genome sequence information is predicted to rise to several thousands. This wealth of new information on pathogens and pests is already being harnessed by plant biotechnologists and plant breeders through effector guide *R* gene selection (see Section Defining the Pathogen-Effector Repertoire to Guide *R* Gene Choice).

Harnessing New Knowledge on Pattern-Recognition Receptor Proteins and R Proteins

To recap briefly, pattern-recognition receptors (PRRs) detect microbes by recognizing PAMPs. Different plant families carry distinct repertoires of PRRs that perceive distinct PAMPs, whereas most resistance proteins directly or indirectly recognize pathogen and pest effectors and this results in the local activation of plant defenses.

Utilizing Cloned Pattern-Recognition Receptor Genes

One biotechnology approach that has been successfully applied to control a range of pathogenic species is to transfer PRRs between plant species. The *Arabidopsis* PRR protein called elongation factor Tu (EF-Tu) receptor (EFR) perceives the acetylated *N*-terminus of the bacterial EF-Tu through binding to the LRR ectodomain. In the solanaceae, the bacterial EF-Tu is not perceived. Transfering the EFR from *Arabidopsis* into tobacco (*Nicotiana benthamiana)* and tomato (*Solanum lycopersicum*) has conferred responsiveness of these recipient plants to bacterial elongation factor Tu and elevated resistance to several phytopathogenic bacteria species representing different genera. The species controlled included *Agrobacterium tumefaciens*, *Pseudomonas syringae*, *Ralstonia solanacearum*, and *Xanthomonas perforans* (Lacombe *et al.*, 2010). These results suggest that extending the PAMP recognition repertoire of crop plants can lead to broad pathogen resistance. The identification of additional functional PRRs and their transfer to a recipient plant species that lacks the orthologous receptor protein could provide a general way of broadening resistance in agriculturally important plant species. In theory, this may even reduce the range of pathogenic species able to cause disease on the recipient plant species and thereby reduce the overall crop protection requirements needed for the crop. With climate change predicted to change gradually the range of important pathogenic species present in a particular geographical region or country, the transfer of species- or family-specific PRRs could potentially become an important route to tackle newly emerging pathogen problems.

The PRRs FLS2 and EFR that recognize bacterial flagellin and EF-Tu, respectively, both require the LRR receptor kinase BAK1 to mediate protein heterodimerization resulting in PTI (Chinchilla *et al.*, 2007, 2009). In rice, overexpression of the interacting protein OsBAK1 was shown to significantly enhance resistance to the rice blast fungus *Magnaporthe oryzae* (Hu *et al.*, 2005; Li *et al.*, 2009). The transgenic OsBAK1 rice plants also had improved grain yield and plant architecture. This indicates that enhancing disease resistance does not necessarily limit the plant's intrinsic potential to grow, develop, and produce an abundant harvest.

Utilizing Cloned Plant Disease Resistance (*R*) Genes

Traditionally plant breeders have introgressed, via time-consuming and lengthy breeding programs, new *R* genes from wild relatives of crop species into elite commercial cultivars to control diseases (**Figure 2(a)**). Within the elite breeding programs, the desired *R* gene introduced via introgression must also be recombined away from any genetically linked bad alleles of other genes coming from the wild relative that may reduce crop performance ('linkage drag'). Often plant breeders try to deploy multiple *R* genes simultaneously in a single elite line, in a breeding strategy known as *R* gene stacking. Through this approach the new cultivar or advanced breeding line possesses multiple *R* genes, each controlling one or at best a few pathogens. However, these *R* genes are located in different regions of the genome and particularly important *R* gene combinations could be lost in subsequent plant generations via genetic recombination. Therefore, marker-assisted selection (MAS) using primer combinations within each *R* gene is needed to ensure that in each breeding generation the required *R* gene stack is maintained (reviewed by Pavan *et al.*, 2010).

The availability of cloned *R* genes now opens the possibility of their direct transfer into elite plant breeding lines by genetic transformation. Plant transformation enables the transfer of several different *R* genes effective against a single pathogen species in a 'cassette' of linked genes that cannot be separated by recombination (**Figure 2(b)**). This multi-*R* gene cassette in theory should slow down pathogen evolution to overcome resistance, because the various *R* genes could only be overcome if, in a single pathogen isolate, several effector genes were simultaneously mutated. However, a major disadvantage of the stacking of single *R* genes is that once the pathogen mutates one of the recognized cognate effectors, plant resistance is no longer triggered by that *R* gene and the overall defense response activated may be weakened. The assembled multiple *R* gene stack would immediately become more vulnerable to further changes in the effector repertoire of the pathogen population.

The introduction of *R* genes by plant transformation also means that the interplant species fertility barriers can be crossed, thereby increasing the repertoire of plant species from which useful novel resistance sources can be obtained, for example, from a distally related wild species. Most *R* gene sequences when transferred from the original plant species to a closely related species confer resistance. However, some *R* genes also function in entirely different plant families. For example, barley Mla can function and confer powdery mildew

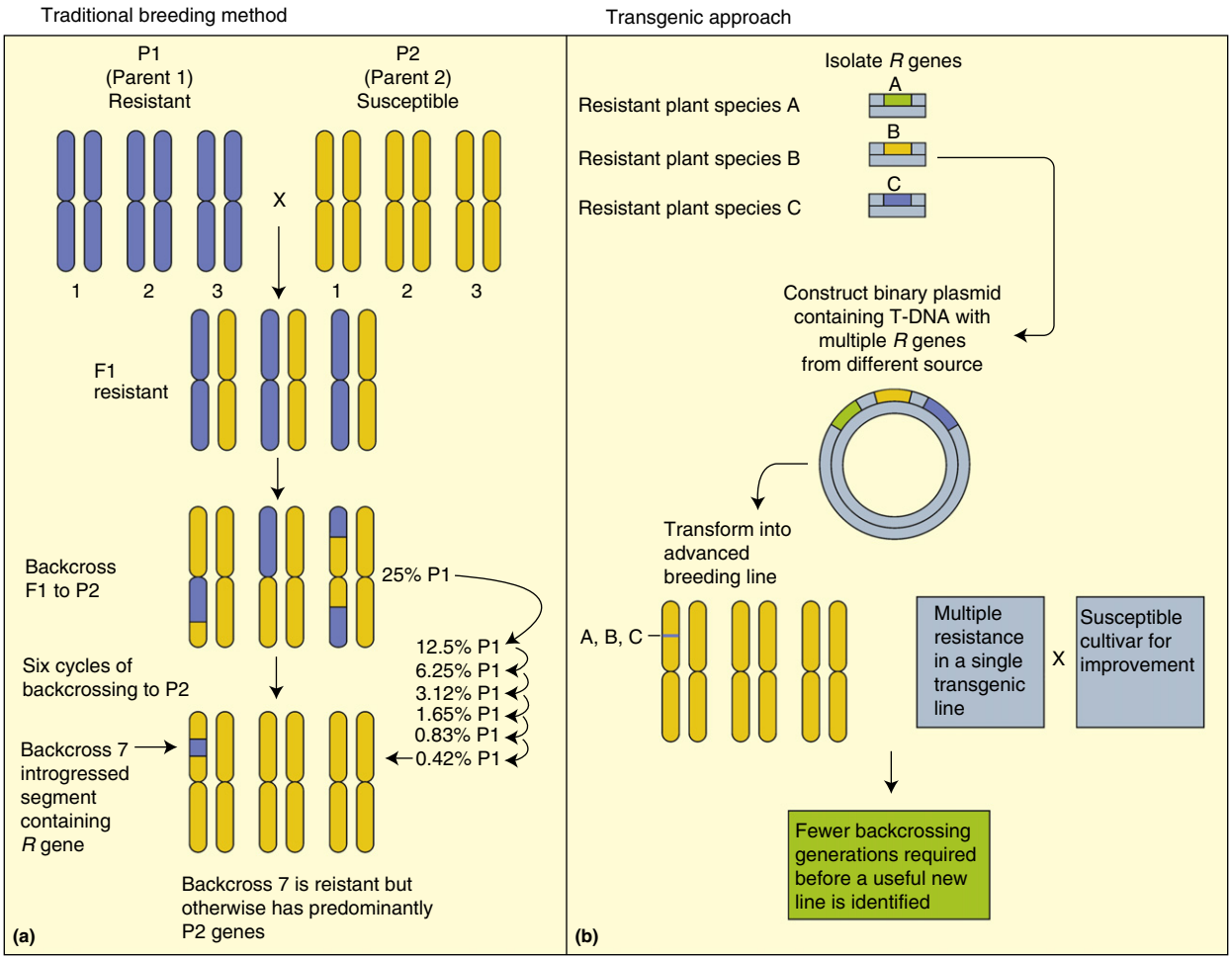


Figure 2 The traditional breeding approach is compared with plant transformation technology to introgress desirable genes into commercial crop plants. (a) In a traditional breeding program, as much as 0.4% of the genome complement from each donor parent can reside in the seventh backcross generation along with the *R* gene of interest (originally from parent 1). (b) By the transgene transformation approach, multiple *R* genes from several initial sources are first assembled into a single Ti plasmid. After T-DNA integration into the plant genome, these *R* genes cosegregate in all subsequent breeding steps, greatly simplifying the subsequent backcrossing program for introducing multiple new traits into a cultivar. When the transgenic transformation approach is used, the entire sequence of the introduced DNA is known, whereas in the traditional breeding program, neither the total extent of the DNA introgressed nor its sequence identity is known. Reproduced from Hammond-Kosack, K.E., Jones, J.D.G., 2000. Responses to plant pathogens. In: Buchanan, B.B., Gruissem, W., Jones, R.L. (Eds.), Biochemistry and Molecular Biology of Plants. Rockville, MD: American Society of Plant Physiology, pp. 1102–1156, with permission from American Society of Plant Biologists.

resistance in *Arabidopsis*, and *Arabidopsis* RPS4 and RRS1 can function in solanaceae (Narusaka *et al.*, 2013). The later success is particularly interesting because the transfer of *R* gene-based defense to a distantly related species required the identification of the correct pair of *R* genes and then their simultaneous transfer. *R* genes that confer resistance to all or almost all isolates/races of a particular pathogen species are particularly attractive candidates for interspecies transfer because it is plausible that they will confer the same broad-spectrum resistance as occurs in their 'native' genomes.

One of the most impressive examples of the use of *R* genes from another species, introduced through plant biotechnology to control a devastating plant pathogen, involves the potato crop and the oomycete pathogen *P. infestans*, which causes late blight disease. *Phytophthora infestans* caused the complete loss of the Irish potato crop between 1845 and 1852 and was responsible for the Irish potato famine that led to the death of ~1 million people and the emigration of ~1.5 million people from Ireland. Currently, most cultivated tetraploid potato varieties are either fully or partially susceptible to *P. infestans* and, as a consequence, a very comprehensive chemical spraying program throughout the growing season is required to control this pathogen, often in excess of 10 foliar sprays per season. In contrast, most accessions of the wild diploid potato species, *Solanum bulbocastanum*, are highly resistant to all known races of *P. infestans*. Using a map-based cloning experimental strategy from a cluster of four highly related *R* genes of the NBS-LRR sequence type, the resistance gene *RB*/*Rpi-blb1* was isolated. Transgenic cultivated potato plants (*Solanum tuberosum*) expressing the *RB* gene show a high level of resistance to nearly all *P. infestans* isolates, including a recent European 'super race' that can overcome all 11 known *R* genes in cultivated tetraploid potato (Song *et al.*, 2003).

Two other *R* genes conferring broad-spectrum resistance to *P. infestans* have been isolated, again from wild potato species, namely *Rpi-blb2* from *S. bulbocastanum* and *Rpi-vnt1.1* from *Solanum venturii* (Dixelius *et al.*, 2012). Transgenic cultivated potato lines expressing both the *Rpi-blb1* and *Rpi-blb2* genes have been evaluated over several years in field trials in the United Kingdom and mainland Europe. Enhanced control of late blight disease has now been achieved via this route (Jones *et al.*, 2014). The use of plant biotechnology to improve plant disease resistance is especially important in plant species like the potato, where conventional plant breeding is inherently difficult and where no useful resistance exists within the germplasm pool available for agriculturally important species.

Many race-specific R proteins are temperature sensitive. For example, at temperatures above 30 °C, *N* gene-mediated resistance to tobacco mosaic virus (TMV) fails and virus particles spread systemically throughout the plant. With climate changes now being experienced in many global regions, inconsistent pathogen control may arise by using temperature-sensitive *R* genes. A lack of correct R protein folding and/or incorrect cellular localization is the most plausible reason for this phenomenon. Plant biotechnologists need to determine carefully the effective temperature range of each *R* gene before their deployment to avoid this undesirable outcome.

Defining the Pathogen-Effector Repertoire to Guide *R* Gene Choice

Whether by breeding or by plant transformation, isolating new *R* genes from wild relatives by map-based cloning is laborious. Before commencing such an approach, it is desirable to prioritize those *R* genes that are most likely to be durable. An analysis of pathogen-effector complements can help. If a *R* gene recognizes an effector that is conserved in all known races of a pathogen, called a 'core effector,' it is more likely to be durable than if the *R* gene recognizes an effector that is absent from many races of the pathogen. In addition, some effectors have been shown to be essential for the full disease-causing ability of the pathogen. By targeting these essential pathogen effectors, resistance is again more likely to be more durable. Emerging knowledge of differences in the effector complement between pathogen races can be extremely helpful when choosing which *R* genes to prioritize for use in plant biotechnology. Within the past 15 years the number of pathogen and pest species for which full genomic sequence information is now available and readily accessible has steadily risen (see Section The Availability of Fully Sequenced Plant, Pathogen and Pest Genomes).

In the potato/*P. infestans* interaction, effector-guided *R* gene deployment is already in use (reviewed by Oliva *et al.*, 2011). This new approach, which in the future can be applied to control many other plant pathogens and pests, is described in detail in **Figure 3**.

In a geographical region where severe disease epidemics have emerged and become commonplace, rapid and inexpensive DNA-sequencing technologies can provide, in just a few days, genome-scale information on natural field isolates of the pathogenic species causing the problem. By this route, it is possible to explore each genome and compare these with the reference genome for the species held 'on line' in various public databases (see Section Relevant Websites). Any effector changes occurring both within and beyond the core effector complement can be rapidly recognized. Effector-guided *R* gene deployment is now being deployed to identify durable resistance genes against the new Ug99-derived races of the wheat stem rust fungus *Puccinia graminis* f. sp. *tritici*, which threatens wheat harvests in Africa and Asia. Recently, the *Sr35* gene that confers near immunity to Ug99 and related races has been isolated from *Triticum monococcum*. The cloning of *Sr35*, which encodes an NBS-LRR protein, opens the door to the use of biotechnological approaches to control this devastating disease (Saintenac *et al.*, 2013).

Cassava (*Manihot esculenta*) is one of the staple crops of East Africa. The causal agent of cassava bacterial blight, *Xanthomonas axonopodis* pv. *manihotis* (*Xam*), can devastate this crop. Full genome sequencing of ~65 *Xam* strains collected over a 70-year timeframe, from 12 countries and three continents has revealed a core effector set, which can now be used to define the repertoire of *R* genes activated by each effector in wild *Manihot* species and potentially other related plants in the family Euphorbiaceae (Dangl *et al.*, 2013). Once several cognate *R*-gene sequences have been identified a transgenic route will be used to rapidly introduce into cassava the most appropriate *R* gene combinations, i.e., an *R* gene stacking approach, in an attempt to achieve durable control as shown in **Figure 2(b)**.

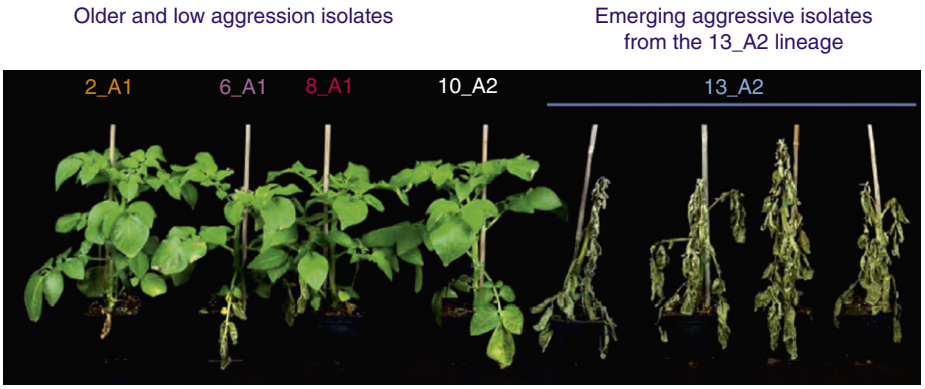
Isolation and Deployment of Broad-Spectrum *R* Genes

For many decades, some plant *R* genes already present in crop species have conferred resistance to many or all races/strains of a single pathogenic species. For example, members of the recessively inherited *mlo* resistance gene family, already functionally characterized in barley, *Arabidopsis*, and tomato, confer resistance to all races of the adapted powdery mildew species (Consonni *et al.*, 2006; Bai *et al.*, 2008). Other *R* genes that confer broad-spectrum resistance include the barley *Rpg1* gene against stem rust infections (Brueggeman *et al.*, 2002; Horvath *et al.*, 2003; Mirlohi *et al.*, 2008), and the *Arabidopsis RRS1-R* against several strains of the bacterial wilt pathogen, *R. solanacearum* (Deslandes and Rivas, 2012). Searching for and isolating other *R* genes from crop species and their wild relatives that provide broad effector recognition capabilities for a particularly problematic pathogen species is a very valuable research activity.

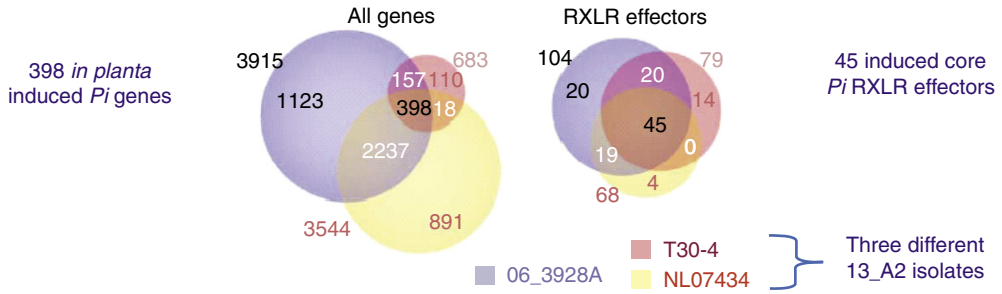
Another set of *R* genes confer resistance to multiple unrelated pathogenic species. For example, the tomato *Mi-1.2* gene, which encodes a NBS-LRR type of R protein, confers resistance to the root-knot nematode *Meloidogyne incognita*, the potato aphid *Macrosiphum euphorbiae*, and the whitefly *Bemisia tabaci* (Nombela *et al.*, 2003). Some other *R* genes confer resistance to different but taxonomically more closely related pathogenic species. For example, the *Lr34* gene in hexaploid wheat, which encodes an ATP-transporter protein, confers resistance to leaf rust (*Puccinia recondita*) and stripe rust (*Puccinia striiformis* f. sp. *tritici*) (Krattinger *et al.*, 2009). The two *Arabidopsis RPW8* genes mediate broad-spectrum powdery mildew resistance (Wang *et al.*, 2009). The deployment of

Effector guided *R* gene deployment

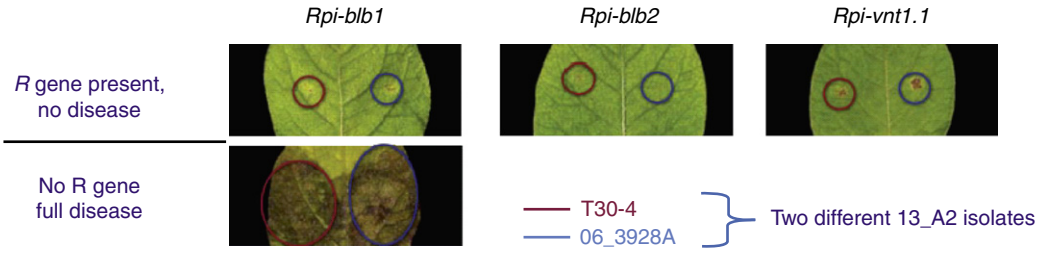
(a) Explore the disease causing ability of historic and current *Phytophthora infestans (Pi)* isolates.



(b) Whole genome sequencing and *in planta* transcriptomics used to identify the 45 'core' RXLR *Pi* effectors present in 3 isolates from lineage 13_A2 that are also expressed early during leaf infection.



(c) The conserved core effectors *Avrblb1*, *Avrblb2*, and *Avrvnt1* are present in all 13_A2 isolates. These are recognized when the corresponding *R* gene is expressed.



(d) Stack *R* genes that recognize different conserved *Pi* effectors to confer durable resistance by plant biotechnology or marker assisted selection.

Figure 3 Effector-guided *R* gene deployment based on the identification of 'core effectors' that lack sequence polymorphism. The core effector-guided *R* gene strategy is currently being used in potato (*S. tuberosum*) to mitigate the impact of the 13_A2 lineage of the late blight pathogen, *Phytophthora infestans.* This pathogen undergoes major population shifts in agricultural systems via the successive emergence and migration of asexual lineages. (a) The aggressive lineage, termed 13_A2, in the European *P. infestans* population, is rapidly displacing the other older lineages. (b) The method used to identify the core effector repertoire in the new aggressive lineage of *P. infestans.* (c) The 13_A2 isolates carry intact and *in planta* induced *Avrblb1, Avrblb2,* and *Avrvnt1* effector genes that trigger resistance in potato lines carrying the corresponding disease resistance genes *Rpi-blb1*, *Rpi-blb2,* and *Rpi-vnt1.1.* This core effector-guided approach can also be used to exclude from the elite potato germplasm improvement scheme any *R* genes already defeated because the cognate core effectors contain sequence polymorphisms that evade plant recognition. (d) *R* gene stacking is achieved by the two methods described in **Figures 2(b)** and **4**. Reproduced from Figures 4A, 7A, and 8B in Cooke, D.E.L., Cano, L.M., Raffaele, S., *et al.*, 2012. Genome analyses of an aggressive and invasive lineage of the Irish potato famine pathogen. PLoS Pathogens 8 (10), e1002940.

broad-spectrum *R* genes is particularly worthwhile in geographical regions where many destructive pathogen and pest species (i.e., disease–pest complexes) are prevalent.

Further isolation and characterization of *R* genes of this type will ensure that the largest tool kit is available for plant biotechnologists to exploit and engineer broader spectrum disease resistance in crops in the future. In particular, analysis of the ever increasing abundance of genome sequence information and transcriptome sequence information available for crop species should reveal the *R*-gene sequences most similar to those genes known to confer broad-spectrum resistance. These can then be preferentially tested for function via plant transformation.

Widening Resistance Protein Recognition Specificity

Within the zig-zag-zig model (Figure 1), two main types of R proteins are recognized: Those that directly bind the cognate Avr effector and those that indirectly confer resistance by guarding another protein, which can itself bind several different effector proteins (Jones and Dangl, 2006; Dodds and Rathjen, 2010; Dangl *et al.*, 2013). This complexity permits a range of plant biotechnology options to be used to widen the specificity of recognition.

Exploiting the Effector-Recognition Domain

Only a small subset of R proteins directly bind the cognate Avr effector. A study of Avr effector recognition in the *Melampsora lini*–flax interaction generated a series of chimeric L-locus (*R* gene) immune-receptors that contained swaps between and within protein domains. Interactions between these modified immune-receptors and the fungal effectors were evaluated *in vitro* and via transient expression *in planta*. Some of these chimeric immune-receptors were found to have an enhanced ability to detect different races of *M. lini* and induce a defensive response. This demonstrates the usefulness of engineering plant receptor proteins to widen the repertoire of Avr effectors (secreted by the feeding fungal haustoria) that are recognized by the plant cells. This new approach to R protein engineering could potentially be used to generate cultivars with disease resistance to other species of rust pathogens in a range of agricultural crops, once the cognate *Avr* and *R* genes are isolated and characterized (Ravensdale *et al.*, 2011, 2012).

Mutagenizing the Leucine-Rich Repeat Recognition Domain

Many plant R proteins possess a LRR domain. The variable regions in the LRR are implicated in microbial effector recognition and in determining resistance specificity (reviewed by Jones and Dangl, 2006; Dodds and Rathjen, 2010). In potato, the Rx protein confers resistance to potato virus X (PVX). The Rx LRR domain recognizes variants of the viral coat protein (CP). By using a novel PCR-based method that permits random mutagenesis specifically in the DNA sequences coding for the LRR domain, artificial *Rx* alleles were generated that conferred resistance to several additional PVX strains and to several strains of the unrelated poplar mosaic virus (Farnham and Baulcombe, 2006). Artificially targeting the 'evolution' of *R* gene sequences in the laboratory appears to have great potential for engineering plant resistance and for broadening natural *R* gene specificity against diverse pathogens. For many R proteins the subdomains in the LRR region conferring microbial effector recognition and determining resistance specificity are already well known and well characterized. The exploitation of this approach depends on the development of rapid and cost-effective ways to identify the novel variant alleles of greatest commercial interest.

Blocking Pathogen-Effector Uptake into Plant Cells

This plant biotechnology approach is only just beginning to emerge as a consequence of the wealth of new knowledge on how some effectors from oomycete and fungal species are taken up into plant cells. Interfering with effector function is a powerful way to control microbial function, albeit potentially only in a pathogen-specific manner. The identification in the *N*-terminus of the highly conserved RxLR (arginine, any amino acid, leucine, arginine) and dEER (aspartate (less conserved), glutamate, glutamate, arginine) motifs in the secreted effectors of many oomycetes, including *Phytophthora*, *Hyaloperonospora*, and *Albugo* species, enabled the identification of a novel mode of effector uptake into host cells that is similar to that deployed by the malaria parasite *Plasmodium* to gain entry into human cells (reviewed by Tyler, 2009; Raeffaele and Kamoun, 2012). The development of a disease control strategy based on blocking effector uptake has been made possible because the mechanisms used in different *Phytophthora* species and different core effectors has been established. For example, in certain species, by applying a blocking agent to prevent phosphotidylinositol-3-phosphate (PI-3-P) binding, effector uptake into the plant cell was inhibited (Kale *et al.*, 2010). Subsequently, cacao plants (*Theobroma cacao* Linn.) were transformed to secrete transiently excess PI-3-P, which somehow inhibited effector uptake. The modified cacao leaves when inoculated with *Phytophthora palmivora* showed a reduction in lesion size, demonstrating the successful application of this concept to lessen the impact of this devastating fungal disease in tropical regions (Tyler *et al.*, 2011). Unfortunately, in other oomycete species binding PIPs has been shown not to be required for effector uptake. Similarly, the well-studied effector protein AvrM secreted by the flax rust fungus *M. lini* has been shown to bind PIPs, but this binding is not required for effector internalization (Ve *et al.*, 2013). Whether this novel plant biotechology approach has wide applicability or instead proves to be a highly species specific control option is currently unclear.

Following on from these impressive oomycete discoveries, researchers are searching for a highly degenerative RxLR-like motif in a wide range of fungi, including plant, insect, and mammalian pathogens. Such a discovery could enable the application of the aforementioned approach, tackling effector uptake, to a wide range of fungal diseases. In this context, the identification of an enrichment of the Y/F/WxC in the *N*-terminus of the mature protein may be important. The first amino acid of this motif is aromatic tyrosine, phenylalanine, or tryptophan, and the last is always cysteine. The high

abundance of the motifs in the predicted secretome repertoires of several unrelated haustoria-forming obligate biotrophic fungal species (i.e., many that cause leaf and stem rusts, or powdery mildew) (Godfrey *et al.*, 2010) is intriguing and may be exploitable in the future. Similarly, in rice blast (*M. oryzae*) research, an important plant-derived structure formed post hyphal invasion, called the biotrophic interface complex (BIC), has been discovered. The BIC transports a subset of *M. oryzae* effectors into the rice cells in advance of fungal infection (reviewed by Valent and Khang, 2010). The BIC provides a new target location inside infected plant cells for possible exploitation by plant biotechnology. In each interaction, blocking uptake of the core effectors is likely to be the most successful route.

Removal of Plant-Susceptibility (S) Targets

Two new genome-editing methods have been developed for use in plants during the past 10 years. These are (1) transcription activator-like effector nucleases (TALENs) (Boch, 2011; Schornack *et al.*, 2013) and (2) clustered regulatory interspaced short palindromic repeat (CRISPR) technologies (Jinek *et al.*, 2013; Gaj *et al.*, 2013). In the future, either technology could be used to remove pathogen-susceptibility targets from crop plant species. In breeding for resistance, elimination of disease susceptibility genes (*S* genes) has been proposed as a viable alternative to exploitation of *R* genes (Gust *et al.*, 2010). Moreover, deploying a single-gene editing approach should ensure that all other genes in the plant genome and especially those in the vicinity of the *S* gene are maintained in elite crop plant germplasm. However, this needs to be cautiously done for two reasons: Some plant proteins are now known to be targeted by multiple effectors that are sequence unrelated. These diverse effectors come from different pathogen species. Therefore, creating resistance to one pathogenic species might increase susceptibility to another species. Second, some susceptibility targets perform other plant functions as well and are required for normal plant growth and development (discussed further by Gawehns *et al.*, 2013).

Arabidopsis RIN4 is a negative regulator of ETI and is targeted by numerous Pseudomonad bacteria effectors. As a consequence, the plasma membrane-tethered RIN4 protein is guarded by several R proteins, including RPM1 and RPS2 (reviewed by van der Hoorn and Kamoun, 2008). This is a classic example of indirect recognition of an effector by an R protein (Jones and Dangl, 2006). The use of CRISPR or TALEN technology to remove this effector-targeted host protein should enhance disease resistance. However, due to genetic redundancy of effector function, this approach might weaken ETI-mediated defense in situations where the pathogen rapidly evolves to recruit and use other effectors for virulence and thereby make better use of an alternative negative regulator of ETI that is less well guarded by R proteins.

For plant-pathogenic bacteria in the genus *Xanthomonas*, TAL (transcription activator-like) effectors called Transcription activator-like effectors (TALEs) contribute to pathogen virulence and the disease formation process by binding directly to host DNA and transcriptionally activating specific *S* genes that are beneficial to the pathogen's growth and dissemination (Boch and Bonus, 2010). To date, these are the only type of bacterial effectors known to function in this way. This discovery led to the description of a new type of DNA-binding protein and opened up the possibility of targeting specific plant genes.

TALEs produced by the bacteria *Xanthomonas oryzae* pv. *oryzae* (*Xoo*) contribute to virulence by transcriptionally activating specific rice *S* genes (Li *et al.*, 2012). Molecular engineering has been used to create a wide array of TAL effector nuclease (TALENs) fusion-proteins (Boch, 2011; Schornack *et al.*, 2013). TALENs contain the DNA recognition repeats of native or customized *Xoo* TAL effectors and the DNA cleavage domains of FokI nuclease. To engineer rice to be resistant to *Xanthomonas*-incited bacterial blight, the promoter of the rice susceptibility gene *Os11N3* (also called *OsSWEET14*) was targeted for TALEN-based disruption. This gene encodes a member of the SWEET sucrose-efflux transporter family. Two *Xoo* TAL effectors, AvrXa7 or PthXo3, activate this *S* gene and divert plant sugars to the bacteria, whereas a third effector PthXo1 targets a different *S* gene. The *Os11N3* promoter contains binding sites for the AvrXa7 or PthXo3 effectors near the TATA box. The TALENs were designed to mutate DNA required for the susceptibility function, but not the development function of Os11N3. Therefore, post transformation the rice lines were first screened by PCR for mutations in both TAL-effector binding sites, but leaving the TATA box intact. This modified *Os11N3* gene was no longer inducible when the rice plants were infected by *Xoo* strains that deliver either the AvrXa7 or PthXo3 effectors into plant cells. The stable TALEN-modified plants showed strong (though recessive) resistance to infection by the AvrXa7- or PthXo3-dependent *Xoo* strains but not the PthXo1-dependent pathogenic *Xoo* strain (Li *et al.*, 2012). So far, natural polymorphisms in the *Os11N3* gene that would confer disease resistance have not been identified in rice germplasm. By using the TALENs to edit precisely a rice gene required for *Xoo* susceptibility, desirable alleles conferring resistance can now be used in rice breeding programs.

In many successful plant breeding programs to control fungi, bacteria, and viruses, recessively inherited disease-resistance genes are well known and well used. In these situations, the lack of a susceptibility protein target or the production of a nonfunctional protein variant is hypothesized to be the underlying cause of these recessively inherited traits. One of the best studied recessive *r* gene is *mlo,* which has functional orthologs in barley, tomato, and *Arabidopsis* (Consonni *et al.*, 2006; Bai *et al.*, 2008). The wild-type *MLO* allele codes for a seven transmembrane-spanning protein that is required for susceptibility to powdery mildew. A subset of the secreted powdery mildew effectors, presumably successfully target MLO to aid fungal infection of the plant's epidermal cell layer. MLO protein families are present in many other crop species, each colonized by different adapted powdery mildew species. Interestingly, the virulence function of the *P. syringae* effector HopZ2 was found to target *Arabidopsis* MLO2, and plants harboring T-DNA inserted into *mlo2* alleles were found to exhibit resistance to this unrelated pathogen (Lewis *et al.*, 2012). Therefore, inactivation of the plant-susceptibility factor MLO in a range of crop species, by using precise genome editing, should confer resistance to different devastating powdery mildew species and potentially other unrelated pathogens.

In *Arabidopsis*, genetic dissection of susceptibility to powdery and downy mildews has identified multiple *S* genes whose impairment results in disease resistance. The *Arabidopsis S* genes *PMR4* and *DMR1* encode a callose synthase and homoserine kinase, respectively, and both genes have functional orthologs in tomato. Single-gene silencing in transgenic tomato plants, using RNAi constructs resulted in resistance to the powdery mildew fungus *Oidium neolycopersici*. However, resistance to *O. neolycopersici* by *DMR1* silencing was associated with severely reduced plant growth whereas *PMR4* silencing was not (Huibers *et al.*, 2013). Therefore, *PMR4* is currently the more suitable candidate gene for immediate deployment via plant biotechnology. This highlights the fact that S proteins have more than one function and are often important for plant growth and development.

Targeting Pathogenicity Factors

Removal of Essential Secreted Biomolecules

In a few fungal and bacterial species the secretion of a single biomolecule has been shown to be essential for the disease-causing ability of the species. In these scenarios, plant biotechnology approaches that either eliminate or reduce drastically the production of these essential biomolecules should enhance disease resistance. This approach has been particularly successful in controlling the necrotrophic fungus *Sclerotinia sclerotorium*, which infects hundreds of crop species. Oxalic acid (OA) secreted by *S. sclerotorium* is a key pathogenicity factor (Cessna *et al.*, 2000). The plant enzyme oxalate oxidase (OXO) can oxidize OA into carbon dioxide and hydrogen peroxide. Transgenic crop plants, including oilseed rape, hybrid poplar trees, potato, soybean, peanuts, and sunflower overexpressing OXO from a range of different cereal plant sources exhibit very high resistance to infection and disease symptom formation (Dong *et al.*, 2008; Stuiver and Custers, 2001). This approach appears to have been particularly successful because the reduced OA production prevents the rapid acidification of the plant tissue that, in turn, probably prevents an arsenal of secreted *S. sclerotorium* enzymes from rapidly macerating the plant cell wall. In addition, the hydrogen peroxide generated would act as a local signal and activate plant defenses.

Bacterial Quorum Sensing

Bacteria have adopted a community genetic regulatory mechanism, known as quorum sensing (QS), to gain maximum benefit in a competitive environment. Many pathogenic and nonpathogenic bacterial species use QS signaling systems to synchronize the expression of specific target genes and thereby coordinate the biological activities locally in the population. *N*-acylhomoserine lactones (AHLs) are well-characterized QS signals in Gram-negative bacteria, which regulate virulence and surface film (biofilm) formation. Several groups of AHL-degradation enzymes have been identified in bacteria and eukaryotes (reviewed by Dong and Zhang, 2005). Expression of these degrading enzymes in transgenic plants has been shown to quench efficiently the microbial QS signaling and thereby block infection by the bacterium (Dong *et al.*, 2001; Dong *et al.*, 2004). Although this approach shows promise, the real impact of overexpressing AHL-degradation enzymes on other plant-beneficial bacteria in the ecosystems is not yet known.

Minimizing Plant Cell Wall Degrading Enzyme Function

Many hemibiotrophic and necrotrophic fungal and bacterial species secrete a cocktail of plant cell wall degrading enzymes (PCWDEs) to facilitate plant infection and subsequent colonization. Owing to high gene copy numbers and functional redundancy, individual types of PCWDEs, for example, endo- and exopolygalacturonases, pectinases, and cellulases, have rarely been shown through reverse genetics experimentation to contribute to pathogenicity (reviewed by Tonukaria *et al.*, 2000). However, when plant polygalacturonase-inhibitor proteins (PGIPs) were overexpressed in various cereal and noncereal species, this led to enhanced resistance to several different ascomycete fungal species (reviewed by De Lorenzo *et al.*, 2001). These results indicate that reducing the effectiveness of pathogen-secreted PCWDE could be an important route to control pathogens that feed on or need to significantly remodel plant cell walls during infection.

Use of Host-Induced Gene Silencing

RNA interference (RNAi), also referred to as posttranscriptional gene silencing, has emerged in the last few decades as a powerful genetic tool in many eukaryotic species. The silencing starts with the initial processing or cleavage of a precursor dsRNA or a structured (hairpin) sRNA into short (20–25 nucleotides) small-interfering RNA (siRNA) duplexes by the highly conserved dsRNase-like enzymes called Dicers. The resulting double-stranded (ds) siRNAs are incorporated into an RNA-induced silencing complex (RISC) containing an Argonaute protein that has an RNA-binding domain and an endonucleolytic activity for cleavage of target RNAs. The activated RISC then unwinds the siRNA in an ATP-dependent reaction, to generate an antisense strand that targets complementary mRNA transcripts via base-pairing interactions. The subsequent cleavage of the targeted mRNA by siRNA-guided RISC causes a reduction in the amount of the corresponding protein (Castel and Martienssen, 2013).

The RNAi mechanism has recently been harnessed to control several globally important fungal pathogens using a novel *in planta* technique called host-induced gene silencing (HIGS) (reviewed by Lee *et al.*, 2012). During HIGS, the silencing mechanism is induced in fungal pathogens by expressing sequences in plants that are complementary to either 'essential for life' or essential pathogenicity genes in the fungus. By an unknown mechanism(s), the silencing phenomenon is transferred from the transgenic host plant cells to the fungal cells during the interaction, and this leads to a dramatic reduction in *in planta* fungal growth (Nowara *et al.*, 2010). Recently, two successful applications of this new approach have been reported. Firstly, in wheat, three *Puccinia triticina* (leaf rust) pathogenicity genes, the mitogen-activated protein kinase 1 (Pt*MAPK*), cyclophilin (Pt*CYC1*), and calcineurin B (Pt*CNB*)

were reported to suppress partially the growth of *P. triticina*, as well as the related wheat-infecting rust species *P. graminis* (stem rust) and *P. striiformis* (yellow or stripe rust) (Panwar *et al.*, 2013a,b). The second success was achieved by devising a stacked RNAi cassette that could target all three paralogous members of a cytochrome P450 lanosterol C-14α-demethylase gene family called CYP51 in the fungus *Fusarium graminearum*. In fungi, the CYP51 proteins are required for ergosterol biosynthesis and the maintenance of membrane integrity and are the target of the globally important sterol demethylation inhibitor (DMI) class of fungicides (Cools and Fraaije, 2008). The *in planta* expression of dsRNA complementary to CYP51A, CYP51B, and CYP51C rendered *Arabidopsis* and barley plants highly resistant to *Fusarium graminearum*, with mycelial growth restricted to the inoculation sites (Koch *et al.*, 2013). These later results are particularly encouraging and suggest that HIGS of CYP51 genes could be used as an alternative to chemical control options for a whole range of fungal pathogens.

Enhancing Plant Defense-Signaling and the Overexpression of Key Defense Components

All plant species mount a multilayered defense response following infection by pathogens or attack by pests. Once the infection/attack is perceived, a sophisticated array of defense-signaling cascades and networks are activated. These, in turn, induce a multifaceted defense response that includes the production of hydrolytic enzymes, antimicrobial compounds, antifeeding compounds, secondary metabolites, ROS, cell wall fortification, and often local programmed cell death (PCD). Most of the early attempts to engineer enhanced plant defense via plant biotechnology were aimed at overexpressing individual components from this complex response (reviewed by Hammond-Kosack and Jones, 2000; Stuiver and Custers, 2001).

Use of Defense-Signaling Components

One approach that has been well tested involves engineering plants to constitutively produce a key defense signal molecule to activate a broader array of defense mechanisms simultaneously, thereby controlling more than one pathogenic species.

Through the molecular genetic dissection of the *R-Avr*-gene-mediated ETI and the SAR response, plant genes such as *NPR1* have been isolated that are required for both the local and systemic-induced resistance. The NPR1 protein interacts with TGA-type transcription factors that control the expression of many defense-induced genes (see Sections Plant Detection of NonSelf and Systemic Plant Defense Responses). Constitutive overexpression of NPR1 from a strong promoter (i.e., 35 S from CaMV or a plant ubiquitin gene) leads to enhanced disease resistance in many species, including *Arabidopsis*, tobacco, wheat, rice, and apple, without apparently causing detrimental effects on other plant traits (Spoel and Dong, 2008; Chern *et al.*, 2005; Makandar *et al.*, 2006). The successful engineering of enhanced resistance via this approach suggests that in untransformed plants these NPR1 proteins are present in limiting concentration, and that elevating protein levels in the transgenic plants results in either the constitutive activation of defense mechanisms or the more efficient activation of defense mechanisms upon infection by a wider array of pathogens. These results also reinforce the view that the activated plant defense responses are not microbe–species specific. However, in the absence of pathogens, elevated expression of regulators such as NPR1 may result in a yield penalty.

In wheat, multiple copies of the *NPR1* gene exist and the family member functionally equivalent to *Arabidopsis* NPR1 has not yet been identified. Therefore, the native *Arabidopsis NPR1* gene was introduced into wheat under the control of the ubiquitously upregulated maize *Ubiquitin1* promoter. The floral tissue of the transgenic AtNPR1 wheat plants had enhanced resistance to the fungus *F. graminearum*, which causes head scab (Makandar *et al.*, 2006). When the wheat plants with AtNPR1 also coexpressed the *nahG* transgene that codes for the enzyme salicylate hydroxylase, which converts the signaling molecule salicylic acid into catechol, full disease susceptibility was restored. This result indicates that modified salicylic acid-mediated signaling can enhance floral defense against some fungal pathogens.

The overexpression of constitutively active forms of plant mitogen-activated protein kinases (MAP kinases) or of transcription factors that control the expression of defense–associated genes was found to confer resistance to several unrelated oomycete and fungal pathogens (Century *et al.*, 2008; Yamamizo *et al.*, 2006). However, several of the transgenic lines exhibited dwarfism, necrotic flecking, or premature senescence. This result reveals that only a carefully selected subset of alleles will go on to have commercial potential.

Several ROS are key signaling molecules produced very early *in planta* and locally during both PTI and ETI, including hydrogen peroxide. In potato, increasing hydrogen peroxide production through the apoplastic expression of a heterologous glucose oxidase enhanced the potato plant's resistance to the late blight pathogen, the oomycete *P. infestans*, the vascular wilt fungus *Verticillium dahliae*, and resistance of potato tubers to the soft-rotting bacterium *Erwinia caratovora* subsp. *caratovora*. (Shah *et al.*, 1995).

The Localized Activation of Programmed Cell Death

Localized PCD at the sites of initial pathogen entry into plants is a frequent response observed in ETI-mediated resistance to biotrophic and hemibiotrophic pathogens. The resulting hypersensitive response (HR) is hypothesized to restrict nutrient supply and this minimizes pathogen growth. Various toxic compounds synthesized by the surrounding living plant cells, predicted to restrict pathogen growth, have also been shown to accumulate preferentially in the dead cells. The infection-specific expression of various transgenes that can induce PCD was made possible by the identification of pathogen-inducible promoters and via the engineering of synthetic promoters using *cis* elements known to be rapidly activated on pathogen infection (Rushton *et al.*, 2002; Gurr and Rushton, 2005). Unfortunately, problems were encountered with the tightness of the regulation of the selected promoters. Often these promoters were subsequently shown to be 'leaky'

(i.e., expression of the PCD-inducing gene occurred in the absence of pathogen infection). As a consequence, engineering of PCD in transgenic crops may reduce infection by biotrophic pathogens or hemibiotrophic pathogens with a long latent infection phase, but favor infection by necrotrophic pathogens that thrive on the induced dead plant tissue. This point is further illustrated by the results obtained using barley plants engineered to overexpress the cell death regulator BAX inhibitor-1 (BI-1), which inhibits plant defense responses (Babaeizad *et al.*, 2009). Transgenic barley plants overexpressing the BI-1 protein grew normally and exhibited enhanced susceptibility to the obligate biotrophic powdery mildew pathogen *B. graminis* f. sp. *hordei*. The same barley seedlings overexpressing the BI-1 protein exhibited enhanced resistance to the hemibiotroph *F. graminearum* when compared with the T_3 progeny which had not inherited the transgene.

Constitutive Overexpression of Inducible Secondary Metabolites and Defense Proteins

Heterologous expression of the grapevine phytoalexin resveratrol was one of the first successful plant biotechnology solutions devised for enhanced crop protection. Tomato and tobacco plants were engineered to express the resveratrol biosynthesis pathway, by overexpression of the enzyme stilbene synthase. This resulted in resistance in tobacco to infection by various fungal species, including the fungal necrotroph *Botrytis cinerea* (Hain *et al.*, 1993) and resistance in tomato to the oomycete *P. infestans* (Thomzik *et al.*, 1997).

Plant chitinases and glucanases that target and degrade pathogen cell walls can normally only be induced following pathogen infection or as plant tissues age. The constitutive overexpression of these hydrolytic enzymes in plants has tended to result in only relatively modest improvements in plant resistance and often the effects are only against a narrow spectrum of pathogenic species. This approach was initially validated in several dicotyledonous crop species and more recently has been shown to enhance plant defense in wheat and rice to various fungal species (Gomez-Ariza *et al.*, 2007; Narasimhan *et al.*, 2009; Shin *et al.*, 2008).

Defensins are small antimicrobial proteins that come from different biological origins, including insects, marine organisms, and plants. In plants, defensins are either found in high abundance in specific organs, for example, seeds or their accumulation is strongly induced on pathogen infection, often when the jasmonic acid/ethylene-mediated defense-signaling pathway has been activated. Specific defensins have been shown to confer weak disease resistance when overexpressed in transgenic plants (Marcos *et al.*, 2008; Rahnamaeian *et al.*, 2009). Defensins directly damage fungal membranes, arrest hyphal tip growth, and cause hyperbranching. The reduced rate of fungal growth presumably gives the plant cells more time to activate additional defenses.

Engineering Nematode Resistance

Nematodes cause annual losses in excess of US$80 billion to world crops (Agrios, 2005). For many crop species, either naturally occurring genes conferring resistance to nematodes are unavailable or the breeding strategies for their deployment are inherently very slow. Transgenic approaches to control nematodes fall into two broad categories: (1) expression of inhibitory proteins and peptides to limit the nematode's dietary intake of protein from the plant and (2) prevention of root invasion but without a directly lethal effect on the nematode (Atkinson *et al.*, 2012).

Nematode feeding sites within the roots can be targeted by the use of plant promoters solely expressed in the induced syncytium or giant cells, where the nematode has lost motility and become sedentary (see Section Different Pathogen and Pest Lifestyles). The best established strategies for nematode control involve overexpression of cysteine proteinase inhibitors (cystatins) to interfere with the nematodes's digestion of plant-derived proteins. This approach has been successfully applied for the control of potato cyst nematodes (*Globodera* species) (Fuller *et al.*, 2008), root-knot nematodes (*Meloidogyne* species) infecting tomato (Chan *et al.*, 2010), as well as the migratory endoparasite species *Ditylendus destructor* that feeds on sweet potato roots (Gao *et al.*, 2011a,b) and *Radopholus similis* and *Helicotylenchus multicinctus* that feed on plantain (*Musa* spp.) roots (Roderick *et al.*, 2012). All plant parasitic nematode species must digest protein. Therefore, a cystatin-based defense can elevate resistance to several different nematode species in a single crop plant. The control of migratory nematode species is important because the root lesion formation encourages secondary fungal and bacterial infections (Duncan and Moens, 2006).

The successful invasion of host plant roots by parasitic nematodes requires each migrating juvenile animal to sense and respond appropriately to a wide range of chemical signals. Two distinct synthetic peptides have been engineered to interfere with cyst nematode chemoperception by binding to either the acetylcholinesterase or nicotinic acetylcholine receptors in the nematode's nervous system (Winter *et al.*, 2002). Transgenic plants engineered to secrete an acetylcholinesterase-inhibiting peptide from the roots decreased development of female beet cyst nematodes by more than 80% in *Arabidopsis* plants and reduced potato cyst nematode development by more than 90% in potato plants. The motile stage of the nematode is particularly vulnerable to sensory intervention (Lilley *et al.*, 2011).

Various proteins secreted from the esophageal glands of root-knot nematodes (*Meloidogyne* species) are now known to mediate infection and parasitism. The parasitism gene 16D10 encodes a conserved *Meloidogyne* secretory peptide that stimulates root growth and functions as a ligand for a putative plant transcription factor. An RNA-interference approach has been used to silence the 16D10 gene in *Meloidogyne*. *Arabidopsis* plants engineered to express 16D10 dsRNA (double-stranded RNA), resulted in effective resistance (63–90%) against the four major *Meloidogyne* species, *M. incognita*, *M. javanica*, *M. arenaria*, and *M. hapla* (Huang *et al.*, 2006).

Enhancing Resistance against Insect Pests

Several alternative approaches to the use of BT toxins to reduce insect pest numbers, plant damage, and the transmission of

harmful viruses have been developed over the past 10 years. These approaches fall into two broad categories: (1) manipulation of plant volatiles either to ward off pests or to attract natural predators and (2) prevention of insect feeding. Both approaches offer considerable promise and could be used in conjunction with BT toxins within a fully integrated pest management system.

Manipulation of Plant Volatiles

Plant volatiles are frequently released at the site of insect feeding. These volatiles can act as both attractants and deterrents to further colonization by the same or other insect species. Changes induced to the air composition in the vicinity of feeding insects have been investigated in combination with sophisticated electrophysiological equipment attached to the insects (Bruce *et al.*, 2005). This type of experimentation has revealed the existence of specific insect-neural stimulations that occur in response to specific plant volatiles. This approach and the fundamental new knowledge on the complexity of insect–plant communication events have already been exploited by plant biotechnologists in several innovative ways.

The largest group of plant volatiles are the terpenes, a diverse class of secondary metabolites that includes monoterpenes (C_{10}) and sesquiterpenes (C_{15}). One plant-produced sesquiterpene, (*E*)-β-farnesene (EBF), has been considered as a potential defense against aphids, because emission of EBF by plants causes aphids to drop off the plant or depart from the feeding site. For many aphid species, EBF is the principal constituent of the aphid alarm pheromone. When the *Ebf* synthase gene cloned from peppermint (*Mentha* x *piperita)* was overexpressed in *Arabidopsis* plants, this caused the emission of pure EBF (Beale *et al.*, 2006). These EBF emissions were shown to reduce the level of attack by aphids as well as increase the time spent on the *Arabidopsis* plants by the foraging parasitoid species *Diaeretiella rapae*. The constitutive production of EBF by plants could hold promise in the control of specific aphid pests. In the United Kingdom, the EBF approach is currently being field tested using hexaploid wheat engineered to overexpress the peppermint *Ebf* synthase gene in an attempt to control two cereal aphid species of major concern in Europe, namely the grain aphid, *Sitobion avenae*, and the bird-cherry oat aphid, *Rhopalosiphum padi* (Pickett *et al.*, 2014). Both of these insect pests are important vectors for disease-causing strains of the barley yellow dwarf virus (BYDV). Therefore, the successful control of aphid vectors should also control important plant viruses.

Following herbivory by the larvae of lepidopteran insects, maize releases a mixture of volatiles that is highly attractive to the females of various parasitic wasp species. The maize volatiles specifically released include EBF, (*E*)-β-bergamotene, and several other sesquiterpene hydrocarbons. The enzyme terpene synthase TPS10 was shown to be responsible for the formation of this mixture of volatiles from the substrate farnesyl diphosphate. Overexpression of the maize *tps10* gene in *Arabidopsis* plants resulted in the emission of high quantities of TPS10 sesquiterpene products identical to those released by maize. Females of the parasitoid *Cotesia marginiventris* learn to exploit these TPS10 sesquiterpenes to locate their lepidopteran hosts, if previously the females had been exposed to these volatiles in association with the host (Schnee *et al.*, 2006). Therefore, this single-gene approach could provide an indirect way to further boost the protection of the maize crop against herbivore attacks. The corresponding sesquiterpene synthase gene *OsTPS3* has now been identified in rice (Cheng *et al.*, 2007), suggesting that this indirect approach will be applicable to other crops and pest species.

The sesquiterpene (E)- β-caryophyllene is emitted by maize (*Zea mays*) leaves in response to attack by lepidopteran larvae like *Spodoptera littoralis* and released from roots after damage by larvae of the coleopteran *Diabrotica virgifera virgifera*. The maize terpene synthase 23 protein (TPS23) was shown to be responsible for the production of the volatile product (E)-β-caryophyllene from farnesyl diphosphate. (E)-β-caryophyllene has been shown to attract different types of natural enemies of both insect pests, namely, entomopathogenic nematodes below ground and parasitic wasps aboveground. The *TSP23* gene is transcriptionally active in teosinte species (a progenitor of maize) and European maize lines. However, for an unknown reason(s), in most North American maize breeding lines, *TPS23* transcription is decreased and this results in the loss of (E)- β-caryophyllene production (Köllner *et al.*, 2008). Restoring *TPS23* gene expression, by use plant biotechnology to introduce a fully transcriptionally active TPS23 gene sequence into North American lines should help to increase the levels of above- and below-ground pest predation and thereby improve the overall level of protection possible against these agriculturally harmful pests.

Reduction of Insect Feeding by Plant-Mediated RNA Silencing

A reduction of insect feeding has been possible for a few species by using plant-mediated RNA silencing. While feeding, many insects metabolize toxic chemicals produced by the plant to resist or evade herbivory. For example, the cotton bollworm (*Helicoverpa armigera*) is able to tolerate otherwise inhibitory concentrations of the cotton metabolite, gossypol, through the overexpression of a specific cytochrome P450, the CYPAE14 protein in its midgut. Engineered plants expressing hairpin RNA directed against CYP6AE14, when eaten by the insect larvae, provide sufficient levels of intact dsRNA to suppress gene expression in their midgut. As a result, the bollworm larvae are unable to metabolize gossypol and loose weight when feeding on cotton plants or an artificial diet containing gossypol (Mao *et al.*, 2007). However, the use of RNA silencing to control insect pests is still at an early stage compared with the use of BT crops.

Combining Approaches to Achieve Sustainable and Durable Crop Protection

In recent years, the DNA sequence length that can be inserted into a vector construct for plant transformation has gradually increased from approxiamtely 10 kb to more than 200 kb. This now means that several genes or gene-silencing constructs can be stacked and simultaneously introduced in a single

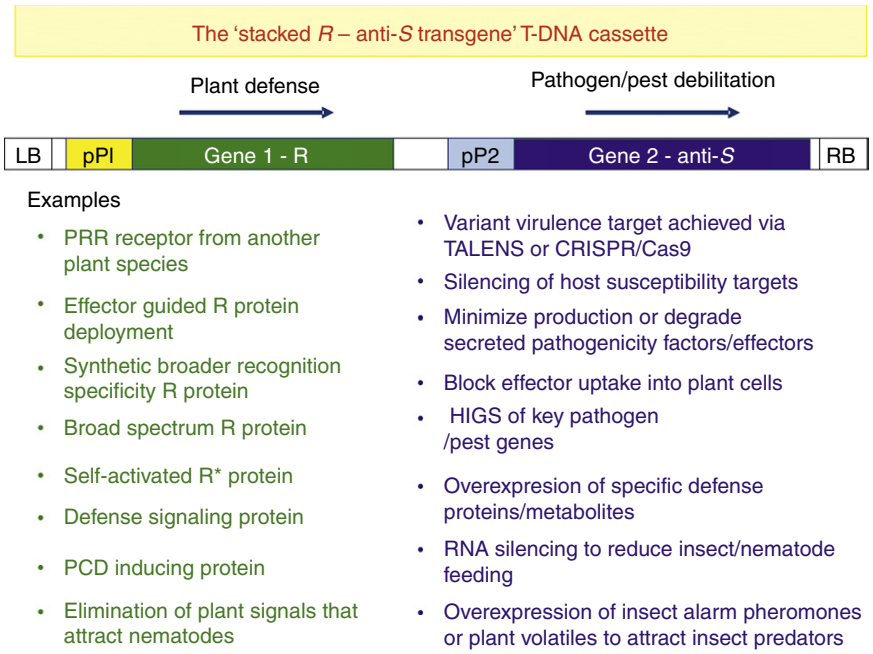


Figure 4 In the future, durable disease control could be achieved using a 'stacked *R* and anti-*S* transgene' T-DNA cassette containing two contrasting promoters and genes. The 'stacked *R* – anti-*S* transgene' T-DNA cassette approach combines the use of an effective resistance protein or defense-signaling mechanism (*R*) with a pathogen or pest debilitation mechanism to minimize plant susceptibility (anti-*S*). The *R* and anti-*S* genes are arranged in parallel and are expressed from two sequence unrelated promoters to ensure T-DNA cassette stability during the plant transformation procedure. As the repertoire of tightly regulated pathogen- or pest-inducible plant promoters gradually increases, this would permit the development of 'double-stacked *R* and anti-*S* transgene' containing two genes for each type. Alternatively, if the emphasis was on preferentially enhancing plant defense or debilitation of the pathogen, a triple-stacked *R* gene and one anti-*S* transgene, or *vice versa* could be engineered into a single T-DNA cassette. Further stacking of the unique T-DNA cassettes could also be achieved through conventional plant breeding, by creating hybrid plants or combining advanced elite pure lines. However, these multiple 'stacked *R* and anti-*S*' T-DNA cassettes (i.e., 2 genes plus 2 genes) achieved through breeding would be inherited as two distinct genetic loci. CRISPR/Cas9, clustered regularly interspaced short palindromic repeats; LB and RB, the left and right borders of the T-DNA construct; PCD, programmed cell death; pP1 and pP2, two different tightly regulated pathogen-inducible or pest-inducible promoters; R, resistance; S, susceptibility; TALENs, transcription activator-like effector nucleases; T-DNA, transferred DNA.

transformation cassette. This desirable approach has three major requirements: (1) a diverse collection of plant promoter sequences to maintain insert stability, (2) maintenance of the correct spatial and temporal pattern(s) of gene expression, and (3) a good repertoire of different gene sequence types that each confers enhanced resistance or reduced susceptibility via a distinct mechanism. In Figure 4, the types of gene stacking that are most likely to generate durable and broader spectrum crop protection are given. So far, very few plant biotechnology routes to crop protection have developed and tested this 'stacked *R* – anti-*S* gene' T-DNA cassette approach.

Conclusions and Future Prospects

The transgenic crop protection control options described have each taken immediate advantage of fundamental scientific discoveries that have advanced our overall understanding of host–pathogen interactions significantly. In each example, a target of potential vulnerability was exposed through the acquisition of new knowledge. Various intervention options were proposed and tested in the laboratory, growth room, or glasshouse and only the very best solutions went on to rigorous field testing and finally commercial release. In addition, many of the proposed single-gene transgenic disease control solutions that failed to make the grade either in early testing or later when tested under field conditions have already provided considerable useful and novel insight into the importance of other plant components and further information on the ways in which pathogens can rapidly evolve to overcome plant defenses.

In a few instances, disease resistance has been engineered using genes of animal origin. For example, one potentially powerful approach is the overexpression of antibodies that recognize microbe-specific cell surface components. Antibodies that specifically recognize a surface antigen of *Fusarium* species were fused with an antimicrobial peptide. Expression of these chimeric proteins in *Arabidopsis* or wheat conferred complete immunity to fungal infection (Li *et al.*, 2008; Safarnejad *et al.*, 2011). Although this approach provides highly efficient crop protection, the application of this technology in agricultural crops that provide human nutrition may raise ethical concerns.

Conventional plant breeding strategies targeted at delivering improved crop protection are now occurring at an accelerated pace through the increased use of high-density

molecular marker maps and wide introgression strategies. However, the pool of high-yielding elite germplasm available to plant breeders is finite. Moreover, the overall rate of evolution of the larger diploid or polyploid crop plant genomes is considerably slower than that of most pathogenic microbial species, which have haploid genomes. The other major route to crop protection is the application of agrochemicals (fungicides, insecticides, and nematicides). These products are costly to make and to apply. For example, several applications within a single growing season may be required to achieve a high level of crop protection. In addition, many active ingredients have been withdrawn over the past decade due to environmental concerns because of the potential effects on nontarget beneficial species, or because the pathogen or pest has mutated, rendering the control ineffective (reviewed by Leadbeater, 2011). The current approaches to chemical control of pathogens and pests are unsustainable in the longer term.

The current challenge is to devise novel ways to utilize the evolutionary genomic information stored in the worldwide diversity of germplasm, whether it be of plant, microbe, or pest origin. Of fundamental importance is the knowledge that most plants are resistant to most pests and pathogens, most of the time. In addition, disease and damage that does occur is usually locally restricted; either a specific part of the plant becomes diseased or damaged, for example, the leaf, root, stem, grain, or fruits, even though most organs are readily accessible. Alternatively, several organs may succumb to a pathogen or pest, but only a single specific plant tissue layer is attacked successfully, for example the epidermis, the mesophyll, or the vasculature. This means that the future solutions to pest and pathogen control already exist in the worldwide germplasm diversity. The current *in situ* and extant plant, pest and pathogen germplasm collections are of increasing importance. These key resources need to be maintained and further improved. This will ensure that these organisms and their genomes, proteomes, and metabolomes can be exploited by fundamental scientific research and for the follow-on application of plant biotechnology. Through this approach the widest possible options to achieve durable and sustainable crop protection will be available for use by current and future generations of scientists and biotechnologists to meet the growing global demands for food, feed, and fibers using less resources and less land.

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See also: Agbiotechnology: Costs and Benefits of Genetically Modified Papaya. Biodiversity: Conserving Biodiversity in Agroecosystems. Biotechnology Crop Adoption: Potential and Challenges of Genetically Improved Crops. Breeding: Plants, Modern. Genebanks: Past, Present, and Optimistic Future. Genomics: Plant Genetic Improvement. Plant Virus Control by Post-Transcriptional Gene Silencing. Transgenic Methodologies – Plants

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Biotechnology: Regulatory Issues

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Introduction

Biotechnology is an excellent, contemporary technological tool complementary to the currently established genetic improvement technologies such as selection, plant breeding, and mutational genetics. Choosing biotechnology provides an important tool for improving food productivity, quality, reducing input costs and it supports sustainable production. Development of biotech crops (or genetically modified crops) for agronomic improvements, reduced pesticides, disease tolerance, postharvest preservation, and improved nutritional quality is one of the selected applications of biotechnology in the agriculture and food sector. With the advent of molecular biology and biotechnology, it became possible not only to identify a desirable phenotypic trait but also to identify the precise genetic material responsible for that genetic trait. Recombinant deoxyribonucleic acid (rDNA) and plant transformation techniques have made it possible to alter the composition of individual plant components such as lipids, carbohydrates, and proteins beyond what is possible through traditional breeding practices. More than 16.7 million farmers around the world use agricultural biotechnology to increase yields, prevent damage from insects and pests, and to reduce farming's impact on the environment. Biotechnology improves crop insect resistance, enhances crop herbicide tolerance, and facilitates the use of more environmentally sustainable farming practices. Biotechnology is also helping to feed the world by (1) generating higher crop yields with fewer inputs, (2) lowering volumes of agricultural chemicals required by crops – limiting the run-off of these products into the environment, (3) using biotech crops that need fewer applications of pesticides and that allow farmers to reduce tilling farmland, (4) developing crops with enhanced nutrition profiles that solve vitamin and nutrient deficiencies, (5) producing foods free of allergens and toxins such as mycotoxin, and (6) improving food and crop oil content to help improve cardiovascular health (BIO, 2011; Phipps and Park, 2002; Mackey and Fuchs, 2001).

Plant biotechnology has been adopted at a higher rate than any other agricultural practice in history. Since 1996, when the first commercial biotech crops were planted, biotechnology has become the fastest technique ever adopted in agriculture. In 2011, the global area of biotech crops increased by approximately 8% from 2010 to reach 160 million hectares, up from 148 million hectares in 2010 as shown in **Figure 1**. This is a 94-fold-hectare increase since 1996. In its annual study, the International Service for the Acquisition of Agri-Biotech Applications (ISAAA) found that in 2011, 16.7 million farmers in a record 29 countries planted biotech crops, an increase of 1.3 million from the previous year. Approximately 90% of the farmers were small-scale and resource-poor farmers from developing countries. Indeed, biotech crops are helping farmers to be more productive and profitable. Biotech crop hectares continue to climb after 15 consecutive years of strong growth, as global population soars to 7 billion. The crops also contribute to a greener environment (James, 2011).

Despite the various benefits of biotech crops, the use of modern biotechnology has become a highly controversial issue in some regions where it has been applied. It has polarized modern society in terms of the potential benefits and risks of the adoption of crop biotechnologies and derived products in food and agriculture systems. The terminology for the application of biotechnology to food and agriculture has been used in various forms, such as genetic modification (GM), genetic engineering (GE), genetic manipulation, gene technology, and rDNA technology. However, the collective term 'genetically modified organisms (GMOs)' is used frequently in regulatory documents and in scientific literature to describe the deliberate introduction of DNA by human intervention into plants, animals, and microorganisms (IFST, 2008). This article covers only the safety and regulatory issues related to plant products derived by modern biotechnology, called biotech crops or genetically modified plants, not for animal products or other organisms.

Trends in the Use, Research, and Development of Foods Produced using Modern Biotechnology

Adoption of Biotech Crops

The adoption of biotech crops by the US farmers rapidly increased since the introduction of biotech crops in the US market, although the increase in adoption rate varied depending on the crops and traits (**Figure 2**). The cultivation of herbicide-tolerant (HT) soybean has increased from 7.4% of US soybean acreage in 1996 to 91% in 2007, and 94% in 2011. Plantings of HT corn, which had been slower in the early period of the last decade, has expanded from approximately 3.0% of US acreage in 1996 to 63% in 2008 and 73% in 2012. Adoption of HT cotton grew from approximately 10% of US acreage in 1997 to 80% in 2012. Plantings of insect-resistant corn and cotton containing the gene from *Bacillus thuringiensis* (*Bt*) also rapidly increased in general, although the adoption of Bt crops will likely fluctuate over time based on the expected infestation levels of major pests.

Adoption of stacked events of corn and cotton containing both HT and Bt traits has become widespread in the US (**Figures 3** and **4**). A few different techniques have been used to develop stacked events, including cotransformation, sequential transformation, or conventional crossing. Some of the already commercialized events are molecular stacks developed by cotransformation of genes included in one insert so that the event can have multiple traits. As such, transforming a host plant with an insert including multiple gene expression cassettes is a straightforward method to develop a molecular stack, which is a new biotech event developed by GE. One technical trouble in developing a molecular stack

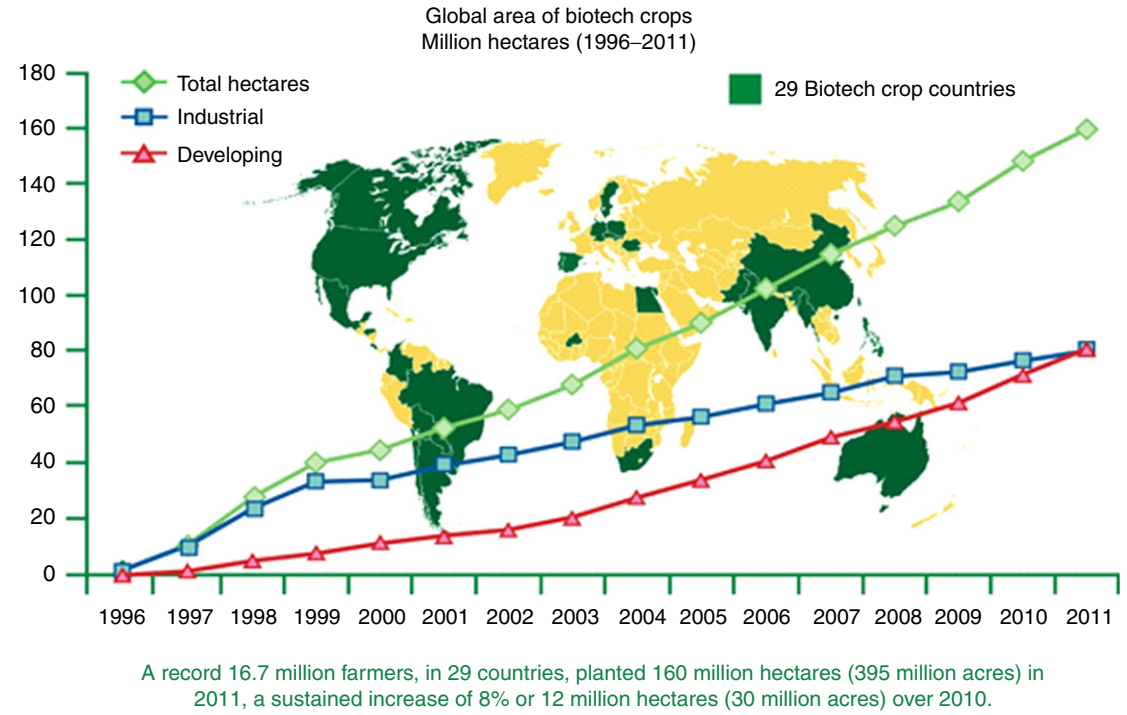


Figure 1 Global area of biotech crops. Reproduced from James, C., 2011. Global Status of Commercialized Biotech/GM Crops: 2011 ISAAA Briefs No. 43.

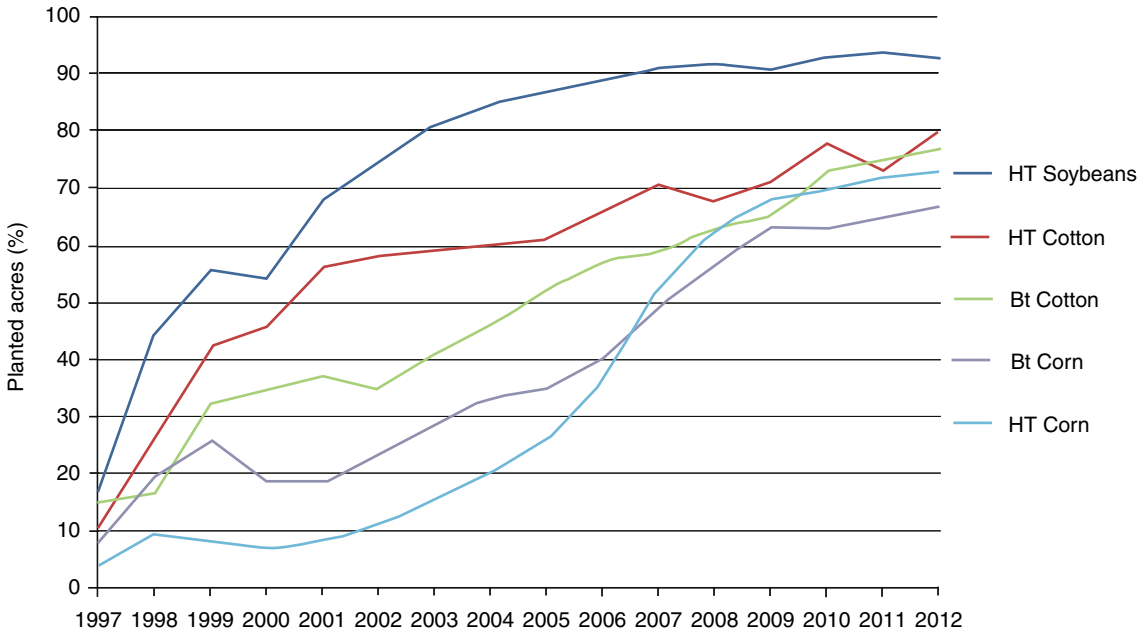


Figure 2 Adoption of biotech crops in the United States Data for each crop category includes stacked events. Reproduced from ERS, USDA, 2012.

having multiple cassettes is that the assembly of a longer insert composed of multiple gene expression cassettes is not easy.

However, genes included in respective biotech events can be combined together in diverse combinations using a conventional method, crossing between different parental lines. It is called a breeding stack. One of the advantages of breeding stacks is the flexibility in a sense that the trait combinations can be more easily tailored to specific market needs depending on prevalent pests. A key objective of pyramiding *Bt* genes in a crop is to delay emergence of Bt protein-resistant insects by stacking multiple *Bt* genes that have different modes of action, as a part of insect resistance management (IRM).

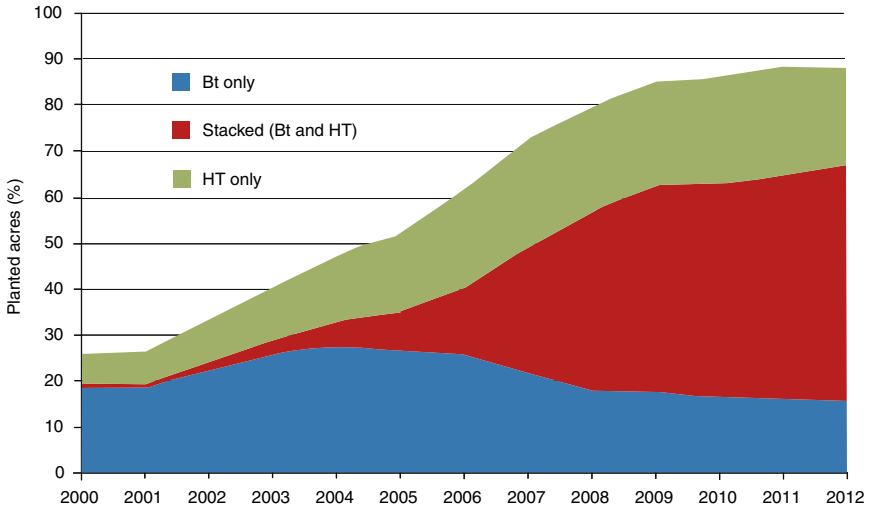


Figure 3 Adoption of biotech cotton in the United States. BT, bacillus thuringiensis and HT, herbicide-tolerant. Reproduced from ERS, USDA (2012).

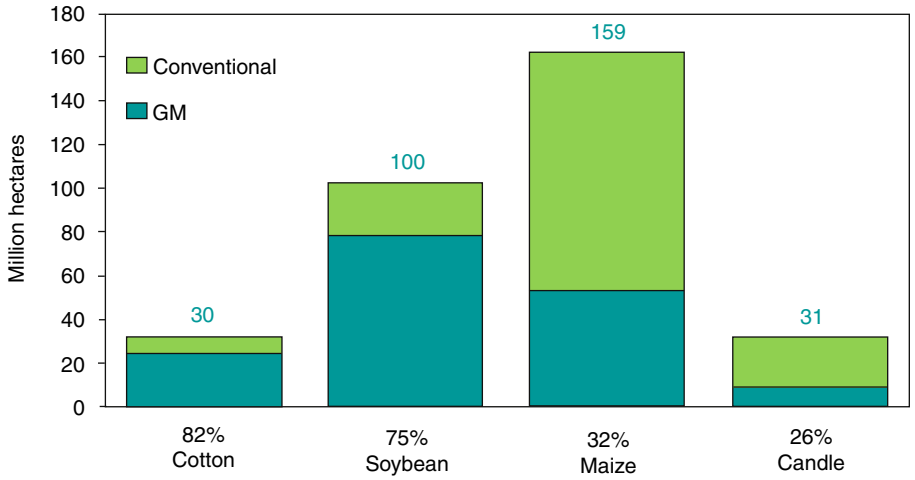


Figure 4 Global adoption rates for principal biotech crops. Reproduced from Clive James, ISAAA (2012).

Global adoption of biotech crops also has become widespread despite the controversy about efficacy and safety in some countries in the region. According to the ISAAA, global planting acreage of biotech crops has increased so that biotech crops covered 160 million hectares and planted by 15.4 million farmers in 29 countries in 2011 (Figure 1).

Commercial Traits and Product Pipeline

Soybean, corn, cotton, and canola have been the most representative of biotech crops as of today. However, in addition to those four crops, biotech alfalfa, biotech sugar beet, biotech papaya, biotech tomato, biotech sweet pepper, and biotech squash were launched and are now commercially available. For soybean, corn, cotton, and canola, insect resistance and herbicide tolerance have been the traits most frequently integrated into these crops since biotech crops were first commercialized in the United States in 1996. Owing to this, cultivation acreage of the biotech versions of cotton, soybean, canola, and corn share significant portions of global planting area of each crop (Figure 4).

Bt genes targeting several different types of lepidopteran or coleopteran pests (Table 1) and HT genes to confer tolerance to a few herbicides have been effectively used in the locations, where the cultivation of biotech crops has been allowed. In comparison to the *Bt* genes, fewer HT genes have been used in commercialized crops. Tolerance to glyphosate has been most widely used in agriculture up to the present, although glufosinate tolerance and sulfonylurea tolerance have been integrated into some crops.

Agricultural use of Bt and HT traits in crops will continue in the future. Theoretically, insect pests can develop resistance to Bt proteins. IRM has been implemented to maintain the effectiveness of Bt proteins by planting refuge crop acres where non-Bt crop is planted. For example, mating between Bt-susceptible insects from the refuge and potential resistant insects from Bt corn acreage largely ensures that susceptibility of pests to the Bt proteins is inherited by the next generation of pests. In the case of HT crops, emergence of glyphosate

Table 1 Bt proteins in commercial crops

Crop	*Bt protein*	*Event name*	*Target pests*
Corn	Cry1Ab	Bt11 (Syngenta), MON810 (Monsanto)	European corn borer
	Cry1F	TC1507 (Dow AgroSciences and DuPont Pioneer)	European corn borer
	Cry1A.105 + Cry2Ab2	MON89034 (Monsanto)	Lepidopteran pests
	Vip3Aa20	MIR162 (Syngenta)	Lepidopteran pests
	mCry3a	MIR604 (Syngenta)	Corn rootworm
	Cry34Ab1/Cry35Ab1	DAS-59122-7 (Dow AgroSciences and DuPont Pioneer)	Corn rootworm
	Cry3Bb1	MON88017 (Monsanto)	Corn rootworm
Cotton	Cry1F	281-24-236 (Dow)	Lepidopteran pests
	Cry1Ac	3006-210-23 (Dow)	Lepidopteran pests
	Cry1Ac + Cry2Ab2	MON 15985 (Monsanto)	Lepidopteran pests

[a]Bt proteins in stacked event, which were developed by conventional crossing of the events listed above, are not listed in this table. Breeding stacks express the transgenes inherited from parental lines.

Source: Reproduced from CropLife International, 2012a. Labeling of Biotech-Derived Products; CropLife International, 2012b. Plant Biotechnology Pipeline. Available at: http://www.croplife.org/view_document.aspx?docId=3631 (accessed 27.08.12).

tolerance weeds in farmlands has been more frequently reported than before, may be due to the intense use of a specific herbicide in biotech crop fields during the last decade. Emergence of herbicide-tolerant weeds and potential development of Bt-resistant insect pests have encouraged developers to continue developing new *Bt* genes and HT genes (Table 2). For example, a soybean event expressing Cry1Ac to control lepidopteran pests of soybean is at its late stage of global regulatory approvals before commercialization. Additional herbicide tolerance traits such as the tolerance to 2-, 4-D, and dicamba are also under regulatory pipelines. New molecular mechanisms to control insect pests are under development, such as RNA interference, which provides a mode of action different from Bt proteins.

In addition to Bt and HT traits, other traits are also gaining increasing importance because of market needs. For example, a high-oleic acid soybean is in its early stage of market launch in the US; some other crops are in the regulatory pipeline or are in the late stages of product development, awaiting their optimized composition (Table 2). Developing biotech events conferring tolerance to abiotic stress such as drought has been one of the hot topics for key developers in the world. One such product, a drought-tolerant biotech corn, is almost ready to be launched in the market in the Americas.

As of today, most of the biotech crops currently on the market have come from key players located in the US and the European Union (EU). However, it is expected that many new biotech events could be brought to market by developers in other countries in the near future, including India, China, and Latin American countries (Stein and Rodríguez-Cerezo, 2010). In terms of crop types, application of agbiotech is increasing so that more diverse biotech crops are anticipated to appear on the market in the future (Figure 4), such as potato, rice, sugarcane, wheat, and some vegetables (Figure 5). Another phenomenon that will be observed after 2014 is the potential of generics of biotech events, as the early patents on biotech crops expire (Gruskin, 2012).

Safety of Biotech Crops

Before commercialization, the safety of biotech crops has been assessed following internationally harmonized assessment principles prepared by concerted efforts of global experts. Only biotech crops whose safety has been confirmed by authorities of countries both cultivating and importing them have been commercialized. In fact, there have been no reported cases that any of the commercialized biotech crops cause human safety problems or environmental problems up to now. Scientific and regulatory authorities worldwide have clearly stated their views that foods from biotech crops are thoroughly evaluated by comprehensive testing for food, feed, and environmental safety and are as safe as their conventional counterparts. However, the critics continue to have concerns about the safety of biotech products, especially biotech crops. Application of biotech in other areas such as protein drugs and enzymes rarely becomes the subject of safety controversy. Likewise, foods developed by traditional breeding methods, which often involve random changes in nucleotide sequence by crossing or using mutagenic radiation, are rarely the cause of safety concerns. Such inconsistencies might indicate that concerns for biotech crops come from outside the science. The safety of biotech crops should, however, be assessed solely based on science. This section outlines what the scientific assessment for biotech crop safety entails.

Safety Assessment Principles and Concepts Applied to Biotech Crops

The safety of biotech crops was first addressed at the Asilomar Conference on California's Monterey Peninsula in 1975. The potential biohazards and regulation of biotechnology was first discussed at the Conference on rDNA. The scientists at the meeting addressed the safety issue presented by handling rDNA technology and proposed the establishment of guidelines for these experiments to ensure the safety of both DNA recombinant technology and its users. The detailed descriptions of the data to be assessed for safety can vary between countries and government agencies, but the assessment principle and criteria for safety assessment of biotech crop is fairly consistent between the nations. This is the outcome of concerted international efforts to harmonize the risk assessment of foods derived from modern biotechnology (FAO, 2008). Table 3 lists some key international consultations addressing

Table 2 Biotech crops in the pipeline

Crop	*Early development*	*Advanced development (next 5–7 years)*
Corn	*Herbicide tolerance* – Dicamba & Glufosinate (Monsanto) – FOPS (Monsanto) – Multiple mode (DuPont Pioneer) *Insect resistance* – Corn borer III (Monsanto) – New modes of action coleopteran III (DuPont Pioneer) – New modes of action lepidopteran III (DuPont Pioneer) – Second generation corn rootworm (Syngenta) – Novel insect traits (Syngenta) *Nitrogen utilization* – (Monsanto, BASF) – (DuPont Pioneer) – (Syngenta) *Stress tolerance* – Drought tolerance II (DuPont Pioneer) – Second generation drought tolerance (Monsanto, BASF) *Crop composition* – Improved corn feed (BASF) – Increased ethanol (Syngenta)	*Herbicide tolerance* – Roundup® hybridization system (Monsanto) – DHT: 2,4-D & FOP (Dow AgroSciences) *Insect resistance* – Corn rootworm III (Monsanto) – Optimum® Intrasect™ insect protection + Agrisure Viptera™ (DuPont Pioneer) – Lepidopteran/Coleopteran DP 4114 (DuPont Pioneer) *Integrated corn rootworm & European corn borer refuge* – Optimum® AcreMax™ XTreme Insect Protection (DuPont Pioneer) *Stress tolerance* – Drought (Syngenta) – First generation drought tolerance (Monsanto, BASF) *Increased yield* – (Monsanto, BASF)
Soybean	*Insect resistance* – Hemiptera/stink bug (DuPont Pioneer) – Lepidopteran (DuPont Pioneer) *Nematode resistance* – Soybean cyst nematode (Syngenta) – Soybean cyst nematode (BASF, Monsanto) *Disease resistance* – Asian soybean rust II (DuPont Pioneer) – (Syngenta) *Fungal resistance* – (BASF) *Increased yield* – Second generation (Monsanto, BASF) *Crop composition* – Increased oil and improved feed efficiency (DuPont Pioneer)	*Herbicide tolerance* – Dicamba (Monsanto) – Multiple mode (DuPont Pioneer) – Hydroxyphenylpyruvate deoxygenase (HPPD) inhibitors (Syngenta, Bayer CropScience) – DHT: 2,4-D & FOP (Dow AgroSciences) – GlyTol® + HPPD + LibertyLink® (Bayer CropScience, M.S.Technologies) – Imidazolinone (BASF, Embrapa/Brazil) *Insect resistance* – Second generation insect-Protected (Monsanto) – Intacta RR2 PRO® (Monsanto) *Increased yield* – First generation (Monsanto, BASF) *Crop composition* – Soymega™ SDA omega-3 (Monsanto-Solae) – Low saturated, zero trans-fat oil (Monsanto)
Cotton	*Insect resistance* – Lygus Control (Monsanto) *Stress tolerance* – Drought tolerance (Monsanto, BASF)	*Herbicide tolerance* – Dicamba and Glufosinate (Monsanto) – DHT (Dow AgroSciences) *Insect resistance/herbicide tolerance* – GlyTol® + LibertyLink® + TwinLink™ (Bayer CropScience) – Next generation IR + GlyTol® + LibertyLink® (Bayer CropScience) *Insect resistance* – Genuity® Bollgard III (Monsanto)
Canola	*Herbicide tolerance* – Dicamba tolerance (Monsanto) *Increased yield* – First generation (Monsanto, BASF) *Crop composition* – Healthy fatty acids (BASF) – Oil quality (Bayer CropScience)	*Herbicide tolerance* – Next-generation Genuity® Roundup Ready® (Monsanto) – Glyphosate tolerance DP 73496 (DuPont Pioneer) – LibertyLink® tolerance (DuPont Pioneer) – Glyphosate tolerance + LibertyLink® tolerance (Bayer CropScience) – Next-generation Genuity® Roundup Ready® LibertyLink® (Bayer CropScience, Monsanto)
Rice	*Herbicide tolerance* – (DuPont Pioneer) *Insect resistance* – Dual Mode of Action Lepidopteran (DuPont Pioneer) – (Bayer CropScience)	*Herbicide tolerance* – LibertyLink® tolerance (Bayer CropScience) *Crop composition* – Beta-carotene content increased – Golden rice 1 (IRRI/Philippines) – Beta-carotene content increased – Golden rice 2 (IRRI/Philippines)

(*Continued*)

Table 2 Continued

Crop	*Early development*	*Advanced development (next 5–7 years)*
	Increased yield	
	– (BASF, Bayer CropScience)	
Other	*Alfalfa*	*Alfalfa*
crops	– Increased yield (Monsanto, Forage Genetics International)	– Reduced lignin (Monsanto, Forage Genetics International)
	Sugar beet	*Beans*
	– Increased yield (BASF, KWS)	– Geminivirus resistance (Embrapa/Brazil)
	Sugarcane	*Eggplant*
	– Insect resistance + Roundup Ready® (Monsanto)	– Insect resistance Bt Brinjal (Maharashtra Hybrid Seeds Company)
	– Increased yield (BASF, CTC)	*Potatoes*
	Wheat	– Potato virus Y resistance (Tecnoplant/Argentina)
	– Herbicide tolerance (Monsanto)	– Late blight resistance (BASF)[a]
	– Increased yield (BASF, Monsanto)	– High amylopectin (BASF, Avebe)[a]
		– High amylopectin (BASF)[a]

[a]Project halted due to refocus of business 2012.

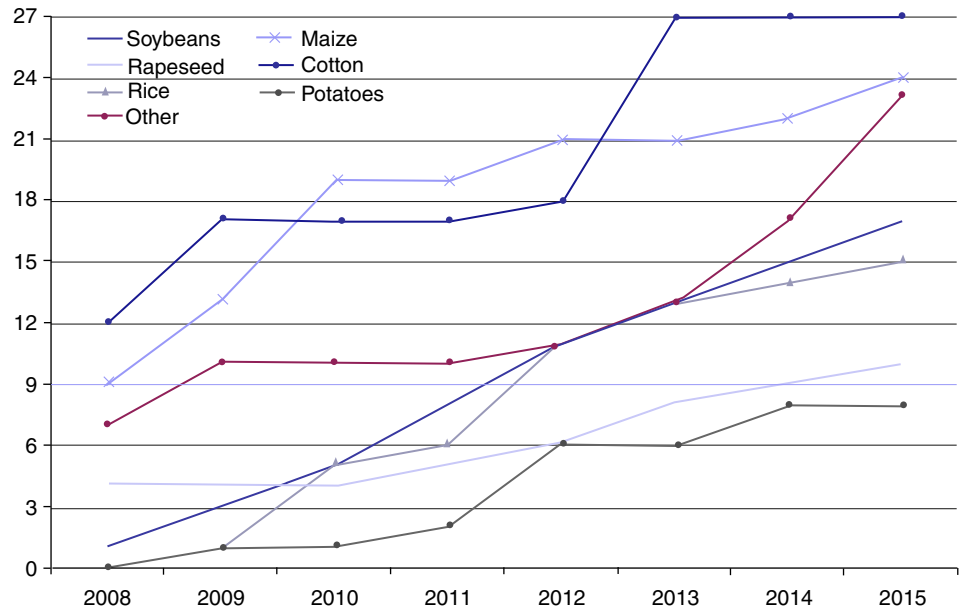


Figure 5 Projected number of events in biotech crops worldwide, by crop. Reproduced from Stein, A.J., Rodriguez-Cerezo, E., 2009. The global pipeline of new GM crops: Implications of asynchronous approval for international trade. Technical Report EUR 23486 EN. Luxemburg: European Communities.

the safety assessment of biotech crops including Food and Agriculture Organization (FAO) of the United Nations, World Health Organization (WHO), Organization for Economic Cooperation and Development (OECD), International Life Sciences Institute, International Food Biotechnology Council, and the Codex Alimentarius Commission (CAC), which have conducted a critical role in the globe.

Comparative Approach and Substantial Equivalency

The goal of the approaches used globally for the safety assessment of biotech crop is to assess whether foods or feeds from a biotech crop is 'as safe and nutritious as' its conventional crops that have an established history of safe use. Conventional crops that have an established history of safe use are considered safe because they are familiar, and not necessarily because of scientific proof. Conventional foods can include hazardous substances, such as endogenous allergens, antinutrients, or toxicants. Other variables not related to the characteristics of the crop can also affect human safety when a food prepared from conventional crops is consumed, such as intake amount, processing methods, physiological characteristics of the specific consumer, etc. Instead, human beings have empirically developed ways to reduce the adverse effects that may come from endogenous food components, such as by cooking, soaking, etc. As a result, a food is regarded safe if "there is reasonable certainty that no harm will result from its consumption under anticipated conditions of use" (OECD, 1993).

Table 3 Some key international consultations addressing the safety assessment of biotech (~2006)

Year	*Organization*	*Title*
1986	Organization for Economic Cooperation and Development (OECD)	Recombinant DNA (rDNA) safety considerations: Safety considerations for industrial, agricultural, and environmental applications of organisms derived by rDNA techniques
1990	Food and Agriculture Organization (FAO) of the United Nations/World Health Organization (WHO)	Strategies for assessing the safety of foods produced by biotechnology, a joint FAO/WHO consultation. Geneva, Switzerland, 5–10 November 1990
1990	International Food Biotechnology Council (IFBC)	Biotechnologies and food: assuring the safety of foods produced by genetic modification. Regulatory Toxicology and Pharmacology, 12, S1–S196
1993	WHO	Health aspects of marker genes in genetically modified plants. Report of a WHO Workshop. Copenhagen, Denmark, 21–24 September 1993
1994	WHO	Application of the principles of substantial equivalence to the safety evaluation of foods or food components from plants derived by modern biotechnology. Report of a WHO Workshop, Copenhagen, Denmark, 31 October–4 November 1994
1996	FAO of the United Nations/WHO	Biotechnology and food safety. Report of a Joint FAO/WHO Consultation, Rome, Italy, 30 September–4 October 1996. FAO Food and Nutrition Paper No. 61
1996	International Life Sciences Institute (ILSI)	ILSI Allergy and Immunology Institute (AII) guidance for assessing the allergenic potential of foods derived from biotechnology
1997	OECD	Report of the OECD workshop on the toxicological and nutritional testing of novel foods
2000	FAO of the United Nations/WHO	Report of a Joint FAO/WHO Expert Consultation on foods derived from biotechnology – Safety aspects of genetically modified foods of plant origin. WHO Headquarters, Geneva, Switzerland, 29 May–2 June 2000
2000	Codex Alimentarius Commission (CAC)	First session of the Codex ad hoc Intergovernmental Task Force on foods derived from biotechnology. Chiba, Japan, March 2000
2001	FAO of the United Nations/WHO	Allergenicity of genetically modified foods, a joint FAO/WHO consultation on foods derived from biotechnology. Rome, Italy, 22–25 January 2001
2001	CAC	Second session of the Codex ad hoc Intergovernmental Task Force on Foods Derived from Biotechnology. Chiba, Japan, March 2001
2002	OECD	Report of the OECD Workshop on the nutritional assessment of novel foods and feeds
2002	CAC	Third session of the Codex ad hoc Intergovernmental Task Force on Foods Derived from Biotechnology. Yokohama, Japan, March 2002
2002	WHO	The stakeholders' meeting on WHO draft document "WHO – Modern food biotechnology, human health and development: an evidence-based study." WHO, Geneva
2003	CAC	Fourth session of the Codex ad hoc Intergovernmental Task Force on Foods Derived from Biotechnology. Yokohama, Japan, March 2003
2003	OECD	Report on the questionnaire on biomarkers, research on the safety of novel foods, and feasibility of postmarket monitoring
2006	FAO of the United Nations	FAO expert consultation on biosafety within a biosecurity framework: Contributing to sustainable agriculture and food production. 28 February–3 March 2006, Rome, Italy

Source: Reproduced from FAO, 2008. GM Food Safety Assessment – Tool for Trainers. Rome: Food & Agriculture Organization of the United Nations.

It is not realistic to establish an absolute safety level of foods containing numerous components regardless of the origin of the food ingredients, be they conventional crops or biotech crops. The conventional toxicological approaches to examine the absolute safety of individual chemicals are unrealistic when applied to the safety assessment of biotech foods. Moreover, conventional agricultural practices and the cultivation of conventional crops are not risk free due to the use of insecticides. Therefore, the ecological risk assessment should compare the novel risks associated with the environmental release of biotech crops against the background risk associated with the existing agricultural practice, projected over the expected lifetime of the release (Hayes, 2004).

Risk assessment of biotech foods and food derived from biotech crops relies on comparative analysis, that is, comparison with their conventional counterparts in order to identify intended and unintended differences. Comparative analysis is based on the assumption that conventional counterparts from which biotech crops have been derived are generally regarded as safe to consume, based on the history of safe use. Information on conventional crops serves as a baseline for food/feed and the environmental safety assessment of a biotech crop (concept of familiarity, concept of substantial equivalence, comparative safety assessment). To that end, the most appropriate comparator analysis for biotech crops should have all traits in common except for the newly introduced traits: near-isogenic line of the biotech crop being tested. The concept of substantial equivalence, a safety assessment framework first described in an OECD publication titled 'Safety Evaluation of Foods Derived by Modern Biotechnology: Concepts and Principles' (OECD, 1993), embodies the idea of a comparative approach mentioned above. This document was developed by some 60 experts from 19 OECD countries, who spent more than 2 years discussing how to assess the safety of foods derived from modern biotechnology (FAO, 2008). One important benefit of the

concept of substantial equivalence is that it provides flexibility, which can be useful in the safety assessment of food derived from biotech crops. This concept of substantial equivalence is often used for the safety evaluation of biotech crops as well. It is a tool that helps to identify any difference, deliberate or unintended, which might be the focus of further safety evaluation (FAO, 2008). Science-based risk assessment, case-by-case approach, and step-by-step approach globally being applied to the risk/safety assessment framework for biotech crops were also developed as the outcome of OECD-led efforts.

Safety/Risk Assessment of Biotech Crops

Establishment of substantial equivalence is not an assessment of safety per se. Substantial equivalence is a starting point in the safety evaluation rather than an endpoint of the assessment (Schauzu, 2000; Kuiper *et al.*, 2001). In principle, all organisms and foods derived from organisms include significant levels of nucleic acids. There are no risks inherent in the use of recombinant technologies as all DNA is chemically and structurally the same. Therefore, the concept of risk assessment of biotech crops is based on any functional and chemical changes resulting from the genetic recombination. A new biotech crop is considered to be substantially equivalent to the conventional crop when the levels of nutrients, allergens, or naturally occurring antinutrients are not substantially different and there are no new allergens or toxins. When foods from biotech crops are concluded as substantially equivalent it is not necessary for further safety testing. However, when there is a substantial difference between a biotech crop and its near-isogenic line, such difference has to be subsequently subjected to risk assessment with respect to its potential impact on the environment, safety for humans and animals, and nutritional quality. For example, the newly introduced expression products such as Bt proteins require risk assessment.

Risk is a function of hazard and exposure (risk= hazard × exposure). Risk assessment arose from the need to make informed decisions in a more objective manner. With the help of risk assessment, individuals can make informed decisions about the impacts from their human-based activities on people and society (Nickson and McKee, 2002). Risk assessment, which follows the same deductive logic as basic scientific research, is the process of determining as accurately as possible the actual likelihood and consequences of the risks presented by exposure to identified hazards. Risk assessment should be science-based and transparent, and it requires scientists to organize and evaluate information so that they can evaluate a product's safety in a systematic way. Risk assessment of biotech crops and the foods/feeds derived from biotech crops involves the elements of hazard identification, hazard characterization, exposure assessment, and risk characterization (**Figures 6–8**; FAO, 2010, 2012).

Food safety assessment

For the risk/safety assessment of the foods derived from biotech crops, the CAC has developed several documents. Out of those documents, two are directly related to the safety assessment of biotech crops: principles for the risk analysis of foods derived from modern biotechnology (CAC/GL 44-2003), and guidelines for the conduct of food safety assessment of foods derived from rDNA plants (CAC/GL 45-2003). This guideline document of Codex provides the principles for the assessment of possible toxicity and allergenicity of expressed substances, compositional analyses of key components, evaluation of metabolites, etc. (FAO/WHO, 2006).

Environmental/ecological risk assessment

Problem formulation is the first step in the risk assessment process (**Figures 8** and **9**). The consistency and utility of environmental risk assessment for biotech crops can be improved through rigorous problem formulation (Wolt *et al.*, 2010; CLI, 2005). Assessment endpoints, valued entities that need to be protected, vary depending on the geography due to the difference of the existing wild species in the environment, etc.

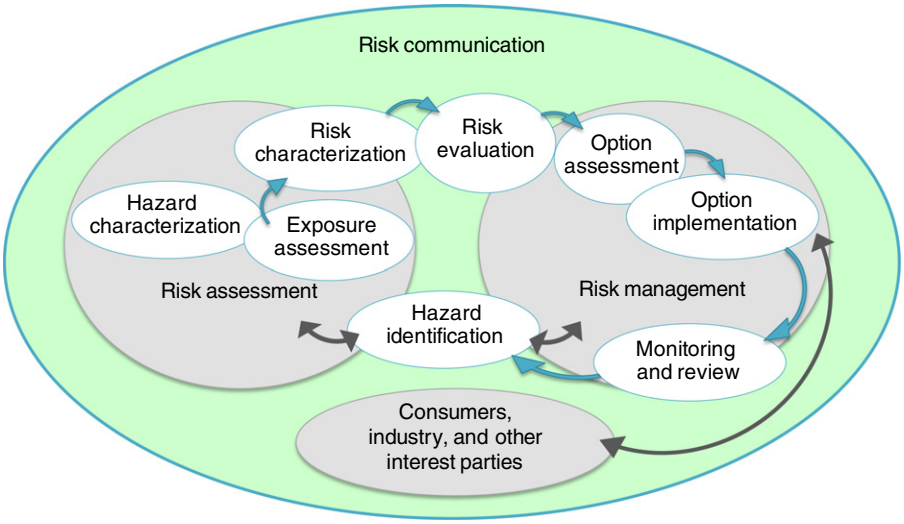


Figure 6 Risk analysis framework for the safety assessment of foods derived from biotech crops. Reproduced from FAO, 2008. GM Food Safety Assessment – Tool for Trainers. Rome: Food & Agriculture Organization of the United Nations.

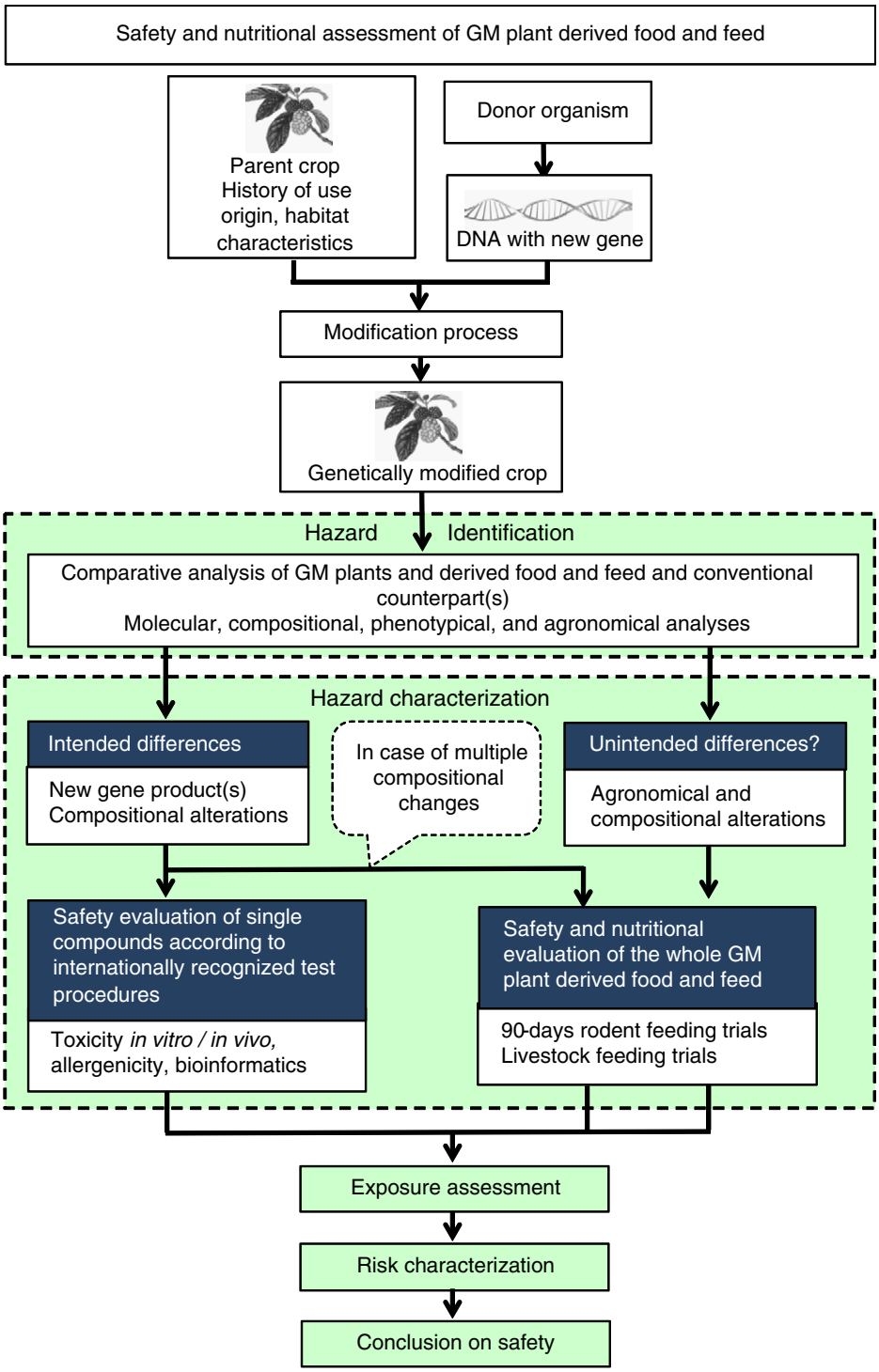


Figure 7 Scheme for premarket safety and nutritional testing of biotech plant-derived food and feed. Reproduced from EFSA GMO Panel Working Group on Animal Feeding Trials, 2008. Safety and nutritional assessment of GM plants and derived food and feed: The role of animal feeding trials. Food and Chemical Toxicology 46 (Suppl. 1), S2–S70.

Therefore, the data to be assessed for environmental risk assessment could vary depending on the environment. For example, interactions of the GM plant with nontarget organisms, plant-to-plant gene flow, weediness potential, etc. can be considered.

Like the Codex food safety guidelines, Annex II and Annex III to the Cartagena Protocol on Biosafety (CPB), especially Annex III, suggest the objective of the risk assessment, general principles, as well as the outline of methodologies. Annex III suggests that the risk assessment should be carried out in a

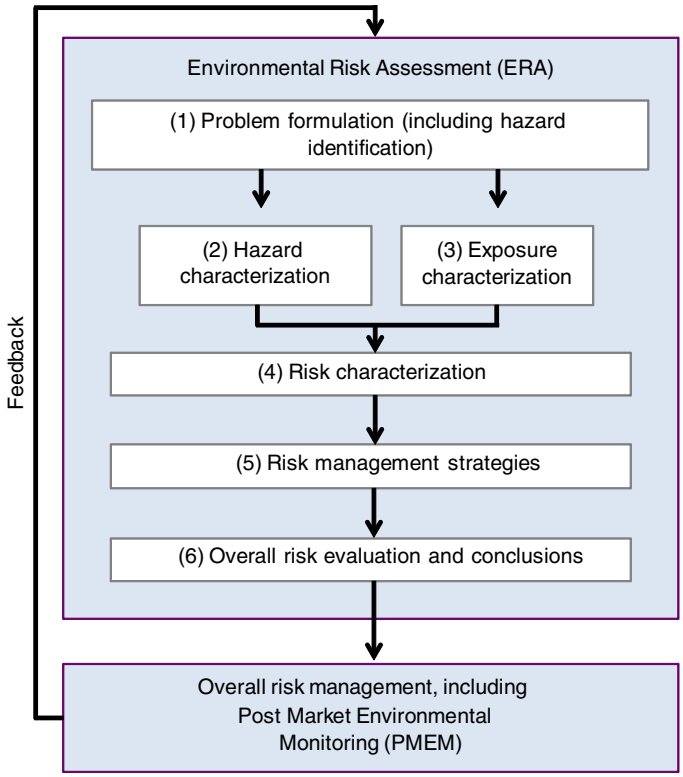


Figure 8 Six steps within the environmental risk assessment. Reproduced from EFSA Panel on Genetically Modified Organisms, 2010. Guidance on the environmental risk assessment of genetically modified plants. EFSA Journal 8 (11), 879.

scientifically sound and transparent manner. At the same time, this protocol also includes words on socioeconomic considerations and precautionary approach. In some countries, it is debatable that science-based risk assessment can be well aligned with socioeconomic considerations and precautionary approach (Raybould, 2010). Socioeconomic uncertainties still remain, and have led in some countries to a continuing emphasis on precaution, which sometimes results in the demand of experimental data less relevant to risk assessment.

Regional and International Regulatory Policy and Instruments on Biotechnology

There are three main elements of international regulations relating to research into, and the trade and use of, GM crops. These are the Codex Alimentarius, OECD consensus documents, and the CPB (FAO and WHO, 2000).

Codex Alimentarius Commission (Codex)

Although there are no specific international regulatory systems, several international bodies are involved in developing protocols for GM crops. The CAC (Codex) is one of them and it is the joint FAO/WHO body responsible for putting together the standards, codes of practice, guidelines, and recommendations that constitute the Codex Alimentarius. The purpose of the CAC is to protect the health of consumers, to ensure fair practices in food trade, and to promote coordination of all food standards work undertaken by international governmental and nongovernmental organizations. The Codex's objectives include consideration of standards, guidelines, or other recommendations as appropriate for foods derived from biotechnology or traits introduced into foods by biotechnology on the basis of scientific evidence and risk analysis. Codex developed principles for the human health risk analysis of GM foods. The principles include a science-based, premarket risk assessment performed on a case-by-case basis, and also an evaluation of both direct effects from the inserted gene and unintended effects that may arise as a consequence of insertion of the new gene. The standards set out by the Codex have been used widely as the benchmark in international trade disputes. Three standards relating to GM crops are (1) principles for the risk analysis of foods derived from modern biotechnology (FAO/WHO Codex Alimentarius, 2003a,b), (2) guidelines for the conduct of food safety assessment of foods derived from rDNA plants (FAO/WHO Codex Alimentarius, 2003a,b), and (3) working principles for risk analysis for food safety for application by governments (FAO/WHO, 2007).

Organization for Economic Cooperation and Development

To address the issues and concerns related to the use of modern biotechnology, the OECD published the guidance book on "Recombinant DNA (rDNA) safety considerations: Safety considerations for industrial, agricultural and environmental applications of organisms derived by recombinant DNA techniques"

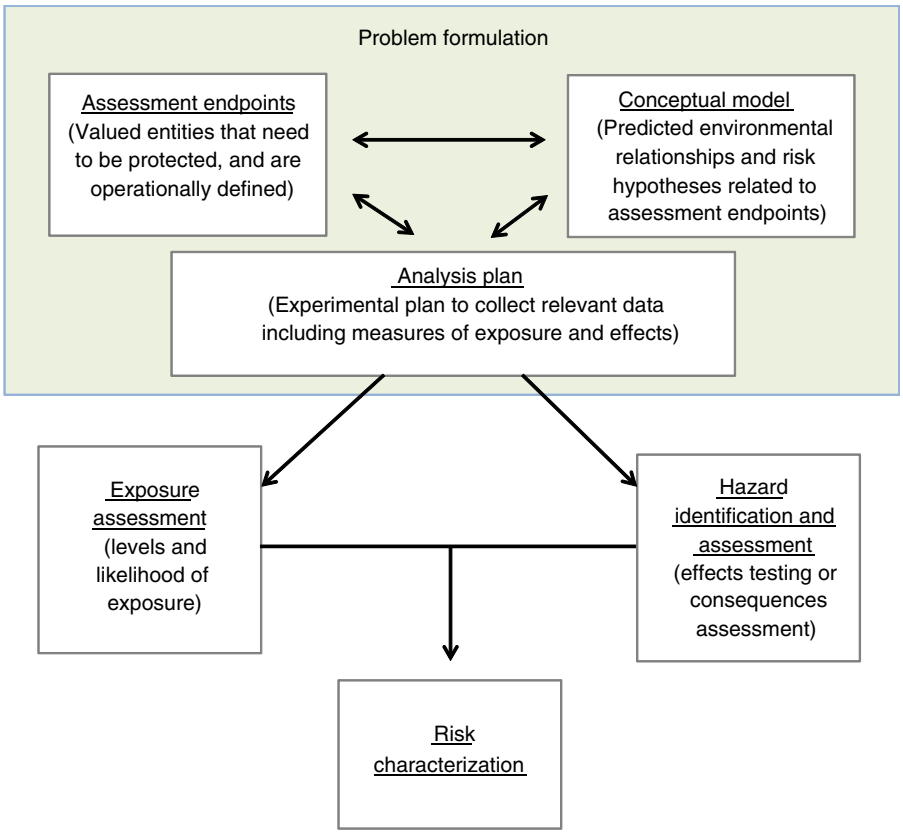


Figure 9 Schematic of problem formulation in the context of the risk assessment process as proposed by the US Environmental Protection Agency. Reproduced from Nickson, T.E., 2008. Planning environmental risk assessment for genetically modified crops: Problem formulation for stress-tolerant crops. Plant Physiology 147 (2), 494–502.

in 1986 called the 'Blue Book' because its cover is blue. This guidance book identified that the "specific aims of rDNA techniques in agriculture are, to reduce vulnerability to environmental stress: to detect and control infectious agents in animals and in the field and postharvest; to reduce dependence on use patterns of chemical pesticides; to decrease dependence on chemical fertilizers and irrigation; and to increase the nutritional qualities of seed, fruits, grains, and vegetables." The book also says that rDNA techniques "represent a development of conventional procedures. They permit precise alteration, construction, recombination, deletion and translocation of genes that may give the recipient cells a desirable phenotype. Moreover, rDNA techniques allow genetic material to be transferred into, and to express in, another organism which may be quite unrated to the source of the transferred DNA" (OECD, 1986). The book has been used as a starting point for countries that need to set up their own biosafety regulation on GM crops. Producing the consensus documents on environmental and food/feed biosafety is one of the OECD's main activities done by the Working Group on the harmonization of regulatory oversight in biotechnology. The objectives of the OECD's working group are (1) to protect the environment, (2) to promote harmonization, while (3) reducing unnecessary barriers to trade. Working group focuses on the safety assessment of GM crops by the development of consensus documents, information dissemination via BioTrack Online, and facilitating regulatory harmonization. Food/feed consensus documents on new crop varieties including soybean, canola, maize, rice, and cotton, etc. were published by Task Force team. These consensus documents are widely used by many scientists throughout the world as an important reference material when they conduct risk assessment for GM crops.

The Cartagena Protocol on Biosafety

Biosafety is one of the issues addressed by the Convention on Biological Diversity (CBD), which was finalized in 1992 at the UN conference and entered into force on 29 December 1993. Modern biotechnology has both positive and negative implications for human health, the environment, and trade. To ensure the safety of biotech products, regulatory regimes began examining the implications of their use. The term Living Modified Organisms (LMOs) is used only in CPB. Biosafety regimes like the CPB tend to stress the risk side rather than the benefits of biotech products. Risks to biological diversity and human health were foreseen when the CBD was negotiated in the early 1990s (Kinderlerer, 2008). After a series of negotiations at the CBD meeting, although concerns on modern biotechnology were raised by many countries, they clearly recognized that "biotechnology also offers new opportunities for global partnerships, especially between the countries rich in biological resources but lacking the expertise and investments needed to apply such resources through biotechnology and the countries that have developed the technological expertise to

transform biological resources so that they serve the needs of sustainable development" (Chapter 16, Agenda 21. UN, 1992). They agreed to establish or maintain means to regulate, manage, or control the risks associated with the use and release of LMOs resulting from biotechnology, which are likely to have adverse environmental impacts that could affect the conservation and sustainable use of biological diversity, also taking into account the risks to human health. To address the issue of biosafety, the development of measures at the national level and the establishment of international legally binding instrument were proposed by CBD parties. After several years of negotiations, the Protocol, known as the CPB to the CBD, was finalized and addressed the transboundary movement of the products of modern biotechnology and ensured that these products would be as safe as possible. The Protocol was adopted in Montreal on January 2000 (Cartagena Protocol on Biosafety, 2000). This international treaty entered into force on 11 September 2003, 90 days after receipt of the 50th instrument of ratification, and currently has 163 member states although many of the countries, such as USA, Argentina, and Canada that currently produce commercial transgenic crops are not members of the CBD (Kinderlerer, 2008; CBD, 2010). The Protocol has the potential to encourage innovation, development, technology transfer, and capacity-building for agricultural biotechnology, while supporting global conservation and sustainable agriculture goals. The Protocol is important because it establishes rules and procedures for the international trade of products of agricultural biotechnology – referred to as LMOs – including products like agricultural commodities, seeds, and research materials in order to protect the conservation and sustainable use of biodiversity. The Protocol requires that exporters of LMOs seek governmental 'advanced informed agreement' before shipping LMOs for intentional introduction into the environment of importing countries. It also requires government decision-making on imports to be based on sound scientific risk assessment and for results of such assessments to be made available through Biosafety Clearing House (CBD, 2000). The Protocol also requires that LMOs be shipped to countries that are Parties to the Protocol, setting of law in their own countries, for contained use, intentional introduction into the environment, or for direct use for food, feed, or processing to be identified in accompanying documentation as specified in the Protocol. Every 2 years, the Parties meet to discuss implementation of the Protocol's provisions. These meetings are called Conference of the Parties serving as the Meeting of the Parties to the Protocol (COP/MOP). The Parties also work in between COP/MOPs to prepare for the discussions and decisions on upcoming meeting agenda items. The sixth Meeting of the Parties will take place 1–5 October 2012 in Hyderabad, India. There are several issues with the potential to impact trade of LMOs, such as (1) risk assessment and risk management, (2) socioeconomic considerations, (3) documentation requirements, and (4) liability and redress (Nagoya-Kuala Lumpur Supplementary Protocol on Liability and Redress) (CLI, 2011).

National Regulatory Framework

The way governments regulate GM foods varies depending on the national and regional situations. In some countries GM foods are not yet regulated. Countries where they have legislation in place focus primarily on assessment of risks for consumer health. Countries that have provisions for GM foods usually also regulate GMOs in general, taking into account health and environmental risks, as well as control trade-related issues such as potential testing and labeling systems. The GMO regulatory systems that countries apply depend on the existing national legislation, their legal systems, and the administrative systems that are in place. UNEP-GEF's (United Nations Environment Program-Global Environment Facility) National Biosafety Framework (NBF) project has been helping underdeveloped and developing countries to establish biosafety regulations and a regulatory framework since early 2000. As of May 2012, a total of 118 countries have completed the majority of development of their NBFs. Their drafts of the NBFs are available online at UNEP (2008, 2012). Immediately after the Asilomar conference, many countries introduced some form of GMO regulation intended to ensure the safe use of the technology. In the USA, for instance, the National Institutes of Health (NIH) produced guidelines that applied to all organizations receiving funding from the USA government (NIH, 2002). These NIH guidelines remain the primary regulatory system for assuring safety in the USA regarding transgenic organisms in containment. For the agricultural use of commercially released GMOs, the US government deliberately chose to use existing agencies and not to change any laws. The US Office of Science and Technology Policy Committee generated the Coordinated Framework for the regulation of biotechnology in 1986 to guide framework for GM regulation (US Department of State, 1999). The USDA works with the Environment Protection Agency (EPA) and the Food and Drug Administration (FDA) to regulate the use of GMOs.

Genetically Modified Organisms Approval in the USA

The US government has played an instrumental role in assuring human, animal, and environmental safety through a rigid review process of all biotech-derived crops. In the US, three federal agencies are primarily responsible for the regulation of biotech crops, and they are involved in reviewing advances in plant biotechnology. Together they provide a coordinated framework to ensure human and environmental safety. The FDA, which oversees food safety and labeling of whole foods and food ingredients; the US Department of Agriculture (USDA), which oversees inspections of GM plants and food stocks, and the EPA, which oversees the registration and regulations of all pesticides, herbicides, and GM crops. Even after the commercialization of any biotechnology product all three regulatory agencies have the legal power to demand immediate removal from the marketplace of any product should new, valid data indicate a question of safety for health or the environment (USGC, 2005).

Food and Drug Administration

The FDA provides voluntary premarket consultations with food companies, seed companies, and plant developers to ensure that biotechnology-derived foods meet the safety standards for safety. Since 1992, the FDA has held the view

that foods from plants produced through modern biotechnology are as safe as those from plants developed through conventional breeding. Therefore, GM foods should be regulated the same as any other foods entering the market. Accordingly, the FDA evaluates the application of biotechnology to food products on a case-by-case basis, as it does with any other food. Under the Food, Drug and Cosmetic Act, the FDA usually focuses on the products, the food, or food ingredients, rather than on the plant development processes used in their production, as the basis for regulation. The same holds true for food and ingredients derived through biotechnology. The FDA offers a series of testing procedures that enable food manufacturers to anticipate safety concerns and to consult with the FDA as necessary for a regulatory review of new plant varieties and products testing under development. The FDA review process focuses on the areas, such as (1) safety and nutritional value of the newly introduced proteins, (2) identity, composition, and nutritional value of modified carbohydrates, fats, or oils, (3) concentration and bioavailability of nutrients for which the food crop is consumed, and (4) potential for allergens to be transferred from one food source to another. To ensure safety, a variety of toxicological and other product safety data are provided to the FDA for food products or ingredients produced through the use of new plant varieties. The FDA requires GMO developers to notify the agency at least 4 months in advance of commercialization of any GM foods or animal feed and supply the food safety authority with their research data for review. In practice, biotech companies have filed notices of commercialization long before the 4-month minimum. The FDA review includes a thorough safety assessment that compares every significant parameter of the GM plant with the traditional counterpart. If no changes are detected, the FDA concludes the GM crop to be substantially equivalent to the conventional crop with respect to nutrition and food safety (USGC and NCGA, 2005).

US Department of Agriculture

The USDA and the EPA are responsible for reviewing the ecological effects of new plants developed through biotechnology. The Animal and Plant Health Inspection Service (APHIS) within the USDA is the primary agency regulating the safety testing of biotech plants that are not insect or disease resistant. APHIS approval must be obtained before proceeding to field test or commercialize a biotech plant. To test a biotech plant in the field, GM crop developers must seek an environmental release permit from APHIS. Once testing is allowed, APHIS and state agriculture officials can inspect the test field throughout the process to ensure that tests are conducted safely. Before GM crops can be grown commercially, a petition must be submitted to APHIS containing the scientific details about the plant, results of field tests, and any indirect effects on other plants. This petition is published in the Federal Register, providing the public time to comment. When the USDA has determined that the product is safe for field use, it is approved for commercialization. There are also four points at which USDA may advance or halt development of a biotech plant product. These are (1) greenhouse approval, (2) field trial authorization, (3) authorization to transport seed, and (4) permission for commercialization (USGC and NCGA, 2005).

Environmental Protection Agency

In addition to APHIS, the EPA also regulates herbicides and has jurisdiction over crops that are insect and disease resistant under the Federal Insecticide, Fungicide, and Rodenticide Act. Environmental exposures to pesticide substances produced in plants are regulated by the EPA to ensure that there are no unreasonable adverse effects on the environment, including nontargeted organisms, such as insects, birds, fish, deer, and other species. The EPA's regulations focus on the pesticide produced by the plant, rather than on the plant as a whole. Such pesticides are subject to registration requirements similar to other pesticides. The agency requires applicants of new plant pesticides to obtain experimental use permits. Before any field testing, EPA officials must review and approve permit plants containing pesticidal properties (USGC and NCGA, 2005).

The European Union

All GMOs need authorization before being placed on the market in the EU. The EU has one of the world's strictest approval procedures for GM products. If, after an extensive scientific risk assessment, the European Food Safety Authority (EFSA), concludes that the product in question is as safe as a comparable non-GM variety, a political decision needs to be made whether or not to authorize the product. This decision-making phase is administered by the EU Commission and involves the member states. The EU legislation requires the EU Commission to stick to the following timelines: upon reception of a positive EFSA opinion, the Commission has 3 months to bring about a vote of the Standing Committee. Once the Standing Committee has voted, if the member states do not achieve a qualified majority for or against the approval, the Commission has to submit the approval dossier to the Appeal Committee within 2 months at the very most. In exceptional circumstances, the Commission may agree with the applicant to align regulatory procedures (EuropaBio, 2012). **Figure 10** shows how EU approves GM food and feed.

Obtaining Approval to Market Genetically Modified Organisms in European Union

Unlike the US, where existing regulations were applied to regulate biotech product, the EU made new regulations to handle the safety of biotech crops. For example, Directive 220/90/EEC relating to experimental releases and marketing of GMOs was entered into force in 1990. With the considerable advances in GM and after substantial revisions, Directive 90/220/EEC was replaced by Directive 2001/18/EC in 2001 to ensure that the regulations of GMOs would meet the demands of EU regulators and consumers. Directive 2001/18/EC on the deliberate release of GMOs into the environment outlines the principles for, and regulates, experimental releases and the placing on the market of GMOs in the EU. Council Directive 90/220/EEC contains the procedures relating to approval of

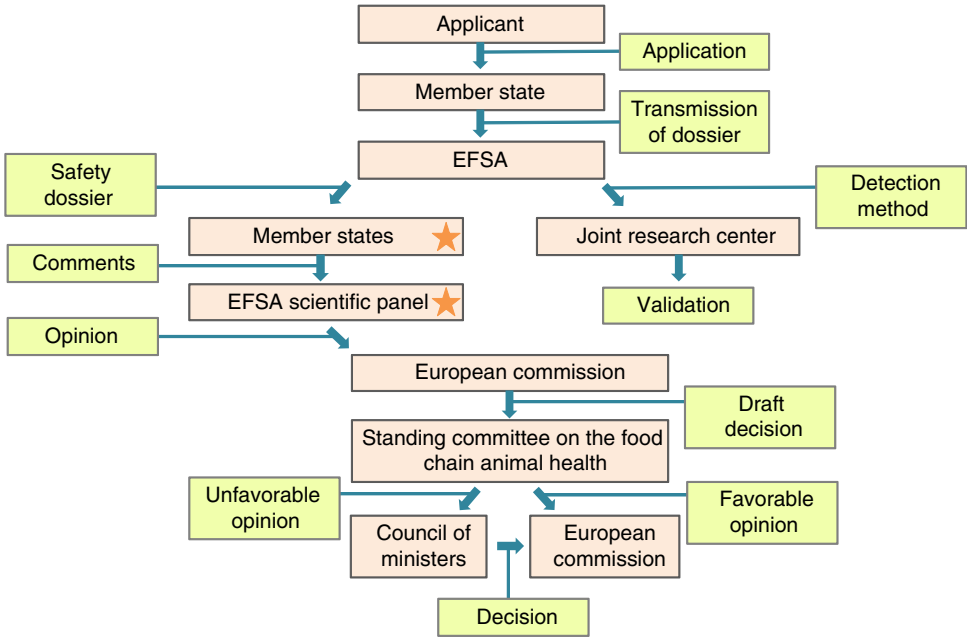


Figure 10 EU approval procedure for GM food and feed. EFSA, European Food Safety Authority. Reproduced from Kleter G., Kuiper, H.A., 2006. EU Regulatory Framework and Status of Genetically Modified Crops. EAAP Workshop. ERIKILT Institute of Food Safety, Wageningen.

the deliberate release of GMOs into the environment for research and development and for placing the GMO on the market (European Commission, 2012a,b; EFSA Panel on Genetically Modified Organisms, 2010). Any person seeking approval to place a GMO on the market must submit a notification to the competent authority of the member state where the product is to be placed on the market for the first time. The notification dossier must describe the risk analysis conducted, show that the products comply with the relevant European Community product legislation, and must describe the environmental risk assessment required by the Directive. The notification also must include specific conditions of use and handling and a proposal for labeling and packaging, which should comprise at least the requirements stipulated in Annex III of the Directive, as amended. On receipt of the notification, the competent authority has 90 days to either forward the notification dossier to the Commission with a favorable opinion or inform the applicant that the proposed release does not fulfill the requirements of the Directive. After receiving a notification dossier, the Commission immediately forwards it to the competent authorities of all member states. If no objections are raised by the competent authorities of the member states within 60 days of the Commission forwarding the notification dossier, then the competent authority that received the notification shall issue a written consent to the applicant and shall inform the other member states and the Commission of that consent. (Maurer and Harl, 1998). Besides the above-mentioned several EU Directives on GMOs, there is a Regulation (European Commission (EC)) 1829/2003 on genetically modified food and feed in the EU to ensure a high level of protection of human health and welfare, environment, and consumer interests, while seeking functioning of the internal market. The Regulation is supplemented by Regulation (EC)1830/2003 to handle traceability and labeling of GMOs placed on the market.

The European Food Safety Authority

The main objectives of the regulations on GM food and feed in EU are (1) to protect human and animal health by introducing a safety assessment of the highest possible standards at the EU level before any GM food and feed is placed on the market, (2) to have in place harmonized procedures for risk assessment and authorization of GM food and feed that are efficient, time-limited, and transparent, (3) to ensure clear labeling of GM food and feed in order to respond to consumers' concerns and enable them to make an informed choice, and to avoid misleading consumers, and (4) to set labeling requirements for GM feed which provide farmers with accurate information on the composition and properties of feed, thereby enabling them to make an informed choice.

The EFSA is the key scientific body of the EU to implement risk assessment regarding food and feed safety. In close collaboration with national authorities and in open consultation with its stakeholders, EFSA provides independent scientific advice and clear communication on existing and emerging risks. EFSA was set up in January 2002, as an independent source of scientific advice and communication on risks associated with the food chain. EFSA was created as part of a comprehensive program to improve EU food safety, ensure a high level of consumer protection and restore and maintain confidence in the EU food supply. In the European food safety system, risk assessment is done independently from risk management. As the risk assessor, EFSA produces scientific opinions and advice to provide a sound foundation for

European policies and legislation and to support the EC, European Parliament, and the EU Member States in taking effective and timely risk management decisions. EFSA's activity covers food and feed safety, nutrition, animal health and welfare, plant protection, and plant health. Regarding the GMO risk review, EFSA's Panel on GMOs provides independent scientific advice on the safety of GMOs, such as plants, animals, and microorganisms on the basis of Directive 2001/18/EC on the deliberate release into the environment of GMOs and GM food and feed, and also on the basis of Regulations (EC) 1829/2003. As shown in **Figure 10**, the EFSA's Panel conducts risk assessments in order to produce scientific opinions and advice for risk managers. Its risk assessment work is based on reviewing scientific information and data in order to evaluate the safety of a given GMO. This helps to provide a sound foundation for European policies and legislation and supports risk managers in making effective and timely decisions. The Panel carries out much of its work in the context of authorization applications, as all GM food and feed products must be evaluated by EFSA before they can be authorized in the EU (EFSA, 2012). The Panel works independently, transparently to deliver timely scientific advice of the highest standards to support the policies and decisions of risk managers. The Panel carries out its work either in response to requests for scientific advice from risk managers or on its own initiative. It frequently sets up working groups involving external scientists with relevant expertise to focus on specific matters and help produce scientific opinions. For any GMO and derived food or feed to be authorized in the EU, a company must submit an application for authorization on placing on the market in line with European legislation. In accordance with EU legislation, an independent scientific risk assessment is to be carried out by the GMO Panel. The Panel's independent scientific advice is then used by the Commission and member states when taking a decision on market approval (EFSA, 2012).

Labeling of Genetic Modification Foods and Consumer Choice

The issue of labeling the food products containing biotech ingredients is one that has been debated at length by both national governments and international standard-setting bodies for many years (CropLife International, 2012a,b). Whether or not to require labeling of GMO is a key issue in the ongoing debate over the risks and benefits of food crops produced using biotechnology. Those in favor of labeling emphasize on the consumers' rights to know what is in their food. Opponents of labeling point out the expense and logistical difficulties of labeling and the fact that no significant differences have been found between GMOs and conventional foods. The issue of labeling GM foods is a complex one that has yet to be resolved. What is clear, however, is that some kind of labeling policy will be adopted by most countries. Right now, the decision to label GM products is not so much related to the actual safety of the product, but rather to the fear associated with such products. The presence of a GM label should not imply that the product is less safe or is significantly different from conventional foods as all GM foods have to meet the safety standards before being approved for placing in the market for sale. The only way to develop and maintain a labeling system that is truthful, not misleading, and verifiable is to ensure that it is based on objective criteria, such as the actual composition of the food, and not on the method of manufacture. (ISAAA, 2004; Caswell, 2000; McHughen, 2001). Consensus among global regulatory bodies on the need for and potential implementation of biotech labeling regimes has been attempted via the CAC – the international food standards setting body established by the UN FAO and the UN WHO. In July 2011, after 20 years of negotiation, Codex adopted a text that does not endorse mandatory labeling; instead the text explicitly states that "any approach implemented by Codex members should be consistent with already adopted Codex labeling provisions." It also clearly states that there is no intent "to suggest or imply that foods derived from modern biotechnology are necessarily different from other foods simply due to method of production." In addition to the work at the international level through Codex Alimentarius, numerous countries have implemented their own domestic rules relating to labeling of foods containing biotech ingredients. Although domestic labeling rules vary considerably, they tend to fall into two categories: mandatory or voluntary labeling. More than 40 countries, including Australia, Brazil, China, India, Russia, Japan, Spain, and the UK, require genetically modified foods to be labeled. These countries have mandatory labeling laws that specify clear rules that must be followed when food products are known to contain biotech ingredients. Other countries, such as Canada and the US, have put in place voluntary labeling frameworks. Labeling regulations around the world differ widely in their scope, labeling exceptions for certain types of ingredients and degree of enforcement. Because of these differences in approaches, a food product with biotech-derived ingredients that must be labeled in one country does not necessarily have to be labeled in another country. Consequently, the observed effects of these policies on consumer choice, consumer information, food marketing, and international trade also vary significantly (CropLife International, 2011).

Canada

In Canada, special labeling is required for all foods where safety concerns, such as allergenicity and compositional or nutritional changes are identified. Labeling must indicate the nature of the change and must be understandable, truthful, and not misleading. Manufacturers can choose to label products to provide information regarding the presence or absence of GM ingredients, so long as the information is factual and neither misleading nor deceptive (ISAAA, 2004).

United States of America

In the USA, all foods must be labeled when there are health concerns, differences in use or nutritional value, or where the common name no longer adequately describes the food derived from the GM plant. In January 2001, the FDA released a Draft Guidance for the Industry: Voluntary Labeling. The document provides guidance to manufacturers in the

appropriate, truthful, and nonmisleading labeling of foods and provides examples of acceptable and unacceptable labeling language (ISAAA, 2004). The US FDA currently requires labeling of GM foods if the food has a significantly different nutritional property; if a new food includes an allergen that consumers would not expect to be present (e.g., a peanut protein in a soybean product); or if a food contains a toxicant beyond acceptable limits. Early in 2001, the FDA proposed voluntary guidelines for labeling food that does or does not contain GM ingredients. USA has a view that mandatory labeling would only be required if a product has been significantly changed nutritionally or if there have been changes in health-related characteristics (CropLife International, 2011).

European Union/United Kingdom

The new EU labeling regulation requires that any food containing GM ingredient or derivative in the amount more than 0.9% will have to be labeled. GM animal feed will also have to be labeled but products of animals fed GM feed, like milk, meat, and eggs, are not required to be labeled. Since 1997, EC regulation on labeling requires that the products intentionally containing GM ingredients must always be labeled, whatever be the level of content. The new regulation extends the range of products requiring traceability and labeling by including derived products – those with ingredients derived from a GM source that are not identifiable by analysis – as well as products consisting of or containing GMOs. Labeling is required for vegetable oils and other highly refined products where the genetically modified DNA or the resulting protein is no longer present or detectable in the final product. Adventitious presence (AP) of GM ingredient no higher than 0.9% requires no labeling (ISAAA, 2004).

Japan

Japan's Ministry of Agriculture, Forestry, and Fisheries (MAFF) is responsible for environmental safety approvals, feed safety approvals, and biotech labeling for foods. On 1 April 2001, MAFF established a labeling scheme that requires labeling for biotech food products if the biotech DNA or protein can be scientifically detected in the finished foods. MAFF regulations require labels for rDNA only if an ingredient is at least 5% of the total weight of the product (ISAAA, 2004).

Korea

The Korea Food and Drug Administration is in charge of inspecting GMO labeling on processed foods that use GM corn, soybean, or soybean sprout, or when these three goods are among the top five ingredients of a processed food product. Minor ingredients are exempt from labeling requirements. The threshold level of unintentional mixture of GMO to those three ingredients is 3%. Korea's Ministry for Food, Agriculture, Forestry and Fisheries also requires labeling for commodity shipments of the three goods if the shipment is destined for direct consumption and if it contains a biotech-enhanced component of 3% or higher. Identity Preservation handling certificate is required for no labeling. Revision of labeling is underway that requires all food, and any ingredients, directly produced from a GMO must be labeled, even if this GMO is undetectable in the final product (ISAAA, 2004).

Implications of Labeling Food

Labeling of GM foods does not advance consumer health information. Before entering the food supply, GM foods and ingredients must be approved for food safety by the national regulatory approval process. All scientific information to date supports the view that there are no health or food safety concerns with products derived from biotechnology. Food labels are often considered one way to support consumer choice and allow for differentiation of products in the marketplace; however, governments considering the implementation of labeling systems must carefully weigh the need to provide necessary and accurate safety information with the additional costs associated with labels that include marketing claims and nonhealth-related information. A study in Canada showed that labeling costs could be equivalent to at least 9–10% of the retail price of processed food products, and 35–41% of the producer prices. The study also concluded that GM and non-GM foods labeled as 'GM free' would be equally affected by this price increase, which amounts to US$700–950 million per year in Canada (KPMG Consulting, 2000). The costs include (1) farmers needing to segregate grains; (2) silos needing to be extremely careful about when they take deliveries to keep GM grains separate; (3) food processors needing to test shipments and so on down to the food chain. For any labeling provisions to be enforceable in relation to GM foods, they should be supported by reliable, validated methodologies for detecting the presence of transgenic protein or DNA. Workable labeling threshold levels for the presence of biotech-derived material in food, feed, and food ingredients are needed to facilitate accurate and truthful labeling. Labeling requirements should be science-based to give consumers meaningful information about the foods they buy and eat. Developing labeling regulations outside these scientific principles distracts attention from the legitimate health, safety, and nutritional issues related to food products. Mandatory GM food labeling provisions are costly to consumers, producers, and governments and can unnecessarily inhibit the development of innovative technologies to help feed a growing global population (CropLife International, 2012a,b).

Costs of Regulatory Compliance

The regulatory approval process for new GM crops is said to be slow and expensive, causing enormous burden to the developers who want to use this new technology to commercialize the biotech products. In fact, estimates of the compliance costs for the full regulatory approval of a GM crop are not available; as such information has been regarded as confidential by the developers of the biotech products. All GM crops are subjected to a series of full safety assessment and regulatory scrutiny during the developments of GM crops. Cost categories, for example, for insect-resistant maize include various experiments and tests, such as molecular characterization,

compositional assessment, animal performance and feeding studies, protein production and characterization, protein safety assessment, nontarget organism studies, agronomic and phenotypic assessments, enzyme-linked immunosorbent assay development, validation and expression analysis, environmental fate studies, toxicology tests, and so on. The compliance costs vary from one regulatory submission of safety documents to another with differences in the number and type of field trials, analytical tests, bioinformatic analysis, animal studies, and other comparative safety assessments, which are basically determined by the target crops, novel trait introduced, number of countries engaged in regulatory approvals, and the type of regulatory approval. Kalaitzandonakes *et al.* (2007) analyzed the compliance costs for insect-resistant maize and for HT maize. A range of costs incurred were estimated to be US$6 180 000–12 510 000 for HT maize, and a range of US$7 060 000–15 440 000 was estimated for insect-resistant maize. In this study, R&D costs were not included and if the indirect costs stemming from the unnecessary and unexpected regulatory delays are considered, the estimated compliance cost might go up. Falck-Zepeda *et al.* (2012) also estimate the cost of compliance with biosafety regulations in developing countries in a range of US$100 000–1.7 million. A recent study by Phillips McDougall (2011) showed (**Table 4**) that the overall cost to bring a new biotech trait to the market between 2008 and 2012 is on average US$136 million. The highest costs were associated with the discovery stages with the aggregated cost of US$31 million, followed by genetic sequence construct optimization procedures with a cost of US $28.3 million. However, collectively the costs of meeting regulatory requirements including testing and registration amounted to US$35.1 million, occupying 25.8% of total costs. A total cumulative time required to complete each stage of activities is approximately 11 years, presenting the longest time for registration and regulatory affairs of 65.5 months.

On the basis of the results of the survey into the actual time associated with each activity stage of the R&D process, the overall time involved in regulatory testing and approval appears to have increased. If this trend is real and continues it could have a significant effect on the cost of regulatory testing and authorization in future years. The results of McDougall's study are indicative of the costs and timelines required to discover, develop, and authorize a new plant biotechnology trait in a large-scale commodity crop, along with the associated import market approvals that are necessary for such a crop to enter the global grain trade, for example, maize, soybean, rapeseed, or cotton (Phillips McDougall, 2011). The compliance costs incurred by GM crop developers appear to be quite high. This can partly be attributed to the shrinking of development and commercialization of new GM crops. Agbiotech innovation and product development have recently slowed down, and high compliance costs for regulatory approval have been cited as one of the key constraints. One example that excessive regulation hinders the release of biotech crops for humanitarian purposes is the Golden Rice case. Ingo Potrykus, who developed provitamin A-enriched Golden Rice, pointed out that overly regulated, unjustified, and impractical legal requirements are stopping genetically engineered crops from saving millions from starvation and malnutrition. He pointed out that genetically engineered crops could save many millions from starvation and malnutrition if they can be freed from excessive regulation. The crop was stalled for more than 10 years by the working conditions and requirements demanded by regulations, including field test permission and safety data collection to satisfy the National Biosafety Authority (Potrykus, 2010; Fedoroff, 2011).

Emerging Issues

AP of biotechnology-derived materials in commodity shipments of grains, oilseeds, and their processed products remains a significant trading issue between the trading partners. It is critical to enable global bulk commodity supply chains to function effectively and efficiently. The term low-level presence (LLP) refers to a specific instance of AP. LLP is the adventitious presence of biotechnology-derived plant material in imported commodities that has completed a full safety assessment and has been approved for use in food, feed, grain, and derived products by the safety authority in one or more countries, including the country of cultivation. Under current bulk-handling systems for grains, there are many opportunities for crops to commingle during crop production, transportation, conditioning, and storage. Although many countries have zero tolerance for unapproved biotech products, LLP in GM crops is currently unavoidable. There are four different cases of

Table 4 Discovery, development, and authorization costs, and time of a plant biotechnology product

Category	*Cost ($ million)*	*Duration in months*
Gene discovery	31.0	46.7
Construct optimization	28.3	32.8
Commercial event production and selection	13.6	34.0
Introgression breeding and wide-area testing	28.01	42.0
Regulatory science	17.9	47.0
Registration and regulatory affairs	17.2	65.5
Total	136.0	268.0

Source: Reproduced from Phillips McDougall, 2011. The cost and time involved in the discovery, development and authorization of a new plant biotechnology-derived trait. A Consultancy Study for CropLife International. Midlothian, UK: Phillips McDougal.

unapproved biotech products that may be found in the food/feed supply. These are the cases where (1) biotech products that have received safety clearance for some use (e.g., feed) but not for others (e.g., food), (2) biotech products that have been approved for all possible uses in one or more countries but not yet in others, a case of asynchronous approvals, (3) experimental GMOs contained in laboratories, greenhouse, or field trials, which are found in the commercial food/feed supply chain, and (4) biotech products that have been reviewed but may have expired (Government of Canada, 2011). In consideration of the potential cases of LLP with structural asynchronicity, biotech industry, governments, and academia have realized in recent years that it may cause grain trade disruption as the biotech pipeline moving toward or awaiting regulatory approval has expanded, whereas regulatory approvals across different countries have become less synchronized. To actively handle any potential food/feed safety or environmental risks from the LLP of unapproved biotech products, some countries have developed their own national LLP policies which they can implement when the need arises. For instance, the Philippines is drafting 'guidelines of LLP risk management' by the formal adoption of Codex annex on LLP into their own policy. International organizations have also sought to facilitate the development of national LLP policies. In 2008, the Codex Alimentarius Task Force on Foods Derived from Biotechnology provided an international guidance for food safety assessment of biotech events authorized as safe for food and feed in one or more countries, including in the country of cultivation, but not yet in the country of import. Details on guidelines are described in the Annex on food safety assessment in situations of LLP of rDNA plant material in food. The Annex foresees that importing countries can undertake a simplified risk assessment in instances of LLP of products that have been fully approved in the country of export in a manner consistent with Codex risk assessment guidelines. Parallel efforts to develop guidelines for supporting environmental risk assessment have also been advanced by an OECD Working Group for the Harmonization of Regulatory Oversight in Biotechnology in the last few years. The OECD Working Group is preparing a technical review for the environmental risk assessment of LLP in seeds and commodities that can function biologically as seeds (International Food & Agricultural Trade Policy Council, 2011). With the increase in the global development of GM products, LLP situations are expected to increase, thus requiring a global approach for LLP. Therefore, it is important for all countries to review their LLP policies to work together to find an effective strategy for managing LLP. There will be a growing need to develop global strategies to manage LLP and to ensure continued and unimpeded trade of grains. When assessing a future LLP policy, several considerations should be taken as follows: (1) ensuring the safety of food, feed, and the environment, (2) minimization of unnecessary trade disruptions, (3) administrative efficiency, transparency, and predictability, (4) promotion of agricultural innovation, and (5) consistency with international guidance on LLP, such as the Codex guidelines, OECD, and FAO/WHO recommendations. As global demand for commodities continues to rise – and biotech crops increasingly produce much needed grain – it will be critical that trade policies support the uninterrupted flow of agricultural and food products to stabilize food supplies and reduce food price volatility. Although new biotech-derived crops will enable farmers to better cope with the effects of climate change, improve resource-efficiency, and increase yields, each new product also raises the potential for trade disruptions due to asynchronous approvals and concerns over the LLP of agbiotechnology products approved in the country of cultivation but not yet in the country of import. To prevent jeopardizing global food security, countries must immediately work toward solutions and exchange policies that minimize the risk to trade that stems from LLP situations. Increasing awareness of the impact of trade policies (or lack of policies) related to LLP, as well as encouraging synchronized approvals and the implementation of LLP policies will be essential to meeting this growing world's food supply demand supported by plant biotechnology. (Lukie, 2011; OECD, 2012).

Conclusion

Since the first commercialization of GM crops in 1996, in countries where GM crops are grown and widely consumed, there have been no reports of them causing any significant environmental damage or human health problems such as toxic, allergenic, or nutritionally deleterious reaction. It is due to the fact that robust scientific tests on GM crops before commercialization have been conducted and that the combination of testing by developers to meet regulatory requirements for safety clearance has been done. Extensive use around the world over a longer period of time with large exposed populations, and the absence of evidence of harm, does provide important proof of safety of GM crop. GM crops have been tested for 30 years, grown commercially for 16 years, and they have been proven safe and reliable as food and for the environment. There have been no cases of GM crops causing ecological harm or human health problems following 16 years of their cultivation and commercialization. The recent report from the EU that involved 25 years of research from 500 independent research groups concluded that GM crops are no more dangerous than other crops and are as safe as crops produced by conventional plant breeding. The EU, the Royal Society, and the US National Academy of Sciences all conclude that GM crops are safe and effective. If GM technology had not been available to the 14 million farmers using the technology in 2009, maintaining global production levels at the 2009 levels would have required additional plantings of 3.8 million hectare of soybean, 5.6 million hectares of corn, 2.6 million hectares of cotton, and 0.3 million hectares of canola. This total area requirement is equivalent to approximately 7% of the arable land in the US, or 24% of the arable land in Brazil (Brookes *et al.*, 2011). Furthermore, GM crops have reduced pesticide use by 390 million kg. GM crops are not the problem, but part of the solution to sustainably feeding 9 billion people. However, despite the fact that GM crops have many advantages to solve world hunger and poverty, there also exist groups who are less convinced, insisting that new technologies have limitations always bringing uncertainties and generating new gaps in knowledge. Strategies that could increase the efficiency of biosafety regulation without burdening GM crop developers with further unnecessary bureaucracy need to be established. There is a clear need for scientific communities to

do more research in a number of areas in biosafety research so that GM crop developers make good decisions in terms of new crop design and target plants, and also to develop products that meet wider consumer needs. The general view of the scientists is that the risks to human health and the environment are very low for GM crops; however, GM crops do present certain potential challenges in risk management. The situation may prove to be more challenging in the future, depending on the crops developed. There is a need to continue to develop safety-assessment technologies to keep pace with the advancement of GM crops with new traits.

Problems that are currently faced with in regard to GM crop regulation is that 'sound science' basis is not properly observed and applied in many countries; instead, most biosafety regulations are based on perceived risks rather than on real risks. The resulting unpredictable and less functional regulatory system causes delays in the approval of new crops. Even the creation of regulatory systems that demand extensive assessment followed by a lengthy decision-making process do more to serve as barriers to trade and new crop development than they do to ensure safety for consumers. It is very important to maintain a global, innovation-friendly regulatory environment – one that is predictable, functioning, transparent, and guided by good science. Science-based and globally harmonized regulation is the most effective way to ensure that farmers have the choice of the best available technologies to help them meet their own agricultural needs in a sustainable way. As new applications of biotechnology are evolving rapidly, regulatory requirements and guidelines also must be able to adapt quickly and applied using on a case-by-case principle. It is fair to say that there is no case where there exists a 100% risk-free situation. Therefore, it is important to have a balanced view on the risks and benefits of GM crops.

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Breeding: Animals

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Glossary

Deoxyribonucleic acid (DNA) sequence Ordered sequence of the DNA nucleotides adenine (A), cytosine (C), guanine (G), and thymine (T). An animal's genome is its complete DNA sequence.

Effective population size Number of animals in an ideal population that would result in the same genetic diversity as an actual, usually much larger, population.

Genetic effects (additive, dominant, recessive, and overdominant) These terms describe the phenotype of the heterozygous genotype compared to the phenotypes of the two homozygous genotypes. When the heterozygote is equal to the average of homozygotes, equal to the smaller homozygote, equal to the larger homozygote, or exceeds the larger homozygote, then gene effects are called additive, recessive, dominant, or overdominant, respectively.

Genetic evaluation A prediction of the genetic value of an animal as a parent. Genetic predictions are used to predict average phenotypic differences between progeny from different parents.

Genotype A genotype describes which form of a particular polymorphism an animal has. An animal with two copies of one form is homozygous and an animal with one copy of each form is heterozygous.

Heterosis The difference in the phenotype of crossbred animals compared to the average of the purebreds used to make the crossbred.

Inbreeding coefficient Estimate of the proportional increase in DNA nucleotide pairs that have identical ancestral origin due to using related parents compared to a base population.

Permanent and residual environment Residual environment is the nongenetic proportion of differences between contemporary animals. Permanent environment describes nongenetic differences that are repeatable over time and repeated measurements.

Phenotype A characteristic or trait of an animal such as weight, milk production, litter size, or hair color.

Polymorphism A difference in DNA sequence among animals. Polymorphisms can be nucleotide sequence changes (e.g., AGG or ACG), deletions of nucleotides, or other differences.

Brief History of Breeding Livestock

Breeding and selection of animals probably began with domestication. Genetic changes in livestock occurred well before herders, shepherds, and caretakers understood genetics or the processes of evolution. Robert Bakewell, an eighteenth-century Englishman and influential livestock breeder, promoted the concepts of breeding to be the best, evaluating breeding animals relative to his concept of an ideal animal, and using inbreeding to fix desired traits. These concepts eventually led to identifying and recording parentage of animals, the formation of breed societies that kept pedigrees and set standards for animals considered as members of the breed, and either deliberate mild inbreeding in breeds and strains or unintentional inbreeding due to a limited number of parents available.

Motivation for Selection

The movement toward development of breeds and strains with pedigreed animals lacked a strong scientific basis. However, the diversity created among breeds and the availability of multiple-generation pedigrees fueled the application of scientific breeding in the twentieth century. Application of the principles of Mendel, mathematics of genetics and evolution, and objective measurements by livestock breeders is making steady and sometimes rapid genetic changes in animal traits and products important to livestock production and consumers.

Although livestock breeders accelerated genetic change, many also shifted from a goal of an ideal animal to emphasize other outcomes. These outcomes often included profit, income, and cost of livestock production. Livestock breeders more closely examined what traits affected income and costs. Usually, examination identified a need for including more animal and product traits in the description of income and costs and in the traits needing genetic evaluation. Some livestock industries integrate breeding through product marketing segments under a single ownership or cooperative. Integration often leads to broader definitions of selection goals compared to owners involved in a single segment of the multisegmented industry. Product pricing schemes can play a role in livestock breeders' selection goals for segmented industries. Payment for milk fluid volume or milk protein sends profit-oriented signals from milk processors through commercial dairy producers to dairy cattle breeders and encourages measurement and genetic evaluation of different milk traits. Appropriate pricing of products can cause livestock breeders to make selection decisions beneficial to their industry even though it could otherwise not be beneficial to their industry segment.

Other desired outcomes of selection are the control or elimination of genetic defects; reduced incidences of disease, parasites, parturition difficulty, and lameness; improved animal well-being through adaptation to management and to the ambient environment; and reduced effects of animals on the

environment. Livestock breeders whose main business is the sale of breeding animals may choose to emphasize traits that differentiate their animals from those of competitors. Many livestock breeders face the dilemma of wanting to simplify their breeding programs while improving the genetics of many traits. Selection to improve some traits might result in negative changes in other traits. Simple approaches to selection may hide negative effects in traits not considered for selection.

The selection index is one of the methods of distributing selection among several traits to predict a desired selection outcome. In its simplest form, the selection index multiplies predictions of genetic differences for several traits by index weightings and sums the products for each animal. Breeders use the index rather than individual trait genetic evaluations. Objectively defined, profit-driven indexes weight traits according to economic values reflecting incremental changes in costs and returns. Subjective weights and constraints can alter economic indexes to address traits that are difficult to value economically like animal behavior. Other weightings of traits can result in proportional genetic changes among traits or preventing genetic change in one or more trait whereas other traits do change.

Modern Genetic Theory and its Adoption

Breeding animals begins with a decision to continue with a current population of animals or to replace part or all of it with new breeds or lines. Region, country, climate, management, prevalent diseases and parasites, product types, import restrictions, and history influence popularity and choice of breeds and lines. For some species and places, livestock producers used the same breeds over long periods, but in other species and places they often changed the breeds. The predominant breed for dairy cattle production is Holstein in many countries with temperate climates. Commercial egg production depends on selected lines developed from Leghorn chickens. Beef cattle, swine, and sheep producers use many breeds to adapt to regional and marketing differences.

Beef cattle, poultry, and swine make wide use of crossbreeding. Crossbreeding uses two or more breeds or lines and can make use of divergent breeds resulting in less focus on a single breed. For beef cattle breeders this lack of focus on a single breed has often led to creating new breeds by combining existing breeds.

Following the choice of a breed or crossbreeding system, livestock breeders make genetic changes by selecting animals that are different from average and use them as parents. A single equation, often referred to as the breeders' equation, captures many features of livestock selection. The equation for genetic change measured in units of genetic standard deviations per year is simply intensity of selection times accuracy of the genetic evaluation at selection divided by age of the parents when progeny are born (intensity $\times$ accuracy $\times$ time^{-1}). Although simply stated, the components are interrelated. Changing one often changes another.

Each livestock species and type of product present a different set of potential changes for intensity, accuracy, and time. These sets of potential changes explain why livestock breeders implement different selection programs for each species. Breeders of livestock producing milk and eggs often rely on progeny information resulting in higher accuracy genetic evaluations, moderate selection intensity, and older parents. Breeders of livestock emphasizing growth in young animals can use information on the parents resulting in less accuracy, more intensity, and younger parents.

Advances in technology alter potential changes for intensity, accuracy, and time. These advances can increase genetic change per year and can lead to changes in the design and operation of selection programs. Reproductive technologies can change intensity of selection by increasing the number of progeny per parent, increase accuracy of genetic evaluation by producing more closely related animals, and decrease parental age by allowing more rapid replacement of parents. Advances in measuring animals can increase accuracy by reducing errors, by making repeated measurements possible, and by adding traits not previously available for genetic evaluation. Measurements modified for use on younger animals can result in earlier selection. Genetics and genomics technology can increase accuracy and allow selection at younger ages.

Selection programs consist of four pathways: sires of males considered for selection, dams of these males, sires of females considered for selection, and dams of these females. These pathways often have different intensities, accuracies of selection, and ages of parents. Intensities of selection for parents of males considered for selection are usually higher than for parents of females and males not considered for selection. Analyzing these pathways guides evaluation and choice among selection programs.

Documenting Genetic Change in Livestock

Livestock breeders made large changes in animals over a long time. Selecting European pigs during the twentieth century resulted in a 90–100% increase in growth rates and a 60–70% decrease in backfat thickness, but little change in litter size (Merks, 2000). Changes in growth rate and backfat thickness accelerated in the second half of the century with greater specialization and adoption of new genetic evaluation technology. Broilers representing 2001 commercial strains weighed 4 times those of strains representing 1957 broilers when fed a 2001 diet and 3.5 times as much when fed a 1957 diet (Havenstein *et al.*, 2003b). Yield of breast meat averaged 20.3% for 2001 broilers versus 11.9% for 1957 broilers (Havenstein *et al.*, 2003a). Comparisons of 2001 and 1957 broilers on 2001 and 1957 diets show that genetic changes are responsible for most of the performance changes. Flock and Heil (2002) reported increase of one-third for eggs laid and a decrease of one-third in feed consumed per weight of egg laid during 24 years of testing commercial laying hens in Germany. Genetic trends in Holsteins show milk yield more than doubling from 1957 to 2010 (Animal Improvement Programs Laboratory website). Rates of genetic change for important traits now exceed 1% annually in many livestock species. In addition to broad genetic changes in the livestock industries, experimental selection demonstrated large genetic changes in many common or uncommon traits like resistance to facial eczema, a disease in sheep (Morris *et al.*, 1994), and increased twinning in cattle (Gregory *et al.*, 1997). Genetic changes in

some of the uncommon traits point to possible future expansion of the definition and goals for livestock selection.

Technology and Organization of Modern Selection Programs

Electronics

Accurate information is paramount to successful selection programs. Information vital to the genetic evaluation supporting these selection programs consists of individual animal identification, pedigree information, and phenotypes. Estimates of the accuracy of the individual's predicted breeding merit complement genetic evaluation results. This accuracy is predicated on the assumptions of the model used to create the predictions of merit being the correct model and on accurate information being recorded. Electronic capture of animal identification and phenotypes improves the integrity of the information contained in the national datasets used for genetic evaluations.

Electronic identification such as Radio Frequency Identification (RFID) equipment, ear tags and ear tag readers, allow livestock producers to scan the identification of an individual directly into a recording system; hence, eliminating the potential errors of human recording. Phenotypic information can often be collected at the same time and hence automatically collated with the identification of that individual. Misidentification or inaccurate association of phenotypes to individuals compromises the precision of the evaluation. Accuracy is a statistical result based on the assumptions of a correct model and errorless information, whereas precision is a concept that relates to the validity of these assumptions.

In some cases, electronically collected data may also be more accurate than the same data appraised by humans. Electronic scales calibrated to obtain weights at stability can be more accurate than the same weights recorded by the person watching the scale. Instrument grading of carcasses for quality measures (e.g., marbling score) is objective and more accurate than visual appraisal for the same measurement.

Electronic transmission of information to central databases expedites the process of data entry into the genetic evaluation database. Previous methods depended on data being transcribed and mailed to central locations and finally entered manually into the database with iterations of checks to validate the integrity of the information. Electronic transmission of digital data allows for immediate submission, electronic queries of the data to check for errors (e.g., data outside of acceptable ranges), and direct database query of the information to ensure consistency of new data with data entered previously into the database (e.g., sex of the individual). Electronic searches of the database provided via the web allow access to genetic evaluation information immediately on creation. Electronic distribution of files of evaluations directly to the owners of the animals speeds up the process of selection. Finally, highly computerized systems of data capture, validation, and synthesis lend support to more frequent genetic evaluations that in turn provide more timely information for selection decisions earlier in an animal's life. An example of frequently run genetic evaluations is the American Angus Association® genetic evaluation that runs weekly (Angus genetic evaluation website).

DNA Technologies

Application of DNA-based technologies for livestock improvement starts with on-farm collection of animal tissue samples. Those samples are then transferred to a laboratory, where DNA is extracted for genotyping and the genotypes are interpreted to provide the livestock breeder with information for selection and mating decisions. Any tissue containing DNA is a possible sample. Blood and hair follicles are common DNA sources for cattle. Ear notches and tips of tails are convenient to collect when processing piglets at birth. Sampling systems must ensure cleanliness and avoid contamination with foreign material and DNA from other animals. It is vital that the system maintains identity of the sample so that DNA-based information corresponds to the animal that was sampled (e.g., creation of a DNA sample collection website). Some systems use prelabeled sample containers and barcoded tissue sampling ear tags. These types of systems use the same identification for sample and animal tag and can reduce labeling errors to maintain consistency between animal and sample identity.

Collection and processing of DNA samples must occur before making decisions. One of the uses of DNA information is identifying genetic defects. Decisions on a carrier animal (one normal DNA copy and one mutated DNA copy) and its parents can occur any time between birth and use as a breeding animal. Information from animals sampled and genotyped soon after birth allows quick use of information in the parents. In purebred animals, breed associations often post identities of carrier and related animals and indicate their carrier status on pedigrees for a few mutations that are verified and important to the breed. DNA sequencing of animals reveals many mutations at very low frequencies that could adversely affect animals if they had two copies of the mutated DNA. Reporting and transmitting DNA mutation information needs to evolve so that livestock breeders can consider many more mutations.

Determination of parentage is a growing use of DNA testing. In many cases, the livestock producers know the mother at birth but the sire might be any one of a group of sires. Results of parentage from DNA tests returned to livestock producers have different formats. Identification of the most likely parent and its reliability is useful to livestock breeders.

Genetic evaluation systems based on phenotypes require parentage. The parent–progeny connection allows progeny phenotypes to contribute to genetic evaluation of parents and also allows parent information to contribute to genetic evaluation of the progeny. For breeding animals, parentage information is critical for either avoiding inbreeding or creating inbred animals. Parentage determined from DNA samples collected soon after birth allow undelayed incorporation of progeny phenotypes into genetic evaluations.

Livestock breeders receive results of early genetic tests based on DNA several ways. Results can consist of actual DNA differences, predicted effects of DNA differences, and categories of predicted effects. Current tests use many DNA differences and

breeders may receive a predicted value based on them. Genetic evaluation service providers also may directly capture DNA test results and incorporate with other phenotypic and pedigree information. DNA tests can occur any time after an animal is born and information should be entered into genetic evaluation systems at the same time. Electronic transmission and modern inventory and tracking systems help maintain fidelity of information across breeders, providers of DNA tests, breed associations, and providers of genetic evaluations in industry-wide genetic evaluation schemes.

Reproductive Technologies

Reproductive technologies have a tremendous effect on the rate of genetic change in domesticated livestock species. Primarily, most of these gains occur because of increases in the number of progeny possible per individual. Examples of these technologies are artificial insemination (AI) and multiple ovulation embryo transfer (MOET). However, adoption rates of some other reproductive technologies are not only less than AI but they also have the potential to increase rates of genetic change.

Cattle producers have had commercial access to AI since the 1940s, with the establishment of standard procedures and organization of AI cooperatives (Foote, 2002). The use of semen extenders, technology to freeze semen and maintain viability, and the ability to divide a single ejaculate into multiple inseminations has overall increased the utility of AI. As of 2010, the percentage of US dairy cows bred by AI exceeds 60%. Other domesticated livestock species, especially swine and poultry, also heavily use AI although the viability of frozen semen is less than it is in cattle. Difficulty with depositing semen through the cervix of ewes has limited the use of AI in sheep though many large international flocks use laparoscopic techniques.

Similar to AI, MO*Et* allows a female to produce more offspring than would be possible using natural service breeding schemes. For this process, the female is superovulated (using a follicle stimulating-like hormone) and then inseminated. Recovery of fertilized embryos occurs before implantation. These embryos are placed in recipient females to produce calves from the donor female. Cryogenically freezing these embryos adds more options for using them. Shipping frozen embryos to multiple locations or delaying their transfer is possible. In general, cost decreases the use of MOET compared to AI. It is also difficult to identify genetically superior females before using MOET because females have few progeny to prove their genetic merit.

For sex-limited traits, such as milk production, both AI and MOET offer advantages to most of the components of the breeder's equation. More progeny increases the accuracy of selection for the parents. For example, dairy bulls have hundreds of daughters tested for milk production using AI. The larger number of progeny increases selection intensity as fewer sires (AI) or dams (MOET) are needed to produce the next generation of breeding animals. MOET can decrease the generation interval because a bull and a cow are more likely to produce progeny to replace themselves from their first mating. Not surprisingly, both of these advances have had their greatest impact on livestock species with low prolificacy.

Several other reproductive technologies can also increase the rate of genetic change per year in the breeder's equation. Two of these technologies are sexing semen and cloning.

It is possible to sex semen because X-containing sperm have approximately 4% more DNA content than Y-containing sperm (Seidel, 2012). As a result, semen can be sorted into highly probable Y-containing sperm (male) and X-containing sperm (female) using laser-based cell sorting and a fluorescence measure of DNA content. Some possible economic and selection advantages from using sexed semen in dairy and beef cattle production are as follows: (1) increased production of bulls to progeny test more quickly in dairy breeding operations decreases generation interval, (2) increased production of females for milk evaluation from the resulting males in dairy breeding herds increases accuracy of selection, (3) production of heifer calves to replace females in fewer matings, and (4) increasing desired sex ratio in herds designed to produce either replacement bulls or cows for crossbreeding (Hohenboken, 1999). This final application is particularly useful when breeding females with a different type of male. The technology is far from mature due to decreased fertility, high costs, and the time required to sort semen for sex differences (Seidel, 2012).

Cloning in the form of zygotic splitting has been possible in mammals since the mid-1980s. More recently, and with much publicity, somatic-cell nuclear transfer was developed to clone animals from adult donors (Wilmut *et al.*, 1997). Both of these technologies have the potential to affect genetic change. However, the advent of nuclear transfer procedures opened up the potential to clone an animal with a known phenotype and a less well-known genetic potential. Still cloning may offer some advantages in the breeder's equation. Van Vleck (1999) offered some possibilities such as improving dairy progeny testing by cloning the best performing cows to reproduce the cow population and by the selection of cloned progeny. General improvement in accuracy or intensity of selection is possible by balancing the testing of clones with selecting from a limited parental pool. Owing to the costs associated with successful nuclear transfer clones, these gains may not offset current costs of cloning. Additionally, predicted increases in accuracy of selection may be less if performance of clones does not completely reflect natural conditions due to transfer to a recipient female.

Communication and Presentation of Genetic Evaluations

Genetic evaluations provide information for selection; hence ideally, the most recent information would be included in the evaluation of an animal at the time of a selection decision regarding that individual. For species with national programs for genetic evaluation, this scenario could be difficult to achieve for all producers involved in that national program. For example, seasonal breeding of a species (e.g., beef and sheep) focuses on the timing of selection for prebreeding. However, even among species where seasonal breeding is predominant, in large geographical regions such as the United States, the timing of breeding can vary by several months. Year-round breeding programs (e.g., dairy and swine) require frequent access to information to ensure inclusion of updated information.

Historically, national and international associations providing genetic evaluation services to their membership published annual or biannual evaluations. Constraints on more frequent evaluations were data collection and reporting, computing capacity to run the large evaluation programs, and time needed to assemble the results in a publication form (e.g., a sire summary). Interesting nuances peculiar to some traits also challenged the incorporation of new information. For example, producers record and report a dairy cow's monthly performance or a hen's weekly egg count but the trait of interest is total lactation production (the accumulation of all monthly production records) or yearly egg production. Yearling weight may be the trait of interest at weaning but at the time of selection all that is available are correlated birth and weaning weights. Lactation projection strategies based on partial records (using available monthly records of a lactation in progress to predict total production) and multiple trait evaluations capturing information from correlated traits are just two examples of strategies designed to improve the timeliness of evaluations for these situations.

As electronic reporting of data became routine and organizations moved to electronic delivery of genetic evaluation results along with or instead of publications, the timeliness of evaluations improved. Web-based programs allow producers to search and obtain genetic evaluation information online to expedite this process (e.g., Angus sire search and Holstein search websites). These searches allowed producers to identify animals that meet specifications in traits of interest quickly.

As computing capacity and electronic movement and access to information improved, the opportunity to provide more frequent evaluations became possible. For example, the American Angus Association provides weekly runs of genetic evaluations. Another strategy used is to provide interim evaluations that evaluate information from a particular producer alone instead of running the entire national program at the time the information is received. Updates of interim evaluations occur when the national program runs.

Awareness and interest regarding the value of genetic information increased in the animal industries, and so did the desire to record and report evaluations for many more traits. For example, at the Angus sire search website breeders can search the database of evaluations for eighteen individual traits. Efficient selection based on individually considering this plethora of traits is difficult. An alternative to considering individual traits is combining the information into indices designed to reflect selection objectives. At the Angus sire search website, one could search the database for animals that excel in indices (expressed as dollar values) for predicted value at weaning of calves, to feedlots, or the value at harvest of the progeny of an animal considered for selection. The dollar value prediction of calves at weaning is an index consisting of 4 of the 18 individual traits reported:

1. Birth weight – influences difficulty during birth and calf survival hence percent calf crop weaned;
2. Weaning weight – influences revenue;
3. Maternal milk – influences weaning weight hence revenue; and
4. Mature cow size – reflect maintenance requirements and hence expense.

The poultry industry began using indices of up to 16 traits for selection in the 1950s (Kashyap *et al.*, 1981). The presentation of information in the form of indices not only expedites the process of identifying animals that are superior for the function targeted by the index but also more accurately combines information on the traits going into the index leading to more accurate selection decisions for the targeted application. Use of predicted index values of possible future progeny makes it easy to decide the pairing of selected males and selected females.

Selection among Breeds and Lines

Diversity among breeds and lines within breeds makes rapid genetic changes in herds and flocks of livestock possible. A change in breed or line is a one-time event with potential for making important adjustments to the genetic base of a herd or flock. However, forming new breeds is not a sustainable approach to continued genetic change.

Breed and Line Formation

Geographical isolation, political boundaries, natural selection for adaptation to the environment, and selection by humans played roles in forming breeds. Breed formation by crossing existing breeds and interbreeding the crossbreds continues today as livestock breeders attempt to combine desirable and moderate undesirable aspects found in different breeds.

The process of forming and propagating breeds necessarily restricts the available number of potential parents that meet the specifications for inclusion in the breed. Typically, many livestock breeders want to maintain high relationships in an even smaller group of animals and ancestors that are influential and sought after in the breed. The genetic relationship between two animals probabilistically describes the shared DNA. Example relationships are 0.5 for parent and a progeny or for two progeny from the same parents, 0.25 for a grandprogeny and a grandparent, and 0.25 for any two progeny sharing a single parent.

Some livestock breeders intentionally mate related animals to maintain even higher relationship to influential ancestors through both sire and dam. Mating related animals results in inbred progeny. Inbreeding coefficients probabilistically describe the proportion of DNA nucleotide pairs with identical parental DNA origin. Inbreeding coefficients of progeny are one-half of the relationship between the parents. Examples of progeny inbreeding values are 0.25 for parent–progeny mating and 0.125 for mating any two progeny sharing a single parent.

Inbreeding also occurs unintentionally over time. Many generations of repeated emphasis on a few animals of every generation cause most animals to have some shared distant ancestry. This results in progeny with low levels of inbreeding that increase over time. Parents with many progeny contribute little more to a population's diversity than parents that produce a few progeny. A concept called effective population size describes the genetic size and diversity of a breed. Effective population size estimates the number of unrelated parents needed to create the same diversity as found in an actual

population that has related parents, some who produce many progeny. Even in breeds with tens of thousands of animals, the effective size may be a few hundred or less. Smaller effective sizes result in larger increases in unintentional inbreeding. McParland *et al.* (2007) estimated an effective number of 75 for the more than 200 000 Holstein-Friesian dairy cattle born in Ireland in 2004. Most long-established breeds fluctuate in popularity and numbers throughout their history. The introduction of breeds into new areas and countries may consist of importing a few hundred animals or less. When numbers are low (called a bottleneck), effective numbers are reduced further and have a lasting effect on unintentional inbreeding in the breed.

Inbreeding increases the proportion of DNA that is identical in paired chromosomes (homozygous). Homozygous DNA increases the predictability of progeny. Some livestock breeders use inbreeding with the objective of producing more uniform and predictable animals. However, inbreeding increases the proportion of homozygous DNA with undesirable effects as well as desirable effects. Inbreeding itself cannot increase desirable homozygous DNA without increasing undesirable homozygous DNA. Inbreeding often reduces reproductive success of parents, vigor of offspring, and growth (inbreeding depression).

Following the early twentieth-century scientific and commercial successes of hybrid corn created by crossing inbred lines, livestock geneticists hypothesized that simultaneous inbreeding and selection might overcome the detrimental effects of inbreeding alone. An expected advantage of inbred lines is increased variation among the inbred lines compared to variation within the original, preinbred breed. Results of many experimental inbred lines developed into different livestock species demonstrated that selection usually could not overcome the undesirable effects of inbreeding on reproductive success and vigor. Inbred lines in low prolificacy species often failed to sustain the line due to low reproduction and survival. Still, a few mildly inbred lines survived and contributed toward improving some breeds (e.g., Line 1 Hereford; MacNeil, 2009). New genomics technologies may enable creating inbred lines with simultaneous selection of desirable homozygous DNA and elimination of undesirable homozygous DNA.

Breed Comparisons

Breeds and lines within breeds arose from different base populations with different selection histories, effective sizes, and are often not farmed or raised together. Unbiased estimates of trait differences are important for deciding how to use breeds and lines. Governments, livestock organizations, international aid organizations, and companies compare breeds and lines for the benefit and education of livestock producers and for internal use and merchandising by companies. The number of breeds and lines compared and the duration of comparisons vary considerably. Some organized comparisons extended for more than 50 years.

Methods to compare breeds and lines depend on many circumstances. The best approach samples the breeds so that they represent the genetics that are available to livestock producers fairly and accurately. Management, environment, nutrition, disease and parasite prevalence, and marketing can all influence comparisons. Usually, conditions that are representative of most livestock production result in the most relevant comparisons. When production occurs in widely different conditions, it may be desirable to compare breeds and lines in more than one set of conditions.

When comparing well-established breeds and lines, one approach is to sample young animals or fertilized eggs, bring them to a common location, and rear them together. Although conceptually simple, some problems can occur. Broad sampling of many animals with low genetic relationships will likely involve many producers. This situation can cause logistical and timing problems, especially when different breeds tend to be in different regions. Effects of different pretest maternal and offspring management may last into the test period and pretest exposure to some diseases may result in more resistance or susceptibility during the test. If any of these or other pretest conditions are different among breeds, then breed differences on test could partially reflect pretest conditions.

Another approach is to sample animals from breeds and lines and use them as parents in a common location. Progeny from these parents are then born and reared together. Comparisons are free of pretest influences but this type of comparison usually requires more resources and time to complete.

Creating new breeds and lines or importing existing ones into a new country or region can make broad sampling of females for testing impractical. Other situations can make sampling and assembling females for testing difficult such as sampling a breed from a large geographical area. In addition, the use of some breeds and lines is mostly as sires of progeny for harvest and the performance of reproducing females is unimportant. In cases like these, sampling sires from different breeds and lines and breeding them with an unrelated population of females can estimate one-half of the differences among them. Keeping daughter progeny for breeding can estimate one-half of the differences in female reproduction.

Crossbreeding Systems

Breeding males and females of the same breed, called straight breeding or pure breeding, is one way to use breeds and lines. Breeding males of one breed with females of another breed is crossbreeding. Many livestock production systems benefit from planned crossbreeding systems. The benefit is derived from two factors known as heterosis and complementarity.

Heterosis has a genetic basis and describes the difference in performance between crossbred animals and the average of the purebreds used to create the crossbred. Several causes of heterosis are possible and not exclusive. Many studies of heterosis in livestock point to dominance as the primary cause but experiments designed to estimate heterosis often have difficulty separating dominance from other possible causes such as epistasis, the effects derived from combinations of two or more differences in DNA. Dominance occurs when DNA at the same location on a chromosome is not identical among animals and those with pairs of nonidentical DNA perform differently from the average of those with identical pairs

of DNA. If dominance causes heterosis, then heterosis is the sum of dominance at many different pairs of nonidentical DNA.

In some ways, crossbreeding and heterosis are the mirror images of inbreeding and inbreeding depression. Crossbreeding and inbreeding both manipulate the proportions of homozygous and heterozygous DNA, inbreeding by increasing homozygosity and crossbreeding by decreasing heterozygosity. One interpretation of heterosis is that it recaptures the accumulated inbreeding since the breeds separated genetically. Partially, heterosis values can differ among breed crosses because breeds separated at different times and have different genetic histories.

Proportional or percentage differences describe the magnitude of heterosis. Low values are near zero, moderate values are 5% or 10%, and a high value is 15%. Heterozygosity of a cross between two breeds is similar for DNA affecting most traits but levels of dominance and therefore levels of heterosis are different. Traits with low, medium, and high heterosis occur in the same cross of breeds and can be measured in or attributed to sire, dam, or progeny. Generally, heterosis for product (egg, meat, milk, and wool) quality traits is low; it is moderate for growth and feed efficiency; and is moderate to high for reproduction and survival. Heterosis for cumulative traits (e.g., a beef cow's lifetime calf production) is often high.

Many different systems of crossbreeding are possible. One factor in deciding among systems is the expected heterosis expressed in sires, dams, and progeny. Expected heterosis depends on the probability of pairing DNA from two different breeds. Multiplication of this probability by estimated heterosis results in expected heterosis.

Three broad types of crossbreeding systems are rotations, terminal crosses, and composites. Comparisons of crossbreeding systems for heterosis utilization usually report proportions of maximum heterozygosity and therefore maximum heterosis. Maximum heterozygosity occurs when two unrelated breeds are mated together to produce a progeny, dam, or sire. A two-breed rotational system mates sires of one breed with dams of a second breed to produce first-generation progeny. Sires of the second breed mated with first-generation progeny produce the second generation. Sires rotate between the two breeds each generation. After several generations, expected proportion of heterosis is 2/3 for dams, 2/3 for progeny, and 0 for sires. If the rotation is expanded to 3, 4, or 5 breeds, then the expected proportions of heterosis are 6/7, 14/15, or 30/31. Rotational systems replace dams from the progeny and do not need an additional source of breeding females.

Another crossbreeding system taking advantage of heterosis is composite formation. Formation of composites begins with creating crossbreds with a desired breed composition and then using them as parents of the next generation. Progeny from the first generation become parents of the next generation and this continues in future generations. Expected heterosis depends on the number of breeds and their proportions in the initial crossbreds. If the initial crossbreds consist of equal proportions of 2 or 4 breeds, then expected proportions of heterosis are 1/2 or 3/4 in later generations. Expected proportion of heterosis in a composite composed of 1/2 of one breed and 1/4 each of two other breeds is 5/8. Composites need large effective population sizes to limit inbreeding and loss of heterozygosity. Composite formation is also a method of creating new breeds by bringing together desirable traits from different breeds and eliminating most of the inbreeding from the contributing breeds.

The simplest terminal system mates sires of one breed with dams of another breed and sells all progeny for harvest or production. In this system, progeny express 100% heterosis but sires and dams express none. In addition, replacing breeding females from another source within or outside the enterprise is a cost to include in evaluating terminal systems. Variations on the simple terminal system use crossbred dams and crossbred sires. These variations not only increase expected heterosis in dams and sires but also increase complexity of the mating system.

A thorough evaluation of crossbreeding systems includes differences in the value of the breeds as well as expected proportions of heterosis. Adding more breeds to rotational or composite crossbreeding systems not only increases heterosis but can also decrease the average value of the breeds used. Progeny and dams in rotational and composite systems have the same breed proportions averaged across generations. Terminal systems have the opportunity to use breeds that excel in maternal traits as dams and breeds that excel in production and product traits as sires of progeny used for those purposes. Complementarity is the term used to describe the ability to take advantage of breeds' strengths in maternal and sire roles. These specialized breed roles in crossbreeding systems also allow for selection within the breeds to enhance their value for the role.

Genetic Evaluation Using Phenotypes

Components of Phenotypes

Genetic evaluation is the process of predicting an animal's value as a parent. Given a choice between two animals to use as a parent, genetic evaluation predicts the average difference between their progeny and the reliability of that prediction. Livestock breeders can then use these predictions of progeny differences for many different traits to select parents.

Phenotypes are basic pieces of information for genetic evaluation. Phenotypes are measurements, counts, and observations of animal characteristics. Animal weight, carcass length, fat thickness, muscle area, and volume of milk produced are examples of phenotypes measured by scales, rulers, and other devices on a continuous scale with many possible values. Eggs laid in a year, pigs born in a litter, number of inseminations per cow, and lambs produced during a ewe's lifetime are examples of counting phenotypes. Presence of horns and hair color are observational phenotypes.

Partitioning phenotypes (P) into components is the first step in genetic evaluation. The simplest partition is two components, genetics (G) and environment (E), or $P = G + E$. The traditional term for the nongenetic component is environment. However, environment does not mean just weather or housing in the context of genetic evaluation. Environment is really everything that appears to cause variation in phenotype but is not genetic. It is the residual phenotype after accounting

for genetics, E = P − G. This can include measurement errors, random interactions with other animals, and an accumulation of minor events in the animal's life.

Repeated measurement of a phenotype throughout the life of an animal can lead to a second level of partitioning. Some repeated phenotypes are milk yield from different lactations of a dairy cattle and litter sizes from different parities of a sow. The same genetic component repeats each time but some of the environment components may also be long lasting and repeated. The simplest way to account for this is to partition the residual (environmental) component into a long-lasting component, traditionally called the permanent environment (PE), and a temporary component (E). The phenotype now consists of genetic, permanent environment, and temporary environment, P = G + PE + E. Two measurements of the same animal repeat the same genetic and PE components but have different temporary environments.

Mothers can affect the phenotypes of their suckling progeny, especially phenotypes like weaning weights measured in young animals. The amount of milk produced by the mother is one maternal factor but general maternal care and the uterine environment are other possible factors affecting progeny. The mother's genetics (GM) may affect any of these factors. A simple partitioning of phenotype affected by maternal genetics is to sum an animal's genotype, mother's genetic effect, and the residual (environment): P = G + GM + E. The animal's genetic component (G) is known as the direct genetic component when both animal and maternal genetics affect a phenotype. The residual component (E) actually consists of two components: maternal residual and calf residual. For some traits like weaning weight, considering the long lasting (PEM) and temporary parts of the maternal residual component is important. Temporary maternal and temporary calf residual components are indistinguishable and combined into a single residual component (E). Components of weaning and preweaning phenotypes usually considered are animal and maternal genetics, long-lasting maternal residual, and temporary residual: P = G + GM + PEM + E. Two animals born to the same mother in different years have the same maternal genetic and long-lasting maternal environment components and share half of the direct genetic component inherited from their mother.

Ascribing phenotypic values of 15 000 kg of milk or 200 eggs to genetics and environment does not mean that genetics account for 6000 kg of milk or 110 eggs and environment accounts for 9000 kg of milk and 90 eggs. Rather, components ascribe differences among phenotypes of animals to genetic and environment. On an average, 2 eggs of a 10-egg difference between hens might be considered genetic and 8 eggs might be due to environment.

For genetic evaluation, identifying systematic sources of environmental differences among animals is desirable. Once identified, options for standardizing the residual environmental component of phenotypes include changes in management, use of correction factors, and statistical adjustment. An example of a management change is distributing related animals across different pens or pastures. Standard adjustment factors apply to weaning weights of calves born to younger mothers producing adjust weights upward to mature cow equivalents. A contemporary group consists of animals treated similarly. A common contemporary grouping is herd-year-season consisting of animals born in the same herd, year, and season. Statistical analyses for genetic evaluations typically adjust contemporary groups simultaneously.

Heritability

Heritability describes how much of the differences in phenotypes among animals treated similarly is due to genetics. It is the most basic connection from phenotype to DNA and genetic evaluation. Heritability is the ratio of genetic variance (VG) to phenotypic variance (VP) and ranges from 0 to 1. High heritability values of 0.5 mean that on average half of the differences among phenotypes of animals are genetic. Low values of approximately 0.1 mean that most of the differences are not genetic. Multiplying heritability times the differences between each animal's phenotype and their average is a simple genetic evaluation. The accuracy of these genetic evaluations is the square root of heritability.

Several types of genetic variance exist. Additive genetic variance predicts permanent and continued response to selection. Other types of genetic variance (dominance and epistatic) do not predict long-term, continuing selection responses. Broad sense heritability describes the ratio of total genetic variance to phenotypic variance as discussed above. Narrow sense heritability describes the ratio of additive genetic variance to phenotypic variance. Genetic evaluation calculations use estimates of additive genetic variances.

Using the average of several measurements of a phenotype can substantially increase heritability. The variance of the average of N independent measurements is 1/N times the variance of one measurement. A phenotype like wool weight is measured each year of a ewe's life. The variance of an average phenotype (VPAV) is the sum of the genetic (VG) and permanent environment (VPE) variances, which are repeated each year, and the residual variance (VE) that is independent from one measurement to the next is divided by N: VPAV = VG + VPE + VE/N. The heritability of an average is VG/VPAV. Table 1 shows how VG and VPE affect heritability of the average phenotype. New technologies may make it easier to measure traits repeatedly leading to higher accuracy genetic evaluations.

Pedigrees

Pedigrees describe genetic connections among animals. Pedigrees record the male (sire) and female (dam) parents of each

Table 1 The relative increases in heritability of an average of repeated measurements from adding an additional measurement is more when genetic variance (G) is lower, variance from permanent environment (PE) is lower, residual variance (E) is greater, and there are few measurements

Variances			*Number of measurements*			
G	*PE*	*E*	*1*	*2*	*4*	*8*
10	15	75	0.10	0.016	0.23	0.29
10	5	85	0.10	0.17	0.28	0.39
30	15	55	0.30	0.41	0.51	0.58
30	5	65	0.30	0.44	0.59	0.70

animal. Relationships like full-sibs (same sire and dam), half-sibs (same sire or same dam), grandparents (grandsire and granddam), and irregular relationships become apparent from accumulating and linking sire and dam relationships. Many breed associations have a long history of recording sires and dams of purebred livestock and creating pedigrees. Individual breeders and companies also maintain private pedigrees for their use internally. Figure 1 shows pedigree diagrams emphasizing ancestors or families.

Related animals share a portion of their DNA. Pairs of close relatives (sire and a daughter; two full-sibs) share more DNA than distant relatives (two animals with the same great grandsire). The phenotype of any animal that shares DNA with a genetically evaluated animal can contribute to that evaluation. The degree of contribution depends on how much DNA they share and the number and relationships to other animals with phenotypes. The coefficient of relationship (R) between two animals in a noninbred population is the average amount of shared DNA between them. Values of R for simple relationships are 0.5 for parent and progeny or full-sibs; 0.25 for half-sibs; and 0.062 5 for animals sharing a single grandparent. Calculation of R usually considers only the paired chromosomes and not the sex chromosomes but it is possible to consider them separately.

Actual livestock populations have many complex relationships among animals. Calculating R in these populations depends on tabular methods and other algorithms that can extend to very large populations and breeds. The result of these calculations is a relationship matrix, an array of values showing an R value for every pair of animals. Table 2 shows a small portion of a relationship matrix in a cattle herd with R values from 0.016 to 0.520 for five animals. Genetic evaluations now use relationships among millions of animals by combining efficient algorithms with rapidly increasing computational capacity.

An animal receives half of its DNA from each parent. Each parents' half in an animal is also a sample of half of the parents' DNA. This limits the accuracy of predicting a progeny only from its parents' phenotypes or genetic evaluations. Sampling parents' DNA means their progeny will still be genetically variable but genetic variability of full-sibs will be half that of unrelated animals. This remaining genetic variation, called Mendelian sampling variation, limits the accuracy of genetic prediction using only parental information to a maximum correlation of 0.71.

There are two ways that phenotypes from relatives can help in genetic evaluation. When potential sires and dams have phenotypes, then relatives with phenotypes can increase the accuracy of evaluation. When potential sires or dams do not have phenotypes, using related animals with phenotypes is necessary. Sex-limited phenotypes like milk or egg production

Table 2 Portion of a relationship matrix in a cattle population

Animal Identity	*98006*[a]	*118052*	*118158*	*118216*	*118227*
98006	1.0[b]	0.037	0.520	0.157	0.065
118052	0.037	1.0	0.037	0.016	0.028
118158	0.520	0.037	1.0	0.157	0.065
118216	0.157	0.016	0.157	1.0	0.115
118227	0.065	0.028	0.065	0.115	1.0

[a]Identification numbers for five animals beginning with animal 98006.
[b]Coefficient of relationship between animal pairs designated by column and row headings showing the range from near zero (118216 and 118052) to greater than 0.5 (98006 and 118052). Values on the diagonal are the genetic relationship of an animal with itself (1.0).

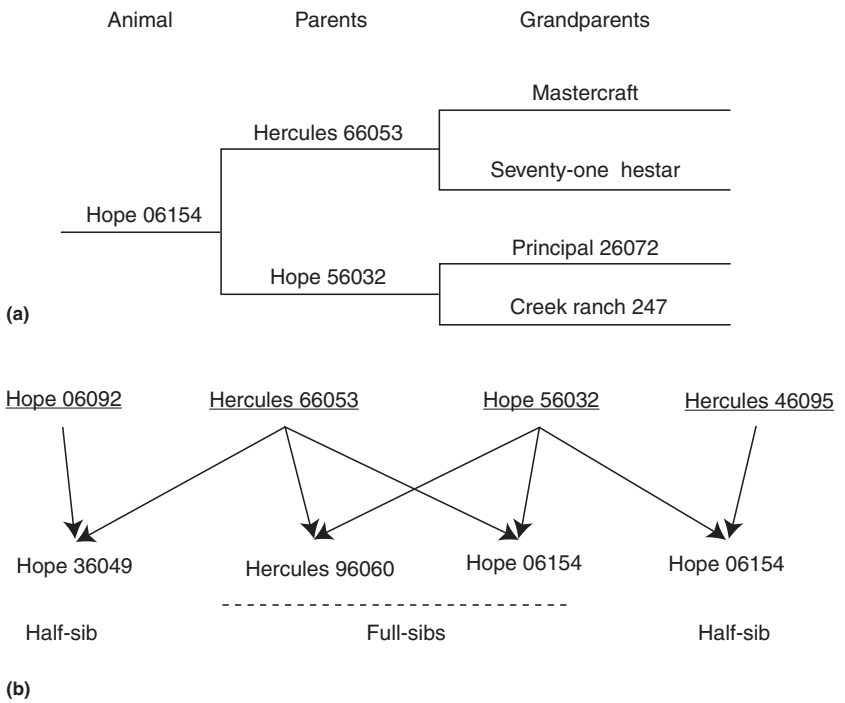


Figure 1 Pedigree diagrams emphasizing (a) ancestors and (b) family structure.

Table 3 Accuracy of animal phenotype, daughter averages, and full-sib averages for different heritabilities and effects of rearing full-sibs in the same litter

Relationship	*Number*	*Litter effect*	*Heritability*			
			0.10	*0.25*	*0.40*	*0.55*
Animal	1		0.32	0.50	0.63	0.74
Daughter average	2		0.22	0.34	0.43	0.49
	4		0.30	0.46	0.55	0.62
	8		0.41	0.59	0.69	0.75
	16		0.54	0.72	0.80	0.85
	32		0.67	0.83	0.88	0.91
Full-sib average	1	Any	0.16	0.25	0.32	0.37
	2	0	0.22	0.33	0.41	0.46
	2	0.2	0.20	0.31	0.38	0.43
	4	0	0.29	0.43	0.50	0.55
	4	0.2	0.24	0.36	0.43	0.48

are examples of phenotypes not measured in males. It is common to base genetic evaluation for dairy and egg production on the phenotypes of sires' daughters. Selection of animals harvested and measured for carcass and meat quality phenotypes is not possible. Some early pig improvement programs harvested a few pigs from each litter to get genetic evaluations for carcass phenotypes on the remaining full-sib littermates. Sometimes being reared in the same litter makes mammalian full-sibs more similar than expected from genetics alone. These litter effects make information from full-sibs less independent than full-sibs raised separately. Because they are less independent, litter effects reduce the value of phenotypes from full-sibs for genetic evaluation.

Table 3 shows how accuracy of an animal's phenotype compares to accuracy of progeny or full-sib averages. Use of many daughters can yield accurate genetic evaluations for sex limited or other phenotypes but it increases the time needed and cost of genetic evaluation. Full-sib phenotypes also yield lower but adequate accuracy, usually without increasing time delays. Opportunities to make use of full-sibs in mammals are limited. When possible, direct measurement of an animal's phenotype is usually the best information for genetic evaluation and selection programs. Technology affects the balance of time and accuracy in the breeder's equation. Reproductive technologies can produce clones, an even closer relative, for harvest phenotypes and sexed semen for more efficient production of daughters. Measurement technologies such as ultrasound can measure harvest-related phenotypes in live animals.

Genetic Correlation

Phenotypic correlation is the term that describes animals with high values for one phenotype also tending to have high (or low) values for another phenotype. Correlations are positive when high values occur together and negative when high values in one trait occur with low values in another. Desirable describes positive correlations of phenotypes selected in the same direction and negative correlations of phenotypes selected in opposite directions. Antagonistic describes positive correlations of phenotypes selected in opposite directions and negative correlations of phenotypes selected in the same direction.

Partitioning phenotypic correlations into genetic and residual components is similar to partitioning variation in phenotype. The genetic correlation describes how the genetic values for two traits associate. A biochemical pathway common to two traits and affected by genetics is one of the causes of genetic correlation. Part–whole associations (birth weight and weaning weight) also create genetic correlations. Another basis is close linkage of DNA differences that affect different pathways. Direct genetic and residual environmental components of phenotypic correlation are often either both positive or both negative but it is possible to have a positive and a negative component.

Livestock breeders use genetic correlations to improve accuracy, reduce time needed for evaluation, and expand the scope of genetic evaluation. Carcass lean meat yield is difficult to obtain. Measurements on harvested progeny can delay accurate genetic evaluation and reduce intensity of selection. Ultrasound and other live animal measurements on correlated phenotypes like fat thickness and muscle area remove some constraints of successful and timely genetic evaluation of lean meat yield.

Litter sizes of sows and carcass fat thicknesses of harvested pigs are examples of phenotypes not measured on the same animal and have no basis for a phenotypic correlation. If the sows and pigs are related, there is a basis for estimating a genetic correlation. Genetic correlations between reproductive and productive phenotypes are important for evaluating any opposing effects from selecting either type of phenotype. Some male reproductive phenotypes predict female reproductive phenotypes in females. Genetic correlations help determine the amount of change possible using phenotypes in one sex to predict those in another.

One use of genetic correlation is to measure correspondence between progeny raised in different environments and management systems measured for the same phenotype. Other uses are substitution of an inexpensive measurement for a correlated expensive phenotype; predicting later life phenotypes from early life ones; and using a phenotype that can be measured several times to improve accuracy of a correlated genetic evaluation.

Statistical and Computational Advances in Genetic Prediction

A goal of genetic evaluation is the prediction of differences in average phenotypes of future progeny, known as breeding values. Knowing the accuracy of these predictions is also important. A basic piece of information used in prediction calculations is the difference in an animal's phenotype from the average of the group of animals it came from. Some groups of animals raised similarly are large and the averages are accurate. In many cases, groups of animals treated similarly are small and poorly estimated. C.R. Henderson at Cornell University developed a statistical technique called Best Linear Unbiased Prediction (BLUP) that overcame many problems of genetic prediction including the simultaneous estimation of group means and other adjustment factors along with breeding

values. BLUP methods are now widely used by livestock industries to predict breeding values.

Steady advances in the adaptation of BLUP techniques to different situations encountered in livestock breeding made this technique increasingly valuable. Advances in computational power, application of numerical analysis methods, and efficient memory storage algorithms also contributed toward its broad adoption. Initial applications of BLUP were restricted to predicting breeding values among sires for a single trait but this expanded to sires and maternal grandsires and then to individual animals (Animal Model BLUP) for direct and maternal breeding values. Additional enhancements included simultaneous prediction of multiple traits and prediction of categorical traits like survival.

Using Molecular Genetics and Genomics in Selection

Polymorphisms

Livestock breeders made important and large genetic changes in animals without knowing or being able to know the specific changes occurring in DNA. Tremendous advances in mapping differences in DNA, called polymorphisms, and sequencing DNA of livestock began in the 1990s. Complete DNA sequences (genomes) of several livestock species are now available (USDA National Animal Genome Research Program website).

Scientific and commercial groups searched genomes for polymorphisms associated with phenotypes beginning with the earliest DNA sequencing and mapping of genetic markers. Genetic markers are biochemical tests that identify particular polymorphisms. A genotype consists of the two polymorphisms found at the same location on a pair of chromosomes and each polymorphism is called an allele. Researchers often underestimated the number of animals needed to identify repeatable associations of phenotype with genetic markers. However, they identified many useful genetic markers associated with phenotypes, especially phenotypes with large or distinct effects like specific malformations.

Association of a polymorphism with a phenotype occurs because it directly causes a difference or because of linkage with another causal polymorphism. Linkage results from two polymorphisms being in proximity on the same chromosome. Linkage causes two polymorphisms to be in the same animal more often than expected if they were independent. A shared ancestor creates linkage in progeny (**Figure 2**) that fades in following generations. A population's historical development can create long-term linkage, usually among very close polymorphisms, called linkage disequilibrium.

Associated effects of alleles and genotypes are categorized as additive, dominant (or recessive), and epistatic. Allele G effects are purely additive if average phenotypes of animals with heterozygous CG genotypes are halfway between average phenotypes of animals with homozygous CC and GG genotypes. If the average phenotype for animals with CG genotypes is closer to GG than CC genotypes, then G is a dominant allele. If phenotypes of CG animals are closer to those with CC genotypes, then G is a recessive allele. The CG genotype of a completely dominant G allele is equal to GG and that of a completely recessive G allele is equal to CC. Overdominance describes a heterozygous genotype with a phenotype beyond the range of either homozygous phenotype. Epistasis is the dependence of additive and dominance effects of an allele on genotypes somewhere else in the genome. **Figure 3** illustrates different allele effects and an example of epistasis.

Many identified genetic diseases in animals are recessive (Ibeagha-Awemu *et al.*, 2008; Online Mendelian Inheritance in Animals website). Bovine leukocyte adhesion deficiency (BLAD) is one such disease resulting in high susceptibility to bacterial infection of cattle. A widely used dairy bull heterozygous for the susceptibility allele produced many sons and daughters in the 1950s and 1960s. Eliminating recessive disease alleles is difficult because animals heterozygous for the disease producing allele have the same phenotype as animals without the allele. Molecular genetics and genomics technology can identify specific DNA variations that cause these diseases. Once identified, developing genetic tests for the disease causing alleles is straightforward. Breeders apply these tests to dozens of livestock genetic diseases. Selection reduces

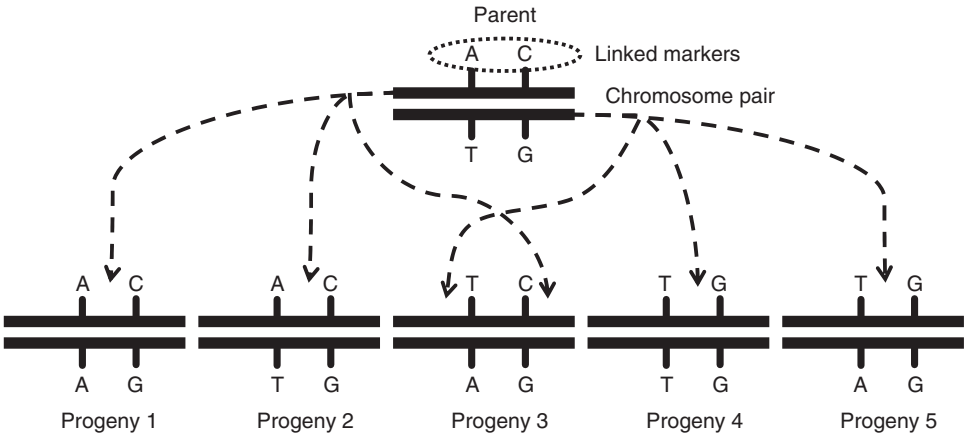


Figure 2 Linked genetic markers on a section of paired chromosomes are often inherited together. Dashed lines show parental chromosome source in progeny chromosomes. Progeny 3 shows mixed chromosomal sources resulting from a crossover in replicating the parental chromosome.

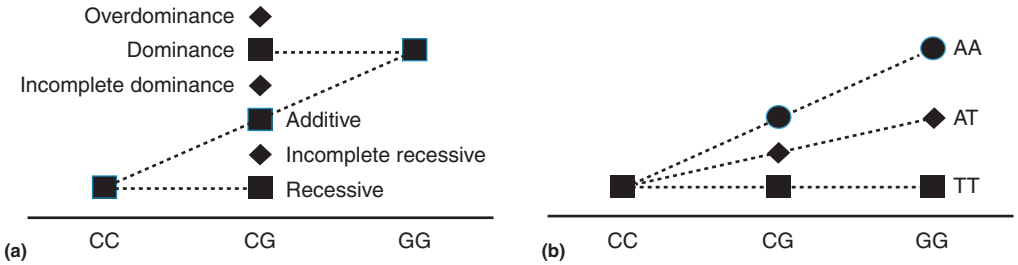


Figure 3 Description of (a) allele G effect depends on average phenotypes of heterozygous (CG) and homozygous (CC an GG) genotypes, and (b) an example of epistasis involving two polymorphisms in different locations.

frequencies of alleles causing many diseases in livestock populations.

Two examples in cattle illustrate differences in controlling genetic diseases with and without DNA tests. Snorter dwarfism is a mutation that was common in US Hereford and Angus cattle during the 1940s and 1950s. Elimination of this mutation took over a decade. The main approach was to eliminate possible carriers having an ancestor who had produced a dwarf calf. Arthrogryposis multiplex, known as curly calf syndrome, became a problem in American Angus cattle in 2007–2008. By the end of 2008, molecular geneticists developed a DNA test for the mutation. Within a year 90 000 cattle were tested to identify 18 000 carriers. A published list of tested carriers enables Angus breeders to manage the defect by avoiding matings of carriers and untested progeny of carriers without eliminating otherwise desirable carrier animals from their herds. The advent of DNA testing for genetic defects has shifted control of defects from disruptive eradication by eliminating all known carriers and their suspect progeny to management of the mutations by testing and not mating known or potential carrier animals. Elimination of the mutation is gradual and mutation-free progeny from otherwise desirable carrier animals retained with DNA testing.

Different causal polymorphisms may result in similar phenotypes. Myostatin is an example of a gene that has several different polymorphisms that cause increased muscling and decreased fat in cattle, pigs, sheep, and other species as well. Multiple causal polymorphisms create genetic ambiguity. Different populations and breeds will tend to have different polymorphisms that result in similar phenotypes. A genetic marker test based on a causal polymorphism will only predict the phenotype in some populations and may only predict some of the animals within a population.

Linkage disequilibrium arises in populations as they fluctuate in numbers of parents and immigrants throughout their genetic history. Any two populations can have both shared and independent parts of their genetic histories. Linkage disequilibrium that arises during their shared genetic history may persist for many generations and be the same in both populations. Linkage disequilibrium arising during their independent genetic histories will not be consistent in the populations. When the basis for a genetic marker test is linkage disequilibrium with a causal polymorphism, then the test is more likely to be valid in populations that share greater and more recent genetic histories.

One of the approaches to identify the strength of linkage disequilibrium is haplotyping. Polymorphisms in strong disequilibrium form inherited groups of alleles. Three polymorphisms with two alleles for each could form eight combinations (AGT, AGC, ACT, TGT, ACC, TGC, TCT, and TCC) but strong disequilibrium may result in only three or four actually occurring (e.g., AGT, AGC, TGT, and TCC). When similar haplotypes occur in different populations, then causal polymorphisms linked to the haplotype should also be similar.

Genetic marker tests derived in one population may not work in another because causal polymorphisms and linkages with the causal polymorphisms can differ in populations because the causal polymorphism in one population might be absent in another population. The National Beef Cattle Evaluation Consortium (NBCEC website) and the SmartGene for Beef project (SmartGene website) conducted validation tests of some genetic markers used in beef cattle and available from commercial companies.

Many traits emphasized in commercially available genetic marker tests are costly, difficult, or available too late in life to evaluate accurately using phenotypes and pedigrees. These include meat quality, disease resistance, fertility, and efficiency. Selection based on genetic markers has the most potential for these traits. However, the same constraints also affect the success of discovering associations of genetic markers with these traits.

Genomic Selection

Beyond simply inherited mutations and traits affected by a single gene or small set of interacting genes with large effects are a myriad of complex diseases and traits influenced by genetics and environmental conditions. Recent genomic technologies enabled development of panels with dozens to hundreds of thousands of genetic markers for livestock species. Genotyping costs for these panels are very economical and open the door to different approaches for using genomic information. Other improvements in DNA sequencers have made sequencing of many individual animals affordable. Targeted sequencing of the 2% of the genome that codes for proteins (exome) is another approach being used to access DNA information across the whole genome. DNA sequence information reveals some of the structure and types of genetic polymorphisms as well as their genotypes across the genome.

Sequencing genomes and exomes and genotyping hundreds of thousands of individual animals are much more affordable now than just a few years ago; however, it is still not

cost effective. A strategy proposed and adopted in some selection schemes is the prediction of missing genotypes through a process called imputation. This process begins by identifying key animals for DNA sequencing or genotyping with panels of tens or hundreds of thousands of genetic markers. Identifying key animals usually begins with sires of males considered for selection, one of the four selection pathways, and then sires of females considered for selection. Other animals descended from key animals are genotyped with smaller panels of hundreds to several thousand genetic markers. Imputing genotypes uses both linkage disequilibrium among the genetic markers and pedigree to fill in all genotypes for animals genotyped only with smaller panels.

Although genetic evaluation using performance and pedigree records has been effective for some traits, including marker genotypes in genetic evaluations can increase accuracy or allow earlier evaluations. If genetic markers accounted for sufficient genetic variation in a trait, then the accuracy of newborn animals could be similar to that of a parent having several progeny measured for the trait. The terms genomic selection and genome-wide selection describe selection based on panels of many markers spread widely across the genome. There are several approaches to implementing genomic selection, and supporting research is rapidly progressing.

One approach to genomic selection begins by genotyping a large training population using imputation with a large panel of genetic markers or from sequencing individual animals. Phenotypes measured in the training population are then associated with genotyped and imputed polymorphisms. One way of applying results from the training population to the population under selection is imputing the same set of genetic markers in the selection population by genotyping a combination of larger and smaller panels of genetic markers. Alternatively, a smaller panel of genetic markers selected from the most highly associated set of genetic markers in the training population is genotyped in the selection population.

Geneticists use both small panels consisting of markers selected based on association with a suite of production traits and large, whole-genome panels having enough markers to ensure unknown causal polymorphisms in the genome will be associated with genotyped genetic markers to explain genetic variation. Low-density panels can reduce costs of genotyping either by direct use of their genetic markers or as a tool to impute large panel genotypes in conjunction with large panel, reference genotypes of influential ancestors.

Another source of training information that works well in dairy and beef cattle is the progeny averages of widely used sires. These sires have hundreds to thousands of progeny measured for some traits. Progeny averages approach half of true genetic differences and eliminate much of the dam and nongenetic variation. If there are enough widely used sires, then genotyping only these sires can lead to good estimates of genetic marker effects. However, this method is limited to traits measured in many progeny. Other important traits that are difficult to measure need other types of training populations.

One of the difficulties of estimating genetic marker effects is that there are often many more genetic markers than training animals. This leads to spurious associations with the markers and erroneous genomic predictions in other populations. Research on statistical methods and other approaches is addressing this problem. Two approaches to limit or prioritize genetic markers for use in genomic prediction include using markers in or near genes that are part of relevant metabolic pathways and using genetic markers with predicted severe effects on proteins.

After genotyping and measuring phenotypes in the training population, a new animal's predicted genomic value for a trait in the selection population is the sum of marker genotypes multiplied by estimated effects of each marker for that trait. Livestock breeders would use these genomic predictions for selection when no other information is available on a trait. Sometimes animals or their relatives will have both genomic, phenotypic, and pedigree information for a trait. One approach to combine this information is an index weighting the genomic values and the genetic evaluations based on phenotypes and pedigree. A second approach uses a standard two-trait and pedigree genetic evaluation treating the genomic breeding values as genetically correlated traits. A desirable byproduct of this approach is an estimate of the proportion of genetic variation explained by the genomic predictions. High proportions indicate that genomic predictions are working well and are appropriate for the population.

Single-step methods simultaneously estimate genetic marker effects and combine either or both genotypes and phenotypes of animals to produce genotype-assisted genetic evaluations. This method uses genomic relationships to replace pedigree relationships when animals have genotypes. Pedigree relationships are expectations of proportions of shared genome based on parentage but genomic relationships measure similarity of genotypes to estimate sharing.

These approaches effectively increase accuracy of young genotyped animals for routinely recorded traits within well-studied breeds and breeding populations, extending the predictions across breeds remains a challenge. Although marker effects estimated in a specific population can account for much genetic variation within that population, applying those effects to genotypes from an unrelated population seldom explains enough variation in the unrelated population to have a meaningful impact on breeding value accuracy. Meeting the challenge of robust genomic predictions applicable across livestock populations could enable meaningful genomic predictions for traits that are economically important but too difficult and expensive to measure routinely.

See also: Advances in Animal Biotechnology. Cloning Animals by Somatic Cell Nuclear Transplantation. Domestication of Animals. Genomics of Food Animals

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Breeding: Plants, Modern

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Glossary

Epistasis The dependence of one gene's effects on the state of a different gene in the same organism.
Genomic selection The use of a large number of genetic markers across the genome to predict breeding values of plants that have not been grown and tested yet.
Germplasm The material representing the genetic diversity available to a breeding program, often stored as seeds or vegetative plant cuttings or maintained in living nurseries.
Linkage disequilibrium Alleles at different genes that cooccur in individuals more often or less often than expected by chance are in linkage disequilibrium; more precisely this is termed 'gametic phase disequilibrium' because it does not require physical linkage on a common chromosome.
Marker-assisted selection Selection for deoxyribonucleic acid markers previously identified as linked to or inside of desired alleles at genes controlling important traits.
Quantitative trait loci (QTL) A chromosomal region associated with variation for a quantitative trait.

Historical Development of Plant Breeding Methods

The Diversity of Mating Systems in Plants

Mating systems in plants are highly diverse, much more-so than in vertebrate animals. Some plant species have exclusively or primarily outcrossing ('allogamous') mating behavior enforced or promoted by sex chromosomes (like domesticated animals), self-incompatibility mechanisms, or spatial/temporal separation of male and female flower development. Typically, these species have morphological and developmental features that represent adaptations to insect and wind-borne pollen dispersal. Primarily outcrossing species tend to have population structures similar to many animal species, characterized by higher levels of genetic diversity within populations, higher levels of heterozygosity within individuals, and more genetic load (recessive alleles that reduce fitness when homozygous). Many perennial tree and forage species have outcrossing mating systems and population structures (Richards, 1997), as do most fruit crops (Janik, 2006). Many annual vegetable crops and some cereals such as maize are also predominantly outcrossing (Allard, 1960).

In contrast, many other important crop species are primarily self-fertilized ('autogamous') annual species. Many self-fertilized species have morphological/developmental features that promote self-pollination (such as maintaining closed flowers until after pollen shed) and often lack the 'showy' floral features of insect/animal pollinated species. Self-fertilized species tend to have significantly lower levels of genetic variation within populations, lower heterozygosity within individuals, and generally suffer little inbreeding depression, presumably because much of their genetic load was purged during the evolution of the self-fertilization mating system. Most of the cereal grass crops (such as wheat and rice) and annual seed legume crops (such as soybean, common bean, pea, and peanut), and a number of other important crops (including tomato, tobacco, cotton, lettuce, and pepper) are predominantly self-pollinated (Allard, 1960).

Still another group of plants reproduces using both asexual and sexual means (to varying proportions). Important crops in this category include potato, sweet potato, sugarcane, and many perennial grasses (Ortiz *et al.*, 2006; Wu *et al.*, 2006). Many ornamental cultivars are sterile interspecific hybrids and are necessarily propagated asexually. Asexual propagation can occur naturally by spreading stem structures, such as rhizomes, or by asexually produced seed ('agamospermy' or 'apomixis'). Apomixis occurs when viable seeds are formed in the absence of sexual reproduction (Richards, 1997). Beyond naturally occurring mechanisms for asexual reproduction, humans have devised methods to propagate vegetative plant parts (by stem or tuber cuttings, grafting, or even tissue culture). Grafting has deep roots (so to speak) in agriculture and was known to the ancients (Janik, 2006). Citrus is an interesting example that demonstrates the reproductive flexibility that even a single plant group can possess. Citrus trees are naturally self-pollinated but also can be outcrossed easily, usually forming seeds from sexual reproduction. Some types of Citrus, however, will also produce seeds asexually, which represent clonal copies of the maternal plant. Some forms of Citrus will produce both sexual and asexual embryos within the same seed (Richards, 1997). Beyond this natural variability in the reproductive mode of citrus, plant breeders have devised methods of asexual propagation from clonal propagation of a genotype by grafting vegetative cuttings to artificially producing novel hybrids by cell fusions (Gmitter *et al.*, 2009).

These mating system and cultivar type divisions do not follow phylogenetic relationships; all types may (and often do) occur within a taxonomic family (Richards, 1997). For example, the grass family, *Poacea*, contains cross-fertilized, self-fertilized, and asexually reproducing groups (Richards, 1997). Furthermore, most perennial grass species can be propagated vegetatively, and some grasses also reproduce apomictically. For plant breeders, the reproductive behavior of a species is almost always the critical determinant of the breeding method that will be most commonly employed for crop improvement (Allard, 1960). Thus, breeders of soybean (a member of the

eudicot family) and spring-sown wheat (monocot family) will use much more similar breeding methods than will wheat and maize (both monocots) breeders. Perhaps more dramatically, breeding methods used for some forest tree species (mostly outcrossed, and with substantial attention paid to measurements of individual plants and their known pedigree relationships with other trees) are fundamentally more like animal breeding methods than wheat breeding methods.

Furthermore, in the same way that plant reproductive systems largely determine the genetic structure of natural populations, the reproductive system also is the most important factor in determining the predominant genetic structure of cultivars. The mating system has two major impacts on cultivar type. First, the mating system has a critical effect on the relationship between heterozygosity and vigor in the species (Allard, 1960; Richards, 1997). Primarily outcrossing species rely on heterozygosity (having two distinct copies of a gene) to shield the plant from the effects of deleterious recessive mutations. Thus, most outcrossing species exhibit strikingly reduced vigor and fitness when inbred (inbreeding depression) and greater vigor when crossed to unrelated plants of the same species (hybrid vigor). In contrast, self-fertilizing species have adapted to a genetic constitution characterized by high homozygosity, with unfavorable and lethal mutations consistently exposed phenotypically. Self-fertilization appears to have evolved from cross-fertilization in many plant lineages when the detrimental effects of inbreeding were outweighed by the advantages of not having to rely on a separate plant for pollen, as could be important in colonization of geographically isolated habitats, for example (Stebbins, 1974). The second major impact of mating system on cultivar types is its effect on the economic efficiency of cultivar propagation and dissemination. For example, even predominantly self-fertilized species may exhibit some hybrid vigor, so F1 cultivars could be an optimal genetic structure in terms of vigor. Yet, these species also tend to have floral structures and pollination behavior that maximizes self-fertilization and makes cross-fertilization difficult. For example, whereas naturally outcrossing maize has separate male and female flowers facilitating easy emasculation for hybrid seed production, manual emasculation of self-fertilizing species is very time-consuming and requires significant experience to perform well without damaging the female organs. In some species, this has been overcome to some extent by genetic or chemical male-sterility systems, but even then, these species tend to shed relatively little pollen, so that manual pollination and a larger proportion of male to female parent plants may be required to produce seed, increasing seed production costs (Li and Yuan, 2010; Wilson, 1984).

In summary, plant breeding methods and cultivar types can be roughly characterized according to the predominant reproductive system of the species. The result of this is that the genetic structure of cultivars can be categorized according to the level of heterozygosity (within-plant genetic diversity) and heterogeneity (among-plant genetic diversity; **Figure 1**). **Figure 1** is an oversimplification, but captures the large pattern of genetic population structure in different cultivar types. Many older landrace varieties (maintained on farm by farmers over long periods of time) contain substantial genetic diversity. In the case of outcrossing species, this diversity is a natural result of the genetic recombination that occurs with each generation of seed production. In the case of self-fertilizing species, diversity is a result of a mixture of seeds from distinct pure lines resulting from recurrent inbreeding spiked by occasional outcrossing to generate new variability (Allard, 1999). Much of the drive of modern plant breeding has been toward uniformity within cultivars, achieved by isolating pure-breeding lines in the self-fertilized species, or by creating uniform but highly heterozygous F1 cultivars in some cross-pollinated species. As mentioned already, some predominantly inbreeding species are

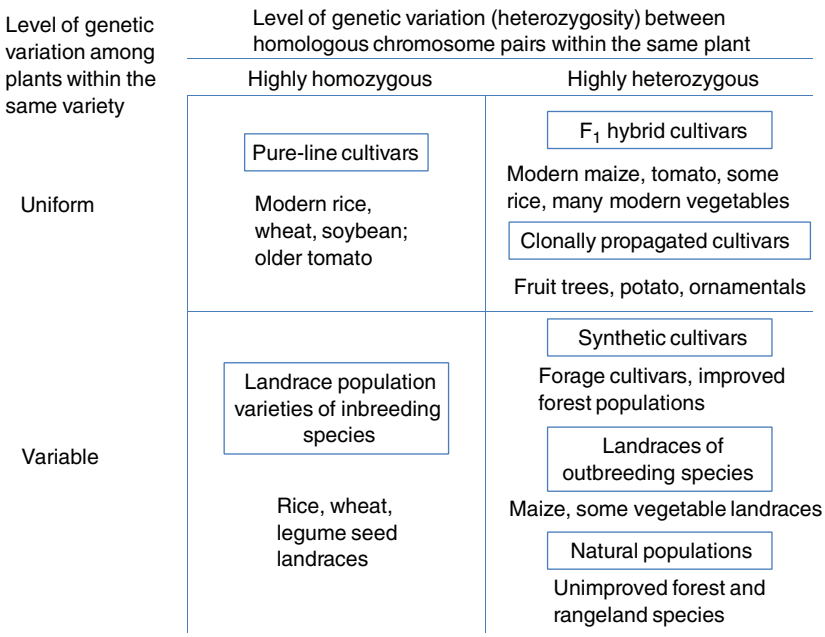


Figure 1 Classification of cultivar types according to genetic diversity among plants within a cultivar and heterozygosity within a plant.

represented by modern F1 cultivars despite the difficulties in seed production, as a way to capture hybrid vigor (which may be limited) and, perhaps more importantly, to more easily combine favorable attributes of different parental lines (e.g., by combining disease resistance with specific fruit quality characteristics).

As with breeding methods, the cultivar types are largely determined by the mating system not the taxonomic grouping of the species, which is why **Figure 1** does not follow a phylogenetic pattern. The predominant genetic structure in most cereal grass cultivars like wheat is a highly homozygous and highly homogenous pure-line variety, whereas maize (an outcrossing cereal grass) cultivars are most often highly heterozygous F1 hybrids.

The Concept of Heritability

Ancient plant domesticators and breeders achieved tremendous gains from selection with no understanding of the biological mechanisms underlying inheritance. Key to this success, however, was the understanding that offspring tend to look more like their parents than unrelated individuals. Thus, it was surely intuitive for ancient plant breeders to use seeds from more desirable plants to sow the next generation. Much less intuitive was Darwin's insight that natural selection, if repeated over many generations, could result in the appearance of new species (Darwin, 1859). Darwin developed his theory of the origin of species by natural selection with an entirely incorrect understanding of the mechanisms of inheritance (Darwin, 1859). Nevertheless, he understood correctly that most traits related to fitness are to some extent heritable from parent to offspring. Thus, absent an understanding of genetics, the concept of inheritance alone is sufficient for effective selection and for basic understanding of the evolution of species.

The synthesis of Darwinian concepts of evolution by natural selection with Mendel's genetics greatly enriched our understanding of both evolution and genetics. The recent developments in genome biology have similarly had profound impacts on these areas of science. Modern plant breeding is a naturally integrative applied field of science, whereby breeders leverage the understanding of inheritance, trait expression, and population dynamics to design more efficient and more effective means of crop improvement. Similarly, plant breeders apply tools and technologies (from genomics, computer science, statistics, agricultural engineering, and so forth) to the extent that their application will help make selection responses better for a fixed input of time and resources. Thus, whereas a simple understanding of inheritance enabled dramatic changes in crops over thousands of years, modern breeders hope that better understanding of the specific details of the inheritance of important traits and the application of tools that permit more accurate discrimination among the potential utility of different plants will greatly speed up the rate of gain from selection. Indeed, recent history suggests that plant breeders have achieved more dramatic gains in the last 100 years in some crops than occurred previously over much longer time scales. The changes in yield potential, stress tolerance, and population genetic structure of maize represent a good example of this phenomenon (Duvick *et al.*, 2004; van Heerwaarden *et al.*, 2012).

A major step toward modern plant breeding was achieved by Johannsen, who studied the inheritance of bean size and weight (Allard, 1960; Johannsen, 1903, 1911), demonstrating that bean populations were a mixture of distinct pure lines, and that selection among those lines would result in heritable changes. Importantly, he noted that while there was also variation among plants within a pure line, selection within lines had no effect on the progeny mean values. He realized this was because there are two components of observable 'phenotypic' variation: (1) 'genotypic' variation because of differences in genetic composition, and (2) variation because of environmental factors. Within a pure line, there is almost no genotypic variation; thus the observed variation is almost entirely because of different reactions of a common genotype to varying environmental conditions. Differences between pure lines are because of both genotypic differences and also environmental differences, so some proportion of those differences will contribute to a response to selection in the progeny. This distinction between genetic and nongenetic causes of variation was critical to providing a sound scientific basis for selection. It made clear that different population structures had different levels of genetic variation, and that selection would have more effect in population structures with more genetic variation. Additionally, by distinguishing the important contribution of environmental effects to observable phenotypes, Johannsen's insights led breeders to consider more carefully how to reduce the contribution of environmental differences among plants under selection, so that selections were determined more by genotype variation rather than nonheritable environmental variation.

Following critical early experiments demonstrating that continuously varying traits could arise as the result of the combined action of multiple genes and the environment (East, 1910, 1916), Fisher (1918) formulated a statistical genetic model that partitioned the overall effect of genotypes into the 'additive' (average) effects of their component genes, dominance interactions between the two copies (alleles) of the same gene in an individual, and epistatic interaction between alleles at different genes. This model led to a formulation of the genotypic variance in a population as the sum of the variation because of additive, dominance, and epistatic effects of component genes.

The importance of conceptually distinguishing the different components of heritable genotypic variation was emphasized by Lush (1945), who coined the term 'heritability' to refer to the proportion of total phenotypic variation observed for some trait in a population that is heritable. Using the terms of Fisher's model, Lush demonstrated that only the additive genetic variance contributes to the heritable genetic variance (Lush, 1940). The reason for this is that in diploid outcrossing organisms, each parent contributes one of the two alleles at each gene in an offspring. Thus, the dominance interaction between the two alleles carried by a parent at a locus is not transmitted to its progeny; dominance effects contribute to variation among individuals, but not to the similarity of parent and offspring. So, if the total genotypic variance (σ^2_G) of a population is composed of additive (σ^2_A) and dominance (σ^2_D) variation (and for simplicity ignoring epistatic effects)

($\sigma^2_G = \sigma^2_A + \sigma^2_D$), then the total phenotypic variance is composed of these components plus environmental variance:

$$\sigma^2_P = \sigma^2_G + \sigma^2_\varepsilon = \sigma^2_A + \sigma^2_D + \sigma^2_\varepsilon$$

The proportion of that total phenotypic variance that is heritable is the heritability (h^2):

$$h^2 = \frac{\sigma^2_A}{\sigma^2_P} = \frac{\sigma^2_A}{\sigma^2_A + \sigma^2_D + \sigma^2_\varepsilon}$$

Lush (1940) referred to this as the narrow definition of heritability; now commonly referred to as 'heritability in the narrow sense' (Falconer and Mackay, 1996) to distinguish it from a broader definition of heritability ('heritability in the broad sense'):

$$h^2_{BS} = \frac{\sigma^2_G}{\sigma^2_P} = \frac{\sigma^2_A + \sigma^2_D}{\sigma^2_A + \sigma^2_D + \sigma^2_\varepsilon}$$

(Falconer and Mackay, 1996).

These two measures have clear and distinct interpretations. Heritability in the broad sense is the proportion of total phenotypic variation that is because of genotypic differences, and refers to the distinction made by Johannsen between genotypic and phenotypic variation. Heritability in the narrow sense has a very important meaning to breeders because it indicates how effective selection will be; in outcrossing populations, the response to selection (R) can be predicted as $R = Sh^2$, where S is the selection differential (the difference between the average of the selected individuals and the whole population). The response to selection refers to the difference between the progeny phenotype values derived from selected parents compared to what the population mean would be expected to be if selection had not occurred (and all parents or a random sample of parents had contributed equally to the next generation).

Lush's definition of narrow-sense heritability is considered the gold standard in quantitative genetics because of its direct relationship with response to selection (Falconer and Mackay, 1996). Note, however, that Lush (an animal breeder) conceived of selection acting on values of individual diploid animals with no possibility of self-fertilization. This is precisely the situation considered by animal breeders and human quantitative geneticists, such that deviations from this definition are considered undesirable and an abuse of the term heritability. Unfortunately, for plant breeders, the reproductive diversity of plants discussed previously immediately causes problems with the definition of heritability (Nyquist, 1991). In addition, polysomic polyploidy of some important crops (e.g., potato, alfalfa, strawberry, many forage, and turf grasses), also creates havoc with the definition of heritability. Finally, the unit of measurement in many plant breeding programs is the total or average production value of a line or family grown in dense populations, such that the measurement of individual values is difficult or meaningless; the result is that the appropriate estimator of heritability in these situations is not the true narrow-sense heritability, but a measure of the heritability of family mean or total values (Falconer and Mackay, 1996; Nyquist, 1991).

Extending Heritability to Polyploidy and Complex Mating Systems of Plants

To demonstrate the more complicated nature of heritability in plants that can arise even in the case of regular outcrossing similar to the animal breeding situation, consider first a relatively simple case of a tetrasomic tetraploid like potato. Each plant carries four homologous copies of each chromosome type (instead of two copies as in diploids). This means that the genotypic value of a potato plant is the sum of the effects of four alleles at the locus, plus all their possible interactions. Each pair of alleles can have a dominance interaction similar to the case in dipoids, however there is also the possibility of higher-order interactions among the alleles at a single locus – the three- and four-way interactions of the alleles. It would be a helpful simplification to ignore the higher-order interactions; unfortunately, substantial evidence indicates that higher-order allelic interactions have a strong effect on yield and vigor in autotetraploids like potato (Mendoza and Haynes, 1974) and alfalfa (Groose *et al.*, 1989). Even if one could ignore all higher-order allelic interactions in a crop like potato, consider that in regular sexual reproduction, each tetraploid parent contributes two alleles per locus to each offspring. Thus a dominance effect because of the interaction of two alleles can be transmitted from parent to offspring, implying that some proportion of the dominance genetic variation should be admitted as part of the definition of heritability in this system (Holland, 2001; Levings and Dudley, 1963).

The situation becomes more complicated when we introduce the more complex reproductive systems of plants (Nyquist, 1991). Consider further the potato breeding situation outlined above. A potato plant can be intermated sexually to generate outbred progeny, which can be subjected to selection based on phenotype, similar in concept to an animal breeding scheme. The utility of a selected cattle sire in a dairy breeding program, however, is in its ability to be mated to dams to generate daughters that can be used in dairy production. Thus, its breeding value really is determined by its additive genetic effects, because all of its daughters carry only one of its alleles. In contrast, if a potato breeder identifies a particularly superior plant, that plant can be vegetatively propagated by tuber cuttings, and those tuber pieces can be used in production by farmers. Thus, the response to selection in this case involves the whole genotype of the plant that is clonally propagated, including all of its additive and dominance effects. So, the response to this selection is a function of the broad-sense heritability, not the narrow-sense heritability in this case.

At the other extreme, a typical breeding method in self-fertilizing species is to make a cross between two varietal parents, then inbreed the progeny from that mating to nearly complete homozygosity. In a pedigree breeding program, selection may be applied at each generation of this process. Note that the proportion of heterozygosity decreases by half with each generation, so that dominance interactions become progressively less important and more of the additive variation becomes partitioned among inbred lineages than within, until one reaches the situation of genotypic variation partitioned entirely among (and not within) pure lines encountered by Johannsen. Modeling the contribution of additive variation to

the genotypic variation among and within lines at each generation is simply a function of the level of inbreeding. However, modeling the nonadditive components of inheritance that contribute to variation among and within lines under intermediate generations is quite complicated (Cockerham, 1983) and measuring those components is exceedingly difficult (Edwards and Lamkey, 2002). In such a case, the appropriate measure of heritability depends on which generations are considered the 'selection units' and which are considered the 'response units.' In the simplest case, a sample of completely homozygous inbred lines from a cross can be evaluated, and only the best lines selected. If those best lines are then propagated as cultivars and considered the end product of that breeding cycle, then the heritability in this situation is a function of total genotypic variance among completely homozygous lines (which includes twice as much additive variance as in the outbred population, no dominance variance, but possibly other higher-order genetic components of variance). Thus, it is entirely appropriate in this situation to use an estimator of heritability that does not match Lush's narrow-sense heritability. In situations where the selected lines are themselves intermated to form a new breeding population, which itself may be inbred, the appropriate heritability estimator depends on the generation of the selected lines as well as the generation of the progeny lines. For this reason, plant breeders would do well to label clearly their estimates of heritability in terms of the 'units of selection' and the 'units of response' to which they apply (Holland *et al.*, 2003).

Enhancing Gain from Selection

For a given trait heritability, there is the possibility of enhancing gain from selection by increasing the selection differential (S in the equation above). This can be accomplished by either selecting fewer, more extreme individuals from the population or by growing a larger population sample for a fixed number of selected individuals. However, there is a tradeoff between having to increase resources to evaluate larger population samples versus the detrimental effects of inbreeding and reduced long-term gains from selection that can occur when the number of selected individuals is too small. Most mature plant breeding programs have more or less a fixed amount of evaluation resources and also some target number of selected individuals at each stage, such that the proportion of selected individuals cannot be widely varied without difficulty. An exception to this are some well-capitalized commercial breeding programs for some major crops, such as commercial maize breeding programs, which have increased substantially in scale in recent years (Crosbie *et al.*, 2006) as a means to increase annual gains from selection in a very competitive seed sales market.

Because dramatic changes in the selection differential are often so costly as to be unfeasible, plant breeders have focused intensely on increasing the heritability of important traits as an alternative means to enhance gain from selection. It follows from the definition of heritability that the greater the proportion of additive genetic variance to total phenotypic variance, the greater the expected response from selection. The additive genetic variance is an inherent function of a particular population and generation of inbreeding. Therefore, the breeder has two general ways to increase the heritability of a trait. One is to concentrate breeding on populations that have more genetic variance. The other is to reduce as much as possible the nongenetic contributions to phenotypic variance.

Populations with more genetic variance generally have greater response to selection, so an obvious strategy is to create populations with greater genetic variance. There are two impediments to this. First is the difficulty in identifying those breeding crosses that produce populations with greater genetic variance before they are evaluated, as methods to predict progeny variance based on parental trait or genetic differences have limited reliability (Hung *et al.*, 2012b). Second, breeders usually face a trade-off between the genetic variance of a population and its mean value, because in elite breeding materials, most variation is in the direction of reduced performance. Criteria for selecting among populations include the usefulness statistic that incorporates both the population mean and its variance (Melchinger, 1987; Schnell, 1983) and the mean value of the best families in a population at some consistent percentile (Goodman, 1965), but, again reliable values for these statistics are available only after the populations have been evaluated. When the local elite breeding pool is lacking in sufficient favorable variation, crosses between local and exotic sources of germplasm (perhaps including wild relatives) may be necessary to incorporate the desired genes into a breeding program. Recurrent backcrossing to local materials or longer term planning may be required for such strategies to be successful.

Reduction of environmental contributions to the phenotypic variance is one avenue for improving gain from selection that breeders can often implement without major difficulty. For the purposes of this discussion, it is well to distinguish variation because of macroenvironmental differences (such as the average performance difference of a population among different locations or over years) from variation because of microenvironmental variation that occurs within a particular year and location combination. Further, when breeding populations are evaluated across macroenvironments, the possibility of genotype-by-environment interaction (differences in relative performance of varieties across environments) must be considered (**Figure 2**). A common breeding strategy is to evaluate a set of families across multiple environments and to select based on their average performance. Each family is tested at all environments such that all family means are averaged over all macroenvironment effects, eliminating the macroenvironment effects from the phenotypic variance of family means. (Even if some data are missing from some environments, one can still estimate mean values that take into account the macroenvironment effects so that genotype comparison are not influenced by the macroenvironment effects.) The heritability of family mean differences across environments is

$$h^2 = \frac{\sigma^2_G}{\sigma^2_G + \frac{\sigma^2_{GE}}{e} + \frac{\sigma^2_\varepsilon}{re}}$$

where the genetic variance among families, σ^2_G, is some function of the additive variance that depends on the type of families

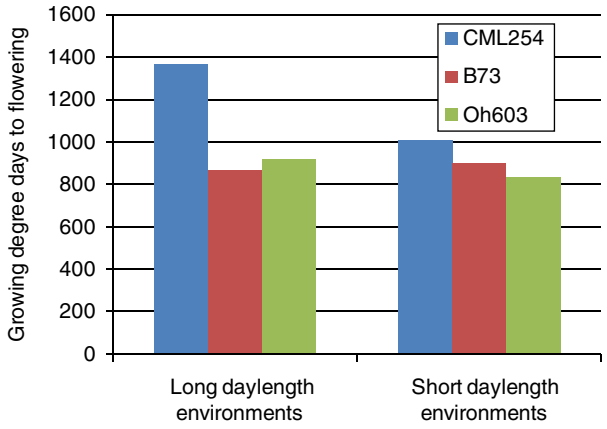


Figure 2 Example of genotype-by-environment interaction: thermal time to flowering of three maize inbred lines grown in long or short daylength environments. Relative ranking of time to flowering for the three lines changes between these two groups of environments. In this particular case, genetic differences in photoperiod sensitivity among lines determines their reactions to different daylengths.

and their inbreeding level, σ^2_{GE} is the genotype-by-environment interaction variance, σ^2_ε is the average within-environment microenvironmental variance, e is the number of environments used for evaluation, and r is the number of replications per family per environment. This equation shows that the heritability, and consequently, the expected gain from selection, can be often increased by increasing the number of testing environments e. If the breeder includes environments that are too distinct, however, the genotype-by-environment variance component may increase and overwhelm the genetic variance component, causing heritability to decrease. In such situations, it pays to identify more homogenous subsets of environments and split the breeding program to select for families that are superior within regions, rather than to continue to search for families that are superior across the whole range of macroenvironments (Ceccarelli, 1989; Simmonds, 1991).

Another component of the heritability equation that the breeder can exercise some control over is the within-environment microenvironmental variation (also known as the experimental error variation). As seen in the equation above, the contribution of this component to the denominator of heritability can be reduced by increasing either the number of testing environments or the number of replications at each environment. There is a nearly direct trade-off in resources between increasing the number of replications evaluated and the number of unique genotypes that can be tested. Fortunately, breeders can avail themselves of experimental designs and statistical analysis methods that can help reduce the experimental error variance without requiring additional testing resources. The major challenge to controlling experimental error in breeding trials is the large number of genotypes to be evaluated. With many genotypes to evaluate, the total physical field size required to plant all of them often become so large that the microenvironments of plots can become quite different across the testing field. Most commonly, soil quality may vary across the field so much that comparing the yield of a variety grown on one side of the field to a variety grown on the other side measures more the difference in soil quality than genetic yield potential. Good crop management is critical to minimize such effects, but experimental designs that break the whole field required for a single complete replication of the entries into subblocks can also help significantly. Lattice, alpha, augmented, *p*-rep, and row-column designs are particularly useful (Cullis *et al.*, 2006; Patterson and Williams, 1976; Williams *et al.*, 2011; Wolfinger *et al.*, 1997). In addition to improved experimental design, newer methods that attempt to model the spatial effects on experimental errors can contribute significantly to improving response to selection (Brownie *et al.*, 1993; Gilmour *et al.*, 1997; Qiao *et al.*, 2004; Smith *et al.*, 2005).

Beyond changing the selection differential and heritability, the breeder has an additional avenue through which the response to selection can be improved: reducing the time required to conduct a cycle of selection. Annual crops can be evaluated for only one generation per year in their target production environment. Breeders may be able to use greenhouses or offseason nurseries (in tropical/subtropical locations or in the opposite North/South hemisphere where seasons are offset) to obtain additional generations per year. Unfortunately, greenhouses and offseason nurseries are not useful for evaluating yield potential in the target production environments. Selection aimed at some traits with simple genetic control (such as major gene disease resistances) may be effective, but for the most part, greenhouses and offseason nurseries are most useful for advancing breeding generations (such as selfing, backcrossing, or making new hybrid combinations for breeding or testing) without selection. This alone is useful, but does not directly increase the number of selection cycles per year. Speeding up backcrossing, however, may enable breeders to more quickly introduce new disease resistance genes or transgenes into elite genetic backgrounds, particularly if they are able to easily select for the presence of the desired gene using deoxyribonucleic acid (DNA) tests or simple phenotypes. Lewis and Kernodle (2009) demonstrated an elegant method to dramatically reduce time to flowering in tobacco by transformation with a flowering time promoter, and using these rapid flowering types as targets for backcrossing a desired gene from an undesired genetic background. After the final generation of backcrossing, the breeder can select against the flowering time transgene and for the target gene to recover the desired gene in the genetic background of the elite parent with its normal flowering phenotype. Breeders have searched for other ways to use these additional generations grown outside of their target production environments, and later in this article, a recent approach using DNA marker information alone to conduct selection in these environments will be discussed.

Another way to reduce the time required to conduct a cycle of selection is the use of doubled haploids in species where inbred lines are created as part of the breeding program (Forster and Thomas, 2005). Doubled haploids require special techniques such as anther/pollen culture, wide crossing, embryo rescue, and inducer stocks. The effort required to obtain sufficient numbers of doubled haploid progeny in some cases has limited the utility of doubled haploids. In maize, however, doubled haploid breeding has gone from a rarely used approach to a widespread method in commercial maize

improvement programs in the past decade. This resulted from the development of genetic stocks that combine a relatively high frequency of haploid induction as a pollinator with a simple color marker that permits rapid visual discrimination among diploid, haploid, and outcross progeny to make the recovery of haploids from new breeding crosses relatively simple and efficient (Rober *et al.*, 2005). Proprietary methods to efficiently double the chromosome numbers of large numbers of haploid plants have probably also made an important contribution to this breeding method.

New Statistical Techniques for Selection

Statistics have long been an important tool for plant breeding; improvements in experimental design have increased the efficiency of selection, as noted in the Section Enhancing Gain from Selection. When experiments are well designed and executed, relatively simple statistical analyses can often remove much of the influence of extraneous macro- and micro-environmental effects from the mean values of the genotypes. To handle nonrandom spatial field effects, however, more complex models may be needed. Such models relaxed the assumptions of standard ordinary least squares analysis of variance, such as the assumption that error effects are uniformly and independently distributed among test plots. Instead, one could test a model that, for example, models the error effects on some pair of plots as having a correlation that is greatest for adjacent plots and decreases in magnitude as the plots considered are more distant physically. To perform such an analysis, however, requires a shift from standard analysis of variance techniques to mixed linear models. The mixed linear models analysis is more computationally intensive and requires specialized software; the necessary computation power and software were not widely available to plant breeders until approximately 20 years ago.

The mixed linear models approach has broadened considerably the range of models that can be tested for plant breeding experiments. One example is the modeling of spatially correlated residual error effects, as just mentioned. More complex models can also be applied to multiple environment trial data sets, such as allowing each environment to have a unique amount of experimental error variance, which is a more realistic model than the constraint of a common error variance assumed by the traditional analysis of variance. An important change in the concept of genotype-by-environment interaction variance has been fostered by the ability to flexibly model different forms of such interactions using mixed models. One example that seems particularly appealing is a model that allows each environment to express a different amount of genotypic variation and allows each pair of environments to have a unique correlation between genotypic values. This allows the breeder to identify easily which pairs of environments produce similar phenotypic responses from a common set of genotypes, and which pairs of environments produce unrelated, or perhaps even negatively correlated phenotypic responses. This helps breeders to select optimal sets of testing environments that will capture as much of the range of environments in the target production region, and can help determine if the breeding program should be partitioned to select for different subsets of genotypes adapted to specific environmental subsets.

Fitting more complex mixed models is not simply an academic exercise in better capturing the nongenetic effects on experiments, however. The mixed model has a different philosophical underpinning for effects that are considered random (meaning that they are samples randomly drawn from some larger population of effects) versus fixed (meaning that the effects studied are the ones of direct interest, and they are not assumed to be drawn from some larger reference population). The practical effect of treating genotypes as random in the mixed model is that their genetic value is predicted with a best linear unbiased predictor (BLUP) instead of estimated with a best linear unbiased estimator (BLUE), such as a mean value (Robinson, 1991). BLUPs and BLUEs may rank genotypes differently, because BLUPs incorporate a shrinkage factor that makes them closer to the overall population mean than their respective BLUEs. The amount of shrinkage depends on the trait heritability (higher heritability traits have less shrinkage) and the amount of information available for a particular genotype. For example, if a genotype has missing data from most environments in a multienvironment trial, but has an outlier phenotype based on a small amount of available data, its BLUP will be shrunk back toward the mean more strongly than genotypes with more data. This is a sort of penalty on those genotypes that have more missing data, and would lead to them being less likely to be selected on the basis of BLUPs, even if their mean BLUE value would have ranked them very highly. The mixed model analysis accounts for the differences among environments in terms of different error variances, amount of genetic variance, correlation with other environments, and so forth, such that the effect of missing data on shrinkage depends on the environment from which the data is missing. Importantly for practical breeding purposes, BLUPs have higher accuracy than mean values, so selection on BLUPs is expected to result in better response to selection (Piepho *et al.*, 2008).

Best Linear Unbiased Predictions Incorporating Pedigree Information

Another key improvement that mixed models and BLUPs have begun to deliver to plant breeding programs is their ability to incorporate information on relationships among lines and individual plants in the breeding pool. This methodology was pioneered by Henderson (1974) and widely adopted in animal breeding before plant breeders began to recognize its utility and applicability to problems in plant breeding (Bernardo, 1996; Panter and Allen, 1995). Plant breeders long recognized that closely related lines have similar phenotypic responses, but Henderson's BLUP methodology allowed precise incorporation of quantitative estimates of genetic similarity based on the amount of shared pedigree between each pair of lines or individuals into the predictions of genetic value (Lynch and Walsh, 1998). The importance of this method is to leverage observed phenotypic information on each line to improve the predictions of other lines to which they are related (Piepho *et al.*, 2008). Extending this idea further, Bernardo (1996) showed that plant breeders could improve

the efficiency of their programs by initially testing a diverse subset of lines, then predict the genetic value of all of those lines, plus the value of untested lines using the known pedigree relationships among the tested and untested lines and the BLUP method. The lines with highest predicted values (whether directly tested or not) could then be identified for further evaluation, thus concentrating testing resources on lines with the best chances of being superior. This concept has evolved more recently into genomic selection (see Section Using Genetic Markers In Selection Programs), where the concept of breeding value prediction has been further refined through the application of genetic marker information.

New Sources of Germplasm

A basic premise of plant breeding is that response to selection occurs by the increase of favorable allele frequencies, and concurrent decrease of unfavorable allele frequencies in breeding gene pools. In the long run, plant breeding that is effective should reduce genetic variability in breeding populations. This poses a problem for breeders: progress from selection depends on genetic variation in breeding populations, but such progress tends to ultimately reduce such variation.

Most crops suffered substantial genetic bottlenecks during the domestication process (Tanksley and McCouch, 1997). Domestication tends to impose strong selection for the domestication type: for grain crops, for example, the nonshattering trait greatly simplifies harvest and was strongly selected for across many species (Harlan, 1992). Domestication also imposed significant selection for traits such as loss of seed dormancy and seed size in seed crops, reduction of thorns and awns, and flavor and fruit size in fruit crops (Allard, 1999). In allopolyploid crops such as wheat and oat, multiple bottlenecks occurred: the interspecific hybridizations and subsequent chromosome doubling occurred naturally, but these are very rare events which involve very small population sizes, and were then followed by the typical population bottleneck during domestication (Sears, 1969). This explains the quite low level of genetic variation in wheat compared to other crops (Cox and Wood, 1999). Acting against this domestication bottleneck were subsequent gene flow between sympatric wild and domesticated species (van Heerwaarden *et al.*, 2011) and human selection for very diverse phenotypes (such as the dramatically different plant forms of cabbage noted by Darwin (1859) and for adaptation to widely divergent environments (Allard, 1999; Ruiz *et al.*, 2008; Wallace and Brown, 1988). Mutation, genetic recombination, mating system, and population sizes were also important factors in shaping the diverse levels of genetic variation among crops.

Seed banks and germplasm repositories represent an important genetic resource holding alleles that have been eliminated from modern elite breeding pools but that may have some value to modern agriculture (Tanksley and McCouch, 1997). Major challenges of using gene bank materials are a lack of relevant information on characteristics that may be of use to a particular breeding program and the linkage of favorable alleles to many generally unfavorable alleles at nearby genes in the unadapted genetic backgrounds of most germplasm resources. Harlan and de Wet (1971) proposed a classification of cultivated plants from the point of view of their practical utility to plant breeding programs. In their system, taxa are organized into primary, secondary, and tertiary gene pools. The primary gene pool consists of all taxa that are fully interfertile with the cultivated species; the secondary gene pool includes taxa that can be crossed to the cultivated species but produce hybrids with low fertility or poor chromosome pairing; the tertiary gene pool includes those taxa whose hybrids with the cultivated species are lethal or completely sterile, such that specialized techniques such as embryo rescue and chromosome doubling are required to obtain any fertility in the progeny (Harlan and de Wet, 1971). This classification emphasizes that most breeding crosses should be restricted to the primary gene pool to have the greatest chance of success of recovering an improved cultivar. Nevertheless, even within the primary gene pool of most crops, there are huge differences in adaptation, productivity, acceptability for commercial production, and genetic load. Thus, breeders usually will attempt to incorporate diversity from already improved materials that are distinct from their elite gene pool, but lack significant problems of adaptation or acceptability. Where such materials do not carry the desired favorable alleles, breeders must access less adapted germplasm and expect to need additional generations to break up unfavorable gene linkages and may need to use backcrossing techniques to reduce the overall contribution of the donor of diversity. Despite these difficulties, there is ample evidence that 'exotic' sources of germplasm within the primary gene pool can be effectively used to improve elite gene pools even for highly polygenic traits such as yield (Goodman, 2004; Simmonds, 1993; Tanksley and McCouch, 1997).

For species such as wheat, which suffered severe bottlenecks during their evolution, the primary gene pool may not carry the genetic variation needed for specific traits. Substantial effort in transferring disease and pest resistances from the secondary and tertiary gene pools has been made in wheat, resulting in the development of numerous specialized techniques to recover progeny from wide crosses, induce recombination, and recover stable cultivated types carrying desired target genes (Friebe *et al.*, 1996; Jiang *et al.*, 1993). These approaches, particularly the use of the tertiary gene pool, require longer-term commitment to successfully proceed from initial crosses to an agronomically acceptable cultivar expressing the trait of interest.

In general, the use of secondary and tertiary gene pools is restricted to the introgression of one or a few genes from a particular donor parent. The objective of introgression programs is to recover a variety that carries the target genes from the donor parent but as little genetic material from that donor as possible. This is usually achieved through repeated backcrossing to the recurrent elite cultivated parent, but if the chromosomal structure of the donor is too different from the cultivated parent, the chromosome segments around the target gene may not pair well and recombination may be suppressed. Without adequate recombination, even many generations of backcrossing may result in the maintenance of large chromosomal segments carrying many genes, which, other than the target gene, are likely to be undesirable (Young and Tanksley, 1989).

Introgression programs aimed at introducing genes from the secondary and tertiary gene pool are more likely to be

successful in polyploid species. Successful examples of this work abound for diverse polyploids such as wheat, potato, and sugarcane (Jansky and Peloquin, 2006; Jiang *et al.*, 1993; Simmonds, 1993), but are unheard of in, for example, diploid maize (despite some effort) (Harlan and de Wet, 1977). This is a result of the greater capacity of polyploid genomes to 'buffer' against the deleterious effects of large chromosomal introductions and unbalances that occur during such breeding schemes.

The use of transgenic technologies (gene transformation) can also be considered as part of the toolkit for introducing genes from the tertiary gene pool. Genetic transformation has expanded the tertiary gene pool (at least for some crops) to include all living species, so, for example, the gene that encodes a protein toxic to lepidopteran insects could be transferred from the bacterium *Bacillus thuringiensis* to crop plants (Koziel *et al.*, 1993; Perlak *et al.*, 1990). Genetic transformation is also sometimes considered the ultimate tool for introgression, as only the desired target gene is introduced into the cultivated crop, conceptually eliminating the accompanying linkage drag of the surrounding chromosomal segments from the donor. Unfortunately, in most crops, transformation is most efficiently conducted with older inferior varieties (because they regenerate better from tissue culture), necessitating backcrossing the transgene from the old variety into the elite.

Using Genetic Markers in Selection Programs

The genomics revolution has provided numerous technologies that facilitate the rapid analysis of sequence variation in crops. Crops such as maize, wheat, rice, and soybean have extensive genomics resources that allow the relatively rapid development of DNA markers that can be used to track inheritance of specific chromosomal positions. Modern sequencing technologies also have contributed to marker development in many other plant species, but the ability to create marker sets that are readily deployable across breeding programs often requires a deeper understanding of genome structure and variation than exists for some species.

The ability to rapidly assay allelic variation at DNA markers can be of considerable utility to plant breeding programs. This technology is of greatest immediate applicability for the selection of desired gene variants that have sizeable effects on an important trait, have been mapped accurately and precisely (with identification of the causal gene and sequence variant most useful), and for which DNA marker assays are cheaper, easier, or faster than phenotypic identification of progenies that carried the desired gene (Collard and Mackill, 2008; Holland, 2004; Tester and Langridge, 2010; Young, 1999). Some examples where this condition is true and for which marker-assisted selection has become routine for at least some breeding programs include:

- Soybean cyst nematode resistance, a difficult trait to accurately phenotype, but for which a few genes have major effects (Cahill and Schmidt, 2004; Young, 1999);
- Disease resistances and submergence tolerance in rice, encompassing a range of difficulty for phenotyping but for which individual genes with large effects have been identified directly or by tight linkage to markers (Collard and Mackill, 2008; Francia *et al.*, 2005; Ismail *et al.*, 2013);
- Numerous disease resistances and simply inherited fruit quality characteristics regularly targeted with markers in commercial tomato breeding programs (Foolad and Panthee, 2012);
- Disease-resistance genes, self-incompatibility, fruit quality in several fruit crops of genus *Prunus* (Dirlewanger *et al.*, 2004);
- Many (>50) simply inherited disease resistance and grain quality characteristics targeted by public wheat breeding programs (Dubcovsky, 2004; Eagles *et al.*, 2001; Gupta *et al.*, 2010; Miedaner and Korzun, 2012).

The experience with marker-assisted selection in wheat breeding is particularly instructive, as this has been done almost entirely in the public sector across several countries. Australia pioneered the practical application of marker-assisted selection on a large-scale by creating centralized genotyping facilities to support the applied breeding programs (Eagles *et al.*, 2001). The USA federal government followed suit by establishing four regional small grains genotyping facilities to conduct marker analysis for both public and private sector breeders and by funding a coordinated multistate project to make genotypic selection widely available to applied breeding programs (Dubcovsky, 2004). By removing the burden of marker development and genotyping from each individual breeding program (which typically do not have sufficient resources to perform marker analyses on substantial proportions of their breeding material), the centralized facilities have enabled the integration of marker-assisted selection into cultivar development in small grains. The USA small grains marker-assisted breeding project assisted in the release of at least 90 cultivars.

The wheat example also highlights the trend seen across the examples of marker-assisted selection in other species: specific markers have been most useful for selection when they identify alleles of relatively large effect. Major disease-resistance genes are the most common example of this: the presence of a particular disease-resistance allele can determine completely if a plant is resistant to a particular race of pathogen. In addition to the targeted gene having a major effect, markers are most useful when they are 'diagnostic' for a phenotypic effect across most breeding crosses that are expected to segregate for the phenotype (Collard and Mackill, 2008; Holland, 2004). Although there are special cases in which linkage relationships between linked markers and causal variants tend to hold in breeding programs, high resolution genetic analysis to identify casual sequence variation that underlies desired phenotypes is usually required to obtain a diagnostic marker (Holland, 2004).

Markers have proven particularly useful to backcross breeding programs, where a panel of markers can be used to select simultaneously for the desired allele from the donor parent, against linked donor alleles (to reduce linkage drag), and against donor alleles on other chromosomes (to reduce the number of generations required to recover most of the recurrent parent genome) (Chen *et al.*, 2000; Collard and Mackill, 2008; Frisch *et al.*, 1998; Randhawa *et al.*, 2009).

Implementing markers for selection more generally in typical breeding schemes that involve generating many new breeding families from crosses among numerous parental lines can be more difficult, as it requires diagnostic markers to be widely useful and efficient. Some effort is often required to determine (based on pedigrees and previous knowledge of which founder lines carry specific alleles of interest) which sets of markers can be fruitfully applied for selection in specific breeding populations.

Marker selection can be most useful if it can be applied to single plants (or seeds) in early generations before substantial effort on phenotyping has been expended (Collard and Mackill, 2008). Rather than attempting to identify a plant or plants homozygous for all of the desired marker alleles in early generations (which would require astronomical population sizes if the number of target genes exceeds a few), gene enrichment strategies that select for plants carrying at least one desired allele at as many genes as possible can be far more efficient and practical for implementation in applied programs (Bonnett *et al.*, 2005; Wang *et al.*, 2007). The key concept is to use markers to identify a subset of the breeding population that has the greatest chance of carrying desired alleles for a number of simply inherited traits so that more expensive field phenotyping for other complex traits of agronomic importance can be concentrated on lineages that are most likely to result in a cultivar possessing most of the desired characteristics. Thus, markers do not replace phenotypic evaluations, but instead help to focus phenotyping resources on lines that are enriched for favorable alleles affecting a subset of traits.

In contrast to the situation where trait expression is largely controlled by one or a few genes and for which marker-assisted selection can be very efficient, traits with complex genetic control have been less amenable to marker-assisted selection. Returning again to the example of wheat breeding, an important trait for both yield and grain quality is resistance to Fusarium head blight disease. Unlike some other wheat disease resistances that are largely controlled by a small number of genes with large effects, such as leaf rust and stem rust, Fusarium head blight resistance is under more polygenic control. Numerous genes with smaller effects contribute to the inheritance of this trait and environments exert substantial influence on the expression of this disease. Therefore, it has been difficult to accurately identify the genome locations and effects of the underlying genes. Instead, regions of the genome have been identified as containing quantitative trait loci (QTL) for Fusarium head blight resistance, but these regions are generally only loosely defined and may contain hundreds of genes (Buerstmayr *et al.*, 2009). Worse, the QTL identified in any one linkage mapping study often have little correlation to those identified in a different cross (Buerstmayr *et al.*, 2009). Thus, at this time, breeders have reliably diagnostic markers for only one Fusarium head blight resistance QTL, which confers only a portion of the resistance in some crosses, and has no effect in other crosses (Buerstmayr *et al.*, 2009). The situation is similar for many other complex traits in wheat, such as grain yield and abiotic stress resistances (Francia *et al.*, 2005). There is no evidence for, nor reason to believe, that a particular marker can be diagnostic for any highly polygenic trait in any species (Bernardo, 2008; Collard and Mackill, 2008; Holland, 2004). Statistical difficulties limit the ability to precisely refine the position of QTL or to estimate their effects even in one breeding family (Beavis, 1998; Schön *et al.*, 2004), and the underlying biological reality is that different sets of genes segregate in different breeding families, reducing the predictive power of QTL markers for complex trait selection (Holland, 2007).

Simultaneous genetic analysis of multiple breeding families representing the range of genetic diversity of a breeding pool can more precisely identify specific genes controlling complex traits and at the same time provide better understanding of the distribution of allelic effects among important breeding stocks (Holland, 2004, 2007). Association analysis and joint multiple population linkage analysis represent complementary approaches to comprehensive genetic analysis of complex traits.

Association analysis attempts to identify allelic variants associated with trait variation across a diverse sample of breeding materials. If linkage disequilibrium decays rapidly with physical sequence distance in the sample, association analysis can provide precise identification of the genomic position of sequence variation affecting a trait, possibly facilitating the identification of a causal gene and its causal sequence variation (Ersoz *et al.*, 2007; Flint-Garcia *et al.*, 2005). In addition to potentially higher resolution than linkage mapping, association studies have the benefits of being directly applicable to existing breeding pools without requiring development of specialized mapping families and sampling a greater diversity of alleles (Breseghello and Sorrells, 2006; Ersoz *et al.*, 2007; Myles *et al.*, 2009). A number of experimental and statistical challenges impact the feasibility of association analysis, including the choice of environments used to measure phenotypes of diverse germplasm sampled from a wide range of zones of adaptation, the accuracy of phenotypic measurements, the frequency of the causal allele, and the ability to measure genetic variation for the trait after accounting for population structure (Breseghello and Sorrells, 2006; Larsson *et al.*, 2013; Morrell *et al.*, 2012; Myles *et al.*, 2009; Yan *et al.*, 2011; Zhu *et al.*, 2008). If the genetic regulation of a trait is already well understood from knowledge of biochemistry or model systems, a relatively small number of genes may be considered candidate genes to be tested for association with the trait, increasing one's chance of identifying a causal gene (Harjes *et al.*, 2008; Wilson *et al.*, 2004; Yan *et al.*, 2010). For many important traits, however, one has little or no understanding of the genes or biochemical pathways that might be involved in their expression. In such cases, genome-wide association studies can be attempted, whereby a very large number of single nucleotide polymorphisms (SNPs) are tested for association, in the hope that some causal variants are in linkage disequilibrium with at least one SNP each (Huang *et al.*, 2010, 2012; Morris *et al.*, 2013; Olukolu *et al.*, 2013; Wisser *et al.*, 2011). Genome-wide association studies also have the advantage that they test for variation in noncoding regions of the genome, which turn out to be over represented in the set of SNPs associated with trait variation in some cases (Li *et al.*, 2012).

Joint multiple population linkage analysis combines information from several related biparental cross populations to improve power and resolution of QTL identification and also to characterize the distribution of allele effects in different founder lines representing some portion of the diversity of a

breeding pool (Blanc *et al.*, 2006; Coles *et al.*, 2010; Holland, 2007). The largest such studies in maize have revealed substantial complexity for most quantitative traits, characterized by numerous genes of relatively small effects at which the allelic effects are dispersed among founder lines (Brown *et al.*, 2011; Buckler *et al.*, 2009), demonstrating the futility of predicting QTL effects across populations for highly polygenic traits.

Joint multiple population linkage analysis can be integrated with genome-wide association study to combine the advantages of well-defined population structure and accurate and inexpensive imputation of dense sequence variation from parents to mapping progenies from linkage analysis to the higher resolution provided by association analysis (Hung *et al.*, 2012a; Kump *et al.*, 2011; Tian *et al.*, 2011). These approaches have permitted the identification of SNPs and other sequence variants associated with complex traits at high power, but again reveal the substantial complexity of quantitative traits at least in outcrossing maize, because most SNPs are associated with only a very small fraction of the observed trait variation. Thus, even identification of specific sequence variants associated with trait variation and their distribution in the breeding pool is not sufficient to enable cost-effective marker-assisted selection, because many markers need to be assayed and the response to selection at any one marker is expected to be too small to warrant its selection. However, even for complex traits, there is usually a distribution of variant effect sizes, and perhaps a few variants might have effects of sufficient magnitude to warrant their targeting for marker selection (Hung *et al.*, 2012a). In addition, association analysis might still be fruitfully applied to traits that are difficult to phenotype but for which a relatively small number of genes are important (Harjes *et al.*, 2008).

An entirely distinct approach to the use of DNA markers for enhancing selection to polygenic traits referred to as genomic selection has developed rapidly in the past decade as a way to address the shortcomings of QTL-based marker-assisted selection. Once again, the seminal work in this area of quantitative genetics-based breeding was done by animal breeders (Hayes *et al.*, 2009; Meuwissen *et al.*, 2001). Plant breeders realized the potential utility of genomic selection and proposed modified schemes that could be integrated into current maize (Bernardo and Yu, 2007), small grains (Heffner *et al.*, 2009; Lorenz *et al.*, 2011), and forest tree (Grattapaglia and Resende, 2011) breeding schemes.

As mentioned already, QTL effects for polygenic traits are difficult to estimate accurately, and this limits the predictive ability of QTL-statistical models even within a single mapping family (Melchinger *et al.*, 1998; Schön *et al.*, 2004), and thus the potential response to marker-assisted selection of QTL (Moreau *et al.*, 1998). QTL models are created by testing each region of the genome for association with the trait and selecting only those marker-tagged regions that appear to have statistically significant effects on the trait. Although the exclusion of markers that do not have strong statistical significance from the prediction model seems sensible, it turns out to limit the predictive power of the models (Moreau *et al.*, 1998). The basic premise of genomic selection is that all markers should be included in the prediction model (Bernardo and Yu, 2007; Meuwissen *et al.*, 2001; Xu, 2003), even when there are more markers than individuals in the test population! Standard regression techniques cannot be used for such 'overfitted' models, so alternative statistical techniques must be used, such as Bayesian analysis, ridge regression, or mixed models with constrained marker variances (Bernardo and Yu, 2007; Meuwissen *et al.*, 2001; Xu, 2003). The details of these analyses are complex, but the key objective of genomic selection is to predict the breeding value of lines in the study as well as lines with genotype information but no phenotype information using the prediction model (Lorenz *et al.*, 2011). Unlike QTL mapping, the prediction models do not attempt to accurately estimate the effects of each genome region, instead they sacrifice accuracy on individual marker effects by overfitting the markers, but increase the accuracy of breeding value prediction based on the net value of markers. In this way, the optimal amount of information about polygenic effects is extracted from the set of lines with both genotypic and phenotypic information (the training data set), providing better predictions for lines with only genotypic data (Heffner *et al.*, 2009), which could represent untested sib lines or progeny generated from crosses among lines in the training data set. Genomic selection models are not expected to provide accurate estimates of the effects of specific genome regions on traits, however.

Bernardo and Yu's (2007) original proposal for implementing genomic selection was in the context of a commercial maize breeding program, in which genomic recurrent selection could be conducted for several cycles on seeds or seedlings in offseason nurseries. Separate genomic selection models could be created for each biparental cross family, which maximizes the consistency of linkage relationships between markers and causal genes over several cycles of selection. Even when genomic marker predictions of phenotypes are less accurate than direct phenotypic evaluations, genomic selection can produce greater gains per unit of time by enabling additional cycles of selection on individuals seeds or plants in offseason nurseries (Heffner *et al.*, 2011a, 2010; Lorenzana and Bernardo, 2009; Massman *et al.*, 2013).

An alternative use of genomic selection is the development of prediction models encompassing lines derived from many different parental combinations rather than just one cross (Crossa *et al.*, 2010; Heffner *et al.*, 2010; Zhong *et al.*, 2009). Cross-validation and simulation studies suggest that this could work (Crossa *et al.*, 2010; Heffner *et al.*, 2011b; Riedelsheimer *et al.*, 2012), but that there are difficulties with combining information across very diverse germplasm sets (Lorenz *et al.*, 2012; Zhong *et al.*, 2009). Windhausen *et al.* (2012) demonstrated that genomic prediction models created by combining diverse maize breeding pools had good accuracy for prediction of germplasm in those same pools, but the prediction accuracy fell to approximately zero when the models were applied to newly created biparental populations. Simply, the training data set used to create the genomic selection model must have a close genetic relationship to the breeding population to which it is derived. Exactly how close this relationship must be is still a matter of investigation. The availability of such large-scale prediction models is likely most useful for well-resourced commercial breeding programs, where the ability to generate and genotype new progeny lines outstrips the ability to conduct high-quality phenotypic evaluations of yield and other complex traits. In this way, the breeding potential of progeny

lines that have never been planted in a field could be predicted, and lines with superior predicted values could be retrieved from storage for future phenotypic evaluations. This approach emphasizes the expenditure of precious phenotypic testing resources for materials that have the best chance of being cultivars or cultivar parents.

Marker-assisted selection and genomic selection are important components of modern breeding programs in many crops. The balance between the use of resources on DNA markers to select for specific gene alleles, genomic selection to select for the 'polygenic background,' and phenotypic evaluations will likely shift as research indicates the best application of each evaluation method. The optimal balance likely will vary among crops and even among different programs in the same crop, as it will depend on the relative availability and cost of genomics resources compared to field testing.

To the extent that genetic dissections of important traits succeed in identifying causal genes and sequence variants (via association analysis, high resolution linkage mapping, or other means), those alleles can be targeted for selection and for incorporation across distinct germplasm groups. This form of 'direct allele selection' (Sorrells and Wilson, 1997) should be more effective at predicting the value of alleles across diverse germplasm than genomic selection models, which are highly dependent on the genetic context in which they are defined. These different selection methods could be combined by identifying a subset of the most important genes and targeting them for direct allele selection, predicting the breeding value of some portion of the remaining background polygenic variation with a genomic selection model, and relying on extensive phenotypic evaluations of a selected subset of lines to make final decisions on cultivar releases. Note that high-quality phenotypic evaluations underlie all three of these aspects of modern breeding.

See also: Crop Pollination. Genebanks: Past, Present, and Optimistic Future. Genomics: Plant Genetic Improvement. Green Revolution: Past, Present, and Future. Transgenic Methodologies – Plants

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Relevant Websites

http://www.cgiar.org/
Consultative Group on International Agricultural Research, which organizes research conducted at non-profit international research centers.

http://www.ars-grin.gov/
Germplasm collections of USDA, including searchable databases of seed collections.

http://maswheat.ucdavis.edu
MASwheat collaborative project on marker-assisted selection in wheat, including technical information on laboratory protocols and outreach and educational materials for the general public.

http://www.extension.org/plant_breeding_genomics
On-line course materials and short tutorials on specific topics from extension Foundation, a network of agricultural extension services of USA land-grant universities.

http://www.plantbreeding.org/napb/
USA National Association of Plant Breeders, includes the plant breeding newsletter.

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Changing Structure and Organization of US Agriculture

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Glossary

Beginning farmer Farm operator of a farm on which all operators have 10 years or less experience in operating a farm.

Commodity specialization Total value of production equaling at least 50% from one commodity or related group of commodities determines a farm's commodity specialization, consistent with the North American Industry Classification System. Farms that do not have a commodity or livestock type composed of at least 50% of production are classified as other crops or other livestock operations.

Contracting Many farmers market their production through contracts in lieu of open market sales. These farmers and their buyers agree to arrangements in the contract signed before harvest (or before the completion stage for livestock), specifying the terms under which products are transferred from the farm.

Family farm There is no hard and fast definition of a family farm in the United States, unlike the farm definition. The United States Department of Agriculture's Economic Research Service (USDA ERS) defines a family farm as one in which the majority of the business is owned by the operator and individuals related to the operator by blood, marriage, or adoption, including relatives who do not live in the operator household. The share of US farms classified as family farms has changed little since 1996, ranging from 97.1% to 98.3% of all farms.

Farm Any place from which US$1000 or more of agricultural products are sold, or normally would have been sold, during a year. A point system developed by the USDA's National Agricultural Statistics Service is used to determine when a farm normally would have sold US$1000 of products, in the event they do not do so. This point system assigns dollar values for acres of various crops and head of various livestock species to estimate a normal level of sales. These point farms have fewer than US$1000 in sales but have points worth at least US$1000 and tend to be very small. Approximately one-quarter of farms have no sales in a typical year, and at least another 30% have positive sales of less than US$10 000.

Farm operator household Farm operator households share dwelling units with principal farm operators of family farms. Multiple operators who do not share the same household operate less than 10% of family farms. In this case, the farm operator household population includes the households of the principal farm operator, but not those of the other operator(s).

Farm operator household income Income from the farm business and from other farming activities, along with income from earned and unearned off-farm sources, comprise total farm operator household income.

Large-scale family farm According to the 1998 National Commission on Small Farms, large-scale family farms produce US$250 000 or more in gross farm sales. However, different users may use different threshold levels for their purposes, especially because agricultural price levels have changed since the level was established.

Nonfamily farm Farms where the majority of the farm business assets are not owned by the principal farm operator and his or her relatives.

Small farm According to the 1998 National Commission on Small Farms, small farms have gross farm sales of less than $250 000. However, different users may use different threshold levels for their purposes, especially because agricultural price levels have changed since the level was established.

Introduction

This article provides a brief description of general characteristics and changes in production agriculture over time. Key influences or drivers of change in structure and organization, as well as other significant drivers of change, are discussed. Detailed measures of farm size and structure are presented and discussed, including the evolution over time. Economics of different types and sizes of farms are explored, including the importance of off-farm income. The implications of significant trends and their challenges to the future structure and organization of agriculture conclude the article.

Although this article is US specific in its measures used to reflect how the structure and organization of agriculture/

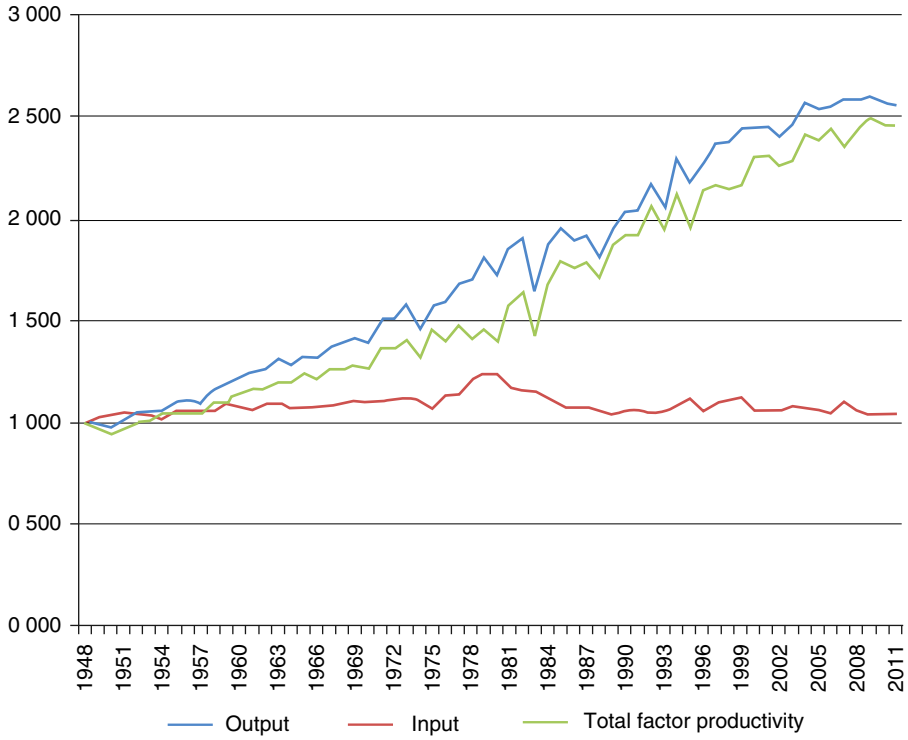


Figure 1 Indices of farm output, input, and total factor productivity, 1948–2011. US Department of Agriculture Economic Research Service, 2013a. Agricultural productivity. Available at: http://www.ers.usda.gov/topics/farm-economy/agricultural-productivity.aspx (accessed 07.07.13).

farming are changing over time, the drivers of change affecting size, structure, and organization of agriculture are largely universal. Quite similar trends are evident throughout most developed countries and are increasingly evident in the emerging commercial farming sectors across Latin America, Africa, and in some other developing countries. The scale and speed of change varies depending on policy, social systems, and cultural preferences, but the key underlying drivers of change are rapidly shared in today's global economy and interconnected world.

Key Drivers of Change in Structure and Organization

Farms in the United States have evolved over time, with more and more production coming from large-scale family farms and a relatively few nonfamily farms. The largest number of farms by far is in the small-size category (under US$250 000 gross farm sales (National Commission on Small Farms, 1998)), with many fewer in the mid-size and large farm-size categories. Small farms produce a relatively small proportion of total agricultural output. This evolution toward a farm sector in which production is concentrated on fewer large farms continues unabated for the most part. Two key drivers of this changing structure and organization of farms are technology adoption and globalization of agricultural markets.

Technology adoption

Increasing size of farms tends to reduce cost of production because of efficiencies in machinery use, cost savings from purchases of larger quantities of inputs at volume discounts, and ability to obtain marketing efficiencies. Larger size farms are often the early adopters of technology derived from research and development, either public or private, leading to increases in productivity. Cost-saving technologies create efficiencies, such as those available from using global positioning systems to guide planting and harvesting machinery and to collect large amounts of site-specific data that facilitate decisions affecting input use, disease-control strategies, and even crop choice. Investments in machinery and accompanying technology have increased significantly, as equipment has become larger and more sophisticated to accommodate increasing scale of operations. The benefit to the producer purchasing such equipment is the efficiency with which planting and harvesting, as well as intermediate field operations, are carried out. The gains partly come from eliminating wasteful overlaps in planting, with accompanying savings in fertilizer and pesticide application costs and in part from the decreased labor time and reduced fuel costs for field operations.

From 1948 to 2011, US agricultural output grew 1.49% per year, whereas the aggregate input use increased only 0.07% annually, so positive growth in the farm sector was mainly due to 1.42% per year productivity growth (Figure 1; USDA ERS, 2013a). Research and development (R&D) leads to technology adoption that often replaces labor and generally reduces costs and increases yields. Technology adoption is fostered by the historic United States Department of Agriculture (USDA)–Land Grant University system wherein basic research findings of the land grant universities established under the Morrill Acts of 1862 and 1890 are transferred to farmers by the state Cooperative Extension programs, which carry out applied research and dissemination

functions, and by private sector firms. The Smith–Lever Act of 1914 authorized these state Cooperative Extension programs in the universities to work in cooperation with the USDA. This collaborative system's success is recognized worldwide, and its structure is often mimicked with varying degrees of success.

Starting in the 1970s, the role of the private sector in carrying out research and development has increased to the point of providing approximately 50% of the combined public and private sector funding for agricultural productivity enhancing research by 2006. This shift was facilitated by expanding intellectual property policy involving animal and plant genetics (Alston *et al.*, 2010). However, the role of the public sector in providing public goods research from which the private sector may not be able to garner profits will continue to be a critical component of technology adoption for agriculture.

Globalization of agriculture

The imports and exports of agricultural and food products tied to globalization put a premium on efficient farm production to hold down costs of exports and to keep lower cost imports from replacing US production. Trade negotiations play an important role in determining the implications of globalization for US domestic agricultural policy and products. Progress in removing or reducing tariffs and import quotas as barriers to trade have facilitated worldwide trade growth in agricultural and food products. Trade negotiations also establish guidelines for the types of food safety or other requirements countries may impose on product quality characteristics. It is critical that standards are not established which are designed primarily to create a barrier to imports from the United States or other countries, which could offset productivity efficiency as a key determinant of trade flows. This is increasingly important amid concerns about food security for the burgeoning world population of poor consumers and a growing middle class demanding improved diets.

Additional Drivers of Change in Structure and Organization

There are numerous other factors that may also drive change in farm size and structure. A number of them are briefly addressed here.

Consumer preferences

Consumer food preferences and expectations are important drivers of change in products sold by retailers. Whether they are also major drivers of change in the size and structure of farms depends on how they influence new opportunities or create challenges for producers. An important preference of consumers is convenience, as more and more households rely on two people in the workforce to provide adequate family income. Food safety is an accompanying concern for consumers who rely on the convenience of food prepared by others, such as packaged produce that has been handled in large-volume processing facilities. Foodborne illnesses, especially occurring in fresh produce and in meats, have received prominent attention in recent years and even partially eroded confidence in safety of the US food system. This led to the passage of the Food Safety Modernization Act (FSMA) in 2011 (Kinsey, 2013). The regulations that implement that Act will have direct implications for costs to producers who will need to increase food safety efforts on the farm. For example, food safety hazard analysis critical control point (HACCP) plans require knowledge about foodborne pathogens and their control. However, as the complexity of products and processes increases, more sophisticated approaches and skills are required to successfully implement an effective HACCP plan. Larger-scale farmers are generally more likely to possess the skills, or to have employees with those skills, to carry out a successful farm-level food safety program based on HACCP plans. This is likely to foster the trend toward larger size farms to spread the cost of such implementation over more units of production. However, farms are exempt from compliance with the FSMA if they sold less than US$25 000 or if they sold less than US$500 000 in the past 3 years and sell at least 51% of product directly to consumers or retail food establishments within their state or a 275-mile radius from their farm. This exemption may offset at least some of the pressure to increase farm size to spread food safety compliance costs over larger acreages.

There is increased interest by relatively smaller segments of the consumer and general population in nonmarket social values – including environmental sustainability, local and regional food systems, humane treatment of food animals, and fair wages for farm workers, to name some of the most prominent. These market segments may increase opportunities for relatively smaller farms to thrive, at least in earlier stages of developing differentiated products for these market niches.

Agricultural policy

There are a number of production-oriented agricultural policies that provide payment to major commodity producers to support incomes. They include such programs as direct payments based on historical yields and acreage, countercyclical payments, loan deficiency payments, disaster assistance programs, or payments tied to conservation practices. Changes in policies over time are surely connected to changes in farming structure (Sumner *et al.*, 2010), although clear causation is difficult to establish. For example, empirical evidence suggests that a share of agricultural program payments are capitalized into the prices of land, but it is difficult to separately identify how that might affect farm structure, apart from the key drivers of structural change (see MacDonald *et al.* (2013) for a review of recent literature).

Other agricultural policy measures may encourage or help to maintain the number of smaller farms. Examples include programs to foster farmers' markets, facilitate purchase of local foods by participants in food assistance programs, and provide federal support for production process verification, which may help smaller producers differentiate their products in the market. However, smaller farms may need to seek out opportunities to collaborate with others to be able to compete successfully in markets, even locally. Individually, they may lack sufficient volume to move much beyond farm stand sales or any local farmers' markets.

Input costs

Input costs, which may be affected by factors outside the control of agriculture, can also be important drivers of changing structure and size of farms. For example, the price of fuel, fertilizer, and debt financing are heavily influenced by factors outside of the agricultural sector. To the extent that their use per unit of farm output varies across farm size, these factors will have an impact on structure. And increases in farm size, perhaps over a number of scattered parcels, may give the farm operator more ability to capture volume discounts for products, transportation, and contracted production services. However, input costs, which they are unable to influence, may put small farmers in a more challenging position in terms of production efficiency.

Risk management

As the size of a farm increases, risk management becomes an evermore challenging element in determining its success or failure. Diversification of production to provide alternative sources of income is one element of risk management that has long been the mainstay of farms from smaller through larger operations. However, with the increasing specialization in a few major commodities in many medium- and large-scale farms in recent years, risk management must be carefully considered in the decision-making processes. Crop insurance subsidized at the federal level, and especially utilized by major field crop producers that tend to be larger than other farms, is one risk management tool that has gained in popularity in recent years. However, research has shown that due to risk-balancing tendencies on the part of a farmer, policies that decrease the variability of farm income could induce farmers to increase their risks elsewhere, such as through increased financial risk (Featherstone *et al.*, 1988). For example, increased financial leverage could provide incentives to increased concentration of production. To what extent insurance will be a mainstay of future farm programs remains to be seen, as policy constantly evolves. Many anticipate increased reliance on insurance programs in the future, in part subsidized at the federal level, as replacing much criticized direct subsidy programs for the major agricultural commodities.

Tax policy

Tax policy involves a variety of provisions that impact how firms and households organize their finances so as to minimize their tax burden and therefore can have indirect impacts on farm structure. For example, tax policy affects the use of capital in agriculture by the provisions associated with expensing of capital acquisition in the calculation of taxable income. The amount of capital costs that can be expensed, rather than placed on a depreciation schedule, are limited, depending on the tax year. For example, in 2000 US$20 000 could be expensed and in 2013 US$500 000 could be expensed. These expensing provisions are especially useful for large and expanding farms. In 2010, 83% of farms with sales of US$500 000 or more made a capital investment, although only 1% of these large farms had capital investments of US $500 000 or more (Durst *et al.*, 2013).

Tax policy may also influence structural change by fostering growth in the number of small farms. Although small farms earn little or nothing in cash income from farming, the key to understand structural change and small farm survivability is to recognize the importance of the full range of returns to farming. Small farm households generally are full owners of their farm land and farm land values have historically, and especially recently, risen rapidly, providing owners with unrealized capital gains (**Figure 2**). However, farm land owners generally receive a reduction in their local property taxes because the land is valued for tax purposes for farm use rather than market value, reducing their cost of investment compared with the cost of owning other real estate.

The majority of farm families reside on their farm property, and therefore many of the expenses associated with the dwelling are included in farm business expenses. According to data from the Internal Revenue Service, since 1980 the aggregate net farm income reported by those that file Schedule F forms (almost 90% of all farms) has been negative. Approximately three-quarters of all Schedule F filers have negative net farm income (Durst *et al.*, 2013). At the same time that farm families may be experiencing rises in the value of their farm land, paying property taxes based on the lower farm use value and having the farm business cover some residential expenses, families with off-farm income benefit from having farm losses that reduce taxes on their nonfarm income. Moreover, many farm residents most likely value the so-called psychic income that comes from a rural lifestyle.

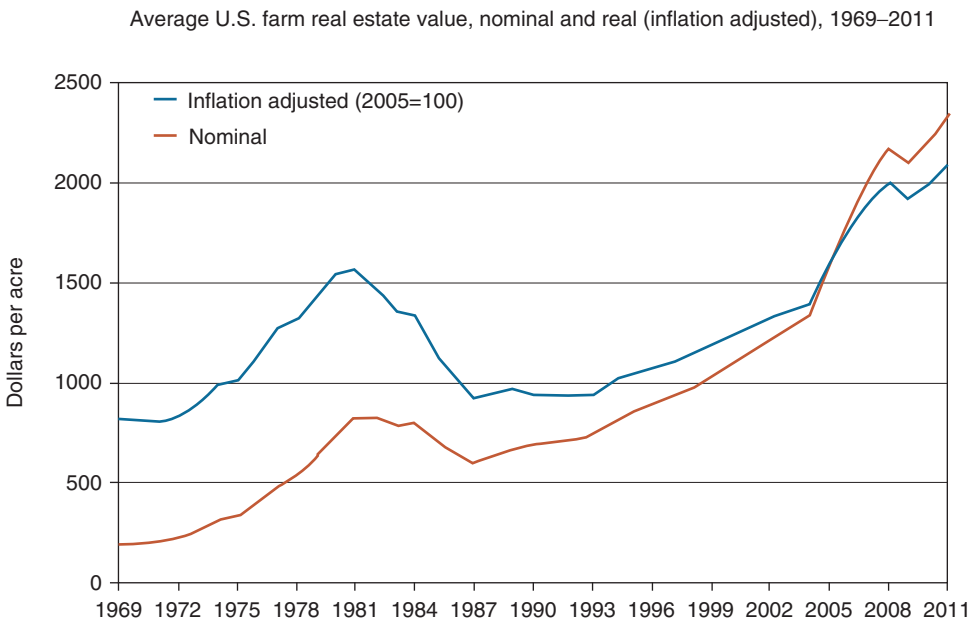
These additional returns to farming were most likely not considered in 1986 when the US Office of Technology Assessment released a report that predicted by the year 2000 there would be 1.2 million farms in the United States. The report stated:

> The projected decline in the number of small farms is dramatic but plausible, given the strong trend in this direction and the persistently negative farm income in this class (U.S. Congress, 1986, p. 96).

The report incorrectly predicted the loss of approximately 500 000 small farms. It also predicted that the 50 000 largest farms in 2000 would produce 75% of all farm products. In fact, in 1997, approximately 180 000 farms produced 75% of the value of all agricultural products. Even in 2007, family farms with greater than US$500 000 gross sales plus nonfamily farms totaled 163 500 (7.5% of total farms) and produced only 71% of total value of production. Adding in the family farms with between US$250 000 and US$500 000 gross sales raises the numbers to 257 000 (12% of total farms) producing 84% of gross farm sales. Although consolidation into large-scale farms has been important in terms of total production, the numbers of farms involved remain quite large compared with earlier projections.

Measures of Farm Size and Structure

Farm size and the relative roles and importance of small family farms, large family farms, and nonfamily farms are integral elements of the structure of agriculture. Family farm income combined from farm and off-farm sources, and the assets owned, compare quite favorably to those of the overall US population.



Note: The gross domestic product chain-type price index is used to convert NASS current-dollar statistics to 2005=100 equivalents (Bureau of Economic Analysis, Dept. of Commerce).
Source: USDA-NASS. Available at: http://usda.mannlib.cornell.edu/MannUsda/viewDocumentInfo.do;jsessionid=F154BA78C7C50C021C8CA924EDB72FD5?documentID=1446 (accessed 29.04.14).

Figure 2 Average US farm real estate value, nominal and real (inflation adjusted), 1969–2011.

Number, Size, and Commodity Specialization of US Farms

After peaking at 6.8 million farms in 1935, the number of US farms fell until the 1970s. The latest Census of Agriculture for 2007 reported 2.2 million farms (USDA National Agricultural Statistics Service, 2009). The current definition of a farm was adopted in the mid-1970s. It is a very inclusive definition and embraces farms operated by households who are retired or attracted to farming for reasons not primarily related to production, such as the rural lifestyle or investment opportunities. In addition, since the definition is dollar based but not inflation adjusted, it becomes more inclusive with each passing year as price levels change. The number of total farms and the average acreage per farm has been very stable (Table 1).

However, the statistics in Table 1 mask significant structural change over the period. Table 2 shows the number and percent of farms in different constant dollar sales classes for 1982 and 2007. During the period, both the number and the share of farms increased in the very smallest class of point farms (with sales less than US$1000 but normally expected to sell at least that amount of agricultural products) and the two largest classes (with sales of US$500 000 or more). The largest declines were in the mid-sizes of US$10 000–249 999 in sales, which went from 51% of all farms in 1982 to 31% of all farms in 2007. This evidence of a declining middle is a continuation of an ongoing trend.

Cash receipts from commodity production indicate increasing nominal value of products sold, reflecting both quantity increases and price increases (Table 3). Several factors have contributed to this rapid rise in cash receipts from all commodities since the turn of the century. In particular, growth of middle-class consumers in developing countries has created demand for oil crops, food commodity crops, and vegetables and fruits as well as for livestock products and therefore feed crops. The extent to which these price increases will be sustained depends on demand recovery from the recession starting in 2008 in the United States and subsequently experienced in most developed and many developing countries, further demand expansion from rising middle-income countries, continued demand for agricultural products as a source of fuel, and trade policy agreements.

Table 4 shows net cash farm income by commodity specialization and provides financial and other characteristics of the various farm types.

Legal Form of Organization and Farm Ownership

The changing structure of farming to larger sized operations facilitates achieving economies of scale to reduce costs and increase farm income. Some are concerned that the future food supply will be controlled by a small number of corporate farms, leading to higher prices to the consumer. But the reality does not bear out this concern.

A distinctive feature of agriculture is that a large number of family farms control most production, whereas publicly held corporations are few in number and control a minor portion of production. To better understand this issue, it is useful to draw the distinction between family and nonfamily farms and legal organization. The family–nonfamily distinction is based on whether or not an extended family owns most of the assets of the farm business, regardless of legal organization and farm size. In 2011, 97.3% of all farms were classified as family farms, and at least since 1996, the percent of nonfamily farms

Table 1 Farms: Number, land in farms, and average farm size, United States, 1985–2012

Year	*Farms (number)*	*Land in farms (1000 acres)*	*Average size of farm (acres)*
1985	2 292 530	1 012 073	441
1986	2 249 820	1 005 333	447
1987	2 212 960	998 923	451
1988	2 200 940	994 423	452
1989	2 174 520	990 723	456
1990	2 145 820	986 850	460
1991	2 116 760	981 736	464
1992	2 107 840	978 503	464
1993	2 201 590	968 845	440
1994	2 197 690	965 935	440
1995	2 196 400	962 515	438
1996	2 190 500	958 675	438
1997	2 190 510	956 010	436
1998	2 192 330	952 080	434
1999	2 187 280	948 460	434
2000	2 166 780	945 080	436
2001	2 148 630	942 070	438
2002	2 135 360	940 300	440
2003	2 126 860	936 750	440
2004	2 112 970	932 260	441
2005	2 098 690	927 940	442
2006	2 088 790	925 790	443
2007	2 204 950	921 460	418
2008	2 200 100	919 910	418
2009	2 200 210	919 890	418
2010	2 192 000	918 840	419
2011	2 181 630	917 000	420
2012	2 170 000	914 000	421

Source: Reproduced from United States Department of Agriculture, National Agricultural Statistics Service, 2013. Quick Stats Data Base. Available at: http://www.nass.usda.gov/Quick_Stats/ (accessed 29.04.14).

Table 2 Number of farms by constant dollar sales class, 1982 and 2007

Sales class (2007 constant dollars)[a]	*1982*		*2007*		*Change*
	Farms (No.)	*Distribution (Pct.)*	*Farms (No.)*	*Distribution (Pct.)*	*1982–2007*
Total farms	2 240 976	100.0	2 204 793	100.0	– 1.6
Point farms[b]	254 097	11.3	688 834	31.2	171.1
US$1000–9999	700 252	31.2	630 327	28.6	– 10.0
US$10 000–49 999	601 840	26.9	403 017	18.3	– 33.0
US$50 000–99 999	253 243	11.3	125 456	5.7	– 50.5
US$100 000–249 999	282 809	12.6	147 500	6.7	– 47.8
US$250 000–499 999	97 894	4.4	93 373	4.2	– 4.6
US$500 000–999 999	34 650	1.5	60 777	2.8	75.4
US$1 000 000 or more	16 191	0.7	55 509	2.5	242.8

[a]Sales class is based on the market value of agricultural products sold.
[b]Point farms have sales of < US$1000 (current dollars) but are still considered farms because they would be expected to normally sell at least $1000 of agricultural products.
Note: Sales and sales classes are defined in 2007 dollars, using the Producer Price Index for farm products to adjust for price changes. Point farms are identified using current dollars – with no adjustment for price changes – because the minimal level of sales in the farm definition is not adjusted for price changes.
Source: Reproduced from Hoppe, R.A., MacDonald, J., Korb, P., 2010. Small farms in the United States: Persistence under pressure. Economic Information Bulletin 63. Washington, DC: USDA ERS and USDA, Economic Research Service, compiled from U.S. Census Bureau, 1982 Census of Agriculture and USDA, National Agricultural Service, 2007 Census of Agriculture. Available at: http://www.ers.usda.gov/topics/farm-economy/farm-household-well-being/glossary.aspx (accessed 29.04.14).

has been between 2% and 3% of all farms (USDA ERS, 2013b). In recent years, nonfamily farms have accounted for between 12% and 15% of the value of agricultural production.

However, legal organization of a farm business is a way to organize ownership and management of the business, largely for tax, liability, and transfer purposes. Legal organization does not require that farms be of a certain size, although large farms are more likely to be organized as corporations than are smaller farms. Legal organization also does not imply a family ownership status. The reality is that many large family farms are

Table 3 Cash receipts from commodity production, 1985–2010

	1985	*1990*	*1995*	*2000*	*2005*	*2010*
			US$1000			
All commodities	143 983 821	169 344 223	188 202 600	192 097 825	240 897 821	321 149 221
Meat animals	38 704 432	51 131 683	44 865 002	53 011 551	64 813 168	69 998 662
Dairy products	18 074 462	20 152 604	19 879 611	20 586 629	26 704 863	31 367 282
Poultry/eggs	11 302 634	15 289 018	19 075 734	21 854 088	28 834 009	35 463 755
Miscellaneous livestock	2 032 948	2 536 205	3 396 768	4 144 299	4 579 063	4 724 711
Food grains	8 863 628	7 480 534	10 356 029	6 525 027	8 611 410	14 104 297
Feed crops	22 276 424	18 671 665	24 504 521	20 545 743	24 589 872	54 812 758
Cotton	3 686 502	5 488 395	6 850 629	2 949 649	6 402 504	7 562 358
Tobacco	2 698 546	2 733 496	2 548 235	2 315 779	1 097 081	1 245 584
Oil crops	12 394 132	12 296 145	15 492 964	13 477 739	18 387 789	36 509 433
Vegetables	8 611 838	11 273 905	14 982 903	15 758 258	17 291 250	20 111 316
Fruits/nuts	6 949 550	9 381 000	11 017 842	12 283 886	17 137 528	21 858 812
All other crops	8 388 725	12 909 573	15 232 362	18 645 177	22 449 284	23 390 253

Source: Reproduced from U.S. Department of Agriculture Economic Research Service, 2013b. Farm household well-being. Available at: http://www.ers.usda.gov/topics/farm-economy/farm-household-well-being.aspx (accessed 07.07.13).

incorporated for sound business purposes. Although the Census of Agriculture asks farms that are organized as a corporation whether or not they consider themselves to be a family corporation, this term does not have a clear definition nor is it a recognized legal form of organization. Census of Agriculture data for 1987, 1997, and 2007 (Table 5) shows that sole proprietors continue to control the lion's share of farm numbers, two-thirds of acres of farmland, and approximately half of total farm sales. Partnerships are next in importance in number of farms and acres and the third most important in farm sales. Although the share of farms organized as partnerships has declined somewhat over the period, the share of their sales has increased. Family corporations control a small portion of farms and gradually growing share of acres as well as sales. Other farms, including nonfamily corporation farms, are a small share of total numbers (under 2%), control approximately 8% of farm acreage, and provide approximately 7% of farm sales.

Table 6 shows the number of farms and amount of farmland operated by the tenure status of farms, i.e., fully own all acres, own part of the acres in the operation, and rent all acres in the operation. More than two-thirds of farms fully own the acreage farmed, but they account for less than 40% of acreage farmed. The share of farms with full ownership increased more from 1997 to 2007 than the share of acres they operated. This is consistent with the increasing share of small farms in the sector over this period, which are more likely than larger farms to be full owners. The share of full tenant farms decreased continuously during 1987–2007. The proportion of land operated by this group of farms has also decreased during that time. Trends indicate that the experience since 1987 is likely to be repeated as structure and size of farms continues to evolve, although the recent historically high rates of increase in the price of farm land may temper the future share of land owned versus leased by large farms.

Finances of Farm Operator Households

The USDA disseminates a wide variety of statistics on farm finances for three general groups of farms. The most closely tracked indicator is the estimate of the aggregated net income of the whole agricultural sector over time. This estimate is the basis for the agricultural portion of the US gross domestic product. The balance sheet of the farm sector is also available at the aggregate level. Although useful to understand the current situation and the outlook of the sector, aggregated statistics provide little structurally relevant information. The USDA also disseminates financial estimates of farm businesses by various structural characteristics, which excludes farms producing relatively small volumes of output and whose operator's major occupation is not farming. Both sets of these farm statistics are available at USDA ERS (2013c). The third farm population for which USDA provides statistics is for family farms, including both farm and off-farm sources of income and wealth. Here the focus is on this latter set of financial statistics because of the important role of off-farm income as a contributor to total family farm income, allowing many farm households to stay engaged in farming and greatly influencing farm sector structure.

Farm Finances

Although small family farms (with gross sales of less than US $250 000) produce a relatively small share (18%) of agriculture's value of production, they controlled 51% of the acreage used in agriculture in 2011 (Table 7) and 64% of farm household assets in 2007 (Hoppe and Banker, 2010). The acreage and assets controlled by the small-scale family farms are down significantly relative to 1990 when they accounted for the vast majority, as reported by Lins (1994). This shift is due to increasing numbers of large-scale family farms and their increased ownership of the acreages farmed compared with the situation in 1990.

On a cash basis, small farms as a group lose money farming. The average small farm cannot generate enough net farm income to support a family farm without outside income sources. Perhaps not too surprising, as farm size increases so too do average farm assets and debt. However, even the smallest farms have large net worth. In 2011, the median net

Table 4 Finances and characteristics of farms by commodity specialization, 2011

Item	*Farm type based on the North American Industrial Classification System*									
	Cash grain	*Soybean*	*Other field crops*	*High-value crops*	*Beef cattle*	*Hogs*	*Poultry*	*Dairy*	*General livestock*	*All*
Number of farms	253 003	65 002	490 840	146 747	654 208	18 042	53 046	53 734	438 222	2 172 843
Percent of farms	12	3	23	7	30	1	2	2	20	100
Farm size (mean operated acres)	941	417	245	125	643	301	119	386	102	415
Percent of acres	26	3	13	2	47	1	1	2	5	100
Percent of total value of production	33	3	7	13	15	6	10	12	2	100
Percent of farms receiving government payments	29	6	31	2	22	1	1	4	4	100
Percent of government payments	46	5	23	3	15	1	1	3	2	100
					Dollars					
Net Cash Farm income, average	119 545	49 538	10 497	110 346	10 799	134 474	57 473	186 755	– 6399	34 324
Net Cash Farm income, median	37 765	10 638	– 968	– 375	– 1 131	12 525	756	60 300	– 5539	– 1 250
Land and building value, mean	1 469 952	893 352	620 939	1 076 490	714 733	1 521 780	732 532	1 307 180	361 521	761 808
Land and building value, median	775 000	530 000	350 000	370 000	328 400	489 640	408 850	760 000	225 000	342 170
Farm assets, mean	2 107 377	1 166 981	720 262	1 344 740	914 849	2 256 112	898 191	2 110 953	444 674	991 810
Farm assets, median	1 231 400	692 698	401 250	458 475	427 250	689 944	523 028	1 193 482	269 000	433 394
Farm debt, mean	204 716	100 360	30 685	126 498	54 196	297 960	174 549	397 588	29 169	81 082
Farm debt, median	29 090	4 125	550	1350	695	64 368	11 456	100 026	463	825
Farm net worth, average	1 902 660	1 066 621	689 577	1 218 242	860 653	1 958 152	723 642	1 713 365	415 505	910 727
Farm net worth, median	1 092 821	655 486	382 739	402 682	398 478	547 818	424 900	953 591	235 400	399 995
					Percent					
Financial position										
Favorable	74	72	67	60	56	57	54	78	45	60
Marginal income	20	21	29	32	39	35	27	12	47	34
Marginal solvency	4	5	2	5	2	6	9	7	3	3
Vulnerable	2	2	2	3	3	1	10	2	5	3

Farm location										
Northeast	3	2	8	18	2	4	12	27	7	7
Midwest	80	81	38	17	25	59	27	59	25	37
South	11	17	37	25	62	26	57	8	48	42
West	6	0	17	40	11	11	4	6	20	15
Principal operator's major occupation as farming	71	57	33	59	45	63	65	98	34	46
Average age of operator	55	58	61	58	60	52	56	51	56	58
Younger than 35 years	8	6	2	3	3	8	4	11	4	4
35–44 years	13	11	6	12	10	21	10	17	12	10
45–54 years	23	19	17	18	20	30	29	30	26	21
55–64 years	31	31	36	41	29	31	31	31	33	33
65 years or older	25	34	38	27	37	10	25	12	25	32
Education of operator (percent)										
Less than high school diploma	4	9	7	7	9	7	11	24	11	9
High school	41	48	41	34	44	30	47	47	40	42
Some college	33	22	23	21	25	42	24	19	25	25
College graduate and beyond	22	21	30	38	22	21	18	11	24	25

Source: Reproduced from USDA Agricultural Resource Management Survey, 2011. Author's calculations based on ARMS data. ARMS is described at: http://www.ers.usda.gov/data-products/arms-farm-financial-and-crop-production-practices.aspx (accessed 29.04.14).

Table 5 Share of farms, sales, and land, by legal organization, 1987–2007

	Sole proprietor	*Partnership*	*Family corp.*	*Other*
Farms (%)				
1987	86.7	9.6	2.9	0.9
1997	86.0	8.9	4.0	1.2
2007	86.5	7.9	3.9	1.7
Sales (%)				
1987	56.3	17.1	19.5	7.1
1997	52.2	18.1	23.3	6.5
2007	49.6	20.9	22.1	7.3
Land (%)				
1987	65.3	16.0	11.0	8.1
1997	62.8	16.0	12.8	8.3
2007	62.3	17.5	12.4	7.8

Note: Other includes nonfamily corporations, estates, trusts, cooperatives, and institutions.

Source: Reproduced from USDA National Agricultural Statistics Service, various censuses. Available at: http://www.agcensus.usda.gov/index.php (accessed 29.04.14).

Table 6 Number of farms and number of acres, by tenure of farm operator, 1987–2007

	1987		*1997*		*2007*	
	No.	*%*	*No.*	*%*	*No.*	*%*
Farms						
Full owner	1 238 547	59	1 146 891	60	1 522 033	69
Part owner	609 012	29	573 839	30	542 192	25
Tenant	240 200	12	191 129	10	140 567	6
Total	2 087 759	100	1 911 859	100	2 204 792	100
Acres						
Full owner	317 787 149	33	316 044 548	34	343 952 327	37
Part owner	519 814 523	54	507 673 344	54	496 344 290	54
Tenant	126 868 953	13	108 077 363	12	81 799 223	9
Total	964 470 625	100	931 795 255	100	922 095 840	100

Source: Reproduced from USDA, National Agricultural Statistics Service, various Censuses of Agriculture. Available at: http://www.agcensus.usda.gov/index.php (accessed 29.04.14).

worth of the 59% of family farms that operated the smallest farms was more than US$440 000, which is more than five times that of the average US family.

Off-Farm Income

A major motivation for the establishment of US agricultural policies in the 1930s was the low incomes of farm families, relative to nonfarm families – the so-called farm problem (Gardner, 1992). Low incomes among farm families are largely a situation of the past, due in no small part to the growth in off-farm income. In 1960, the ratio of farm to US household income was 0.65, compared with 1.25 in 2011. In the past two decades, the rate of increase in the average incomes of farm families has surpassed that of the average US household (Figure 3).

One of the factors contributing to the reversal in the income gap between US and farm households is educational attainment. Formal education is an especially important factor not only in the nonfarm job market but also in today's highly technical farming industry. In the early 1960s, only 4% of principal farm operators had a 4-year college degree, compared with 8% of the general US population. By 2011, the college attainment levels were nearly comparable, 25% for principal operators compared with 28% for the general population (Table 8). Moreover, the US population now has a higher share of the population that has not attained a high school degree, compared with the farmer population (15% compared to 9%). The closing educational attainment gap is even more noteworthy when one considers that the farmer population has a significantly older age structure than the general US population and the educational attainment is higher for younger people in general.

The importance of off-farm income in maintaining the large numbers of farms and acreage along with other assets held by small- and medium-size family farms has been understood for some time (Ahearn, 1986a, b). Without off-farm income sources to sustain family expenses, many of those farmers would likely disappear, greatly reducing the number of farms and likely shifting the ownership of the acreage to larger sized operations. This means that farms located near urban areas or in rural areas with significant industrial or service sector businesses are more likely to have the ability to remain in farming. Beginning farms often rely on off-farm sources of income as they enter agriculture, and the majority of farm families benefit from someone in the household engaged in off-farm work that often provides the family with health insurance.

The shares of income from farm and off-farm sources vary significantly by size of family farm (Table 7). The differences in off-farm income by farm size are consistent with the differences in major occupation of the principal operator. Of the 59% of the smallest family farms, 31% of the operators reported to have a major occupation of farming, compared with more than 90% of the largest 10% of family farms. In 2011, almost 60% of family farms had gross sales of less than US $10 000 and had negative average farm incomes, typically receiving all of their household income from off-farm sources. On an average, they received more than US$77 000 in income from off-farm sources in 2011, which is more than family farm households operating larger farms typically received.

Family farms with gross sales of US$10 000–249 999 represented 30% of family farms in 2011. Although still considered to be small farms, the households operating these farms earned, on an average, positive returns from their operations. They earned less from off-farm sources compared with households operating the very smallest farms, but with their positive farm earnings, they had higher total household incomes than those operating the smallest farms in 2011. Their average (mean) household income was US$79 780 and their median household income was US$60 990, in 2011.

Ten percent of family farms in 2011 had gross sales of US $250 000 or more. Although receiving less in off-farm income than those operating small farms, these larger family farm households earned significantly more on the farms they operated. As a result, they had average household incomes nearly three times the level of smallest farm households. The average household income of farm families operating the larger farms was US$205 000, and the median was US$127 000, in 2011.

Table 7 Characteristics of principal farm operator households, by gross farm sales, 2011

Item	*Gross sales of farm*			
	> US$10 000	*$10 000 to $249 999*	*$250 000 or more*	*All*
Number of family farms	1 255 816	639 430	219 422	2 114 668
Percent of family farms	59	30	10	100
Number of total operators	1 780 709	934 757	359 816	3 075 282
Number of family members	3 206 600	1 671 371	642 113	5 520 084
		Income, mean dollars per household		
Farm income	– 6 538	8 061	154 859	14 623
Off-farm income	77 045	71 719	50 356	72 665
Earned income	54 080	51 390	35 861	51 376
Unearned income	22 965	20 329	14 494	21 289
Total income	70 507	79 780	205 215	87 289
		Percent		
Mean farm income as a percent of total farm household income	– 9	10	76	17
		Income, median dollars per household		
Farm income	– 4112	3065	84 649	– 2 250
Off-farm income	55 000	51 031	29 250	53 424
Earned income	35 433	28 298	12 500	32 500
Unearned income	14 250	9 000	2 750	12 500
Total income	52 262	60 990	127 009	57 050
		Balance sheet, mean dollars per household		
Total assets	694 202	1 247 897	3 295 304	1 131 522
Farm assets	428 523	965 582	2 988 918	856 589
Nonfarm assets	265 679	282 315	306 385	274 933
Total debt	69 092	109 232	444 793	120 213
Farm debt	20 045	60 865	376 616	69 387
Nonfarm debt	49 047	48 368	68 177	50 827
Total net worth	625 110	1 138 664	2 850 511	1 011 309
		Balance sheet, median dollars per household		
Total assets	500 427	895 669	2 227 713	672 500
Farm assets	287 363	663 751	1 973 951	412 300
Nonfarm assets	184 881	163 250	172 806	178 500
Total debt	17 061	33 755	207 576	34 300
Farm debt	421	2 325	145 896	800
Nonfarm debt	1 500	0	250	250
Total net worth	444 212	800 974	1 924 793	597 767
		Farm and household characteristics		
Percent of total value of production	1	17	82	100
Percent of all acres	14	37	49	100
Farm size (mean acres operated)	89	475	1809	384
Share of beginning farms				
Established farm	74	84	91	78
Beginning farm	26	16	9	22
Farms receiving government payments	256 434	320 229	164 574	741 237
Percent of all farms receiving payments	35	43	22	100
Percent of farms within group receiving payments	20	50	75	35
Percent of all payments	9	31	60	100
Major occupation of principal operator				
Farm or ranch work	31	61	92	46
Work other than farming/ranching	50	33	7	41
Currently not in the workforce	19	6	0	13
Education of principal operator				
Less than high school	10	8	5	9
High school and some college	65	67	70	66
4-year college degree or more	25	24	25	25

(*Continued*)

Table 7 Continued

Item	*Gross sales of farm*			
	> US$10 000	*$10 000 to $249 999*	*$250 000 or more*	*All*
Race and origin of principal operator				
White, not Hispanic	83	90	90	86
Nonwhite or Hispanic	17	10	10	14

Source: Reproduced from USDA Agricultural Resource Management Survey, 2011. Author's calculations based on ARMS. ARMS is described at: http://www.ers.usda.gov/data-products/arms-farm-financial-and-crop-production-practices.aspx (accessed 29.04.14).

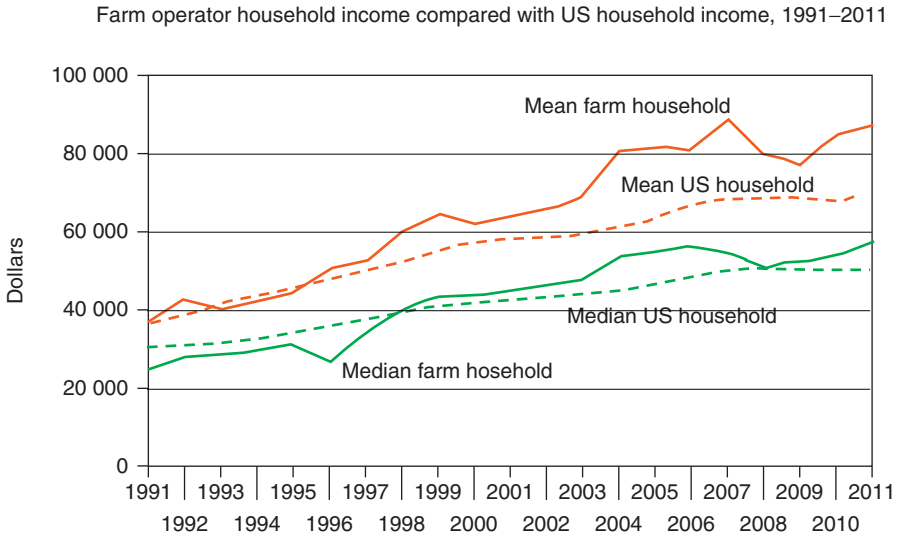


Figure 3 Farm operator household income compared with US household income, 1991–2011.

Table 8 Percent of persons by educational attainment, for farm and US population, selected years 1960–2011

Year	*Less than high school*	*High school*	*Some college*	*4-year college degree or more*
		Principal farm operators		
1964	66	24	6	4
1979	34	38	18	9
1988	24	42	22	13
2000	15	41	25	19
2011	9	41	25	25
		US population, 25 years and older		
1960	59	25	9	8
1970	48	31	11	11
1980	31	37	15	17
1990	25	30	25	20
2000	20	29	27	24
2011	15	29	29	28

Source: Reproduced from USDA, Census and ARMS; U.S. Bureau of the Census. The 1964, 1979, and 1988 data for principal farm operators are Census of Ag available at: http://www.agcensus.usda.gov/index.php. The principal farm operators data for 2000 and 2011 are author's calculations based on ARMS: http://www.ers.usda.gov/data-products/arms-farm-financial-and-crop-production-practices.aspx; and for the US population, the data are from the Census of Population and the Current Population Survey, years available at: http://www.census.gov/hhes/socdemo/education/ (accessed 29.04.14).

Significant Trends

A number of trends or issues facing agriculture are most likely to impact the future structure and organization of the industry. Some are derived from consumer demand for product characteristics and others are a matter of demographics, whereas still others are policy driven.

Sustainable, Organic, and Local Foods

There has been growing consumer interest in sustainably produced food, including organic and more recently local. Sustainable integrates in concept economic profitability, minimum environmental impacts, and social equity and economic opportunity issues. The growth of niche farm categories, such as organic, sustainable, local market oriented, and other extra-market intervention-driven categories, have an increasing role to play in farm structure. They may provide an opportunity for smaller or new operations to gain a foothold in agricultural production. But there are challenges related to producers gaining market access, establishing themselves as selling differentiated products from normal market channels and gaining consumer acceptance as reliable suppliers for products that meet the standards for the specific type of sustainable production. With the possible exception of organic products that are USDA certified, there is no way for consumers to ascertain whether producers met these credence attributes for how the product was produced or to what extent they provided other promised benefits, such as to the local economy, humanely produced, etc. In many instances, sustainability criteria are rather loosely defined. Short descriptions of organic and many other environmentally relevant topics are provided by Osteen *et al.* (2012).

Organic production is the one area of sustainable production that has strict standards for what comprises it. The Organic Foods Production Act of 1990 established requirements for organic production. Subsequent regulations codified a set of criteria that must be met to allow foods to be labeled organic. The USDA has established a certification program to assure consumers that the production attributes promised in organic products have indeed been followed. This is a necessary condition for building trust in such products for which consumers are unable to observe or taste the characteristic they desire. Producers must make the necessary investment of time and resources to comply with the well-defined organic criteria and submit to verification of the practices involved to assure product compliance.

The recent push for local foods has been highly promoted by various interest groups. Local foods can be a challenge to define, and the term is frequently used in conjunction with other sustainable production criteria, including organic. A national standard contained in the Food, Conservation, and Energy Act of 2008 limits local or regional foods to those produced within 400 miles of the market, or within state borders. The local foods category lacks standards that lead to consistency across states or markets, has no strict organizational structure or framework to certify compliance with whatever standards are specified, and has no way to evaluate outcomes (McFadden, 2013). One pragmatic approach is to define local food by the way it is marketed, for example, through farmers markets or through regional food hubs (Low and Vogel, 2011). According to the Census of Agriculture, in 2007 only 6.2% of farms marketed their product directly to consumers for human consumption. Even fewer farms marketed their product through regional food aggregators, although the farms engaging in marketing at that level are more likely to be profitable due to the economies of size advantages.

Overall, sustainable production lacks criteria that provide clarity for what are process-based characteristics. Although there have been various definitions of sustainable used and even defined in agricultural policy through the farm bill, there still remains substantial leeway in what is considered to fall in this category. There has been some interest in using food miles as an indicator of sustainability that could be quantified. However, there is no scientific basis for using food miles as a standard and in fact research has shown that common assumptions about food miles are not valid. Foods produced in highly efficient large-scale operations and transported across the country may be more efficient in economics and environmental impact than locally produced foods from inefficient, small-scale operations, which may use more fuel per unit of product (King *et al.*, 2010).

Nonetheless, this general category of sustainable agricultural production is most likely to continue to expand in the foreseeable future and offer opportunities to smaller producers or new entrants to establish niche production operations. This will allow some of them to compete in the market more easily than in major commodity markets, which are highly competitive and generally require increasing size of operations to remain viable. But as the experience with organics has shown, establishing the stronger criteria to assure product integrity opens the door for larger size operations to compete as well in the niche markets. In fact, many large farms have already established themselves as competitors in these various sustainable market niches, which proponents most likely did not anticipate. Proponents of stronger criteria for organic production perceived the niche as one in which small farms would thrive and provide more environmentally friendly production (Kinsey, 2013).

Aging Principal Operators and Beginning Farmers

As a group, US principal farm operators are older than the typical US household head. In 2011, more than 30% of principal farm operators were of age 65 or older (**Table 4**). The average age of principal operators in 2011 was 58 and has been greater than 50 since at least the 1974 Census of Agriculture. One reason for the advanced age structure of farmers is the farm's status as the family home. Approximately 40% of principal farm operators in the 65+ category reported being retired from farming and 20% had land enrolled in the Conservation Reserve Program. Although principal farm operators less than 35 years of age operate only 4% of all family farms, their farms tend to be larger than those run by older principal operators. A major reason for the small share of farmers who are young is the significant startup costs of a typical farming operation that make it especially difficult to accumulate wealth and acquire control of the land and capital they need. The bulk

Table 9 Characteristics of beginning family farms differed by age of principal operator in 2011

Item	*Age of principal operator*				
	< 35 years old	*35–49 years old*	*50–64 years old*	*65 years old or more*	*All beginning family farms*
Farm characteristics					
Percent of family farms	14	33	40	12	100
Percent by gross sales class					
< US$10 000	43	67	85	83	73
US$10 000 to US$249 999	46	27	14	16	23
US$250 000 or more	11	6	1	1	4
Farm size (operated acres)	255	276	125	179	200
Percent with principal operators farming as their major occupation	47	27	20	29	27
Share of beginning family farms (%)	14	33	40	12	100
Share with farm major occupation (%)	47	27	20	29	27
Farm household finances					
Average farm income ($) 1/	15 651	7 095	− 6 195	− 1 304	1 902
With negative farm income (%) 1/	52	76	75	76	72
Average off-farm income ($)	49 686	84 036	101 615	105 909	89 015
Average farm net worth ($)	318 534	359 236	428 491	511 997	400 273

Note: 1/ Calculation of farm income reflects the expenses associated with reported depreciation.

Source: Economic Research Service, USDA, based on USDA Agricultural Resource Management Survey, 2011. Author's calculations based on ARMS. Description of ARMS available at: http://www.ers.usda.gov/data-products/arms-farm-financial-and-crop-production-practices.aspx (accessed 29.04.14).

of production from family farms (three-quarters) was produced on farms run by principal operators aged 35–64 years (USDA ERS, 2013b).

For more than two decades, the share of farms operated by beginning farmers – those operating farms on which all operators have 10 years or less experience operating a farm – has been in decline. Beginning farms and ranches account for 22% of US family farms and ranches, and provide 10% of production on family farms. It is natural to assume that most beginning farmers are relatively young. Indeed, when compared with the operators of more established farms, beginning farmers do tend to be younger. The average age of the principal operators of beginning farms in the US was 49 in 2011, compared with 60 for established farms. However, only 14% of beginning farmers were less than age of 35 years in 2011 and just more than half were greater than 50 years (Table 9). Many of the older beginning farmers who come to farming late in life operate very small farms and are more likely attracted to the rural lifestyle that they are able to afford by working at established careers off the farm. Although easily surpassing the 1% of principal farm operators who were less than 35 years of age on established farms in 2011, the low share of young beginning farmers helps to account for the decline in the share of all farms operated by young farmers in recent decades (Ahearn, 2013).

Younger beginning farmers tend to operate larger farms than older operators of beginning farms. In 2011, 11% of beginning operators less than age of 35 years had gross farm sales of $250 000 or more, compared with 6% of those aged 35–49 years and 1% of those aged 50 years and older. As a result, young beginning farm households tend to earn more income on their farm and less off farm than older beginning farm households. Still, more than half of young beginning farmers report losses and, on an average, have much higher debt-to-asset ratios than older beginning farmers. And although beginning farmers less than age of 35 years have more debt than older beginning farmers and have lower average net worth, a higher share of young beginning farmers operate profitable farm businesses. One factor in the viability of young beginning farmers is the degree to which they can cash flow their operations, while growing their operations to a more profitable scale.

Contracting and Supply Chains

Producers operate in a marketing system, which increasingly involves supply chains and contracts for the type of output that retailers need in order to deliver desired products to consumers. In the past, farmers produced and then sold the outputs from their farms through distant markets. That system started evolving in the 1950s to vertical coordination whereby processors or food manufacturers specified contract terms that controlled the types of products they wished to buy and how much they would pay for certain product characteristics. Eventually decision-making power shifted from the food manufacturers and major brands to retailers, who obtained detailed data about consumers purchasing behavior. That information empowered the retailers to determine what is produced and sold (Kinsey, 2013). The supply chain carries value implications at various levels in the production and marketing system but manifests itself at the farm level through production or marketing contracts in order for producers to access market outlets.

Contracting expanded significantly from 2001 and will most likely continue to expand for field crops as larger

operators become more tied in with supply chains that continue to evolve in the agricultural industry. Production contracts specify services provided by a producer, the compensation for the services, and the contractor's role in providing inputs. Production contracts are widely used in livestock production, where 90% of poultry and 68% of hog production were under such contracts in 2008. Poultry producers often specialize and are, therefore, quite dependent on poultry processing contractors, often a single one in a given area that puts the poultry producers at a disadvantage in negotiating contract terms. Hog producers using contracts are generally part of the larger and more diversified farming business, and therefore hog income is not the only source of income from the farming operation. Further, they tend to have alternative contract production outlets (MacDonald *et al.*, 2004; MacDonald and Korb, 2011). Production contracts are also commonly used in vegetable and horticultural crops.

Marketing contracts are used for a number of specialty crops and increasingly in field crops. They specify pricing, or methods to determine price, for product characteristics delivered for a given quantity, but the farmer maintains control of the production process. Crops were sold under contract for approximately 32% of total crop production in 2011; and larger corn, soybean, and wheat farmers using contacting often do so for more than half their crop (MacDonald *et al.*, 2013). Larger farms in general use marketing contracts specifying product attributes delivered for a substantial share of their production as one form of risk management for their operation. One example is provided by tobacco and peanut producers who shifted to contracts following termination of Federal marketing programs, which for years limited their price risks (McDonald and Korb, 2011).

In addition to supply chain contracts in the marketing function, some producers – outside the prominent production contracts in poultry and hog supply chains – contract for certain production inputs. One example is the role of labor contracts as an important element of large-scale specialty crop production. Rather than hiring individual workers, the farms often rely on firms specializing in providing the needed labor over the crop season. In 2009, there were 14 103 firms that provided agricultural labor support, including machines, employing 292 000 wage and salary workers. Out of those, 2166 firms provided 149 546 field workers and crew leaders (U.S. Bureau of Labor Statistics, 2013).

Policy Role in Farm Size and Structure

How US agricultural policy, various regulatory policies, and international trade policy affect farm size and structure are ongoing concerns and are subject to potential change. They have previously and will likely continue to influence the structure of agriculture and farm size.

Government Payments

Current US agricultural policies are rooted in the 1930s and have been redesigned over time, currently approximately every 5 years. Commodity and conservation programs are a major feature of farm policies and include payments to farmers and farmland owners who are eligible for a variety of programs offered at any one time. Most commodity program payments go to larger scale operations, whereas many of the conservation land retirement payments, such as the Conservation Reserve Program designed to protect fragile lands in permanent crops or trees go to smaller operations. Commodity programs – primarily providing subsidies for food and feed grains, cotton, and oilseeds production – are based on the amount of cropland enrolled, currently or historically, and yield history. They comprised approximately 75% of all government payments to farmers in 2007. The commodity programs exclude most specialty crops as well as livestock, although these latter producers may receive periodic disaster payments authorized by Congressional action. Some nonprogram commodity and livestock producers may still receive payments based on program commodities that they also produce currently or did in the past (Hoppe and Banker, 2010).

Conservation payments are available to a much wider range of producers, with nearly all crop and livestock producers eligible for at least one conservation program. See Hoppe and Banker (2010) for a brief description of the various types of farm program payments. As shown in **Table 10**, 35% of all farms received government payments in 2011. The large farms, with US$250 000 or more in sales, received approximately 60% of all payments. Given the design of the programs, 77% of the commodity program payments were received by the 10% of farms classified as large farms. In contrast, the large farms received a smaller share of conservation payments, or 35%. The largest conservation program is the Conservation Reserve Program, which requires that working land is put into conserving uses to maximize environmental benefits.

Subsidized crop insurance is the other major government program. Originally targeted to crops covered in the farm bill commodity programs, it has become more widely used for a broader range of agricultural commodities. In 2010, the program covered 255 million acres, with four commodities – corn, soybean, wheat, and cotton – accounting for three-quarters of those acres. As most of the acreage in these commodities is on large farms, the majority of participating farms are larger farms. Under the program, the producer pays a share of the premium and the government subsidies the rest. Currently, the government share is approximately 60%. Unlike other government farm programs at the present time, crop insurance premium subsidies have no means testing against participants' income levels nor is there a total payment limit. The cost to taxpayers of heavily subsidized crop insurance has steadily increased – from US$2 billion in 2001 to US$9 billion in 2011. The current budget projections are for spending on crop insurance to outpace spending on traditional commodity programs over the next 10 years (Shields, 2010).

Regulations

Producers are subject to or affected by an increasing array of regulations – including environmental, conservation, food

Table 10 Government payments, by gross farm sales class, 2011

Item	*Gross sales of farm*						
	< US$10 000	*US$10 000–49 999*	*US$50 000–249 999*	*US$250 000–499 999*	*US$500 000–999 999*	*$1 000 000 or more*	*All*
Number of farms	1 281 537	365 771	292 193	100 454	79 997	52 891	2 172 843
Percent of farms	59	17	13	5	4	2	100
Farms receiving any farm payments							
Percent of all farms receiving payments	34	18	25	10	8	5	100
Percent within group receiving payments	20	38	64	77	75	66	35
Percent of all payments	9	11	20	17	20	24	100
Farms receiving commodity payments							
Percent of all farms receiving payments	15	17	35	15	12	7	100
Percent within group receiving payments	5	21	54	70	69	57	21
Percent of all payments	1	4	19	20	26	31	100
Farms receiving conservation payments							
Percent of all farms receiving payments	51	17	15	7	6	5	100
Percent within group receiving payments	14	17	17	24	26	30	16
Percent of all payments	22	24	19	12	10	13	100
Average payments per farm				*Dollars*			
All payments (including other)	538	2 396	5 404	13 639	19 687	36 332	3 687
Commodity payments	43	390	2 578	7 902	13 155	23 851	1 868
Conservation payments	449	1 673	1 633	2 961	3 331	6 255	1 178
Average payments per receiving farm							
All payments (including other)	2 631	6 262	8 392	17 793	26 347	54 745	10 512
Commodity payments	815	1 876	4 786	11 369	19 032	41 608	8 899
Conservation payments	3 256	10 062	9 378	12 229	12 992	20 727	7329

Source: Reproduced from USDA Agricultural Resource Management Survey, 2011. Author's calculations based on ARMS. ARMS is described at: http://www.ers.usda.gov/data-products/arms-farm-financial-and-crop-production-practices.aspx (accessed 29.04.14).

safety, and trade regulations. All of these have potential to impact the structure of agriculture, as farms adjust to comply with the regulations.

Some of the more prominent and contentious environmental regulations of the US Environmental Protection Agency involve the Endangered Species Act, the Clean Water Act, and the Concentrated Animal Feeding Operations Act. These three acts have been the source of ongoing conflict between farmers and those concerned with potential impacts on various species and on water and air quality. Lawsuits have been frequent and are more likely to continue. In contrast, USDA programs to promote good environmental stewardship have involved paying farmers and farmland owners to adopt good practices. Not too surprisingly these are less contentious because they are voluntary and involve payments. However, participation in some commodity programs requires cross-compliance with environmentally sound practices and even these requirements have been controversial at times.

Ecosystem services is a concept receiving increased attention and in many ways represents a coalescing of issues encompassed in environmental and conservation regulatory programs. To the extent that agriculture is required to meet more stringent environmental regulations to protect ecosystem services provided by the environment to agriculture and by agriculture to the environment for enjoyment by other citizens, producers will more likely face increased costs. Unless exemptions are made for smaller operations, such regulations are more likely to provide incentives for further consolidation of production into larger operations. The typical expectation of exemptions for smaller operations may not be realized, given that larger operations may be able to better manage and monitor outcomes of their practices designed to minimize any damage to ecosystems from the farming operation.

Food safety has become a much more prominent issue in recent years as consolidation within the food industry has increased the likelihood of a food safety event affecting many states or a wide area, rather than being more localized as was earlier the case. Most recently, the FSMA of 2010 updated the food-related elements of the Federal Food, Drug, and Cosmetic Act administered by the Food and Drug Administration (FDA). It significantly expanded authority of the FDA related to food regulation, including authority to mandate recalls of contaminated food products to replace what had been a voluntary system. However, the FSMA does not cover the USDA-regulated meat, poultry, and egg products. It is possible that additional legislation will bring the USDA-administered food safety programs into alignment with the FSMA, but that remains to be seen. Meanwhile, the FSMA has implications for costs to farms that will need to adopt more stringent good agricultural practices to meet expectations of the food handlers and processors facing requirements to adopt HAACP systems at all levels in the food supply chain. See the earlier discussion of Consumer Preferences under Additional Drivers of Change in Structure and Organization for potential implications of the FSMA for farm structure and organization.

Trade regulations, including World Trade Organization (WTO)-negotiated and individually negotiated bilateral or multilateral trade agreements between the United States and one or more countries, often contain provisions that limit farm program payments to producers. They provide interesting dilemmas for long-standing US commodity programs, which in some cases have been challenged in the WTO and under other trade agreements. Several of those cases have been lost by the United States and farm programs had to be adjusted or are still to be brought into alignment with the decision's required or proposed remedies. In some instances, the US programs have continued unabated and fines were paid in lieu of changing the program. In others, adjustments have been made that resulted in farmers being more exposed to market price risks. To the extent that future negotiations or dispute settlements eliminate farm program protections, the need to manage risks may lead to greater consolidation of production into larger units more capable of such risk management.

Future Challenges

The preceding data, trends, and discussion suggest a number of issues that will affect the future of agriculture's structure, profitability, and role in the US and world economies. Some issues are internal to the agricultural industry, whereas others are driven by consumer interests and concerns, environmental factors, and domestic and international trade policies. Managing the challenges of the several risks discussed below cuts across the range of these issues.

Climate Change

To the extent that scientific expectations about climate change leading to more variable and severe weather events are accurate, weather risks faced by producers are more likely to be greater in coming years. This will provide incentives for producers to adapt crops they cultivate through adopting improved varieties designed to better cope with weather events, such as prolonged drought, excessive moisture, or extreme heat, or even to change crops produced on their farms. Further, shifts in climatic zones create the potential for costly pest problems from plant and animal diseases, invasive weeds, insects, microbes, and fungi that spread to new geographic areas.

Climate change, along with other challenges discussed here, will put a premium on risk management at the producer level, either through insurance programs or through other risk management strategies, such as futures market hedging and crop diversification. These factors will continue to provide incentives for growth in size of farming operations to spread the costs of insurance, hedging, and crop diversification over larger acreages and output.

Technology

Technology will most likely continue to evolve – including genomics and other branches of biotechnology that will most likely have major implications for plant and animal breeding – and hence farm size increases are to be expected. New technologies typically are expensive, at least in the early stages of implementation, and this creates an incentive for farmers to spread the cost over larger acreages. Although some technologies are truly size neutral, such as genetically modified

seed, many are too expensive for smaller to medium sized operations to economically adopt. This suggests that public opinion about the structure of agriculture may influence future R&D funds to be allocated somewhat differently to assure that research results are more truly size neutral.

Increasing total factor productivity has meant that individual farm sales have expanded rapidly due to technological changes adopted at the farm level. This trend has been a major contributor to the increasing size of farm operations and the phenomena of a small percent of total farms producing the vast majority of agricultural output. However, a critical issue is to what extent future public sector support for agricultural productivity enhancing research will be at levels sufficient to keep the United States competitive in a global economy in which emerging countries are investing heavily in this type of research. There are heightened concerns in the agricultural science community that the United States and other developed countries are underinvesting in public agriculture R&D (Executive Office of the President, 2012).

Food Safety

Supply chains designed to deliver retail-level products with characteristics that consumers desire have expanded significantly as an organizational tool in the agricultural and food industry in recent years. Further processing of most food products, including even raw produce processed into more convenient product forms ready for the table or food service use, makes food safety a constant concern in the food supply chain. To successfully compete for opportunities in the supply chains, producers are required to adhere to strict food safety guidelines incorporated into contracts within the supply chain for products delivered to the next level. This facilitates traceability from the consumer back to the farm level of any products that may cause foodborne illness outbreaks. Thus, it may be expected that more use of HAACP-type programs will be required of supply chain participants even at the farm level, and the expense of such systems will be at least in part absorbed by the producers. This will provide further incentives for growth in farm size to spread the costs involved over larger amounts of product.

Globalization

Ongoing growth of emerging market and developing country demand will create an opportunity for more US exports. It may also open the door to more imports into the United States from new production areas designed to serve expanding markets. Globalization will continue to create challenges, as witnessed by the current international debate on the acceptance of genetically modified agricultural products. But even with increased globalization, domestic agricultural policy will remain a major factor impacting farm size and structure in the foreseeable future.

The extent to which the US producer thrives from developing market opportunities will depend at least in part on trade negotiations and the implications for US domestic agricultural policy and products. It will be important that the United States maintain strong food safety standards for any products imported and meet the food safety requirements of other countries in order to gain exports. Trade negotiations will need to help establish guidelines about the types of food safety or other requirements countries may impose on product quality characteristics, so that standards are not established, which are designed primarily to create a nontariff barrier to imports from the United States or other countries.

Concluding Comments

The future size and structure of US farms, number of farms and farmers, and the relative economic prosperity of agriculture will be determined by the factors identified above and others. Similar changes are to be anticipated in most developed countries and in those developing countries with large commercial farming sectors. The next few decades will most likely see changes that have similar impacts to those experienced over the past several decades. The exact nature of the changes, the structural implications, and the opportunities created for farmers to provide food, feed, fiber, and fuel profitably will be determined by market forces, social systems, climatic conditions, environmental and other regulations, and agricultural and trade policies, among other factors. It will be an exciting time to be involved in the globally connected agricultural sector.

Disclaimer

The views expressed here are the authors' and do not necessarily represent the views of the USDA.

See also: Agribusiness Organization and Management. Agricultural Mechanization. Climate Change, Society, and Agriculture: An Economic and Policy Perspective. Critical Tracking Events Approach to Food Traceability. Crop Insurance. Farm Management. Food Marketing. Global Food Supply Chains. Government Agricultural Policy, United States. International Trade. Investments in and the Economic Returns to Agricultural and Food R&D Worldwide. Markets and Prices. Production Economics

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Climate Change: Agricultural Mitigation

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Glossary

Adaptation Adjustment to changing conditions (including climate change); can refer to adjustment during the lifetime of an organism or system or to cross-generational genetic changes.

Additionality The environmental impact, for example, emission reduction, achieved in comparison to a 'business as usual' development pathway.

Agriculture, Forestry and Other Land Uses (AFOLU) Intergovernmental Panel on Climate Change guidelines for accounting of land-based greenhouse gas emissions (successor to the land use, land-use change, and forestry guidelines, but not yet formally accepted by United Nations framework convention on climate change (UNFCCC)).

Clean Development Mechanism Part of the Kyoto accord of the UNFCCC

Intergovernmental Panel on Climate Change The science/policy boundary organization that reviews evidence on climate change in a 5-year cycle of reporting.

Land use, land-use change and forestry Guidelines for accounting of land-based greenhouse gas emissions (superseded by AFOLU).

Leakage The unintended effect on emissions elsewhere (beyond the project scale).

Mitigation (in context of climate change) Reducing the net emissions of greenhouse gasses to the atmosphere.

Value chain A representation of a sequence of actions that transform raw materials (or land use enhancing C sequestration) into marketable products (certified emission reduction) that an end user could buy.

Introduction

Perspectives on agricultural mitigation have evolved from the first report of the Intergovernmental Panel on Climate Change (IPCC) (Sauerbeck, 1993), through the second (Cole *et al.*, 1996; Paustian *et al.*, 1997), third, and fourth (Metz *et al.*, 2007; Smith *et al.*, 2008) to current discourse (Ericksen, 2008; Beddington *et al.*, 2012; Burney *et al.*, 2010; Vermeulen *et al.*, 2012; Baker *et al.*, 2012; Neufeldt *et al.*, 2013). There has been (1) a refinement of numbers on current emissions and their sources, with agriculture currently responsible for 11% of global emissions (UNEP, 2013), (2) more integration in scenario modeling than cross sectoral borders (Golub *et al.*, 2009), (3) responses to some of the accounting system anomalies that allowed global emission displacement around biofuels to be counted as emission reduction, (4) separate efforts to deal with forestry emissions under the REDD+ (efforts to reduce emissions from deforestation and forest degradation) agenda that showed the challenges of a partial approach in what is an integrated landscape (van Noordwijk *et al.*, 2013), and (5) a greater appreciation of action opportunities on the demand side of the equation. Part of the food system industry is responding to consumer action and demand for low-carbon-footprint products, whereas formal governance systems and international negotiation arenas are slow to respond effectively. Current global greenhouse gas (GHG) emission levels are already considerably higher than would be allowed in 2020 in scenarios that keep global warming below a 2 °C target (UNEP, 2013). Experiments with carbon markets have captured the imagination beyond actual performance, but there certainly are considerable opportunities to reduce net GHG emissions while meeting rising global demands, compared to a 'business as usual' extrapolation of past trends. The challenge is how to provide economic incentives for 'clean development' across scales, without a huge bureaucracy and network of intermediaries whose pay and transaction rents compete with real actions on the ground. This article starts with defining the scope of mitigation and agriculture, before reviewing current emission estimates of the three main GHGs involved – nitrous oxide (N_2O), methane (CH_4), and carbon dioxide (CO_2) – across the agricultural spectrum, and discuss how projected increases in demand from a growing and more wealthy global population can be reconciled with emission reduction in macro-level scenarios. Finally, this is followed by considering the experiments with micro-incentive systems currently under way. Although there is a wealth of studies and syntheses in the technical literature, the focus here will be on bridging the 'supply' and 'demand' side approaches to achieve the overall objective of the United Nations Framework Convention on Climate Change (UNFCC) (UNFCCC, 1992) as stated in its second article, to 'stabilize GHG concentrations in the atmosphere at a level that would prevent dangerous anthropogenic interference with the climate system.' As one would note, there are several weaving errors in the regulatory tapestry set up for achieving the UNFCCC objective, made up of a warp of countries, a weft of sectors, and shades of colors ranging from mitigation to adaptation and vulnerability. As will be discussed below, neither the terms 'mitigation' nor 'agriculture' as defining concepts are as clean and clearly separated from other aspects as it might appear.

Mitigation as Part of the Climate Change Discourse

Mitigation Plus Adaptation

The term mitigation originally meant softening, as it is derived from the Greek mitis=soft, rather than from the kiSwahili

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miti = forest. It has obtained a specific meaning in the international climate change discourse: it has become shorthand for reducing the net emissions of GHGs to the atmosphere that are seen as the primary drivers of global climate change, because such climate change is considered a risk for humanity and the future of planet Earth as known. Mitigation was defined as the primary line of defense in the chain of events (Figure 1) that caused a reduced quality of life due to the human activities that induce an increase of atmospheric concentrations of GHGs. The atmospheric concentration of GHG's, net result of emissions and uptake by oceans and terrestrial systems, together with solar irradiation, reflection (albedo), and hydrological cycle shape the climate system; the current rate of change will soon bring us beyond the safe planetary boundaries of our coping range (Rockstrom *et al.*, 2009). This will lead to direct human vulnerability and to indirect effects on human welfare through ecosystem changes. Adaptation is a second line of defense, which reduces vulnerability in the face of exposure to change, but which implies a failure of the UNFCCC to achieve its primary target. Adaptation shifts the concept of what is 'dangerous,' but does not reduce interference with the climate system. Nor can it deal with the risks of run-away, positive feedback loops such as changes in ocean current systems, inducing further change once thresholds are crossed. One does not know exactly where those thresholds are, so the precautionary principle should be applied (Ramanathan and Feng, 2008; Rockstrom *et al.*, 2009). Early warning signs of real change have been around for at least two decades (Smith *et al.*, 2009). Synergy between mitigation and adaptation is feasible in land use (Verchot *et al.*, 2007; Smith and Olesen, 2010).

Direct Micro- and Meso Climate Forcings?

There is an alternative perspective to the conventional cause–effect-impact relationship between agriculture and climate. It does not solely or even primarily relate to the global GHG effects – as indicated a bypass to the macroclimatic GHG route (Figure 1). Pielke *et al.* (2007) discussed the diverse local and regional climate forcing that impact agricultural systems and represent effects of local land cover change and aerosol production on local climate and geographically explicit

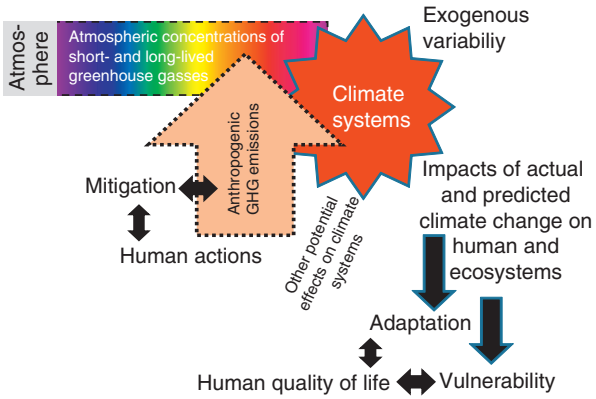


Figure 1 Feedback loop from human actions via GHG emissions to climate change, impacts on human and ecosystems and vulnerability and ultimately quality of life where these impacts exceed the coping range, potentially adjusted by adaptation measures.

teleconnections, relationships between local effects and distant but geographically explicit causes. In their view, agricultural assessments of risk to climate change and variability should start with a bottom-up perspective of understanding local climate, as a complement to global top–down modeling. Actions to mitigate climate change may similarly be seen from a new angle if a coadapt approach is taken (van Noordwijk *et al.*, 2011) that allows for local actions with local effects to add up to global impacts; tree effects on the microclimate of agriculture begin to get recognized (van Noordwijk *et al.*, 2014c). New perspectives on 'rainbow water' that relate terrestrial evapotranspiration to rainfall elsewhere on the same continent showcase specific teleconnections (van Noordwijk *et al.*, 2014a).

Accounting for Anthropogenic Emissions per Area, Activity, Capita, or Sector

The concept of anthropogenic interference with climate systems is an aggregate that needs disaggregation before it can be dealt with. This is where the problem starts. The totality of emissions can be derived from summing over all people and their per capita emissions, from summing over all land areas and the change that occurs per unit of space or from summing over all sectors and subsystems of human activity:

$$\text{Anthropogenic interference} = \mathrm{f}(\Sigma \mathrm{E}_{\mathrm{GHG}}) = \mathrm{f}(\Sigma_i E_{\mathrm{GHG},i}) = \mathrm{f}(\Sigma_j E_{\mathrm{GHG},j}) = \mathrm{f}(\Sigma_k E_{\mathrm{GHG},k}) = f(\Sigma_n E_{\mathrm{GHG},n}) + M \quad [1]$$

where i sums over all pixels (units of space) on planet Earth, j over all people and their per capita emissions and k over all sectors and types of human activity with associated footprints. The summation over all nations n requires an additional term M for the international waters and international transport that are not otherwise attributed.

In principle, the first three approaches can all lead to a consistent result. However, what we currently have in the policy debate is a hybrid, which contains elements of all three (national emissions, per capita calculations, and product footprints), but is at risk of double-counting as well as having gaps. Although emissions are of primary interest, which are fluxes, there are good reasons to approach them through changes in directly observable stocks (e.g., carbon stored in soils or vegetation) for part of the accounting system, but again hybrids of flux and stock accounting are problematic. Linked to the United Nations framework in which the UNFCCC was developed, nation states are the primary accounting units. This implies primarily a territorial and citizen-based approach to accounting, but has challenges with multinational companies, international (cross-border) trade and is trapped in a political dichotomy of 'developed' versus 'developing' countries (diplomatically termed 'Annex I' vs. 'Nonannex I'), where the major share of emissions shifted to transitional economies such as China (Peters *et al.*, 2011). In absolute levels, developing (and transitional) countries accounted in 2010 for approximately 60% of global GHG emissions (UNEP, 2013). Davis and Caldeira (2010) estimated that 23% of global CO_2 emissions (6.2 Pg CO_2) were traded internationally, primarily as exports from emerging markets to consumers in developed countries. Sharing

responsibility for emissions embodied in trade among producers and consumers could, in their view, facilitate international agreement on global climate policy – agreements now hindered by concerns over the regional and historical inequity of emissions. The emissions embodied in trade concept also applies to agriculture and associated global trade flows (Minang *et al.*, 2010). For example, local nutrient cycles became global nutrient flows (van Noordwijk, 1999), with continued dependence on new inputs and associated GHG emissions.

Footprint Accounting

In the face of the failure of the nation states to achieve convincing collective action at par with the challenge, a global citizen-based approach has emerged with attention on the 'footprint' of all goods and services that they use for their lifestyles and diets (Pandey *et al.*, 2011; Peters, 2010). This follows from a simple disaggregation of the citizen based accounting system:

$$\mathrm{f}(\Sigma_j E_{\mathrm{GHG},j}) = \mathrm{f}(\Sigma_s \Sigma_m P_s * L_{m,s} * F_m) \quad [2]$$

where P is human population size per social stratum s, L is lifestyle and per capita use of goods and services for social stratum s, and F is the footprint or emissions per unit goods and services (indexed m). Controlling P is a politically sensitive and religiously contested domain for public policy, and investment in access to education for girls may well be the only widely supported long-term approach. There is a large current disparity between social strata in L and there are valid aspirations to increase the average under the heading of 'development.' That leaves F, or the efficiency with which goods and services are produced, as the primary degree of freedom. Increasing efficiency is a potential win-win solution in many environment/economic tradeoffs.

Territorial, Sectoral, and Demand-Based Interpretations of 'Agriculture'

Turning now to agriculture, elements of all accounting approaches are seen coming together, with several challenges for transparent and comprehensive accountability. Agriculture uses land – but as a land use category it has a fuzzy boundary with 'forestry' (Watson *et al.*, 2000), as well as with 'wetlands.' These three land uses are adjacent chapters in the Agriculture, Forestry and Other Land Uses accounting system designed by IPCC (2006). Agriculture uses inputs such as fertilizer and machinery, which are derived from mining and manufacturing industry, as well as fossil fuels for farm operations and transport of products. In a sectoral approach these need to be accounted in one, and only one sector. However, farm-level decisions about alternative approaches then have cross-sectoral consequences that require consistency of policies across the various sectors involved. Agriculture is the basis of a food supply systems, with considerable waste along the chain, as only a fraction of the food that is produced is consumed (Parfitt *et al.*, 2010). What part of the food wasted is attributable to agriculture, what part not? Agriculture together with forestry provides a large share of the fiber supply systems with textile, paper, and other applications that also have fossil fuel–based alternatives. Jointly the two are still the primary source of energy for a large share of the rural population, with options to substitute firewood, charcoal, and dried-manure by fossil fuel use. On the other side of the spectrum, agriculture- and forestry-based biofuels resubstitute for fossil fuel. Emission reduction in one 'sector' can be achieved by shifting product flows and associated emissions to another sector, without decreasing the anthropogenic interference with the climate systems. The sectoral map of the world has dotted lines as boundaries (**Figure 2**). Rigidity of concepts such as an agriculture concept that does not allow overlap with forestry, as in Food and Agriculture Organization databases, is thus seriously challenged to deal with trees outside forest and agroforestry as intermediate land use system (de Foresta *et al.*, 2013). Rigidity implies considerable cost to the rationality of decisions based on them.

Multiple Perspectives

Compared to the discussions on 'Mitigation in Agriculture' in the first IPCC report (Sauerbeck, 1993), the current discourse (Beddington *et al.*, 2012) has brought greater recognition for the demand side, with attention to waste and lifestyle choices of human diets. It also acknowledges that there are planetary boundaries to ambitions for all to emulate the American dream and diet. Thus the current debate encompasses multiple aspects, accounting principles, and outstanding issues of agriculture (**Table 1**).

There may be a general trend to move from an area-based emissions per unit of agricultural land, to efficiency/footprint-based concepts (emissions per unit end-user satisfaction with goods and services), but these still have an area-based component in the calculation. Consequently, it requires productivity data. A concept of 'indirect land use change' that has emerged in the biofuel debate (Plevin *et al.*, 2010) applies to any new or existing crop and is a challenging one. To what degree can a new use of a crop be held accountable for the additional conversion of land into agriculture elsewhere in the world? Will the new use have left some of the original demand unmet? Is every parcel of land that once supplied a product for a certain type of use bound to keep going that forever? With such concepts we appear to be trapped in the rigidity of artificial accounting concepts and need to go back to the basics of the totality of anthropogenic interference with climate systems. All this leads to a hot debate about the optimum level of intensity of land use, in the face of the nonlinear relationship between inputs, emissions, and yield per unit area (Doré *et al.*, 2011; Jackson *et al.*, 2010, 2012; Matson *et al.*, 2012). As intensification influences various aspects of the accounting system, optimization from a GHG perspective can only be done at national aggregated level. In terms of GHG accountability, a focus on imports rather than local food production is a very attractive choice at national level – similar to the transfer of high-emission industries to countries without emission reduction commitments. However, from an atmospheric impacts perspective, focus should be on reducing the total of net GHG emissions directly or indirectly associated with the sum total of global agricultural production.

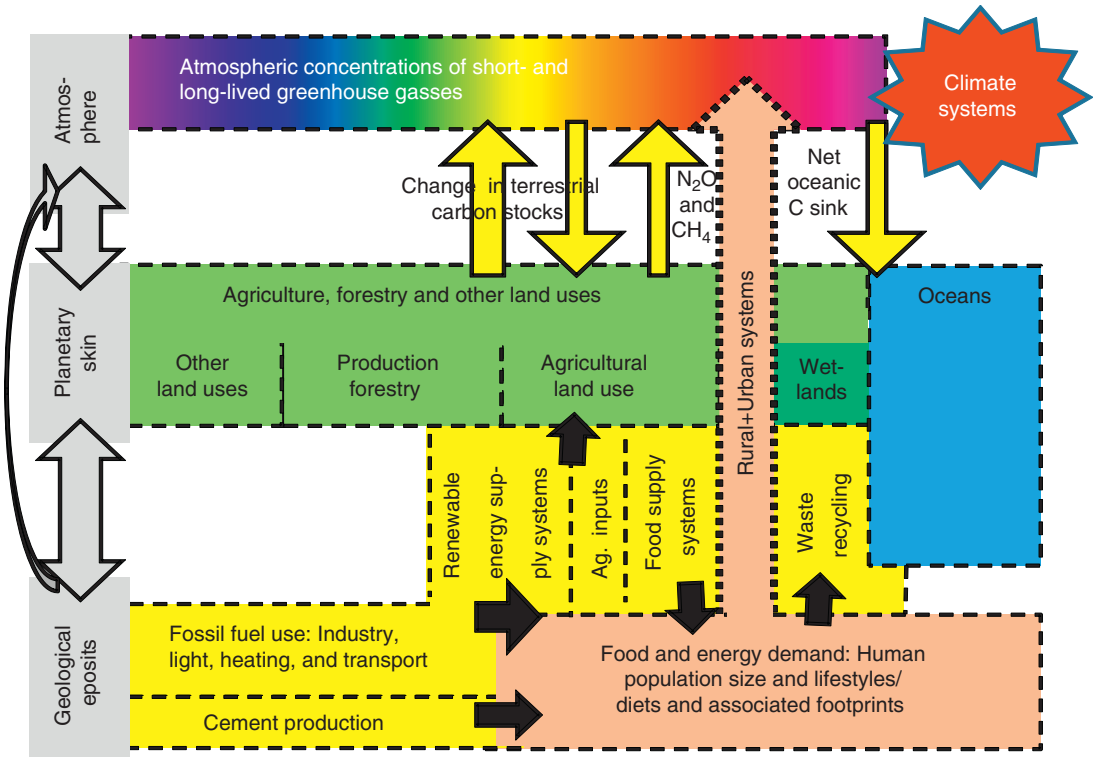


Figure 2 Agriculture as part of the anthropogenic GHG emissions: It relates not only to an important part of land use (interfacing with forests, wetlands, and oceans as basis for food supply systems, as well as energy supply systems), but also with direct energy consumption for agricultural inputs and transport, and with (missed opportunities) for waste recycling; ultimately agriculture responds to the shifts in demand, that are based on human population size multiplied with the goods and services required for lifestyles and diets, modified by the footprints per unit good and services.

Current Emission Estimates

In 2008, agricultural production, including indirect emissions associated with land-cover change, contributed 80–86% of total food system emissions. This was 19–29% of global anthropogenic GHG emissions, releasing 9.8–16.9 Pg of carbon dioxide equivalent (CO_2e) to the atmosphere (Vermeulen *et al.*, 2012).

CO_2, N_2O, and CH_4 Compared

The 'greenhouse effect' impacts of nitrous oxide and methane can be expressed in carbon dioxide-equivalent quantities based on their global warming potential. This includes the direct heat trapping effect of the gasses as well as their expected residence times in the atmosphere. Conventionally, a hundred-year time frame is used in defining the default CO_2e values per unit N_2O and CH_4 at 296 and 25, respectively, Evaluated over shorter time frames, the global warming effect of CH_4 would be rated higher.

Forest-to-Agriculture Conversion

Agriculture and the size of the human population have risen as a consequence of deforesting the earth to create farm land (Williams, 2006; Gibbs *et al.*, 2010). The logarithm of human population size accounts for 70% or more of the variation in forest cover at national and subnational scales, with 80% of data within plus or minus 10% of the predicted forest cover. However, the emission consequences of this conversion differ by the carbon density of the natural forest and the specific pathway of change, which can be gradual or direct; but the net effect on CO_2 emissions does not depend on the pathway taken. Yet, 46% of the agricultural lands have at least 10% tree cover (Zomer *et al.*, 2009), and trees are compatible with agricultural production (de Foresta *et al.*, 2013). Fortunately, simple approaches to quantifying the net carbon loss from change in tree cover are available (Hairiah *et al.*, 2011), compatible with IPCC (2006) guidelines. Methods for other GHG emissions are also becoming simpler (Milne *et al.*, 2013). The net emissions per unit agricultural product vary along the forest or tree cover transition curve (Rudel *et al.*, 2009; Meyfroidt and Lambin, 2011), depending on the preceding land cover that was converted and on how far back in history the accountability rules apply.

Soil Carbon Transition Curves

Soil carbon stocks express a balance between organic inputs and their stepwise decomposition by soil biota. The stock ($tC\ ha^{-1}$) can be estimated as the sum over annual inputs ($tC\ ha^{-1}\ year^{-1}$) multiplied with mean residence time (year)

Table 1 Multiple perspectives on agriculture in relation to mitigation issues

Perspective on agriculture	*Accounting principle*	*Challenges*
1. Agriculture as land use, modifying above- and belowground C stocks in comparison to forests and wetlands and increasing or decreasing methane emissions	Area-based emission accounting as per AFOLU (or its predecessor LULUCF; for CO_2 emissions this is primarily based on change in above- plus belowground stocks, for N_2O and CH_4 on summation of fluxes	What about trees outside forest and agroforestry? What about anthropogenic reduction of natural (e.g., wetland) ecosystem emissions?
2. Agriculture as transformer of solar energy + CO_2 + water + nutrients into usable organic matter + waste + N_2O + CH_4	N_2O emissions from agriculture are estimated as fraction of total fertilizer use	What about N_2O emissions based on biological N_2 fixation or organic fertilizer inputs?
3. Extensive rangelands grading into natural ecosystems, as start of intensification	Accounting per unit livestock, CH_4 emission profiles depending on feeding regimes	N-rich feeds reduce CH_4 emissions per animal, but increase N_2O emissions of the manure
4. Relations with oceans, coastal and freshwater fisheries, aquaculture, and animal feed stocks	Productivity and CH_4 + N_2O emissions are accounted separate from the nitrogen and phosphorus transfers from agriculture that influence them	International waters remain outside of any accounting system
5. Agriculture as driver of transport and input industry	Transport emissions are accounted outside the agricultural sector	Can locally produced biofuel, be counted as carbon neutral?
6. Agriculture as basis of food system value chains, responding to demand signals	Footprint concepts and efficiency of output in usable products per unit emissions. Nonutilized production as consequence of supply-demand mismatch is not handled separately	Where does accountability of agricultural sector end and that of other parts of the food system take over?
7. Agriculture as potential basis for 'bioenergy,' recyclable 'waste'	Domestic use of biofuel or methane capture from waste recycling is accounted through its reduction of fossil fuel dependency Where international trade is involved and products cross borders, ad hoc footprint efficiency criteria apply to bioenergy feed stocks	Attempts have been made to include international wood trade into the system, and the same might apply to other organic exports, but this creates loopholes and inconsistencies

similar to tree cover transition. Conversion into agriculture reduces annual inputs, as more of the carbon gets exported from the field with harvested products, whereas it reduces the mean residence time as tillage speeds up decomposition and mineralization. With a switch in management practice a soil carbon transition can be induced similar to the tree cover transition. Such transitions can also result from increased cropping frequency and associated root inputs to the soil (Minasny *et al.*, 2011; van Noordwijk *et al.*, 2014b).

Livestock

Livestock is accountable for emissions both through the way feed is produced with consequences for changes in C stocks and N_2O emissions and though methane emissions at the animal level that depend on feed quality (IPCC, 2006; Herrero *et al.*, 2009, 2010). In the context of global land cover data, the handling of the transition from grazed dry forest to wooded savanna and to rangeland with trees is a challenge for consistency: with seminomadic and transhumance livestock systems being more easily accounted per head than per area grazed. Deforestation in the humid forest zone of Latin America has been historically dominated by extensive livestock production, whereas in Africa *Trypanomosiasis* prevented similar livestock systems, whereas in Asia the regional supply/demand situation did not make such conversion attractive.

Rice Paddies

Methane emissions by cultivated paddies or natural wetlands is the net result of methane production in the anaerobic zones of submerged soils by methanogens, and its oxidation into CO_2 by methanotrophs in the aerobic zones of wetland soils and in upland soils (Le Mer and Roger, 2001). Net methane emissions can be approximately 10 mg CH_4 m^{-2} h^{-1}, whereas methane oxidation by aerobic upland soils (forests are most active) is two orders of magnitude less. Submersion and organic matter addition increase methane emissions. Intermittent drainage and utilization of the sulfate forms of N-fertilizers reduce CH_4 emission (Le Mer and Roger, 2001). Conversely, the methane oxidation potential of upland soils is reduced by cultivation, especially by ammonium N-fertilizer application.

Peatland Use

Globally, peatlands store more than half of total soil carbon. Both in the northern temperate and tropical zones peatlands are in agricultural use, with annual emissions per unit area that are a factor 100 or more above those on mineral soils. Peatland emissions derive from the use of fire in land clearing, the increased decomposition due to drainage and fertilization. Together these make the organic residues that took thousands of years to accumulate disappear in one or a few decades.

Where natural and disturbed wetlands and peats emit methane, methane oxidizers become effective once the water table is below 30 cm of the soil surface. Conversion of tropical peatland for plantation crops such as oil palm has become a major issue Agus *et al.* (2013).

Projected Increases and Relevance of Demand-Side Adjustments

Shifts in Diets and Lifestyles

The recurrent debate on how a human population of 9 billion can be fed with sufficient and sufficiently nutritious food has different answers depending on the degree of freedom in dietary choice that is assumed for future generations (Nelson *et al.*, 2010; Shindell *et al.*, 2012). Poverty reduction and expansion of a middle class has large consequences for the composition of the human diet, and its associated emissions and waste (Beddington *et al.*, 2012; Parfitt *et al.*, 2010). The different dietary options to meet daily human needs have very different footprints in terms of carbon and other GHG emissions.

Although there are broad patterns associated with product food groups and their trophic position, there can be a considerable 'management swing potential' (Davis *et al.*, 2013) that differentiates the best from the worst management practice in the production of goods that are otherwise indistinguishable. For example, palm oil can be both the best and the worst vegetable oil in terms of carbon emissions per unit product, depending on whether it is grown on peat or mineral soil, and whether the deforestation history of the site is still attributed to the current plantation. This equally applies if such palm oil would be used as biofuel source, rather than for the food industry, but focus of the debate has been disproportionally on such potential biofuel use.

Although a more vegetarian lifestyle and diet has substantial benefits in reducing footprints, its direct consumption of soybean, rather than via an animal stage in a food chain, does not release it from the issues around the soybean carbon footprint that are primarily attributable to direct and indirect land use change (van Middelaar *et al.*, 2013)

Bioenergy on the Agricultural Accounting Plate?

Within the UNFCCC accounting rules, one of the simplest ways to meet emission reduction obligations is to move high-emission industries, such as agriculture, across the accounting border. As land-based products can be subsequently used as biofuel and reduce dependency on fossil fuels without a change of lifestyle or transportation systems, a very attractive pseudosolution became available to policy makers. Crutzen *et al.* (2008) pointed to this accounting anomaly in the case of biofuels, and there have been several attempts since to redress the issue.

If a substantial part of global energy needs in the future are to be met by biofuel sources, the land required for agricultural production may double – which shows the level of challenge involved. Although there have been hyped expectations of miracle biofuel crops that can be highly productive on marginal soils without dependency on inputs, reality is otherwise, as many farmers have learned the hard way (Iiyama *et al.*, 2012).

Technical Opportunities for Efficiency Gain Plus Emission Reduction

Vermeulen *et al.* (2012) estimated agriculture's net GHG emissions along the food chain as:

- 3.8–5.2% due to production of fertilizer, pesticides, and feed transport (mostly CO_2).
- 40.8–55.7% due to direct emissions in production stage (mostly N_2O and CH_4).
- 23.9–43.8% due to indirect emissions and initial land conversion (mostly CO_2).
- 10.2–16.7% due to postproduction processing, transport, and cooling (CO_2, N_2O, and CH_4).

Opportunities to reduce emissions exist throughout the chain, with the direct and indirect emissions offering the largest reduction options. The author will first focus on the direct emissions.

Reducing the Temporary Excesses of Available Nitrogen that Allow for High N_2O Emissions

Mosier *et al.* (1998) and more recently Reay *et al.* (2012) found current N_2O estimates to be reasonably consistent at the global scale between accounting for measured atmospheric change and known emission sources, but that a lack of direct measurements makes national and subnational estimates highly uncertain. Although continued intensification of existing lands is essential in meeting future needs (Matson *et al.*, 2012; Zhu and Chen, 2002), increased nitrogen nutrition of crops is needed. However, options exist to achieve that without increasing nitrous oxide emissions by increased N uptake efficiency at the farm scale, although these require appreciation of spatial heterogeneity in fields currently managed as if they were homogeneous (van Noordwijk and Wadman, 1992; Gebbers and Adamchuk, 2010; Cao *et al.*, 2012). Expanding the buffer zone between nutrient excess and deficiencies in access is crucial (van Noordwijk and Cadisch, 2002) and requires location-specific solutions to increase synchrony, synlocation, and buffering (Hillier *et al.*, 2012). In the transition from a primarily nutrient-constrained agriculture (Giller *et al.*, 2006), overshoot into excessive fertilizer use is likely and leads to situations where emission reduction by reducing N fertilizer use can both increase yields as well as economic returns from farms (Kahrl *et al.*, 2010). For N-rich regions in China, 15% of N fertilizer can be saved without yield loss, by increased nutrient use efficiency, whereas in N-poor regions of the same country, additional N fertilizer use would benefit yield (Wang *et al.*, 2011b; Yunju *et al.*, 2012).

Reducing CH_4 Emissions by Better Feeding Regimes of Ruminants

Methane emissions from ruminants are a consequence of an excess of carbon over nitrogen in the digestive system, and

they can be controlled by a more nutritious diet. Livestock will also grow faster when well fed, and thus the CH_4 emissions per unit production are reduced from both sides of the ratio (Herrero *et al.*, 2009, 2010). For dairy cattle, the conversion of paddy rice to fodder grass production is economically attractive in certain areas; whereas cut-and-carry systems make livestock compatible with forest protection on slopes (Lusiana *et al.*, 2012). The flipside of improved nutrition is an increase in N_2O emissions from the N rich manure produced. On balance, however, intensification of livestock management can reduce emissions per unit livestock product – but an increased share of such products in the diet of a wealthier human population is increasing the human footprint. More radical solutions are to make more insect protein attractive for human consumption (van Huis, 2013).

Reducing CH_4 Emissions by Less inundation of Rice-Fields

Methane emissions from rice agroecosystems depend on the water regime, straw incorporation, and nitrogen fertilizer levels (Wang *et al.*, 2012). Substantial methane emission reduction without negative yield effects is possible by careful timing of inundation periods, which also help in weed control, and dryland conditions (Green, 2013). Not only the water level, however, but also water flow within the field needs to be taken into account in methane reduction strategies (Rizzo *et al.*, 2013).

Wiser Use of Peatlands

As the collapse and subsidence of drained peat interacts with the water management, agricultural use that is compatible with a water table of approximately 30 cm can substantially reduce emissions although maintaining agricultural production. Banning the use of fire in peatland clearing is one of the most cost effective ways to reduce emissions, but a reorientation of agricultural intensification to mineral soils is highly desirable in a mitigation context. Peatland agroforestry options exist (Tata *et al.*, 2013; Mulia *et al.*, 2013) and are worthy of further exploration.

Better Waste Recycling

Waste is a secondary resource. Organic material can be used for its energy content (by direct burning or in a methane digester producing biogas), for its role in protecting the soil during a surface decomposition process, or by incorporation into the soil enhancing soil organic matter formation. There are tradeoffs between these functions. If N-rich biomass is left on the surface, such as clippings from leguminous trees, N_2O emissions can be high (Verchot *et al.*, 2006), but it is an open debate how important aboveground residues are for soil carbon formation relative to root inputs in no-till agricultural systems. If not needed for surface protection, they might be harvested as fodder or for energy content without harm to longer term soil carbon storage. However, the smoke of manure or crop residues used as fuel tends to contain a high particulate matter content, which forms aerosols and has a direct impact on regional climates through particulates in haze, as well as on global climates (Granier *et al.*, 2011; Mahowald *et al.*, 2011).

Increased Carbon Storage in Soils

The third IPCC assessment identified increased soil C storage as the primary option for agriculture to directly contribute to climate change mitigation (Smith *et al.*, 2008). Most of this change was expected to come from widespread adoption of conservation agriculture systems with reduced tillage. There is considerable debate, however, on the interpretation of the data available, especially where the relative distribution of crop roots and soil organic matter is influenced by a change in soil tillage (VandenBygaart and Angers, 2006). Assessment in the top 100 cm of the soil profile may show less effect than an assessment in the top 30 cm, whereas the most impressive changes in soil carbon are obtained in the top 5–10 cm (Stockmann *et al.*, 2013). Soil carbon needs a long-term perspective, with most of current understanding based on the very few long-term experiments that have primarily been used to calibrate the dominant soil carbon models (Powlson *et al.*, 2011). There is evidence, however, of a soil carbon transition curve as a side-effect of agricultural intensification (Minasny *et al.*, 2011; Xu *et al.*, 2011; Stockmann *et al.*, 2013), but with specific attention to incentives, increments might be faster. On mineral soils, however, it requires many years of high organic matter inputs to increase the soil carbon content by 20 tC ha^{-1}. The case for recovery of soil carbon in overgrazed and degraded drylands is sufficiently strong to warrant action, as the areas involved are large (Wang *et al.*, 2011a).

Increased Carbon Storage in Trees in the Agricultural Landscape

Increments in aboveground soil C storage of 20 tC ha^{-1} can be more easily achieved by incorporating trees into farming systems. If in a rotational system, trees are harvested when they reach a 40 tC ha^{-1} stock level, the time-averaged C stock over the rotation length is approximately 20 tC ha^{-1} (Hairiah *et al.*, 2011). Double this amount is quite feasible, and aboveground gains in C stock are thus more easily made than belowground ones. Given the prominence of trees outside forest and trees spread in agricultural landscapes (de Foresta *et al.*, 2013; Zomer *et al.*, 2009), a reassessment of the relative importance of tree versus soil carbon-based strategies from the third IPCC assessment report (Smith *et al.*, 2008) may be needed (Aertsens *et al.*, 2013; Mbow *et al.*, 2014). Trees moreover have many direct impacts on local climates, including their roles as windbreaks and as providers of topsoil moisture during periods of water stress (Bayala *et al.*, 2008). They are a key element in the bypass loop from human activity to climatic conditions influencing people (**Figure 1**), outside of the formal reach of 'mitigation' as understood in UNFCCC, but well aligned with local knowledge and perceptions (van Noordwijk *et al.*, 2011; van Noordwijk *et al.*, 2014c). Many trees additionally produce food and nonfood products, which have income and livelihood benefits for the local population (Leakey, 2012; Mbow *et al.*, 2014).

Indirect Emissions, Emission Displacement, and Macrosolutions

As indicated, summaries such as Vermeulen *et al.* (2012) see land use change and the conversion of land to agriculture as a large component of current agricultural emissions. This implies that obtaining higher yields from existing agricultural lands, even if it increases area-based emissions, may be an overall mitigation strategy (Lambin, 2012). If instead of a global a national perspective is taken, however, the issue of indirect emissions is missing from the current accounting systems. If, however, indirect emissions are introduced into product-based footprint calculations, the outcome is controversial.

Historically, many countries have been able to transit out of an economic dependence on primary agricultural production, with positive consequences for their forest area and tree cover. Part of the forest recovery is the consequence of the pull of rural populations toward urban and industrial areas elsewhere. Part is also due to the push for labor-extensive, profitable tree production systems, once the opportunities for essentially free harvest from natural forests are gone. However, as analyzed by Meyfroidt and Lambin (2009, 2011), countries that reported an increase in forest, such as Vietnam, have generally achieved this by increasing their external footprint. On an area basis, half the gain in forest cover is offset by expansion elsewhere.

Where indirect land use change emissions are included in a product-based footprint, all producers of the same crop are supposed to have a joint responsibility on how production is managed. This goes substantially beyond the responsibility of a land manager for the specific conditions under which she/he produces the crop, in the upper or lower part of the management swing potential (Davis *et al.*, 2013). Inclusion of indirect land use change in the rules thus has consequences for the possible incentive systems to achieve agricultural mitigation by reducing the footprint of the marketed products and reducing the net emissions from the total agricultural area while increasing total yields.

Carbon Markets and Other Experiments with Micro-Incentive Systems

In response to consumer concerns, the food and agricultural processing industry has learned to respond to environmental concerns, including those on carbon footprints. Where the swing potential is large, as in the case of palm oil, the part of the food industry that targets markets with critical consumers (especially in European markets), it is keen to get associated with the upper segment of the swing potential, by creating voluntary standards of good performance. The Round Table on Sustainable Palm Oil (RSPO) has been pioneering this approach, but similar initiatives exist on other commodities. It is unclear, however, at what scale and time frame such efforts contribute to global mitigation, as substantial emission displacement can occur through a switch of the production in the lower segment of the swing potential to markets that are not accountable and not interested (e.g., palm oil export to other Asian countries).

A major challenge in incentive systems, such as a carbon market, is whether it can provide investment in a shift to other development trajectories that can become financially sustainable on their own, or whether it only implies offsetting opportunity costs and will have to be continued, as a form of payment for environmental services (PES) for an indefinite period of time (van Noordwijk *et al.*, 2012). The EU AgriEnvironment scheme, as one of the largest such efforts to support public policies in the rural landscape, has tried to introduce more conditionality of payment against environmental performance, including a requirement of increase in soil C content, but there are strong countervailing forces. There are many issues with economic incentives for agricultural mitigation (**Table 2**), operating in different policy domains, and with different challenges of achieving additionality (environmental performance above baseline) and avoiding leakage (negative environmental effects outside the primary accountability domain).

Closing Remarks

There is a probability that current efforts to achieve mitigation have actually made things worse. Franks and Hadingham (2012) gave examples how a farm-focused effort at emission reduction in selected countries can lead to increases rather than decreases of global emissions. Henders and Ostwald (2012) in their overview of leakage in a forest context, also included relations with agricultural land use. Two decades of international climate negotiations to effectively implement the agreed framework convention, dealing with the additionality and leakage issues, have made very little progress. There may be some progress in bridging current debates on REDD + and Nationally Appropriate Mitigation Actions in developing countries, but we are far from a Reducing Emissions from All Land Uses ideal.

The dominant focus of the UNFCCC framing of the climate problem on GHG emissions is under scrutiny, with consequences for the way mitigation is perceived, especially in the land use sector. Firstly, there is growing recognition of the Faustian choice that derives from the net effect of air pollution on a global cooling, masking 50% of the committed GHG warming from the Industrial Revolution (Unger, 2012). Aligned with that view, is the enhanced visibility of global climate change after industrial sulfur dioxide emissions were reduced. Aggressive reduction of air pollutants, including fine particulate matter from biomass burning that causes haze, would increase climate warming (Jacobson, 2004; Lamarque *et al.*, 2010). Within the air pollutants, however, methane through its effect on ozone decay (Fiore *et al.*, 2008), is a candidate for selective reductions in warming air pollutants, which may provide a way to mitigate near-term warming by complete pollution control until CO_2 reductions take effect (Unger, 2012). Worldwide implementation of current CH_4 emission control technologies in waste management, agriculture, and the extraction and transport of fossil fuels by 2030 would lead to a reduction in anthropogenic CH_4 emissions of 24% (relative to 2010 levels) and decrease the global mean warming by an estimated central range of 0.2–0.4 °C relative to a business-as-usual scenario (Unger, 2012).

Table 2 Incentive systems for achieving agricultural mitigation

Accounting principle	*Economic incentives to mitigate net greenhouse gas emissions from agriculture*	*Additionality*	*Leakage*
Area-based (Annex-I countries)	National (or European Union-level) emission reduction commitments translate into incentive systems to reduce agricultural emissions, and into formal carbon markets that might in future allow agricultural emission reduction credits to be exchanged for fossil fuel emission permits; the carbon market in Europe is currently restricted to fossil-fuel emission rights	Currently, agricultural mitigation is a cobenefit from other actions to make agricultural landscapes multifunctional and make agriculture sustainable	As international agreements do not yet include the land use sector, leakage is not a big risk
Area-based (outside of Annex-I countries)	Voluntary action to reduce emissions, often project-based; naming and shaming of export-oriented agriculture with high emissions leads to shifts in behavior; in North America, outside of Kyoto protocol and its compliance rules, carbon markets have emerged that support a shift to conservation agriculture for its C storage effects	A/R-CDM rules for additionality have been simplified for small-scale projects, but still are not widely used; voluntary carbon market standards such as VCS support well-intentioned action, limited in scope and reach	Leakage risk in restoration is small; leakage has been the primary challenge for protection of C stocks in REDD+, and require accountability at national scale
Product-based (footprint and efficiency criteria)	Consumer choice for products with lower footprint, often supported by forms of ecocertification and industry self-regulation, allows some linkage between consumers and producers, but is challenged by indirect emission concepts as it can cherry-pick the cleanest part of production systems without impact on the sector as a whole	If footprints calculations would cover all activities and value chains, a real reduction in environmental impacts per capita may be expected	Indirect land use change represents 'leakage,' but is controversial in its application

Abbreviations: A/R-CDM, afforestation and reforestation as part of the clean development mechanism; REDD+, efforts to reduce emissions from deforestation and forest degradation; VCS, voluntary carbon schemes.

Second, non-GHG influences of land cover and land use on rainfall, windspeed, maximum daily temperature, and other aspects of climate fall technically outside of the remit of the mitigation agenda. However, they may well have been underestimated in the public and policy discourse on climate modification that became overly carbon-centric.

Third, and sadly, public discourse remains interested in oxygen supply by plants, rather than the carbon balance and GHG effects, even though this is a nonissue in any place other than a space capsule (van Noordwijk and Lusiana, 2013).

Franks and Hadingham (2012) concluded that auditing methodology of the Kyoto Protocol is at fault. They suggest that a consumption, rather than a territorial/production, approach could be more effective, especially if it includes GHG emissions that are a consequence of farmer's decisions including overseas land use change. However, current life-cycle accounting is often still partial; allowing the term waste to be used. Waste is a wasteful concept, without specifying how and where it returns to global cycles of nutrients (and other elements), and links to energy/entropy flows. The current deficiency in recycling/reuse has multiple rationales, but it partly represents major progress in public health in breaking the life cycle of human parasites and causal agents of diseases. Closing the urban–rural loop in food production, consumption, and waste management would represent real and lasting agricultural mitigation.

See also: Agroforestry: Complex Multistrata Agriculture. Agroforestry: Fertilizer Trees. Agroforestry: Fodder Trees. Agroforestry: Hydrological Impacts. Agroforestry: Practices and Systems. Agroforestry: Participatory Domestication of Trees. Biodiversity and Ecosystem Services in Agroecosystems. Biodiversity: Conserving Biodiversity in Agroecosystems. Ecoagriculture: Integrated Landscape Management for People, Food, and Nature. Food Security: Yield Gap. Soil: Nutrient Cycling

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Climate Change and Plant Disease

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Glossary

Disease management Methods to prevent and control diseases and their effects on crops.
Emerging disease A disease that is increasing in incidence, host or geographical range, or virulence and/or has been newly discovered.
Environment The biotic and abiotic elements surrounding an object or organism.
Epidemic Increased occurrence of disease in a population.
Host A living organism that is invaded or infected by a parasite and from which the parasite obtains partial or total nourishment.
Incidence The number of plants affected by a disease within a population, commonly expressed as a percentage.
Inoculum Pathogen or its parts that can cause infection.
Pathogen An organism capable of causing disease in a host.
Resistance The inherent ability of an organism to prevent or reduce the effects of a damaging agent (antonym: susceptibility).
Severity Measure of damage in a plant tissue area caused by a disease.
Symptom Internal or external manifestation of disease on a host.
Vector A living organism capable of transmitting a pathogen from one plant to another and spreading disease.

Plant Diseases and Weather

Plant disease can be defined as any disturbance of a plant that interferes with its normal growth and development, economic value, or esthetic quality and leads to development of symptoms (Shurtleff and Averre, 1997). Plant disease is addressed using a narrower definition – disease as a consequence of infections caused by pathogens (Buczacki and Harris, 1981). Weather plays a key role in disease development and pathogen dispersal from one plant to another, facilitating or limiting new outbreaks and generating epidemics. Under climate change scenarios, changes are expected in epidemic rates and geographical distributions, emerging and reemerging diseases, and overall alterations in economic, social, ecological, and agricultural dynamics driven by plant diseases.

Humanity has suffered disastrous effects of plant disease epidemics. Thus, to understand the biological and environmental factors that contribute to epidemics is crucial, and such knowledge should help one to design the principles, practices, and, strategies for effective plant disease management (Campbell and Madden, 1990).

Plant Diseases and Their History

Historically, the emergence of plant pathology as a science began in the eighteenth century. The use of words now common in plant pathology, like 'plant parasite' or 'epidemic,' originated at that time (Rapilly, 2001), as well as the introduction of the concept of 'a living agent causing human, animal, or plant diseases' by Richard Bradley in 1721 (Santer, 2009). This fundamental idea in modern medicine, veterinary science, and plant pathology was denied by the scientific community at the time. The effects of pathogens on crops have been a commonplace for human society since the invention and practice of agriculture. Porta Puglia and Vannacci (2012) discussed how plant diseases were recorded early in human history by authors like Homer, along with reference to plant diseases in the Old Testament.

The Greek philosophers Democritus and Theophrastus identified some plant diseases and speculated about the causes and origins of those phenomena. Romans were also aware of the consequences of crop pathogens, and authors such as Lucretius, Pliny, and Columella, among others, recorded some cases. As an example of the awareness of plant pathogens in Roman times, a religious ceremony was created in order to appease the anger of Rubigo, a deity that was believed to cause rust diseases on small grains (Porta Puglia and Vannacci, 2012).

The examples of plant diseases described in ancient times are not unique to Europe or the Middle East. In AD 400–800, Mayans experienced a decline in corn production, probably as a consequence of plant diseases. Before the Spanish Conquest of the Americas, Mexican indigenous society identified *Chauiztli* or *Chahuixtle*, now known as corn rust. As early as 1590, records of potato late blight were found in Peru and in Colombia, Brazil, and Mexico in the seventeenth century (Nolla and Valiela, 1976). The history of plant diseases started with the beginning of agriculture, and new diseases continue to emerge.

Plant diseases have affected the economy and the development of the culture, as the following examples illustrate. Some of these diseases are still a threat to food security around the world.

Irish potato famine and German famine

Potato late blight, caused by *Phytophthora infestans*, caused yield losses that resulted in massive human migration from

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Europe to America. This disease was favored by cool, wet weather (Campbell and Madden, 1990). Potato was the main staple at the time in Ireland and this disease devastated the crop between 1845 and 1849, destroying up to 80% of production. Approximately one million people left Ireland for the United States and Canada in one of the largest human migrations in modern times (Ristaino, 2002), and approximately 2 million people died of starvation (Rossman, 2008). Some neighboring countries – Belgium, Germany, Holland, France, Switzerland, Italy, England, and Scotland (Ristaino, 2002) – suffered the effect of the epidemic, but consequences for them were less dramatic because they depended less on potato as a primary food (Porta Puglia and Vannacci, 2012).

A second case of famine produced by *P. infestans* occurred during 1916–17 in Germany. Copper, commonly used in late blight management, was in short supply because of its use during World War I. As a consequence, disease management was less effective, reducing the potato supply for the German people. It is speculated that reduced food availability affected army morale and could have influenced the outcome of the war (Mitzubuti and Fry, 2006).

American chestnut and its decline in the United States

The American chestnut, once a major forest species in the eastern United States, was reduced to a minor forest component by the fungus *Cryphonectria parasitica*, the causal agent of the disease chestnut blight (Anderson *et al*., 2004). The North American distribution of American chestnut was from the states of Georgia and Mississippi to Michigan and Maine, including some areas in Ontario, Canada (Agrios, 2005; Campbell and Madden, 1990). In a period of 50 years starting in 1904, when the disease was first reported in New York, native American chestnut stands were practically wiped out after the introduction of the pathogen from Japan during the late nineteenth century. This loss has been called by McKeen in 1995 as "the greatest single catastrophe in the annals of forest history," given not only the loss of chestnuts but also the resulting ecological impacts. These forests were the most important source of hardwood for many purposes (furniture, fences, poles, and railroad ties) and were also a source of tannins for the leather industry (Campbell and Madden, 1990). Another consequence of the loss of American chestnuts was the replacement of natural tannins produced by trees with synthetic agents in the leather industry. The timber loss was estimated conservatively to be 30 billion board ft (Campbell and Madden, 1990).

Coffee rust and its impact on former Ceylon's economy during the nineteenth century

During the 1870s, Ceylon, a former British colony known today as Sri Lanka, was the largest coffee producer in the world, satisfying the demand for the former British Empire's preferred hot beverage (Campbell and Madden, 1990; Fletcher, 2011). A rust epidemic caused by a fungal pathogen (*Hemileia vastatrix*) was responsible for replacing the once predominant coffee crops in Ceylon with tea plantations. Coffee rust, the most destructive disease of coffee (Agrios, 2005), was reported for the first time in 1861 (Lake Victoria, Kenya) in wild coffee. Then it was reported in Ceylon in 1869, where the disease took 28 years to change the agroecosystem (Staples, 2000). It is commonly suggested that as a consequence of this disease, Britain became a tea-drinking society (Ainswort, 1969), although other social and economic factors probably also played a role in this transition (Madden, 2013). What is clear is that coffee production moved to other countries in South and Central America. A new epidemic was then discovered during 1971 in Brazil, and from there the pathogen spread over South and Central America in countries whose economies depend on coffee production (Campbell and Madden, 1990; Staples, 2000). The coffee rust epidemic of 2013 threatened the livelihoods of many smallholder farmers in the Americas, amid speculation about the role of climate change.

The great Bengal famine: Brown spot of rice

During 1943 the region of Bengal – today Bangladesh and the state of West Bengal in India – suffered a devastating famine in which 2–3 million people died from starvation (Islam, 2007). Rice in the region was destroyed by brown spot (caused by *Bipolaris oryzae*). The brown spot epidemic and bad management decisions during the crisis by the administrative entities were responsible for the catastrophic famine (Islam, 2007; Padmanabhan, 1973). One of the factors contributing to the development of the epidemic was the unusual weather: heavy rains, prolonged cloudy weather, and warmer temperatures (Padmanabhan, 1973).

Southern corn leaf blight

In 1970 in the United States, the fungus *Bipolaris maydis* caused a Southern corn leaf blight epidemic that generated losses of approximately US$1 billion. That year in February, the disease was found in Florida in corn hybrids, which previously were resistant to *B. maydis*. All infected plants had something in common: they were produced using the gene for Texas cytoplasmic male sterility. This observation was frightening, because nearly 85% of corn in the United States was produced using this breeding technique. By May, the pathogen was well established in the southern part of the United States and weather conditions were extremely favorable to spread of the disease to the north. Tropical storms moved the inoculum from the Gulf of Mexico into the Midwest in July and the weather conditions were perfect for the pathogen to infect and reproduce (Campbell and Madden, 1990). This is a dramatic example of how host population homogeneity, when it includes susceptibility to a particular pathogen species or subpopulation, can have devastating epidemiological and economic consequences. At the time, almost 100% of the corn planted in the Midwest was genetically similar and had the Texas male sterile cytoplasm that was susceptible to the virulent type of the pathogen (Race T) (Rossman, 2008).

Ergot and ergotism: lysergic acid diethylamide and the holy fire

Claviceps purpurea is a fungus that infects rye, producing a structure on grains called a sclerotium, or ergot, that contains large amounts of alkaloids, like lysergic acid diethylamide (LSD). The consumption of bread made with rye flour contaminated with sclerotia generates a variety of symptoms, including fever, hallucinations, and even death depending on the amount of alkaloid ingested. The plant disease, also

called ergot, was first recorded around AD 857 in the Rhine valley, Europe, where thousands of people died. The human disease is known as Ergotism but was colloquially named 'the holy fire' because of the symptoms produced in humans. A second epidemic occurred in France during AD 1039. The disease was also present from the eleventh to the thirteenth centuries in France and Germany and in Russia during 1722, potentially contributing to the defeat of Peter the Great of Russia. In the United States it is believed that ergot caused symptoms in some people that influenced the witchcraft accusations in Salem, Massachusetts in 1692. Recent times have also witnessed ergot epidemics, such as during 1951 in the south of France, causing 200 cases of severe illness, 32 cases of insanity, and 4 deaths. Cases of the disease were also found in Ethiopia in 1977–78 (Campbell and Madden, 1990).

Current Case Studies

Plant diseases continue to threaten food security and natural plant systems. These current examples of epidemics illustrate the importance of pathogens and plant diseases and the need for continued development of improved management strategies, including adaptation to climate change.

Other recent Phytophthora epidemics

Phytophthora species cause a wide range of symptoms and in some cases are difficult to diagnose, allowing the pathogen to remain incognito (Frankel and Hansen, 2011). *Phytophthora cinnamomi* can cause disease in more than 1000 species of plants and has damaged Australian natural plant communities. *Phytophthora ramorum* is the best studied, monitored, and managed forest pathogen species in the United States because of its important impact on trees and other plant species (Frankel and Hansen, 2011; Garbelotto and Pautasso, 2011). This pathogen is the causal agent of diseases such as sudden oak death and ramorum blight of coast live oak and tanoak in native forests, especially in the western US states California and Oregon. Other tree species in European and American forests are also affected (Grunwald *et al.*, 2009). The management of this disease is complex and needs to address three levels: the individual plants affected, the forest, and regional/international management and policies (Rizzo *et al.*, 2005).

Phytophthora infestans caused a pandemic during 2009 and 2010 in the Northeastern United States. A large proportion of organic tomato growers, home gardeners, and some commercial producers lost their production. Losses were up to 100% in some regions. The outbreak of the disease occurred mid- to late-June over most of the Northeastern United States (Fry *et al.*, 2013). This is a very interesting case because of the pathway of epidemic spread. Initially, it followed the shipping network among different retailers. Plants were sold in shops from Pennsylvania to Maine. By mid-August all counties in New York reported the presence of the disease. The weather in the region was relatively favorable for the disease, allowing plants infected in home gardens to sporulate, disperse, and infect neighboring plants, generating the epidemic (Fry *et al.*, 2013). This is an example of how an epidemic can develop in a short period of time, with important economic consequences.

Cassava mosaic virus

Cassava (also called yucca) is the sixth most important food crop worldwide and the third most important source of calories in the tropics. More than 800 million people depend on this plant – tubers and sometimes leaves – as their main staple (Burns *et al.*, 2010). Cassava is the principal source of carbohydrates in several of the poorest countries in Sub-Saharan Africa. *Cassava mosaic virus* (CMV) is a key pathogen affecting cassava in Africa, Sri Lanka, and India (Otim-Nape and Thresh, 2006) and can be transmitted both by whitefly (*Bemisia tabaci*) and through vegetative propagation (Fargette *et al.*, 2006).

CMV was first reported in 1894 in Tanzania (Fargette *et al.*, 2006). The first epidemic during the 1920s in East and West Africa coincided with the increase of cassava production in Africa. The second and third epidemics occurred in the 1930s in Cape Green and Nigeria and during the 1940s in Madagascar, with a more recent epidemic in Uganda in the 1990s (Otim-Nape and Thresh, 2006).

In 1990, a famine in Uganda was caused by a shortage of cassava due to an outbreak of CMV. This epidemic spread to neighboring countries (Kenya, Tanzania, Burundi, and Rwanda) acquiring the status of pandemic and threatening other cassava-producing regions. Cassava production is mainly on a small scale and the virus remains prevalent in many areas. There was evidence of African crop losses ranging from 15% to 24% (Otim-Nape and Thresh, 2006).

Consequences of this epidemic were a decline in cassava production, a decrease in planted area, a rise in prices, and also increased theft of cassava as its price increases. Affected families relied heavily on cassava as a subsistence crop and suffered a decrease in their income. Some positive consequences, like allocation of funds for cassava rehabilitation projects and increased use of resistant varieties, have been observed during and after the epidemic. Recent analyses of CMV impacts in Africa – nowadays confirmed as involving at least two geminiviruses (*African cassava mosaic virus* (ACMV) and *East African cassava mosaic virus* (EACMV)) (Fargette *et al.*, 2006) – indicated losses of 47% of production, generating local famines (Burns *et al.*, 2010).

Canola diseases

Important recent epidemics in canola of Sclerotinia stem rot, caused by *Sclerotinia sclerotiorum*, occurred in England in 1991 and in 2007. In 2007, 5.7% of plants were affected by the disease, generating the worst epidemic since 1991 (Gladders *et al.*, 2008). It has been suggested that weather factors and variation in inoculum were main factors in the development of the epidemic. As a consequence, higher production of inoculum in the coming years was predicted (Gladders *et al.*, 2008). During 1991, disease levels were very high with incidence of 46% and an average of 5.5% of plants affected. Weather factors were conducive for the disease in early May and early June (Gladders *et al.*, 1993).

Wheat stem rust

Wheat stem rust, caused by *Puccinia graminis* f.sp. *tritici* (**Figure 1**), had been effectively managed in many parts of the

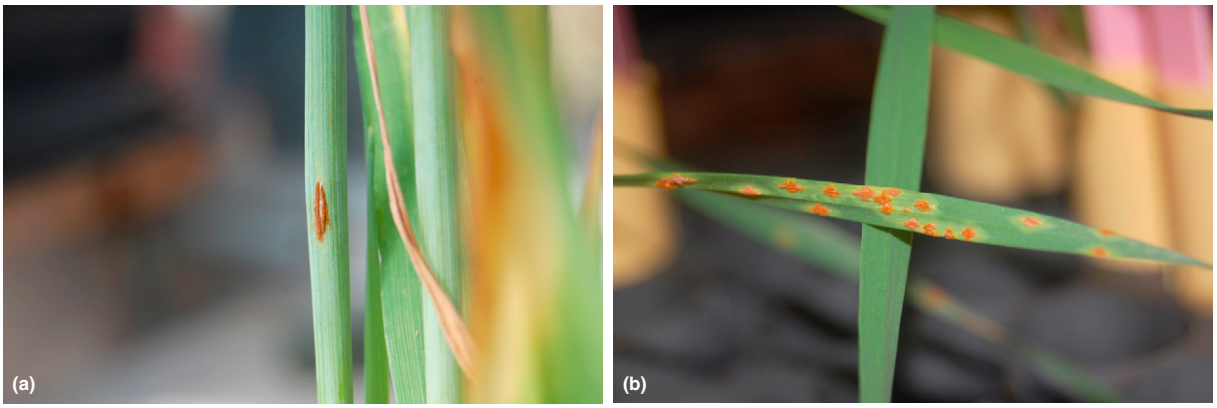


Figure 1 Symptoms (pustules) of wheat stem rust, caused by the fungus *Puccinia graminis* f.sp. *tritici*, on a wheat stem (a) and leaf (b). Photo by John Fredy Hernandez Nopsa.

world using genetic disease resistance. Ug99, a new pathogen race that can overcome common forms of resistance, had the capacity to cause disease in approximately 90% of the wheat population worldwide (Ayliffe *et al.*, 2008; Singh *et al.*, 2011). Given that wheat is the second-largest small grain crop worldwide (FAO, 2013) and that it provides approximately 55% of the carbohydrates and 20% of humankind's calories (Joshi *et al.*, 2011), new pathogens are important challenges to food security. Current management efforts include development of new resistant cultivars, chemical control, and the development and improvement of epidemiological tools that help farmers, producers, and scientists to predict when an epidemic will occur.

General Taxonomic Groups of Pathogens

Plant pathogens cause a wide range of diseases in plants that affect the quantity, quality, and safety of food products; restrict agro-based industries; and affect the biology of ecosystems. Taxa that have evolved mechanisms to parasitize plants include fungi, bacteria, viruses, nematodes, parasitic plants, viroids, protozoans, and algae. Pathogens fall on a continuous scale from facultative saprophytes (that can survive in soil and plant debris) at one end to obligate pathogens (that cannot survive without a host) at the other. They enter plants via a variety of methods, including direct penetration into the host, through natural wounds and openings, vector feeding, and through seed and other propagation methods. Plant pathology, or phytopathology, is the study of the biology, ecology, and epidemiology of plant diseases, ultimately aiming to identify management tools to limit damages associated with plant diseases. The first step is to understand plant disease etiology.

Fungi

Fungi are an important group of plant pathogens that cause a high proportion of plant diseases. Organisms in the kingdom Fungi are eukaryotic, comprised of hyphae or yeast cells, and reproduce by sexual or asexual spores (Figure 2) dispersed by rain splash, wind, humans, animals, seed, and soil movement. Fungal plant pathogens are distributed in all major phyla,

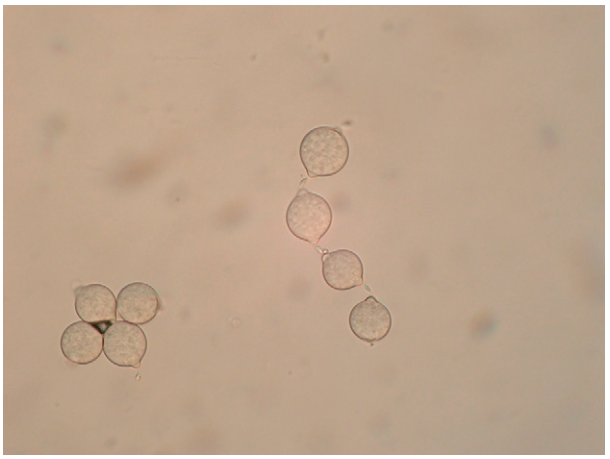


Figure 2 Typical chain of conidia (asexual spores) of the ascomycete *Monilinia vaccinii-corymbosi* that causes mummy berry disease on blueberries. Photo by Sara Thomas-Sharma.

including Ascomycota, Basidiomycota, Zygomycota, Chytridiomycota, and Deuteromycota. Fungi can survive as mycelium in a host or organic material tolerating wide temperature and moisture ranges (Agrios, 2005). They produce an array of spores for dispersal (such as conidia and urediniospores) and also produce sexual and asexual structures for survival (such as chlamydospores, sclerotia, zygospores, and teliospores). Some fungi have complicated life cycles with multiple spore types and different hosts (such as many rust fungi), whereas others have simple life cycles. Fungi can utilize direct penetration (e.g., *Magnaporthe oryze*) or natural openings (stomata and lenticels) and wounds (e.g., *Botrytis cinerea*) to gain access into the host. During the plant parasitic phase of their life cycle, fungi can produce haustoria (feeding organs) inside the host cell to draw nutrients (biotrophic fungi) or produce enzymes that kill host cells ahead of mycelium development (necrotrophic fungi). This results in a variety of symptoms, including leaf spots, blights, rots, wilts, etc. Some fungi also produce toxins that may aid in plant colonization. These mycotoxins can be toxic to humans and animals, such as deoxynivalenol and zearalenone produced by *Fusarium*

graminearum (Figure 3), fumonisins produced by other species of *Fusarium*, ergotoxin produced by *Claviceps* spp., and aflatoxins produced *Aspergillus* spp. Detection and diagnosis of fungal plant pathogens rely on symptomatology, culturing, spore and fruiting body morphology-based identification, and nucleic acid-based detection techniques.

Oomycetes

Colloquially called water molds, oomycetes are classified in the kingdom Chromista and are fungus-like eukaryotic organisms. They have a cell wall composed of cellulose and glucans (unlike chitin in fungi), aseptate hyphae, and produce sexual spores called oospores (resting spores), and asexual spores called zoospores. They are mostly aquatic or soil inhabiting and cause many devastating plant diseases, such as late blight (*P. infestans*); damping-off in seedlings (*Pythium* spp.); downy mildew diseases on many crops, including *Peronospora manshurica* in soybean (Figure 4); and white rust (*Albugo* spp.). As for fungal pathogens, detection and diagnosis of oomycetes rely on symptomatology, characteristics of oospore and sporangia, and nucleic acid-based detection techniques.



Figure 3 Wheat spike showing the typical symptom of Fusarium head blight, a disease caused by the fungus *Fusarium graminearum*. Photo by John Fredy Hernandez Nopsa.

Viruses

Plant viruses have been among the earliest viruses studied, with *Tobacco mosaic virus* (TMV) discovered by Martinus Beijerinck in 1898. Plant pathogenic viruses are parasitic nucleoproteins that vary in size, chemical composition, physical structure, and number of genomic units. They are transmitted in various ways, including by vectors (insects, mites, fungi, nematode, and parasitic plants), vegetative propagation, pollen, seed, and by contact. Movement of viruses within a plant generally occurs via plasmodesmata for between-cell movement and via phloem for long distance transport. Symptoms associated with plant viruses include mosaic patterns, vein clearing, streaking, stunting, and hypo- or hyperplasia. However, plants can also maintain viruses without any obvious symptoms. Detection and diagnosis of plant viruses can be challenging and are conducted using transmission studies, symptomatology, electron microscopy, serological, and nucleic acid-based techniques.

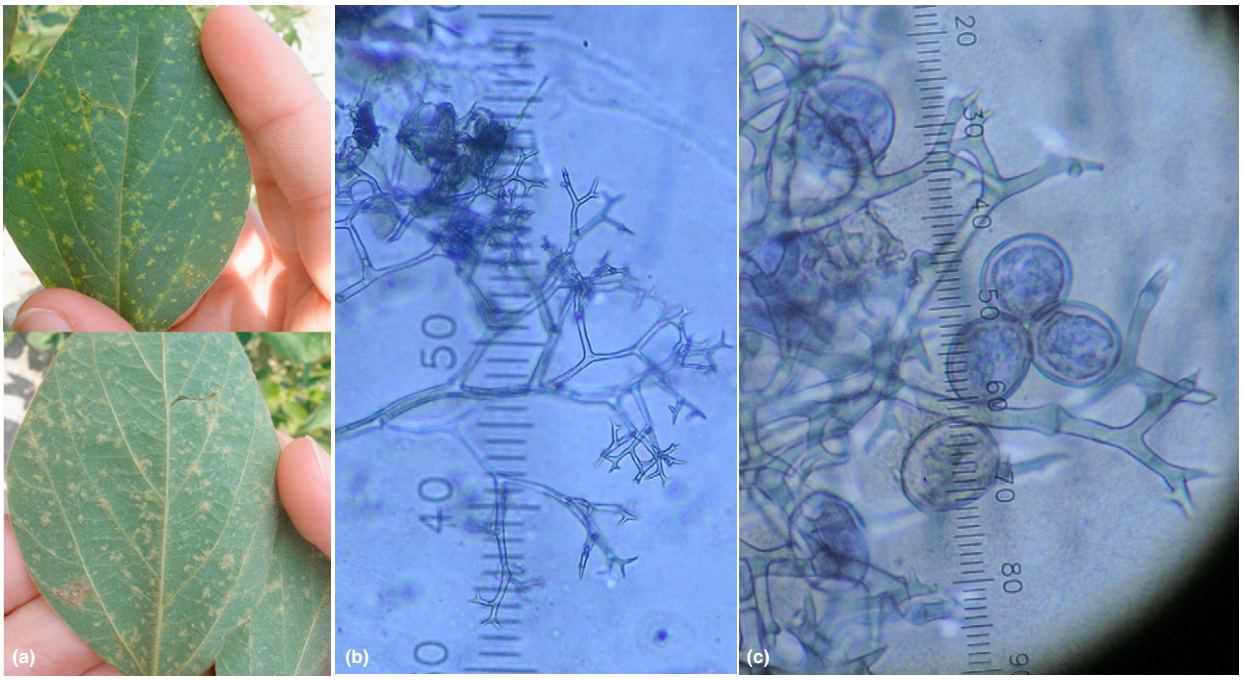


Figure 4 Downy mildew on soybean. (a) Pale green to light yellow spots on the upper surface of soybean leaves and developed grayish mycelia of the oomycete on the lower foliar surface of a soybean leaf; (b, c) determinate growth of sporangiophores showing unattached oval-shaped sporangia (200 × and 500 ×, respectively). Photo by Maria Valeria Avanzato.

Bacteria

Bacteria are prokaryotic microorganisms that belong to kingdom Monera (Prokaryota), with well-known examples including *Agrobacterium tumefaciens*, used routinely for plant transformation, and *Ralstonia solanacearum*, causing wilt diseases in various hosts. Many plant pathogenic bacteria are rod shaped (with an exception of *Streptomyces* spp., which is filamentous), reproduce rapidly by binary fission, can be motile or nonmotile, and are Gram-negative (with some Gram-positive exceptions such as *Clavibacter* spp.). The bacterial cell wall is composed of peptidoglycans, but certain cell wall-less bacteria called Phytoplasmas (class Mollicutes) are also serious pathogens in plants. Plant pathogenic bacteria are found in the soil as saprophytes or on plant surfaces as epiphytes, both of which require natural openings or wounds to gain entry into the host. Inside the plant host, bacteria grow in the apoplast and use secretion systems to release a variety of extracellular virulence factors, such as enzymes, polysaccharides, toxins, and growth regulators, to manipulate host machinery. Many of these processes are population density dependent, allowing bacteria to aggregate before attacking the host. Symptoms associated with bacterial diseases include water soaking, spots, cankers, blights, rots, tumors, wilts, etc. Detection and diagnosis of bacteria is based on symptomatology, culturing and colony morphology, and nucleic acid-based detection techniques.

Nematodes

Nematodes, in the kingdom Animalia, are worm-like in appearance and generally soilborne (with exceptions such as *Aphelenchoides*, a foliar nematode). Although numerous saprophytic nematodes exist in soils, they differ from plant pathogenic nematodes in that the latter have stylets that allow feeding on plants. Nematodes hatch from eggs laid by females either after mating with males or parthenogenetically. The juveniles go through four molts, where in some species the first and second stages do not feed on plants. Soil moisture, aeration, and temperatures greatly affect nematode survival and movement. Plant pathogenic nematodes can be ecto- or endoparasites depending on their feeding location in the root and sedentary or migratory depending on their movement during feeding. Nematode feeding on plants can cause mechanical injury and alter cell physiology because of enzymes in their saliva. Consequent symptoms on plants include yellowing, stunting, hyperplasia at feeding sites such as root knots and root galls, root lesions, etc. Further, nematodes can predispose plants to infection by other soilborne pathogens, often producing wounds that facilitate pathogen entry. Diagnosis of nematode diseases relies on identifying the nematode species based on morphology, by first isolating nematodes using soil isolation techniques, such as Baermann's funnel method, sieving method, and centrifugation or sugar floatation methods (Agrios, 2005). Symptomatology and nucleic acid-based detection techniques are also used.

Others

Other microorganisms such as protozoa, viroids, and algae also cause serious plant diseases (Agrios, 2005). Some such examples include phloem necrosis of coffee (*Phytomonas leptovasorum*), coconut cadang-cadang disease (*Coconut cadang-cadang viroid*), and algal leaf spot of magnolia (*Cephaleuros virescens*). Certain higher plants such as dodder (*Cuscuta* spp.), mistletoe (*Viscum* spp.), and witchweed (*Striga* spp.) are parasitic on plants and can cause significant yield losses in poorly managed crop fields.

How Weather Affects Plant Diseases

Plant diseases result when a susceptible host and infective pathogen interact with each other under favorable environmental conditions. This concept, illustrated by the disease triangle (Figure 5), can be further expanded to incorporate the influence of environment on each biotic component, including the interactions among pathogen, host, pathogen environment, and host environment, and how these interactions change over time (Dixon, 2012).

Thus, environmental factors (in both air and soil) can individually or in combination favor or deter the development of the host, pathogen (and vector), and consequently disease. The prevailing environmental conditions contribute to plant disease variability, affecting disease initiation, development, intensity, and spread. Further, as small changes in these variables can translate into substantial changes in pathosystem dynamics, climate change has the potential to have an important impact on plant disease epidemics.

Temperature

Differences in temperature optima of host, pathogen, and vector play an important role in restricting plant diseases to different geographical areas. Climate change, and the resulting poleward shift of agroclimatic zones, would thus shift regions with temperature optima, potentially increasing the spread of diseases (Coakley *et al.*, 1999). High temperatures can break down resistance in some hosts with heat-sensitive

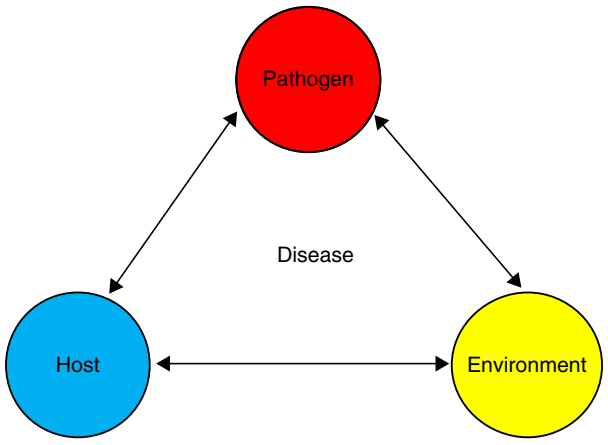


Figure 5 The plant disease triangle. The three necessary causal factors of disease are positioned at the vertices, and the disease occurs with the combination of a conducive environment, a competent pathogen (and in some cases a competent vector), and a susceptible host. Adapted from Francl, L., 2001. The disease triangle: A plant pathological paradigm revisited. The Plant Health Instructor. APSnet. Available at: http://www.apsnet.org/edcenter/instcomm/TeachingArticles/Pages/DiseaseTriangle.aspx (accessed 01.04.13).

resistance genes (Coakley *et al.*, 1999; Garrett *et al.*, 2006). Elevated temperatures can modify the stresses experienced by plants, in turn affecting defense signaling and secondary metabolite pathways that alter plant resistance (Garrett *et al.*, 2006). Temperature changes can also affect pathogen and vector dynamics. Elevated temperatures are known to increase the replication and systemic movement of viruses in plants, alter the accumulation pattern of viruses in mixed infections, and increase virus evolution rates (Canto *et al.*, 2009; Jones and Barbetti, 2012). For bacteria, diseases caused by thermophylic xanthomonads are expected to increase in prominence unlike those caused by thermophobic pseudomonads (Jones and Barbetti, 2012). Similarly, prolonged heat waves are expected to reduce the severity of plant pathogenic bacteria that are temperature sensitive (Jones and Barbetti, 2012). In vectored pathogens, temperature can alter the predominant vector in a region, consequently changing the diseases vectored. For example, in the Andean region of South America, populations of cold-tolerant whiteflies, such as *Trialeurodes vaporariorum*, are displacing the less cold-tolerant *B. tabaci* in higher altitudes, consequently changing the incidence of Potato yellow vein disease (transmitted by *T. vaporariorum*) (Jones and Barbetti, 2012). Higher temperatures are also predicted to increase the reproductive rates of insects. Aphid populations were estimated to increase by five generations per year for a 2 °C increase in global temperatures (Yamamura and Kiritani, 1998). Soil temperatures can also affect the profile and physiology of soilborne pathogens and vectors. For example, the feeding of *Longidorus macrosoma*, a nematode vector of *Raspberry ringspot virus*, was inhibited at high temperatures, reducing virus infections in cucumber (Jones and Barbetti, 2012).

Precipitation

Many plant pathogens, such as nonfastidious bacteria, nematodes, oomycetes, and certain fungi, rely on water for their dispersal. Thus, precipitation patterns serve as drivers of these epidemics and any alteration can change the prevalence and spread of these diseases. In semiarid and arid regions of the mid-latitudes, the incidence of non-vector-borne bacterial diseases that have high moisture requirements are expected to decline (Jones and Barbetti, 2012). Similarly, the Dothistroma needle blight epidemic (caused by the fungus *Mycosphaerella pini*) in North America may be moving north due to higher temperatures and altered rainfall patterns (Woods *et al.*, 2005). In general, there is a correlation between the number of precipitation events per season and the number of infection cycles for pathogens (Agrios, 2005). Vector-borne viral and bacterial diseases can also be affected by changes in precipitation patterns. Long dry seasons, for example, can increase the number of *B. tabaci* generations, consequently increasing the incidence of begomoviruses (Jones and Barbetti, 2012). Similarly, increased soil moisture and temperature in temperate regions may increase epidemics of fungi-transmitted viruses because vector spores will be more easily dispersed. Thus, epidemics of furoviruses and bymoviruses, such as *Soil-borne wheat mosaic virus* and *Wheat spindle streak mosaic virus*, are expected to increase in Canada, Northern USA, Northern Europe, Northeast Asia, and Southern South America (Jones and Barbetti, 2012). However, in rain-fed fields of India and Africa, where reduced rainfall is predicted, the incidence of fungus-vectored diseases like *Peanut clump virus* (PCV) and *Indian peanut clump virus* would be reduced (Jones and Barbetti, 2012). Frequent heavy rainfall can not only wash insect vectors, such as aphids, whiteflies, and thrips, off the plant but also wash bacteria into natural openings and wounds, increasing bacterial diseases. In addition, the success of chemical control strategies could be affected by increased precipitation, because plant protection chemicals can be more easily washed off plant surfaces (Coakley *et al.*, 1999).

Extreme rainfall-related events

Extreme rainfall-related events, such as droughts and floods, can significantly affect plant diseases. Drought and disease can interact in damaging crops, as demonstrated by severe epidemics caused by *Xylella fastidiosa*, *Beet yellows virus*, and *Maize dwarf mosaic virus*, increasing economic losses (Jones and Barbetti, 2012). In other cases, cross-talk between abiotic stress-related pathways and defense signaling can make drought-stressed plants more resistant to disease. Prolonged droughts can have adverse impacts on pathogens and vectors by limiting their population sizes and affecting their dispersal and survival mechanisms. Certain contact-transmitted viruses, such as TMV, that are easily inactivated in aerated soils (rich in antagonistic microflora) can benefit from compact soils in drought-affected areas and waterlogged soils (Jones and Barbetti, 2012). Similarly, nonsaprophytic bacteria like *Xanthomonas citri* subsp. *malvacearum*, causing bacterial blight on cotton, can have greater survival in drought-prone areas. Waterlogged soils (that are not anaerobic) will have higher activity of fungal and nematode pathogens and hence a higher incidence of diseases they cause or vector (Jones and Barbetti, 2012). In contrast, pupal stages of thrips and oviposition of whiteflies are negatively affected by waterlogging, reducing diseases they transmit (Jones and Barbetti, 2012).

Relative humidity

Many fungal pathogens require high relative humidity, and associated surface moisture, for germination and dispersal of their spores. Oomycetes (for most of their life cycle) and bacteria need leaf surface moisture to aid with their movement into natural openings and wounds. Powdery mildews are an exception to this, causing maximum infection in low (50–70%) relative humidity environments (Agrios, 2005). Similarly, flight patterns and multiplication rates of insect vectors can be adversely affected by high humidity. Plants become more succulent and tender under high humidity scenarios, making them more susceptible to contact-transmitted viruses (Jones and Barbetti, 2012).

Wind

Wind drives plant disease epidemics by affecting dispersal of pathogen propagules, increasing drying of host surfaces, and increasing wounding of hosts. Certain spores of fungi (such as urediniospores) and readily airborne insect vectors can be dispersed around the globe by high intensity winds and storms. Periodic increases in wind velocity, consequent to climate change, however, can limit the dispersal of winged aphid vectors and lower the incidence of the diseases they transmit (Jones and Barbetti, 2012). The prevailing wind

direction can also determine the direction of spread of epidemics and disease outbreaks.

CO_2

The CO_2 concentration in the atmosphere affects the rate of photosynthesis, especially in C_3 plants, by altering internal carbon dioxide concentrations (Ziska and Bunce, 1997). Thus, elevated CO_2 improves photosynthesis; increases plant size attributes, such as leaf thickness, area, longevity, and number of leaves; and also increases tillering, stem and root length, and dry weight (Coakley *et al.*, 1999). Such changes alter plant architecture and density, creating more humid microclimates, conducive for many fungal diseases. In addition to this, changes in CO_2 concentrations can alter secondary metabolite pathways in plants, in turn altering the nutritive value of leaves to disease vectors and affecting plant defense signaling. Higher carbon:nitrogen ratios in these plants would also result in slower decomposition of plant litter and greater survival of pathogen resting structures (Coakley *et al.*, 1999). Changes in CO_2 concentration can also affect host–pathogen interactions in different pathosystems. In barley powdery mildew caused by *Blumeria graminis*, an increase in CO_2 results in a reduction in the rate of primary penetration of the host, but increases the growth rate of the pathogen once established (Coakley *et al.*, 1999). Such contrasting results are also seen in virus pathosystems where high CO_2 is predicted to suppress pathogen-induced virus resistance but shown to increase resistance to *Potato virus Y* in tobacco. Similarly, among bacterial pathogens, soft rot of tomato caused by *Pseudomonas marginalis* was inhibited by higher CO_2 concentrations, but incidence of bacterial wilt (*R. solanacearum*) on pepper increased (Jones and Barbetti, 2012). Thus, the effects of CO_2 on plant diseases are pathosystem-specific, making generalizations difficult.

How Climate Change Can Affect Plant Disease

Climate change can directly affect plant diseases by altering the favorability of different environmental conditions for pathogen, host, and vector development. It can also indirectly affect disease development by altering other biological components (such as weed host abundance, vector predation, and symbiont associations) in agricultural and natural ecosystems. The effects of climatic change can also vary from microscopic (leaf wetness and soil temperature) to macroscopic (global temperature, hurricanes, and other extreme weather events) scales. Thus, predicting the overall consequence of climate change on plant disease epidemics requires a thorough understanding of each of these elements and how they interact.

Changes in Pathogen Range

Pathogen range expansions are directly related to host range as well as vector range for vectored pathogens. With climate change, regions in high latitudes and elevations are predicted to become more favorable for many plant species. Resulting host range expansions will provide opportunities for indigenous pathogens to infect new host species and exotic pathogens to move (with their host or vectors) into new geographical areas. Under these new environmental conditions, factors that improve rates of reproduction and survival abilities (ability to oversummer and overwinter) will affect pathogen fitness. For example, predictions for the generalist plant pathogen *P. cinnamomi* in Europe include improved ability to persist under increased temperatures and consequent range expansions (Bergot *et al.*, 2004). In vectored pathogens, pathogen range expansions would also require increases in vector ranges. In temperate countries, insect vectors are expected to have greater survival in warmer winters and faster reproduction with higher summer temperatures. In Europe, aphid-transmitted viral diseases, like potato leaf roll and yellow dwarf in cereals, are predicted to increase under higher temperatures (Jones and Barbetti, 2012). In addition to responses to host and vector range shifts, pathogens can be directly affected by climate change. Generalist viruses, less affected by temperature fluctuations and adapted to wider host ranges, are more likely to expand under climate change scenarios (Jones and Barbetti, 2012). Similarly, fungal, oomycete, and nematode pathogens that depend on water for transport will more likely have reduced expansion in tropical climates with lower predicted precipitation and more frequent droughts. In addition, extreme weather events, like torrential rains, hurricanes, and storms, can transport pathogens across large geographical distances into new regions. A recent expansion of soybean rust (*Phakopsora pachyrhizi*) into North America occurred in November 2004, probably when the spores were introduced by hurricane Ivan.

Changes in Local Disease Severity

Environmental variables can affect disease severity through multiple mechanisms. Temperature may alter the stability of resistance genes, the rates of multiplication of pathogens and vectors, and seed transmission rates of certain viruses (such as *Arabis mosaic virus*). In rice, for example, bacterial blight resistance gene *Xa7* was found to have greater effectiveness against *Xanthomonas oryzae* pv. *oryzae* under increased temperatures (Webb *et al.*, 2010). Low temperature scenarios reduce the effectiveness of plant antiviral mechanisms (such as gene silencing), increasing severity of virus diseases. Further, rates of replication and systemic movement of viruses (such as *Potato virus X* and TMV) in plants are expected to be higher at higher temperatures, resulting in greater disease severity (Jones and Barbetti, 2012). Altered patterns of precipitation can affect dispersal of pathogens as well as the severity of fungus- and nematode-vectored viral diseases. Extreme rainfall events, floods, and droughts can specifically favor or deter diseases depending on the pathosystem. Further, increased rates of reproduction of different pathogens, overlap of areas with different mating types, and higher evolution rates can facilitate the generation of new pathogen strains that are more virulent to crops.

Changes in Pathogen–Vector–Host Associations

Climate change can cause outbreaks of previously uncharacterized disease complexes, reemergence of existing plant

diseases, and alter the relative importance of endemic diseases. In viral diseases, changes in temperature can modify the rates of virus multiplication, accumulation pattern in mixed infections, and transmission efficiency of vectors (Jones and Barbetti, 2012). Taken together with host range expansions, these provide excellent opportunities for the outbreak of new disease complexes. In the Iberian peninsula, where warming is double the global average, diseases such as citrus tristeza, tomato leaf curl, tomato necrosis, tomato mosaic, and cucurbit vein yellowing have emerged in recent years (Canto *et al.*, 2009). Displacement of vectors under different climate change scenarios and their increased activity can change the importance of diseases locally. Examples include the emergence of begomovirus epidemics in the middle latitudes and reduced importance of PCV in the tropics (Jones and Barbetti, 2012). Temperature also affects host–pathogen interactions by allowing host resistance to be overcome by pathogens in some cases. This could be aided by increases in host tissue and morphological and physiological changes in the host (Juroszek and von Tiedemann, 2011).

Changes in Evolutionary Processes

Increases in CO_2 and UV-B radiation have the potential to accelerate evolutionary process in pathogens, allowing them to overcome host resistance more rapidly (Chakraborty *et al.*, 1998, 2000; Garrett *et al.*, 2006). Stages in the life cycle of pathogens, such as production of inoculum, infection, and other stages, are driven by favorable weather conditions. Thus, climate change can influence pathogen evolution. Experiments under elevated CO_2 indicated that the plant pathogen *Golovinomyces cichoracearum* increased in aggressiveness and the host *Arabidopsis thaliana* exhibited different leaf characteristics, making it potentially more susceptible to pathogens. This may represent an acceleration of plant pathogen evolution (Lake and Wade, 2009). The rate of evolution of organisms is influenced by the number of generations per time interval. Temperature has a direct impact on the reproductive process in many pathogens, and in many cases higher temperatures may support faster evolution rates. Longer and warmer seasons may make it possible for pathogens to become more virulent, to become pathogenic in different systems, and to be more aggressive (Garrett *et al.*, 2006). Pathogens may adapt to new climate scenarios and potentially become more virulent. Just as pathogen life history traits influence the rate at which pathogens may overcome host resistance genes (McDonald and Linde, 2002), they will also influence the response of evolutionary rates to climate change.

Changes in Management and Management Efficacy

Biological control agents may become less effective if there is a greater fluctuation in temperature, humidity, rain periods, and other weather conditions under climate change scenarios (Garrett *et al.*, 2006; Juroszek and von Tiedemann, 2011). System-level effects of climate change – such as changes in productive zones, increases or decreases in crop area and diversity, and changes in yield – may produce a direct effect on pesticide use, pesticide activity, and the volumes needed and applied in a given region (Miraglia *et al.*, 2009). An increase in the number of outbreaks could lead to greater use of pesticides, increasing the risk of pest resistance to pesticides. Additionally, faster crop growth may shorten the time between applications, having direct effects on producers, economics, environment, and food safety (Juroszek and von Tiedemann, 2011).

General Predictions for Plant Disease under Climate Change

North American Forests

During the last 50 years, temperatures in Northeastern North America have increased at an estimated rate of 0.25 °C per decade (Dukes *et al.*, 2009). Given that 23 pest species, 8 invasive plant species, and 18 pathogens are predicted to cause negative effects in the region's forests (Dukes *et al.*, 2009), this temperature increase has the potential to cause a number of changes. Precipitation patterns may have influenced the Dothistroma needle blight epidemics in pine in Western Canada (Woods *et al.*, 2005). Forests adapt slowly to environmental change, given the long generation times of trees, a factor making climate change adaptation strategies in forestry more challenging (Boland *et al.*, 2004; Jones and Barbetti, 2012; Sturrock, 2012).

Northern European Agriculture

For high-latitude regions, increases in precipitation are expected during winter and summer seasons. With higher temperatures, an increase in the melting rate of land ice and snow cover is predicted, although snow cover has the potential to increase along with higher temperatures in boreal regions. Driven by higher levels of CO_2 and higher temperatures, increases in plant tissues and leaf surface areas, with associated changes in microclimate conditions (humidity and wetness), may facilitate pathogenic infections and outbreaks of new diseases. For example, warmer temperatures in winter increase the probability of rust overwintering (Pfender and Vollmer, 1999). Many pathogens may experience more conducive overwintering conditions under climate change and so serve as inoculum for the following season. Potato late blight in Finland has been observed earlier in the year over recent decades, although the effects of changes in potato cultivars are confounded with weather effects (Hannukkala *et al.*, 2007).

Tropical Agriculture and Developing Countries

In tropical Africa, precipitation is predicted to increase during the wet season (winter). However, in Central America, a decrease in precipitation is predicted. Pathogens have an advantage over plants because their reproductive cycles are in general faster than plants and their number of generations per time unit is greater, giving them the potential for more rapid adaptation to new climate conditions (Garrett *et al.*, 2006). This pathogen advantage may be even more pronounced in tropical agriculture when long or year-round growing conditions make it possible for continuous pathogen reproduction.

Unfortunately, geographical regions predicted to have significant risks associated with climate change are often regions

with lower abilities to adapt to such risks due to technological and economic resource constraints (Hoffmann, 2011). In developing countries, national program research to help mitigate plant diseases under climate change scenarios – such as development of varieties with stable resistance genes, better vector monitoring and management tools, and improved disease management practices – is often limited. Further, unmonitored range expansions of crops and use of infected seed can result in unanticipated invasions of existing diseases or emergence of new diseases. In both cases, the role of anticipatory research is crucial to alleviate such losses. All the same, developing countries have also shown resilience to climate fluctuations in the past. In the West African Sahel region, rainfall decreases of 25–33% have altered pastoral cultivation and agricultural practices over the years (Adger *et al.*, 2003). Thus, integrating experiential and indigenous knowledge with formal research efforts will be important to manage plant disease under climate change scenarios.

Additional Reading

There are a number of good recent reviews on the subject of climate change and plant disease in addition to those cited above (Chakraborty and Newton, 2011; Eastburn *et al.*, 2011; Gregory *et al.*, 2009; Juroszek and von Tiedemann, 2011; Luck *et al.*, 2011; Newton *et al.*, 2011; Pautasso *et al.*, 2010, 2012; Savary *et al.*, 2011b; Sutherst *et al.*, 2011); this continues to be an active area for synthesis. Reviews have addressed soilborne pathogens, which are generally less studied compared with foliar pathogens but have the potential for particularly strong and potentially surprising responses to climate change (Chakraborty *et al.*, 2012; Garrett *et al.*, 2012; Pritchard, 2011). The effect of climate change on beneficial microbes also merits more attention (Compant *et al.*, 2010). As for forests, plantation production offer challenges because of the long-lived nature of the perennial plant hosts (Ghini *et al.*, 2011).

The inclusion of plant disease and its management in greenhouse gas budgets may support prioritization of management strategies (Carlton *et al.*, 2012; Mahmuti *et al.*, 2009). The complexity of pathogen–host–environment interactions is an important problem for scenario analyses (Garrett *et al.*, 2011; Shaw and Osborne, 2011), and the need for better long-term data sets to validate scenario analyses is an ongoing issue, with some intriguing exceptions (Bearchell *et al.*, 2005; Jeger and Pautasso, 2008). Work is ongoing to develop disease risk assessments at the scales needed for effective prioritization (Savary *et al.*, 2011a; Sparks *et al.*, 2011). The impact of variability in climate patterns, especially extreme events, is an important challenge for scenario analysis for plant disease (Garrett *et al.*, 2013; Rosenzweig *et al.*, 2001; Scherm, 2004; Scherm and van Bruggen, 1994).

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See also: Biotechnology: Plant Protection. Climate Change: Agricultural Mitigation. Climate Change: Animal Systems. Climate Change: Cropping System Changes and Adaptations. Climate Change: New Breeding Pressures and Goals. Climate Change, Society, and Agriculture: An Economic and Policy Perspective. Emerging Plant Diseases. Food Safety: Emerging Pathogens. Food Security: Postharvest Losses. Food Security: Yield Gap. Mathematical Models to Elaborate Plans for Adaptation of Rural Communities to Climate Change. Mineral Nutrition and Suppression of Plant Disease. Pathogen-Tested Planting Material. Plant Disease and Resistance. Plant Health Management: Biological Control of Plant Pathogens. Plant Health Management: Crop Protection with Nematicides. Plant Health Management: Fungicides and Antibiotics. Plant Health Management: Pathogen Suppressive Soils. Plant Health Management: Soil Fumigation

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Climate Change: Animal Systems

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Glossary

Carbon footprint The total GHG emissions caused by an activity or product.

Enteric methane (CH_4) emissions Emissions of the greenhouse gas, methane, from the animal's digestive tract that result from microbial activity. Emissions are greater from ruminant species compared to nonruminant species of livestock.

Global warming potential (GWP) The potential for greenhouse gases (GHG) to trap heat in the atmosphere based on its atmospheric lifetime and radiative forcing.

Life cycle assessment (LCA) An evaluation of a given product's environmental impact over its entire production chain.

Production efficiency Minimizing the inputs (e.g., feed and fossil fuels) and undesirable outputs (e.g., greenhouse gas emissions) required to produce a given quantity of animal product (e.g., pork, beef, and milk).

Introduction

Anthropogenic (human-caused) climate change is both impacting animal agricultural systems and influenced by those systems through emissions of greenhouse gases (GHG). Concurrent with global climatic change, global demand for animal agricultural products (e.g., meat, milk, and eggs) is rising with the growing population and increasing per capita incomes in developing nations. The world population is expected to surpass 9 billion by 2050 and demand for meat and dairy products are expected to increase by 58% and 74%, respectively (Garg, 2012). Consequentially, understanding how our animal systems are impacted by and contribute to climate change needs to be discussed within the context of certain growing demand for animal-derived products. Strategies to adapt and mitigate the impacts of these systems on climate change will be an interdisciplinary challenge that will require the cooperation of farmers and ranchers, researchers, extension educators, regulators, and policymakers. Advancements in animal production to address climate change will be a combination of extending current knowledge, innovative research, and effective dissemination of research findings.

The scientific consensus that human activity is contributing to global climatic change among climate scientists is strong (Oreskes, 2004), with several independent attempts to reconstruct global surface temperatures over the last several thousand years leading to the same conclusion; there has been a clear warming trend in the past century, which has occurred at an unprecedented rate (Mann *et al.*, 2008; Marcott *et al.*, 2013). The major cause for the warming trend is increasing concentrations of GHG in the atmosphere, which has been primarily driven by the combustion of fossil fuels since the beginning of the Industrial Revolution. It has been known for more than 100 years that carbon dioxide (CO_2) influences temperature (Arrhenius, 1896), and along with methane (CH_4) and nitrous oxide (N_2O) forms the major GHG emissions that result from animal systems. However, CO_2, CH_4, and N_2O do not all contribute to warming temperatures equally. Each of these gases has a different radiative forcing, or potential to trap heat in the atmosphere, along with a different atmospheric lifetime, which has led to the creation of global warming potentials (GWP) to standardize the impacts each GHG has on temperature (Seinfeld and Pandis, 2006). The Intergovernmental Panel on Climate Change (IPCC) has established GWP as CO_2 equivalents (CO_2e) on a 100 year timescale for CO_2, CH_4, and N_2O as 1, 25, and 298, respectively, meaning CH_4 has a 25 times greater potential and N_2O has a 298 times greater potential to trap heat in the atmosphere than CO_2 on a 100 year time horizon (Solomon *et al.*, 2007). In addition to the concerns about the rapidly changing climate due to human activity, it is also important to note that GHG play an important role in keeping the global average surface temperature of the Earth in a range which is hospitable to life. If the longwave radiation from the Earth's surface was not partially trapped via GHG in the atmosphere, the global average surface temperature would have been −19 °C, rather than 14 °C as it is today (Le Treut *et al.*, 2007).

The impacts of climate change on animal agriculture are expected to be far reaching. Animals will be directly impacted by increased temperatures, which can lead to higher incidence of heat stress resulting in decreased productivity (e.g., decreased milk yield and growth rates), and in periods of prolonged increased temperatures, higher death losses occur (Mader *et al.*, 2009; St-Pierre *et al.*, 2003). Beyond the direct physiologic impacts on animals, climate change will likely impact animal feed crop quality and yield, commodity prices, disease and pest prevalence and distribution, and lead to a higher incidence of extreme weather events (e.g., floods and heat waves) (Craine *et al.*, 2010; Walthall, 2012; Wheeler and Reynolds, 2012). For the purpose of this article, adaptation of animal systems to climate change will not be discussed, but rather the sources of GHG emissions and GHG emission mitigation opportunities will be explored. However, as climate change and variability impact animal productivity, GHG mitigation techniques discussed in later sections of this article will be related in part to the adaptation of animal systems to climate change.

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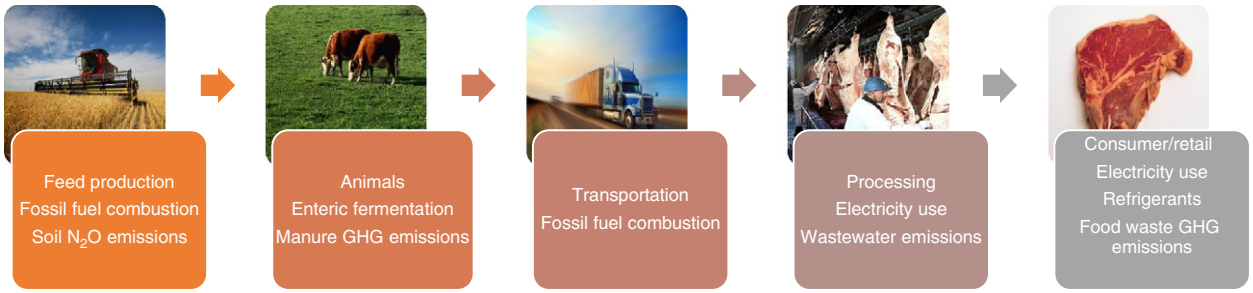


Figure 1 Example of the phases of production and greenhouse gases (GHG) emission sources that would be accounted for in an Life Cycle Assessment (LCA) of beef's GHG emissions or carbon footprint. Methodologies and sources considered often vary from industry to industry and analysis to analysis, which can lead to challenges when attempting to compare across LCA.

Sources of Greenhouse Gas Emissions from Animal Systems

Sources of GHG emissions from animal agriculture systems can be broken down as either direct or indirect GHG emissions. Direct GHG emissions are those that occur directly from the animals (i.e., enteric CH_4 emissions from ruminants) and its waste (GHG emissions emitted from manure). Indirect GHG emissions can be defined as those that occur from processes and activities that are ancillary, but essential for the production of animal products. Indirect sources include on-farm activities (e.g., GHG emissions from farm equipment and fertilizer application) and GHG emissions associated with activities both pre- and postfarm gate (e.g., GHG emissions associated with the production of purchased feedstuffs and transportation of animal products). For the discussion of indirect GHG emission sources, the term prefarm gate will refer to all CO_2e emissions resulting from activities before the animal product (i.e., fresh raw milk, eggs, live cattle, sheep, pigs, and poultry) leaves the site of production (i.e., the farm, ranch, feedlot, etc.) bound to a processing facility. Postfarm gate will refer to CO_2e emissions resulting from activities after the animal product has left the site of production.

An accounting system that considers direct and indirect emissions is consistent with Life Cycle Assessments (LCA) that account for GHG emissions along the entire production chain of a given product. The final inventory for all GHG emissions along the production chain would then be divided by the total product produced to calculate a metric of GHG emissions in CO_2e per unit of product (e.g., CO_2e per kilogram of milk), also referred to as the functional unit (Thoma *et al.*, 2013). However, by analysis, variations in GHG emission inventory infer that the scope and scale of animal agriculture product LCA are not homogeneous. Therefore, comparisons across LCA can at times lead to inappropriate comparisons and conclusions if methodological differences are ignored. Some LCA do not consider the entire product chain, but rather part of the chain (e.g., the GHG emission to the farm gate, which would not include processing, transportation, retail, etc.). Additionally, an LCA may be global, national, or subnational (i.e., a US state) in its scale, which makes extrapolating conclusions from an LCA at one scale to another inappropriate (Pitesky *et al.*, 2009), which is due to the disparate management strategies, climates, animal types, feedstuffs, etc. used in different regions around the world (Place and Mitloehner, 2012). See **Figure 1** for a beef industry example of what processes and segments of the animal agriculture product chain are considered for LCA of GHG emissions.

Direct Sources

Enteric

Enteric CH_4 emissions are one of the major sources of GHG emissions from ruminants (e.g., cattle, goats, and sheep) agriculture systems (Pitesky *et al.*, 2009; Thoma *et al.*, 2013). The production of CH_4 represents a loss of the gross energy (GE) value of the animal's feed, which depending on the diet and level of intake can be a loss of 2–12% of dietary GE for ruminants (Johnson and Ward, 1996). Enteric CH_4 emissions from nonruminant animals do occur from hindgut fermentation processes, but are minor compared to ruminants, with CH_4 emissions typically representing less than 1% of dietary GE for pigs and lower still for poultry (Christensen and Thorbek, 1987; Jørgensen, 2007; Wang and Huang, 2005).

When a ruminant animal consumes feed (e.g., forages and grains), the feed nutrients will undergo fermentation processes resulting in the production of volatile fatty acids (VFA) that are absorbed through the rumen wall and metabolized by the animal, during this process, CO_2 as well as hydrogen (H_2) is produced. Methane emissions do not result directly from the fermentation processes, but rather occur from methanogenesis carried out by methanogenic archaea residing within the rumen. The most prevalent substrates for methanogenesis in the rumen are H_2 and CO_2 (Janssen and Kirs, 2008), with methanogens reducing CO_2 to CH_4 with H_2 summarized in the following equation:

$$CO_2 + 4H_2 \rightarrow CH_4 + 2H_2O$$

Other substrates used in methanogenesis include formate, methanol, and acetate (Russell, 2002). With CO_2 being abundant in the rumen due to the continuous fermentation processes, the pool of H_2 available is one of primary determinants for the total yield of CH_4 from rumen methanogenesis and many mathematical models predict rumen CH_4 production by modeling the rumen H_2 balance (Ellis *et al.*, 2008). For further detailed information, Janssen (2010) conducted an excellent in-depth review of the influence of H_2 on rumen CH_4 formation. The rumen partial pressure of H_2 gas is kept very low through the action of methanogens, which is

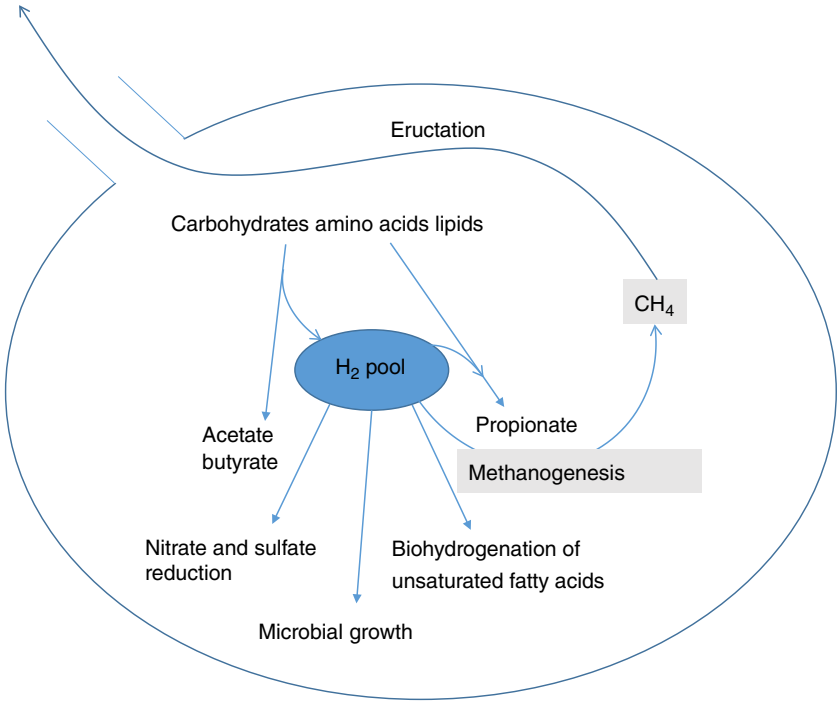


Figure 2 A simplified model of the rumen processes that determine enteric CH_4 emissions from ruminant livestock species.

important as H_2 acts as a feedback inhibitor to fermentation (Immig, 1996). Fermentation pathways that lead to the net production of H_2 include the production of the VFAs acetate and butyrate, while the production of propionate leads to a reduction in H_2 available for methanogenesis (Ellis *et al.*, 2008). The proportions of each of these VFA in relation to total rumen VFA production is greatly determined by diet, with diets higher in fermentable carbohydrates (i.e., starch) yielding more propionate than diets high in fiber (Johnson and Johnson, 1995). Alternative H_2 sinks include the biohydrogenation of unsaturated fatty acids, microbial growth, nitrate reduction, and sulfate reduction (Ellis *et al.*, 2008; Johnson and Johnson, 1995). A simplified model of rumen fermentation and the major H_2 sinks and sources is shown in **Figure 2**.

For animal systems, respiratory CO_2 emissions are usually not counted toward net CO_2e emissions, as it is assumed that the CO_2 released as the result of animal metabolism is equal to the CO_2 used by plants in during photosynthesis, which the animals have consumed (Steinfeld *et al.*, 2006).

Nonenteric

The predominant nonenteric direct GHG emissions source both from ruminant and nonruminant animal agriculture systems (e.g., swine and poultry) is manure (i.e., urine and feces mixed). Manure GHG emissions typically occur from manure storage systems and land-applied manure. The primary GHG emissions from stored manure are CH_4 and N_2O. Fresh manure (e.g., manure on the floor of animal housing areas) results in little or no CH_4 or N_2O emissions (Shaw *et al.*, 2007; Sun *et al.*, 2008). For land-applied manure, N_2O is the major GHG emitted (more discussion in the Sections Indirect Sources and Mitigation). As with respiratory CO_2 emissions from livestock, CO_2 emissions from manure are considered carbon neutral.

Like in the rumen, emissions of CH_4 occur from manure stored in anaerobic or oxygen-free conditions. However, unlike the rumen that has digesta passage rates of upto 20% per hour, manure storage systems often allow fermentation processes to occur undisturbed for weeks or months (Russell, 2002). Consequently, methanogens that can utilize VFAs for methanogenesis can thrive, but in the rumen environment these species are virtually nonexistent due to the high rates of passage and removal of VFAs through the rumen wall (Russell, 2002). Additionally, manure storage systems are typically not kept within a narrow temperature range as in the rumen, and this temperature variability influences the metabolic activity of the microbial populations. Hence, in Northern latitudes, CH_4 emission rates are typically higher during warm summer months than in winter months from manure storage systems (Husted, 1994; Park *et al.*, 2006).

Hydrolysis, fermentation (and acetogenesis), and methanogenesis are the three major steps in CH_4 formation from manure (Gilroyed *et al.*, 2011), which is shown in the simplified equation below:

$$\text{Organic polymers} \overset{\text{Hydrolysis}}{\Longrightarrow} \text{Monomers} \Longrightarrow$$

$$\text{Fermentation/acetogenesisVFAs (acetate)} \overset{\text{Methanogenesis}}{\Longrightarrow} CH_4$$

Organic polymers include carbohydrates, proteins, and lipids. Besides storage conditions and management, the nutrient content of animal manure can influence the CO_2e emission potential of manure. The nutrient content and digestibility of

the animal's diet can impact the carbon (C) and nitrogen (N) availability in the manure and the subsequent CH_4 and N_2O emissions resulting from the manure (Külling *et al.*, 2003).

Nitrous oxide emissions primarily occur from bacterial denitrification processes; however, N_2O emissions also occur from nitrifying bacteria and ammonia oxidizing bacteria (Bremner, 1997). The denitrification process reduces nitrate (NO_3^-) to dinitrogen gas (N_2), which is environmentally benign and composes 78% of the Earth's atmosphere. One of the intermediate products of the pathway is N_2O, hence emissions of N_2O can result from denitrification. Most of the N in fresh manure is in the form of organic N (in a carbon-containing compound, like amino acids) or ammonium (NH_4^+). Thus, very little NO_3^- is present for denitrification. However, if microbial nitrification processes occur, which require aerobic conditions to oxidize NH_4^+ to NO_3^-, the potential for N_2O emissions from the manure will greatly increase. Often, manure storage conditions do not allow for significant enough oxygen presence for nitrification to occur. Such storage systems include anaerobic lagoons and anaerobic digesters, and consequently N_2O emissions from these systems are typically low (Chadwick *et al.*, 2011). However, solid manure storage systems and compost bedded pack systems where manure is used as a bedding source for animals and is periodically aerated can allow for the necessary nitrification and denitrification microbial processes to occur that result in N_2O emissions (Rotz, 2004).

For extensive animal systems (i.e., where animals are primarily housed outdoors) manure is unmanaged and distributed where animals defecate and urinate in the pasture or rangeland. Emission factors for N_2O emissions in g of N_2O–N per kilogram of N excreted from urine and dung patches are often higher than manure spread on croplands for fertilizer due to the higher N concentration in the patches, which encourages N_2O emissions (Mosier *et al.*, 1998). Additionally, N_2O emission potential per unit of N excreted is higher for urine patches compared with feces patches, as most N in urine is excreted as urea (vs. organic N in feces), which is typically rapidly hydrolyzed to NH_4^+ and then available to undergo nitrification–denitrification processes (Oenema *et al.*, 1997).

Indirect Sources

Prefarm gate

Indirect prefarm gate emissions include GHG emissions released as a result of feed production for animals (e.g., N_2O emissions from cropland soils and CO_2 emissions from fossil fuel combustion in farm equipment) and on-farm electricity use. Crop production that is destined for animal consumption is typically fertilized either with animal manure or synthetic fertilizer. Nitrous oxide emissions will occur from soil in cropland from the same microbial processes as previously discussed. In addition to the availability and form of N in the soil, N_2O emissions are influenced by the amount of soil C, soil moisture conditions, pH, and temperature (Smith *et al.*, 1998). Emissions of N_2O will be higher with increasing soil C availability, water content, temperature, and pH (Bouwman, 1996).

Methane emissions from soil used for livestock crop production are virtually nonexistent in well drained soils, and CH_4 uptake by soil can occur after tillage (Omonode *et al.*, 2007). Soil CO_2 emissions can occur during the tillage of soil as a result of aerobic decomposition of organic matter; however, plants typically assimilate more C through photosynthesis than C is released from plant and soil respiration processes (Chianese *et al.*, 2009). In assessments of animal system GHG emissions, long-term C balances of croplands are assumed to be zero as the C assimilated by plants or added to the system (e.g., C from manure) will be equal to the C leaving the cropland in the form of feed biomass and CO_2e emissions (Rotz *et al.*, 2010). However, if previously tilled cropland is shifted into permanent grasslands, there can be a net reduction in CO_2e emissions from an animal system due to C sequestration, as long as the grassland is not tilled in the future (Rotz *et al.*, 2009).

Indirect CO_2 emissions occur from fossil fuel combustion in farm equipment, and from electricity generation in power plants that burn fossil fuels, such as coal. Although fossil fuel combustion is not a large prefarm gate emission source for animal systems, the total contribution of these sources to total CO_2e emissions per unit of product depends on the animal agriculture sector considered. For example, a low input grass finished beef system would likely have a lower proportion of its total CO_2e emissions per unit of product originating from fossil fuel use than an intensively managed dairy farm, where cattle are housed in mechanically ventilated barns and are milked twice per day by a milking system using energy off the electricity grid. Furthermore, the contribution of indirect prefarm gate emissions can vary within a sector of animal agriculture based on the management systems used and the geographic location of the farm, which influences climate and the crops that can be grown. Rotz *et al.* (2010) used the DairyGHG model to conduct a partial LCA (to the farm gate) of five simulated US dairies in Pennsylvania and California of different herd sizes (ranging from 60 to 2000 cows) and management strategies (grazing, confined, and drylot). Fuel use on-farm for tractors and other farm equipments ranged from 5.8% to 9.8% of the net CO_2e emissions from the simulated dairy farms. Secondary CO_2e emissions were also considered, which included the GHG emissions from the production of fuel, electricity, fertilizer, machinery, pesticide, and plastics used for feed production, for managing the animals, and manure management. The secondary emissions were found to be 18.9–25% of net CO_2e emissions of the five simulated dairies to the farm gate, which may be higher than some estimates, as the authors included CO_2 sequestration from cropland (Rotz *et al.*, 2010). The simulated 60 cow grazing dairy in Pennsylvania had a lower proportion of its total CO_2e emissions per kilogram of energy-corrected milk coming from on-farm fossil fuels and secondary sources compared with the other systems, which would be expected due to the lower inputs (e.g., less machinery use, electricity use, etc.) of the system (Rotz *et al.*, 2010).

Postfarm gate

The emissions that occur postfarm gate include emissions from fossil fuel burning during transportation, refrigeration of products (leakage of refrigerants that have high GWPs), and

energy usage during processing and for food preparation at retail, restaurants, and in consumer homes. Although there is often a perception that transportation is a large part of the carbon footprint of food (i.e., the total CO_2e emissions associated with the food product) and purchasing local food is prescribed as a solution (e.g., the locavore movement), the contribution of transportation to the total CO_2e emission per unit of animal product is often quite small (Capper, 2011b). Thoma *et al.* (2013) found that 72% of CO_2e emissions per kilogram of milk produced in the US occurred prefarm gate whereas transportation accounted for 7.7%. Ledgard *et al.* (2011) found 80% of CO_2e emissions per kilogram of lamb meat occurred prefarm gate for New Zealand lamb production, whereas only 5% was attributed to transportation, despite the assumption in the LCA that the lamb was exported to the UK.

The GHG emissions prefarm gate are predominately CH_4 and N_2O emissions, whereas postfarm gate GHG emissions are dominated by CO_2 and refrigerant gas emissions. Leakage of refrigerant gases (mainly hydrofluorocarbons) is a significant source of GHG emissions from the postfarm gate segment of the animal system production chain, as these gases have high GWP that depending on the gas can be several hundred or several thousand times that of the 100 year CO_2 GWP (Solomon *et al.*, 2007). In the past several decades, refrigerant leakage rates have been declining (Calm, 2002); however, supermarket average leakage rates are still estimated to be approximately 25% (EPA, 2009). Additionally, CO_2e emissions result from the production of packaging materials for animal products (e.g., boxes, cartons, and containers) that are used during processing, transportation, and retail.

Food waste at the retail, restaurant, and consumer stages of the supply chain of animal products is another important source of CO_2e emissions postfarm gate. A 1997 USDA Economic Research Service study found that 32% of edible dairy products, 31% of edible eggs, and 16% of edible meats (including poultry and red meats) were wasted from the retail, foodservice, and consumer phases of the food supply chain (Kantor *et al.*, 1997). In the US, food waste composes 20% by weight of municipal solid waste entering landfills where it can be a source of CH_4 emissions (EPA, 2013). In addition to the CO_2e emissions that directly result from food waste in landfills, the embedded or embodied energy of food waste can be substantial. Embodied energy of a given product or service is calculated as the total direct and indirect energy required for its production (Costanza, 1980). Cuellar and Webber (2010) estimated that the embodied energy in wasted food represented approximately 2% of US annual energy consumption in 2007.

Mitigation

Metrics for Mitigation of Greenhouse Gas Emissions from Animal Systems

One faces a paradox of mitigating the CO_2e emissions from human activity, including animal systems while meeting the nutritional and material needs of a growing world population during climatic change and variability. Meeting these challenges will require a nuanced analysis and understanding of the implications of policy changes, and dedicated efforts to make concrete, quantifiable on-the-ground modifications that result in lower global CO_2e emissions and increased carbon sequestration. Critical to these efforts is having the appropriate CO_2e emissions measurement system that takes into account the productivity or usefulness of the activity or industry. To this end, CO_2e emissions per unit of output for animal systems is an appropriate way to assess the impacts of animal systems on climate change while recognizing the nutritional benefit of those systems.

Direct Sources Mitigation Opportunities

Enteric

Mitigation of enteric CH_4 emissions is important to ruminant systems as these emissions are one of the largest sources when considering CO_2e emission prefarm gate or the entire product chain to the consumer. Thoma *et al.* (2013) found that 25% of CO_2e emissions per kilogram of milk were from enteric CH_4 emissions when evaluating the entire 'cradle-to-grave' production chain of US fluid milk production. Beauchemin *et al.* (2010) conducted a whole-farm GHG emissions LCA of western Canadian beef production for an 8-year period using Holos, a whole-farm model developed by Agriculture and Agri-Food Canada. Enteric CH_4 emissions were found to account for 63% of the whole farm emissions of the beef production system that included a cow-calf phase, a feedlot finishing phase, and GHG emissions associated with crop production and emissions from pasture (Beauchemin *et al.*, 2010). The same model was used to simulate whole farm GHG emissions from dairy production in eastern Canada for a 6-year period, and it was found that enteric CH_4 accounted for 48% of total CO_2e emissions (Mc Geough *et al.*, 2012). Consequently, mitigating enteric CH_4 emissions per unit of production for ruminant systems would be one of the most impactful ways to mitigate GHG emissions from ruminant meat and milk production systems.

Dietary manipulation and the use of feed additives are the major ways enteric CH_4 emissions can be directly reduced per animal. Specifically, enteric CH_4 emissions can be impacted by changing the diet's forage-to-concentrate ratio, digestibility, and lipid content. Feed additives that can potentially impact enteric CH_4 emissions include alternative hydrogen sinks (e.g., nitrates and sulfates), ionophores, tannins, saponins, and essential oils. Additionally, attempts have been made to eliminate protozoa from the rumen (known as defaunation) to reduce CH_4 emissions as many ciliate protozoa produce H_2 through their metabolic processes and methanogens are often closely associated with protozoa in the rumen (Finlay *et al.*, 1994). Defaunation has been shown to reduce CH_4 emissions by 20% in sheep (Morgavi *et al.*, 2008); however, the research on defaunation's impacts in live animals is scarce and due to the impractical methods currently available to defaunate a ruminant, commercial adoption of the practice seems unlikely (Hegarty, 1999).

Altering the forage-to-concentrate ratio and the type and digestibility of the carbohydrates of the diet impacts enteric CH_4 emissions by shifting fermentation pathways from acetate production to propionate production. As discussed, higher fiber diets (i.e., high forage-to-concentrate ratio diets) yield

higher proportions of acetate and higher enteric CH_4 emissions. Consequently, ruminants fed diets high in fermentable carbohydrates (e.g., finishing beef cattle in feedlots fed a 75–90% grain diet) produce lower CH_4 emissions per unit of feed intake compared to ruminants fed high forage diets (e.g., grazing cattle and dairy cattle in confinement systems fed 50–60% forage diets). Aguerre *et al.* (2011) demonstrated the impact of the forage-to-concentrate ratio on CH_4 emissions from dairy cattle fed diets from 47% upto 68% forage and found a linear increase in CH_4 emissions per cow per day and per kilogram of dry matter intake with increasing dietary forage percentage.

However, simply decreasing forage consumption of all ruminants worldwide is not a viable, sustainable CO_2e emission mitigation solution for ruminant production systems. Diets very high in fermentable carbohydrates can lead to rumen acidosis resulting in health issues, such as liver abscesses and laminitis (an inflammation of the laminae of the hoof that cause of lameness) (Brent, 1976; Kleen *et al.*, 2003; Owens *et al.*, 1998). However, the efficiency of gain (i.e., amount of feed required for 1 kg of body weight gain) when feeding diets high in fermentable carbohydrates has historically been more economically profitable than high forage diets for ruminant meat animal systems during the finishing phase (the last period of the animal's life before slaughter). Subsequently, most beef cattle in North America are finished in feedlots where they consume high grain diets (e.g., 75–90% corn or barley). However, in recent years due to sustained increases in commodity prices, the profitability of such feeding systems has suffered. Furthermore, ruminants' ability to utilize forages and byproducts (e.g., distiller's grains, cottonseed, citrus pulp, and almond hulls) is a form of valuable nutrient recycling, particularly when considering cellulose (Oltjen and Beckett, 1996). Cellulose is the most abundant organic (carbon-containing) compound on Earth; however, it is indigestible to humans and large-scale, commercial cellulosic ethanol production for use in internal combustion engines is yet to become a reality. Therefore, one of the primary ways humans are able to capture the energy potential of the C fixed via photosynthetic processes of plants is through ruminants and their symbiotic relationship with the microbial populations residing in their digestive tracts. In the context that agriculture at its core is about transforming nutrients and natural resources of low value to humans to higher value food and fiber products, the ability of ruminants to use low protein quality, high fiber feedstuffs and convert them into high quality protein cannot be discounted if we are to meet growing human nutritional needs and should be weighed against the impacts of enteric CH_4 emissions from ruminants.

Lipids included in the diets of cattle has been shown to reduce enteric CH_4 emissions per animal per day (Beauchemin *et al.*, 2009; Odongo *et al.*, 2007), though some of the reduction can be attributed to decreases in intake and digestibility (Beauchemin and McGinn, 2006; Beauchemin *et al.*, 2007). Ruminant diets are typically low in fat ($<5\%$) and increasing dietary fat concentration above 5–6% of the diet can negatively impact rumen fermentation and decrease feed intake (Odongo *et al.*, 2007). Lipids and more specifically, unsaturated fatty acids, can reduce CH_4 emissions via two ways. First, unsaturated fatty acids are saturated by rumen bacteria by a process known as biohydrogenation, which requires H_2 to be used, diverting it from potentially being used for methanogenesis (Ellis *et al.*, 2008). The second, more impactful way unsaturated fatty acids can influence enteric CH_4 emissions is through their toxic impacts directly on methanogens and on H_2 producing bacteria and protozoa (Janssen, 2010).

Alternative hydrogen sinks of nitrate and sulfate reduction can reduce CH_4 emissions because both sulfate and nitrate reducing bacteria compete with methanogens for H_2. In fact, both these processes are more energetically favorable than methanogenesis, but sulfate and nitrate concentrations are often low in ruminant diets (Ellis *et al.*, 2008; van Zijderveld *et al.*, 2010). However, widespread adoption of sulfates and nitrates in ruminant diets currently seems limited in its potential as a enteric CH_4 emissions mitigation technique due to the toxic impacts of some of the intermediates of nitrate and sulfate reduction to the animal (Ellis *et al.*, 2008; van Zijderveld *et al.*, 2010).

Ionophores, such as monensin and lasalocid, can potentially reduce CH_4 emissions by targeting H_2 producing bacteria and protozoa and giving a competitive advantage to propionate producing bacteria, thereby reducing H_2 available for methanogenesis (Russell and Houlihan, 2003). Ionophores are antimicrobials typically fed to cattle to reduce the incidence of rumen acidosis and bloat, and improve feed efficiency (Duffield *et al.*, 2012; Duffield *et al.*, 2008). Past experiments with cattle have shown variable results with ionophores, with some studies demonstrating reductions in CH_4 emissions (Guan *et al.*, 2006; Odongo *et al.*, 2007), while others have not (Grainger *et al.*, 2010; Hamilton *et al.*, 2010). A meta analysis of monensin's impact on CH_4 emissions from beef and dairy cattle found that monensin had a more consistent reduction of CH_4 emissions from beef cattle (−19 g CH_4 per day), which was attributed to the higher concentration of monensin in beef diets (mean dose 32 mg kg^{-1} of dry matter intake) compared to dairy diets (mean dose of 21 mg kg^{-1} of dry matter intake) (Appuhamy *et al.*, 2013). Appuhamy *et al.* (2013) concluded that due to the higher feed intake of dairy cattle, higher doses of monensin may need to be fed to reduce CH_4 emissions, which may be a challenge as the maximum US Food and Drug Administration (FDA) approved daily dose of monensin for dairy cattle is 660 mg day^{-1} or 24 g kg^{-1} of dry matter (FDA, 2006). As some high producing dairy cattle can consume 30 kg or more of dry matter per day, an increase in the FDA maximum dose may be necessary to achieve widespread CH_4 emission reductions from US dairy cattle. Beyond the US, ionophores are restricted in their use or banned in some nations (i.e., the European Union), which limits their global enteric CH_4 emissions mitigation potential.

Tannins, saponins, and essential oils are plant compounds or extracts that have garnered interest as potential enteric CH_4 emission mitigation feed additives that could be considered natural alternatives to antimicrobials. However, with all of these plant extracts little research has been done *in vivo*, with many of the studies that have not showing much promise for mitigation (Beauchemin *et al.*, 2007; Beauchemin and McGinn, 2006; Holtshausen *et al.*, 2009), and few showing a

reduction in enteric CH_4 emissions from ruminants (Mao *et al.*, 2010). A more thorough investigation of these plant compounds' effects in ruminants may be warranted, along with analyses of their cost effectiveness, before they are recommended for feeding as a viable enteric CH_4 emission mitigation strategy.

Attempts to establish acetogens (microbes that use CO_2 and H_2 to create acetate rather than CH_4) in the rumen have been made; however, these organisms cannot outcompete methanogens for H_2, which leaves little potential for their use in mitigating enteric CH_4 emissions from ruminants (Ellis *et al.*, 2008; Lopez *et al.*, 1999). Additionally, attempts have been made to vaccinate ruminants against methanogens with mixed results on enteric CH_4 emissions (Williams *et al.*, 2009; Wright *et al.*, 2004), yet the concept holds promise if further research and development of vaccines is pursued (Krause *et al.*, 2013).

Manure storage

Capturing and reducing GHG emissions through manure storage design and manure treatment offers opportunities to mitigate GHG emissions from animal systems. If manure is stockpiled in solid form (>15% dry matter) with little or no management or treatment, the GHG emission potential from the manure is high (Gilroyed *et al.*, 2011). Manure treatments can reduce GHG emissions, as well as address pathogen load and odors from the manure, which are other areas of concern for animal systems. For anaerobic manure lagoons where manure is stored in a liquid form (<7% dry matter), adding a cover to the lagoon can capture the GHG emitted. By flaring off the accumulated gas containing CH_4, more of the total C emissions are oxidized to CO_2, which reduces the net CO_2e emissions from animal manure. Additionally, covers can allow manure surface crusts to develop (by not being disturbed by precipitation), which some research has suggested allow methanotrophs (organisms that oxidize CH_4 to CO_2) to develop (Clemens *et al.*, 2006; Petersen *et al.*, 2005).

Anaerobic digestion of animal manure has increased in popularity in recent years as a way for farmers to create an on-farm energy source through the production of biogas, which consists of primarily CH_4 (60–70%) and CO_2 (30–40%) (Cantrell *et al.*, 2008). The biogas can then be further refined for use in equipment or combusted to generate electricity that can be used on-farm or put on the grid, which can offset fossil fuel use in the animal system (Asgedom and Kebreab, 2011). However, costs, both for construction and operation, can be a prohibitive factor that can keep animal agricultural operations from adopting anaerobic digestion of manure. For individual operations, the costs can be difficult to overcome, though through public policy efforts it is possible to increase anaerobic digestion capacity of animal manures. The European Union has set a goal of 25% of its energy use to come from renewable sources by 2020, which can encourage further development of anaerobic digestion of animal manure that is already well underway in nations like Germany and Denmark (Holm-Nielsen *et al.*, 2009). In the US, there have been efforts to have utility customers pay a premium for electricity generation, with the premium allowing dairies with anaerobic digesters to cover construction and operation costs (Wang *et al.*, 2011). An evaluation of the program found that grants to offset the initial cost of constructing the digester system were critical for its success, as was sustained cooperation between farmers, the community, utility companies, and government (Wang *et al.*, 2011).

Composting manure is a treatment for solid manures that encourages aerobic decomposition of organic matter, which can reduce odors and pathogen load (Gilroyed *et al.*, 2011). However, composting's potential to reduce CO_2e emissions seems limited or nonexistent (Hao *et al.*, 2004; Hao *et al.*, 2001), which makes it a manure treatment practice that cannot be currently recommended as a way to reduce CO_2e emissions from animal systems (Asgedom and Kebreab, 2011).

Altering the diets of the animals to reduce CO_2e emissions from manure storage systems is a strategy that has tradeoffs and mixed results. In general, the CH_4 emission yield of manure is greatly determined by the manure's volatile solids content, which generally is inversely related with the amount of fermentable carbohydrate in the diet (Hashimoto *et al.*, 1981; Møller *et al.*, 2004). For swine, diets lower in fermentable carbohydrates may result in lower CH_4 emissions from manure; however, the practice can increase the potential of ammonia emissions due to a higher manure pH, which is another undesirable gaseous emission from animal agriculture (Aarnink and Verstegen, 2007).

Production efficiency

After the discussion on ways to reduce GHG emissions via reducing CO_2e emissions per animal per day or from manure per day, other opportunities exist to reduce CO_2e emissions per unit of product through production efficiency. Production efficiency for animal systems can be defined as minimizing the inputs (e.g., feed and fossil fuels) and undesirable outputs (e.g., GHG emissions) required to produce a given quantity of animal product (e.g., pork, beef, and milk) (Place and Mitloehner, 2010). Capper and Bauman, 2013 conducted an excellent review of the role productivity plays on the environmental sustainability that can be referenced for further details. Improved production efficiency can be achieved through increasing productivity (e.g., milk yield and growth), optimizing the productive lifetime of individual animals and populations, and minimizing waste. Production efficiency should not come at the cost of animal health and well-being, as reducing environmental impacts per unit of animal product at the cost of shirking the social responsibility of humans toward animals is not a sustainable solution. However, there is often much overlap between enhancing animal health and well-being and lowering CO_2e emissions per unit of product. Additionally, production efficiency gains can be made within all animal systems by a variety of methods, and therefore, can be seen as a one-size-fits-all solution with a long list of customizable answers depending on the operation, industry, location, etc.

Further explanation of the potential of production efficiency to mitigate CO_2e emissions from animal systems per unit of product can be gained through historical comparisons. Capper *et al.* (2009) compared US dairy production in 1944 with the 2007 system and found a 63% reduction in the CO_2e emissions required to produce 1 billion kilogram of milk for the 2007 system. A similar comparison of the 1977 US beef production system to the 2007 system found a 16.3%

reduction in CO_2e emission per 1 billion kilogram of beef produced for the 2007 beef system (Capper, 2011a). In both industries, reductions in carbon footprint were largely achieved by reducing the number of animals required to produce a given quantity of animal product, which was made possible by advancements in genetics, nutrition, and management. Similarly, when comparing animal systems across nations, differences in those systems production efficiency are translated into different carbon footprints. Gerber *et al.* (2011) demonstrated how carbon footprints can be reduced by diluting out CO_2e emissions across a larger volume of production by conducting a global LCA for dairy production disaggregated by nation. For the 155 countries analyzed, a strong relationship between CO_2e emissions per kilogram of fat- and protein-corrected milk (FPCM) and milk yield per cow was found, with reductions from 10 to 12 kg CO_2e per kilogram FPCM when annual milk yield per cow was 500 kg FPCM to 2 kg CO_2e when milk yield per cow increased to 3000 kg FPCM per year (Gerber *et al.*, 2011).

Continued improvements can be achieved by optimizing an animal's productive life, which impacts the total inputs required to produce a given quantity of animal product. For example, for female animals (e.g., sows and beef cows) that are producing the next generation of food animals, extending the time between parturitions beyond the time necessary (e.g., due to reproductive failure), increases the amount of feed, water, electricity (if housed in confinement), etc. required to maintain those animals. Additionally, extending the time to first parturition for females (e.g., the age at first calving for a dairy heifer) beyond an ideal of what could be achieved with superior genetics, nutrition, and management, increases the animal's lifetime requirements for maintenance inputs. Time-to-slaughter is another example. If meat animals have slow growth rates due to poor genetics, management, environmental conditions, or nutrition, those animals will require a longer life to reach an ideal slaughter weight and composition compared to animals with high growth rates. Consequentially, the slower growing animals will have higher input requirements to create the same amount of product for human use and consumption. The CO_2e emissions associated with those inputs can be viewed as a mitigation opportunity if the productive lifetime and productivity of animals can be optimized. Optimized, rather than maximized, is key. A point of diminishing returns, which would vary by species, management system, and location, will exist both economically and in terms of animal welfare. Health issues associated with productivity (i.e., growth rate) and animal welfare are apparent when examining the broiler industry. Through better nutrition and breeding for faster growth rates and improved feed conversion efficiency (reducing the feed required for 1 kg of growth), a broiler in 2001 took one-third of the time to reach 1.8 kg in weight (32 vs. 101 days) and did so with 3 times less feed (Havenstein *et al.*, 2003). With the gains in efficiency, CO_2e emissions per unit of product (i.e., kg of chicken) have likely declined from the production phase of the entire poultry production chain over time. However, the rapid early growth that these birds achieve has led to an increased incidence of metabolic disorders, including skeletal problems that can lead to deformities and decreased mobility in the later stages of the animals' lives (Angel, 2007). The break point at which a cost to animal welfare overcomes any continued improvements in production efficiency will be influenced by subjectivity of how the welfare of animals is defined and the value animal welfare carries, which will likely change over time and be influence by the society's culture where the animal production system is located.

However, in many cases animal health and well-being are strongly positively related to production efficiency and offer potential opportunities to simultaneously address animal welfare issues and CO_2e emissions of animal systems. The potential for improvement in these issues can be seen in the variability of their prevalence across animal agriculture operations. The dairy industry experiences high rates (30–50%) of clinical lameness in lactating cows, as has been observed on dairy farms in Canada, the UK, and the US (Barker *et al.*, 2010; von Keyserlingk *et al.*, 2012). However, the rates of lameness across farms in these studies ranged widely, which suggests management, facility design, etc. could be altered in those farms with high rates of clinical lameness to achieve the rates seen in the herds of their contemporaries. Lameness can reduce milk yield and productive lifetime of dairy cows (Bicalho *et al.*, 2007; Bicalho *et al.*, 2008), and reduce the productive lifetime of sows (Anil *et al.*, 2009), which represents a potential opportunity to reduce inputs, and their associated CO_2e emissions, from the dairy and swine industries if lameness rates can be improved.

Additionally, heat stress in livestock and poultry is an animal well-being issue that is interrelated with the production efficiency of animal systems. Heat stress occurs when an animal's ability to dissipate heat to its environment is overwhelmed. Heat stress can have far reaching negative impacts on animal growth, lactation, reproduction, and lead to higher rates of mortality (Lin *et al.*, 2006; West, 2003; Wettemann & Bazer, 1985). Often these impacts of heat stress are thought of with regard to their economic impact on animal agriculture industries. St-Pierre *et al.* (2003) modeled the impact of heat stress in the US and found that annual losses to the dairy, beef, swine, and poultry industries cost US$1.7 to US$2.4 billion annually due to decreased productivity and reproduction, and increased mortality. Presumably, the inputs required in all of these industries and the CO_2e emissions associated with those inputs are substantially higher during heat stress to produce a given quantity of animal product. As climate change leads to higher average global temperatures, strategies to mitigate heat stress' impacts on livestock and poultry should be viewed as a way to address both mitigating CO_2e emissions per unit of product and adapting animal systems to climate change.

Indirect Sources Mitigation Opportunities

Opportunities exist both pre- and postfarm gate to mitigate indirect CO_2e emissions from animal systems. Prefarm gate, reducing emissions from feed production represents a major area of opportunity, with soil N_2O emissions from manure and fertilizer application contributing a significant portion of prefarm gate emissions (Ledgard *et al.*, 2011; Rotz *et al.*, 2010; Thoma *et al.*, 2013). Soil N_2O mitigation opportunities revolve around ways to better match, spatially and

temporally, plant N needs with the N supplied. The timing and method of fertilizer and manure applications are important drivers dictating the amount of manure or fertilizer N that plants will uptake versus the N lost to the environment as N_2O emissions. Avoiding fertilizer and manure applications when soils are wet, conducting frequent soil testing to determine agronomic N application rates, and splitting applications to match when plants require N for growth can reduce the potential for N_2O emissions from feed production (Dalal *et al.*, 2003; Millar *et al.*, 2010). Additionally, nitrification inhibitors have been proposed as a way to mitigate N_2O emissions. By inhibiting the conversion of NH_4^+ to NO_3^-, nitrification inhibitors act to limit the amount of NO_3^- available for denitrification and potentially reduce N_2O emissions. Di and Cameron (2003) demonstrated that N_2O emissions from urine patches in grazing systems could be reduced by the application of a nitrification inhibitor; however, the practicality and economics of such a practice likely prevent its widespread adoption (Rotz, 2004). In general, more research on the effectiveness and the causes of variation on N_2O emissions of nitrification inhibitors is needed before they can be recommended as a CO_2e emission mitigation technique (Asgedom and Kebreab, 2011).

Efficiency of fuel use or use of alternative fuels with lower net CO_2e emissions throughout the production chain for transportation and electricity generation (i.e., wind and solar) can lower CO_2e emissions per unit of animal product. Postfarm gate, optimizing transport routes, driver behavior, and transport vehicle design (e.g., low resistance tires and aerodynamic design) can all contribute to decreasing CO_2e emissions from the transportation portion of the animal system product chain (Léonardi and Baumgartner, 2004).

Further reducing refrigerant leakage or switching to refrigerants with lower GWP could help reduce postfarm gate CO_2e emissions from animal systems. Moreover, advancements in packaging that use fewer raw materials in their production and have innovative designs to reduce wasted space during transport and distribution could reduce CO_2e emissions per unit of animal product.

Anaerobic digestion of wastewater at processing plants and abattoirs offers another potential CO_2e emission opportunity, which can both minimize CO_2e emissions from the waste and by reduce fossil fuel-derived electricity use if the biogas is used for electricity generation. Hassan and Nelson (2012) provide an excellent review of the microbiology and biochemistry of anaerobic digestion, as well as the digester designs that can be used for the anaerobic digestion of dairy food wastewater. Similar opportunities exist for livestock and poultry abattoir facilities to adopt anaerobic digestion of their organic wastes (Salminen and Rintala, 2002).

Food waste

Although there has been much discussion and analysis in recent years with regard to the potential climate impacts of changing diets from those higher in animal product content to those lower in animal product content (Garnett, 2011; Jones and Kammen, 2011; Weber and Matthews, 2008), the actual implementation of massive global dietary change seems unlikely, especially in the face of projected increasing worldwide demand for animal products (Garg, 2012). Addressing the issue of wasted edible food would be a more effective approach to reduce CO_2e emissions due to its tangible economic costs to the consumer (Dorward, 2012).

Waste of edible food can be viewed as a total loss. The labor, natural resources, animals, etc., and associated CO_2e emissions, that were required to produce the wasted product have essentially been used and expended for naught as the resulting food has not provided any human nutritional value. Minimizing food waste and waste at all phases of the production chain may be one of the most effective ways to address the paradox of meeting growing global nutritional needs with finite resources. Considering it is estimated that 30% of edible food is wasted worldwide (Gustavsson *et al.*, 2011) whereas there are currently 870 million people (one in eight) in the world who are undernourished (FAO *et al.*, 2012), the reasoning to address food waste goes beyond climate change and becomes a moral issue. Additionally, capturing and converting food waste back into a useful product or energy (i.e., through anaerobic digestion) rather than letting the waste enter a landfill can reduce CO_2e emissions that result from the animal system product chain. In general, reducing food waste and finding ways to convert the waste to into value (i.e., energy) rather than a net source of CO_2e emissions, is not just important sustainability issue for the animal system, but for the entire global food system.

Conclusion

Animal agriculture systems face a challenge in the coming decades to meet growing global demand for animal-derived products with finite resources. Additionally, animal systems must meet growing demand while adapting to climate change and variability, which animal systems contribute to through the emissions of GHG. The sources of GHG emissions from the entire animal production chain (from the farm to the consumer's plate) are varied and derived from microbiological, chemical, and physical processes. Mitigating GHG emissions can come from different strategies of animal feeding, animal management, manure management, and increasing efficiency and reducing waste throughout the animal production chain. Efficiency improvements and reduction of food waste can potentially address the challenges of meeting growing demand and mitigating environmental impacts simultaneously. Ultimately, a concerted, multifaceted global effort that includes farmers, researchers, and policymakers is required to create tangible, positive change surrounding the issues of climate change and animal systems.

See also: Air: Confined Animal Facilities and Air Quality Issues. Air: Greenhouse Gases from Agriculture. Animal Welfare: Stress, Global Issues, and Perspectives. Beef Cattle. Climate Change: Agricultural Mitigation. Climate Change, Society, and Agriculture: An Economic and Policy Perspective. Dairy Animals. Energy and Greenhouse Gases Footprint of Food Processing. Food Security: Postharvest Losses. Human Nutrition: Malnutrition and Diet. Swine Diseases and Disorders

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Intergovernmental Panel on Climate Change.

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US Environmental Protection Agency Climate Change.

Climate Change: Cropping System Changes and Adaptations

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Glossary

Carbon dioxide Gas in the atmosphere consumed by plants during photosynthesis.
Chilling hours The duration of temperature below a given threshold required for plants to flower.
Direct effects Effects of climate on plants or animals, for example, direct effect of temperature on plant growth.
Diseases Pathogens in the environment which cause a reduction in growth or reduce the quality of the product.
Indirect effects Effects of climate on an organism which affects the growth or productivity of the economic product, for example, increase in disease pressure induced by climate on a given plant.
Pests A combination of insects, diseases, or weeds which affect either plants or animals.
Plant productivity The rate of generation of biomass used for food, feed, fiber, or fuel consumption.
Precipitation Water which is deposited from the atmosphere onto the earth's surface as either snow or rain.
Soil resources A combination of all the properties of the earth's surface suitable for supporting human activity, for example, agriculture, buildings, and/or roads.
Temperature A numerical measure of heat or cold in an object.

Introduction

In the past 10 years, there has been renewed discussion about the implications of climate change for agriculture. Increasing evidence that our climate is changing and impacting agriculture is leading to understanding of the potential pressures on our ability to ensure an adequate food supply for the increasing human population. Rising carbon dioxide (CO_2), increasing temperatures, and more variable precipitation affect agricultural systems and no region of the world will be exempt from these effects. Understanding these effects on plants will help us develop cropping systems that are resilient to climate stresses and identify adaptation strategies to cope with climate change. Our goal in this article is to provide an understanding of the implications of climate change on cropping systems.

Climate has been changing and during the past 50 years there has been an increase in CO_2 concentration from 325 to 390 ppm with a projection of further increases to nearly 500 ppm by the middle of the twenty-first century (IPCC, 2007a). During the twentieth century, global average air temperatures increased by approximately 0.74 °C (0.56–0.92 °C) (IPCC, 2007a) with projections of further increases in surface air temperatures of between 1.1 and 2.9 °C by 2100 under emission scenarios, which have adopted aggressive methods to reduce CO_2 emissions, and by up to 2.0–5.4 °C under scenarios with higher emission rates. For agricultural cropping systems, trends in average temperature are not as important as the diurnal range, and projections are for increasing minimum temperatures more than maximum temperatures. Winter temperatures have increased more rapidly than summer temperatures, and nighttime minimum temperatures have warmed more than daytime maximums. Across the US (and elsewhere), record high temperatures are three times higher than the number of record cold events (IPCC, 2007a; Meehl *et al.*, 2009). Meehl *et al.* (2007) summarized that on a global basis "it is very likely that heat waves will be more intense, more frequent, and longer lasting in a future warmer climate. Cold episodes are projected to decrease significantly in a future warmer climate. Almost everywhere, daily minimum temperatures are projected to increase faster than daily maximum temperatures, leading to a decrease in diurnal temperature range." Observations of temperature have shown that 10 of the warmest 11 years have occurred since 2001 (Hansen *et al.*, 2012). Coupled with these changes is the decrease in the number of frost days by 10% in the eastern half of the US and an increase in the length of the growing season by over 10 days (Karl *et al.*, 2009). Temperatures are increasing and there are implications for plant growth and also the rate at which plants transpire water because as temperatures increase so does the saturated water vapor in the air creating an atmosphere with an increased rate of water use by crops.

Trends in precipitation are more difficult to assess; however, overall precipitation amounts and heavy precipitation events have increased in most regions of the world; while occurrences of drought has been increasing, particularly since 1970 (IPCC, 2007a; Allison *et al.*, 2009). Karl and Knight (1998) found that more than half of the observed increases in total annual precipitation across the US between 1910 and 1996 were due to increases in frequency of large events (upper 10 percentile of measured daily values). Groisman *et al.* (2005) examined records of measured daily rainfall data across land areas of the world and found trends of increased probability of extreme events for many regions outside of the tropics.

In addition to temperature, precipitation, and CO_2 changing, there is evidence that other components of the atmosphere changing as well. Solar radiation is one of the primary factors affecting plant growth because plants capture sunlight and convert this energy into sugars without which they would not grow. The amount of solar radiation reaching the surface of the earth is affected by cloud cover and the amount of

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particulates in the atmosphere. Under climate change, there is a projected increase in water vapor (humidity) and more cloud cover, causing a decrease in incoming solar radiation. Observations from around the world have shown that this effect has already begun to occur. Thus, Stanhill and Cohen (2001) found that there was noticeable reduction of nearly 3% per decade over the past 50 years, with current solar radiation totals reduced by approximately 5–7% from the midsummer values in the midlatitude regions. Changes in solar radiation directly affect crop water use and evapotranspiration but have less effect on crop growth because other factors (e.g., water and temperature), often limit productivity (Hatfield *et al.*, 2011). Furthermore, changes in solar radiation are not uniform across any continent and after a thorough evaluation, Stanhill and Cohen (2005) suggested that post-1950 there has been a decrease in solar radiation in the US, with sites in the Northeast, West, and Southwest showing the most significant declines. Solar radiation is more easily estimated by computer simulation models compared with other climate variables, and the use of the models by different researchers has confirmed the observations. A study on solar radiation by Medvigy and Beaulieu (2011) concluded that there was an increase in solar radiation variability around the world related to increases in precipitation variability and convective cloud formation and presence. Any change in solar radiation resources under climate change will affect the agricultural system in different ways and it is important to understand which climate factor is affecting crops.

Changes occurring in the climate are not uniform across any region of the world and it is important to realize that under climate change, variability within and among years, and among locations will likely increase. These changes will create more variation in crop growth and development within individual regions for all of the plant species we depend on for our food, feed, fiber, and fruit supply. Understanding these changes and the implications that flow from them will help us prepare a way to maintain an adequate global food supply. This having been said, agriculture has developed under a changing climate scenario because regional and global patterns of climate have changed and fluctuated since the beginning of cultivated agriculture. The ability of agriculture to adapt to a changing climate is evidenced in the continual increase in crop production throughout the world as exemplified in world maize, rice, and wheat production (**Figure 1**). These increases in production over time also show variation among years caused by the weather. In recent years, notable events including drought and heat waves in Russia in 2010, drought in China in 2012, and droughts in the US in 2011 and 2012, have all had a major impact on agricultural production in these areas.

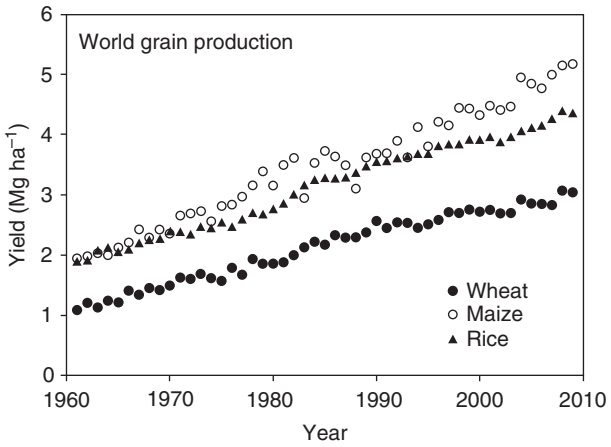


Figure 1 World grain production for wheat, maize, and rice since 1960 (www.fas.usda.gov).

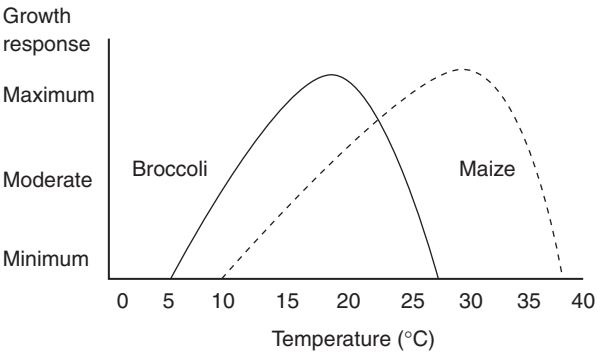


Figure 2 Idealized temperature response for plants showing the maximum, minimum, and optimal temperatures for a warm-season crop (maize) and a cool-season crop (broccoli) (Hatfield *et al.*, 2011).

Climate Parameters: Physiological Effects on Crops

Temperature

Each species responds differently to temperature throughout its life cycle and has a defined range of maximum and minimum temperatures within which growth occurs, and an optimum temperature at which plant growth progresses at its fastest rate. The response of plants to temperature is not symmetrical around the optimal temperature with greater effects of temperatures above the optimum than below (**Figure 2**). Furthermore, there are differences among plants as typified by a cool-season (broccoli) and warm-season (maize) growth response. Growth rates slow as temperature increases above the optimum and cease when plants are exposed to temperatures greater than their maximum. One of the classic methods of describing plant response to temperature has been through the use of a growing-degree-day concept (calculated as growing degree days (GDDs) $= (T_{max} + T_{min})/2 - T_{base}$) where T_{max} and T_{min} are the maximum and minimum air temperatures, respectively, for each day. This approach is commonly used and GDDs calculators are available on the Weather Channel website (www.weather.com) for an individual to evaluate GDDs for their location and compare with average conditions. This approach assumes (1) a base temperature (T_{base}) below which the plant does not grow, (2) the growth rate increases with temperature up to an optimum, and (3) then decreases until the maximum temperature is reached and growth no longer occurs. In most estimations of GDD, temperatures above the maximum are set equal with the maximum and do not detract from growth. Vegetative development usually has a higher optimum temperature than

reproductive development, which means that plants perform best when temperatures are cooler during the development of fruit, grain, or fiber. There are differences among annual (nonperennial) crop species in their cardinal (lower and upper temperature limits) temperature values as detailed in Hatfield *et al.* (2008, 2011).

There are wide ranges in the temperature responses of plants, for example, rice has an optimum temperature of 33 °C for vegetative growth but only 26 °C for reproductive growth; broccoli, a cool-season crop, has range of temperatu res for growth between 5 and 25 °C and 16 and 18 °C for reproductive growth, whereas warm-season tomato has a range for growth between 12 and 30 °C and an optimum for fruit development between 20 and 25 °C. For many plants as air temperatures increase, there is a greater chance that they will be exposed to conditions that exceed their optimum temperature (**Figure 2**).

As temperatures increase, the rate of progression through phenological stages (observable stages of plant development, for example, emergence of the plant seedling from the soil, the first leaf, the first flower, fruit development, and maturity) increases, which typically results in a smaller plant. One critical stage in plant development is pollination during which pollen is shed and flowers fertilized. Pollen is very sensitive to exposure to high temperatures, which renders it infertile and causes a failure in pollination. The predicted increase in more extreme temperature events will cause problems with pollination if they occur during flowering. In rice this means that varieties that flowered early in the morning are better able to tolerate high temperatures than ones that flower in hotter parts of the day (Hatfield *et al.*, 2011).

In other plants particularly many perennials, another effect of temperature is the need for a certain amount of chilling before flowers form. Chilling hours are defined as the hours below a given threshold temperature, usually defined as 7 °C. Chilling hours vary among perennial species, for example, grapes require 400–2000 h, strawberry from 300 to 400 h, and apples between 1000 and 1600 h. As temperatures warm, especially during the winter, the chilling requirements for perennial plants may not be achieved. Luedeling *et al.* (2009) estimated that with the current rate of warming, the chilling hours for the central valley of California would drop from 1000 h to between 500 and 750 h, and that perennial crops requiring more than this amount would not produce fruit. A different response has been predicted in the Northeast US perennial specialty cropping systems. Wolfe *et al.* (2008) analyzed the future chill requirements of the Northeast and found that a 400-h chilling requirement will continue to be met for most of the Northeast during this century regardless of emissions scenario. However, crops with larger chilling hour requirements (>1000 h) could be negatively affected, particularly in southern sections of the Northeast. Yields will be negatively affected if the chilling requirement is not completely satisfied because flower emergence and viability will be low.

According to Wolfe *et al.* (2008), an extended frost-free period projected for the Northeast will benefit perennial specialty cropping systems requiring a relatively long growing season, such as apples, peaches, and grapes. The warmer winter temperatures produced a longer frost-free period allowing for earlier growth in the spring; however, these warmer temperatures caused a more variable fruit set in the spring. Increased summer heat stress and drought could reduce yield and crop quality in fruit crops. Wolfe *et al.* (2008) found that apple yields for western New York (1971–82) were lower in the years when winters were warmer than average (based on accumulated degree days >5 °C from January 1 to budbreak). Midwinter warming can lead to early bud burst or bloom of some perennial plants, resulting in frost damage when cold winter temperatures return. Warm temperatures also affect fruit quality, and perennial crops exposed to high temperatures during fruit development produce smaller fruit and poorer quality.

One effect of increasing temperatures is to increase the transpiration rate of the plant. Water use or transpiration is affected by the amount of solar radiation intercepted by the plant canopy, windspeed, vapor pressure gradient between the plant and the atmosphere, and the amount of water available to the plant. The vapor pressure gradient is affected by air temperature because the maximum amount of water the air can hold is a positive exponential function of air temperature. This effect causes plants to use water more rapidly and without an adequate supply plants rapidly show signs of water stress, such as wilting, rolling of the leaves, or in severe cases of water shortage, death.

Precipitation

Precipitation supplies water to the soil from which plants extract water. Precipitation is one of the most difficult climate parameters to predict into the future; however, there is evidence that precipitation events will be more intense and there may be shifts in its seasonality. Across the Midwest US, the projection is for more precipitation to occur in the spring and for a reduction in summer. These shifts have significant implications because Midwestern cropping patterns have developed to utilize the precipitation occurring during the summer and any decline during that period reduces the available soil water leading to a reduction in plant growth. As the water supply in the soil is reduced, the plant is no longer able to extract sufficient amounts of water and stomates begin to close. As they close they no longer allow water to exit (thereby reducing cooling benefits), while also limiting the amount of CO_2 that enters from the atmosphere into the leaf. Without CO_2 being converted into sugars in the leaf, the plant is no longer growing and productivity suffers.

Because the plant is dependent on the soil to supply the water needed for plant growth, there is an important role for soil in response to climate change. Soils absorb and hold water because of their organic matter content and high-quality soils with large amounts of organic matter store more water. Organic matter content in soils is replenished by adding organic material and avoiding excessive tillage. These processes have been recently reviewed by Hatfield and Wright-Morton (2013) in which they discussed how soils become marginal in their functionality because of the loss of organic matter content and erosion. Maintenance of the soil to increase water availability can help reduce the impact of the increasing uncertainty in precipitation. Soil management to decrease the potential for erosion from the increased intensity of precipitation events will be necessary to maintain crop cover either as growing

plants or as crop residue on the surface to protect the soil surface from the impact of rain during these intense storms.

Changing precipitation patterns and intensity will affect soil erosion. Precipitation causes erosion through the interacting effects of storm energy and maximum prolonged precipitation intensity (Nearing *et al.*, 2005). The dominant variable causing erosion is rainfall intensity, the amount of rainfall reaching the soil surface per unit time, rather than total rainfall amount (Nearing *et al.*, 2005). Soil erosion processes are affected by (1) erosive effects of rainfall, irrigation, snowmelt, and wind; (2) plants, cropping, and management; (3) soil erodibility; (4) conservation practices; and (5) topography. Climate change and the impact on precipitation frequency, intensity, and seasonality will most likely have the greatest effects on the first three of these factors. O'Neal *et al.* (2005) showed there was a relationship between expected patterns of precipitation under climate change and crop management practices. Agricultural production depends on a high-quality soil resource and degradation of the soil via erosion will limit the ability to continue to efficiently produce crops. To offset these potential impacts in the future, agriculture will have to aggressively utilize conservation practices to provide protection to the soil (Delgado *et al.*, 2011).

Supplying water to the soil via irrigation can offset the effects of inadequate precipitation or timing of precipitation with crop water demand. An example of the timing issue occurs in the Central Valley of California, which has a Mediterranean climate in which virtually all precipitation occurs during the winter. To produce a crop, water must be stored from the winter period and then supplied to the soil during the summer. In many areas of the world, irrigation from ground water or surface water storage is used to supplement precipitation during the growing season. However, given the requirement for increasing amounts of fresh water to support human activities, agriculture will have to become more efficient in its use of water for production.

Carbon Dioxide

Carbon is one of the fundamental building blocks for all plant compounds. Through the process of photosynthesis, CO_2 is converted into sugars which are ultimately converted into proteins, starches, amino acids, etc. through a variety of metabolic processes. Rising levels of CO_2 in the atmosphere has a positive effect on plant growth and development. Even using conservative estimates, the current levels of approximately 390 ppm will increase at a faster rate than originally expected to nearly 450–500 ppm by 2050 (Karl *et al.*, 2009). To assess the effect of increasing CO_2 on plant growth, enclosed chambers and free-air CO_2 enrichment (FACE) studies have been conducted in which plants have been exposed to higher levels of CO_2 typical of what may be expected in future climates. These studies have shown a positive effect on plant growth (Kimball, 1983, 2011) with increasing CO_2 concentrations increasing growth by ~10% in plants such as maize and sorghum, which already have the highly efficient C_4 photosynthetic pathway, to increases in growth of greater than 30% in C_3 plants, such as beans, peanut, rice, wheat, soybean, and others. In general, doubling CO_2 caused an approximate 30% increase in reproductive yield of C_3 species and a less than 10% increase for C_4 species. Differences among the species are due to differences in internal metabolic pathways that determine how the plant incorporates CO_2 into sugars and how respiration processes (release of CO_2 from metabolic processes) release CO_2 into the cells.

Respiration is the process of converting C-based compounds back into CO_2 – a process that occurs in all living organisms. Although the process of photosynthesis is controlled by the amount of solar radiation, respiration is controlled by temperature. In biological studies, the Q_{10} temperature coefficient measures the rate of change in biological activity, for example, respiration, for every 10 °C change in temperature. For most biological systems this coefficient ranges between 2 and 3. Thus there is a doubling of respiration rate for every 10 °C rise in temperature, so that as the air temperature increases there is a concomitant increase in the respiration rate. The importance of this response is because nighttime temperatures are increasing more rapidly than daytime temperatures, which are likely to lead to higher respiration rates in plants. Higher respiration rates will result in lower plant growth because CO_2 that is captured during the day will be released back into the atmosphere at night rather than being utilized for growth. Plant temperatures at night tend to equal air temperatures so that any increase in air temperature directly affects respiration rate. The implication of the effect of climate change on respiration is a significant challenge to increasing plant productivity.

One of the interesting aspects of the plant's response to increased CO_2 links photosynthesis with transpiration. Increasing CO_2 decreases the transpiration rate of the plant while increasing the photosynthetic rate. This effect occurs because the CO_2 concentration gradient is larger than that for water vapor between the leaf and the atmosphere, and there is actually a decrease in the stomatal opening causing a reduction in the rate of movement of both gases. The net effect of this change is to increase water use efficiency, meaning that plants grown under high CO_2 concentrations have higher photosynthetic rate than transpiration rate. Observations from scientific studies around the world have shown that a doubling of CO_2 reduced stomatal conductance by nearly 34–40% (e.g., Kimball and Idso, 1983; Morison, 1987; Ainsworth *et al.*, 2002) so that an atmospheric CO_2 concentration of approximately 450 ppm, as estimated to occur between 2040 and 2050, will likely cause 10% reductions in stomatal conductance. The magnitude of these reductions in stomatal conductance will lead to decreases in transpiration and have potential positive impacts on crop water use efficiency, that is, they will be more water use efficient in the amount of growth they make relative to their rate of water use.

The effect of reduced water use by plants will be especially important in rainfed environments where plant growth is dependent on rainfall during the growing season. This effect has been observed in field conditions by Bernacchi *et al.* (2007) where they found soybean plants grown under ambient CO_2 (control plants) showed a large reduction in water use when their water supply decreased. In contrast, plants grown under increased CO_2 (FACE plots) continued to transpire because of the water conservation compared with control plots. This allowed plants in the FACE plots to continue to photosynthesize and grow for a few days longer, whereas the control plants ceased growth. Under rainfed agriculture, which often

experiences periods of drought, the net impact of elevated concentrations of CO_2 would be to enable conservation of soil water, thus sustaining crop productivity for longer than at today's CO_2 levels. Understanding these relationships between ambient environmental conditions and plant physiology helps to develop production systems, which can cope with the increasing stress levels likely to occur under climate change.

Ozone

Although attention has been directed toward CO_2 increases as part of climate change, less attention has been given to ozone (O_3), although concentrations of this gas have increased in rural areas of the US over the past 50 years, and are expected to increase further over the next 50 years. Currently, Midwest and Eastern US have some of the highest rural O_3 levels on the globe. Ozone concentrations increase toward the east and south, showing levels in Illinois exceed those in Nebraska, Minnesota, and Iowa. Only Western Europe and Eastern China have similar (high) levels. Argentina and Brazil and most of the Southern Hemisphere have much lower levels of O_3, and expect to see little increase in O_3 over the next 50 years. Increasing O_3 levels will impact crop production, and efforts to increase O_3 tolerance will be important to maintain agricultural productivity. Future trends in global O_3 concentrations are linked to Intergovernmental Panel on Climate Change scenarios, so that agricultural impacts from O_3 can be considered along with the other components in climate change. Modeled predictions for O_3 based on expected economic development and planned emission controls in individual countries estimate significant increases in the annual mean surface O_3 concentrations in major agricultural areas of the northern hemisphere (Dentener *et al.*, 2006).

Physiological responses to increased O_3 concentrations have been studied using similar approaches to assessing the effects of increased CO_2. After uptake through the leaf's stomata, ozone interacts with plants' cellular processes, inhibiting photosynthesis, growth, and yield. Detrimental effects result from a combination of chemical toxicity and physiological responses that either amplify or inhibit injury and in many regions of the US and worldwide (Booker *et al.*, 2009; Morgan *et al.*, 2006) current ambient O_3 levels are already impacting yields of crops such as alfalfa, bean, clover, cotton, peanut, potato, rice, soybean, sugar cane, and wheat. In some grass species, changes in leaf chemistry from elevated O_3 exposure have caused reduced nutritional quality of the grass used to support grazing animals. This loss of nutritional quality in these grasslands may be more significant than biomass losses (Muntifering *et al.*, 2006). Ozone changes are often not considered part of the climate change puzzle; however, the changing temperature and humidity of the atmosphere combined with continued fossil fuel combustion will create conditions favorable for O_3 formation and higher atmospheric concentrations.

Crop Growth and Yield Response to Climate Change

Grain crops

Grain crops, for example, wheat, oats, rice, corn, soybean, and beans, all have different responses to a changing climate

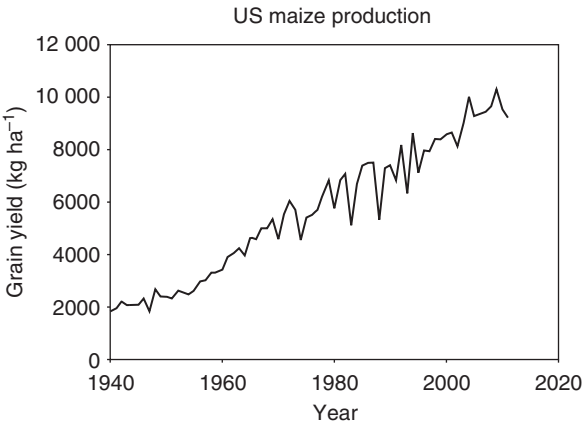


Figure 3 Variation in annual corn (maize) yields for the United States to demonstrate the effect of weather variability among years (USDA-NASS, 2013, www.nass.usda.gov).

(Walthall *et al.*, 2012). Examination of among-year yield variation shows that within-year weather conditions have an impact on production. Most of this reduction in grain yield is associated with the lack of sufficient water to maximize grain production and exposure to the short-term water deficits may reduce yields from their potential by 5–20% (Hatfield, 2010). Increasing variation in rainfall across many areas of the world may exaggerate the effect of climate change on grain production because of the increased frequency of water stress during the growing season. This effect will be increased in soils with lower water-holding capacity or eroded topsoil because the limited amount of soil water available to the plant during the growing season (Hatfield, 2012; **Figure 3**).

There is evidence that the increasing temperatures over the past 20 years have already begun to impact growth and Lobell *et al.* (2011) suggested that yield declines from 4 to 5% have occurred in many growing areas of the world. Other studies have suggested that maize yields in the Midwest US would decrease 2 to 3% with a temperature increase of less than 1 °C (Hatfield *et al.*, 2011). Grain yield of soybean demonstrate a differential response to changing temperatures by region depending on where the projected temperatures fall on the growth response to temperature relationship (**Figure 2**). In the southern US, soybean yields are projected to decline because temperatures will begin to exceed maximum temperatures for optimal growth, whereas in the Midwest, soybean yields will increase because rising temperatures will actually benefit the plant (Hatfield *et al.*, 2011). In an evaluation of the likely impacts of temperature change in the Central Valley of California, Lee *et al.* (2011) found that all crops except alfalfa showed a decline in production as temperatures increased. Decreases in production were as large as 30% by 2100 because of increased temperature stress on the plant and disruption of optimum physiological function.

Winter wheat and other small grain crops exhibit a large sensitivity to increasing temperatures. The warmer the temperatures, the faster the rate of development leading to reduction in grain yield. An interesting observation in wheat is the decline in grain quality with the changing climate and an associated emerging challenge will be to understand and

quantify these impacts. It has been observed that growing wheat under low nitrogen (N) conditions coupled with high CO_2 reduced grain quality, and a steady decline in grain protein in Australia from the late 1960–2000 was related to increasing CO_2 concentrations (Conroy and Hocking, 1993). Other research results on barley have concluded that nutritional and processing quality of flour will diminish for cereal grown under elevated CO_2 and low N fertilization. These observations point out the need to increase our understanding of these interactions because they will provide insights into crop response to climate change and how we can ensure nutritional quality of grain production under climate change. The quality of grain is not the only product affected by climate change, in cotton, there is a decrease in fiber quality when plants are exposed to high temperatures during boll development when lint fibers are being formed (Pettigrew, 2008).

Forage crops

Forage grasses exhibit the same responses to temperature as other plant species; however, grasslands are made up of mixtures of plants and rising temperatures may cause a change in the relative dominance of different species in the community. These changes in community structure have been discussed and evaluated relative to climate change by Izaurralde *et al.* (2011). The quality aspect of forages is even more critical than in grains because of the direct consumption of the forage as the primary source of nutrition for the animal. Efficient animal production from pastureland and rangeland systems depends on both forage quality and quantity. Positive and negative changes in forage quality are possible as a result of atmospheric and climatic change when we examine the potential vegetation changes and environmental effects on forage protein, carbohydrate, and fiber content. Studies on forage quality have helped to reveal the linkage between changing CO_2 concentrations and a plant's ability to extract N from the soil. Warming temperatures cause N concentrations in the forage to decrease partially because of the positive effect of increasing CO_2 on enhancing vegetative growth (Morgan *et al.*, 2004). The fact that these effects will vary among species highlights the need to understand interactions among all the plant species in a community and how they respond to climate change.

Forage growth is directly linked to precipitation because many of the production areas are in regions with limited precipitation during the growing season. Increasing variation in precipitation will lead to increased variation in forage production which, in turn, will affect livestock production. These variations in forage production will have worldwide impacts on animal production.

Specialty crops

Annual specialty crops include many vegetable and fruit plants, each with their own environmental ranges. Climate change will have an impact on them in a similar way as grain crops; however, because these crops are often directly consumed, the effects of temperature or water stress are more noticeable.

Temperature is a major environmental change expected to affect production of annual specialty crops as temperature responses vary more widely among specialty than other crops, for example, tomatoes have a warmer temperature response than cool-weather crops, such as broccoli, potato, lettuce, and onion (Hatfield *et al.*, 2008). The sensitivity of these different species to stress depends on when during the life cycle the stress is imposed and the nature of the stress itself for example, periods of hot days, overall growing season climate, minimum and maximum daily temperatures, and timing of stress in relationship to developmental stages. In specialty crops, mild heat stress (a 1–4 °C above optimal growth temperature) often results in moderate reductions in yield (Timlin *et al.*, 2006; Tesfaendrias *et al.*, 2010; Walthall *et al.*, 2012). Specialty crops are vulnerable to exposure to high-temperature stresses during pollen development, which typically occurs 7–15 days before pollination. The pollination period is critical to the development of fruit and exposure to temperature extremes and intense heat stress (>4 °C over the optimum temperature) during this period may cause a failure in fruit set and consequent yield loss (Tesfaendrias *et al.*, 2010; Walthall *et al.*, 2012). Protection of the plants against exposure to high temperatures during this phenological stage may be a critical step in ensuring fruit or vegetable production.

Water is a critical component in specialty crop production and maintaining an adequate water supply is necessary to achieve high yields and product quality acceptable for consumers. Observations in strawberry have shown that inadequate water results in reduced leaf area, root development, and smaller berries causing less harvestable yield (Bordonaba and Terry, 2010). Potato production is reduced when plants are grown under water stress coupled with high temperatures because the plant is unable to maintain the optimal level of starch production needed for tuber development. Each crop species has a different amount of water required to produce fruit, for example, tomato, 2.58–11.88 kg m^{-3}; potato, 1.92–5.25 kg m^{-3}; melon, 2.46–8.49 kg m^{-3}; watermelon, 2.70–14.33 kg m^{-3}; and cantaloupe, 4.18–8.65 kg m^{-3}. This suggests that future efforts will have to be directed toward management practices that can maintain water supplies to these crops. In many specialty crop production regions, there is extensive use of irrigation to avoid water stress.

Perennial crops

Perennial crops are typically considered as those that are more permanent, requiring a number of growth cycles before fruit is produced. One of the characteristics of these plants is their requirement for winter chilling before flowering the next spring. As discussed earlier in the Section Temperature, there is evidence that with warming winter temperatures some perennial crops may not have their chilling hour requirement satisfied, which will limit flowering and ultimately fruit set. An additional concern is that warm winters may promote early bud and flower development and late season frost events will damage these flowers and fruit or nut formation. Perennial crops are valued for a combination of their total production and the quality of the harvested product, for example, size of a peach or apricot, the red blush on an apple, oil content of olives, or the quality of wine produced from a particular vineyard. By nature, perennial crop production is long-term and climate change will create interesting problems for production because production areas have less flexibility in their location after establishment and because the production

cycle is often measured in decades rather than single growing seasons.

Apples provide an excellent example to show how climate stress will impact growth throughout the year and across years. High temperatures occurring during the year before harvest affect floral initiation (occurs in June–July) and can reduce the number and vigor of potential floral buds. When the tree is dormant, exposure to extreme cold can kill buds and intermittent warming periods can cause flower buds to be more susceptible to winter damage before growth resumes in spring. Flowers can emerge too early in the spring and if frost occurs, will be killed. During the development of fruit in the spring, exposure to high temperature reduces cell division causing smaller fruit size. During the summer months, high temperature may cause sunburn damage reducing harvest quality, accelerating maturity, reducing fruit firmness and color development, and/or decreasing the suitability of fruit for short- or long-term storage. These effects will be exaggerated if there is an occurrence of water deficit during the same period. It is often not recognized that climate stress may occur at multiple times during the growing season; however, in perennial crops this is a common phenomenon.

Indirect Effects of Climate Change on Crops

Plant production is affected by a combination of direct impacts from different climate variables and indirectly for example, insects, diseases, and weeds, which are themselves directly impacted by these same climate variables. The indirect effects may have as large an impact on productivity as the direct impacts and also affect the quality of the fruit, grain, or feed from these plants. To fully appreciate the impacts of climate change on plants it is important to understand the indirect impacts on plants.

Insects

Increasing air temperatures are beneficial to insect pests and like plants, rising temperatures accelerate every aspect of an insect's life cycle, and warmer winters reduce winter mortality. Insects, like plants, have an upper threshold of temperatures above which there is mortality. Similar to plant response, warming temperatures will cause some insects to thrive and expand their range, whereas others will have a reduced viability. Warmer temperatures during the summer increases the growth of insect populations; however, a more positive benefit on insect populations is caused by lengthening of the growing season, which results in more damage to plants (Bradshaw and Holzapfel, 2010). Increasing air temperatures also affect the range of insects because they encounter a wider range of environments in which they can survive; however, each insect species has a specific range of temperatures in which it develops, so not all insect populations will automatically expand with warmer temperatures. Insects also require water for survival and limited water supplies will affect populations.

Temperature plays a large role in the geographic ranges of insect pests because of the impact it has on the ability of insects to survive winter conditions and the presence, and nutritional quality of the plants upon which they feed. Insects are mobile and both local dispersal and long-distance migration allow some to invade colder regions. Spring emergence is generally defined by temperature, whereas winter dormancy is cued by photoperiod or a combination of photoperiod and temperature. Insects are capable of withstanding all but the most extreme precipitation events, thus rainfall affects growth and survival principally through increased cloud cover, which can reduce activity, and changes in the nutritional quality of plants. Insects, especially small ones and those with aquatic life stages, will desiccate and die without ready access to water. Humidity influences the prevalence of insect diseases, as well as plant diseases that insects carry.

Increasing air temperature results in reduced cold stress over the winter and when there is no substantial increase in heat stress during the summer, which will affect insect life cycles and survival by removing temperature stress during the winter period allowing greater insect populations to be maintained (Bradshaw and Holzapfel, 2006). Decreased soil temperatures can occur in areas with reduced frequency of snow cover leading to greater winter insect mortality (Bale and Hayward, 2010) because arousal from winter dormancy is generally dependent on accumulated temperature (growing-degree days). Increasing air temperatures are causing phenology to advance faster than previously observed within a growing season (Gordo and Sanz, 2006; Harrington *et al.*, 2007; Gregory *et al.*, 2009; Bale and Hayward, 2010). This is a similar response to that observed for plants with warmer temperatures causing faster rates of development. The effect of the longer growing season has caused some insects with multiple generations per season to produce more generations per year (Tobin *et al.*, 2008; Altermatt, 2010). However, as for crops, insects have optimal temperatures under which they thrive, so not all insect populations will increase with increasing temperature.

Diseases

Leaf and root pathogens will be favored by increases in humidity and the frequency of heavy rainfall events projected for many parts of the world will create a more conducive environment for many different pathogens (Garrett *et al.*, 2006, 2011). Increases in temperature also favor populations of pathogens because the growth rate of these organisms is temperature dependent. Incidences of warm, moist environments will increase the potential for disease to occur on plant leaves and fruit (Wu *et al.*, 2011). However, it is difficult to develop general statements that the incidence of pathogens will increase because even, short- to medium-term droughts reduce the duration of leaf wetness causing a reduction in pathogen attack on leaves. The development of a better understanding of the effect of climate change on pathogens remains a challenge for agriculture and a major topic for future investigation. Protection of the growing plant, and the harvested product placed into storage, from pathogens remains a challenge. Improving our understanding of the role climate has on these organisms will increase our ability to ensure a secure food supply for the future.

Weeds

Weed species are a range of plants which exist within plant production systems that compete with crops for water, light,

and nutrients while often also serving as hosts for some pathogens or insects. Weeds have a much greater response to increasing CO_2 concentrations than has been observed in cultivated plants (Ziska, 2004). This implies that weed management may become more difficult because weeds will become more vigorous and invasive under climate change and thus lead to greater impacts on plant productivity (Ziska, 2010). Temperature controls weed species success with the same effects on weeds as on cultivated plants (Woodward and Williams, 1987). A warming climate will affect the dissemination of weeds with subsequent effects on their growth, reproduction, and distribution. Indeed, warmer temperatures, in particular an increase in the number of frost-free days, may allow a northward expansion of aggressive weeds into areas where weed populations have been less of a problem in the past. Weed management under climate change will become more of a challenge because of the nature of these plant species and their positive response to warming temperatures, more variable precipitation, and increasing CO_2 concentrations.

Adaptation in Cropping Systems

Ensuring future supplies of food, feed, fiber, and fruit depends on our ability to develop adaptation strategies to allow plants to cope with climate change. In this quest it is important to remember that we are dealing with complex biological systems, which respond to a range of different factors and that within each species there is a wide range of response. Adaptation science is just beginning to emerge and climate change will present a challenge to our ability to not only quantify the responses of different species to climate variables, but also develop and evaluate methods that can be employed to reduce the negative effects of climate stress on plant growth and yield. There are two avenues whereby we can address this problem, we can evaluate differences in genetic responses to different climate variables or determine the role of management practices to alleviate or avoid the effect of climate on plants.

Genetics

All species show a range of genetic responses to selection pressures. Tolerance of plants to high temperatures can be assessed by evaluating phenotypic traits that promote heat tolerance during flowering, increased harvest index (ratio of reproductive production to total biomass production), smaller leaves, or diverting more growth into root systems to increase water uptake. One adaptation strategy would be to select plants for peak flowering times in cooler periods of the day to assist pollen survival and increase grain set (Prasad *et al.*, 2006). Another selection target would be to identify plants that demonstrate different recovery responses to high temperature or water stress. Observations that plants show increased transpiration efficiency with increasing CO_2 suggest that there may be genetic differences in these responses; however, these relationships have not been fully evaluated to determine if there is potential in genetic variation to achieve enhanced transpiration efficiency through genetic manipulation.

Assessing the genetic response of plants to climate variables has not been the focus of many studies partly because they require specialized facilities capable of inducing temperature and water stresses typical of future climate scenarios on a range of genetic stock within a species. As we continue to develop more detailed gene maps of different species, there is optimism that these tools will help identify genes or gene sequences associated with responses to climate stress.

Management

Management as an adaptation strategy offers the most immediate promise to alleviate the effects of climate change. One obvious management strategy is to provide water by irrigation to supplement inadequate precipitation. Irrigation has proven very effective in many parts of the world and efforts to increase irrigation use efficiency and reduce waste have proven beneficial to enhancing production under limited water supplies. Use of drip or trickle irrigation to supply water only to the plant has shown promise in many parts of the world. However, for irrigation to be effective there has to be an adequate supply of surface or ground water to meet crop demands.

Other management practices involve changes in planting dates so that plants grow and mature during times of the year with reduced probability of high temperature or water stress. There are limits to the range of potential planting dates in many environments because plant growth may be limited by cold in the early spring if the temperatures are below the lower threshold for development (**Figure 2**). A more simple management approach may be to alter plant selection and grow plants which have a different temperature response curve. An example of this would be to produce wheat or other small grain, which can be planted in the fall and matures in the early summer before the primary occurrence of high temperatures or increased water demand, in place of corn, which is planted in the spring and is producing grain during the warmest and least rainy period of the year in a number of environments. Another alternative would be to replace corn with sorghum or millet, which is much more tolerant of water stress conditions than corn, and under water limited environments performs better in producing a grain. In many arid environments these types of management decisions offer the potential for ensuring a grain supply.

There are observations collected from ongoing research on grain quality, which suggests that management of nutrient supply for plants should be considered in adaptation strategies to cope with climate stress. Nutrient management is a portion of the soil management complex, which may hold some keys to helping build more resilient crop production systems to the changing climate. As part of the soil management complex, we need to ensure that soils have maximum water-holding capacity and nutrient cycling capabilities because these are related to negating the negative effects of climate stress on plant growth and development. Strategies to achieve these goals were recently reviewed by Hatfield *et al.* (2011). There is no single solution to this problem and development of effective adaptation strategies will require efforts which integrate across a number of approaches.

Conclusion

Climate change is occurring with the expectation for increased temperatures, more variable precipitation, increasing CO_2,

increasing O_3, and higher humidity over the next few decades. Agriculture has been subjected to climate change in the past and we have evolved our production systems to cope with interannual and annual variations in weather. The concern is that the rate of climate change and the magnitude of the change may begin to exceed the capacity of some plant species to adapt resulting in a decline in production. To place this in perspective, recent analysis for the impacts of increased temperature on wheat production in India by Ortiz *et al.* (2008) shows the fragile nature of our production systems. The consequences of increasing temperatures, which are in the moderate range of those suggested by climate scientists, would create a shortage of wheat production in India and cause the transition from a self-sufficient country to an importer of wheat to meet population demands.

Climate change impacts all plant growth and productivity and understanding how to develop production systems, which can cope with the increasing temperature and water stress offers a challenge to be able to maintain adequate food supplies for the increasing population. The effects of different climate variables on plant growth, development, and yield demonstrated shows where we need to begin to focus our efforts to meet this challenge.

See also: Agroforestry: Conservation Trees and Erosion Prevention. Biodiversity and Ecosystem Services in Agroecosystems. Climate Change: Agricultural Mitigation. Climate Change, Society, and Agriculture: An Economic and Policy Perspective. Climate Change: Animal Systems. Mathematical Models to Elaborate Plans for Adaptation of Rural Communities to Climate Change. Climate Change: Horticulture. Climate Change: New Breeding Pressures and Goals. Climate Change and Plant Disease. Food Security: Yield Gap. Plant Abiotic Stress: Temperature Extremes. Plant Abiotic Stress: Water. Plant Biotic Stress: Weeds. Soil: Carbon Sequestration in Agricultural Systems. Soil Greenhouse Gas Emissions and Their Mitigation. Soil: Nutrient Cycling

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Climate Change: Horticulture

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Glossary

Chilling requirement Minimum quantity of exposure to cold temperatures required to break dormancy allowing the tree to flower normally.
Evapotranspiration The sum of evaporation and plant transpiration from the Earth's land surface to atmosphere.
Phenology The study of periodic plant and animal life cycle events and how these are influenced by seasonal and interannual variations in climate.
Photoinhibition Description of reactions that decrease the efficiency of photosynthesis.
Transpiration The loss of water vapor from parts of plants, especially from leaves but also from stems, flowers, and roots.

Introduction

Horticulture Species Range

The horticulture industry is represented by a diversity of perennial and annual crops, ranging through fruits, nuts, vegetables, edible fungi, and extractive crops (essential oils), with amenity horticulture, cut flowers and turf also categorized as horticultural crops. Globally, in 2010 approximately 600 million tons of fruit, 9 million tons of tree nuts, and more than 1.7 billion tons of vegetables were produced (FAOSTAT, 2012). In contrast to many other agricultural industries, horticultural products are of high value and are often grown on relatively small areas of land and under dry-land, irrigated, or covered conditions. There often exists a high level of management input aimed at ameliorating climate risks (e.g., via irrigation) despite this, many activities retain considerable exposure.

Horticulture Geographical Range

Horticultural crops are grown across most latitudes in the world with representations from temperate and Mediterranean (30–40°), subtropical (20–30°), and tropical (0–20°) regions. Because of the nature of horticultural products, transport over long distances can require refrigeration and become expensive. So, where possible, much horticultural production is undertaken in proximity of population centers, and are therefore also at risk from urban expansion. Horticultural production can range from vast enterprises, family owned farms, to plantings by individuals in their own gardens.

An overall increase in horticultural production has been observed over the recent past, driven by demand from rapid population increase and facilitated by the introduction of trade agreements and the emergence of an international horticultural market (Dehnen-Schmutz *et al.*, 2010). A marked increase in production from the Asian region for fruits, tubers, and vegetables has been contrasted by a decline in European production (**Figure 1**). Over recent decades since 1980, there has been an increase in exports from developing countries like Africa (Mathooko and Mutui, 2011) and Asia (Xue and Revell, 2009). China, for example, ranked second in the world as an exporter of processed vegetables and fourth for unprocessed vegetables in 2005 (Xue and Revell, 2009). Some production declines in cooler growing regions of Europe have been related to increasing oil prices affecting costs of greenhouse heating. Increasing labor costs, and in some countries a shortage of seasonal workers, has also been a factor in productivity decline in Europe (Dehnen-Schmutz *et al.*, 2010).

Horticulture Economic Importance

In 2010, global horticulture produce made up approximately 43% of gross production value of crops (approximately US $600 billion), with US$255 billion for fruits and nuts, and US $370 billion for vegetables (FAOSTAT, 2012). Key fresh fruit species (in order of production tonnage in 2010 and representing all fruits above 1% of world production) include bananas, watermelons, apples, oranges, grapes, mangoes/mangosteens/guavas, plantains, other melons (including cantaloupes), pears, tangerines/mandarins/clementines, peaches and nectarines, pineapples, lemons and limes, papayas, and plums and sloes. The production rankings of these vary by region. Key vegetables (in order of production tonnage in 2010 and representing all vegetables above 1% of world production) include potatoes, cassava, tomatoes, sweet potatoes, onions (dry), cabbages and other brassicas, cucumbers and gherkins, yams, eggplants (aubergines), carrots and turnips, chilies and peppers (green), lettuce and chicory, pumpkins, squash and gourds, garlic, spinach, green beans, cauliflowers and broccoli, and green peas (FAOSTAT, 2012; **Table 1**).

Flowers, turf, and amenity horticulture are also important horticultural production entities. In Australia, turf production (sod) in the 2005–06 growing season has been estimated to have been worth AUS$213.8 million and future growth in this industry is expected (Aldous and Holborn, 2012). The United States is the third-largest producer of cut flowers in the world and production was valued at US$424 million in 2001 (Bonarriva, 2003).

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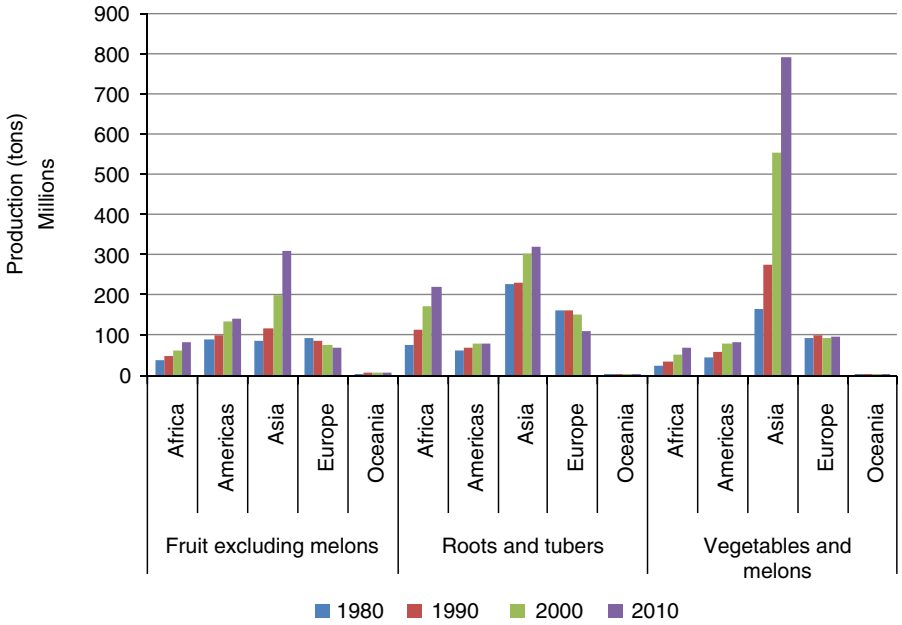


Figure 1 Horticultural production of fruits and vegetables from 1980 to 2010 from different regions of the world (FAOSTAT, 2012).

Projected Climatic Changes

Mean Climate Change

Global warming estimates and representative ranges have been documented in the Intergovernmental Panel on Climate Change (IPCC) Special Report on Emission Scenarios (Nakićenović and Swart, 2000). By 2030, assuming rapid population growth and a mix of future energy sources (a mid-range IPCC emission scenario), the globe is estimated to warm by an average of 0.9 °C (0.5–1.4 °C) (IPCC, 2007). Patterns of change for temperature and precipitation taken from simulations of 23 climate models were projected for 2030 under this A1B scenario (Watterson and Whetton, 2011; **Figure 2**). The models indicate that the Northern Hemisphere is expected to warm faster than the Southern Hemisphere and continental regions will warm at a faster rate than coastal regions.

A range of projections for rainfall change from among climate models indicate that some regions of the globe will likely get wetter and others drier (**Figure 2**), with regionally varying levels of model agreement, hence certainty (not shown in the figure, see IPCC, 2007). The pattern of rainfall change broadly shows subtropical regions have a drying trend whereas increasing rainfall is projected in some equatorial and high-latitude regions (IPCC, 2007; **Figure 2**).

Extreme Weather

Extreme weather and climate events such as frost, drought, heat waves, hail, cyclones, and floods all have the potential to impact severely on horticultural production. Under global warming, changes in the frequency, intensity, spatial extent, duration, and the timing of extreme weather is likely. It should be appreciated that some climate extremes (e.g., droughts) may be the result of a combination of weather events that are not extreme when considered independently (IPCC, 2012).

An increase in the frequency of extreme events has been observed already (Alexander *et al.*, 2006) and it is very likely that extreme heat events, heat waves, and heavy precipitation events will become more prevalent. Based on a range of climate models, tropical cyclones (typhoons and hurricanes) are projected to become more intense, with larger peak wind speeds and heavier precipitation associated with continual increases to tropical sea surface temperatures (IPCC, 2007).

Observed decreases in the number of cold days and nights (Alexander *et al.*, 2006) may point to a possible advantage of climate change for horticultural production, except in the case of winter chilling requirements. These observations in conjunction with projected warming of the climate (IPCC, 2007) may reduce the number of frost days, decreasing crop loss and damage from cold events.

Climate Change Impacts on Horticulture

Selection of favorable sites involves understanding the plant environment – physiology relationship in order to minimize deleterious impacts resulting from growing species in sub-optimal conditions (Schaffer and Andersen, 1994). With climate change, important environmental conditions for production will be modified. Interpretation of the potential effects of these changes is required to minimize adverse impacts through adaptation and take advantage of possible benefits.

Both negative and positive impacts on production are expected to transpire under future climate conditions. These impacts are dependent on the plant species, geographical region, and future changes to the spectrum of climatic variables that influence plant production. Generally, perennial crops will be more vulnerable than annuals to changes in the climate. Perennial crops are characterized by high investment permanent plantings often with long productive life spans, whereby measurable changes to climate will occur over the

Table 1 Ranking of major (fresh) horticultural production categories (tons produced) in different regions and globally

	Africa	*Americas*	*Asia*	*Europe*	*Oceania*	*World*
Fruit (fresh)						
1	Plantains	Oranges	Watermelons	Grapes	Grapes	Bananas
2	Bananas	Bananas	Bananas	Apples	Bananas	Watermelons
3	Oranges	Grapes	Apples	Oranges	Apples	Apples
4	Watermelons	Apples	Mangoes, mangosteens, and guavas	Watermelons	Oranges	Oranges
5	Mangoes, mangosteens, and guavas	Plantains	Oranges	Peaches and nectarines	Kiwifruit	Grapes
6	Grapes	Pineapples	Grapes	Pears	Pineapples	Mangoes, mangosteens, and guavas
7	Dates	Watermelons	Other melons (including cantaloupes)	Plums and sloes	Watermelons	Plantains
8	Pineapples	Lemons and limes	Pears	Other melons (including cantaloupes)	Peaches and nectarines	Other melons (including cantaloupes)
9	Apples	Mangoes, mangosteens, and guavas	Tangerines, mandarins, and clementines	Tangerines, mandarins, and clementines	Pears	Pears
10	Other melons (including cantaloupes)	Papayas	Peaches and nectarines	Strawberries	Tangerines, mandarins, and clementines	Tangerines, mandarins, and clementines
Vegetables (fresh)						
1	Cassava	Potatoes	Potatoes	Potatoes	Potatoes	Potatoes
2	Yams	Cassava	Sweet potatoes	Tomatoes	Sweet potatoes	Cassava
3	Potatoes	Tomatoes	Tomatoes	Cabbages and other brassicas	Tomatoes	Tomatoes
4	Tomatoes	Onions, dry	Cassava	Onions, dry	Yams	Sweet potatoes
5	Sweet potatoes	Maize and green	Cucumbers and gherkins	Carrots and turnips	Taro (cocoyam)	Onions, dry
6	Onions, dry	Lettuce and chicory	Onions, dry	Cucumbers and gherkins	Maize, green	Cabbages and other brassicas
7	Taro (cocoyam)	Chillies and peppers, green	Cabbages and other brassicas	Lettuce and chicory	Carrots and turnips	Cucumbers and gherkins
8	Chillies and peppers, green	Carrots and turnips	Eggplants (aubergines)	Pumpkins, squash, and gourds	Pumpkins, squash, and gourds	Yams
9	Cabbages and other brassicas	Sweet potatoes	Carrots and turnips	Chillies and peppers, green	Onions, dry	Eggplants (aubergines)
10	Pumpkins, squash, and gourds	Pumpkins, squash, and gourds	Garlic	Cauliflowers and broccoli	Onions (including shallots), green	Carrots and turnips

Source: Reproduced from FAOSTAT, 2012. Food and Agriculture Organization of the United Nations website. Available at: http://faostat.fao.org/default.aspx (accessed 14.01.14).

productive life of the plant. Some cultivars additionally have extended juvenile periods (early life phase dominated by vegetative growth), such as pecan (up to 10 years) (Thompson and Grauke, 2003). These long lead times to production increase vulnerability to future changes. Annual crops, however, can be modified more easily to incorporate different varieties or management strategies and they also produce on shorter timeframes.

Temperature Impacts on Growth, Yield, and Quality

Temperature is a key determinant in the successful production of horticultural products. With climate change, warmer temperatures may act to hasten developmental phases of plants. For annual crops such as lettuce (Pearson *et al.*, 1997), French bean (Wurr *et al.*, 2000), and tomato (Maltby, 1995), this may allow for more cropping cycles per year, resulting in increased production.

Changes of timing in winegrape ripening has been observed in Europe (Jones *et al.*, 2005; Le Roy Ladrie, 1988; Seguin and de Cortazar, 2005) and Australia (Petrie and Sadras, 2008). A recent study of 44 vineyard sites from 12 regions located in southern Australia reported a trend to earlier maturity of wine grapes in 43 of the blocks (Webb *et al.*, 2011; **Figure 3**). In the one site where an advance in ripening was not observed, Margaret River, the region had also not experienced

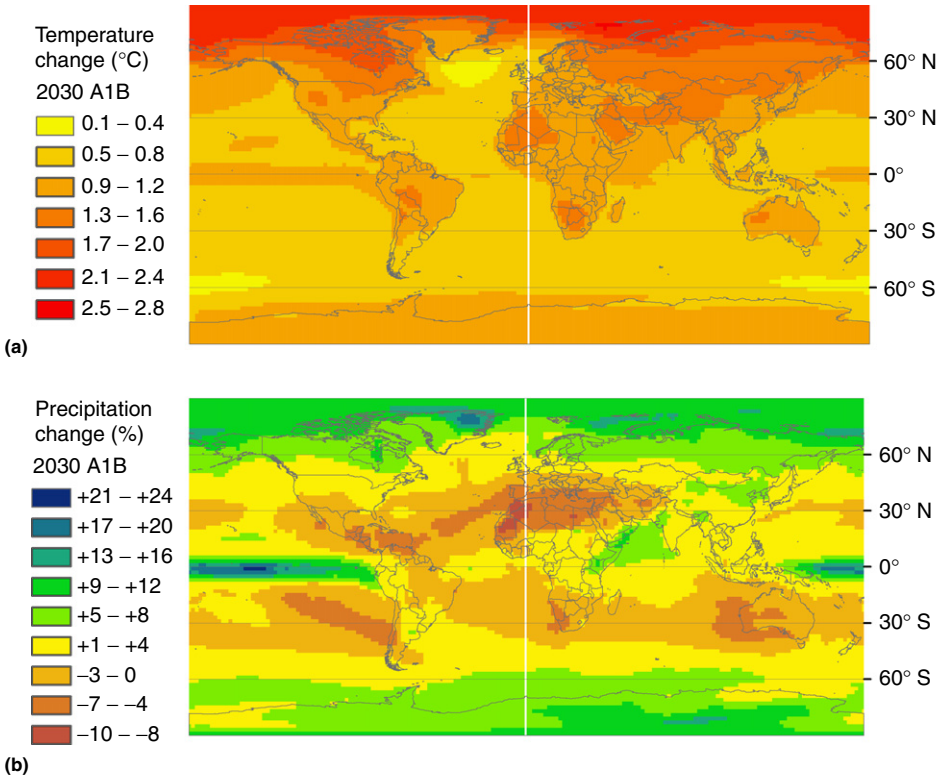


Figure 2 Projected annual temperature change (°C) (a), and annual rainfall change (%) (b) by 2030 (A1B emission scenario) as it varies spatially across the globe. Results depicted indicate the median of 23 CMIP3 climate models (Watterson and Whetton, 2011).

a warming growing, season for the period of observation. Over the more recent period, that is, 1993–2009 the average advance was 1.7 days per year, whereas for the period 1985–2009 the rate of advance was 0.8 days per year on average. With projected warming, ripening is anticipated to occur even earlier and in hotter climatic windows (Webb *et al.*, 2007b, 2012). Early ripening can have an adverse impact on wine quality with higher temperatures associated with altered balance of flavor and aroma compounds (Marais, 2001), hastening acid degradation (Liu *et al.*, 2006), and increasing the speed of sugar development (Sadras and Moran, 2012). Changes to wine styles and cultivar suitability are anticipated in the future (Webb *et al.*, 2013).

Many other crops across the globe have similarly recorded changes to phenophase timing in agreement with those expected from climate change (Rosenzweig *et al.*, 2008). For instance, the timing of apple flowering in France has been observed to advance by 2.6–3.0 days per decade in response to warming (Legave *et al.*, 2008). In contrast, observations in Australia are less pronounced with some apple growing regions recording a delay in flowering timing (1.4 days per decade) (Darbyshire *et al.*, 2013b). If observed advancements to flowering continue, interruptions to important production processes may transpire. For example, some crops require cross-pollinating varieties for fruit development (e.g., sweet cherries, pears, and apples). Asynchronous advancement of flowering between cross-pollinating varieties may cause misalignment of the flowering periods, potentially affecting pollination success, and, therefore, fruit set and yield. As well as tree cultivars losing synchronicity, pollination vectors may become climatically isolated from their food source, for example, butterflies and *Prunus* spp. (Doi *et al.*, 2008).

Many perennial deciduous fruit and nut trees require exposure to cool temperatures over winter to break dormancy and enter normal spring growth. Insufficient exposure to these winter chilling temperatures can lead to protracted and reduced bud break, poor pollination, abnormal fruit development, and small fruit sizes (Oukabli *et al.*, 2003; Petri and Leite, 2004; Saure, 1985; Voller, 1986; Maggs, 1975). Globally, it is expected that most temperate fruit and nut producing regions will face lower chill conditions in the future (Luedeling *et al.*, 2011). These chill conditions may drop below varietal threshold requirements leading to adverse production outcomes. Higher latitude regions are predicted to be minimally affected and in some circumstances accumulated exposure to chill is expected to increase (Luedeling *et al.*, 2011). Temperate growing regions may be significantly affected by declining winter chill, for example, Australia (Darbyshire *et al.*, 2013a).

Simulations of projected changes to pome fruit tree (e.g., apple and pear) flowering indicate that, depending on the cultivar selection, the physiological characteristics of the plant and expected climate change, flowering time may be delayed, advanced, or remain unchanged (Darbyshire *et al.*, 2013b). These different responses are the result of the opposing actions of delayed winter chill accumulation and acceleration of the time required to develop flowers (**Figure 4**). Exactly how a warming climate will affect the timing of budburst is not straightforward. For example, in a cool region (**Figure 4(a)**)

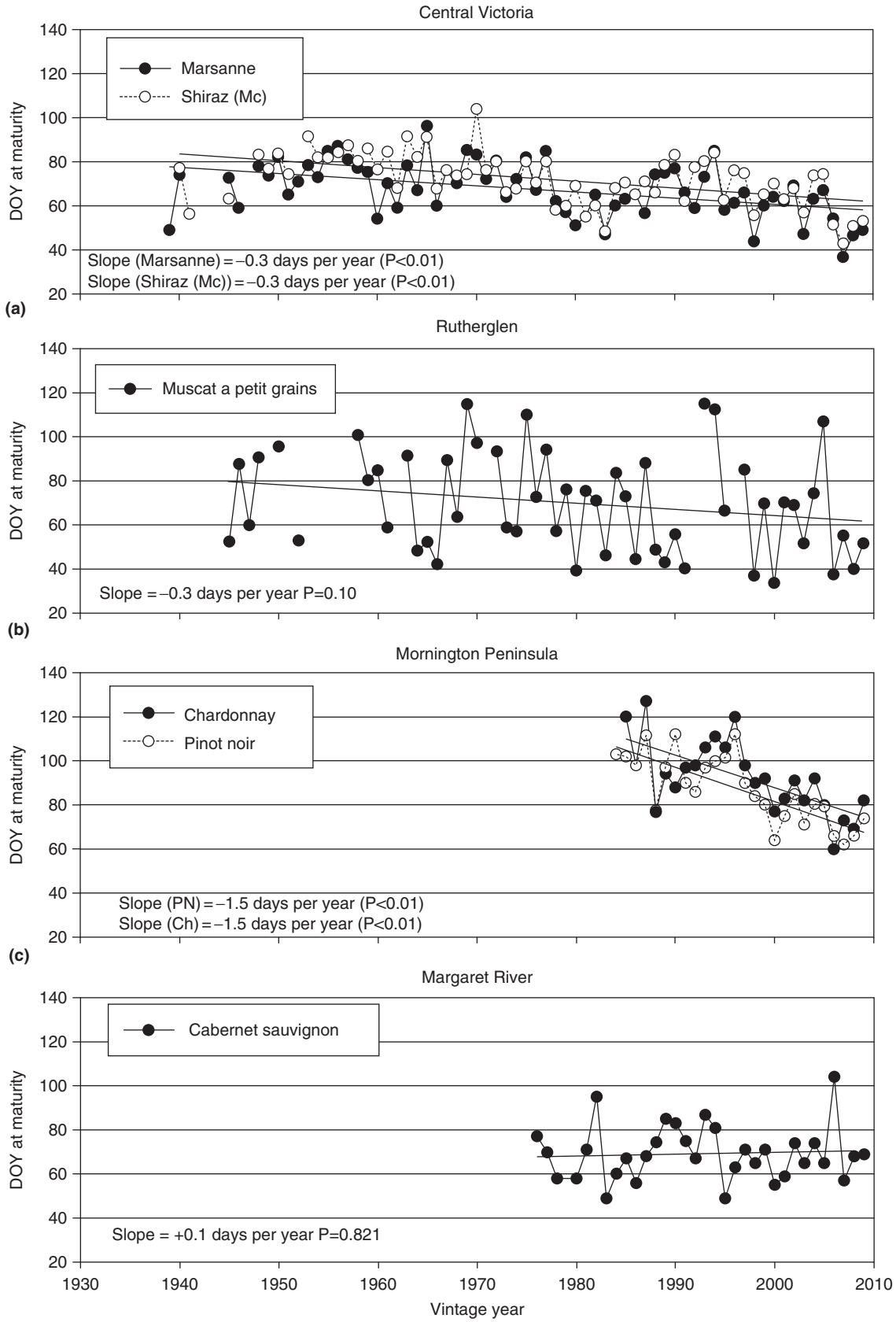


Figure 3 The observed day of year (DOY) at maturity recorded for six blocks from four regions (a) Central Victoria: Marsanne (1939–2009) (solid circles), Shiraz (Mc) (1940–2009) (open circles) and (b) Rutherglen: Muscat a Petit Grains (1945–2009) (c) Mornington Peninsula: Chardonnay (1985–2009) (solid circles) and Pinot Noir (1984–2009) (open circles), and (d) Margaret River: Cabernet Sauvignon (1973–2009). The best fit linear regression indicates the average trend in the maturity day (Webb *et al.*, 2011).

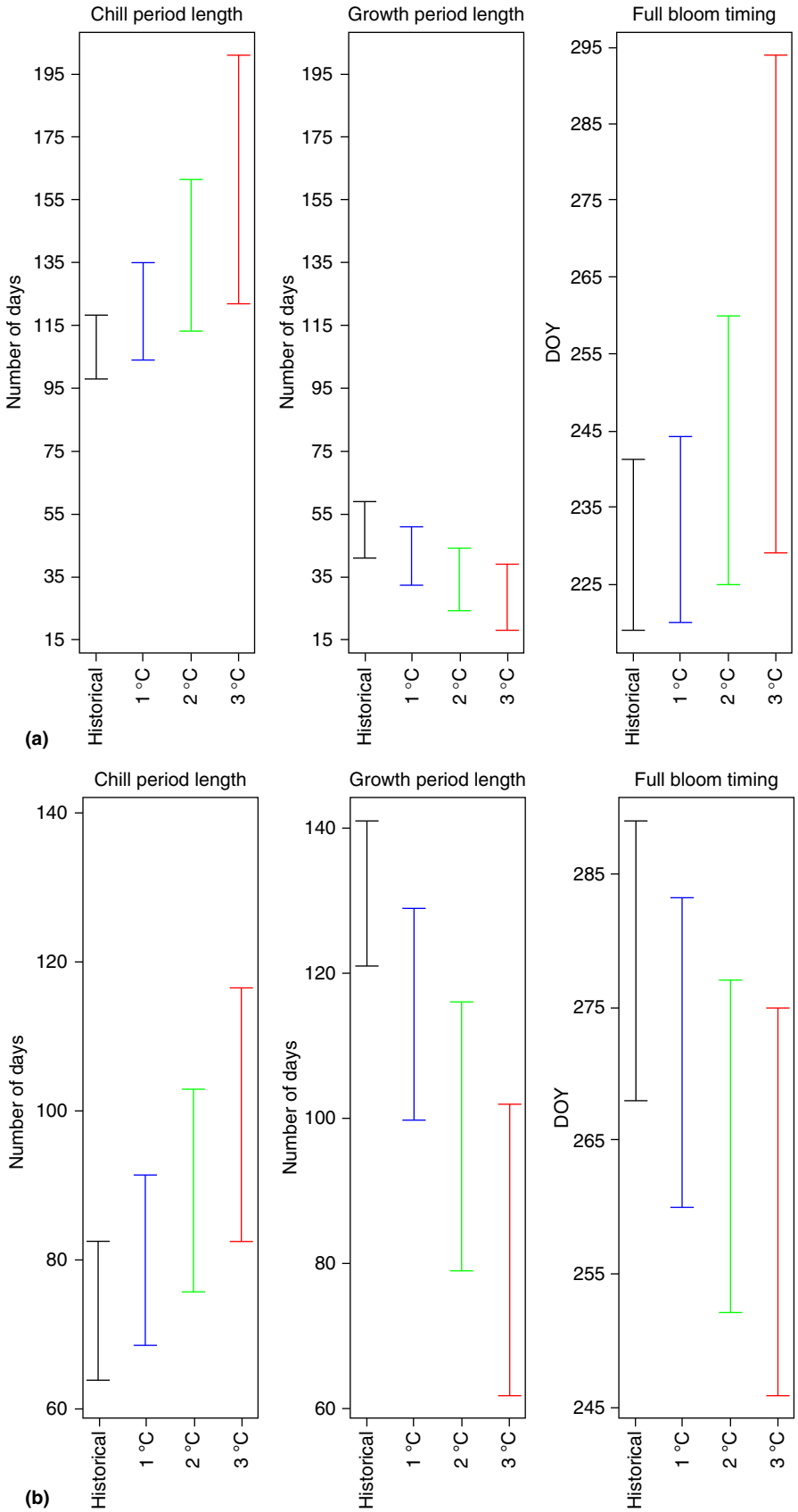


Figure 4 Alternate simulations for projected changes to pome fruit full bloom timing at (a) cooler and (b) warmer location. Projections are relative to +1, 2, and 3 °C increases to mean global temperatures. The relative influence of the chill and growth periods on expected flowering timing led different prediction of flowering delay or flowering advancement (unpublished data).

although chill is prolonged with a warming climate, the projected warmer spring still dominates the dormancy-breaking process, leading to earlier bloom time. In contrast, in a warmer region (**Figure 4(b)**), chill accumulation is already marginal in the current climate. With warming, chill is noticeably delayed and the limited influence of warming in spring does not compensate for this, leading to an overall delay in budburst. This regional variation in response has implications for future changes to frost incidence during the flowering period for apples (Darbyshire *et al.*, 2013c).

It should be appreciated that changes to the timing of flowering is yet to be fully understood from a physiological point of view, with greater research into phenology–temperature relationships, as well as development of models to represent these, required (Darbyshire, 2013).

The physiology of tropical crops may also be influenced by warmer winters. Temperatures between 11 and 14 °C are optimal for flower growth in lychee (Gao and Huang, 2004). Winter temperatures higher than this optimal may encourage vegetative over floral growth and thereby decrease the productive output of the plant (Chen, 2012).

Changes to springtime temperatures may also influence production with excessively warm temperatures during bloom or early fruit set known to induce abscission (premature fruit fall) in citrus fruit (Rosenzweig *et al.*, 1996), capsicum, and chilies (Murison, 1995), and adversely affect pollination of avocado (Schaffer *et al.*, 2002) and some tomato varieties (Sato *et al.*, 2000). High spring temperatures can cause reductions to peach yields (Lopez *et al.*, 2007), and modeled impacts have shown that future yields of almonds, table grapes, oranges, walnuts, and avocados are likely to be affected (Lobell *et al.*, 2006; Stöckle *et al.*, 2010). Berry collapse in table grapes (Tilbrook and Tyerman, 2008) has been associated with high temperature conditions during postberry set.

High-temperature impacts can be negative for quality and yield across many varieties. Reduced sugar content in products such as pea, strawberry, and melon produced under warmer nights is often attributed to increased night-time respiration. However, this effect may also be caused by high temperatures reducing the period over which fruit develops (Wien, 1997). An increase in maximum temperatures may negatively impact yield and quality of leafy crops such as lettuce and spinach (Titley, 2000). Bolting (premature formation of the seed head/flowers) is an example of a negative impact resulting from growing these crops in high temperature regimes (Dioguardi, 1995). The timing of elevated temperatures has been shown to reduce vitamin C levels in fruit production in woody perennials (Richardson *et al.*, 2004).

Production of anthocyanins (pigments responsible for the red, purple, and blue colors) for apple, pear, purple potato, pomegranate, legumes, and grapes is often related to commercial quality and the health advantages of foods (for a review, see Tsuda, 2012). The accumulation of anthocyanins is partly dependent on environmental conditions with cool minimum temperatures during maturation promoting production whereas high maximum temperatures act to destroy the compound (Lin-Wang *et al.*, 2011; Marais *et al.*, 2001; Steyn *et al.*, 2004; Xie *et al.*, 2012). As such, coloration may be degraded due to both higher minimum temperatures and higher maximum temperatures. Citrus fruit quality, with respect to both development of sugars and color, is also influenced by warmer temperatures, with a decrease in tree storage time and rind regreening increasing as temperatures rise (Rosenzweig *et al.*, 1996). The red color of ripening capsicums develops between 18 °C and 25 °C. But if temperatures rise above 27 °C during the ripening, a yellowish color results (Murison, 1995). Yellowing can also occur in tomatoes experiencing high temperatures when ripening (Maltby, 1995).

After harvest, many products including beans, melons, cherries, and strawberries require cooling so as to remove field heat quickly (Alique *et al.*, 2006; Coombs, 1995). With projected temperature rises, the costs and benefits of shifting harvest time to a cooler part of the day, or increasing refrigeration, will need to be assessed. Further, higher growing temperatures may negatively impact the shelf-life of lettuce (Rogers, 2007).

Benefits to horticultural production from increasing temperatures are also likely. For instance, mangoes grown in the subtropics can suffer from leaf yellowing when winter temperatures fall below 10 °C, due to photoinhibition of the photosynthetic apparatus (Sukhvibul *et al.*, 2000). This low temperature photoinhibition has also been reported for lychee and rambutan (Diczbalis and Menzel, 1998) and banana (Damasco *et al.*, 1997). In a warmer climate, cold-induced photoinhibition will be reduced and greater agronomic potential may exist in some areas currently considered to be marginal. Further, there may be benefits for Solanaceous vegetable crops (e.g., tomatoes and capsicum), which are currently seeded in heated glasshouses and transplanted into the field when the danger of frost has past (Peet and Wolfe, 2000). These crops may be directly seeded at locations where frost risk reduces, lowering production costs. Production of dried fruit, such as Thompson Seedless (sultana) and raisins, could also benefit as solar drying capacity increases as temperatures rise and humidity and rainfall decrease in regions with Mediterranean climates (Possingham, 2008).

Water Balance Impacts

Access to adequate water supply is a fundamental requirement for horticultural production. Generally, rain-fed systems are likely to be more vulnerable to future climate changes than irrigated crops. Nevertheless, irrigated horticulture may still face challenges for regions with predicted decreases to rainfall and increased evaporation leading to lower inflows into catchments, reducing the water available for irrigation (Cai *et al.*, 2009; Daccache *et al.*, 2011; Potter *et al.*, 2008). Similarly, reduced winter snow accumulation in colder regions may reduce stream flows due to lower snow melt run-off, with projections for Yakima basin in Washington State indicating such water shortages are likely to increase with future warming (Vano *et al.*, 2010). Compounding lower stream flows, competition of water resources from other sectors, such as for environmental, urban, or industry use, may further restrict water available to horticulturalists. In addition to changes in water availability and accessibility, crop water requirement will increase under warmer conditions. This puts greater pressure on water resources although increase in humidity and atmospheric CO_2 may counter the effects of elevated temperature on crop evapotranspiration (Snyder *et al.*, 2011).

Extreme Event Impacts

Changes in the frequency and severity of extreme events are likely to pose a substantial risk to future horticultural production. In a survey study of the effects of a heat wave event on grape vines in Australia, Webb *et al.* (2010) presented a range of impacts including stalled development, leaf burn, leaf drop, berry sunburn, and berry shrivel. The authors of the study suggested that the stalled or delayed sugar accumulation of up to 3 weeks was attributed to leaf damage during the heat wave (Kliewer and Dokoozlian, 2001), caused by heat-stress induced lack of water (Thorne *et al.*, 2006). The greatest delays occurred in the region where there was a cool lead-up to the heat wave, and the vines were not acclimatised to the heat. It is understood that consistently higher temperatures throughout the growing season have been shown to produce higher thermostability of photosynthesis functionality in grapevine leaves (Zsofi *et al.*, 2009). Through this same heat wave, citrus, apple, pear, and grapes were all adversely affected by direct radiation (**Figure 5**).

Future temperature projections indicate fewer frost days (IPCC, 2007) so it might be expected that horticulturists would experience less frost damage. However, if flowering occurs earlier, frost risk may not be reduced or stay the same (Darbyshire *et al.*, 2013c; Eccel *et al.*, 2009). In some regions, lower rainfall in spring and associated drier soils, fewer clouds, and lower dew points may even increase frost risk (Webb and Snyder, 2013). Furthermore, an increase in day-to-day climate variability may lessen any 'positive' impact of mean warming on reducing frost frequency (Rigby and Porporato, 2008). Changes to timing of frost events are important for horticultural production. For instance, the last observed frost day appears to have been delayed at Tatura, VIC, an important horticultural location in Australia (**Figure 6**). Such a delay will likely increase risk of damage to crops even if the overall number of frost events decline.

Increasing concentrations of carbon dioxide in the atmosphere have been found to render plants more susceptible to potential frost hazard (Woldendorp *et al.*, 2008). Nevertheless, for annual crops, a reduction in risk may be possible as planting/sowing dates can be managed.

Drought intensity and duration is projected to increase in some seasons and regions due to reduced precipitation or



Figure 5 Impact of direct radiation damage to (a) oranges, (b) apples, (c) pears, and (d) wine grapes during the 2009 summer heatwave in South-east Australia (pome fruit photos courtesy Malcom McCaskill, Vic DPI).

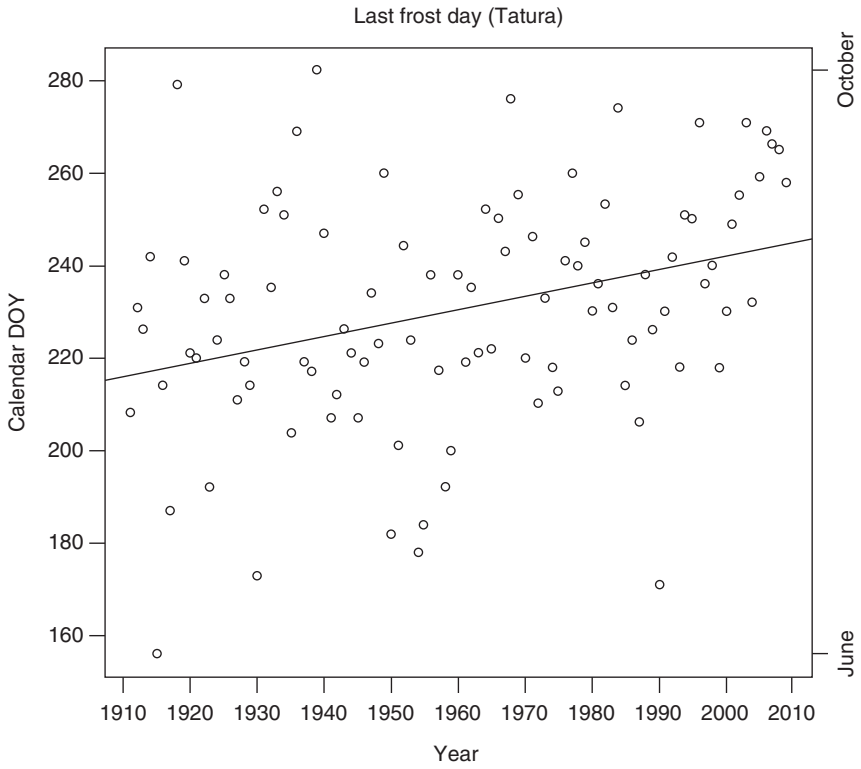


Figure 6 Observed day of year (DOY) relating to the last frost event (daily minimum temperature ≤ 0 °C) at Tatura, Australia (unpublished data).

increased evapotranspiration (IPCC, 2012). Economic impacts are often large with, for example, the 1999–2000 period drought in Iran reducing gross domestic product by 4.4% (Salami *et al.*, 2009).

In contrast to periods of drought, more extreme rainfall periods can also be problematic. Direct damage to the crop can result from high rainfall events. Splitting or cracking in cherry fruit arise from excess water uptake close to harvest. The degree of damage will vary with variety and seasonal effects (Measham *et al.*, 2009). Water logging of the root zone of most woody plants has a negative impact on physiology. Inadequate oxygen supply is the primary cause of damage (Flore, 1994). Flow on effects of excessive rainfall to management such as a delay to farm operations can disrupt production and add costs (Falloon and Betts, 2010). Further, with an increased incidence of extreme events (e.g., heat and flooding), the timing of spraying, harvest, pruning, and planting may be affected. Access to fungicides through flood events may be problematic if the recent Australian experience is any indication (Webb, 2011).

Australian region studies indicate a likely increase in the proportion of tropical cyclones in the more intense categories but a possible decrease in the overall frequency of cyclones (CSIRO and Australian Bureau of Meteorology, 2007). However, globally, there is low confidence in any observed long-term (i.e., 40 years or more) increases in tropical cyclone activity (i.e., intensity, frequency, and duration), after accounting for past changes in observing capabilities (IPCC, 2012). The magnitude of the impact cyclones can have is demonstrated by Severe Tropical Cyclone Larry (Australian Bureau of Meteorology, 2006), which crossed the Queensland coast of Australia in 2006. Devastating crop loss of AUS$300 million to the banana industry was initially caused, with a further AUS $150 million being required for replanting, renovating, and rebuilding after the cyclone (Leahy, 2006).

Hail can cause direct damage to crops and lead to large economic losses (Ogurtsov *et al.*, 2008). A recent study in the Netherlands showed that by 2050 annual hailstorm damage to outdoor farming could increase by between 25% and 50%, with considerably larger impacts on greenhouse horticulture in summer of more than 200% (Botzen *et al.*, 2010).

Climate change may also influence the characteristics of bushfires/wildfires (Lucas *et al.*, 2007). Smoke from bushfires (or controlled burning) can reduce the sensory characteristics of wine, leading to 'smoke taint' (Kennison *et al.*, 2008) and unsalable wine. Smoke taint due to bushfires cost Australian grape growers more than AUS$7.5 million during the 2003 and 2004 vintages (Whiting and Krstic, 2007). With the incidence of forest-fires projected to increase in the Mediterranean area (Moriondo *et al.*, 2006), a region with many vineyard plantings, the risk of smoke taint is likely to increase.

Human factors need to be considered when discussing impacts of climate change on horticulture. Direct impacts of climate change include increasing heat stress levels of workers. Where workforces are likely to be exposed to more extreme conditions, changes to current practices may need to be undertaken to avoid potential negative human health outcomes (Kjellstrom *et al.*, 2009). Other impacts of drought on the community can be subtle and difficult to economically quantify although of significant social concern. In Australia, research has indicated that during periods of drought rates of suicide in males in rural areas notably increases (Hanigan

et al., 2012). Aspects of social activities can also be affected, further impacting communities. For example, a recent extended drought in Australia reduced access to sporting fields occurred as turf could not survive (Sport and Recreation Victoria, 2007).

Pest, Disease, and Weed Impacts

Elevated temperatures may increase pest and disease pressure due to higher populations caused by shorter life cycles and decreases to generation times (Aurambout *et al.*, 2006). Conversely, other factors such as lower rainfall and humidity may reduce disease pressure (Coakley *et al.*, 1999). Increased survival of pests that normally do not withstand cold winters, for example, the cabbage moth (*Phitella xylostella*) (Deuter, 1989), is of some concern in a warmer climate. Disease threat may also increase, as in the case of citrus canker, where warmer winter temperatures would support a continuous life cycle in subtropical and temperate regions and potentially favor establishment in regions outside its historic range (Aurambout *et al.*, 2006). A 1.0 °C rise in temperature is expected to dramatically increase the cost of controlling the Queensland fruit fly in Australia without accounting for any increased risk to current fly-free zones (Sutherst *et al.*, 2000).

The range and severity of Phoma stem canker (blackleg, *Leptosphaeria maculans*), an internationally important disease of wild and cultivated brassicas, may increase with projected climate change (Evans *et al.*, 2008). Models also predict an increase in severity of downy mildew (*Plasmopara viticola)* epidemics on grapes in an important Italian wine-producing region near Turin in 2030, 2050, and 2080 (Salinari *et al.*, 2006).

It is likely that anywhere where rainfall or humidity are projected to increase, the incidence of infections with fungal pathogen will increase (Magarey *et al.*, 1994; Webb, 2006). An increase in the frequency of extreme rainfall events, especially in combination with higher temperatures, may also lead to conditions that favor root-invading fungus like *Phytophthora cinnamomi*, which affects avocado (Howden *et al.*, 2005). Wet soils may predispose crops to rot development, whereas dry and warm conditions favor insect population growth and viral vector epidemics (Rosenzweig *et al.*, 2001).

Temperature changes, altered wind patterns, or flooding may allow tropical and frost-tolerant weed species to move into temperate regions. Competitiveness both between different weed species and between weeds and crop species may be altered (Fuhrer, 2003). Changes to weed seasonal survival can interact with pest pressure, with persistence of weed hosts for crop pests prevailing through winter, increasing the ability of pests (e.g., the Silverleaf Whitefly) to overwinter (known as a 'green bridge') (Aurambout *et al.*, 2006).

Finally, the direct effect of elevated CO_2 concentrations may also influence pest and disease pressure. High CO_2 concentrations can change host morphology and phenology, pest fecundity and life cycle, and plant disease epidemiology (Chakroborty, 2004). The confluence of changes to climate variables, host physiology, and pest and disease characteristics will dictate changes to plant susceptibility under climate change conditions.

Impacts from Changes to Carbon Dioxide

Direct impacts from changes to CO_2 concentrations may also influence future production of horticultural products. Higher concentrations of CO_2 may improve plant water use efficiency (Grant *et al.*, 2004; Morgan *et al.*, 2004) and reduce stomatal conductance. This reduced conductance could lower transpiration rates assuming the smaller aperture does not result in a very large increase in leaf temperature. Whether this affects water use efficiency of the whole plant depends on whether the leaf area increases, caused by the increased growth in enriched carbon dioxide environments, counteracts the effect of reduced stomatal conductance (Drake *et al.*, 1997; Rosenberg *et al.*, 1990).

For C3 crops, research suggests that elevated CO_2 may have many positive effects; including yield stimulation, improved resource-use efficiency, more successful competition with C4 weeds, reduced ozone toxicity, and in some cases better pest and disease resistance (Fuhrer, 2003). Across all horticultural species, the effects of elevated CO_2 on plant growth and yield will depend on photosynthetic pathway, species, growth stage, and management regime and its implications for water and nitrogen applications (Easterling *et al.*, 2007). Thus, it is likely that horticultural crop responses vary. Wurr et al. (2000) found a null response of French bean to CO_2 enrichment, whereas positive effects have been reported for onion (Daymond *et al.*, 1997), beetroot and carrots (Wurr *et al.*, 1998), avocado (Schaffer *et al.*, 2002), citrus (Rosenzweig *et al.*, 1996), and banana (Schaffer *et al.*, 1996).

As well as assessing the implications of these crop-specific CO_2 enrichment effects, interactions with related temperature and water supply changes will be imperative. These changes will modify, and often limit, direct CO_2 effects on plant growth (Easterling *et al.*, 2007). For instance, with lettuce, increasing CO_2 should increase yield, but this will be partially offset by warmer temperatures (Pearson *et al.*, 1997). Positive effects of CO_2 on potato crop growth counteracted the negative effects of warmer temperatures depending on the initial temperature regime (Miglietta *et al.*, 2000). In contrast, Rosenzweig *et al.* (1996) found minimal compensating effect of CO_2 on potato yields. Wurr *et al.* (1998) found carrots had a temperature optimum of approximately 15.8 °C for maximum responsiveness to CO_2 enrichment.

The quality of products may also be influenced under a CO_2-enriched atmosphere. Plant responses to elevated atmospheric CO_2 may increase the carbon to nitrogen ratios in plant tissue (Drake *et al.*, 1997; Morison and Lawlor, 1999). This can reduce the nutritional value of some vegetables to human consumers. In stating this, however, a review of many free air CO_2 enrichment studies has reported that this effect is small (Ainsworth and Long, 2005).

Horticultural Adaptation to Climate Change

Site Selection

Site selection for horticultural production is a practice critical to crop success even in a stable climate. Temperature, the dominant factor that determines where and when horticultural

crops are grown, has a significant influence on crop performance (i.e., time to harvest, product quality, and, to a lesser extent, yield). In a warmer future climate, this practice of carefully selecting appropriate sites for annual crops will continue. However, when selecting sites for perennial species it is imminently more important and urgent to consider the changing climate. This is because some of these crops (e.g., fruit trees and grape vines) have an average life of more than 30 years. Within that time-frame global average warming of at least 1 °C is anticipated (Rahmstorf *et al.*, 2007), and crops planted today are expected to remain productive.

By selecting more elevated sites, or avoiding north-westerly aspects in the Southern Hemisphere and south-westerly aspects in the Northern Hemisphere, horticultural potential can be extended where regions may otherwise become too warm. Ultimately, if climate warming increases to a level whereby the region becomes too hot for the particular crop, pole-ward shifting of horticultural zones will enable production to continue, with increasing suitability of currently cold-marginal regions (Olesen and Bindi, 2002). For example, horticulture production is currently limited by winter temperatures and late spring frost in northern European regions like Scandinavia and Siberia (Dehnen-Schmutz *et al.*, 2010) and the UK (Daccache *et al.*, 2011). Further, an assessment of the productive range of apples in Finland for the year 2040 found that land suitable for production will increase northward as will the range of varieties available for cultivation (Kaukoranta *et al.*, 2010).

Mapping of threshold temperatures and other relevant aspects of the climate for a range of future climate regimes can expose risky, or less-risky, areas in which to plant crops. With a potential reduction of frost-prone areas under climate change, the area suitable for growing tropical and subtropical crops is projected to expand, such as for olives (Olesen and Bindi, 2002), citrus, avocados, and bananas in the Mediterranean region of Europe (Houerou et al. 1992) and for avocados and pecan nuts in Southern Africa (Schulze and Kunz 1995).

Changing average rainfall conditions may increase or reduce suitability for growing certain crops. Note that where crops are irrigated the catchment may be remote from the production area. In these cases information regarding projected rainfall over the catchment region will be essential for planning purposes (Chiew et al., 2009).

A global-scale increase in extreme rainfall may mean increasing risk of floods or erosion (IPCC, 2012). Impacts are complex and influenced by localized factors, but avoiding low-lying sites and considered planting of erosion-prone slopes may help avoid some of the potential impacts from these precipitation events. In tropical regions, although the number of cyclones is projected to reduce in future, the intensity of these may increase, so selecting sites to avoid cyclone hazard, for example, away from the coast, may be advisable.

Crop Management

The timing of management activities, such as planting, fertilizing, and irrigation can be adjusted in response to climate shifts (Krug, 1997). Because climate change is expected to reduce the duration from sowing to harvest for some annual crops there can be consequent reductions in yield (Olesen *et al.*, 1993). These yield decreases may be compensated by sowing annual crops earlier. Where crops mature more rapidly, it may be necessary to plant smaller areas of crop more frequently in an attempt to reduce market supply fluctuations (e.g., for cauliflower) (Olesen and Grevsen, 1993). In some areas, autumn soil temperatures could become too high for good germination of celery so planting later in the season can be an option (Peet and Wolfe, 2000). For potatoes, however, planting later in the season to avoid very hot temperatures may be compromised by the shorter day lengths later in the year, which have a negative impact on yield (Rosenzweig *et al.*, 1996). Thus, any planned change in sowing needs to be accompanied by considerations of day length requirements. As the timing of winegrape harvests has been linked to soil–moisture status, crop load, and temperature (Webb *et al.*, 2012), water management or crop-load manipulation could be used to manage undesirable shifts in timing under climate warming.

Given chilling levels are projected to reduce in temperate regions (Luedeling *et al.*, 2011), managing variable and protracted bloom of pome and stone fruit and nut trees may be necessary (Saure, 1985). For example, pesticides with longer residual action may be required to protect the crop if the flowering period is substantially lengthened. Application of hydrogen cyanamide, to promote budburst as an adaptation option for inadequate chilling, is becoming more common in perennial fruit-growing operations (e.g., table grapes; George and Nissen, 1990), though concerns regarding risks due to human exposure have been reported (Schep *et al.*, 2009). Evaporative cooling by water sprinkling (Nir *et al.*, 1988; Erez and Couvillon, 1983) can also be used to lower winter temperatures and thereby increase chill accumulation. However, this adaptive strategy needs to be balanced against water supply and security. Rootstock selection is a promising area for future research to adapt to lower chill conditions yet retain the same variety mix. Finetto (2004) considered the influence of rootstock on chilling requirements of Golden Delicious apple. Rootstock was found to be important with plants on M-11 rootstock appearing to require less 'chill' than those on either M-26 or M-27.

Extreme rainfall is likely to increase in frequency (IPCC, 2012) and consequently flooding may also occur in some regions. Schultz (2000) explains that in Europe, shifts in precipitation patterns may necessitate introduction of cover crops between vine rows in order to minimize soil erosion. Such measures could include the planting of interrow groundcover using 'drought-tolerant' grass and legume species (Pardini *et al.*, 2002). Plastic shelters are another way used to minimize damage from untimely or extreme rainfall events reducing berry splitting and berry drop in table grape production (Possingham, 2008).

Diverse management approaches enacted before and during a severe heat wave in Australia in 2009 have been documented (Webb *et al.*, 2010). Variations in management of water application, canopy cover, row orientation, and phenological stage were found to affect the level of impact. For example, water application before the heat wave was found to be useful in ameliorating the level of impact (**Figure 7**). If the leaf canopy protected the grape bunches from radiation,

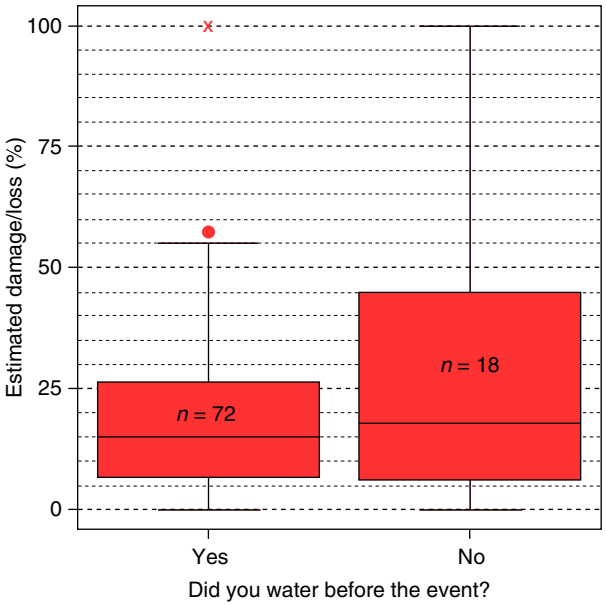


Figure 7 Survey results showing estimated damage/loss (%) of individual growers' winegrape crop in relation to timing of irrigation application with regard to the 2009 summer heatwave in south-eastern Australia (Webb *et al.*, 2010).

reduced fruit damage was also reported (Webb *et al.*, 2010). In the case of perennial tree crops, consideration of canopy structure could also be scored for useful traits such as natural self-shading ability. In some cases, however, increased canopy management in an enriched CO_2 environment may need to be addressed if CO_2 stimulates vegetative growth causing intra-canopy shading.

Hail netting has been found to be particularly suited to high-yielding, intensive apple orchard systems in Australia to reduce fruit sunburn, improve color and skin finish, and eliminate bird damage (Middleton and McWaters, 2002). Commercial kaolin-based coatings (also used as a pest repellent) can also be used to reduce sunburn (Thomas *et al.*, 2004). Further, evaporative cooling from overtree sprinklers can lower fruit temperature (**Figure 8**), reduce sunburn (Parchomchuk and Meheriuk, 1996), and improve color in apple (Thomaia *et al.*, 1998).

Lower levels of management and cost saving may also result from climate warming. For instance, many horticultural crops are grown in glasshouses to protect against unfavorable weather. In higher latitude climates these are often artificially heated adding cost to production. With a warming climate, a reduced need for heating will lower energy costs to the producers (Storck, 1978) and improve returns.

Varietal Selection and Crop Breeding

Every winegrape variety has specific genetically determined phenology (McIntyre *et al.*, 1982), which results in very different times of harvest (Gladstones, 1992; Kerridge and Antcliff, 1996). Matching of the phenology of the different varieties to a particular climate is a fundamental aim for every vineyard manager (Jones and Davis, 2000). The impact of climate change on varietal suitability in viticulture sites in European (Kenny and Harrison, 1992; Schultz, 2000) and Australian regions (Webb *et al.*, 2007a) have been examined. A global intercomparison of projected climate changes offers winegrowing practitioners a chance to assess the spatial variability of the changing climate and provides analog future climates for comparison (Webb *et al.*, 2013). As such, variety selection for replanting can be made in view of phenology traits that will be anticipated in future climates.

Approaches to matching varieties to climate also exist for annual crop production. In some cases, long season varieties may be more suited to a future climate than short season varieties (e.g., onion) as the hastened progression through phenological stages can be somewhat negated (Daymond *et al.*, 1997). One advantage of this is that ripening in a later and possibly cooler part of the season could reduce the risk of potential curing problems (Salvestrin, 1995). Alternatively, double-cropping could be practiced using shorter season varieties at some sites with some crops (Meza *et al.*, 2008), though this has implications for increased water use.

Crop or cultivar selection and planting dates can be changed to either suppress flower initiation, in the case of celery, onion, or cabbage, or delay flowering, in the case of broccoli and cauliflower (Coombs, 1995). Crops with extended flowering periods like peas and pumpkin are less sensitive to periods of heat stress compared with those that have more tightly determined flowering times (e.g., cauliflower and broccoli) (Peet and Wolfe, 2000).

Breeding for improved tolerance to heat and enhanced water use efficiency, with consideration of the interactive effect of increasing concentrations of CO_2 on physiology, provides an adaptation option for crops growing in subtropical regions, where a warming and likely drying climate is projected. There exists great potential to enhance the adaptive capacity of grapevines through conventional breeding or genetic manipulation. With a large pool of genetic variants (both varieties and clones) (Thomas and Van Heeswijck, 2004), and 500 million bases of the *Vitis vinifera* genome now sequenced (Velasco *et al.*, 2007), the research community is in a strong position to address the future and continuing challenges the changing climate. Breeding varieties more adapted to high temperatures can also reduce quality concerns with regard to lettuce (Rogers, 2007) and yield concerns with peas (Olesen *et al.*, 1993) and potatoes (Manrique and Bartholomew, 1991).

Stone-fruit varieties are defined by the chill requirements of the tree (Saure, 1985). To combat this restrictive feature, low chill stone-fruit are being bred for subtropical areas where very low winter chilling is experienced (Topp *et al.*, 2008; Topp and Sherman, 2000; Wilk, 2005). These varieties can also be utilized in areas expected to experience lower winter chill conditions.

Water Management

In many regions of the world, horticultural production occurs where the water requirement of crops is far higher than that provided by effective rainfall. In these places irrigation has been widely adopted to maximize yield and quality, giving more surety of harvest dates and also facilitating marketing

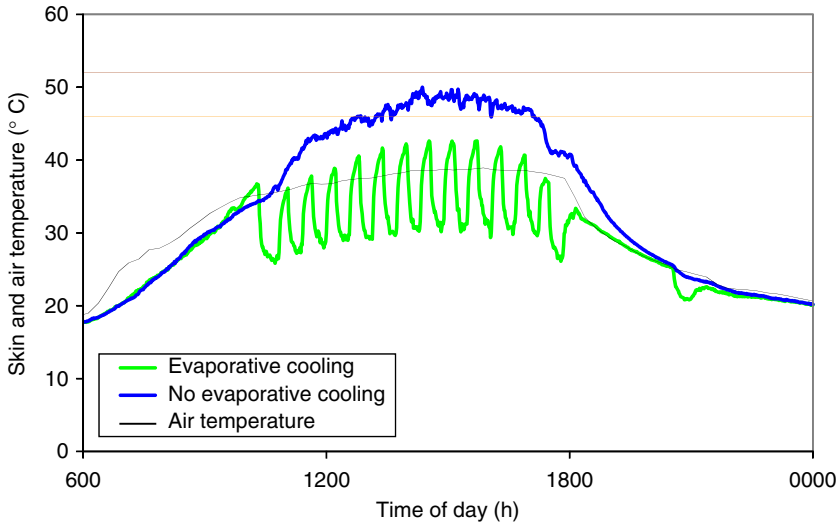


Figure 8 The effects of evaporative cooling on skin temperature of fruit exposed to direct sunlight in a commercial Royal Gala apple orchard in southern Australia. Evaporative cooling was imposed by applying water through permanent overtree microjets. Water was applied for 20 min and then turned off for 15 min. The horizontal lines represent thresholds for sunburn browning and sunburn necrosis (unpublished data).

plans of growers. With projected drying in subtropical regions, irrigators may need to reassess their irrigation strategies. In the United Kingdom, for example, modeling studies indicate that by the 2050s the capacity of existing irrigation schemes would fail to meet future irrigation demands for potato production in approximately 50% of years (Daccache *et al.*, 2011).

Options to reduce on-farm water needs include investing in improved irrigation management to match crop water requirement, and irrigation equipment to increase application uniformity and efficiency (Daccache *et al.*, 2011). Estimating crop water requirement from weather data with feedback from measurements of soil moisture, deep drainage, and crop water stress will improve irrigation management. Many vegetable growers use drip irrigation technologies, which provide a significant improvement to water use efficiencies when compared to furrow or sprinkler irrigation systems (Fereres *et al.*, 2003). The best irrigation practice to implement, however, can vary with soil type and crop morphology (Al-Jamal *et al.*, 2001). Deficit irrigation strategies like partial root-zone drying (Zegbe-Domíngueza *et al.*, 2003) and regulated deficit irrigation (Kriedemann and Goodwin, 2003) are strategies that could be explored more rigorously in some horticultural cropping regimes. Modifying soil structure to improve soil moisture retention (Bronick and Lal, 2005) or mulching the soil surface with organic matter can reduce the loss of water through evaporation (Tindall *et al.*, 1991). Night-time watering may result in reduced evapotranspiration losses. Applying saline water strategically may assist some growers to cope with severely reduced access to water in drought situations, though effects on soil structure will need to be considered (Clark, 2004). Cost and efficiency of distribution, holding dams, dam evaporation, and water quality maintenance will also need to be reviewed (Van Dijk *et al.*, 2006).

Drought is a common occurrence in the United States, (14% of the country experiences severe or extreme drought at any one time). So a national database of drought impacts and the economic losses associated with these impacts is being developed and is anticipated to provide comprehensive and timely information for researchers, planners, policy makers, and the general public (Ding *et al.*, 2011).

Increased use of reclaimed wastewater for horticultural enterprises can be considered. A summary of the major impediments to the use of reclaimed water by the Australian horticultural industry has been compiled (Hamilton *et al.*, 2005). Insufficient knowledge of impacts on market acceptance and of food safety issues, inadequate understanding of consumer perceptions and uncertainty about pricing of reclaimed water were raised as some of the potential issues that need to be resolved.

In some regions rainfall may increase on average in future. Disadvantages of increases in rainfall may be an increase in the need for plant protection from diseases, the risk of nutrient leaching, and the turnover of soil organic matter (Olesen and Bindi, 2002). More vigilance in disease management, as well as monitoring soil fertility will offer some adaptive potential, though both these options will add to the cost of production.

Whether elevated atmospheric CO_2 concentration reduces transpiration depends on the effects on leaf area index as well as stomatal conductance (Drake *et al.*, 1997), interactions between stomatal conductance, and increased vapor pressure deficit. Although increases in plant water use may result from possible increases in leaf area index, balancing this and possible reduced water use due to decreased stomatal conductance will need to be better understood to determine future water requirements for crops.

Weeds, Pests, and Diseases

Management of horticultural pests using pesticides, cultural practices, and biological control methods in relation to current climate variability depends on effective monitoring and predictive systems (e.g., Hetherington, 2005), varies with crop type, and is undertaken as a matter of course by horticulturists.

Certain existing preventive plant protection measures, such as use of a diversity of crop species in cropping systems, adjustment of sowing or planting dates, use of crop cultivars with superior resistance or tolerance to diseases and abiotic stress, use of reliable tools to forecast disease epidemics, application of integrated pest management strategies, and effective quarantine systems, may become particularly important in the future (Juroszek and von Tiedemann, 2011).

Under climate change, disease-assessment models should account for projected changes to overwintering of a wide range of insect pests and plant diseases and changes in the timing and severity of pest outbreaks. To date, the most common bioclimatic models used to predict potential range shift of species under climate change are 'CLIMEX' and 'BIOCLIM' (Aurambout *et al.*, 2006). Geographically sensitive models that use projected climate information focused on the use of biopesticides and natural enemies can be constructed to improve pest control. CO_2 effects on disease and hosts have to be considered when addressing future disease risks.

There is a clear requirement for consistently utilizing, adapting, and improving crop protection strategies and tools and enhancing the relevant knowledge base (Juroszek and von Tiedemann, 2011). Improved understanding of the drivers of disease cycles, epidemic development, and host responses will continue to be a fundamental prerequisite to enable farmers and advisors to predict and manage diseases under changing local conditions (Chakroborty, 2004).

Integrating Knowledge

Rain, or the threat of rain, may cause growers to pick early to reduce risk of disease (Jackson and Lombard, 1993). Short-term forecasting of extreme rainfall events close to harvest will become crucial given the projected increase in these events. Farmers can incorporate knowledge of seasonal forecasts, informed by improved information regarding patterns of regional climate drivers (e.g., El Niño-Southern Oscillation; Meinke and Stone, 2005). However, to benefit from seasonal climate forecasts, the decision capacity of the smallholder farmers needs to be improved and greater emphasis should be placed on farmer involvement and a demand-driven participatory approach (Selvaraju *et al.*, 2004).

Consumer Behavior

Availability of most horticultural crops (e.g., strawberries) tends to vary throughout the year and may be reduced in some seasons due to production difficulties caused by effects of higher temperatures, droughts, or other climatic events. In these cases consumers can pay higher prices to growers or pay more for an imported product (if available). In Australia, banana prices increased dramatically after Severe Tropical Cyclone Larry devastated the crop in 2006 (Clements and Maesepp, 2011). Color or nutrition levels of produce could be impacted by climate change, with some of the possible esthetic impacts identified being regreening of oranges, and yellowing of tomatoes and capsicums. Ongoing marketing programs are increasing consumer awareness of new and varied alternative produce.

Conclusion

The effects of climate change on crop quality will vary. The magnitude and extent of these impacts will be governed by the present climate of the region, the rate of projected change of climate and crop type. Management inputs available to ameliorate any adverse climatic impacts will be determined by the value of the crop and grower capacity. Because overall vulnerability will be crop- and site-specific, it is difficult to determine this for the horticulture industry as a whole, especially at a global scale.

Adapting to a changing climate may occur autonomously. For instance, farm managers currently adjust to gradually increasing temperatures by modifying timing of planting on a year-by-year basis. In some instances management may become easier, for example, frost avoidance mechanisms may not need to be implemented. Glasshouses may not require as much heating, though cooling requirements may be increased. However, planned adaptation will also be needed, particularly for high value, long-lasting permanent perennial crops (e.g., apples) with the associated infrastructure.

A focus on conventional breeding programs and biotechnology, once some of the potential vulnerabilities of horticultural crops have been identified, can build resilient cultivars that are more suited to future climates, for example, drought-tolerant cultivars. Considering the impacts of rising CO_2 on crops (and the interaction of CO_2 with increased temperature) would assist this endeavor.

Seasonal forecasts can be utilized to address interannual climate variability to enable effective use of resources (e.g., labor and planting material). As knowledge of climate systems improves, these forecasts should become more accurate and sophisticated and could include considerations of climate change trends.

Validation of climate indices that determine locations of current horticultural enterprises can be modeled relatively quickly so that predictions of potentially suitable crops for each region, or potentially suitable sites for particular crops, can be assessed. Risks associated with climate extremes can be assessed at the same time as suitable macroclimates and mesoclimates are being evaluated. Substantial benefits can be achieved if damaging temperature threshold events can be avoided in future.

Similarly, calculating the risks associated with changes to water availability may alleviate any adverse impacts with regard to allocating water to various agricultural sectors in the future, or in avoiding flood-prone areas. It will be possible to assess the water requirements for horticultural crops more accurately if the effect of rising CO_2 on crop water use is better understood. It will remain necessary to continue improvements in irrigation technology.

After identifying relevant, crop-specific, climatic thresholds, it will be possible to estimate whether climate change will increase or decrease the risks of growing crops in particular geographic locations. Some new regions may be identified as becoming more suitable for horticultural production, whereas others may become less suitable. An increase in production from subtropical and tropical regions could see new products being introduced, or a changed accessibility of produce. This

change will most likely be gradual and marketing strategies will need to adjust accordingly.

See also: Climate Change and Plant Disease. Climate Change: Cropping System Changes and Adaptations. Climate Change: New Breeding Pressures and Goals. Computer Modeling: Applications to Environment and Food Security. Mathematical Models to Elaborate Plans for Adaptation of Rural Communities to Climate Change. Plant Abiotic Stress: Temperature Extremes. Tree Fruits and Nuts. Water: Water Quality and Challenges from Agriculture

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Climate Change: New Breeding Pressures and Goals

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Glossary

Anthropogenic Caused or influenced by humans.
Aquifers An underground layer of permeable rock, sediment (usually sand or gravel), or soil that yields water.
Forward genetics Comprise of genetics techniques that aims to identify genes/mutations that produce a certain phenotype.
Genebanks Type of biorepository which preserves the genetic material. In plants, this could be by freezing cuts from the plant or stocking the seeds.
Genetic engineering Direct manipulation of the genes in an organism, with the intent of making that organism better, using biotechnology.
Glaciers A huge mass of ice slowly flowing over a land mass, formed from compacted snow in an area where snow accumulation exceeds melting and sublimation.
Ice sheets Layer of ice covering extensive regions of the world, notably Antarctica and Greenland.
Marker-assisted selection A process whereby a marker (morphological, biochemical, or one based on deoxyribonucleic acid (DNA)/ribonucleic acid (RNA) variation) is used for indirect selection of a genetic determinant or determinants of a trait of interest (e.g., productivity, disease resistance, abiotic stress tolerance, and quality).
Near-isogenic lines A term used in genetics and is defined as lines of genetic codes that are identical except for differences at a few specific locations or genetic loci.
Reverse genetics An approach to discover the function of a gene by analyzing the phenotypic effects of specific gene sequences obtained by DNA sequencing.

Climate Change

Climate changes are occurring and the discussions on their impact are rising. Climate changes are already providing significant challenges to natural systems. The discussion on the consequences of climate changes concerns different knowledge areas. Most of the observed increases in global average temperatures since the mid-twentieth century are very likely due to the observed increase in anthropogenic greenhouse gas (GHG) concentrations. The Fourth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC, 2007) indicates that the warming of the climate system is unequivocal, as it is now evident from observations of increases in global average air and ocean temperatures, widespread melting of snow and ice, and rising global average sea level. Significant changes in physical and biological systems have already occurred on all continents and in most oceans, and most of these changes are in the direction expected with warming temperature (Rosenzweig *et al.*, 2008). Global climate change is predicted to lead to extreme temperatures and severe drought in some parts of the world, whereas other parts will suffer from heavy storms and periodic flooding (Marshall *et al.*, 2012).

Estimates of changes in the global temperature are still uncertain. For the future, best estimates of temperature increases are in the range of 1.8–4 °C in 2090–99 relative to 1980–99, depending on the scenario of future GHG emissions that is used to drive the climate models (IPCC, 2007). Nevertheless, however low they may be, the consequences will be felt by all humanity to a greater or lesser degree. The most relevant fact is that most of the effects of these changes will affect developing countries (Lobell *et al.*, 2008).

There is a broad scientific agreement that the climate conditions are being changed on a global scale by human activities. Burning of fossil fuels, deforestation, and a variety of agricultural practices and industrial processes are rapidly increasing the atmospheric concentrations of CO_2 and other GHGs (IPCC, 2007). Projections to the year 2100 indicate that CO_2 emissions are expected to increase by 400% and CO_2 atmospheric concentration is expected to increase by 100% (Cline, 2007). Some studies have predicted increasingly severe future impacts with potentially high extinction rates in natural ecosystems around the world, and also, provided strong evidence of ongoing dramatic changes in the Earth's climate system. Among them, the long-term temperature records from ice sheets, glaciers, lake sediments, corals, tree rings, and historical documents demonstrate that every decade in the late twentieth century has been warmer than the preceding decades (Williams *et al.*, 2003; Thomas *et al.*, 2004; Hansen *et al.*, 2012; Jones *et al.*, 2009).

The most recent 50 years likely have been the warmest worldwide in at least the last 1300 years (IPCC, 2007), and 10 of the 11 warmest years on record have occurred since 2001 (Hansen *et al.*, 2012). Observations since 1961 show that at depths of at least 3000 m, the average temperature of the global ocean has increased; this deep storage of heat together with the higher heat capacity of water is causing the ocean surface to warm more slowly than the land surface (IPCC, 2007). Changes in snow, ice, and frozen ground have resulted in more, and larger, glacial lakes, increased ground instability in mountain and other regions, and led to changes in some Arctic and Antarctic ecosystems (Walker, 2007). The mountain glaciers and ice caps, as well as snow cover, are receding in most areas of the world. Both the Greenland and Antarctic ice sheets are now losing mass at increasing rates. The extent and thickness (volume) of Arctic Sea ice is declining, and lakes and rivers freeze later in the fall and melt earlier in the spring (IPCC, 2007; Allison *et al.*, 2009).

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The main climate changes that are occurring affect the level of the oceans, precipitation, and temperature. The global sea level has increased by approximately 12–22 cm during the twentieth century, but satellite records confirm that the rate of sea level rise has now almost doubled to approximately 3.4 mm year^{-1} (IPCC, 2007; Allison *et al.*, 2009). Precipitation is highly variable and trends are more difficult to isolate, but the overall precipitation and heavy precipitation events have increased in most regions; at the same time the occurrence of drought has also been on the rise, particularly since 1970 (IPCC, 2007; Allison *et al.*, 2009). Winter temperatures have increased more rapidly than summer temperatures, and nighttime minimum temperatures have warmed faster than the daytime maxima (IPCC, 2007; Meehl *et al.*, 2007).

All climate changes will have additional impacts via changes in the ecosystem, losses in agriculture, and of genetic diversity and changes to biotic and abiotic interactions with other species and ecosystem processes. These impacts are potentially very significant in determining the effects of climate change.

Climate Change on Agriculture

Agriculture is extremely vulnerable to climate change, and global warming is already changing agriculture in some parts of the world. Higher temperatures, changing patterns of rainfall, more extreme droughts and floods, eventually reduce crop yields without discouraging weed, disease, and pest challenges. Changes in precipitation patterns increase the likelihood of short-term crop failures and long-term declines in production. Although there will be gains in some crops in some regions of the world, the overall impact of climate change on agriculture is expected to be negative, threatening global food security. All will have an impact on food production in the future (Nelson *et al.*, 2009; Smith, 2011). Moreover, the impact of climate change on agriculture has repercussions that extend far beyond the supply of food. Agriculture accounts for 29% of the gross domestic product (GDP) in developing countries and provides jobs for 65% of their populations (Smith, 2011). In this scenario, the consequences will be catastrophic, not only for farmers, but for the economy as well. Using the results from formal economic models, it is estimated that, in the absence of effective counteraction, the overall costs and risks of climate change will be equivalent to a 5% decrease in global GDP each year (Stern, 2005). If a wider range of risks and impacts is taken into account, the estimates of damage could rise to a 20% decrease in GDP or more, with a disproportionate burden on and an increased risk of famine in the poorest countries (Altieri and Koohafkan, 2003).

It is possible to isolate some critical challenges that agriculture will face from climate changes, for example, water availability. In many regions water is extremely scarce and with increasing demand, the competition for its use will increase, especially with decreasing precipitation and the river flow changes. In Asia, rainfall changes and snow melt in the glacier, probably, are the biggest threats. In Africa, many people depend directly on rain for food and livelihood, and any change in the rainfall represents a great risk. Water quality is also a problem, the saline water will increasingly affect agricultural systems due to seawater intrusion, overexploited aquifers, and unsustainable irrigation practices (Moorhead, 2009). At mid- to high latitudes, crop productivity may increase slightly for local mean temperature increases of up to 1–3 °C, depending on the crop, whereas at lower latitudes, crop productivity is projected to decrease for even relatively small local temperature increases (1–2 °C). In the tropics and subtropics in general, crop yields may fall by 10–20% by 2050 because of warming and drying, but there are places where yield losses may be much more severe.

Higher temperatures will challenge many agricultural systems. Plants are sensitive to high temperatures during critical stages such as flowering and seed development. Often combined with drought, high temperatures can mean disaster to farmers' fields. Carbon dioxide levels also have implications for crop plants, although impacts are complex and need further research.

Many pests and diseases of crops, animals, and humans are sensitive to climate, and one can expect these to change in currently unpredictable ways. Some will become prevalent in areas where they were previously unknown, when the climate becomes favorable in those areas. Natural ecosystems are equally at risk from climate change.

Smallholder and subsistence farmers, pastoralists, and artisanal fisher folk will suffer complex, localized impacts of climate change, due both to constrained adaptive capacity in many places and due to the additional impacts of other climate-related processes such as snow-pack decrease and sea level rise.

Furthermore, changes in the frequency and severity of extreme climate will have significant consequences for food production and food security; not alone the mean climate change that will have an impact. Increasing frequencies of heat stress, drought, and flooding events are estimated to be likely, even though they cannot be modeled in any satisfactory way with current levels of understanding of climate systems, but these will have adverse effects on agricultural and natural systems over and above the impacts due to changes in mean variables alone.

Many recent studies have identified environmental climate changes and stresses as major threats on food production, food quality, and global food security in the twenty-first century (Ashmore *et al.*, 2006; Atkinson *et al.*, 2008; Battisti and Naylor, 2009). One of the predictions is that the number of undernourished people would have increased by 150% in the Middle East and North Africa and by 300% in sub-Saharan Africa by the year 2080, compared with 1990 (Tubiello and Fischer, 2007). Currently, millions of hungry people subsist on what they produce. If climate change reduces production while populations increase, there is likely to be more hunger. In addition, the impacts of climate change include reductions in calorie consumption and increases child malnutrition. Thus, aggressive agricultural productivity investments are needed to raise calorie consumption enough to offset the negative impacts of climate change on the health and well-being of children (Nelson *et al.*, 2009; Ramalho *et al.*, 2009). Therefore, improving biomass production and seed yield per area under suboptimal water availability due to drought and other abiotic stresses by improving the plants themselves is now even more pressing. Food and Agriculture Organization estimates that the

current soybean worldwide production (~220 million tons) must increase by a staggering 140% to meet food demands of a growing human population by 2050 (Bruinsma, 2009).

With decreasing availability of well-watered agricultural areas, attempts to reach such future production levels will require the use of existing or new cropping areas having limited water supply (Sinclair *et al.*, 2010). Abiotic stress factors, such as drought, heat, soil salinity, tropospheric ozone, and excess UV radiation are already causing significant agricultural yield losses and will become even more prevalent in the coming decades due to the effects of global change (Ashmore *et al.*, 2006; Ortiz *et al.*, 2008; Battisti and Naylor, 2009; Feng and Kobayashi, 2009; Fuhrer, 2009; Wassmann *et al.*, 2009). For the sake of objectivity, this article will focus on drought, heat, and flooding stress.

Drought and Heat Stress

Water stress may arise as a result of two conditions, either due to excess of water or water deficit. The more common water stress encountered is the water-deficit stress known as the drought stress (Mahajan and Tuteja, 2005).

Drought is a major abiotic stress factor that affects the growth and development of plants (Harb *et al.*, 2010). It can also affect crop productivity, through insufficient rainfall or altered precipitation patterns (Toker *et al.*, 2007). Drought or soil water deficit can be chronic in climatic regions with low water availability or random and unpredictable due to changes in weather conditions during the period of plant growth. The effects of drought are expected to increase with climate change and growing water scarcity (Harb *et al.*, 2010). Drought is often accompanied by relatively high temperatures, which promote evapotranspiration and affects photosynthetic kinetics, thus intensifying the effects of drought and further reducing crop yields. Plant responses to soil water deficit have been extensively investigated at developmental, physiological, and molecular levels and the complex nature of growth regulation under stress conditions has been highlighted (Passioura, 1996; Bray, 1997; Shinozaki and Yamaguchi-Shinozaki, 2000; Harb *et al.*, 2010; Hirayama and Shinozaki, 2010). Severe water stress may result in the arrest of photosynthesis, disturbance of metabolism and finally the death of plant (Jaleel *et al.*, 2008). Water stress inhibits cell enlargement more than cell division. It reduces plant growth by affecting various physiological and biochemical processes, such as photosynthesis, respiration, translocation, ion uptake, carbohydrates, nutrient metabolism, and growth promoters (Jaleel *et al.*, 2008; Farooq *et al.*, 2008). In plants, a better understanding of the morphoanatomical and physiological basis of changes in water stress resistance could be used to select or create new varieties of crops to obtain better productivity underwater stress conditions (Nam *et al.*, 2001; Martinez *et al.*, 2007). It is also anticipated that the occurrence of drought in many food-producing regions will increase significantly in response to climate change (Collins *et al.*, 2008; Reynolds and Ortiz, 2010).

High temperature also reduces the antioxidant enzyme activities and the intensity of the reactions decrease as the plants age (Balla *et al.*, 2007). Warmer temperatures and longer growing seasons will increase crop water demand, whereas summer rainfall will remain about the same or possibly decline. Some of the drought challenges are declining and more variable yields of rain-fed crops and decline in quality of high-value fruit and vegetable crops. The solutions for drought conditions are to increase irrigation capacity, particularly for high-value crops, shift to drought-tolerant crop varieties and shift plant dates to avoid dry periods (Smith, 2011).

The reactions of plants to water stress differ significantly at various organizational levels depending on the intensity and duration of stress as well as plant species and its stage of growth (Chaves *et al.*, 2002; Jaleel *et al.*, 2008). Understanding plant responses to drought is of great importance and also a fundamental part for making the crops stress tolerant (Reddy *et al.*, 2004; Zhao *et al.*, 2008).

Flooding Stress

The man-induced world climate change will increase the frequency of precipitations of higher magnitude as well as tropical cyclone activity (IPCC, 2007). As a result, the occurrence of flooding events on flood plains (i.e., lowlands) and cultivated lands is expected to be higher (Arnell and Liu, 2001). Under flooding conditions, the water table rises above soil level and envelopes some aerial portions of the plant. Soil water excess determines a severe decrease in the oxygen diffusion rate into the soil (Ponnamperuma, 1972, 1984; Armstrong 1979). Shortly after the soil is flooded, the respiration of roots and microorganisms depletes the remnant oxygen and the environment becomes hypoxic (i.e., oxygen levels limit mitochondrial respiration) and later anoxic (i.e., respiration is completely inhibited) (Blom *et al.*, 1994; Bailey–Serres and Voesenek, 2008; Wegner, 2010).

When flooding results in complete submergence, and in normally submersed aquatic plants, availability of carbon dioxide, light, and oxygen to the shoots typically diminishes (Jackson and Ram, 2003). Plant roots suffer hypoxia or anoxia. The first constraint for plant growth under flooding is the immediate lack of oxygen necessary to sustain aerobic respiration of submerged tissues (Armstrong, 1979; Vartapetian and Jackson, 1997; Voesenek *et al.*, 2004).

Under conditions of water excess, the soil type and its features will be crucial in determining how deep the stress will influence plant development. With the reduction of the soil redox potential a range of potentially toxic compounds appear, such as sulfides, soluble Fe and Mn, ethanol, lactic acid, acetaldehyde, and acetic and formic acid, and may injure plant tissues by impairing proper cell metabolism (Kozlowski, 1997; Fiedler *et al.*, 2007). Therefore, lack of oxygen and later the accumulation of such compounds are the major constraints that plants suffer under flooding conditions. A major constraint resulting from water excess, at least for poorly adapted species, is an inadequate supply of oxygen to submerged tissues; diffusion of oxygen through water is 104-fold slower than in air (Armstrong and Drew, 2002). In addition to the oxygen deficiency, excess water also leads to other changes in the soil that influence levels the hormones ethylene in the plants (Smith and Russell, 1969; Jackson, 1982).

Soil waterlogging and submergence are abiotic stresses that influence species composition and productivity in numerous plant communities. In rice farming, flooding regimes are manipulated (e.g., paddy rice) or are accommodated by genotype selection (e.g., deepwater rice) to secure much of the world's production of this staple crop (Grist, 1986). There have also been recent advances toward developing cultivars for lowland areas prone to short duration flash flooding (Siangliw *et al.*, 2003; Toojinda *et al.*, 2003). For most other crops, excess water is a major constraint to productivity in many regions and situations (Jackson, 2004), adversely affecting grain yields (Setter and Waters, 2003) and growth of pasture species (Gibberd and Cocks, 1997; Gibberd *et al.*, 2001).

The concentrations of oxygen (O_2), CO_2, reactive oxygen species (ROS), and ethylene change upon flooding and can occur in various combinations, as determined by the flooding regime. Tolerant plant species exploit the escape strategy based on a suite of (inducible) morphological and anatomical traits allowing reaeration of flooded tissues by the formation of aerenchyma; or those that adopt a quiescence strategy composed of traits that conserve the use of energy and carbohydrates to prolong underwater survival (Bailey–Serres and Voesenek, 2008; Colmer and Voesenek, 2009).

Responses and Adaptation of Plants to Climate Change

Increasingly erratic rainfall and extreme weather events can affect growth and development of plants, influencing the physiology, behavior, abundance, and distribution of many species. Plants are invariably intolerant to the current major abiotic stresses (that are likely to be further aggravated by climate change, such as drought, submergence, and salinity). These stresses reduce yields in millions of hectares in production areas that have had impact. Tolerance to abiotic stresses is very complex, due to the intricate interactions between stress factors and various molecular, biochemical, and physiological phenomena affecting plant growth and development (Razmjoo *et al.*, 2008). Agricultural yield losses due to abiotic environmental stresses are obvious and have been well documented (Mackill *et al.*, 2010).

Plants are sessile organisms that cannot escape from environmental constraints and, as a result, have evolved numerous adaptive responses to cope with environmental stresses. Stress is an altered physiological condition caused by factors that tend to disrupt the equilibrium. Strain is any physical and chemical change produced by a stress (Gaspar *et al.*, 2002). Stress being a constraint or highly unpredictable fluctuations imposed on regular metabolic patterns cause injury, disease, or aberrant physiology. Plants are frequently exposed to many stresses, such as drought, low temperature, salt, flooding, heat, oxidative stress, and heavy metal toxicity, while growing in nature, caused principally by environmental stresses (Jaleel *et al.*, 2009).

Drought and flooding can cause serious constraints to production. Effects of drought stress change the morphological characteristics. It has been established that drought stress is a very important limiting factor at the initial phase of plant growth and establishment. It affects both elongation and expansion growth and also affects the yield, but the tolerance of any species to this menace varies remarkably (Anjum *et al.*, 2003; Bhatt and Srinivasa, 2005; Kusaka *et al.*, 2005; Shao *et al.*, 2008). A ramified root system has been implicated in the drought tolerance and high biomass production primarily due to its ability to extract more water from soil and its transport to the above-ground parts for photosynthesis. In addition to other factors, changes in photosynthetic pigments are of paramount importance to drought tolerance (Jaleel *et al.*, 2009).

Other very important effects from climate change are the excess rainfall that will increase the frequency of precipitation of higher magnitude as well as tropical cyclone activity that cause stress for flooding. Those natural disturbances affect crop and forage production worldwide (Bailey–Serres and Voesenek, 2008; Colmer and Voesenek, 2009). Plants develop a suite of anatomical, morphological, and physiological responses in order to deal with partial submergence imposed by flooding (Armstrong, 1979; Kozlowski and Pallardy, 1984; Vartapetian and Jackson, 1997; Striker *et al.*, 2005; Colmer and Voesenek, 2009).

The most common anatomical response is the generation of aerenchyma in tissues, which facilitates the transport of oxygen from shoots to roots (Justin and Armstrong, 1987; Seago *et al.*, 2005; Colmer, 2003). At the morphological level, usual responses to flooding include adventitious rooting and increases in plant height and consequently, in the proportion of biomass above water level (Naidoo and Mundree, 1993; Grimoldi *et al.*, 1999). This also helps to facilitate the oxygenation of submerged tissues through the aerenchyma tissue (Laan *et al.*, 1990; Colmer, 2003). At the physiological level, flooding modifies water relations and carbon fixation in plants. Closing of stomata, with or without leaf dehydration, reduction of transpiration, and inhibition of photosynthesis are responses that can occur in hours or days, depending on the tolerance to flooding of each plant species (Bradford and Hsiao, 1982; Else *et al.*, 1995; Insausti *et al.*, 2001; Striker *et al.*, 2005; Mollard *et al.*, 2008, 2010).

Plant species can also adjust to these novel climate conditions through phenotypic plasticity, that is the range of phenotypes a single genotype can express as a function of its environment, or adapt through natural selection or migrate to follow conditions to which they are adapted; these options are not mutually exclusive, that is, the capacity of a given plant to alter its physiology, morphology, or phenology and allows it to tolerate, avoid, or escape a certain stress condition (Nicotra *et al.*, 2010; Grime *et al.*, 1986). The phenotypic plasticity is understood to be genetically controlled, heritable, and of potential importance to species evolution (Bradshaw, 2006; Lande, 2009). With mounting evidence from molecular and developmental biology, the understanding of the mechanisms of plasticity, which will be crucial for predicting changes in species distributions, community composition, and crop productivity under climate change will be easier (Van Kleunen *et al.*, 2007; Van Kleunen and Fischer, 2001).

Biotechnology Tools in the Breeding for Climate Change

As a complement to changes in agronomic management, plant breeding is a convenient technological response to

environmental challenges (Yadav *et al.*, 2011), but considerable time and investment is required to deliver changes in the productivity or quality of varieties. The genetic basis of adaptation to environments is complex, and it is difficult to unravel what sets of genes are required for optimal performance and to explain the interactions of genes controlling any given trait. Investment in plant breeding requires assessment of when and where this is the most economical response for an industry in dealing with climate change (Chapman *et al.*, 2012).

Biotechnology techniques can help to accelerate the improvement of performance under harsh environmental conditions, particularly because breeding for abiotic stress tolerance sometimes has linkage drag issues, i.e., undesirable genes are also transferred along with desirable traits; and also because reproductive barriers limit the transfer of favorable alleles from diverse genetic resources. For instance, advances in genomics coupled with bioinformatics and stress biology can provide useful genes or alleles for conferring stress tolerance. Two biotechnology approaches have a key role in this work, the molecular breeding (MB) and genetic engineering (GE), and their integration with conventional breeding to develop crops that are more tolerant of abiotic stresses (Varshney *et al.*, 2011).

Molecular Breeding

The detection and exploitation of genetic variation have always been an integral part of plant breeding. DNA-based molecular markers are useful for detecting the genetic variation available in germplasm collections and breeding lines. During the past two decades, many different molecular markers have been developed for most major crop species. These markers have been used extensively for the development of saturated molecular genetic and physical maps and for the identification of genes or quantitative trait loci (QTLs) controlling traits of economic importance for marker-assisted selection (MAS) (Varshney *et al.*, 2009). Despite the great collaboration performed by molecular markers, the genomics-assisted breeding approaches have greatly advanced with the increasing of genome and transcriptome sequence data for several model plant and crop species, such as rice (IRGSP, 2005), poplar (Tuskan *et al.*, 2006), sorghum (Paterson *et al.*, 2012), maize (Schnable *et al.*, 2009), and soybean (Schmutz *et al.*, 2010).

The MB approach involves first identifying QTLs or genes for traits of interest, such as tolerance to abiotic stresses, after identifying the markers associated with QTLs or genes; the candidates can be introgressed in elite lines through marker-assisted backcrossing (MABC). For two most important abiotic stress, heat and drought, some QTLs for tolerance were identified in important crops, such as wheat rice and maize (Paliwal *et al.*, 2012; Changrong *et al.*, 2012; Almeida *et al.*, 2013).

There are two general approaches to understand the function of a gene: forward genetics and reverse genetics (Alberts *et al.*, 2007). Reverse genetics is a particular approach in discovering the function of a gene. It begins with a well-characterized phenotype and works toward identifying the gene(s) responsible for the phenotype. Genetic mapping approaches, such as QTL mapping and association mapping, are part of forward genetics and are often used because gene transfer is not required (Tierney and Lamour, 2005; White *et al.*, 2007).

QTL mapping can be defined as the marker-aided genetic dissection of variation of complex phenotypes in segregating progenies. The objectives of QTL mapping analysis are: to provide knowledge toward fundamental understanding of individual gene and interactions, enable positional cloning, and improve breeding value estimates and selection response through MAS in plants and animals (Holland, 2004; Collard *et al.*, 2005).

Anticipated changes in climate and its variability, particularly extreme temperatures and changes in rainfall, are expected to make crop improvement even more crucial for food production (Varshney *et al.*, 2011). The objective of plant breeding for stressing environments is to accumulate favorable alleles that contribute to stress tolerance in a plant genome. Genes that confer stress resistance can be sourced from germplasm collections, including wild relatives of crops that are held in genebanks or organisms that currently live in habitats of water deficit or excess, extreme temperature, and salinity conditions and have evolved to cope with such conditions (Nevo and Chen, 2010). Thus, the genetic variation for stress tolerance is the engine that drives advances in plant breeding (Fridman and Zamir, 2012).

The abiotic stress is considered one of the most important factors affecting yield all over the world, mainly those stress provoked by climate changes, such as drought, heat, and flooding. The detection and genetic location of tolerance gene candidates and QTL for these stresses, together with the development of molecular markers, linkage maps, and genetic association studies have largely contributed to the purpose. There exists a vast array of gene for tolerance abiotic stress in several crops and studies using QTL mapping approaches and the major QTLs/candidate genes have been widely described.

Quantitative Trait Loci Mapping for Drought and Heat Stress

Drought and heat are the most significant environmental stresses in agriculture worldwide and improving yield under these conditions is a major goal of plant breeding. Identification of genetic factors involved in plant responses to drought stress will provide a solid foundation to improve drought and heat tolerance. To achieve progress in plant yield in drought-prone environments, it is necessary to develop new tools to understand the complex network of drought-related and heat-related traits. Molecular genetic approaches have uncovered many QTLs affecting yield under drought and heat or the expression of abiotic stress tolerance-related traits. Across many species, upon water stress by drought, the accumulation of biomass increases the root/shoot ratio (Sharp and Davies, 1989).

QTLs studies with recombinant inbred lines (RILs) and near-isogenic lines identified several genomic regions associated with resistance to preflowering and postflowering drought stress in sorghum. Four genomic regions associated with the stay-green trait were identified using a RIL population developed from B35 × Tx7000. These four major stay-green QTLs

were consistently identified in all field trials and accounted for 53.5% of the phenotypic variance (Sanchez *et al.*, 2002).

The mapping population Bala × Azucena RILs (Price *et al.*, 2000) was used to identify QTLs for drought avoidance in rice. A total of 15 clusters of QTLs for drought avoidance were detected (Khowaja *et al.*, 2009). Although QTLs were found on chromosomes 1, 3, 4, 5, 6, 7, 8, 10, and 12, the major gene clusters were found on chromosomes 3, 6, and 7. From these, for only three drought meta-QTLs, deeper root systems may be explaining drought avoidance. The complex regulation mechanisms and the large number of regions associated with drought avoidance point out that further investigations are still needed to better understand the genetic basis of this trait. Moreover in rice, a QTL on chromosome 12 was detected in a large population from the cross of Vandana/Way Rarem that accounted for approximately 50% of the genetic variance, and was expressed consistently over 2 years (Bernier *et al.*, 2007). This QTL seems to be related to increased water uptake of plants under stress (Bernier *et al.*, 2009). A chromosome 3 QTL had a large effect on drought tolerance in the cross between the tolerant variety Apo and the widely grown susceptible variety Swarna (Venuprasad *et al.*, 2009). This is a very promising QTL for use in MAS, because the variety Swarna is widely grown in drought-prone environments due to its high yield and other desirable traits. QTLs for grain yield under drought stress have been mapped in many rice populations (Babu *et al.*, 2003; Lafitte *et al.*, 2004; Lanceras *et al.*, 2004; Bernier *et al.*, 2007; Kumar *et al.*, 2004). Despite large efforts, no successful application in marker-assisted breeding (MAB) has been yet accomplished. So far, repeatability problems and the complex nature of gene interactions involved in drought response suggest that further investigations are needed to better understand the genetic basis of this trait (Swamy *et al.*, 2011).

High temperature (>30 °C) at the time of grain filling is one of the major causes of yield reduction in wheat. To identify QTLs for heat tolerance under terminal heat stress, a set of 148 RILs were developed by crossing a heat-tolerant hexaploid wheat (*Triticum aestivum* L.) cultivar (NW1014) and a heat-susceptible (HUW468) cultivar. The F5, F6, and F7 generations were evaluated in two different sowing dates under field conditions for 2 years. Three QTLs that explained the phenotypic variation were identified and can be used in MAS for heat stress in wheat (Paliwal *et al.*, 2012).

Quantitative Trait Loci Mapping for Flooding Stress

Rising temperatures due to the accumulation of GHGs are expected to result in declining crop yields. One of the abiotic stresses that are anticipated to worsen as the consequence of climate change is flooding or waterlogging stress. Therefore, submergence tolerance is an important trait where short-term 'flash' flooding damages crops. Flooding causes a reduction of oxygen supply and inhibiting respiration. Highly tolerant varieties such as FR13A from Orissa, India, have been used in breeding programs (Vergara and Mazaredo, 1975; Hille-RisLambers and Vergara, 1982; Mackill *et al.*, 1993). Tolerance in these varieties is controlled by the *Sub1* locus on chromosome 9 (Xu and Mackill, 1996). This major QTL has been cloned and successfully transferred to cultivated rice genotypes, *Submergence1* (*Sub1*) (Xu *et al.*, 2006). A cluster of three genes, *Sub1A*, *Sub1B*, and *Sub1C*, which encode putative ethylene responsive factors (ERFs) were found to be associated with the phenotype, but a major effect of *Sub1A-1* was observed after its overexpression (Xu *et al.*, 2006). Another QTL was mapped in the cross C9285 (deepwater rice) × Taichung 65 (Hattori *et al.*, 2009). Two genes on chromosome 12 (*Snorkel1-SK1* and *Snorkel2-SK2*), which possess a putative nuclear localization signal and a single APETALA2/ERF domain were described. The ERF domains are very similar to those of *Arabidopsis thaliana* ERF1, *O. sativa* ERF1, and SUB1A-1. A comparison between the effects of SK1 and SK2 showed that the latter is more effective at internode elongation in water. Some other common QTL related to flooding have been found in rice (Kamoshita *et al.*, 2002; Zheng *et al.*, 2003, 2008; Zheng, 2006). They include regions near markers RM315 (C1), RZ 318 (C2), between RM338 and RZ284 (C3), near RZ70 (C5), and on the telomeric region (C9). Several of these QTLs have been mapped closely or together with root trait QTLs when well drained and drought conditions were compared.

Soil waterlogging also is a major environmental stress that suppresses soybean (*Glycine max* (L.) Merr.) growth and yield. A study was conducted with the goal of identifying QTL associated with the tolerance of soybean to soil waterlogging, where 208 recombinant inbred (RI) populations were subjected to 2 weeks of waterlogging when the plants were at the early flowering stage (Vantoai *et al.*, 2010). A single QTL was identified, linked to marker Sat_064, from the Archer parent which was associated with improved plant growth (11–18%) and grain yields (47–180%) in waterlogged environments.

In maize (*Zea mays* L.) soil waterlogging is also a major environmental stress that affects growth and yield. To identify the QTL associated with waterlogging tolerance at the maize seedling stage, an F_2 population consisting of 288 $F_{2:3}$ lines were created from a cross between two maize genotypes, 'HZ32' (waterlogging-tolerant) and 'K12' (waterlogging-sensitive) (Qiu *et al.*, 2007). A total of 25 and 34 QTLs were detected in two experiments, respectively. The effects of each QTL were moderate, ranging from 3.9% to 37.3%. Several major QTL determining shoot dry weight, root dry weight, total dry weight, plant height, and their waterlogging tolerance coefficient each mapped on chromosomes 4 and 9. These QTLs were detected consistently in both the experiments. Secondary QTLs influencing tolerance were also identified and located on chromosomes 1, 2, 3, 6, 7, and 10. These QTLs were specific to particular traits or environments.

Genetic Engineering

The terms GE or genetic modification (GM; also used for 'genetically modified') have been used for the processes of transforming plants (Lawlor, 2013). Crop GE with signaling components and transcription factors (TFs) lead to the expression of their target transcriptome that consists of several genes involved in stress adaptation. However, only a few crops, such as rice (Xiao *et al.*, 2009; Oh *et al.*, 2009), maize (Nelson *et al.*, 2007; Castiglioni *et al.*, 2008), and canola (Brassica napus) (Vanderauwera *et al.*, 2007; Wang *et al.*, 2005), expressing the desired TF and other genes, have been tested

under real field stress conditions. GE-derived crops still have a long way to go to gain universal acceptance and reach farmers' fields. Even though the benefits to small and resource-poor farmers have been demonstrated and the GE technology is becoming more popular, the political will to facilitate this process is weak (Farre *et al.*, 2010). Indeed, there have been many calls for the global harmonization of regulations, which would make the requirements compatible and consistent (Ramessar *et al.*, 2008). Regulatory harmonization would help remove artificial trade barriers, expedite the adoption of GE crops, protect developing countries from exploitation, and bring the benefits of GE products to the consumer. Eventually, the adoption of biotech crops to mitigate abiotic stresses that are expected to increase in frequency and intensity in coming years will depend on public perceptions and public acceptance, as well as on cultural and institutional processes in developing countries (Varshney *et al.*, 2011).

Climate Change on the Future of Plant Breeding

With the climate change a new scenario is established. The higher temperatures will reduce crop productivity. An increase in CO_2 concentration is certain with both direct and indirect effects. The increase in the frequency of drought, the increase in the areas affected by salinity, and the increase in the frequency of biotic stress are also highly probable (Ceccarelli *et al.*, 2010).

The developing world already contends with chronic food problems. Climate change presents yet another significant challenge to be met. The estimate for Africa is that 25–42% species habitats could be lost, affecting both food and non-food crops. Habitat change is already underway in some areas, leading to species range shifts, changes in plant diversity which includes indigenous foods, and plant-based medicines (McClean, 2005). In developing countries, 11% of arable land could be affected by climate change, including a reduction of cereal production in up to 65 countries, approximately 16% of agricultural GDP (FAO, 2005).

The considerable efforts needed to prepare for climate-related impacts and the time required for agriculture, forestry, and fishery production systems to adapt is the crucial point. Success depends on factors relating to biology, ecology, technology, and management regimes. Those countries with limited economic resources and insufficient access to technology will be least able to keep up with the changes (FAO, 2007).

The future is always uncertain, but it is what we will live in. In the scenario of climate change, these uncertainties are even greater. Despite all technological advances, models of climate forecasts in the medium and long term will still need to be corroborated. It is, however, not known, how much the impact will increase and the effect it will cause on the planet and the living creatures in it.

Numerous research efforts in all knowledge areas are being implemented to mitigate as much of the predicted problems as possible. In this scenario, given that plant breeding has been a success story in increasing yield, it can help in developing new cultivars with enhanced traits better suited to adapt to climate change conditions using both conventional and genomic technologies (Dixon *et al.*, 2006; Habash *et al.*, 2009). These traits include drought and temperature stress resistance, resistance to pests and disease, which continue to cause crop losses, salinity, and water logging (Humphreys, 2005; Oerke, 2006). The genetic improvement of plants, based on experiences of the past, is an area that can make contributions to the adaptation of plants to the new agricultural scenario of the coming years (Ramalho *et al.*, 2009).

Experience has shown that biotic and abiotic stresses occur together, although not necessarily all at once. Normally, when temperatures are elevated, water stress on plants is strong and pest incidence, among other stresses increases. To identify more tolerant cultivars to all these factors the available alternative, with proven efficiency, is to evaluate the progeny and/or cultivars in the conditions in which the crops will be grown (Ramalho *et al.*, 2009).

In this context, the main drawback to the work of breeders is the interaction of genotypes with environments. In other words, genotypes respond differently to environmental stimuli. Therefore, especially under tropical conditions, where the diversity of climate and management adopted by farmers is higher, the interaction of genotype by environment is the greatest challenge to be met. Cultivars must be well adapted and more stable.

See also: Breeding: Plants, Modern. Genomics: Plant Genetic Improvement. Plant Abiotic Stress: Salt. Plant Abiotic Stress: Temperature Extremes. Plant Abiotic Stress: Water

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Climate Change, Society, and Agriculture: An Economic and Policy Perspective

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Glossary

Climate change A change in the state of the climate that can be identified (e.g., by using statistical tests) by changes in the mean or the variability of climate properties and that persists for an extended period, typically decades or longer. Climate change may be due to natural internal processes or external forces or due to persistent anthropogenic changes in the composition of the atmosphere or in land use.

Climate change adaptation An adjustment in natural or human systems in response to actual or expected climatic stimuli or their effects, which moderates harm or exploits beneficial opportunities.

Climate change mitigation A human intervention to reduce the human impact on the climate system; it includes strategies to reduce greenhouse gas (GHG) sources and emissions and enhance GHG sinks.

Command-and-control policy In the climate change case, this involves a government-imposed limit on greenhouse gas emissions where the limit should reflect a balance between the damages from emissions and the cost of reducing emissions.

Externalities Occur when a change in the production or consumption of an individual or firm affects indirectly the well-being of another individual or firm. Externalities can be positive or negative.

Greenhouse gas (GHG) Those gaseous constituents of the atmosphere, both natural and anthropogenic, that absorb and emit radiation at specific wavelengths within the spectrum of thermal infrared radiation emitted by the Earth's surface, the atmosphere itself, and by clouds. This property causes the greenhouse effect. Water vapor (H_2O), carbon dioxide (CO_2), nitrous oxide (N_2O), methane (CH_4), and ozone (O_3) are the primary GHGs in the Earth's atmosphere. Moreover, there are a number of entirely human-made GHGs in the atmosphere, such as the halocarbons and other chlorine- and bromine-containing substances, dealt with under the Montreal Protocol. Besides CO_2, N_2O, and CH_4, the Kyoto Protocol deals with the GHGs sulfur hexafluoride, hydrofluorocarbons, and perfluorocarbons.

Private party adaptation Adaptation actions initiated by private agents acting in their own best interests. Such individuals alter operations to better adapt to climate. This is also often called autonomous adaptation.

Public party adaption Actions collectively implemented by governments or other societal organizations. Generally, this resolves adaptation deficits arising due to public goods characteristic where private party adaptation is insufficient, so public agencies have to step in to take actions.

Tradable emission permits In the climate change case, this involves a government-imposed limit on GHG emissions in the form of permits for emissions but allows the permits to be traded.

Transactions costs When GHG offsets are sold, the transactions typically will involve cost. These are three types of transaction costs: (1) preproject costs that include search costs, negotiation costs, baseline determination costs, approval costs, validation costs, review costs, and registration costs; (2) project implementation costs that include monitoring costs, verification costs, review costs, certification, and enforcement costs; and (3) trading costs that include transfer costs and registration costs.

Introduction

In recent decades, climate change has become a popular and controversial topic debated intensively worldwide. This is mainly due to the complex, distinctive features of the climate change issue, such as the uneven distribution of effects and emissions, global and long-term causes, and key interrelationships with energy and economic growth. In this study, the authors have examined aspects of climate change as observed and projected, causal factors, policy approaches, and findings. Throughout the article, the authors have emphasized economics and agriculture and forestry (AF).

Basics of Climate Change

A lot of scientific endeavor has been devoted to documenting what has been happening with climate change, why this might be happening, and what is likely to happen? Here, the authors have overviewed some of that literature as background to the reset of the document.

What Have been Seen?

Many have assembled data, showing that the world is facing growing global temperatures (see the NOAA data represented in **Figure 1**, IPCC (2007a), and the United States Global Change Research Program (USGCRP)). Such data show that 11 of the 12 warmest years in the Earth's recorded history have happened since 2000.

In addition, reports like the IPCC (2007a,b) or the National Academy of Sciences (2011) show a long list of effects including (1) global sea level is rising; (2) ice melting in the past 25 years that took 1600 years to form; (3) rainfall patterns are changing; and (4) weather is becoming more extreme, leading to costly events, including huge losses in the agricultural sector. For example, the Texas Extension Service estimates that the drought in the US Southwest in 2011 entailed net loss of US$7.6 billion.

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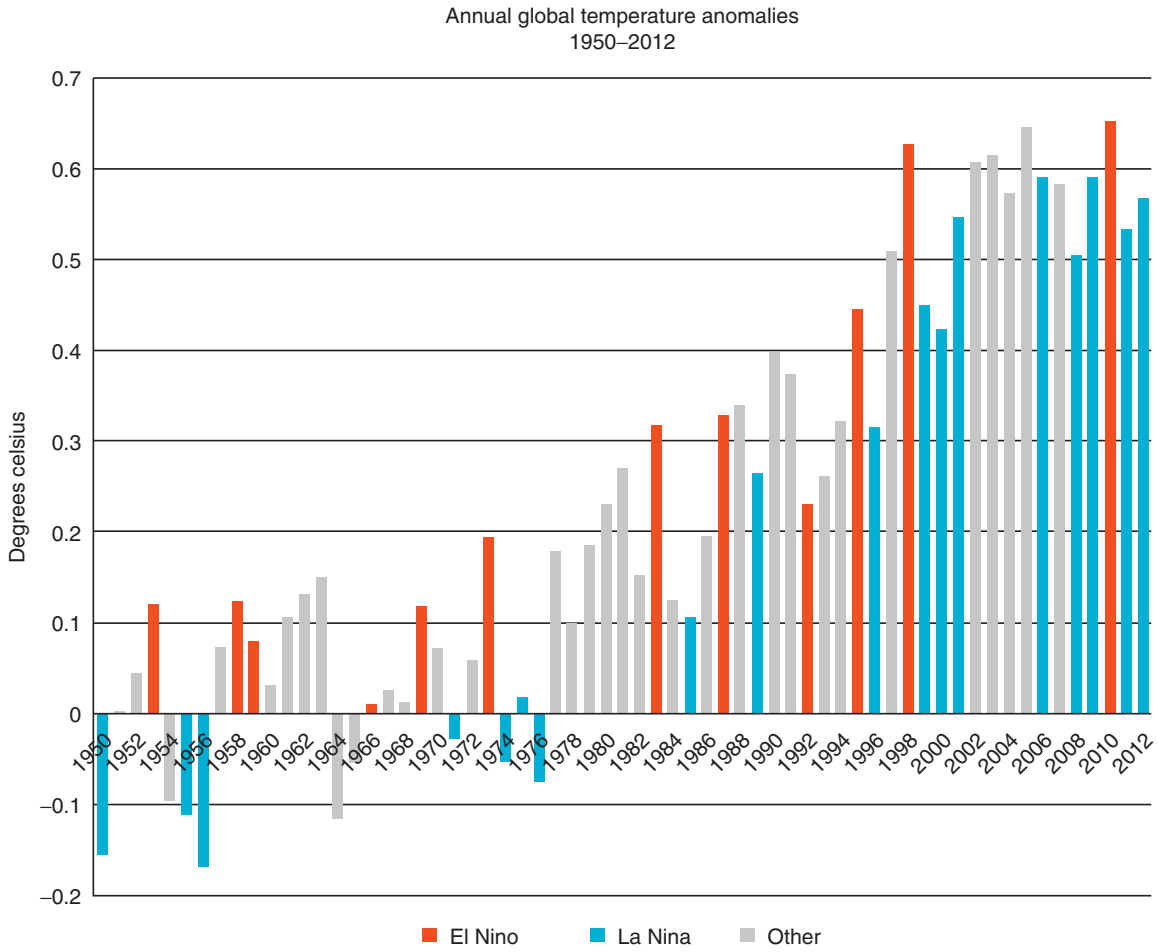


Figure 1 Temperature evolution from 1950 to 2012. NOAA, State of the climate, Global Analysis – Annual 2012 (http://www.ncdc.noaa.gov/sotc/global/2012/13).

Why is This Happening?

Many acknowledge that they see the climate change, although there is not a broad social consensus on the causality. However, scientists are largely arguing that societal emissions of greenhouse gases (GHGs) are a strong causal factor. For example, the IPCC (2007a) states "Since pre-industrial times, increasing emissions of GHGs due to human activities have led to a marked increase in atmospheric GHG concentrations," whereas the United States National Academy states "Climate change, driven by the increasing concentration of greenhouse gases (GHGs) in the atmosphere, poses serious, wide-ranging threats to human societies and natural ecosystems around the world" (Fri *et al.*, 2010). Globally, IPCC (2007d) estimates that 69% of the GHGs originate from energy consumption, whereas 14% arise from food production and 17% from deforestation. Meanwhile, energy use, food use, and land use change, and thus emissions generally expand with incomes and population. In fact, historical emission data show that global GHG emissions and concentrations have been increasing at an increasing rate (**Figure 2**). Society has tried to mitigate GHG emissions but is making slow progress. Climate stabilization requires that emissions peak then drop to low levels (Fri *et al.*, 2010). Unilateral action by any one country would not be effective and thus has to be a global endeavor.

What is Projected?

Given continuing emissions, a changed future climate is expected in terms of temperature changes, as projected in **Figure 3**, along with associated precipitation and other changes (Knutti and Sedláček, 2012). In turn, this would cause changes in such things as fresh water supplies; snow pack; location of agricultural crop production; extreme event incidence; sea level; coastal inundation; and pest, diseases, bird, animal, and plant ranges.

Damages and Economic Dimension

Before probing into policy responses to this multifaceted issue, the authors have reviewed damages and economic effects.

Is Climate Change Causing Economic Damages?

Climate system changes affect many items, some beneficial, detrimental, minor, and major with differential effects across

locations and periods (Tol, 2014). Market influences can also spread the effects to many sectors. Suppose the supply of goods from one sector shrinks due to climate change effects then the price of those goods will go up accordingly. If this commodity is used as an input to produce another commodity (for instance, corn is a feed for cattle) then the production cost of the other commodity will increase as its sale price. For consumers, higher prices will give rise to less consumption and smaller consumers' surplus. Producers, as Adams *et al.* (1990) found, may benefit from higher prices. Nonetheless, in most cases, total welfare will decrease due to climate change effects.

Numerous economic studies have examined climate change effects on production and welfare.

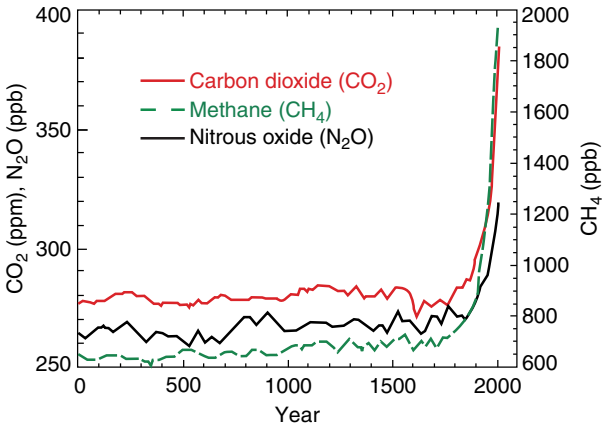


Figure 2 Expansion of GHG emissions for three major GHGs from 0 to 2005. Reproduced from IPCC, 2007a. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.

Production

With regard to the agricultural sector, climate change can alter yields and crop acreage (Adams *et al.*, 1990, 1999; Reilly *et al.*, 2002; IPCC, 2007b). Climate change has diverse implications involving the effects of carbon dioxide, temperature, precipitation (amount, distribution, and intensity), and extreme events (droughts, hurricanes, floods, etc.). All of these, in turn, alter production, as a number of authors have reviewed.

Using a historical statistical approach, Chen *et al.* (2004) found that crop yield effects of temperature and precipitation changes varies with crop. This has been subsequently verified by others (Tack *et al.*, 2012; Schlenker and Roberts, 2009). Studies have also investigated the effects of climate extremes, such as hot days, standard deviation in temperature, precipitation intensity, and droughts (McCarl *et al.*, 2008; Huang and Khanna, 2010). Studies have also been carried out using crop simulators finding temperature and precipitation effects (Parry *et al.*, 2004; Tubiello *et al.*, 2002; Backlund *et al.*, 2008; Iglesias *et al.*, 2012).

Yield effects also arise from increased atmospheric concentrations of carbon dioxide, where it serves as a fertilizer, simulating some species of crops to grow faster (C3 crops, including wheat, potatoes, etc.; Darwin and Kennedy, 2000). However, this is not the case for C4 crops (corn, sorghum, etc.), where benefits appear to arise only under moisture stress (Leakey, 2009). Attavanich and McCarl (2011) included this in a statistical investigation by merging the United States Department of Agriculture data with crop data from field-level free air carbon enrichment experiments (Long *et al.*, 2006) finding that in some cases yields are substantially influenced and possibly confused with technical progress.

Changes in crop production also affect crop prices, economic returns, and land allocation with substantial shifts projected (Adams *et al.*, 1990, 1995, 1999; Reilly *et al.*, 2002; McCarl, 2011).

Climate change can also alter resources for production. Kjellstrom *et al.* (2009) concluded that heat exposure caused

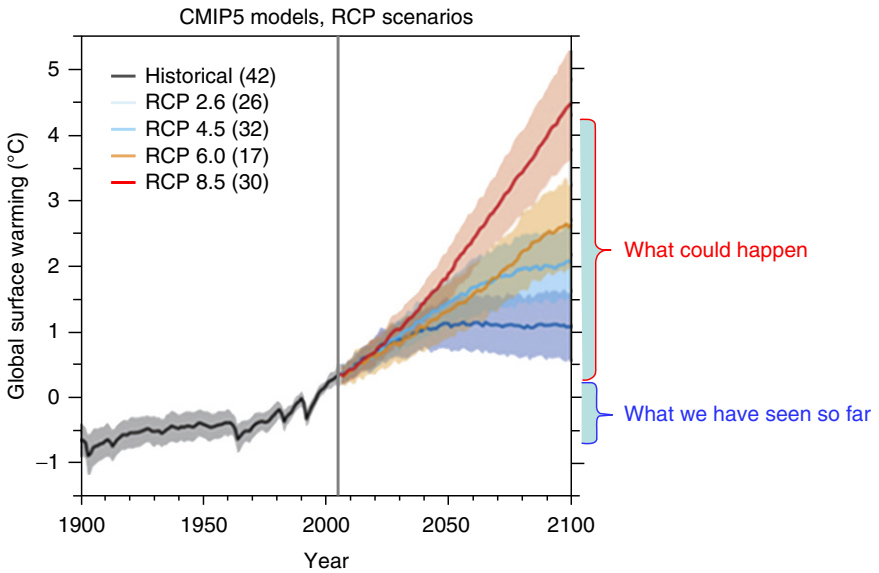


Figure 3 Global temperature change from new coupled model intercomparison project phase 5 (CMIP5) climate model projections. RCP, representative concentration pathways. Adapted from Knutti, R., Sedláček, J., 2012. Robustness and uncertainties in the new CMIP5 climate model projections. Nature Climate Change 3, 369–373.

by global climate change may substantially impair labor productivity. A number of authors have examined water finding regionally detrimental effects (Gleick *et al.*, 2000; Bates *et al.*, 2008; Chen *et al.*, 2001).

Welfare

Efforts have been made to estimate the economic consequences of climate change on agriculture in terms of land values and social welfare in terms of producer income and measures of consumer satisfaction. A series of studies initially found climate change to be detrimental for the welfare of those involved with agriculture but as the crop scope, carbon dioxide effects, and adaptation possibilities were added, it became beneficial (Adams *et al.*, 1990, 1995, 1999; Reilly *et al.*, 2002; McCarl, 2011). However, others argued that it would be detrimental, and appraisals in countries like Mali, Butt *et al.* (2005) certainly showed that. In terms of land value, Mendelsohn *et al.* (1994) analyzed a cross-section dataset consisting of 3000 counties in the United States and found that higher annual temperatures reduced average farm values. Broader scoped studies have shown varying results depending on location with some regions benefiting but some warm regions losing (see the review and results in Van Passel *et al.*, 2012).

In terms of water resource effects, Hurd and Rouhi-Rad (2012) and Adams and Peck (2008) stated that climate change effects on water give rise to economic welfare loss through lower consumer surplus resulting from higher water prices and costs of actions taken due to water shortage.

Forestry is sensitive to climate change as well. However, Alig *et al.* (2002) showed that in the United States small welfare increases would arise. In terms of global timber markets, Sohngen and Mendelsohn (1998) found that supply of timber would increase and bring benefit to the whole timber market.

In terms of more aggregate measures, Tol (2014) reviewed 17 multisector studies and concluded that the initial net effects are positive but they become negative in the long run.

All in all, as shown above, climate change poses a serious and persistent threat to portions of the world and to increasingly larger parts as changes become larger.

If Greenhouse Gases Are Causing Climate Change, Why Are They Still Emitted?

Up to here, the authors have built the argument that climate change is occurring, in all likelihood caused by GHG emissions, and such emissions are more likely to continue increasing the degree of climate change. Furthermore, this climate change has caused changes in production and welfare plus portends future risks as it proceeds. The next question then is: Why do the emissions proceed? In economics, such emissions are commonly called an externality. GHGs are not purposefully emitted; they are rather a by-product emission from activities such as energy generation/use, agricultural fertilization, livestock raising, coal mining, cement manufacture, and many other activities. Furthermore, there is generally not a direct way that people damaged by climate change now and in the future can reflect the damages they incur on those now involved in the generation of the GHG emissions. In more concrete terms, the carbon dioxide emitted by industrial activities increases the level of GHGs in atmosphere and causes some degree of climate change. In turn, climate change causes some damage, but those who are damaged bear the costs without any compensation. Furthermore, they have no way of reflecting those costs on the entities causing the emissions. Such an effect is the externality, resulting in a greater degree of GHG emissions than desired, which economists call a market failure.

There are complex issues involved with potential resolution of the externality. One aspect is that GHG emissions reduction is a public good (Tol, 2014), with everyone living on the earth potentially benefitting without reducing the utility others gain. In turn, this motivates free riding activity with parties motivated to enjoy the benefits of reduction without paying for it. Another aspect is that gasses spread globally and reductions by any one party or country have small implications, thus coordinated global emissions reductions are required (Stern, 2007; Fri *et al.*, 2010). Yet another aspect is that GHG emissions have persistent impacts spanning decades, benefitting parties in the future, but the costs of reducing them are borne by current parties raising intergenerational equity concerns. Other complex characteristics include the following: uncertainties associated with the long-run implications of emissions (a precise estimate of economic effects is not possible and is debatable), irreversible economic damages are possible, tipping points may be involved, effects are unevenly distributed across regions and social strata, and nonmarginal change (IPCC, 2007b; Stern, 2007; Fri *et al.*, 2010).

Basic Policy and Social Action Approaches

Three broad policy and social action approaches have been used to address the climate change issue and a fourth is possible. One involves investing in the development of information on the climate change degree, consequences, and potential outcomes (monitoring and projecting consequences). There are also three damage-reducing approaches. These are commonly called adaptation, mitigation, and geoengineering.

- Mitigation involves actions aimed at reducing the magnitude of climate change drivers, like reducing GHG emissions. Such actions are designed to reduce current and future atmospheric concentrations. In turn, such actions are designed to limit future climate change along with ocean acidification (IPCC, 2007d; Fri *et al.*, 2010).
- Adaptation involves actions to reduce the damage arising from a given amount of climate change plus exploiting the positive opportunities. This involves manipulating management, information dissemination, infrastructure investment, and enterprise choice to improve coping mechanisms.
- Geoengineering (also climate engineering) involves purposeful intervention in the Earth's climatic system with the aim of reducing climate change. The two basic thrusts involve solar radiation management and carbon dioxide removal (Izrael *et al.*, 2009). The subject is controversial and

widely debated (Barrett, 2007; Boyd, 2008; Robock, 2008; Schneider, 2008; Pelley, 2009; Bellamy *et al.*, 2012). Interested readers are referred to those references and the topic will not be further discussed here.

Note that these basic policy directions are not mutually exclusive and the first three are currently being used to various extents plus there is considerable room for increasing activities in all three spheres. In this study, the authors have discussed these directions in more detail.

Information Efforts

Information Value

One policy approach where there has been a lot of investment involves information development. Coping with climate change involves decisions across multiperiods based on information available to decision makers. Under climate change, decisions are often made in the face of uncertainty and are adjusted over time. In fact, information on climate change and its impacts are insufficient today. First, science and technology have not been developed yet to accurately assess and predict climate change. There are still numerous unexplored problems associated with climate change. Moreover, it is costly to collect and disseminate all relevant information, particularly in developing countries (Berrang-Ford *et al.*, 2011; Bryan *et al.*, 2009; Deressa *et al.*, 2009).

Because the information is crucial for decision making, there is implicit value associated with it. The authors have used Figure 4 to shed light on the value of information within the climate change context. Here, they focus mainly on information for adaptation. Similar arguments can be extended to mitigation decisions.

The curves in Figure 4 represent different agricultural productions in terms of value of activity on land in response to climate variables, for instance, temperature in this case. As temperature goes up to specific levels, the production should switch from one crop to another in order to maintain the highest possible value. For example, temperature T_1 is the threshold for switching between wheat and corn, whereas T_2 is the threshold for switching between corn and grazing. In this example, the authors assume that actions are taken instantaneously against climate change.

Under temperature T_3, a rational farmer would plant wheat with realized land value at Point B. Now consider the temperature changes from T_3 to T_4 due to climate change. The farmer would change the crop from wheat to corn, ending up with land value at Point A. However, this adaptive action requires that the farmer possesses complete information about climate change before cropping decisions are made. If the farmer is unaware of the ongoing climate change, wheat can still be planted on the land, which results in the value of planting wheat at Point C. Planting wheat generates less value than planting corn under temperature T_4. Hence, the value loss ΔV due to lack of information could be interpreted as the value of information associated with climate change.

In the face of information needs to aid decision making, large investments have been made in information generation, particularly involving the following:

- Developing information on how the climate has been changing globally, regionally, and locally; the forces causing these changes; the nature of natural and human responses; economic consequences; projections of future levels of causal agents; climate change; and economic consequences. Certainly the long-standing efforts by the IPCC (1990, 1996, 2001, 2007a,b,c,d and the ongoing fifth assessment effort) and country efforts like the United States (USGCRP and National Academy studies) fall into this domain.
- Developing information on possible policy actions and their effectiveness. Many studies have worked on the role of information on adaptation (National Academy of Sciences, 2011; United Nations Framework Convention on Climate

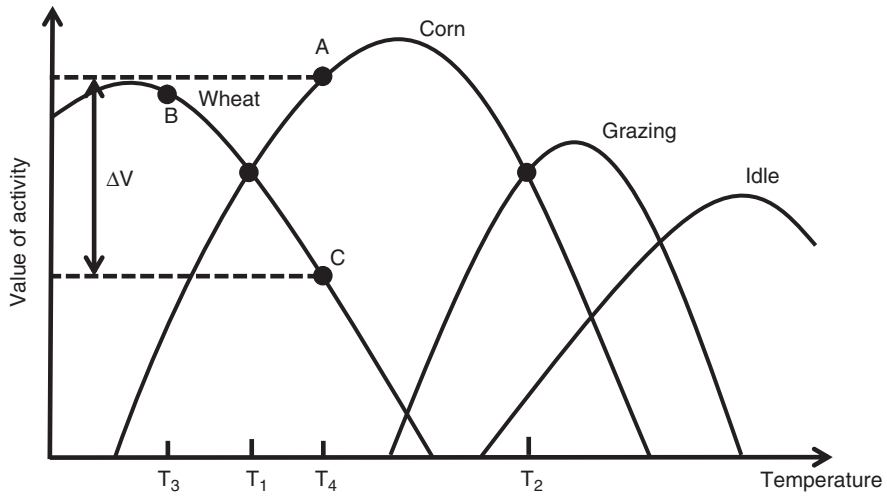


Figure 4 Value of activity on land in response to temperature. Adapted from Mendelsohn, R., Nordhaus, W., Shaw, D., 1994. The impact of global warming on agriculture: A Ricardian analysis. American Economic Review 84 (4), 753–771 and Kelly, D.L., Kolstad, C.D., Mitchell, G.T., 2005. Adjustment costs from environmental change. Journal of Environmental Economics and Management 50(3), 468–495.

Change (UNFCCC), 2007; World Bank, 2010), mitigation (IPCC, 2007d; National Academy of Sciences, 2011), social dimensions (Mearns and Norton, 2010), and geoengineering (Bellamy *et al.*, 2012).

Information and Dynamic Decision Making

It is generally impossible for people to accurately predict the future climate and the consequences of alternative GHG concentrations. Consequently, climate change decision making involves a series of decisions and revisions as time and information grows. A number of studies suggest utilizing flexible approaches to cope with climate change that can benefit from continuous learning/information accumulation (Berkhout *et al.*, 2006; Pelling *et al.*, 2008; Leary, 2009; Fri *et al.*, 2010; Hallegatte *et al.*, 2011).

Climate Change Mitigation

The first active policy considered relative to climate change involved mitigation (or limiting GHG emissions) and thereby the future extent of climate change (Fri *et al.*, 2010). The United Nations formed the Framework Convention on Climate Change in 1994, and today there are 195 countries that are Parties to the Convention. The convention aims "to stabilize greenhouse gas concentrations at a level that would prevent dangerous anthropogenic (human induced) interference with the climate system." In 1997, the UNFCC formulated the Kyoto Protocol, which commits its parties by setting internationally binding GHG emission reduction targets and remains in force for much of the world today.

AF will be directly or indirectly involved in mitigation as these sectors are both emitters and providers of sinks that sequester GHGs in the ecosystem. This merits explicit mention in the Kyoto protocol that mentions emissions from enteric fermentation, manure management, rice cultivation, soil management, field burning, and deforestation along with sinks of afforestation and reforestation. In the following sections, the AF in climate change mitigation are discussed, followed by economics of the issue, and then some challenges and future research needs.

Policy Approaches to Climate Change Mitigation in Agriculture and Forestry

Externalities have long affected society, and various methods have been formulated to deal with them. Classically, one basically tries to reflect the costs imposed by the emissions on the emitter generally by the government in a way to improve private decision making and the market result (Mankiw, 2012). This has been done by regulation, taxation/subsidization, and imposition of trading schemes. Their basic characteristics are as follows:

- Regulation or command-and-control policy involves a government-imposed limit on GHGs emissions, where the limit should reflect a balance between the damage from emissions and the cost of reducing emissions. Obviously, command-and-control policy is a simple and direct approach to reduce emissions. But, in order to determine the appropriate level of emission regulation, government needs thorough knowledge of the regulated activity and the damage caused plus an ability to monitor and enforce compliance. Also, the burden of the regulation can be quite different depending on the emitters' production characteristics possibly causing substantial inequities (Tol, 2014).
- Emissions taxation involves imposing a cost to emit, whereas subsidies give benefits to emissions reductions. Nordhaus (2008) stated that the appropriate taxation level should represent the discounted present value of damage resulting from an additional ton of emissions. The tax acts like a penalty that will be paid by people emitting GHGs. While imposing the tax, the government needs to know this appropriate tax level but is uncertain in terms of the amount that emissions will be reduced (Mankiw, 2007). Generally, subsidies have similar effects as taxes in the short run, but one of the differences from taxes is the redistribution of money (Tol, 2014): in terms of taxes, money is transferred from consumers to governments; in terms of subsidy, the trend of money flows reverse, that is, from governments to consumers.
- Tradable emission permits involve a government-imposed limit on GHGs emissions in the form of permits for emissions but allows the permits to be traded. It permits emitters that would incur high cost in reducing emissions to buy permits from those who can reduce emissions at a lower cost, lowering the overall cost of emissions (Nordhaus, 2008). The Kyoto protocol advocates such a scheme and spawned the multisector, multicountry European Union's Emissions Trading Scheme in 2005.

Generally speaking, economists prefer market-based trading or taxation methods to direct market regulation. Through such mechanisms, policy makers internalize the externality: providing emitters with incentives to reduce emissions and innovate in developing new, lower emitting technologies (Nordhaus, 2008).

Recently, attention has been paid to voluntary participation in emission reduction programs with emitters allowed to opt in and choose to produce carbon offsets. If emitters choose to join the program (opt in), then they are going to be directly paid for the GHG abatement and will also be provided with liability for any future GHG emissions. Also, AF is generally mentioned as sectors that are not capped but ones that may sell emission reductions or sequestration increases into the market place.

Beyond the market and command-and-control approaches, a number of other policy approaches are possible. For example, Fri *et al.* (2010) mentioned:

- Pursuit of near-term emission reductions including (1) increasing energy efficiency in production and use/conservation and (2) increasing the use of low GHG-emitting electricity generation like those relying on renewables, new-generation nuclear power, power plants equipped with carbon capture and storage technology, and low GHG-emitting transportation options.
- Accelerated retirement, retrofitting, or replacement of emissions-intensive infrastructure.
- Increased research and development on low-emitting technology choices.

How Agriculture and Forestry Can Participate in Mitigation Efforts?

IPCC (2007d) presents estimates that AF are the source of approximately 30% of anthropogenic GHG emissions mainly in the form of methane, nitrous oxide, and carbon dioxide. Main sources for methane emissions are rice, ruminants, and manure. For nitrous oxide, main sources are manure, legumes, and fertilizer use. For carbon dioxide, the main emissions arise from fossil fuel usage, soil tillage, deforestation, other land-use change, biomass burning, and land degradation.

AF management can be altered to reduce emissions by a number of means. For example, in many cases management can be improved, cattle diets can be changed, fertilization practices altered, tillage and associated energy use reduced, irrigation pumping efficiency improved, rice management altered, land moved into more perennials, and many other strategies (McCarl and Schneider, 2000).

In terms of sinks, AF annually absorb atmospheric CO_2 as plants and trees grow, and then release it as they decay. Retention (sequestration) can be increased in soils and standing vegetation by altering practices. Such practices include cropland retirement (conversion to native vegetation), residue management, less-intensive tillage, land use conversion into pasture, afforestation, restoration of degraded soils, avoided deforestation, longer forest rotations, and forest management practices, can contribute to mitigation and storing carbon in wood products (McCarl and Schneider, 2000; Krankina and Harmon, 2006; Wilson, 2006).

Fossil fuel-intensive products can also be replaced with substitute products of AF. Certain AF products can be used to replace building materials, such as steel and concrete. Also, AF biomass can directly be used in fueling electrical power plants or can be processed into liquid fuels, such as ethanol and biodiesel. Using biomass as energy feedstocks reduces net CO_2 emissions because the carbon in the feedstock is drawn from the atmosphere via photosynthesis. However, this offset is not perfect as feedstock's growth, refining, and related transport emits GHGs. Furthermore, one must also consider the leakage or indirect land-use effects when land is diverted from traditional commodity production resulting in potential land conversion or other emissions increasing activities elsewhere (Murray *et al.*, 2004; Searchinger *et al.*, 2008; Fargione *et al.*, 2008). Other potentially significant indirect negative effects, such as rebound effects in energy consumption due to changes in the price of energy, are also probable (Rajagopal *et al.*, 2010).

Economic Work on Costs of Agriculture and Forestry Greenhouse Gas Mitigation

There have been a wide variety of efforts addressing the extent to which AF can produce cost-competitive supplies of GHG net emission reductions. These studies have looked at the issue in terms of particular strategies and across a portfolio of strategies. In terms of individual strategies, McCarl and Schneider (2000) reviewed cost estimates across a variety of emission reductions, sequestration, and substitute product options.

In terms of individual strategy appraisals:

- A long history of forest sequestration studies show that cost-competitive possibilities exist in terms of afforestation and forest management (Moulton and Richards, 1990; Adams *et al.*, 1993, 1999; Parks and Hardie, 1995; Plantinga *et al.*, 1999; Stavins, 1999; IPCC, 2000; Stavins and Newell, 2000; Kauppi and Sedjo, 2001; Sohngen and Mendelsohn, 2003; Latta *et al.*, 2011). Later, studies enter more complexity and show increased costs of offsets (Latta *et al.*, 2011).
- Agricultural soil carbon has been shown to be competitive at lower prices (Pautsch *et al.*, 2001; Antle and Capalbo, 2001) but of relatively short duration (15–20 years or so for tillage and up to 50 years for land-use change; West and Six, 2007).
- The cost-competitive sequestration amount has been found to be substantially lower than the total estimated potential with the differences narrowing as carbon price increases (McCarl and Schneider, 2001).
- A large number of studies have looked at individual agricultural emissions reduction and biofuel strategies as reviewed by McCarl and Schneider (2000), IPCC (2007d), and Smith *et al.* (2006).

In terms of portfolios:

- A range of emission reductions and offsets have been found to be cost-effective strategies for GHG offsets with different ones being superior at alternative price levels (McCarl and Schneider, 2001; Murray *et al.*, 2005; Baker *et al.*, 2010).
- Large potential options include agricultural soil carbon and forest management at low prices and in the near term with afforestation and bioenergy in the longer term (Lee *et al.*, 2007; Murray *et al.*, 2005).
- Competition between strategies significantly alters results from single-strategy appraisals. For example, soil carbon increases as price initially increases but then falls at high levels in favor of forestry and bioenergy (McCarl and Schneider, 2001; Schneider and McCarl, 2003; Lee *et al.*, 2007).
- Agricultural emission offsets are competitive with food production. For example, McCarl and Schneider (2001) found substantial decreases in food production and increases in food prices at higher carbon prices.

Renewable energy has been found to have a large role in achieving ambitious climate mitigation targets (McCarl and Schneider, 2001; Schneider and McCarl, 2003; Murray *et al.*, 2005; Hoogwijk *et al.*, 2009), but effects on market prices and sequestration in key areas, like rainforests, are a major concern. Johansson and Azar (2007) focused on the competition between bioenergy and food production and found a similar result. Searchinger *et al.* (2008) and Fargione *et al.* (2008) argued that such results would be expected.

Distributional Effects of Mitigation and Cobenefits

Distributional effects of mitigation strategies have been examined. A number of studies show that mitigation activity stimulated by GHG prices generally improves producers' welfare and decreases consumers' welfare (McCarl *et al.*, 1999; United States Department of Agriculture, Global Change Program Office, 1999; Konyar and Howitt, 2000; McCarl and Schneider, 2001; Schneider and McCarl, 2005; Baker *et al.*,

2010). Murray *et al.* (2005) showed that effects and strategies used vary regionally. Sparovek *et al.* (2009) showed that welfare effects may be negative across different societal groups with some regions/groups experiencing losses. Also, some mitigation policies also benefit other environmental or economic items. For instance, Elbakidze and McCarl (2007) discussed the coeffects of mitigation on water and air quality; however, they also indicated that full consideration of these benefits was quite complex.

Challenges in Mitigation

Although many studies show that AF may be able to supply low-cost mitigation opportunities, it is important to consider some challenges raised in the Kyoto protocol. These are commonly known as additionality, leakage, permanence, and uncertainty. It is also important to consider transaction costs.

- *Additionality* For economic efficiency, mitigation activities need to provide GHG emission reductions that are additional to what would have occurred in the absence of mitigation activity. However, actors who adopt strategies in advance of a mitigation program generally have an interest in being paid for their actions. Murray *et al.* (2007) discussed this issue.
- *Leakage* Another mitigation challenge is leakage. Leakage embodies the idea that mitigation gains in one place could be offset due to mitigation-induced reductions in commodities produced and offset, emissions increasing, and production elsewhere. Mitigation options like diverting land from production of food crops to bioenergy crops or afforestation may lead to emission increasing agriculture expansion elsewhere. The result is a lower effect on emissions (Murray *et al.*, 2004) and possibly an emission's increase or a long-term emission's debt (Searchinger *et al.*, 2008; Fargione *et al.*, 2008).
- *Permanence* Certain activities only provide offsets for a limited time and store potential emissions. In particular, biological sequestration in soils and standing trees only uptake carbon until equilibrium is reached (West and Six, 2007) and on practice reversal, the stored carbon is released. This raises the possibility of a price discount for such activities as discussed by Kim *et al.* (2008).
- *Uncertainty* There is uncertainty in the magnitude of the GHG offsets developed by many potential AF projects due to the effects of forces like climate, fire, and pests. Kim and McCarl (2009) discussed possible discounts and the value of widely spread portfolios.
- *Transactions costs* When GHG offsets are sold, the transactions typically will involve cost. Michaelowa and Jotzo (2005) classified transaction costs for GHG projects into three different groups: (1) preproject implementation costs that include search costs, negotiation costs, baseline determination costs, approval costs, validation costs, review costs, and registration costs; (2) project implementation costs that include monitoring costs, verification costs, review costs, certification, and enforcement costs; and (3) trading costs that include transfer costs and registration costs. There would also be costs of brokers assembling projects as discussed in Post *et al.* (2009) and Kim (2011).
- *Other difficulties* Costs and benefits of mitigation can arise over a long period. Discounting of impacts over long time horizons can be problematic (Weitzman, 2007; Dietz and Stern, 2008). Also, many impacts are extremely complex and their consideration and monetary valuation can be complicated. Moreover, there are usually no compensation mechanisms that may well balance costs and benefits among different stakeholders (Söderholm and Sundqvist, 2003).

Adaptation in Climate Change

There is a likely inevitability to a substantial amount of climate change. GHG emissions and atmospheric concentrations are on a strong increasing upward trend, whereas climate stabilization requires close to zero net emissions. IPCC (2007c) presents a series of atmospheric GHG stabilization scenarios and these show substantial climate change, even if GHG emissions peak now and then trend toward zero. In such a setting there is a need to address adaptation to a changed climate (Rose and McCarl, 2008).

Adaptation is used in a climate change setting to refer to "adjustment in natural or human systems in response to actual or expected climatic stimuli or their effects, which moderates harm or exploits beneficial opportunities" (IPCC, 2007b). Some studies have shown that with adaptation AF could, to a large extent, moderate the damage caused by lower levels of climate change (Easterling *et al.*, 1993; Adams *et al.*, 1999; Reilly and Schimmelpfennig, 1999; Yu and Babcock, 2010; Zilberman *et al.*, 2012).

Who Adapts?

Climate adaptation can be initiated by actors across multiple levels, such as individuals, firms, and public entities. In general, such adaptation actions are undertaken by private and public parties with important distinctions.

Private party adaptation (also called autonomous adaptation – IPCC, 2001; Smith *et al.*, 2000) is initiated by private agents acting in their own best interests. Such individuals are altering operations in reaction to climate. Much private party adaptation has been done in AF for centuries (McCarl, 2007). Adaptations can be observed today. For example, in AF, Seo and Mendelsohn (2008a) found evidence of shifts in livestock populations as climate evolves, whereas Mu *et al.* (2013) found evidence of land use and stocking rate shifts and Park (2012) found evidence of crop mix shifts.

Public party adaptation, sometimes called planned adaptation, is collectively implemented by governments or other societal organizations. Activities in this domain correct for market failures in the classical public good sense (Samuelson, 1954) where private parties do not reap the full gain of adaptation or where private parties cannot adapt due to limited resources, knowledge, or capability (Speranza *et al.*, 2010; Hallegatte *et al.*, 2011).

Means of Agriculture and Forestry Adaptation

A wide variety of adaptation actions are possible. In managed AF settings, private adaptation decisions include altering

planting and harvesting date, crop varieties, crops mix, livestock species, irrigation, pest management strategy, shade provision, insurance use, fire control, etc. (Klein *et al.*, 1999; McCarl, 2007). In unmanaged AF ecosystems, natural adaptation is occurring but perhaps at an undesirable pace and thus shifting to more active management may be possible. On the public side, a number of possible strategies can be pursued, including the following, as summarized by McCarl (2007):

- Research investment in crop varieties, management practices, etc.
- Extension investment in disseminating adaptation information.
- Infrastructure investment in transport, flood control, water provision, coastal protection, etc.
- Adaptation adjustment assistance, like education, migration of facilities, etc.
- Support for new industries, developing new institutions, and relocating industry, etc.
- Trading policy allowing more imports or exports to alleviate lost production and cope with surpluses.

Economic Aspects of Agriculture and Forestry Adaptation

A number of studies have addressed economic aspects of adaptation. These can be separated into studies of climate change offset ability, observed historical levels of adaptation, and modeling adaptation in an economic sense.

Basic AF adaptation concept

Figure 4 above shows the basic adaptation concept. In particular, a producer will pick the production system that is most economically attractive, given the climate regime at a location. Suppose that the curves in Figure 4 show the returns to various enterprises on a parcel of land as the temperature varies. In turn, under a temperature level of T_3, a rational farmer would plant wheat as it is superior to the other possibilities. Now suppose the temperature rises from T_3 to T_4, then the farmer would adapt by changing from wheat to corn to seek higher economic returns. Further temperature increases cause additional shifts as well.

Climate change offset ability

Adaptation can reduce the adverse effects of climate change to some extent or enhance the benefits. For example, technological advances, such as genetically modified crops and more efficient irrigation systems, can help to maintain agriculture productivity at the level before climate change. Adams *et al.* (1995) and Tubiello *et al.* (2002) found that changes in planting date and crop maturity can substantially improve production. Yu and Babcock (2010) showed that yield losses of corn and soybeans in the United States Corn Belt from drought have decreased over time due to effort being devoted to research on drought-tolerant crops. Adams *et al.* (1999) showed that changes in crop mixes have substantial benefits.

Observed adaptation

Contemporary adaptation has been examined by looking at how AF practices vary over space and respond to climate conditions over time (Chen and McCarl, 2001; Seo and Mendelsohn, 2008a,b; Seo *et al.*, 2009a,b). For example, findings indicate variations in many fields:

- observed agriculture yield, where changes under climate change are smaller than agronomic results, indicating that effective adaptation is occurring (Mendelsohn and Dinar, 2003);
- input usage associated with climate, where, for example, Chen and McCarl (2001) found increased pesticide costs incurred as climate got warm;
- mix of animals and crops (Seo and Mendelsohn, 2008a,b; Mu *et al.*, 2013);
- land allocation between crops and livestock (Seo and Mendelsohn, 2008a; Mu *et al.*, 2013);
- crop varieties and planting dates (Tubiello *et al.*, 2000); and
- livestock breeds (Zhang *et al.*, 2013).

Modeled adaptation

A number of studies have tried to examine potential adaptations by predicting their nature and implications using modeling. In such efforts, adaptation can only employ possibilities portrayed in the model, so it is important to have an augmented set of production possibilities that can be used in the face of climate change. A number of findings have arisen from such studies. For example:

- There are significant adaptation benefits from alterations in cropping systems, planting dates, harvest dates, and varieties (Adams *et al.*, 1995, 1999; Easterling *et al.*, 1993; Tubiello *et al.*, 2000, 2002).
- Crop mix shifts are more likely beneficial (Adams *et al.*, 1999) but cause shifts in needed infrastructure (Attavanich *et al.*, 2013).
- Adaptation can alter income effects substantially and reduce the risk of hunger effects (Butt *et al.*, 2005, 2006; Reilly *et al.*, 2002).
- Producers in low- to mid-latitude forests can adapt using short rotation plantings, bringing down timber prices (Sohngen *et al.*, 2001; Spittlehouse and Stewart, 2003).

Effort Allocation and Economic Tools for Climate Change Analysis

Effort Allocation between Information, Mitigation, and Adaptation

One big question involves the societal allocation of effort between conventional matters and climate change-related efforts. Conceptually, this involves an allocation problem considering the opportunity costs of allocated funds and their marginal returns in various climate change activities (McCarl, 2012). Some economic studies have dealt with the allocation issue regarding adaptation and mitigation (de Bruin *et al.*, 2009; Wang and McCarl, 2013).

Economic Tools

Many studies have been done regarding climate change issues. Broadly speaking, these have involved a statistical, spatially observed data approach and a simulation, structural approach

(Schimmelpfennig *et al.*, 1996). In the remaining of this study, the authors have provided a few comments on the nature, strengths, and weaknesses of both.

Statistical spatial modeling

Statistical, spatial-based models examine climate change effects, adaptation, and mitigation using historical data on practices employed and their consequences. Typically, statistical or econometrical approaches over panel datasets are used, separating those factors that could account for different effects in different places. In the effects and adaptation arenas, one looks at data across space and time characterized by alternative climates and can infer the following: (1) effects of climate change on land values (Mendelsohn *et al.*, 1994), crop yields (Chen *et al.*, 2004), or input use (Chen and McCarl, 2001) or (2) adaptation in terms of land use (Mu *et al.*, 2013), crop mix (Park, 2012), livestock species (Zhang *et al.*, 2013), or livestock type (Seo *et al.*, 2009b). In the mitigation arena, one looks at how productivity is altered by adoption of mitigation strategies and infers the cost of achieving mitigation (Antle and Capalbo, 2001).

Advantages of this method are that the behavior of farmers and changes in the environment are both embedded in the data and in the estimated model and one can control a number of factors, like soil quality (Adams *et al.*, 1998). Disadvantages are that prices are assumed to be constant, that there is generally no cost for farmers or companies to adapt to climate change, and that the model cannot completely capture phenomena in the dataset or beyond the range of the dataset (like high CO_2 levels) (McCarl *et al.*, 2010).

Structural modeling

A structural modeling approach generally combines biophysical and economic models under climate change data to project the effects of climate change issues (Lambi and Molua, 2007). In general, it uses an assumed behavioral economic model often based on mathematical optimization. For instance, researchers often used welfare maximization under climate change to simulate market reactions (Adams *et al.*, 1990, 1999; Reilly *et al.*, 2002).

The strength of this approach is that it presents comprehensive responses and adjustments from physical and economic aspects of agriculture to climate change examining phenomena beyond the scope of the current data (Schimmelpfennig *et al.*, 1996). For instance, Butt *et al.* (2005) and Arndt *et al.* (2012) used structural methods to simulate the effects of climate change in developing countries without large data requirements. Also, changes in market prices can be captured and then employed in welfare analysis (Adams and Hurd, 2002).

However, this type of model assumes the motivation for decision making (i.e., profit maximization) and the mechanism for market clearing. The strength of the adaptations and mitigation modeling is purely dependent on the production possibilities included in the model (Adams *et al.*, 1998; McCarl *et al.*, 2010) and can lead to under- or overestimates (Adams and Hurd, 2002). Another problem associated with this method is that one usually extends the conclusions of some regionally specific experimental cases to more general and diverse agricultural situations (Schimmelpfennig *et al.*, 1996).

Combined methods

Even though the authors categorize the above as two different methods, the relationship between them is often complementary, instead of mutually exclusive (Schimmelpfennig *et al.*, 1996; Lambi and Molua, 2007). For example, the United States national assessment used a combination of both modeling approaches in its appraisal (Reilly *et al.*, 2002).

Concluding Comments

The authors have reviewed the evidence for climate change, the causes and the projections followed by a review of possible information, adaptation, and mitigation actions. In the discussion, they have attempted to provide the reader with an introduction to the vast literature by extensive referencing. Given the vastness of the issue, this was intended only to be an introduction and a guide to where one might go to learn more.

See also: Air: Greenhouse Gases from Agriculture. Climate Change: Agricultural Mitigation. Climate Change and Plant Disease. Climate Change: Animal Systems. Climate Change: Cropping System Changes and Adaptations. Climate Change: New Breeding Pressures and Goals. Computer Modeling: Applications to Environment and Food Security. Computer Modeling: Policy Analysis and Simulation. Economics of Natural Resources and Environment in Agriculture. Government Agricultural Policy, United States. Mathematical Models to Elaborate Plans for Adaptation of Rural Communities to Climate Change. Simulation Modeling: Applications in Cropping Systems. Soil: Carbon Sequestration in Agricultural Systems. Soil Greenhouse Gas Emissions and Their Mitigation. World Water Supply and Use: Challenges for the Future

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Cloning Animals by Somatic Cell Nuclear Transplantation

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Glossary

Clone An organism that is an exact genetic copy of another.
Cryopreservation Maintenance of viable tissues, cells, or embryos at very low temperature.
Enucleation The process of removing the recipient cell chromosomes or nucleus.
Epigenetics Heritable changes to DNA and its associated proteins that control/establish gene expression patterns without affecting the underlying DNA sequence.
Nuclear reprogramming The process of returning a differentiated cell nucleus to a totipotent state.
Recipient cytoplast An oocyte that has had its DNA removed.
Somatic cell nuclear transfer (SCNT) A technique that allows the production of cloned animals.
Transgenic animal An animal in which there has been a deliberate modification of its genome, such as addition or deletion of genes.
Zona pellucida (ZP) A glycoprotein membrane that surrounds the plasma membrane of the oocyte.
Zygote The one-cell embryo formed by the union of sperm and oocyte.

Introduction

Animal Cloning and Nuclear Reprogramming

A clone is an organism that is an exact genetic copy of another. Many plants and animals in nature utilize cloning as a form of reproduction. Somatic cell nuclear transfer (SCNT) is a technique that allows the production of cloned animals. With this technique, the nucleus of a donor cell, containing an animal's genetic material, is introduced into an enucleated oocyte called the recipient cytoplast. Embryonic development is then induced and, providing that the right conditions are maintained, the reconstructed embryo can develop into an individual that will be genetically identical to the one from which the nuclear material was derived (**Figure 1**).

The process by which the somatic cell nucleus is transformed into an embryo is called nuclear reprogramming and involves changes to the epigenetic mechanisms that control gene expression and cell differentiation status. Most cells in an organism contain the same genetic information, which is stored in their deoxyribonucleic acid (DNA). Epigenetics refers to heritable changes to DNA and its associated proteins (collectively referred to as chromatin) that control/establish gene expression patterns without affecting the underlying DNA sequence. As embryonic cells differentiate into different tissues and cell types, the DNA remains the same, but the cells acquire different epigenetic modifications. The normal development of an embryo and fetus depends on a precise sequence of chromatin configuration changes, which are usually related to methylation of genomic DNA and modifications to the histone proteins to which DNA is wrapped around. These epigenetic changes are heritable from cell to cell and are acquired in a progressive and sequential manner as cells differentiate. The presence of these epigenetic marks and their ability to be passed to daughter cells after cell division is a mechanism to maintain the functional and differentiation status of the cells. This mechanism explains why when a cell in the skin divides, its daughter cells continue to be skin cells and do not turn into neurons or any other cell type. It was thought that development of an embryo to an adult was a unidirectional process and the differentiation status of a cell, and thus its epigenetic modifications, were fixed and irreversible. Cloning using adult differentiated somatic cells disproved that dogma (Gurdon, 1962; Wilmut *et al.*, 1997), demonstrating the enormous plasticity of the mammalian epigenome. Successful cloning by SCNT involves epigenetic reprogramming whereby the gene expression profile and the epigenetic memory of the differentiated cell is abolished and the new embryo-specific gene expression and epigenetic profile is established, driving correct embryonic and fetal development. This includes abrogation of the expression of approximately 8000–10 000 genes in the somatic cell and initiation of the embryonic program with approximately 10 000 genes (Niemann and Lucas-Hahn, 2012). Failure to reprogram the donor genome is thought to be the main reason for the low efficiency of cloning (Rideout *et al.*, 2001; Bourc'his *et al.*, 2001; Dean *et al.*, 2001). Thus, cloning efficiency depends on the ability of donor cells to be totally reprogrammed to an embryonic state and the ability of the recipient cytoplasm to reprogram the exogenous (i.e., donor) nucleus.

The oocyte is one of the few cells that have the ability to induce the necessary changes to a somatic cell nucleus, so that embryonic development can proceed to term. This capacity probably extends from the natural role oocytes have during normal development. When the oocyte and sperm, two highly differentiated cells, meet at fertilization in order to generate a new individual, their genomes must be combined and rendered amenable to embryonic and fetal development. This process includes extensive and dynamic epigenetic remodeling.

Historical Perspective

The original idea of generating an animal from a somatic cell was proposed by Spemann in the early 1900s (Spemann, 1914) as a way to test the developmental potential of a cell's

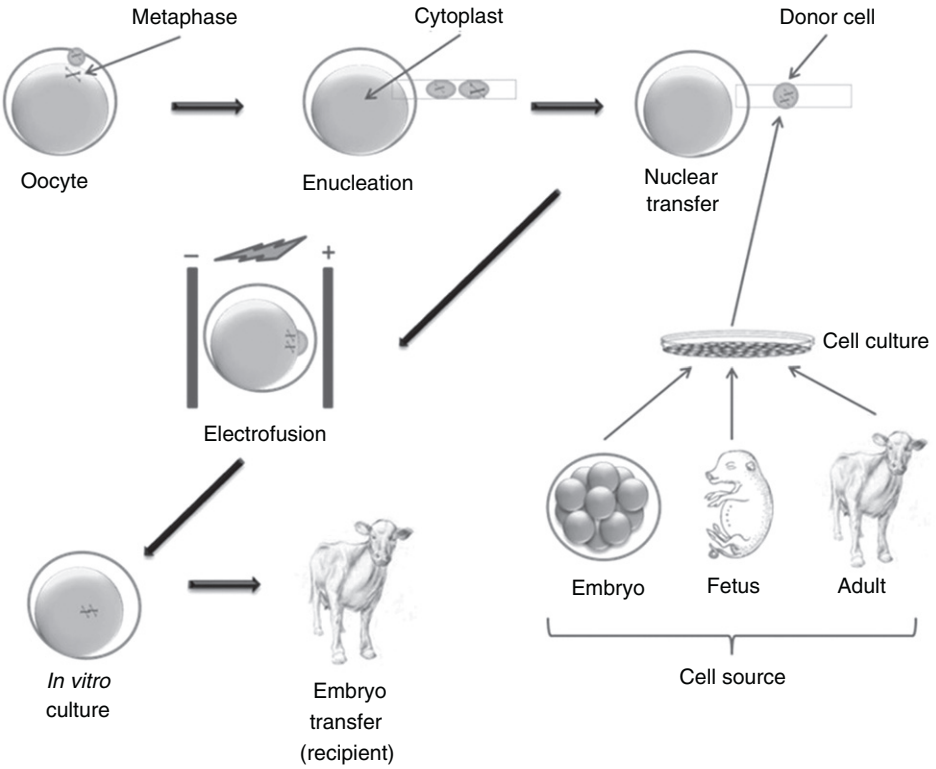


Figure 1 Cloning animals by nuclear transplantation.

nucleus. However, the required technology to perform Spemann's proposed experiment was not available until the 1950s, when Briggs and King developed nuclear transfer techniques in amphibians (*Rana pipiens*), obtaining adult animals when injecting embryonic cells into enucleated oocytes (Briggs and King, 1952). In 1962, John Gurdon used a similar technique to produce frogs (*Xenopus tropicalis*) from intestinal cells, demonstrating that a somatic cell nucleus has all the genetic material necessary for development of a complete individual (Gurdon, 1962). Gurdon was awarded the Nobel Prize for these accomplishments.

In mammals, nuclear transfer technology was developed several decades later as technological improvements allowed scientists to work with the smaller mammalian embryos. The transfer of an embryonic nucleus into an enucleated mouse zygote (1-cell embryo) was reported by Illmensee and Hoppe in 1981, resulting in the development of adult animals (Illmensee and Hoppe, 1981). However, controversy surrounded these results, as other groups were unable to replicate them. McGrath and Solter (1983) developed a more efficient technique by which the donor cell was fused with, instead of being injected into, an enucleated zygote; however, they were not able to produce offspring when two-cell and older embryos were used as cell donors. In 1986, Willadsen used sheep mature oocytes as recipient cytoplasts instead of zygotes and was able to obtain offspring after the transfer of cells from early stage cleavage embryos (up to a 32-cell embryo) (Willadsen, 1986). The embryo cloning approach developed by Willadsen provided the opportunity for producing a limited number of clones from a single embryo. This technique was then successfully applied to several species, including cattle (Prather *et al.*, 1987), rabbits (Stice and Roblm, 1988), pigs (Prather *et al.*, 1989), mice (Kono *et al.*, 1991), and monkeys (Meng *et al.*, 1997), with some commercial companies providing embryo-cloning services for more than a decade.

In the mid-1990s, Keith Campbell and Ian Wilmut hypothesized that synchronizing the cell cycle of the donor and recipient cells could be the key to efficiently cloning from adult animal cells. Their experiments led first to successful cloning from embryonic cells cultured *in vitro* (Campbell *et al.*, 1996) and soon after to the birth of the first mammal cloned from an adult somatic cell – Dolly the sheep (Wilmut *et al.*, 1997). Dolly was cloned from a somatic cell nucleus derived from mammary gland cells cultured *in vitro*. Only one viable animal was produced from the 277 reconstructed embryos created, a relatively low efficiency that remains unimproved to this day. After the sheep was cloned, several other mammalian species followed, including the cow (Cibelli *et al.*, 1998), mouse (Wakayama *et al.*, 1998), goat (Baguisi *et al.*, 1999), pig (Polejaeva *et al.*, 2000), gaur (Lanza *et al.*, 2000), mouflon (Loi *et al.*, 2001), rabbit (Chesne *et al.*, 2002), cat (Shin *et al.*, 2002), rat (Zhou *et al.*, 2003), white-tailed deer (Westhusin, 2003), mule (Woods *et al.*, 2003), horse (Galli *et al.*, 2003), banteng (Janssen *et al.*, 2004), African wildcat (Gomez *et al.*, 2004), dog (Lee *et al.*, 2005), ferret (Li *et al.*, 2006), wolf (Kim *et al.*, 2007), buffalo (Shi *et al.*, 2007), red deer (Berg *et al.*, 2007), and the camel (Wani *et al.*, 2010).

Efficiency of Cloning by Somatic Cell Nuclear Transfer

Typically, the success of obtaining a live birth after mammalian somatic nuclear transfer is low. In general, only 1–5% of

embryos transferred to surrogate mothers result in live offspring; however, since the first successful attempt, progress has been made that reflects improved technical skills and increasing knowledge of the underlying mechanisms (Niemann and Lucas-Hahn, 2012). For example, in cattle, efficiencies of 20–25% of live offspring are not uncommon for experienced commercial and research laboratories (Panarace *et al.*, 2007; Kues *et al.*, 2008). In pigs, although the average yield of live births per embryo transferred is only 3–5%, by transferring a large number of embryos per recipient sow, pregnancy rates can reach 80% with litter sizes averaging 6 cloned piglets; which, although lower than that of natural breeding (~10%), is a significant advance.

Interestingly, the *in vitro* development of SCNT embryos to the blastocyst stage is similar to that attained by *in vitro* fertilization (IVF). Also, after initial embryo transfer, a similar pregnancy rate was observed between SCNT- and IVF- or *in vivo*-derived bovine embryos (Kuroiwa *et al.*, 2004; Hill *et al.*, 2000; Heyman *et al.*, 2002). However, high incidences of pregnancy loss occur during the first trimester of gestation (Hill *et al.*, 2000; Heyman *et al.*, 2002; Zakhartchenko *et al.*, 2001). Also, late gestation losses are higher in SCNT pregnancies as compared with IVF- and *in vivo*-derived pregnancies (Heyman *et al.*, 2002). Fetal and placental abnormalities are often reported. Finally, high proportions of cloned offspring die soon after birth or require intensive care. The losses during gestation and in the early postnatal period are the main causes for the low overall efficiency of cloning by SCNT.

The majority of clones that survive to 6 months of age continue to develop normally and do not differ from naturally conceived animals in terms of blood and urine biochemistry (Chavatte-Palmer *et al.*, 2002), immune system (Lanza *et al.*, 2001), and reproductive parameters (Enright *et al.*, 2002) among others. Also, there is no difference in the composition of meat and milk from clones of cattle compared with their naturally produced counterparts of the same age, and similar results have been reported for cloned pigs (Archer *et al.*, 2003).

Some abnormalities manifested in animals derived from SCNT include 'Large Offspring Syndrome,' diabetes, pulmonary hypertension, viral infection, dystocia, kidney problems, leg malformations, pneumonia, heart defects, liver fibrosis, osteoporosis, joint defects, anemia, and placental abnormalities (Cibelli *et al.*, 2002). However, all the abnormalities seen in clones disappeared in the clone's offspring, leading to the conclusion that the abnormalities must be of epigenetic rather than genetic origin.

Applications of Somatic Cell Nuclear Transfer: Why Clone Animals?

Cloning by nuclear transfer has the potential to contribute substantially to animal agriculture, biotechnology, biomedicine, and the preservation of endangered species. The success of adult SCNT with almost all agriculturally important species confirms its usefulness for the clonal expansion of animals with superior genotypes (**Table 1**). Also, the ability to generate a complete individual from an *in vitro*-cultured cell provides an efficient means of making transgenic animals carrying complex genetic modifications. Furthermore, cloning can be used as a tool for aiding in the preservation of endangered species and has even been proposed as a means to rescue already-extinct ones. Finally, cloning offers a research model for studying the basic mechanisms of cell fate commitment, cell differentiation, and epigenetic reprogramming while providing new avenues for biomedical research and application.

Multiplication of Superior Animals

Cloning has the potential to allow the rapid dissemination of superior genetics. The dissemination of genetics with superior production potential directly to farmers and producers could dramatically increase animal production and reduce variability in production systems and products. Specific genotypes could be developed for different conditions and provided to farmers to match their particular environmental conditions and production systems. However, this would require that the efficiency of clone development closely matches that achieved by natural reproduction or currently used reproduction biotechnologies, such as artificial insemination and embryo transfer. Currently, embryos produced by SCNT cloning have a 10–50× lower developmental potential than naturally produced embryos, which limits its application and results in a high cost for cloned-animal production. Therefore, current agricultural applications of cloning are limited to animals of high economic value, such as those with elite genetics used for breeding purposes. Expanding the number of animals with highly desired genetics provides opportunities for increased embryo or semen production, increased breeding opportunities, and extended generational influence from clones of elite animals. Furthermore, a common application of cloning is the ability to recover the reproductive potential from animals that otherwise cannot produce offspring, such as the case with castrated animals, animals exposed to the stress of high athletic performance, and diseased animals. In the latter case, cloning can also offer a form of insurance against the natural or accidental death of an elite or prized animal.

The agricultural application of cloning technology is directly related to the safety of food products derived from these animals and their offspring (Rudenko *et al.*, 2007; Fox, 2008). Extensive studies from multiple regulatory agencies in several countries have concluded that meat and milk products from clones and their offspring are as safe for human consumption as those from naturally bred animals EFSA, 2010, 2012; FDA, 2008. Some concerns, especially with cloned individuals, are that the inefficient epigenetic reprogramming

Table 1 Somatic cell nuclear transfer in farm animals

Species	*References*
Sheep	Wilmut *et al.* (1997)
Cow	Cibelli *et al.* (1998)
Goat	Baguisi *et al.* (1999)
Pig	Polejaeva *et al.* (2000)
Rabbit	Chesne *et al.* (2002)
Mule	Woods *et al.* (2003)
Horse	Galli *et al.* (2003)

inherent to current cloning methodologies can lead to abnormal epigenetic profiles, which, in turn, may alter meat and/or milk qualities. Also, animal welfare issues generated by the current methodologies, related to the increased incidence of pregnancy complications and need for additional early postnatal care of cloned animals, are of further concern. As these are reasonable concerns, more studies related to the influence of cloning on epigenetic status and the effects on food products derived from cloned animals are required.

Production of Genetically Modified Animals

Because cloning can be performed from *in vitro* cultured cells, it is possible to induce precise genetic modifications to the cells in culture, screen for correctly modified cells, and then use them to generate a transgenic animal. This ensures that all animals produced carry the genetic modification and that every cell type within the animal, including the germline, is transgenic. In spite of the inefficiencies of cloning by SCNT, this technique remains the most efficient one for generating transgenic farm animals. Furthermore, SCNT can be used for generating animals with precise genetic engineering, such as adding, deleting, or modifying specific genes at specific locations. Using this approach, cattle that lack the prion gene, responsible for bovine spongiform encephalopathy (mad cow disease), have been produced (Kuroiwa *et al.*, 2004). Targeted modifications have also been successfully achieved in sheep (McCreath *et al.*, 2000) and pigs (Lai *et al.*, 2002). Agricultural traits that have been considered for genetic modification are improved feed utilization, resistance to disease, reduction of animal waste, and diversification of agricultural products, i.e., providing new economic opportunities in rural areas and generation of new consumer products. A major hurdle to the advancement of transgenic technologies for agricultural applications are concerns about the cost and time associated with the regulatory processes necessary to bring products to market and potential consumer acceptance issues.

A higher economic incentive is associated with the production of genetically engineered animals for human medicine applications. Genetically engineered animals that can be used as bioreactors for the production of pharmaceuticals have been created. Many therapeutic proteins require production in animal cells, as mammalian cell culture bioreactors are expensive and inefficient. Genetically modified animals offer an opportunity for producing large quantities of animal proteins in their milk or blood and at a much lower cost.

Also, transgenic livestock, especially pigs, are being produced as biomedical research models for various human diseases, including Alzheimer's, diabetes, cystic fibrosis, and cardiovascular disease among others. The combination of precise genetic modifications and cloning by nuclear transplantation is being used to develop pigs whose cells, tissues, and/or organs will not be rejected if transplanted to humans. The cloning of pigs with genes from other species artificially introduced into their cells opened new doors in the field of medicine. These animals could provide an alternative source of organs for transplantation into humans (Nagashima *et al.*, 2012). For now, xenotransplantation – the transplantation of organs from a 'foreign' species – is not viable because different species are not immune compatible, causing organ rejection; however, a goal is that through genetic engineering, pigs with human-compatible organs could be produced.

Preservation of Endangered Species

Cloning using SCNT can be a useful tool for conserving exotic or endangered animal species and even for recovering extinct species. Cloning can be used to improve genetic diversity by recovering animals that would otherwise disappear from the population and by introducing genetics from animals that otherwise would not contribute to the genetic pool because of death and infertility associated with age or disease, even for animals that were too young to reproduce. For example, SCNT was used to clone the last surviving animal of the Enderby Island cattle breed (Wells *et al.*, 1998). Also, cloning could potentially be used to reintroduce specific genetic resources from captive to wild habitats, such as in cases where adults would not adapt well to wild conditions. A limitation of cloning endangered species is the source of oocytes and recipient animals to perform SCNT and produce offspring, respectively. A solution that has been proposed to solve this problem is the so-called interspecies SCNT, whereby oocytes from a species different to the donor cell are used for cloning and the resulting embryos can sometimes be gestated in a related species. Interspecies nuclear transfer was used to clone a Gaur (*Bos gaurus*) – an endangered species – by transferring Gaur somatic cells into cow oocytes and the embryos to a surrogate cow mother (Lanza *et al.*, 2000). A similar approach was used to clone the wild European Mouflon – an endangered breed of sheep – with tissue collected from dead animals (Loi *et al.*, 2001). So far, interspecies nuclear transfer has only been successful across subspecies. One of the potential limitations to the success of interspecies SCNT is nuclear–mitochondrial incompatibility, because mitochondria are provided by the oocyte and molecular incompatibility between reprogramming factors in the recipient cytoplast and the donor cell nuclear chromatin can occur (Beyhan *et al.*, 2007; Jiang *et al.*, 2011).

Furthermore, cloning by nuclear transplantation can be used to recover extinct species as long as genetic material from the species can be recovered. The feasibility of cloning a recently extinct species was recently demonstrated. The Pyrenean Ibex (*Capra pyrenaica pyrenaica*) is a wild goat species that went extinct in 2000. Investigators transferred cells from a specimen collected in 1999 into goat oocytes and implanted the embryos into surrogate goats in order to obtain a live clone (Folch *et al.*, 2009). Although this animal died a few hours later, it represented the first case in which an extinct species was brought back to life, even if for a few hours. Furthermore, the sequencing of the woolly mammoth nuclear genome from permafrost remains and the production of cloned animals from mouse cells cryopreserved without cryoprotectants suggest that revival of long-extinct species may be possible. However, for purposes of conservation biology, cloning is not generally accepted as an alternative to animal conservation, and there is an ongoing debate among scientists and experts on the role of cloning in animal conservation and rescue. At the very least, it seems appropriate to consider the cryobanking

of somatic cells from endangered species as insurance against possible losses in genetic diversity.

Cloning Animals: Methodological Approaches

A cloning program involves multiple components including: harvesting of recipient oocytes, isolation and preparation of a donor cell, nuclear transplantation (oocyte enucleation, nuclear transfer, and oocyte activation), culture of cloned embryos, transfer of embryos to recipients, pregnancy monitoring, delivery of cloned animals, and perinatal care of clones.

Many of these components are common to other animal reproductive biotechnologies such as IVF and embryo transfer. Each step of the process has crucial importance, as many factors can influence not only clone development but also the epigenetic status of the embryo, with potential consequences for later clone health.

Source of Biological Materials

Recipient cytoplasm

Only a few cell types in an organism have the potential to reprogram a somatic cell nucleus to allow for development of a whole individual. These include oocytes (the female gamete) and zygotes (the one-cell embryo). A metaphase recipient cytoplasm appears to be important for correct reprogramming of a somatic cell nucleus, in part because this allows for removal of the genetic materials without depleting all of the nuclear components. Meiotic metaphase II (MII) stage oocytes are the most commonly used recipient cytoplasm for nuclear transplantation, because it has proven to be capable of inducing reprogramming of transplanted nuclei from a variety of sources and species. Also, metaphase stage zygotes have been successful in producing live offspring after nuclear transfer in mice and cattle.

For most livestock species, oocytes are typically harvested from slaughterhouse-derived ovaries. This provides an abundant and economical source of gametes. Alternatively, oocytes can be collected from live animals by ultrasound-guided oocyte aspiration or by laparoscopy. In general, immature germinal vesicle oocytes (prophase I of meiotic division) are collected, which have to be *in vitro* matured before being used for SCNT. In cattle, sheep, and goats, *in vitro* oocyte maturation takes 22–24 h, and 42–44 h in pigs. *In vivo*-matured oocytes have also been used to produce cloned cows, pigs, and sheep, with typically better results than that when using *in vitro*-matured oocytes; however, the cost and extra labor associated with recovering matured gametes has resulted in most laboratories using *in vitro*-matured oocytes.

Donor cell

The donor cell has a key role in cloning and can be determinant of the success or failure of the procedure. In general, the efficiency of cloning is considered inversely proportional to the differentiation state of the somatic cell. Adult somatic cells are usually more difficult to reprogram than fetal cells, whereas embryonic cells often result in the greatest cloning efficiency. However, there is great variability between individual cell lines in determining the efficiency of clone animal production. This variability is associated not only with cells from different tissues and individuals but also between different subcultures of the same cell line. To date, the characteristics of a successful cell line for cloning by SCNT have not been identified.

Donor cells in the G0/G1 phases of the cell cycle are typically used for production of clones. Synchronization of the cell cycle in the G0 stage can be accomplished by reducing the concentration of serum in the culture medium or inducing contact inhibition by growing cells to confluence. Synchronization in the G1 stage can be achieved by first selecting cells in mitosis and then allowing those cells a short time (1 h) to complete mitosis and enter the G1 stage. Also, mitotic cells have been used to produce mouse clones, although this is a less-common approach in farm animals. Cells from different tissue types may be used as donors in cloning. Some of the cell types that have been successfully used include mammary gland epithelial cells, cumulus cells, oviductal cells, granulosa cells, hepatocytes, endometrium cells, myocytes, Sertoli cells, T and B lymphocytes, neurons, and fibroblasts (Brem and Kühholzer, 2002; Miyoshi *et al.*, 2003; Campbell *et al.*, 2007). Easy accessibility and ability of the cells to grow *in vitro* are characteristics that facilitate cloning programs. Skin-derived fibroblasts are one of the most commonly used cell types for SCNT cloning in livestock species, given that they can be easily obtained from a small skin biopsy and are easily cultured.

Oocyte Enucleation and Nuclear Transfer

Three main approaches are most commonly used in livestock nuclear transplantation. These include traditional nuclear transfer, hand-made cloning (HMC), and zona-free nuclear transplantation. Traditional nuclear transfer involves enucleation of the oocyte by aspirating the metaphase II plate with a sharp micropipette in a zona pellucida (ZP)-intact oocyte in order to remove the chromosomes, then transferring a whole donor somatic cell into the perivitelline space of the oocyte, and finally fusing together the donor cell to the oocyte recipient and thus delivering the somatic cell nucleus into the oocyte cytoplasm. HMC consists of oocyte halving with a sharp micro scalpel and fusing the two nonnucleated oocyte halves with a somatic cell. Finally, zona-free nuclear transfer involves removing the ZP of the oocyte, enucleation with a blunt-end needle, and fusion of the enucleated oocyte to a somatic cell.

Traditional nuclear transfer

The traditional method for nuclear transplantation is without a doubt the most commonly used technique for the production of cloned animals. This technique makes intensive use of micromanipulation and thus requires highly specialized equipment and personnel. Oocyte enucleation is performed under a high-power microscope (200–400 × magnification) using a sharp glass micropipette to aspirate the metaphase plate, thus removing the recipient cell chromosomes leaving only cytoplasm. Typically, the first polar body (PB) is also removed by aspiration. The manipulations are assisted by

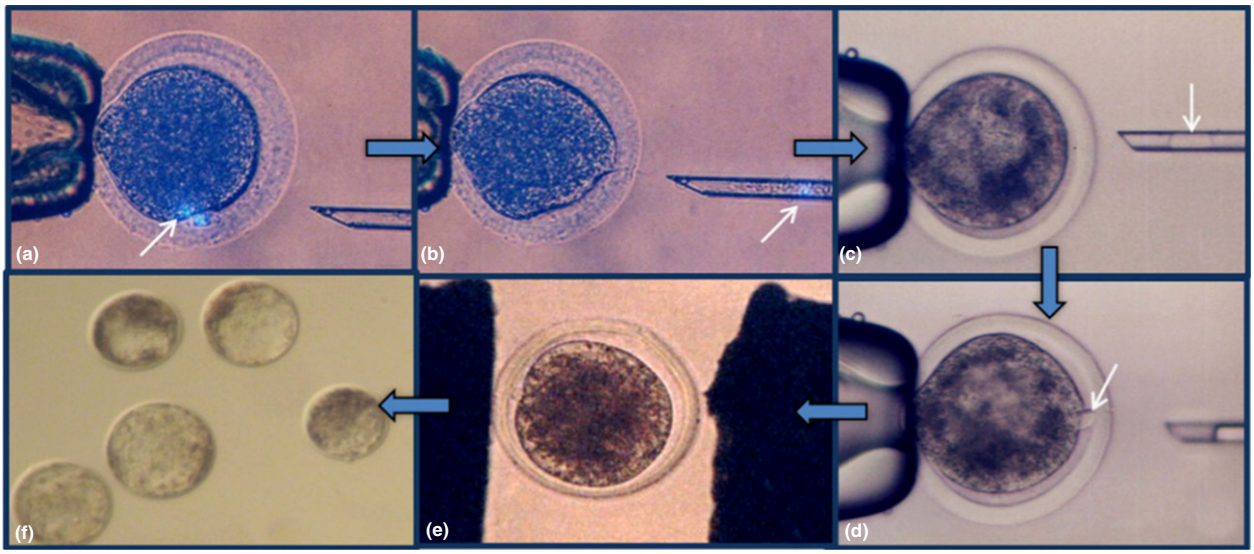


Figure 2 Traditional nuclear transfer. (a) Oocyte (arrow: DNA stained with Hoechst 33342); (b) Enucleation (arrow: aspirated metaphase plate); (c) Donor cell inside the transfer micropipette (arrow); (d) Nuclear transfer (arrow: donor cell in perivitelline space); (e) Fusion; and (f) Blastocysts produced by traditional nuclear transfer.

holding the oocyte in place using another micropipette. As oocytes from most farm animals are dark, because of high lipid content, the metaphase plate cannot be directly visualized. Therefore, visualization of the metaphase plate can be aided by DNA staining using a live fluorescent dye such as Hoechst 33342. As staining and visualization under UV light can damage oocytes, blind enucleation can also be used by removing the cytoplasmic material in proximity to the PB, although this is not always successful and residual DNA may be left behind.

After oocyte enucleation, a donor cell is transferred into the perivitelline space of the oocyte (between the oocyte membrane and the ZP), also through micromanipulation. For transfer, the same hole in the ZP created during enucleation can be used; however, it is usually more efficient to make a new perforation of the ZP in order to transfer the somatic cell. Finally, the nucleus of the donor cell is delivered into the oocyte cytoplasm by fusing the two cells together. This is usually achieved by applying a short high-voltage electric direct current (DC) pulse perpendicular to the apposed cell membranes. This electric pulse creates holes in the cell membranes of the donor cell and recipient cytoplasm and as the membranes are repaired they fuse together at their point of contact. Once fused, the oocyte cytoplasm containing the nucleus of the donor cell is called a reconstructed embryo.

A modification to traditional cloning that is more common in rodents, but that has also been successfully applied to livestock species, involves intracytoplasmic injection of the somatic cell nucleus rather than fusion of oocyte and somatic cell. For injection into the oocyte cytoplasm, a piezoelectric device is normally used. Piezo-driven injection of the donor nucleus has been successfully accomplished in oocytes from horses, cattle, swine, mice, and rabbits (Onishi *et al.*, 2000; Choi *et al.*, 2002; Gao *et al.*, 2004; Du *et al.*, 2009). Other modifications to the enucleation and transfer procedures exist, such as using chemicals to facilitate oocyte enucleation (e.g., demecolcine) or using Sendai virus to induce cell–oocyte fusion Figure 2.

Hand-made cloning

The cloning technique called HMC (Figure 3) is considered easier to perform and requires less equipment when compared with other techniques (Vajta *et al.*, 2005), thus reducing the initial investment for implementing a cloning program.

For HMC, the ZP of the oocyte is removed by enzymatic treatment (typically using pronase). Then, zona-free oocytes are manually bisected using an ultrasharp blade. This step is typically performed under a low-power stereoscope (20–60 × magnification) and does not require micromanipulation equipment. Hemioocytes are then stained with a fluorescent DNA stain (Hoechst 33342), screened for nuclear material under UV light, and nonnucleated ones selected. For embryo reconstruction, two nonnucleated hemioocytes (hemicytoplasts) and one donor cell are fused together by electrical stimulation, achieving approximately 100–120% of the original oocyte cytoplasmic volume. Phytohemagglutinin (PHA) is commonly used to facilitate adherence of hemicytoplasts and somatic cells. After treatment of hemicytoplasts with PHA, the somatic cell is 'glued' to the surface of the cytoplast, which facilitates cell alignment and fusion.

Embryos produced by HMC or any other technology that involves removal of the ZP need to be cultured individually in a conical container, in order to prevent embryo aggregation and cell dispersion, respectively. Normally, HMC embryos are cultured in microwells using the well-of-the-well (WOW) system, which consists of small depressions or microwells on the surface of a plastic embryo culture dish (Vajta *et al.*, 2000).

Zona-free nuclear transplantation

This technique combines concepts of traditional cloning techniques and HMC (Figure 4; Oback *et al.*, 2003). As in HMC, the ZP of the oocyte is removed, which simplifies the

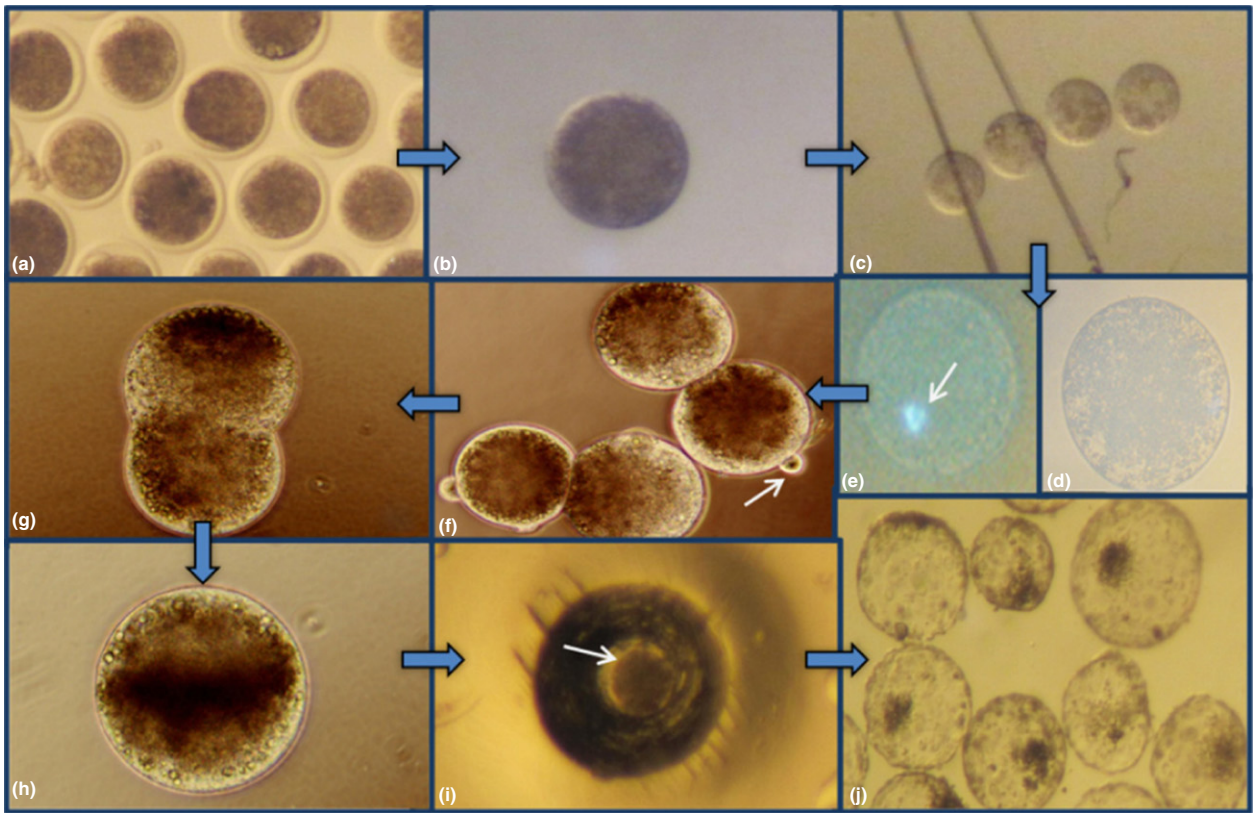


Figure 3 Hand-made cloning. (a) Oocytes; (b) Oocyte without zona pellucida; (c) Hand-bisected hemioocytes; (d) Hemioocyte without DNA; (e) Hemioocyte with DNA (arrow indicates DNA – this hemioocyte is discarded); (f) Donor cell (arrow) attached to two hemicytoplasts; (g) Fusion; (h) Reconstructed embryo; (i) Reconstructed embryo (arrow) inside well-of-the-well; and (j) Blastocysts produced by hand-made cloning.

procedures for enucleation and nuclear transfer and requires less technical expertise and the production of more basic micromanipulation tools. After removal of the ZP, the oocyte is supported in a holding pipette, and with the aid of a blunt enucleation pipette, a portion of the oocyte cytoplasm where the PB is localized is aspirated. For reconstruction and nuclear transfer, one enucleated oocyte is quickly exposed to PHA and then attached to one donor cell. Following attachment, the cell and cytoplast are electrofused. After assessment of the fusion outcome, the reconstructed embryos are activated and individually cultured in the WOW system.

Oocyte Activation

The natural activation of an embryo, and consequently the beginning of the first cleavage divisions, are caused by oscillation of intracellular calcium triggered by the sperm. Because somatic cells do not carry this sperm capacity, artificial activation of SCNT embryos is absolutely required. Numerous procedures have been developed to activate mammalian oocytes (Machaty, 2006). As calcium is a key regulator of oocyte activation, several approaches to artificial oocyte activation rely on inducing single or repetitive rises in calcium levels. In livestock, oocyte activation can be achieved through a variety of protocols (Machaty, 2006). The most prevalent protocols induce a single intracellular increase in calcium, which can be achieved by physical or chemical means (Alberio *et al.*, 2001). Electrical stimulation by administration of DC pulses in the presence of exogenous calcium induces calcium influx through pores formed in the plasma membrane (Fissore and Robl, 1994). This activation method was successfully used in cloning the first sheep and goats (Baguisi *et al.*, 1999; Wilmut *et al.*, 1997). The most commonly used activation protocols in bovine SCNT utilize a calcium ionophore, such as A23187 or Ionomycin (Machaty, 2006). Ionophores allow passive diffusion of calcium though the plasma membrane and thus induce a single large increase in calcium (Nakada and Mizuno, 1998). Because a single calcium surge is not enough to completely activate the cell cycle and initiate embryonic development, the calcium stimulus is supplemented with chemicals that help to regulate the cell cycle (Alberio *et al.*, 2001). Among them, DMAP, a kinase inhibitor, can be used after ionomycin treatment to induce high rates of oocyte activation (Susko-Parrish *et al.*, 1994). This activation treatment was used in production of the first cloned calves (Cibelli *et al.*, 1998) and is widely used today. Another possible way to regulate the cell cycle is by using protein synthesis inhibitors. Cycloheximide is a protein synthesis inhibitor that has been used to activate cloned bovine embryos (Zakhartchenko *et al.*, 1999). Other methods to induce repetitive calcium rises include injection of sperm extracts or recombinant sperm factors.

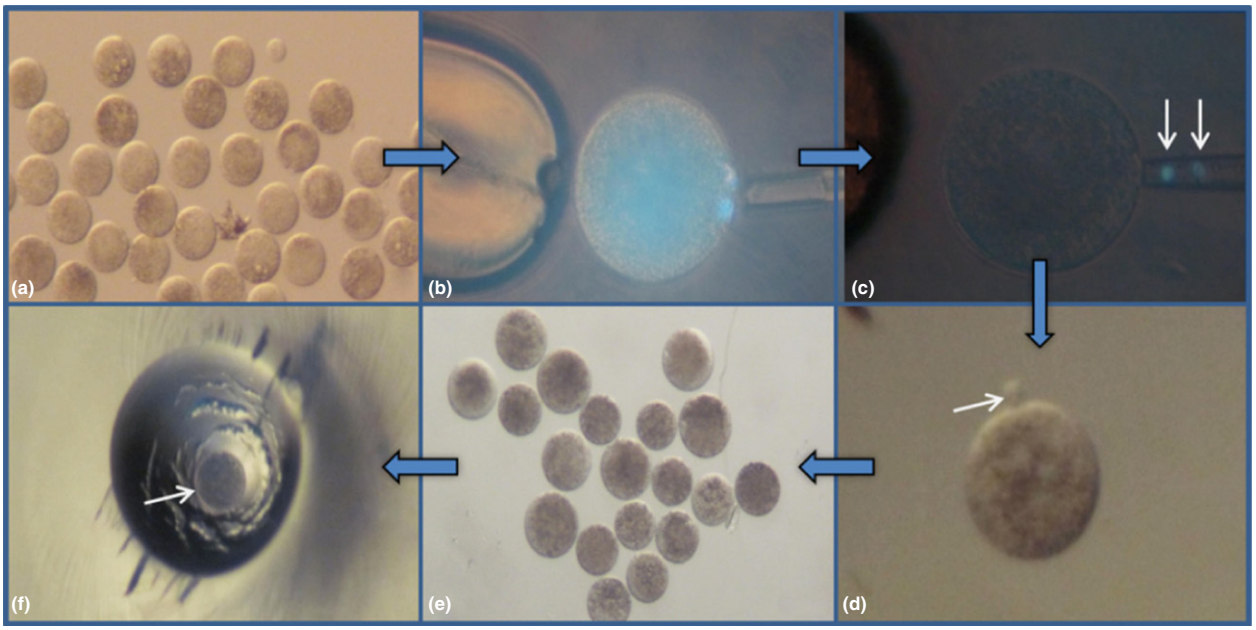


Figure 4 Zona-free nuclear transplantation. (a) Oocytes without ZP; (b) Visualization of oocyte DNA before enucleation; (c) Enucleation (arrows: PB and metaphase plate inside enucleation mircopipette); (d) Cell transfer (arrow: donor cell attached to cytoplast); (e) Fused reconstructed embryos; and (f) Reconstructed embryo (arrow) inside WOW.

In vitro Culture and Embryo Transfer

After the activation period, embryos are cultured with *in vitro* systems that mimic the oviductal or uterine environments. The success rates of *in vitro* culture are variable among species. Culture systems for bovine embryos are well advanced and allow routine production of 30–45% blastocysts from *in vitro*-fertilized bovine oocytes isolated from abattoir ovaries (Gandhi *et al.*, 2000). In the case of cattle, the reconstructed embryos can be cultured *in vitro* to the morula/blastocyst stage (5–7 days) to assess the initial developmental competence before transfer into a foster mother. In contrast, the requirements for proper growth of embryos in other species are not well established and *in vitro* embryo culture is less efficient. In pigs and goats, although it is possible to obtain blastocysts cultured *in vitro*, the pregnancy rates achieved with these embryos are low. With small ruminants, the best results are obtained when the embryos are cultured for shorter periods such as 1–2 days. In contrast, porcine reconstructed embryos are normally transferred immediately after activation (Petersen *et al.*, 2008).

The timing of *in vitro* culture will determine which stage the clones' embryos will be transferred. Typically, bovine embryos are transferred at the morula or blastocyst stage directly into the uterus of recipient females with their estrous cycle synchronized to the age of the embryo. In cattle, the transfer is performed using the same nonsurgical techniques developed for regular embryo transfer. In small ruminants and pigs, the reconstructed embryos are often transferred directly into the oviducts of recipient females by laparoscopic or surgical methods.

Pregnancies from cloned embryos need to be closely monitored, given the higher incidence of potential complications. This typically involves regular ultrasound examinations to check fetal viability and sizes of the placenta and umbilical cord, among other parameters. Delivery of clones must also be closely monitored and planned, usually requiring cesarean section. Finally, cloned animals often require extreme perinatal cares such as oxygen supplementation, respiratory assistance, blood glucose normalization, among other considerations. Once a cloned offspring passes the neonatal period, they do not typically need any more attention than that given to naturally reproduced animals.

Conclusion

The ability to produce offspring from cultured somatic cells allows the rapid propagation of superior genotypes, genetic improvement of domestic species, the production of biopharmaceuticals and nutraceuticals by cloned animals, organs for xenotransplantation, genetically engineered animal models of human diseases, and preservation of endangered species. Although these applications for SCNT are far reaching, its broad implementation has been hindered by low efficiency.

Although advances in recent decades have allowed improvement in the preimplantation development of cloned embryos, their full-term developmental potential remains low. High rates of early pregnancy loss are often observed along with an increased incidence of abortions in late pregnancy. Moreover, high mortality rates of offspring from cloned embryos are reported, which makes the overall efficiency of SCNT range between 1 and 5%.

The inefficiencies of cloning negatively affect the economic and commercial viability of SCNT. However, a wealth of

knowledge has been generated in an attempt to solve these problems and many fields of science are emerging and consolidating as a result, especially areas that try to understand the mechanisms of epigenetic reprogramming and specific physiological aspects of pregnancy and neonatal development.

Regulatory agencies around the world have agreed that food from cloned animals and their offspring is safe for human consumption. However, SCNT raises new questions about the ethical and moral status of animals and their welfare, which have caused controversial discussions around the world. As technical refinements and increased knowledge of the mechanisms underlying nuclear reprogramming continue to develop, improvements in the success rate of cloning and decreases in the potential for adverse events should occur. This will result in lowered costs for cloned animal production, increased acceptability for products derived from clones and their offspring, and a more widespread application of this technology in commercial enterprises.

See also: Advances in Animal Biotechnology. Breeding: Animals. Stem Cells. Transgenic Methodologies – Plants

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Cloning: Plants – Micropropagation/Tissue Culture

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Glossary

Acclimatization The process of hardening or conditioning micropropagated plants so that they will survive in the greenhouse or field.

Adult plant A plant that is physiologically mature enough to flower under normal inductive conditions. Compare with juvenile plant.

Adventitious bud, root, or shoot An organ that forms at an 'unexpected' location, such as roots on a stem or leaf, or shoots on a root or leaf.

Callus Unorganized group of cells that forms on plant parts or explants as a result of wounding or application of plant growth regulators, such as auxins and cytokinins.

Clone A population of organisms (plants) that is asexually derived and can be traced back to an original individual.

Dedifferentiation When differentiated (specialized) cells return to the meristematic condition often to replace a missing or wounded part, such as a root or shoot. This is a typical wound healing response for plants, and is utilized in vegetative plant propagation, such as rooting cuttings and microcuttings, grafting, and other vegetative propagation techniques.

Differentiation When cells become more specialized than the meristematic condition. Meristematic cells have one function: division (mitosis). All other cell types differentiate from cells produced in meristems via cell division.

Embryogenesis Formation of embryo-like structures *in vitro* or in planta, derived directly from explant cells or indirectly from callus cells.

Ex vitro The environment outside of the vessels containing plant tissue cultures. Typically the greenhouse and field are referred to as *ex vitro* environments for micropropagated plants.

Explant The plant tissue or organ that is removed from the stock plant and is first placed *in vitro* during the micropropagation process. Subcultured shoots are also typically called explants.

In vitro The vessels containing plant tissue cultures. Although originally meaning 'in glass,' now all micropropagation is said to be *in vitro*, regardless of the material used for the container.

Juvenile plant A plant that is in a vegetative state and incapable of responding to flower induction stimuli that would usually lead to flowering in an adult plant (see adult plant). Cuttings root more readily and micropropagation is facilitated if juvenile stock plants are used.

Laminar flow hood An enclosed, protected chamber (transfer chamber) that passes air through a specialized filter to create an atmosphere free from contaminants where micropropagation transfers take place using sterile techniques.

Meristem Tissue composed of dividing cells. Primary meristems are shoot and root tips, secondary meristems are the vascular and cork cambia, and adventitious meristems form at unexpected locations and will give rise to roots or shoots; meristem culture is employed to produce disease-free stock plants.

Organogenesis Initiation of adventitious organs, such as roots or shoots.

Somaclonal variation When plants produced *in vitro* exhibit phenotypic differences because of mutation, epigenetic, chimera separation and other reasons. Adventitiously produced plants, especially from callus have an increased likelihood of showing somaclonal variation, whereas the clonal uniformity is maintained by utilizing an axillary shoot multiplication system.

Totipotency Theory that all living cells contain all the genetic information necessary to develop into a complete intact organism.

Introduction

In 1902, Gottlieb Haberlandt broached the subject of plant tissue culture and micropropagation in his seminal publication (Haberlandt, 1902) in which he endeavored to explore totipotency and morphogenesis in plants. His efforts were largely unsuccessful, primarily related to a lack of knowledge about the requisite medium components. Subsequently, plant scientists vigorously pursued definition of conditions necessary to successfully produce viable cell, tissue, and organ cultures (Read, 1992). In the more than a century that has elapsed, there have been thousands of reports related to attempts to refine media, environmental conditions (both *in vitro* and *ex vitro*), and other parameters conducive to successful *in vitro* culture resulting in micropropagation success and commercialization. Murashige produced an excellent review in which he presents detailed descriptions of the stages of the process and constituents of media successfully employed for plant micropropagation (Murashige, 1974). At that time he was able to list information related to micropropagation of more than 100 genera from more than 50 plant families. That number has expanded greatly to include most food, fiber, ornamental, medicinal, and other important plants.

A wide range of factors are required for successful micropropagation, including the source of explant material (the 'stock plant,' donor plant, or mother plant), environmental conditions under which the stock plant is grown, the culture environment (both in the culture vessel and the culture's

external environment, constituents of the *in vitro* medium, and subsequent procedures employed for multiplication, rooting, and acclimatization).

Why did not Haberlandt's experiments yield successful micropropagated plants? As often is the case in science, requirements for success were yet to be discovered. A major step was accomplished when Went (1929, 1934a,b) reported on the root-forming substance, initially referred to as rhizocaline, later identified as indoleacetic acid (IAA) or auxin (Went, 1934a,b; Thimann and Went, 1934). Subsequently, analogs of IAA, indolebutyric acid (IBA) and naphthaleneacetic acid (NAA), although not endogenous, were discovered to have even stronger abilities to stimulate root formation (Zimmerman and Wilcoxon, 1935, Thimann, 1935) than IAA. Numerous reports of research employing auxin followed in the next decades. Nobecourt and Gautheret, working in different laboratories in France with carrot cultures, demonstrated successful callus growth and Phillip White in the USA reported successful culture of an organ (tomato roots, White, 1963). Previously, Knudson (1922) demonstrated that a defined medium could be employed to germinate and culture seeds of tropical orchids. His Knudson C medium is still commonly used commercially for seed germination and tissue culture of orchids (Knudson, 1951).

Despite the success of Gautheret and White in repeated cultures of tomato root callus – indeed they could culture such callus in a defined medium almost indefinitely – regeneration of intact plants from plant tissue cultures remained essentially impossible. It was not until Miller and Skoog's laboratory group at the University of Wisconsin isolated kinetin from autoclaved herring sperm and described the action of this compound in cultures of tobacco pith tissues, that plant regeneration *in vitro* became a reality (Skoog and Tsui, 1948; Skoog and Miller, 1957). They referred to the class of compounds to which kinetin belongs as cytokinins (cyto = cell, kinesis = division, hence compounds that stimulate cell division). Skoog and Miller (1957) further described the relationship of ratios of auxin to cytokinin in the culture medium; they determined that when auxin predominates in the medium, root formation is stimulated, when cytokinin is in excess, bud and shoot formation occurs. If neither auxin nor cytokinin activity predominate, only callus is formed.

At approximately the same point in the history of plant tissue culture, Morel and Martin (1952) showed that by culturing excised meristems of dahlia, endogenous viruses that cause serious diseases could be eliminated. Morel later reported that similar results could be attained with meristem culture of *Cymbidium* orchids (1960). As a consequence of his research with meristem culture of orchids, he discovered that following initiation of meristem culture, plants could be multiplied *in vitro*, leading to a clonal propagation system that is still practiced today (Morel, 1964). In 1967, Marston and Voraurai reviewed the literature on clonal propagation of orchids by utilization of meristem culture techniques.

The foregoing noted accomplishments ultimately led to the landmark paper by Murashige and Skoog that revolutionized plant tissue culture (Murashige and Skoog, 1962). The medium formulation developed by their work formed the basis for thousands of studies in which the now-famous Murashige and Skoog (MS) medium was employed. Indeed a preponderance of medium formulations used for micropropagation research and commercial multiplication of elite clones of a myriad of plant species are based on the MS medium.

It would be nearly impossible to list all of the researchers and plant species and genotypes that have been reported since the Murashige review, but a few of the classic examples should be noted. Ball's work with sterile cultures reported in 1946 helped lay the foundation for the work that followed (Ball, 1946), including that already noted for Murashige, Skoog, Miller, and Morel. Nitsch and Nitsch were contemporaries who conducted numerous tissue culture experiments and provided other medium formulations employed in later research (Nitsch and Nitsch, 1956). They even reported on flower induction of *Plumbago* stem segments cultured *in vitro* (Nitsch and Nitsch, 1967). Reinert's work with embryogenesis (Reinert, 1959; Reinert and Mohr, 1967; Reinert *et al.*, 1967) and that of Steward (Steward *et al.*, 1958) contributed greatly to the fields of embryogenesis, suspension culture, and medium composition. Many other researchers also worked with cell suspensions, liquid culture, and medium constituents named after them when used in later research, for example, Gamborg's Medium (Gamborg *et al.*, 1968; Vasil *et al.*, 1964; Norstog, 1965).

As research with plant tissue cultures progressed, especially with callus suspension and embryogenic cultures, it became clear that aberrations would frequently occur. The resulting plants often would be different genetically and phenotypically from the plant from which the explant was taken. This was readily apparent when asparagus *Asparagus officinalis*, tobacco *Nicotiana tabacum*, carnation *Dianthus caryophyllus*, and other plants were regenerated from callus or cell suspension cultures (Wilmar and Hellendoorn, 1968; Murashige and Nakano, 1966). Sometimes such changes could be advantageous, for example, changes in scented geranium (Skirvin and Janick, 1976). Shepard *et al.* (1980) demonstrated wide-ranging variability in 'Russett Burbank' potato regenerated from leaf protoplasts. Larkin and Skowcroft (1981) coined the term 'somaclonal variation' and espoused the value of somaclonal variation for plant improvement. Likewise, Cocking's (Cocking, 1960) demonstration of the potential of culturing plant protoplasts has also exhibited promise for plant regeneration, parasexual hybridization, and plant improvement, but also will not be addressed in this article. Later, Grosser (1994) described methodology for protoplast isolation and somatic hybridization in citrus, also with encouraging results. Murashige (1974) commented that off-type plants commonly occur when plants are adventitiously regenerated from callus and stated "The frequency of genetically aberrant plants can be reduced considerably, even avoided entirely, if the plant multiplication can be achieved through an enhancement of axillary shoot formation." The authors therefore have chosen to restrict our discussion to use of techniques that to a high degree retain the genetic and phenotypic identity of the plant being cloned via micropropagation.

Murashige's review suggested three stages of micropropagation: Stage I, Establishment of the aseptic culture, Stage II, Multiplication of propagule, and Stage III, Preparation for re-establishment of plants in soil (Murashige, 1974). Subsequently, general micropropagation practice, both for

research and commercial production, has been to consider five stages: (0) stock plants, (I) establishment, (II) multiplication, (III) pretransplant, and (IV) transplant (Anderson, 1980; Murashige, 1978). These four stages have been used for the discussion preceded by Stage 0, that is, the Stock Plant stage.

Stage 0: Stock Plants

The plant from which the explant intended for micropropagation is taken may be referred to as the stock plant, donor plant, or mother plant. The overall characteristics of this stock plant are critical to the success of the micropropagation process (Read, 1990; Read, 1992). Freedom from endogenous pathogens such as viruses, bacteria, and fungi is essential because micropropagation of a virus-infected plant is simply a way to produce many more unwanted virused plants. Hence, it is important and obvious that the propagator must start with a healthy plant.

Explant Selection

Many researchers have shown that explants taken from juvenile stock plants or from juvenile parts of the stock plant perform better *in vitro*; this response is similar to the better rooting of cuttings taken from juvenile plants when compared with cuttings from mature plants such as *Hedera helix* (Hackett, 1983). Sources of juvenile material are depicted schematically by Preece (2008) in which he notes the 'cone of juvenility,' epicormic shoots, stump sprouts, and root suckers, among others. Similarly, it has been demonstrated that explants secured from tissue culture-derived stock plants frequently respond better *in vitro* than explants taken from greenhouse or field-grown stock plants. This was shown for azalea (Economou and Read, 1986) and strawberry (Liu and Sanford, 1988). Furthermore, when location on the stock plant is considered, for example, apical bud versus lateral bud, the best results vary with species: lateral buds were superior for deciduous azalea (Economou and Read, 1986), but apical explants responded better for *Fagus sylvatica* (Vanderschaege and Debergh, 1988). Genotypic differences have been widely reported to lead to varying *in vitro* performance, for example, *Pelargonium* shoot tips and organogenesis in sweet potato (Pillai and Hildebrandt, 1968a,b; Gunckel *et al.*, 1972). With a relatively easy to micropropagate species such as petunia, shoot-forming ability from leaf segment explants varied by as much as fivefold, depending on cultivar (Read, 1990).

Nutrition of the Stock Plant

The classic work of Kraus and Kraybill (1918) demonstrated that nutrition of tomato stock plants had a marked effect on rooting of cuttings. The authors in their research found similar impact on tomato leaf segments cultured *in vitro* (Read *et al.*, 1979). When explants were taken from stock plants receiving high amounts of nitrogen, fewer shoots were produced *in vitro* when compared with explants from stock plants receiving a lower, but adequate for normal growth, amount of nitrogen fertilizer. They also found that nitrogen and potassium levels provided to hydroponically grown *Salix* stock plants exerted a strong influence on organogenesis of *in vitro* cultures of explants excised from such stock plants (Read *et al.*, 1982, 1983). In this case, however, nutrition of the stock plant was insufficient to overcome poor performance *in vitro* of inherently recalcitrant genotypes. It seems apparent that not only adequate nutrition of the stock plant is important to tissue culture success, but excess nutrients will not substitute for inadequate nutrition in the culture medium.

Light Level, Quality, and Photoperiod Stock Plant Effects

Conflicting reports are found in the literature regarding the effect on explant performance when stock plants receive high or low levels of light or no light at all. Dunwell and Perry (1973) found enhanced haploid plantlet production from anthers taken from stock plants grown under high photon flux, whereas Hughes *et al.* (1978) obtained higher protoplast yield if the donor plants were grown under low light. A complicating factor was that in both cases the stock plants were grown under short days. Some plants are sensitive to photoperiod, so their normal physiological responses may parallel *in vitro* performance. It is possible that rooting, as Mes (1951) proposed, is reduced under high light levels due to a reduction in auxin content, whereas the enhanced shoot production noted by Yu and Meredith (1986) for shoot tips of shaded grape stock plants may have been related to high cytokinin content because filtered light may increase the red light component (Yu and Meredith, 1986; Economou and Read, 1986; Read, 1990). Petunia stock plants that received 30 min of light rich in red light at the end of each growing day produced explants that proliferated more shoots than explants receiving far-red light at the end of the day. This suggests a possible phytochrome effect, because red light followed by far-red reduced the shoot-stimulating effect of red light (Read *et al.*, 1978). Similarly, petunia leaf segments cultured on cytokinin-free medium provided with 15 min of light at the end of the day produced more shoots than explants taken from cultures receiving far-red light (Economou and Read, 1987).

Stock Plant Temperature Effects

The temperature under which the stock plant has been grown may have a profound impact on explant *in vitro* performance, although this topic has only been sporadically studied. Heide (1965) found an interaction between temperature and auxin and cytokinin levels when culturing begonia leaf segments. Stimart and Ascher (1981) reported that duration of storage at 4 °C influenced bulblet formation from lily bulb scale segments and the authors found differing responses to storage temperature and time in storage when hyacinth bulb scale segments were cultured *in vitro* (Read *et al.*, 1984; Ko, 1986). This was in contrast to the work of Pierik and Ruibing (1973) who suggested that bulblet production was not significantly affected by duration of storage. A stimulation of adventitious bud and root formation was affected when leaf discs of *Streptocarpus* were excised from stock plants subjected to a cold period (12 °C) before leaf harvest (Appelgren and Heide, 1972). In general, however, limited research has been pursued

with regard to stock plant temperature, suggesting that this could be a field for further research.

Plant Growth Regulator Treatment of the Stock Plant

Inclusion of hormone-like growth regulators in the culture medium has been extensively investigated and is discussed in the Section 'Stage I: Establishment.' Treatment of the stock plant to 'program' the explant tissue before culture has proved to be an approach that can be helpful in micropropagation. This approach was pursued by DeLanghe and DeBruijne (1976) with tomato leaf segment culture. In their research a growth retardant, chlormequat chloride, was sprayed onto the stock plants at 2000 ppm, leading to an increase in shoot proliferation. This response was repeated in our laboratory with tomato and with daminozide (another growth retardant) applied to dahlia stock plants (Read *et al.*, 1979). Similarly spraying petunia stock plants with daminozide led to greater shoot proliferation from leaf segments cultured *in vitro* than from leaf segments from stock plants sprayed with water (Economou and Read, 1980)

Preculture Treatment of Explants

Growth-regulating chemical treatments to the explants themselves before culture has been hypothesized as an approach that could obviate the need for inclusion of the compound in the medium. Dipping petunia leaf segments into cytokinins such as benzyladenine (BA) and culturing on cytokinin-free medium led to equivalent shoot formation to that of cultures containing BA in the medium (Economou and Read, 1982). Treatment of the explant offers some advantages over placement of the growth regulator in the medium and often has resulted in better quality plants than the traditional method of incorporating cytokinins in the medium.

Shoot Forcing

Forcing solutions

Woody plant tissue culture has often proved to be difficult, primarily because cells or tissues of woody plants are cellulosic and lignified. As a result, the period of time when soft, non-lignified shoots can be obtained often is limited to a brief period in the spring when the first flush of growth occurs. Employing a solution such as those used commercially for extending the keeping quality and longevity of cut flowers, such as roses, chrysanthemums, and carnations, has enabled relatively clean, soft tissue to be obtained for explant use. The solution used mimics the one used for cut flowers: 58.4 μM sucrose (2% solution) and 592 μM 8-hydroxyquinoline citrate (200 ppm). Woody stems are cut from the stock plants and the cut bases placed into vessels containing the forcing solution (**Figure 1**). A fresh cut is made to remove 1–2 mm from the base of the stem and the solution replaced every 2–3 days. Delivery of plant growth-regulating chemicals via the xylem uptake from the forcing solution may be accomplished by inclusion in the forcing solution (Read *et al.*, 1984, 1986). Buds from dormant woody stems have been stimulated to emerge and elongate in spite of an endodormant condition by preforcing treatments and by inclusion of gibberellic acid (GA_3) in the forcing solution. A preforcing treatment with 15% bleach solution hastened bud break and promoted shoot elongation (Yang and Read, 1992), whereas GA_3 at 10 mg l^{-1} in the forcing solution consistently led to earlier bud break and shoot elongation (Yang and Read, 1989, 1997). In addition, including BA in the forcing solution increased the number and size of shoots formed *in vitro*, but had minimal effects on days to bud break. Inclusion of auxins, such as IAA and NAA, in the forcing solution delayed bud break, but shoots produced from such forcing treatments could be useful for rooting as softwood cuttings. Because silver thiosulfate (STS) became a common treatment for enhancing cut flower longevity, studies with STS in the forcing solution to determine potential for improving bud break were initiated. It was found that 5 μM STS in the forcing solution reduced time to bud break and increased both percent bud break and shoot elongation for several woody species (Hamooh and Read, 2000).

Forcing large stem sections

An alternative approach for obtaining soft growth for explants was reported by Vieitez *et al.* (1994) when they forced branch segments of mature *Quercus robur* to obtain explants for micropropagation. This technique takes advantage of the production of epicormic shoots and can exploit the juvenile portion of a plant for propagation purposes and has been refined and exploited by Preece and colleagues (**Figure 1**). They have successfully forced epicormic shoots of numerous deciduous woody species, including maple, black walnut, hibiscus, and others, providing quality explants for micropropagation (Van Sambeek *et al.*, 1997a,b; Henry and Preece, 1997a,b; Ledbetter and Preece, 2003). The technology for forced epicormic shoots from mature woody stems is summarized in Preece and Read (2003) and Preece (2008) and descriptions of environmental and medium considerations were presented by Aftab *et al.* (2005).

Serial grafting

Stems of a number of woody species have been 'rejuvenated' by repeatedly grafting mature stems onto juvenile rootstocks. The process often needs to be repeated several times, depending on species/genotype, in order for juvenility to be re-established (Debergh and Maene, 1985; Bonga and Von Aderkas, 1992). Franclet (1987) and Boulay (1987) have reported extensively on this process, especially with conifers. Using small shoot tips as scions enhanced rejuvenation in avocado when conducted *in vitro* (Pliego-Alfaro and Murashige, 1987) and was studied for juvenile and mature clones of *Sequoiadendron giganteum* by Monteuius *et al.* (1987).

Stage I: Establishment

The primary objective of Stage I is to successfully introduce the explant onto the medium by using clean explants and aseptic techniques (**Figure 2**). Because the objective of micropropagation is to produce a population of uniform genotype (cloning, asexual propagation), this article focuses on use of existing meristems. Although much research has

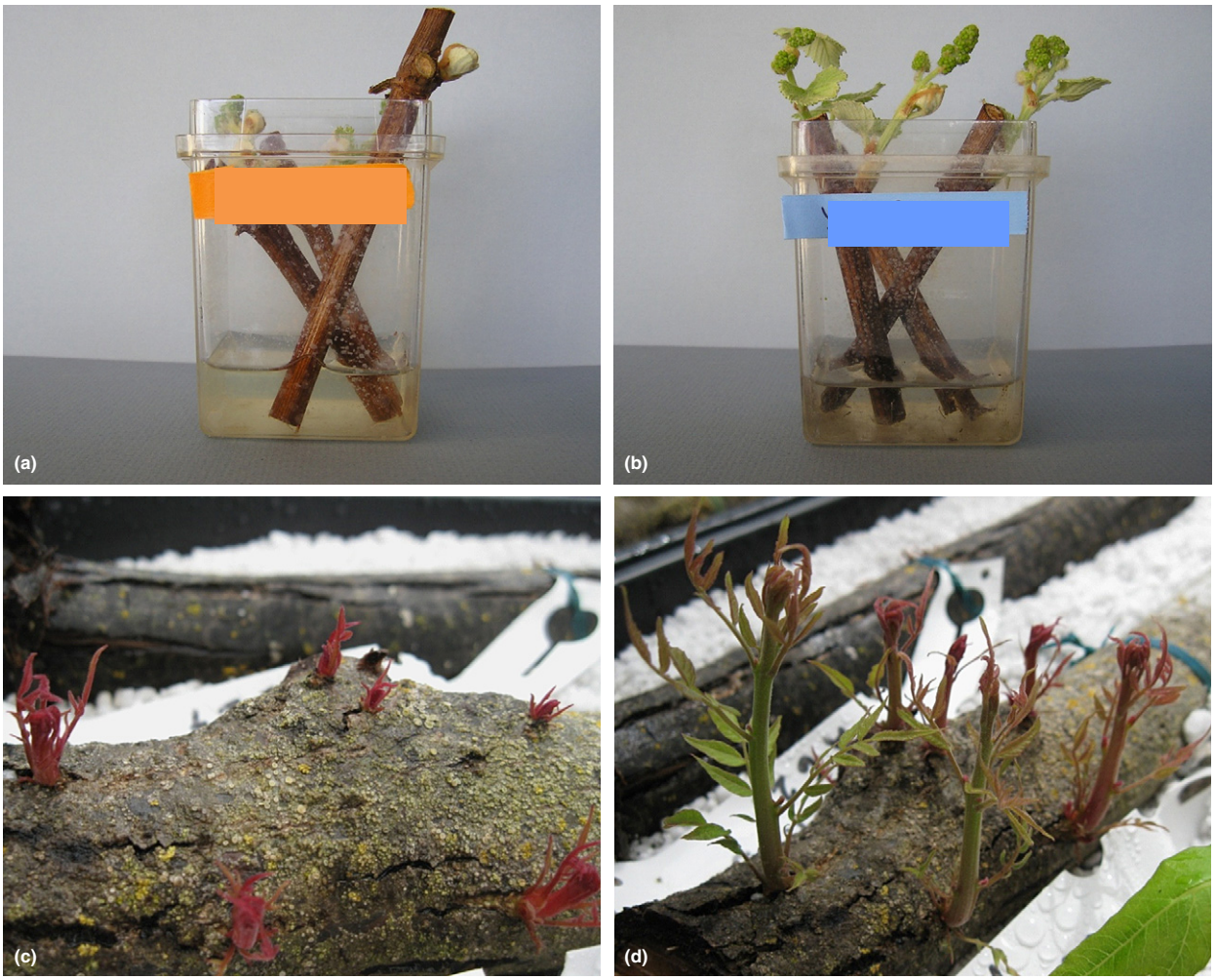


Figure 1 (a) and (b) Shoot forcing technology. (a) Cut woody stems of grape (*Vitis* spp.) with bases immersed in forcing solution and buds beginning growth. (b) Shoots elongated sufficiently to be excised for use as explants for micropropagation. (c) New recently emerged red epicormic shoots being forced on a 4 cm diameter walnut stem segment. (d) 2–5 cm long forced shoots ready to be excised for use as explants for micropropagation.

been accomplished and will continue to be pursued in the fields of organogenesis and embryogenesis, those topics will not be considered further.

Explant Disinfestation

Nearly all reports regarding culture establishment initially describe the disinfestation technique, which employs a chemical treatment to kill organisms on the surface of the explant. Bacterial cells, fungal spores, and some arachnid or small insect pests may inhabit the explant surface and when the explant is placed on the culture medium these contaminants can multiply and destroy the explant. The most common disinfestant procedure employed is soaking the explants in bleach (sodium or calcium hypochlorite solutions), a potent oxidative agent that in optimal concentrations and durations will kill the undesirable organisms. A wetting solution such as Tween 20 usually is added to the bleach solution. This will aid in good surface contact and improved kill of unwanted organisms. The bleach soak is often preceded by several soapy water rinses to remove dust and other extraneous material from the explant. Treatment with sodium dichloroisocyanurate (NaDCC) has been reported to be as effective as sodium hypochlorite for greenhouse and field-grown *Citrus* (Niedz and Bausher, 2002). Other chemical treatments have also been utilized such as ethanol, hydrogen peroxide, and mercuric chloride. The latter chemical and other poisonous compounds are dangerous to the operator and often represent a disposal problem; their use is therefore discouraged. Newer chemicals, such as zerotol (Aftab *et al.*, 2005), have exhibited promise as disinfesting agents and no doubt additional compounds will be found for future use.

Medium Disinfestation

The most common method to sterilize the medium is the use of an autoclave to provide heat treatment under pressure. A typical treatment is 121 °C for 20–30 min. Times may vary and when using a new autoclave one or more test runs is



Figure 2 (a) Green, leafy walnut shoot harvested for micropropagation explants. The leaves are removed, as in (c) and surface disinfested. Following disinfestation and rinsing in sterile water, the shoot is cut into nodal and apical explants (b). (c) Hibiscus nodal explants with new growth, toward the end of Stage I.

recommended. In recent years, especially for small-scale research or commercial operations, the use of a microwave oven is an inexpensive alternative to an autoclave (Tisserat *et al.*, 1992).

Medium Gelling

Choice of gelling agent or use of liquid medium can have an impact on the success of the micropropagation process. Debergh (1983) compared seven different brands of agar at five different concentrations for gelling Murashige and Skoog (1962) medium when micropropagating *Cynara scolymus* and *Oreopanax nymphaeifolia*. He found numerous differences in gel strength and chemical characteristics of the medium with differences in a defect referred to as hyperhydricity, and related to cytokinin and water availability. Agar gel strength was related to water availability, with a more firm gel providing less water availability and therefore less hyperhydricity. Working with more defined agar sources and agar alternatives Wetzstein *et al.* (1994) observed that gel strength was influenced by gelling agent and by choice of medium. Woody Plant Medium (WPM) and Gamborg B5 (GB) was generally more firm than MS, Gel-gro had greater gel strength than either agar tested, and autoclaving caused a decrease in pH of all media. Like Debergh, they emphasized the importance of medium choice, gelling agent, and sterilization protocols. Use of agitated liquid medium was employed by Morel (1964) and Preece (2010) has shown that large shoot masses can be micropropagated successfully in shallow stationary liquid medium (**Figure 3(c)**). It is important to use agars of high purity for plant tissue culture. Gelcarin gums are also widely used in micropropagation. They create a gelled clear medium compared with the gelled cloudy medium with agar. Gelcarin gums may result in better shoot growth *in vitro*, but hyperhydricity can be a problem. To solve this, a mixture of half strength agar with some gelcarin gum results in low hyperhydricity and good shoot growth.

Medium Composition

It is acknowledged that the culture medium must provide adequate nutrition and an energy source because unlike an intact plant, the explant generally cannot adequately produce its needs. A typical micropropagation medium contains both inorganic macro- and micronutrients; an energy source, usually sucrose, although other sugars and complex carbohydrates are sometimes employed; organic chemicals such as vitamins, amino acids, and hormone-like plant growth regulators, such as auxins, cytokinins, gibberellins, and occasionally others. In some medium formulations complex substances are included such as coconut water (liquid endosperm), tomato juice, and purees of other fruits and vegetables. A comparison of several commonly used media is presented in Hartmann *et al.* (2011). Nas and Read (2004) developed a medium based on the chemical composition of hazelnut (*Corylus* spp.) kernels, making the assumption that nourishment of explants *in vitro* could be consistent with the nutritional needs of the developing embryo *in situ* during germination. They also presented a comparison of the constituents of the Nas and Read medium with MS and other media.

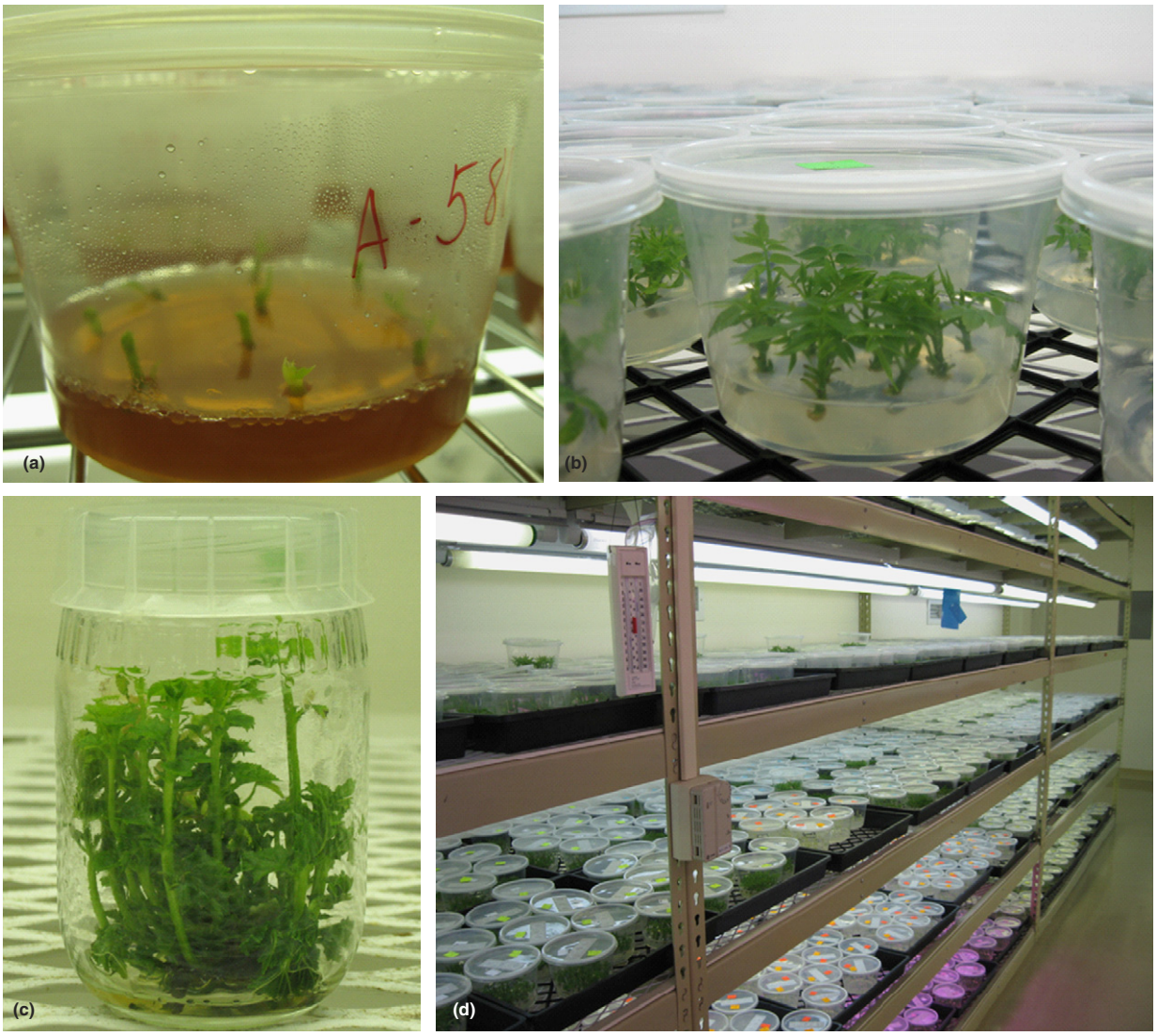


Figure 3 Stage II cultures. (a) Stage II walnut microshoots subdivided into nodal segments with axillary buds that elongate into microshoots (b) that can be further subdivided into nodal segments as in (a), or recut and placed on rooting medium or rooted *ex vitro*. (c) Hibiscus axillary shoot proliferation on stationary liquid medium. (d) Growth room for Stage II cultures.

Culture Environment

A clean room for aseptic transfer and subsequent growth of the explants (Figure 3) is essential to the success of any micropropagation enterprise. Light level (photon flux), photoperiod, and light quality are all important, particularly when green leafy explants are used. In some cases, absence of light is preferred, as in the case of *Anthurium andreanum* (Pierik *et al.*, 1979), and Miller and Murashige (1976) showed that tropical foliage species – which often are jungle understory species – benefited from culture under relatively low light. However, many researchers have reported that higher light levels promote shoot growth and more photosynthetic activity by green explants (Werckmeister, 1971; Pennazio and Radolfi, 1973; Hasegawa *et al.*, 1973). Reported optimum photon flux levels are varied, but many fall into a range of 70–80 μmol m^{-2} s^{-1} (Hutchinson, 1984; Economou, 1982; Villalobos *et al.*, 1984). Optimum light levels vary with the species, and the literature should be consulted when beginning with any new species.

When considering photoperiod, species that are physiologically responsive in nature, i.e., flowering under short days (SD, chrysanthemum) or long days (LD, carnation) and tuberization (SD, dahlia), will likely respond similarly *in vitro*. However, in most cases of such morphological responses, for example, flowering in chrysanthemum, the response is undesirable for *in vitro* culture because such responses will be competitive with the desired goal of micropropagation. Typically microcultures are incubated under 16 h photoperiods. This is especially necessary with woody species to keep them from going dormant.

Light quality, as mentioned earlier regarding stock plants, can likewise influence endogenous hormone levels and thus affect *in vitro* performance. If there is a predominance of red light, it may increase endogenous cytokinin levels and enhance

shoot proliferation (Economou and Read, 1986b). Research on light quality is continuing and may have additional impact on practical micropropagation in the future. Most commercial and research laboratories use cool white fluorescent lamps, or fluorescent lamps designed for growing plants.

Temperature in Micropropagation

As is true for intact plants, temperature governs numerous processes and plant growth in general. Within limits, growth and development increase with rising temperature. Culture temperatures in the range of 20–27 °C are commonly used. When considering appropriate culture temperatures, the natural habitat of the species to be cultured should be considered, for example, 32–39 °C for species of tropical origin.

Culture Atmosphere

The atmospheric constituents in the culture room and in the culture vessel could logically have a profound impact on explant responses *in vitro*. Generally, little research has been done on the culture room atmosphere, but humidity, carbon dioxide, oxygen, and ethylene levels have been investigated. Typically the gaseous atmosphere inside the culture vessel is 90% relative humidity or higher. This high humidity presents a problem for acclimatization, which is addressed under Stage IV in this article. Maximum relative humidities are highest for liquid cultures and those that employ low levels of gelling agents; high concentrations of agar, for example, approximately 1.0%, create a stiffer medium and lower relative humidity (Debergh *et al.*, 1981; **Figure 5**).

Carbon dioxide levels in the culture atmosphere can influence photosynthesis for green leafy explants. Reuther (1987) demonstrated advantages for CO_2 enrichment of grape, *Spathiphyllum*, and African violet micropropagation. Researchers have pursued autotrophic culture to enhance micropropagation efficiency (see Stage IV, Kozai (1991)) and the addition of CO_2 to combat the detrimental influence of ethylene buildup in the culture (Van der Plas and Wagner, 1986).

Ethylene inhibition of explant growth and organogenesis is an important consideration, because it is clear that cultures that contain auxin in the medium and contain living tissue (explants) can produce ethylene. When ethylene builds up in sealed vessels, it can inhibit and even kill the plant material being cultured. Gavinlertvatana *et al.* (1979) reported growth suppression of petunia and dahlia and Mingo-Castel *et al.* (1976) showed that ethylene inhibited tuber formation in etiolated potato sprouts, but elevated CO_2 levels stimulated tuberization. The negative effects of ethylene have been counteracted by the treatment of explants with silver nitrate or cobalt chloride, but scrubbing ethylene from the vessel atmosphere with potassium permanganate had little effect on ethylene-induced growth suppression. Economou (1991) has reviewed the positive and negative effects of ethylene on *in vitro* cultures.

Because oxygen is required for respiration of all living cells, it would seem obvious that oxygen levels could be important for micropropagation. Agitation of liquid cultures aerates the medium when propagating orchid meristems, for example. Stationary liquid medium can be used if it is sufficiently shallow to allow the shoot cultures adequate oxygen (Preece, 2010). Gelling agents support the plant material allowing good aeration.

When working with gelled cultures, oxygen in the head space atmosphere is also important, although oxygen enrichment of the culture atmosphere has not been investigated to a large extent and both stimulation and inhibition have been reported for culture atmosphere enrichment.

Meristem Culture

The apical meristem area is often free from pathogens, including viruses, because vascular differentiation occurs in daughter cells that differentiate from meristematic cell divisions, not in the cells in and immediately around the apical meristem (Preece, 2003). Because it is difficult to excise only the meristem, young leaf primordia are also included, making the explants micro shoot tips, typically 0.4–0.5 mm in diameter. Micro shoot tips are widely used to escape viruses in perennial, clonally propagated crops. Frequently stock plants or cultures also receive thermotherapy as a further measure to produce plants free from important pathogens.

Morel (1960) used this technique to produce virus-free orchids. In practice, the process involves starting with an elite plant that usually receives heat treatment, from which the meristem tip is excised and used as the explant. Following culture, possibly several re-cultures of the micro shoot tip, resulting shoots and plants are tested for freedom from those pathogens that can be detected. This latter step may involve indexing for viruses, bacteria, or other diseases. It is standard practice to obtain specific pathogen-tested stock plants for a wide variety of asexually propagated crops, including potato, banana, pome fruits, several citrus species, chrysanthemum, and many others (Klopmeyer, 2000). An interesting example is the use of meristem cultures for the elimination of Pierce's disease in Muscadine grape, *Vitis rotundifolia* (Robacker and Chang, 1992). For a review of the process of escaping pathogens using this technique, see Sangwan *et al.* (1987) and Milošević *et al.* (2012).

Stage II: Multiplication

The multiplication stage capitalizes on the stimulation of axillary buds from the explant, which in turn can produce many more shoots that have axillary buds that with repeated subculturing can result in an exponential increase of explant numbers. Subsequently these shoots can be cut into numerous pieces, each with at least one axillary bud, for further subculturing. The resulting shoots can then be induced to produce adventitious roots and grown on as intact plants (see Stages III and IV, **Figures 2–4**).

As noted earlier, cytokinins, or a ratio of cytokinin to auxin in which cytokinin dominates, can lead to bud production, shoot proliferation, and potential new plantlets. When using an agar-gelled medium, the shoots may not elongate well or produce adventitious roots in a satisfactory manner. Maene and Debergh (1985) demonstrated that liquid additions to existing 'exhausted' cultures could help to alleviate this



Figure 4 (a) Walnut microshoots that have been cultured in darkness to etiolate the shoots to enhance adventitious root initiation. (b) and (c) *In vitro* rooted microshoots of trifoliate orange ready to transplant to flats ultimately to be used as clonal rootstocks for citrus. (d) *In vitro* rooted microshoot of cherry, ready for transplanting into greenhouse growing medium.

problem. By adding liquid MS medium that contained kinetin instead of the BA that had been used in the multiplication medium, they were able to stimulate shoot elongation of *Philodendron* and *Cordyline*. Inclusion of charcoal in the liquid medium added to *Philodendron* cultures, along with kinetin, gave uniform elongation of the microshoots. They theorized that the charcoal overcame the after-effect of high BA in the Stage II cultures. Stationary liquid medium can also be used to enhance shoot elongation, and is useful on species that are not prone to hyperhydricity (Preece, 2010).

A large number of plant species and gentypes have been successfully micropropagated in the decades since Murashige's (1974) listing of over 100 species and more than 50 genera that had been micropropagated to that date. Examples of herbaceous and woody plants are now routinely micropropagated, among many, including the following:

- Herbaceous/ornamentals:
  - *Aechmea* – Cueva *et al.* (2006)
  - *Gardenia* – Hatzilazarou *et al.* (2006)
  - *Philodendron* – Jámbor-Benczár and Márta-Riffer (1990)
  - *Pulmonaria* – Stimart *et al.* (1998)
  - *Tillandsia* – Cueva *et al.* (2006)
- Woody ornamentals:
  - *Acanthopanax* – Yang and Read (1997)
  - *Acer* – Preece *et al.* (1991a,b)
  - *Berberis* – Uno and Preece (1987)
  - *Cercis* (red bud) – **Figure 8**
  - *Hibiscus* – Airò *et al.* (2009, **Figures 2** and **3**)

- Fruits:
  - *Citrus* – **Figure 4**
  - *Malus* (apple) – Zimmerman (1984)
  - *Olea* – Leva (2011)
  - *Passiflora* – Faria and Segura (1997)
  - *Prunus* –**Figures 4** and **6**
  - *Rubus* – **Figure 7**
  - *Vaccinium* – Grout and Read (1986)
  - *Vitis* – Gago *et al.* (2009, **Figure 1**)
- Nut crops:
  - *Castanea* – Yang *et al.* (1986)
  - *Corylus* – Nas and Read (2001)
  - *Juglans* – Leslie *et al.* (2010, **Figures 1–4**)
  - *Pistachia* – Benmahioul *et al.* (2012)
- Medicinals and herbs
  - *Allium* – Mohamed-Yasseen *et al.* (1993)
  - *Balanites* – Gour *et al.* (2007)
  - *Hypericum* – Karppinen *et al.* (2006)
  - *Rosemarinus* – Tawfik *et al.* (1992)
  - *Satureja* – Arrebola *et al.* (1997)

At times, the available plant material may be limiting, leading researchers to be concerned about reliability of their investigations and commercial propagators to question new protocols. One approach to addressing this problem has been the studies of Nas *et al.*, (2005) in which experimental designs were tested when there was a limited amount of potential explant material. They employed two designs that they proved to be effective when explant material is limited, Plackett–Burman Design (PBD) and fractional factorial design (FFD). Although limiting information on treatment interactions when PBD or FFD are used, their results indicated that several factors could be tested when explant material is limited and would facilitate prioritizing the most important factors. Subsequently these results can provide guidance when sufficient numbers of explants become available for larger experiments.

Stage III: Pretransplant Stage

Steps in the Adventitious Rooting Process

The goal with Stage III is both root initiation and development to complete the formation of new clonal plants that will grow in the greenhouse or field. Rooting can be accomplished *in vitro* in the tissue culture incubation room or *ex vitro* in a greenhouse or growth chamber. When rooting is *ex vitro*, Stages III and IV, rooting, and acclimatization are combined, which gains efficiency if both rooting and acclimatization percentages are high. With some species, especially herbaceous plants, including many foliage plants, rooting occurs during Stage II, the shoot proliferation stage, thus allowing Stage III to be skipped. However, rooting during Stage III is critical for many species, especially woody plants, including ornamentals and fruit and nut crops.

The process of adventitious root formation from stem cuttings and microcuttings follows a predictable path with changing requirements as the new root system forms. Rooting is essentially a wound healing process. Plants have the remarkable ability to regenerate missing parts after wounding. Propagators have for centuries been utilizing the plant wound healing responses to propagate billions of superior plants by generating roots on stem cuttings and stems on root and leaf cuttings. The result is the production of uniform clonal crops of the best selected individuals.

Root formation. Both microshoots and stem cuttings are composed entirely of cells and tissues that formed and grew as parts of shoot systems and consist of cells that constitute the buds, stems, and leaves. For rooting to be successful, a small portion of the cells in the stems near the vascular tissue must convert into root meristematic cells that will divide and subsequently form a functioning root with a vascular connection to the shoot. This must happen at multiple locations around the stem for optimum root distribution and anchorage.

Rooting has long been recognized as a multistep process of induction, initiation, and expression (Kevers *et al.*, 1997, 2009). Rooting microshoots and normal 'macro' stem cuttings follows the same sequence of events. Cells that formed as part of a stem must change to perceive a signal, such as auxin and polyamines, which induces them to become root meristematic cells that will begin a coordinated series of cell divisions to form a root initial. That initial must then elongate to express a functioning root, providing anchorage, support, and both water and mineral nutrient uptake.

Not all cells in a stem have the competence to perceive a signal that will induce them to begin dividing to form root meristems (growing points). Christianson and Warnick (1985) divided the process of adventitious shoot or root production into acquisition of cellular competence, those cells being induced, and then the differentiation and growth of the organ. Viewing these three phases as separate events, with each one subsequently depending on the previous phase makes various procedures used for rooting microshoots more understandable.

Rooting varies among genotypes, including among cultivars of the same species. This is an indication that the ability to acquire cellular competence is blocked or inhibited in some genotypes (Christianson and Warnick, 1985). The ability to acquire cellular competency changes during the ontogeny of many perennial species with cuttings from juvenile forms generally rooting in higher percentages with more roots than cuttings from adult forms of the same plants (Hartmann *et al.*, 2011; Preece, 2003, 2008). Cellular competency is induced by etiolation of whole shoots (**Figure 4(a)**), or by excluding light from the bottom of cuttings (Murray *et al.*, 1994). Additionally, cellular age and position in relation to other cells affects acquisition of competency (Wilson, 1994).

Auxin has been considered an important signal for adventitious root initiation since the 1930s (Cooper, 1935; Hitchcock, 1935; Zimmerman and Wilcoxon, 1935). Auxin occurs naturally as IAA and phenylacetic acid (PAA), with IAA often having greater activity. Exogenously applied auxins are primarily IBA and NAA. These can be incorporated into the nutrient medium for *in vitro* rooting, or applied to the bases of microshoots or macrocuttings before planting in a rooting medium.

Polyamines, especially putrescine, are also important for root initiation. For example, during the induction period of adventitious root formation of mung bean (*Vigna radiata*) from 0 to 24 h, both IAA and putrescine levels increased (Nag *et al.*, 2001). When rooting *Nothofagus nervosa* microshoots,

Martinez Pastur *et al.* (2007) found that polyamine content in the tissue was highest before root emergence and therefore added 10 μM spermine to their culture medium when rooting.

Auxin is used predominantly for rooting microshoots and macrocuttings. Polyamines likely play an important endogenous role, but are seldom used when rooting cuttings or microshoots. Microshoots themselves contain and produce natural auxins, such as IAA, which also contribute to rooting. The addition of exogenous auxin makes rooting possible in some genotypes and greatly increases rooting percentages and root numbers per microshoot in many others.

Induction is when cells that have acquired competence, cells are induced by the rhizogenic action of auxin and other plant growth regulators, such as polyamines. Induction occurs in a short time of hours or days depending on genotype (Christianson and Warnick, 1985). Once induced, microcuttings can be transferred to medium with no auxin and root development will proceed. Within 24 h of exposure to 3 μM IBA, there was an increase in starch accumulation in vascular bundles and surrounding cells of 1 mm stem slices of apple microshoots (Jasik and De Klerk, 1997), which is likely an early step in dedifferentiation into a root meristem.

Caution must be exercised when using auxins for rooting. Although they appear essential for root initiation at relatively low concentrations, at relatively high concentrations they inhibit root elongation. A typical sign of auxin overdose is short, larger diameter than normal, very slow growing roots. Higher amounts of auxin act as herbicides and damage or kill plants. Therefore, it is important that a concentration of IBA or NAA is applied as a short exposure or that the concentration will be sufficient to stimulate root initiation without being inhibitory to elongation.

Although not visible to the propagator, new root meristems can form quickly. New cell divisions were visible 48 h after apple microshoot stem slices were exposed to IBA and were forming meristems after 72 h (Jasik and De Klerk, 1997). The initials of root primordia were detected 96 h after IBA treatment. That is why the auxin treatment can be removed after a short exposure with no subsequent effect or the removal may even result in improved rooting.

The remainder of the adventitious rooting process is normal root growth activity. The new root apical meristematic cells divide and daughter cells differentiate and form the tissues of functioning roots. During this process, each new root establishes a vascular connection with the shoot to supply it with water and mineral nutrients in return for photosynthate.

Methods for Rooting Microshoots

If microshoots do not form roots during the multiplication stage, they must receive special treatments to initiate and grow an adventitious root system. Microshoots may be rooted *in vitro* and then acclimatized to the ambient environment, or they may be rooted *ex vitro*, thus combining rooting and acclimatization.

Ease and success rate of rooting determine which method is used on a particular cultivar. The more cost-effective method is to root microshoots *ex vitro*. *Ex vitro* rooting saves an additional *in vitro* transfer to rooting medium and speeds acclimatization making micropropagation more efficient. *In vitro* rooting is used if *ex vitro* rooting and acclimatization facilities are lacking, if success rates are low with *ex vitro* rooting, and at the discretion of the laboratory manager.

In vitro rooting. The ingredients in the medium and the incubation conditions are easy to change when *in vitro* conditions are used to promote root initiation and early development. Nutrient salt formulations may remain the same, be changed, or reduced, often to half strength macrosalts, and relative humidity reduced by the use of ventilated lids (**Figure 5**). The light and temperature culture incubation conditions can be changed for rooting. Many microshoots are incubated in darkness for a period for root initiation and then transferred to lighted conditions.

The rooting nutrient medium on which freshly cut microshoots are placed generally contains auxin. Typically micromolar concentrations of IBA and/or NAA are added to the medium before autoclaving. The concentration of auxin depends on the species and cultivar. This information is typically available online using a scholarly search engine, such as Google Scholar http://scholar.google.com/. Typically the name of the plant, the words '*vitro*' and 'root' (or adventitious root) in the search string will yield specific information. If the literature is lacking for a particular plant, use close relatives in the search to determine how they responded.

Because it is recognized that the same concentrations of auxin that stimulate adventitious root initiation can inhibit root development, some use a two media approach. When microshoots of *Cotinus coggygria* were on medium containing 10 μM IBA for 5 days before transfer to auxin-free medium, 100% rooted; whereas only 40% rooted with continuous culture on medium with the 10 μM IBA (Metivier *et al.*, 2007). Padilla and Burgos (2010) cultured olive microshoots on media containing up to 4 μM IBA for 2 weeks followed by transfer to basal medium without auxin that resulted in 65–93% rooting, depending on cultivar.

In some cases, IBA solutions have been applied to microshoots as a basal dip for one minute or more. Tsvetkov *et al.* (2007) obtained their best rooting of *Sorbus domestica*

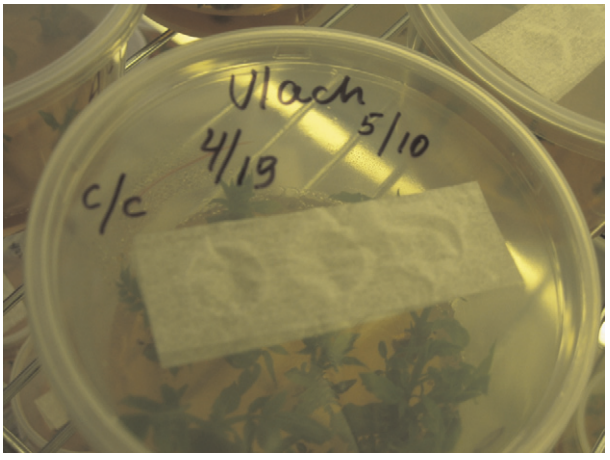


Figure 5 Surgical micropore tape provides ventilation to this vessel of shoots being rooted; this helps reduce relative humidity and prepares the new plants for the greenhouse environment.

microshoots when they were dipped in a 14.8 μM IBA solution for 80 s before being placed on basal medium.

Darkness during or before rooting can increase rooting success and synchronicity of rooting among microshoots. Etiolation, development of shoots without light, will increase cellular competency for adventitious rooting (Murray *et al.*, 1994). When walnut microshoots were etiolated, rooting was better with faster emergence of roots than from green shoots (Leslie *et al.*, 2010); however, the etiolated shoots were brittle and required more careful handling.

Culturing green microshoots on rooting medium in darkness for a relatively short period can greatly enhance rooting. A period of darkness for 4–7 days on a half strength Murashige and Skoog medium containing 1 μM phloroglucinol and 1.4 μM IBA followed by incubation under lighted conditions resulted in better rooting of 'Delicious' apple microshoots than if cultured only in light or in darkness for longer periods (Zimmerman, 1984). When culturing 'MM106' apple rootstock microshoots on medium with 4 μM IBA in darkness for 0–10 days, it was discovered through histological investigation that root induction occurred during the first 3 days or less in darkness and that conical root primordia were visible by day 7 (Naija *et al.*, 2008). Timing of treatment in darkness is critical and may need to be determined for each crop or genotype; nevertheless, it can greatly enhance rooting success.

Some species root best if the tops of the microshoots are lighted and the basal portion in the medium is in darkness, similar to the way that macrocuttings are rooted in a greenhouse medium under mist. Darkening of the medium can be achieved by painting the outside of culture vessels black to slightly above the level of the medium and covering the medium with sterile polycarbonate granules or other light excluding substance or darkening the medium itself by adding activated charcoal. At times a greenhouse medium, such as vermiculite, which also excludes light is used for *in vitro* rooting after being wetted with the nutrient medium.

It was shown that darkening the bases only of microshoots increased rooting of almond, peach, and olive (Rugini, 1988) and apple (Mencuccini and Rugini, 1993) compared with controls incubated either in darkness or under lights. However, in a separate study, Mencuccini and Rugini (1993) reported that basal darkening had little effect on rooting almond, apricot, chestnut, jojoba, and olive microshoots and was inhibitory to walnut. Therefore, if rooting success is below what is desirable, basal darkening may be helpful.

Ex vitro rooting. If rooting percentages are similar, *ex vitro* rooting can be more efficient and cost effective than *in vitro* rooting (Leva, 2011). Costs are higher when rooting *in vitro* because of the ingredients, preparation time, autoclaving media, labor for transfers and moving cultures, and incubation space. Movement to the greenhouse is similar between *in vitro* and *ex vitro* rooting, and transplanting time may be similar or slower when there are roots on the microshoots (**Figures 4** and **6**). Efficiency is gained by rooting *ex vitro*. It has been reported that the root quality of walnut microplants is superior when the roots form *ex vitro* under fog than *in vitro* in a gelled medium (Leslie *et al.*, 2010).

Ex vitro rooting can be an improvement on *in vitro* rooting. Although *in vitro* microshoots of *Gardenia jasminoides* rooted in 10 days, compared with 14 for *ex vitro* microshoots, all microshoots rooted *ex vitro* survived acclimatization compared with 80% survival for *in vitro*-rooted microshoots (Hatzilazarou *et al.*, 2006). Poorer survival of microshoots rooted *in vitro* compared with *ex vitro*-rooted microshoots was also reported for walnut (Leslie *et al.*, 2010).

It may be necessary to treat microshoots with auxin before planting in rooting medium for *ex vitro* rooting. Pistachio microshoots treated with 2% IBA in talc rooted *ex vitro* at 79% compared with 48% rooting for the controls (Benmahioul *et al.*, 2012).

Improved *ex vitro* rooting can also be obtained with auxin applied as a liquid dip applied to the basal portion of microshoots. A 15 min pulse in 250 μM IBA caused 90% of the tree species *Melia azedarach* microshoots to root compared with no rooting on control microshoots (Husain and Anis, 2009). A 2 h dip in an aqueous solution of 588 μM IBA caused 90% of *Malus zumi* microshoots to root compared with 20% rooting of controls (Xu *et al.*, 2008).

Perhaps because of a reversion to juvenility, increasing time being multiplied *in vitro* can increase rooting of microshoots. Leva and Petruccelli (2012) tested rooting up through seven subcultures and found that rooting was best after the seventh subculture.

Facilities, the species, shipment method, customer demand, and managerial preferences all dictate how microshoots are rooted. Species that root very easily or root during the shoot proliferation phase can be acclimatized to the *ex vitro* environment quickly. It is the challenging species that receive special attention, regarding lighting, auxin treatment, rooting *in vitro* or *ex vitro*, and other factors. The clones that are difficult to root demand greater prices from customers because rooting is an impediment to efficient production. Rooting can be improved if it is approached as a multistep process of acquiring competency, root initiation, and subsequent root growth. All of these steps must be considered and addressed, especially with the more difficult-to-root clones.

Stage IV: Acclimatization

Acclimatization of microplants to the *ex vitro* environment of the greenhouse and field can be a time of the greatest losses of plants in the micropropagation process (Preece, 2001, 2010; Preece and Sutter, 1991). Shoots, and leaves in particular that form *in vitro* on many species are uniquely unsuited to the ambient environment, consequently there must be a gradual hardening process during which microplants produce new leaves in the acclimatization and post-acclimatization environments. See the leaves on the plantlets in **Figure 7**, the majority were formed during and after acclimatization compared with the leaves in **Figures 4** and **6** that formed *in vitro*.

Humidity Control

A primary challenge with establishing microplants in the ambient environment is the change in relative humidity. The *in vitro* environment is typically 100% relative humidity



Figure 6 (a) and (b) *In vitro* rooted micropropagated cherry plantlets ready for transplanting into a sphagnum peat greenhouse medium before placement under high relative humidity for acclimatization. (c) The cherry plantlets being planted as the first step in greenhouse acclimatization. (d) Walnut plantlets being planted in a flat before being placed under high relative humidity in a greenhouse.

(see the condensation inside of the culture vessels in Figure 4b). The leaves that form on these *in vitro* microshoots do not develop the same mechanisms to prevent water loss as plants growing at lower humidity levels. In the saturated *in vitro* atmosphere the development of the waxy cuticles on leaves is greatly reduced compared with the same clone grown *ex vitro* (Hazarika, 2006; Preece, 2001, 2010; Preece and Sutter, 1991). Additionally, the stomatal apparatus often does not function and the stomata remain continuously open, even at night or during dessication.

Perhaps because of a combination of low light and the high humidity, there are much greater air spaces and less tight packing among the cells of the *in vitro*-produced leaves than those grown in the ambient environment (Brainerd and Fuchigami, 1981; Preece and West, 2006; Preece, 2010). Leaves produced *ex vitro* are approximately three times thicker in cross section and the palisade cells containing chloroplasts are tightly packed and often stacked in multiple layers, whereas *in vitro*-produced leaves have only one layer of palisade cells with intercellular spaces. During acclimatization, the first new leaves that form are thin and similar to *in vitro* leaves; however, as new leaves develop, they gradually become more like normal leaves that grow on plants in the greenhouse or field. Initially the new leaves that form during acclimatization have tightly packed palisade cells, indicating a transition to higher light and lower relative humidity.

In vitro rooting is often in vessels with ventilated lids (Figure 5), which can lower humidity and begin the transition of microplants to the *ex vitro* environment. For example, ventilation caused lower water content, which thus increased epicuticular waxes on the leaf surfaces, and resulted in a higher resistance to water loss on jojoba propagules (Mills *et al.*, 2001), which all contribute to acclimatization success.

If ventilated lids still maintain a high relative humidity, loosening, tilting open, and removing lids of culture vessels following *in vitro* rooting but before transplanting will help prepare microplants for the ambient environment. With desert date (*Balanites aegyptiaca*) it was necessary to gradually unscrew lids of culture vessels before transplanting into vermiculite to



Figure 7 Rooting and root development on clonal microplants immediately following acclimatization. (a) and (b) Walnut plantlet being acclimatized and showing root development through a peat pot containing a sphagnum peat-based container (a) or in a similar medium removed from a plastic container. (c) Blackberry plantlet showing root development along the outside of the sleeve containing a similar peat-based medium. (d) and (e) Root development on clonal walnut rootstock micropropagated plants after acclimatization and removal of the growing medium.

achieve a 43% survival of this recalcitrant species (Gour *et al.*, 2007).

In vitro-rooted microplants should have a good, healthy root system at the time of transplanting, as with any transplant (Figures 4 and 6). To provide good anchorage, new adventitious roots should emerge from all sides of each new microplant. Before transplanting, new microplants must not be allowed to overheat, become too cold, or desiccate. Microplants are typically transplanted into small pots, starter blocks, or flats containing suitable growing medium and then moved to the acclimatization environment where new roots will begin to grow and shoots will elongate in a short time, or after a lag period of little or no growth, depending on the species and cultivar (Figure 7).

Because of the poor adaptability of *in vitro* leaves to the *ex vitro* environment, it is essential that the microplants be placed in a high relative humidity environment, such as under fog or intermittent mist located in a greenhouse or humidity tent (Figure 8). The goal is to minimize transpiration and not to soak the plants. Multiple types of enclosures are available to



Figure 8 Acclimatization areas. (a) Clonal walnut rootstock plants being acclimatized within a clear plastic tent. (b) 'Forest Pansy' Red Bud (foreground) and blackberry plants during acclimatization under a white plastic humidity tent with evenly spaced overhead mist nozzles. (c) and (d) Walnut microplants being acclimatized in a greenhouse with a fog system filling the greenhouse with humidity in (d).

provide a highly humid environment, and can be as simple as a plastic bag over a potted microplant, to benches covered with clear or white plastic, plastic tunnels, hard plastic and vinyl, or glass domes or other enclosures (Preece, 2010). Plastic and other tunnels may contain fog or intermittent mist systems.

The relative humidity should be gradually reduced as the plants adapt to the acclimatization environment. An example is a gradual reduction in relative humidity from the initial 100–60% over a 3-week period, which worked well for *Vitis vinifera* 'Albariño' (Gago, 2009). This gradual reduction in humidity can be achieved by venting humidity tents and other enclosures, adjusting the mist or fog system controls to decrease the 'on' times and increase the 'off' times.

Shading

In addition to high relative humidity, microplants are often acclimatized under shade. *In vitro* leaves are shade leaves because they develop under approximately 35–80 μmol m^{-2} s^{-1} and are therefore poorly adapted to sunlight. In separate studies, when different levels of shade or light were tested, survival of *Heliconia bihai* (lobster claw) was highest (>90%) under the highest levels of 70% or 80% shade (Rodrigues *et al.*, 2005). *Musa* (banana) microplants acclimatized best under the highest levels of 50% or 70% shade (Scaranari *et al.*, 2009) and *Doritaenopsis* orchids had best growth and survival when acclimatized under the lowest light levels of 50–150 μmol m^{-2} s^{-1} (Hahn *et al.*, 2009).

Shade can be provided by using a semiopaque plastic for a humidity tent, rather than clear polyethylene. Various shading materials are used, including shade cloth or fabric that is available from approximately 20–90% shade in various increments. Wood or aluminum lath is also an effective way to apply shade to plants. For acclimatization, the fabric should provide at least 50% shade and typically should be combined with intermittent mist or fog.

Substrates

There are many different greenhouse media used during acclimatization, ranging from plugs and starter blocks (**Figure 7**) to sphagnum peat- or tree bark-based media in flats or pots (**Figure 6**, Preece, 2010). The specific acclimatization environment dictates which substrate will be cost effective and contributes to the production of high-quality plants. For example, a medium that holds too much or too little water for

the situation will result in reduced acclimatization success. A well-drained medium, such as perlite, vermiculite, or sand might be appropriate in a wet environment, such as under mist, or either peat or bark mixed with the perlite or vermiculite might be suitable for fog or other high humidity conditions.

An ideal medium will provide good water-holding capacity for the situation; have adequate pore spaces to provide a balance of air (especially oxygen) and water-holding capacity; be easily wettable; provide good anchorage; be of a proper pH for the crop; if used to grow the plants, be able to hold nutrients (high cation exchange capacity); be inexpensive and readily available; and be free from pathogens, insects and pests, and toxic substances. Some media are hydrophobic when dry, such as sphagnum peat and some tree barks. These can be used if a detergent-type wetting agent is added to break the surface tension of the water. Otherwise, water will run off and not soak the medium creating droughty conditions for the microplants, often leading to stunting or death.

Beneficial soil microflora can be considered during acclimatization and may contribute to acclimatization success. In particular, inoculations with mycorrhizal fungi have been shown to be very helpful. *Vitis vinifera* 'Pusa Navrang' microplants grown in medium inoculated with single or mixed strains of arbuscular-mycorrhizal fungi had an 81–91% survival rate compared with only 45% for noninoculated plants (Krishna *et al.*, 2004).

Mycorrhizal inoculation can also enhance subsequent growth and quality of the fully acclimatized plants, resulting in a higher quality product. For example, the following species had both greater survival and growth compared with control plants when inoculated with the arbuscular-mycorrhizal fungus *Glomus viscosum*: *Cynara cardunculus* (Cardoon), *Cucumis melo* var. *inodorus* (melon), *Origanum vulgare* subsp. *hirtum* (Greek oregano), and *Spartium junceum* (Spanish broom, Ruta *et al.*, 2009).

Some growers add the beneficial fungi *Trichoderma* spp. to their peat-based medium for acclimatizing microplants and their subsequent growth (Hoare, 2001). *Trichoderma* spp. are avirulent plant symbionts that colonize plant root surfaces protecting the roots from several pathogens, as well as often enhancing root growth, nutrient uptake, abiotic stress tolerance, and overall productivity (Harman *et al.*, 2004). Addition of *Trichoderma* can be beneficial whenever growing plants.

Encapsulated Vegetative Explants

Sodium alginate, gelled with calcium chloride ($CaCl_2$) can be used to encapsulate nodal explants for storage, or to use in a manner similar to an artificial seed that can be planted for growth and acclimatization. The alginate matrix protects the nodal segment and emerging plant from desiccation and provides the nutrients of the tissue culture medium within the matrix. Results have varied with species and acclimatization conditions.

Microbial infection can be a problem when planting encapsulated nodal segments because of the ingredients in the alginate matrix (nutrient medium salts, organics, sugar, and others). Researchers have addressed this problem. Bapat and Rao (1990) previously had experience with microbial infection when planting alginate beads containing 0.5 cm long nodal segments of mulberry (*Morus indica*). These were planted in autoclaved soil in Petri dishes. When the encapsulation matrix contained 50 mg l^{-1} Carbendenzim, 63% formed plants, whereas when the matrix contained 50 mg l^{-1} Bavastin, only 21% formed plants. Refouvelet *et al.* (1998) used the carbamate eserine, *p*-hydroxymercuribenzoate (*p*-HMB), which was applied as a spray every 4 days, to encapsulated lilac (*Syringa vulgaris*) buds before preacclimatization in an enclosed chamber on Sorbarods® in a nonsterile environment for 45 days. Survival was up to 81% in the greenhouse.

Problems with decay, necessitating the use of pesticides may be related to planting condition. Preece and West (2006) used no fungicides and found that the only encapsulated nodal segments of hardy hibiscus (*Hibiscus moscheutos*) that survived were planted in vermiculite under intermittent mist. None survived if under fog or hand watering, or if planted in perlite or a peatlite medium (two sphagnum peat: one vermiculite: one perlite (by volume)). Because survival was only 20% and because Sarkar and Naik (1998) gave a lighted pretreatment to encapsulated potato nodal segments with no pesticide, West and Preece also tested an *in vitro* lighted pretreatment. When encapsulated nodal segments were placed under light in the laboratory for 2–3 weeks, 100% acclimatization success was achieved under intermittent mist uncovered, in 1 cm deep furrows in vermiculite. Kumar *et al.* (2010) also achieved high acclimatization success without pesticide, but had to transfer encapsulated jojoba (*Simmondsia chinensis*) shoot tips to *in vitro* medium containing IBA for 4 weeks to produce rooted shoots for acclimatization.

Therefore, with the correct pretreatment to induce both root and shoot growth, alginate-encapsulated nodal segments can be planted like small plugs, which can be very efficient. This must be tested by genotype, and efficiencies in the encapsulation process are necessary to be cost effective.

Acclimatization under Commercial Conditions

Nurseries typically receive Stage II, freshly cut microshoots; Stage III, *in vitro*-rooted nonacclimatized microplants; or Stage IV, fully acclimatized plantlets from commercial micropropagation laboratories. Freshly cut microshoots must be rooted and acclimatized and are priced lower to the nursery than rooted or acclimatized microplants. Fully acclimatized plantlets are sold to growers for direct field planting and nurseries for growing to profitable size.

Carlton Plants, Oregon, USA (Anderson, 2001); Skagit Gardens Inc., Washington, USA (Hoare, 2001); and Meadow Lake Nursery Co., Oregon, USA (Armstrong, 2001) purchase microcuttings. Carlton Plants places microcuttings into a one sphagnum peat: one pumice medium with fertilizer, Skagit Gardens uses a seven sphagnum peat: three perlite medium with both fertilizer and *Trichoderma* and then intermittent mist with bottom heat for 4–7 days (Hoare, 2001). Meadow Lake Nursery may refrigerate the microcuttings until they can be planted. Applications of hydrogen dioxide (Zerotol®) can eliminate algae and foliar diseases.

Manor View Farm, Inc., Maryland, USA (Jones, 2001); Carlton Plants, and Skagit Gardens receive nonacclimatized rooted Stage III microplants. Manor View Farm transplants them into 72- or 98-cell plug trays and then places them into a tent with a mist system. Skagit Gardens and Meadow Lake Nursery handle them the same way as the Stage II microcuttings.

Some nurseries specialize in acclimatization and sell or grow-on microplants. With all or a portion of a nursery having focus on acclimatization, the grower gains great expertise with this system. Early recognition and control of pathogens, such as *Botrytis* (gray mold) is crucial to successful acclimatization. *Botrytis* can appear as a gray fuzzy mold and thrives in humid, stagnant environments such as those found within acclimatization tents and other enclosures.

Conclusion

Clonal micropropagation is an important component of the propagation, nursery, and orchard industries. This technology has allowed the Oregon hazelnut industry to abandon grafting and transplant micropropagated trees growing on their own roots. The California walnut industry has, for the first time, clonal rootstocks available only because of micropropagation. Walnut cuttings root poorly and not at commercially viable rates.

The micropropagation industry is having an economic impact on companies that sell the supplies and equipment, the trucking and transportation industry, the nursery industry, the forestry industry, the landscape industry, and others. Commercial companies would not devote their resources to purchase micropropagated plants unless there were sufficient demand for the product. Clearly, there is a place for micropropagation and although micropropagation will never replace grafting, layering, and rooting cuttings, it is an important component of the commercial propagation industry.

Whether grown commercially, for research, or personal pleasure, all clonal micropropagation follows the same basic pathway through the stages of micropropagation. Because axillary shoot proliferation is important, initial explants must include nodes. Axillary buds are induced to grow from the nodes, and when desired, excised, rooted, and acclimatized.

Care must be exercised to avoid adventitious shoots and only axillary shoots should be produced to ensure clonal fidelity. Adventitious shoots can show a tendency to exhibit somaclonal variation and the resulting plants may not be true-to-type. Commercial laboratories have failed because of selling plants derived via adventitious shoot organogenesis. The lack of uniformity among the plants disappointed customers, who did not make additional purchases.

Clones that establish, proliferate shoots, root, and acclimatize successfully are the easiest for meeting customer demand and the most cost effective to produce. Genotypes that offer more production challenges and either grow and multiply, root, and/or acclimatize slower and less successfully are more expensive to produce and for customers to purchase than easier genotypes. Typing 'micropropagation laboratories' into an Internet search engine will access sites with additional information about micropropagation.

See also: Agroforestry: Practices and Systems. Biodiversity: Conserving Biodiversity in Agroecosystems. Biotechnology: Pharming. Biotechnology: Plant Protection. Breeding: Plants, Modern. Climate Change: Horticulture. Genebanks: Past, Present, and Optimistic Future. Heterosis in Plants. Medicinal Crops. Pathogen-Tested Planting Material. Plant Cloning: Macropropagation. Quarantine and Biosecurity. Tree Fruits and Nuts

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Computer Modeling: Applications to Environment and Food Security

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Glossary

Agricultural System Model A mathematical model of soil–water–plant–climate management system.
Cover crops Short-duration crops that are planted after harvest of main crop (e.g., corn) and planting of the next main crop in rotation (e.g., soybean).
Crop simulation Computation of plant growth processes with a mathematical model.
Crop water production function Crop biomass or grain yield at different levels of water use; transpiration, evaporation and transpiration, or water supplied in the soil.
Emission scenarios Level of greenhouse gas (GHG) concentrations in the atmosphere depending upon the different scenarios of emission from various sources. In the 2000 report, the Intergovernmental Panel on Climate Change defined four possible emission scenarios in the order of increasing GHG concentrations as A1, A2, B1, B2.
Filed capacity Water retained in the rootzone after complete wetting, followed by gravity drainage for 48 hours, expressed as volume of water per volume of soil.
Plant available water (PAW) Part of the water in the rootzone that the plant can uptake, which is the difference in soil water contents between field capacity and wilting point.
Water use efficiency Crop biomass or grain yield per unit of crop transpiration or PAW.
Wilting point Water content in the rootzone at which the plants start to wilt.

Why Models in Agriculture?

The use of system models in agricultural research has accelerated in the past two decades due to increasing knowledge of the soil–plant–atmosphere system, our ability to collect massive real-time field data, unlimited computing power, and the need to address more difficult and complex issues facing us in the twenty-first century. The continued increase in world population requires continued increases in agricultural production. However, the increase in the use of fertilizers, pesticides, and water to increase production with the new higher yielding crop varieties is causing environmental problems and soil degradation. The ground and surface water quality is seriously affected by excessive leaching and runoff of agricultural chemicals at many places. The increase in soil salinity, decline in soil organic matter, and increase in soil erosion remain major problems in intensively farmed areas. The environmental concerns of the general public are challenging producers to modify farm management to protect water, air, and soil quality, while staying economically profitable. At the same time, global warming and the increased frequency of droughts and floods, water shortages due to increased urban use, and market-based global competition in agricultural production are threatening economic viability of the traditional agricultural systems, and require the development of new and flexible production systems. The solution or mitigation of these changing and multiple problems requires continual adaptation and optimization of agricultural systems, using a quantitative systems approach integrated with field research. The process-level models of agricultural systems, based on synthesis and quantification of available interdisciplinary knowledge, provide the systems approach for evaluating and optimizing the effects of varying management practices, crops, soils, water, and climate to attain sustainable production and maintain environmental quality. Fortunately, the new electronic technologies can provide a vast amount of real-time dynamic information regarding crop and soil conditions via remote sensing with satellites or proximal sensing with ground-based instruments. System models can (and are essential to) assimilate this information to further enhance site-specific management. Models can serve as an evolving theoretical backbone of complex agricultural system research and information transfer to policy makers and farm managers to maintain food security and environmental quality.

System modeling has been a vital step in many scientific disciplines. We would not have gone to the moon successfully without the combined use of knowledge, good data, and computer models. In designing automobiles and airplanes, computer models of the system are increasingly replacing the scaled physical models of the past. Models have also been used extensively in designing and managing water resource reservoirs and distribution systems, and in analyzing waste disposal sites. However, a lot more work is needed to bring agricultural system models to the level of physics and hydraulic system models and to enhance their structure and usability. Agricultural system models have matured enough that, with some good data to serve as reference, they can be used for many practical applications in research and management (Jones *et al.*, 2003; Ahuja *et al.*, 2002; Matthews and Stephens, 2002). The effect of management practices of tillage or no-tillage, different crops and varieties, crop rotations, fertilizers and manures, water application levels, and tile drainage on

production and water quality can now be modeled (Ma *et al.*, 2000; Andales *et al.*, 2003; Saseendran *et al.*, 2005). Their integration with field research will expose knowledge or conceptual gaps in the models that will then be filled with new research. In a Dutch publication, 'Method in Our Madness' International Service for National Agricultural Research (ISNAR), 2004, a case is made for applying modeling tools and processes in planning and implementation of natural resources research and making sense of the vast amount of data. The CGIAR Science Council (2005) noted in their Research Priorities: "Modeling and the ability to combine data from different sources, promises to revolutionize understanding of processes affecting management of natural resources. Thanks to strategic accumulation of data, tools, and modeling resources in the coming decade, one can expect the development of a more predictive approach to agriculture." Integration of field research with system models has the potential to significantly enhance efficiency of agricultural research and raise agricultural science and technology to a higher level, leading to improved production and protection of the environment.

Over the past few decades, many models have been developed to address the same agricultural issue with slightly different objectives. Most, if not all, are fit for the purpose they were developed. Therefore, it is difficult to select one model for a given problem, without going into details of the model components. The purpose of this article is not to give such details of the models that the users can obtain on their own, but to give examples of model applications that make a compelling case that models are important tools that can be used to evaluate and manage the environment and food security. The examples pertain to three critical resource areas: (1) water quality, a major environment issue; (2) water quantity, a major emerging issue, important to both environmental quality and food security; and (3) projecting climate-change effects and identifying adaptation and mitigation strategies for both the environment and food security.

Model Applications to Manage Nitrogen for Crop Production and Water Quality

The use of system models can greatly help N management to maintain or improve crop yields without detrimental environmental impacts, even though N is the most difficult component to simulate with models because of the interactions among several components and the fate of N in soil: plant N uptake, mineralization of organic soil N, nitrification, denitrifcation, ammonia volatilization, NO and N_2O emissions, N fixation, and N movement with soil water. All system models with a plant growth component have the capability of simulating N fate in an agricultural system, but with different levels of detail for each N process. Correct simulation of plant N uptake has been identified as a crucial process in determining N fate in the environment (Ma *et al.*, 2007). Most models can simulate crop response to N application as well as N leaching under different N treatments adequately. A wide range of agricultural management practices to help reduce N pollution of surface and groundwater can also be simulated well. These practices include: optimizing rate and timing of N applications, winter cover crop, controlled subsurface (tile) drainage, nitrification inhibitors, and buffer strips. The main agricultural management practices that result in N pollution of groundwater are N fertilizer and manure applications.

Minimizing Nitrogen Loss to Subsurface Drainage (Tile Flow)

In the Midwest, USA, N loss to subsurface (tile) drainage contaminates streams that feed the Mississippi River and causes hypoxia (lack of oxygen for the fish). Considerable research has been conducted by the United States Department of Agriculture, Agricultural Research Service, and the State universities in the region on management practices to minimize this pollution, including degree of tillage, crop rotations, and timing and rates of manure versus fertilizer applications. One example is a comprehensive study at Nashua, IA. **Figure 1** presents the synthesis and quantification of 14 years of data at Nashua, using RZWQM2 (the enhanced Root Zone Water Quality Model), for corn and soybean yields, annual tile drainage flows, N in tile flow, and the weighted average N concentration in tile flow (Ma *et al.*, 2007). The data represented values averaged over multiple plots and a number of management practices for a number of years. Very high spatial variability of the tile flow, caused by unknown lateral groundwater flow below the tiles, was calibrated for each plot. Individual plot and management simulation results were within the variation of the observed data (Ma *et al.*, 2007). The results in **Figure 1** show a good synthesis of the overall data. On the basis of these results, Ma *et al.* (2007) used the model to develop a chart on the effects of different management practices on N leaching in tile flow as a guide to minimizing leaching while maintaining production for corn–soybean cropping systems (**Figure 2**). As shown in **Figure 2**, higher N loss to tile flow was simulated under continuous corn rotation than under corn–soybean rotation due to N applications every year for continuous corn, and under free drainage than under controlled (reduced) drainage. Tillage effects on N loss were not significant.

The research in Iowa further showed that cover crops, such as rye grass or clovers, planted after corn help to remove residual nitrates from the soil profile and thus reduce its leaching to the tile flow (Kaspar *et al.*, 2007). The research also confirmed that reducing tile flow by raising the tile outlet during fall and winter season following corn raises the water table that helps to denitrify nitrate and reduce its leaching (Crabbe *et al.*, 2012). The scientists in Iowa used the field-tested RZWQM2 model to evaluate the effectiveness of cover crops (**Figure 3**) and controlled drainage (**Figure 4**) in reducing nitrate leaching in different parts of the US Midwest to guide on-farm management.

Optimizing Nitrogen Prescriptions

In the past two decades, N management for maximum crop yield as a single goal has changed to maximum crop yield along with minimum N leaching as a double goal. Matching just the right soil N availability with plant N demand is the key to this double goal. For this purpose, split application of N is usually a desirable method, at least when the added cost of application is not a major issue. Other considerations are to

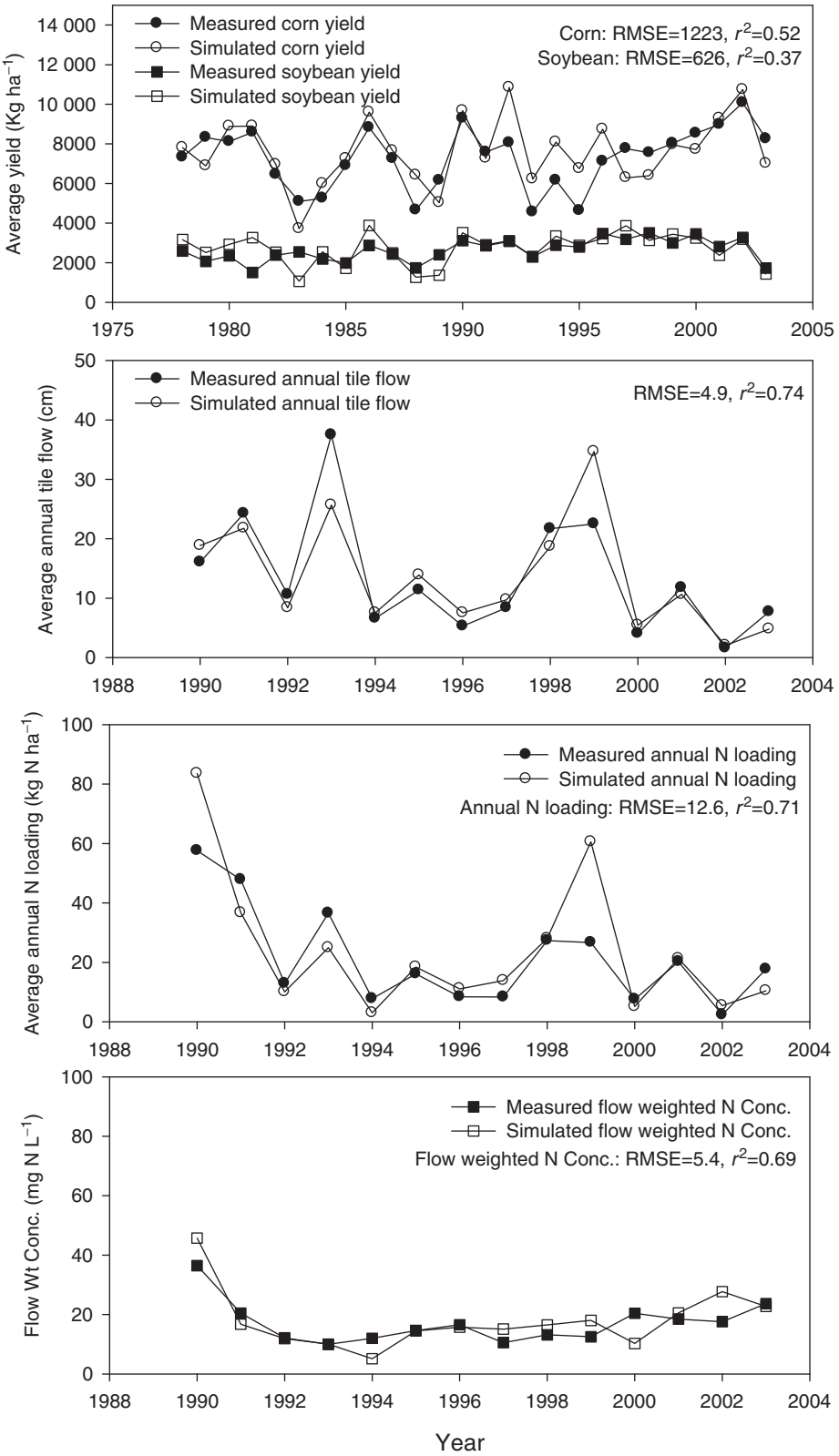


Figure 1 Simulated and measured average corn and soybean yield, yearly tile flow, yearly N loading in tile flow, and flow-weighted N concentration in tile flow across all treatments over 13 years, at Nashua, IA, USA. The results give confidence in the model for identifying best management of N. RMSE, root mean square error; r^2, coefficient of determination. Reproduced with permission from Ma, L., Malone, R.W., Heilman, P., *et al.*, 2007. RZWQM simulation of long-term crop production, water and nitrogen balances in Northeast Iowa. Geoderma 140, 247–259.

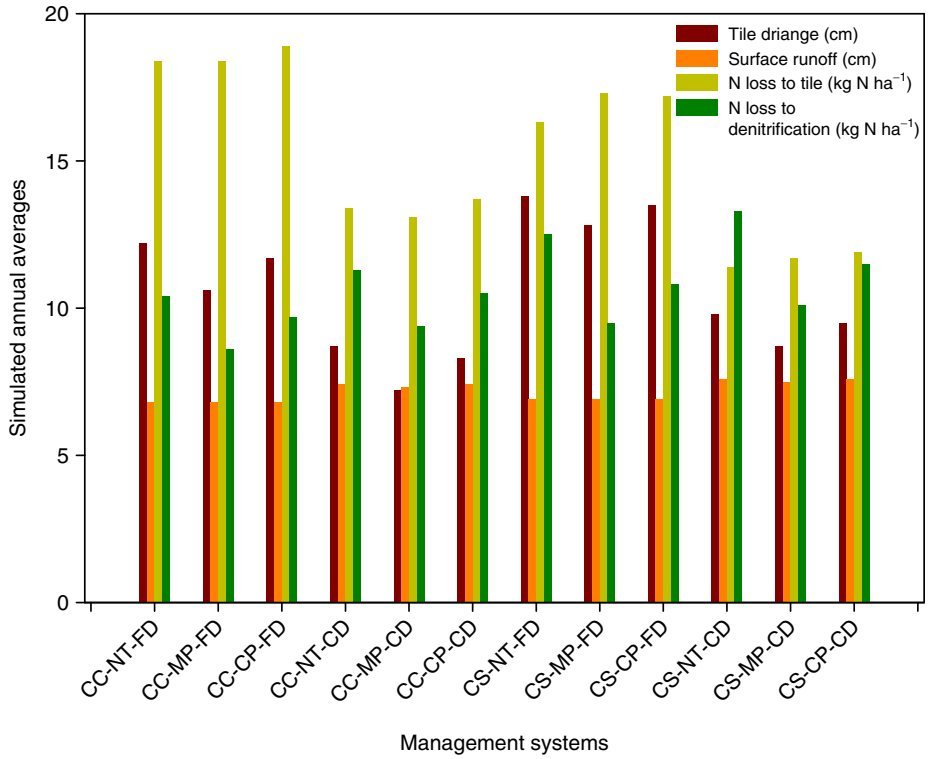


Figure 2 Simulated average annual tile drainage, surface runoff, N loss to tile drainage, and N loss to denitrification for various management systems based on calibrated model from a study in IA, USA. CC, continuous corn; CS, corn–soybean rotation; FD, free drainage; CD, controlled drainage; NT, no-till; MP, moldboard plow; CP, chisel plow. The model runs were from 1979 to 2002. The results serve as a guide to management. N losses are expressed on a per year basis. Reproduced with permission from Ma, L., Malone, R.W., Heilman, P., *et al.*, 2007. RZWQM simulation of long-term crop production, water and nitrogen balances in Northeast Iowa. Geoderma 140, 247–259.

match N application rate with water availability (rainfall or irrigation) (Saseendran *et al.*, 2004) and with other soil conditions that influence productivity (Thorp *et al.*, 2006).

Using the CERES-wheat model calibrated for three growing seasons and five N treatments (0, 28, 56, 84, and 112 kg N ha^{-1}), Saseendran *et al.* (2004) developed probability distribution functions of wheat production using more than 90 years of historical weather data for Akron, CO, USA (**Figure 5**). The model results suggested that an application rate of 56 kg N ha^{-1} was sufficient under dryland conditions for most years in Colorado, without too much residual soil N at harvest (**Figure 5**).

In the North China Plain (NCP), Fang *et al.* (2008) used the calibrated RZWQM2 to investigate the response of long-term crop yield and N leaching to different N application rates (100, 200, and 300 kg N ha^{-1}) and irrigations based on initiation at and recharge to certain levels of field capacity. As shown in **Figure 6**, the highest grain yield was obtained when irrigation was triggered at 50% field capacity and recharged to 70% field capacity at 200 kg N ha^{-1} per crop, indicating that N application rate at approximately 200 kg N ha^{-1} per crop was generally sufficient to obtain high crop yields in the wheat–maize double-cropping system in the region. Compared with 300 kg N ha^{-1} application rates, nitrate-N leaching at 200 kg N ha^{-1} per crop application rate was reduced by 63% for the wheat seasons, and by 60% for the maize seasons (**Figure 6**). However, constrained by limited water resources in the region, the current irrigation amounts are less than 300 mm for wheat, and little or no irrigation for maize. This amount of available water can only sustain an autoirrigation triggered at 40% and recharged to 60% field capacity and produce a potential wheat yield of 76% and a potential maize yield of 86%. At this irrigation level, the N application rate should be reduced to between 100 and 200 kg N ha^{-1} for wheat, to match the limited available irrigation water resource in the region for efficient use of N and water and minimal nitrate-N leaching loss (**Figure 6**). For maize, irrigation was not necessary due to adequate rainfall, and 100 kg N ha^{-1} per crop application rates are reasonable considering the high risk of nitrate-N leaching potential (**Figure 6**).

Thorp *et al.* (2006) used the calibrated CERES-Maize model to prescribe N rate for a heterogeneous field in Iowa, USA, using long-term weather data (37 years) to study maize production and N leaching risks at different levels of precision nitrogen (N) management. The value in using long weather records could be expanded to discuss risk assessments of decision making and probabilities of 'success.' Nitrogen was applied uniformly in the spring; for each rate of application, the field was divided into 100 grid cells and the model was run for each cell for 37 years. To maximize farmers' net returns, an average of 56.2 kg N ha^{-1} overall grid cells was left in the soil as residual N, which was subjected to leaching (**Figure 7**). To achieve an average residual soil N at harvest under 40 kg ha^{-1} in 80% of the growing seasons, the producer's opportunity

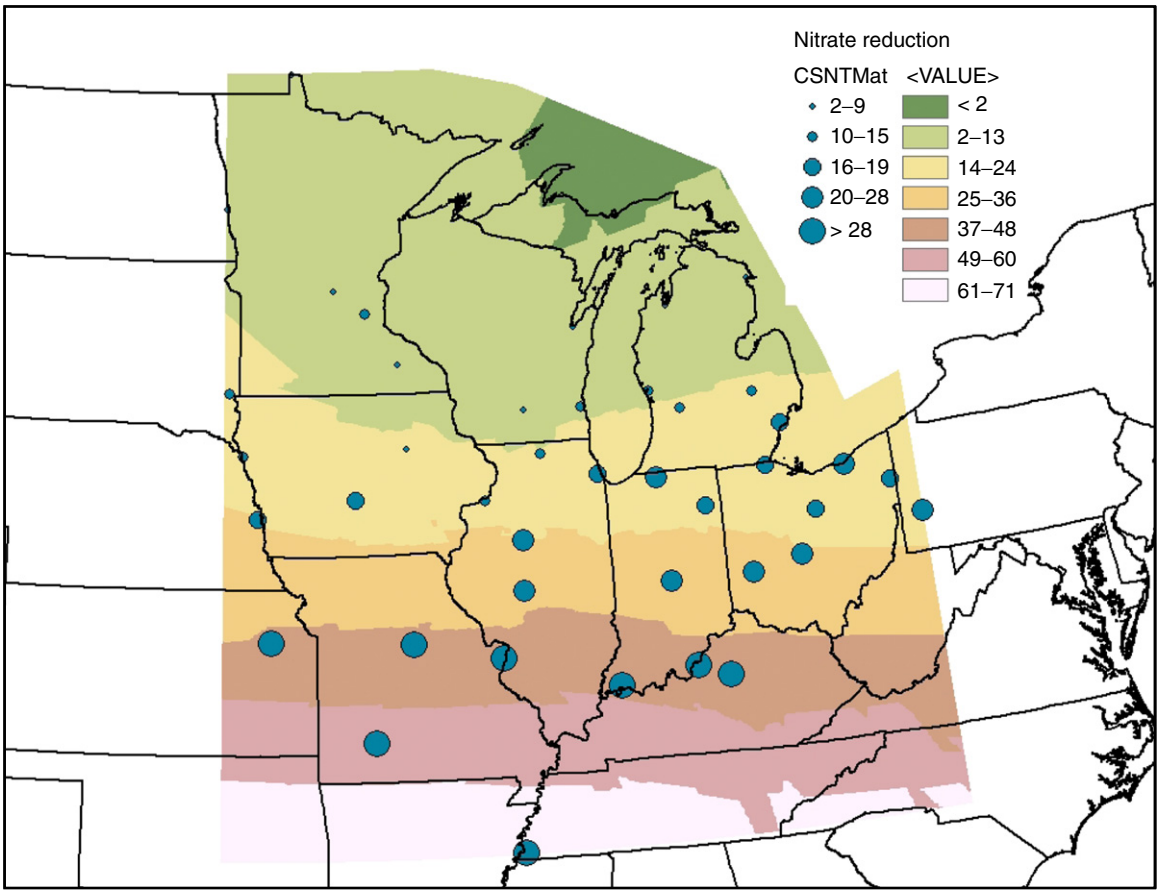


Figure 3 RZWQM2 model used to calculate annual nitrate reduction in tile water by cover crop in the US Midwest region (kg N ha^{-1} $year^{-1}$). Reproduced with permission from Malone, R.W., Jaynes, D.B., Kaspar, T.C., *et al.*, 2014. Cover crops in the upper Midwest USA: Simulated effect on nitrate leaching with artificial drainage. Journal of Soil and Water Conservation.

cost that reduced the maximum return was estimated to be US \$48.12 ha^{-1} (Figure 8).

Model Applications to Optimize Water Use in Crop Production

The use of irrigation system models to estimate crop yield responses to water in general and to allocate limited water resources is widely documented in the literature. The use of the detailed soil–water–plant growth–climate system models for optimizing the use of available water through optimum rates and times of irrigation application is relatively new, but is improving and making progress.

Optimizing the Use of Limited Water through Irrigation Scheduling

One approach for optimizing limited water is by scheduling irrigation at the right time and in amounts to match the crop–water demand. However, this scheduling will vary from year to year due to variations in timing and amount of rainfall and other weather conditions that determine the crop demand. At any location, the models can be run over a long time period of historical weather conditions to help devise optimum scheduling over this period and assess risks. The value in using long weather records could be expanded to discuss risk assessments of decision making and probabilities of 'success.' Figure 9 shows the evaluation of decision support systems for agrotechnology transfer (DSSAT) version 4.0 CERES-maize model against multiyear experimental data for the response of corn to different water levels at Akron, CO, USA. The model provided a good synthesis of the data. This field-tested model was then used to create a graph of corn yield for different amounts of controlled water applications during the entire growth period to aid optimal management of limited water for three different scenarios, run over 90 years of weather data, at Akron, CO, USA (Saseendran *et al.*, 2008). The initial soil water content at planting was assumed to be what is commonly observed at Akron; the top 30 cm of soil was at field capacity, and deeper depths at half the field capacity. The response to water applications was studied at two N levels, a fixed amount of N (168 kg ha^{-1}) denoted as 'with N stress' and with assumed 'No N stress' in the crop model. The data points in Figure 10 are mean values over 90 years of weather and the vertical bars on the data indicate one standard deviation of simulated points around the mean. The yield

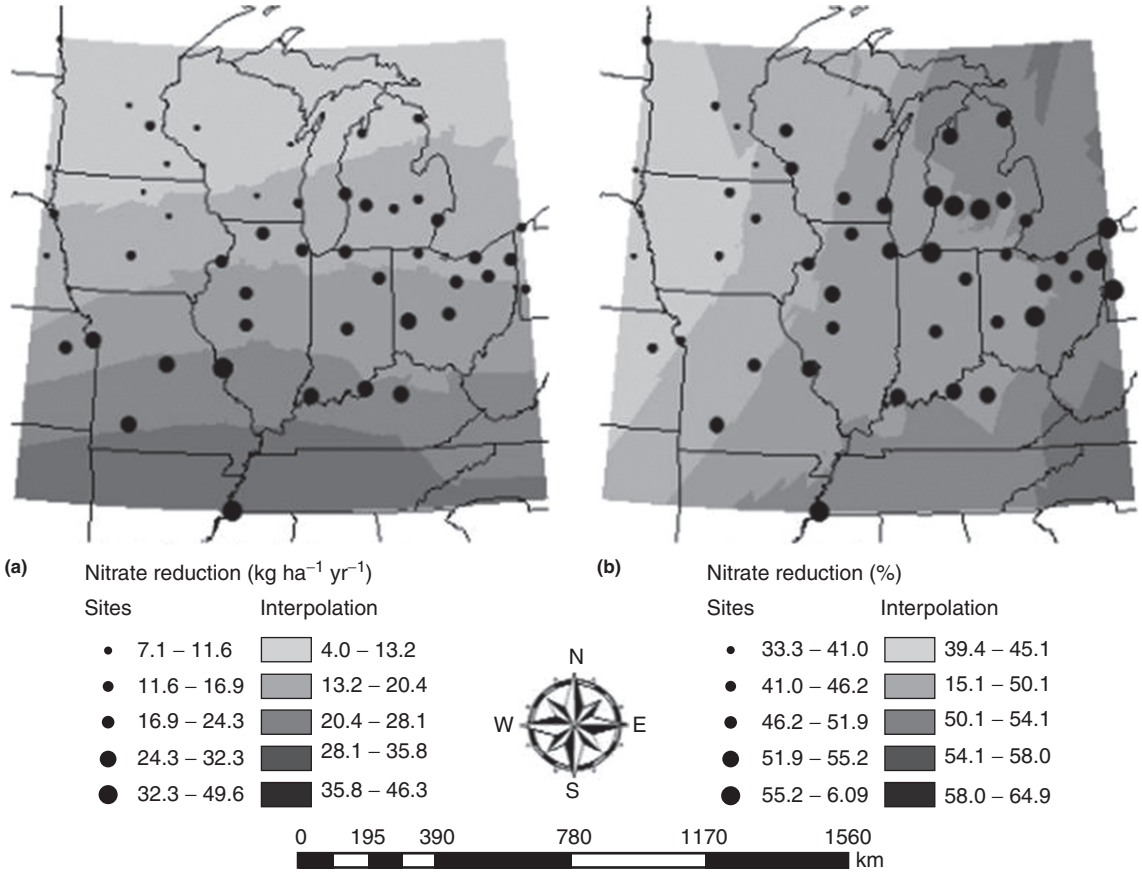


Figure 4 RZWQM2 used to calculate annual nitrate reduction in tile water by 'controlled' drainage in the US Midwest region (kg N ha^{-1} year^{-1}). Reproduced with permission from Thorp, K.R., Jaynes, D.B., Malone, R.W., 2008. Simulating the long-term performance of drainage water management across the Midwestern United States. Transactions of the ASABE 51 (3), 961–976.

increased with water application level, up to a maximum at approximately 400 mm of water application, and started to decrease thereafter due to N leaching in the 'with N stress' treatment, whereas it leveled off with 'No N stress' (Figure 11). In one of the water application scenarios (50%V and 50%R), half of a given total amount of water was applied during the vegetative growth stages and the other half during the reproductive growth stages. In another scenario (20%V and 80%R), the same total amount of water was split in a way that 20% was applied during the vegetative growth stages and 80% during the reproductive stages; in the third scenario, the split was 40% during the vegetative stages and 60% during the reproductive stages. The 20–80 split was the best as an average over the years, although the results depended on weather from year to year, as indicated by the vertical bars. A corresponding graph was generated for nitrogen balance components – plant uptake, leaching below the root zone, and residual in soil, at different irrigation levels for each scenario (Figure 11).

The N uptake by the crop had the same trend of variation with water levels as the yield in Figure 10. It increased with water level up to a maximum of approximately 400 mm water application, and did not change much thereafter. The N leaching increased mildly with water level up to 400 mm level, and then more rapidly. The residual N left in soil at the end of the growth period decreased with water level. The 20:80 split application of water had the least leaching of N as compared with 50:50 and 40:60 splits. The graph in Figure 11 can be used to optimize the amount of N application with respect to the amount of water available and expected crop yield, instead of applying the same N amount for each year, irrespective of rainfall or irrigation water available. The optimization of N application will save the farmer's input costs and minimize effects on groundwater quality by reducing leaching during the growth period or reducing the residual N subject to leaching during fall and winter. The graphs in Figures 10 and 11 help both research and management for optimizing the use of water and nutrients.

Optimizing Water Productivity of Limited Water by Applying Water at Sensitive Growth Stages and Rationing Water between Crops in China

Fang *et al.* (2010) applied the RZWQM2 model to a double-cropping system (wheat–maize) in the NCP, using historical long-term weather data. They found that a higher wheat yield could be obtained when a single irrigation was applied at the stem extension stage than when it was applied at booting or grain filling stage. These results indicated that the stem extension stage was the most sensitive growth stage of wheat to

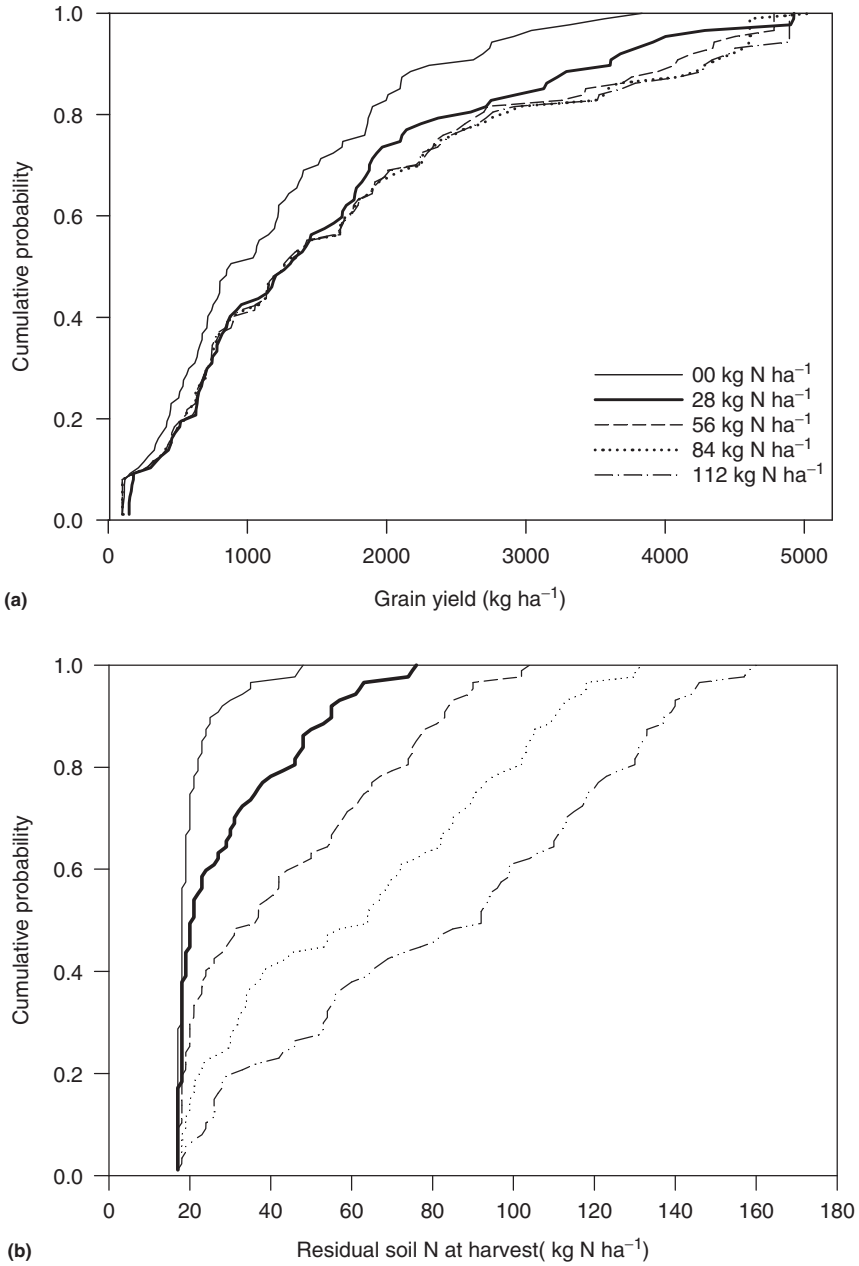


Figure 5 Cumulative probability distribution function plots of winter wheat grain yields and residual soil N at harvest simulated by CERES-wheat model under different N application rates. N was broadcast and the crop was planted every year. Reproduced with permission from Saseendran, S. A., Nielsen, D.C., Ma, L., Ahuja, L.R., Halvorson, A.D., 2004. Modeling nitrogen management effects on a winter wheat cropping system using RZWQM and CERES-wheat. Agronomy Journal 96, 615–630.

water stress. However, in short-term field experiments, the most sensitive stages of wheat to water stresses were extended from stem extension to grain filling stage. Higher crop yield and water-use efficiency (WUE) could be obtained when two irrigations were applied at stem extension and booting stages than applied at other stages. These higher yield and WUE treatments also had lower deep drainage and N leaching. Irrigation for maize was generally unnecessary except when the initial soil water is too low for germination.

Another long-term simulation was designed to optimize the limited water between wheat and maize seasons for high WUE and minimum drainage. Water distribution between the wheat and maize seasons was tested at six ratios: 50:50; 60:40; 70:30; 80:20; 90:10; and 100:0, for each of the four assumed total amounts of water available, applied at different growth stages (Fang *et al.*, 2010). Wheat yields increased linearly with the distribution ratios varying from 50:50 to 100:0 (**Figure 12**), whereas maize yield decreased slightly. The WUE of wheat increased with the irrigation ratio from 50:50 to 100:0 at 100 and 150 mm available water, whereas at 200 and 250 mm available water level, WUE reached the highest values at ratios of 80:20 and 60:40, respectively. For maize, WUE

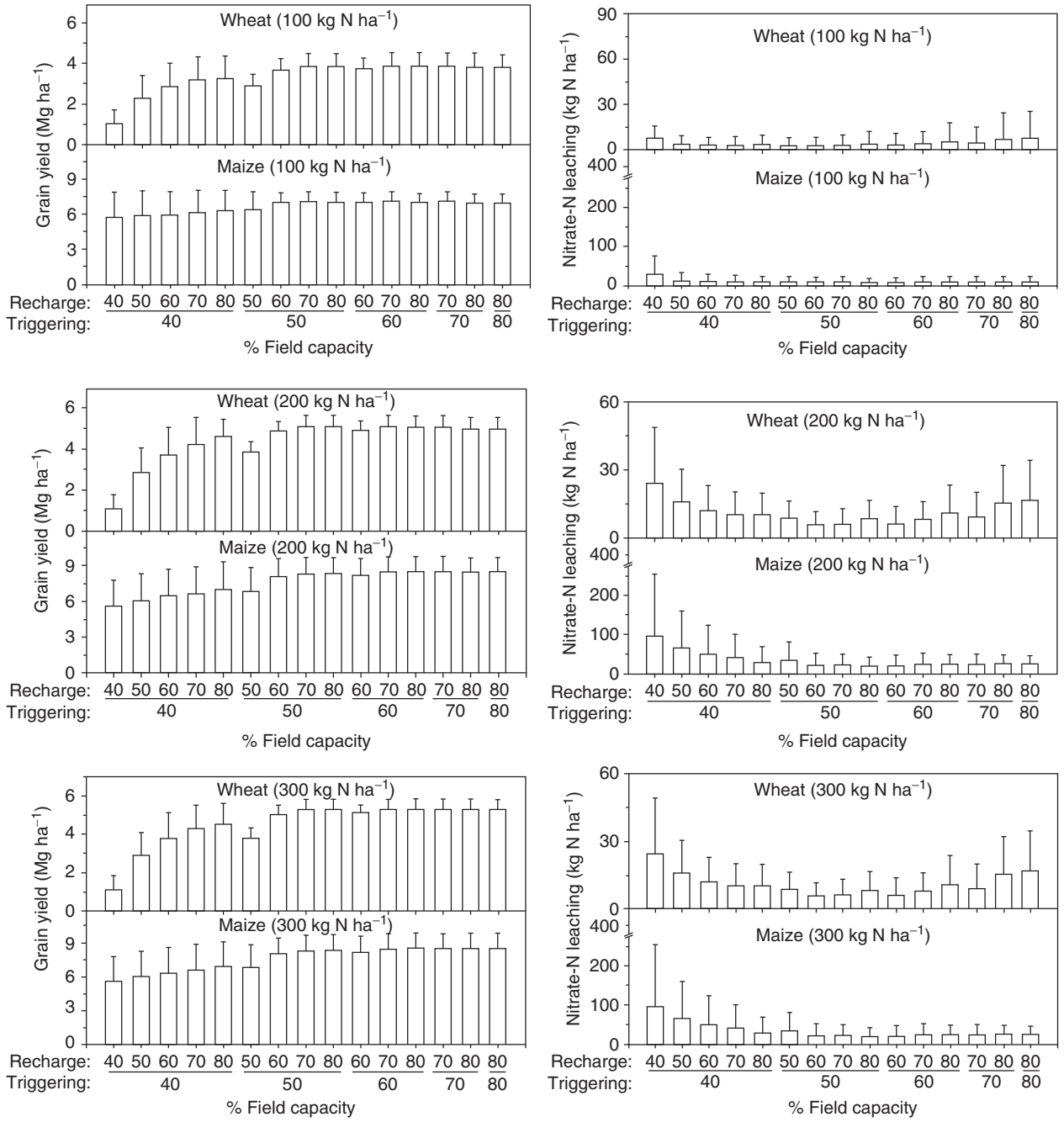


Figure 6 Average grain yields and nitrate-N leaching across seasons under irrigations triggered at varying levels of % field capacity (FC) and stopped after root zone recharge to selected levels of %FC and at different N application rates (100, 200, 300 kg N ha^{-1} per season) simulated by RZWQM2 from 1961 to 1998. Bars indicate +1 standard derivation across 38 years of simulation (1961–98). Reproduced with permission from Fang, Q., Ma, L., Yu, Q., *et al.*, 2008. Modeling nitrogen and water management effects in a wheat-maize double-cropping system. Journal of Environmental Quality 37, 2232–2242.

increased slightly with the irrigation ratio varying from 50:50 to 100:0 and with a decrease in available water from 250 mm to 100 mm (Figure 12).

Combining both wheat and maize seasons in a year, wheat and maize yields and WUE were maximum at the distribution ratio of 80:20 at both 200 and 250 mm available water. Drainage and N leaching were the lowest for the distribution ratio of 80:20 at 100, 150, and 250 mm available water and the lowest for the distribution ratio of 90:10 at 200 mm available water. Therefore, it can be concluded that the most reasonable distribution ratio for available water between the wheat season and the maize season was 80:20 at the four limited available water levels to obtain the highest crop yield and WUE and the lowest water drainage.

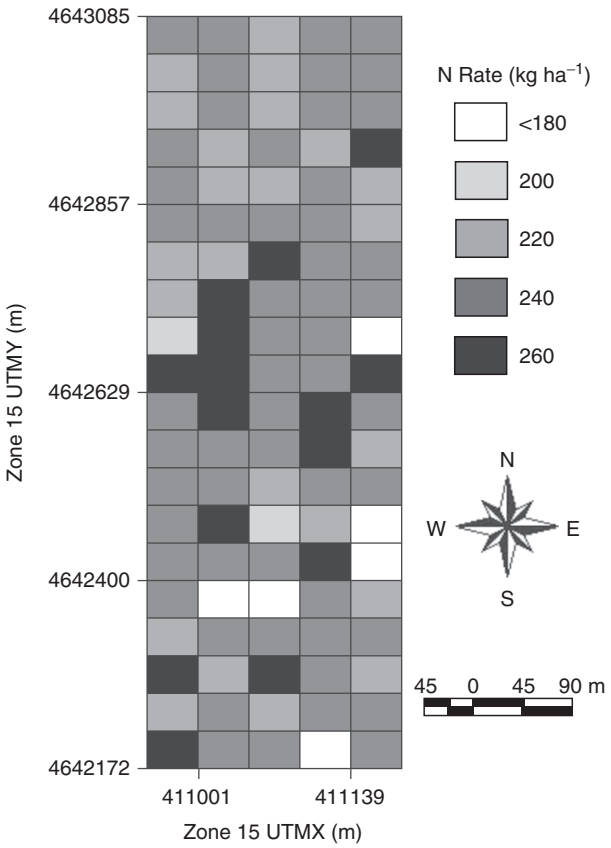


Figure 7 Nitrogen prescription for maximum farmer's profit in a variable land area that left an average 56.2 kg N ha^{-1} of unused N at harvest in IA, USA. Reproduced with permission from Thorp, K.R., Batchelor, W.D., Paz, J.O., Steward, B.L., Caragea, P.C., 2006. Methodology to link production and environmental risks of precision nitrogen management strategies in corn. Agricultural Systems 89, 272–298.

Better Water-Use Efficiency through Crop Rotations

The models can be used to help maximize precipitation use efficiency by more intensive cropping, such as adding an appropriate summer crop in the traditional dryland (rainfed) wheat–fallow rotation in the Great Plains of the USA. However, the choice of the summer crop will vary from year to year depending on the soil water stored at planting and the anticipated rainfall during the growing season. The models can be used to determine the choice of the summer in relation to soil water planting over long-term weather conditions at any given location. Figure 13 shows RZWQM2 synthesis of dryland crop production data for four different crop rotations at Akron, CO, USA. The tested model was then used to evaluate the performance of different summer crops for rotation with the primary crop of winter wheat over 97 years of weather conditions, at four different levels of plant available soil water (PAW) during planting of these crops. Figure 14 gives the mean and variance of net return from five different crops at each level of PAW. The forage crops give higher returns than the corn and canola crops at all levels of PAW at the prevailing crop prices at the time of the study. This graph serves as a guide to choose the summer crop in any year based on known PAW and crop prices.

Better Crop Selection and Deficit Irrigation

Figure 15 shows a RZWQM model synthesis of corn response to different levels of limited irrigation at Greeley, CO, USA. The tested model was then used to develop long-term average Crop Water Production Functions (yield vs. water consumed and water applied) for several counties of Colorado (Figure 16). Similar water production functions were obtained for other crops. The authors have used these functions to develop a 'Colorado Water Optimizer' to help farmers with decisions on the best use of limited irrigation water in Colorado, including the options of selecting which crops to irrigate, deficit irrigation of crops, areas irrigated, and leasing water to the Denver municipality or other urban uses.

Evaluating Agricultural Systems and Management Effects on Greenhouse Gas Emissions

In general, agriculture (this excludes emissions from livestock) is a minor to moderate source of greenhouse gas (GHG) emissions. It is generally accepted that N fertilizer is a major contributor to GHG production in an agricultural land. The emission of GHGs from agricultural land, mainly CO_2, N_2O, and CH_4, shows high spatial and temporal variability, associated with agricultural management practices (fertilizer and irrigation application, tillage, cover crop, and cropping system), as well as climate and soil conditions (Liebig *et al.*, 2005; Snyder *et al.*, 2009). Various models have been explored to simulate GHG emissions from soil at laboratory, field, and regional scales (Chen *et al.*, 2008; Pattey *et al.*, 2007). The process-based field-scale models, such as denitrification–decomposition (DNDC; Li *et al.*, 1992), DAY CENTURY (DAYCENT) (Parton *et al.*, 1998), agricultural production systems simulator (APSIM; Probert *et al.*, 1998), and water and nitrogen management model (WNMM; Li *et al.*, 2007), have been most widely used to quantify the effect of alternative agricultural managements on GHG emissions across different time and spatial scales.

The DNDC model has been applied worldwide for GHG emission simulation and identifying management strategies for mitigation. In the United States, soil tillage and fertilizer use were the most important farming practices contributing to N_2O emissions at the national scale; even manure applications to corn increased N_2O emissions in Iowa, although it enhanced carbon storage in soils (Li *et al.*, 1996). Farahbakhshazad *et al.* (2008) concluded that no-till practice slightly increased N_2O emissions, but increasing fertilizer application depth with nitrification inhibitor substantially reduced N_2O emissions in central Iowa. However, in a wheat–maize cropping system in North China, manure amendment or crop residue incorporation mitigated GHG emissions from the cropping system (Li *et al.*, 2010). Wang *et al.* (2011) also concluded that residue return was a more efficient method of mitigating GHG emission than decreasing fertilizer N application rate in Northwestern China. However, in an agricultural

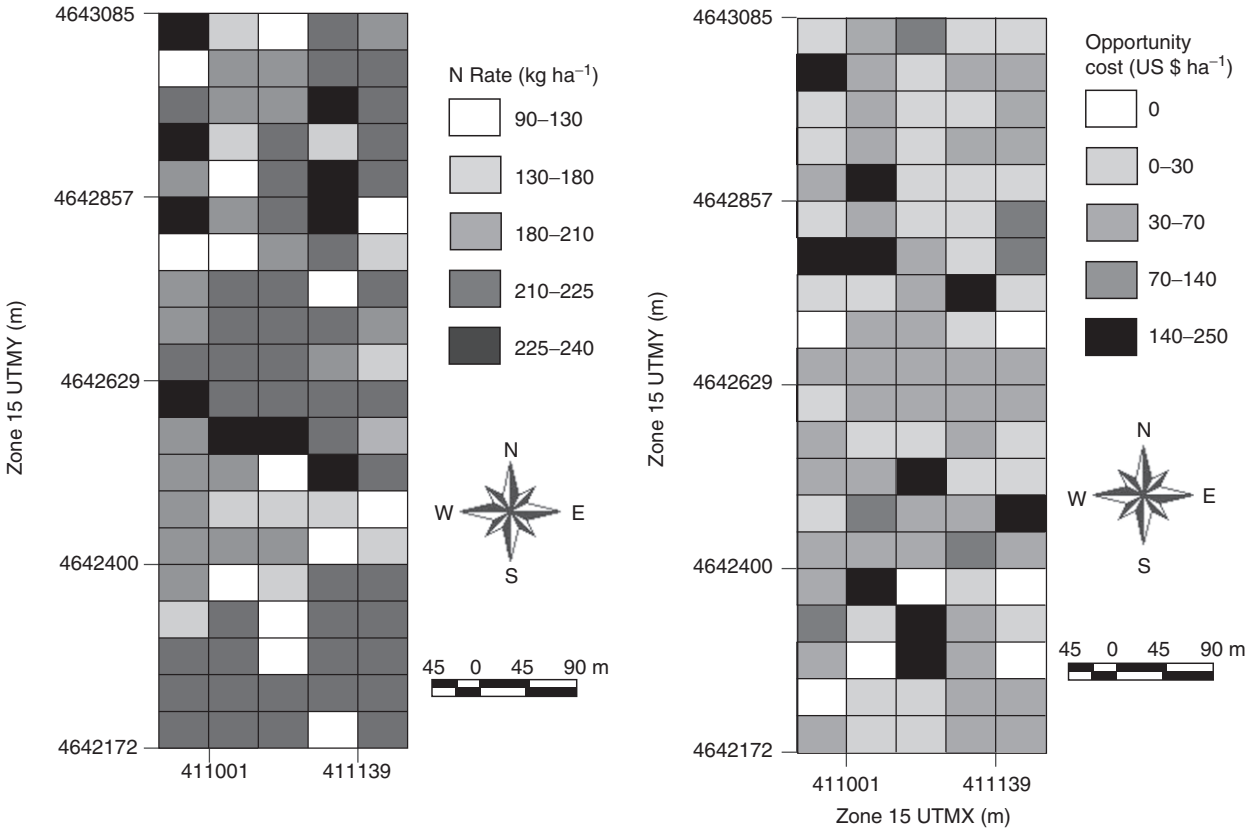


Figure 8 N rate and opportunity cost for leaving less than 40 kg N ha^{-1} of unused N in the soil 80% of the time. Opportunity cost is the additional cost that reduces the maximum profit. Reproduced with permission from Thorp, K.R., Batchelor, W.D., Paz, J.O., Steward, B.L., Caragea, P.C., 2006. Methodology to link production and environmental risks of precision nitrogen management strategies in corn. Agricultural Systems 89, 272–298.

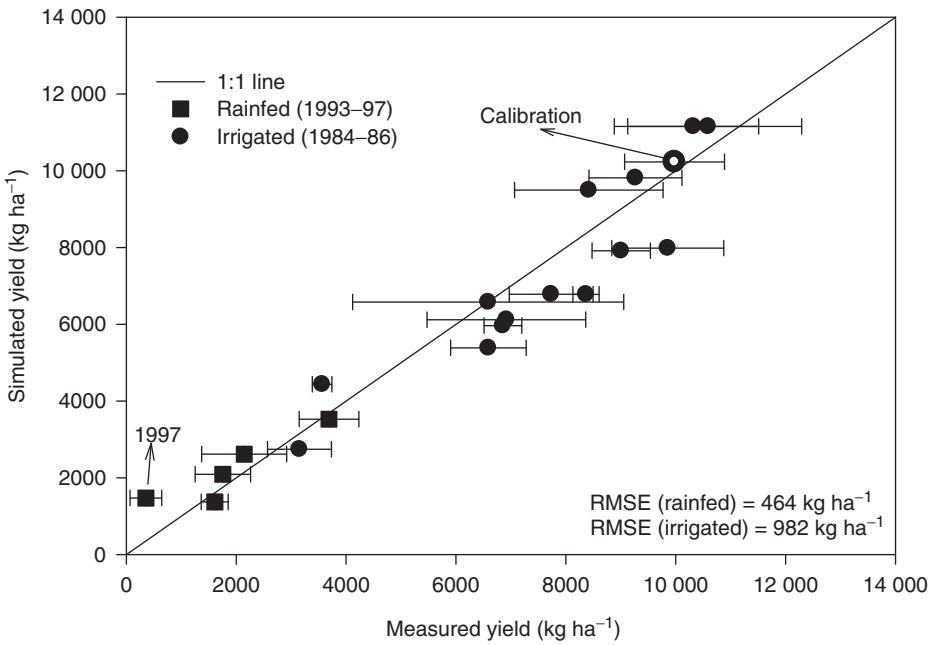


Figure 9 Measured and simulated corn grain yield in the irrigated (1984–86) and rainfed experiments (1993–97) at Akron, CO. Error bars indicate one standard deviation about the mean of the treatment replications. RMSE, root mean square error. Reproduced with permission from Saseendran, S.A., Ahuja, L.R., Nielsen, D.C., Trout, T., Ma, L., 2008. Use of crop simulation models to evaluate limited irrigation management options for corn in a semiarid environment. Water Resources Research 44, W00E02. doi:10.1029/2007WR006181.

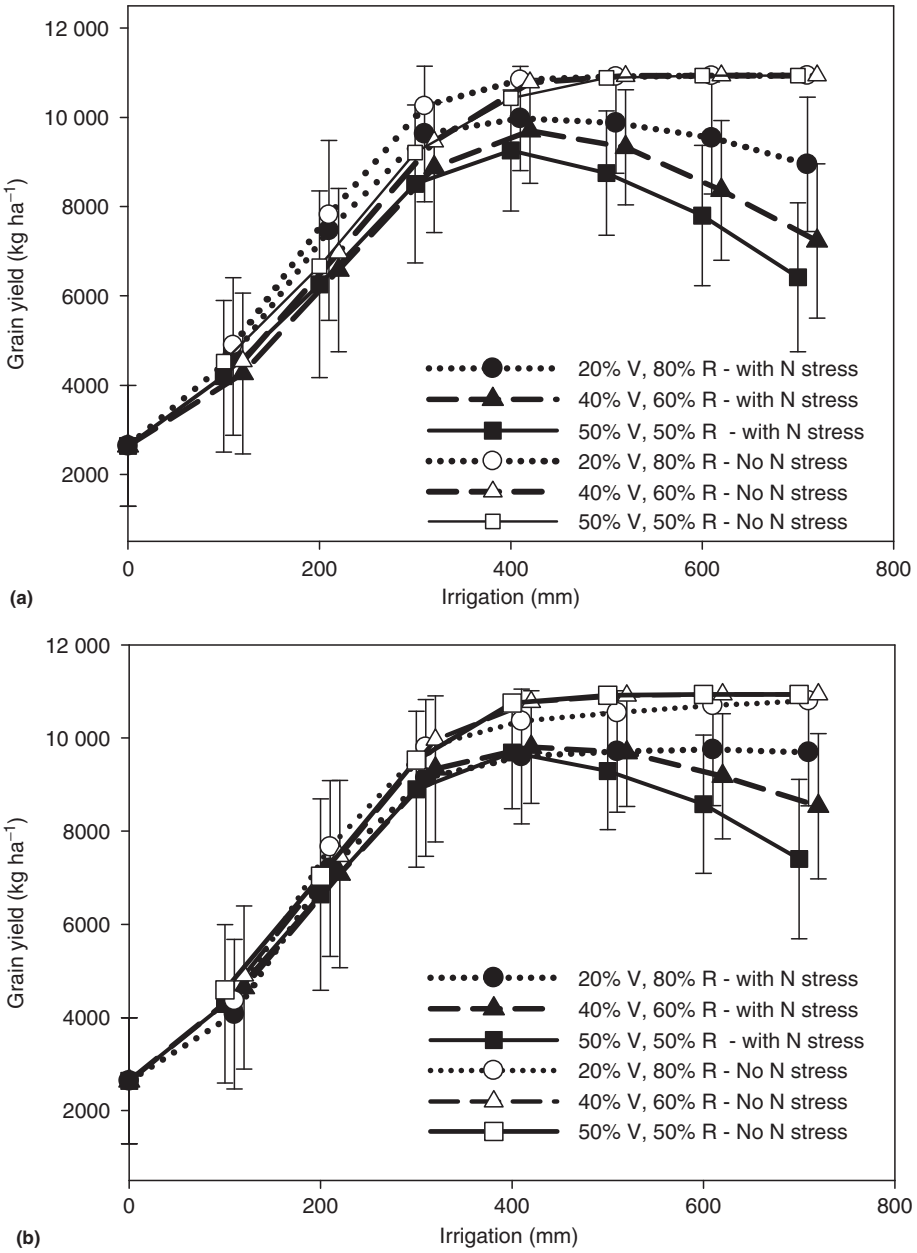


Figure 10 Simulated grain yield response to 100–700 mm irrigations (gross irrigation), split between vegetative and reproductive stages at 20:80, 40:60, and 50:50 with (a) 22 June and (b) 15 July as cutoff dates differentiating between growth stages for corn grown at Akron, CO. Distribution of average seasonal potential evapotranspiration demand between the vegetative and reproductive growth stages was (a) 38:62 and (b) 55:45. Error bars represent one standard deviation from the mean. Deviations of grain yields from the mean value were due to variation in rainfall, temperature, and solar irradiance during the crop growth period from 1912 to 2005. Average crop season rainfall was 284 mm. Reproduced with permission from Saseendran, S.A., Ahuja, L.R., Nielsen, D.C., Trout, T., Ma, L., 2008. Use of crop simulation models to evaluate limited irrigation management options for corn in a semiarid environment. Water Resources Research 44, W00E02. doi:10.1029/2007WR006181.

freeze zone in North China, Ouyang *et al.* (2012) observed that both manure amendment and N fertilizer enhanced the global warming potential (GWP), but the return of residue to the soil was a win-win solution for soil carbon and GWP. In Ireland, Lugato *et al.* (2010) simulated an accumulation of 1100 kg C ha^{-1} of soil organic carbon and lower N_2O emission with conversion of conventional to minimum tillage for maize, whereas residue removal led to high soil C depletion and GHG emissions. Rafique *et al.* (2011) simulated a $\pm$9% and $\pm$17% change in N_2O emissions under $\pm$50 kg inorganic N and slurry N application rate, respectively, which was much lower than the estimated change of 50% based on Intergovernmental Panel on Climate Change (IPCC) default emission factor (EF).

The DAYCENT model is another popular model applied for GHG emission simulations. In the Great Plains, USA, Del Grosso *et al.* (2002) observed that the dryland soils and cropping systems are net sources of GHGs, although they can

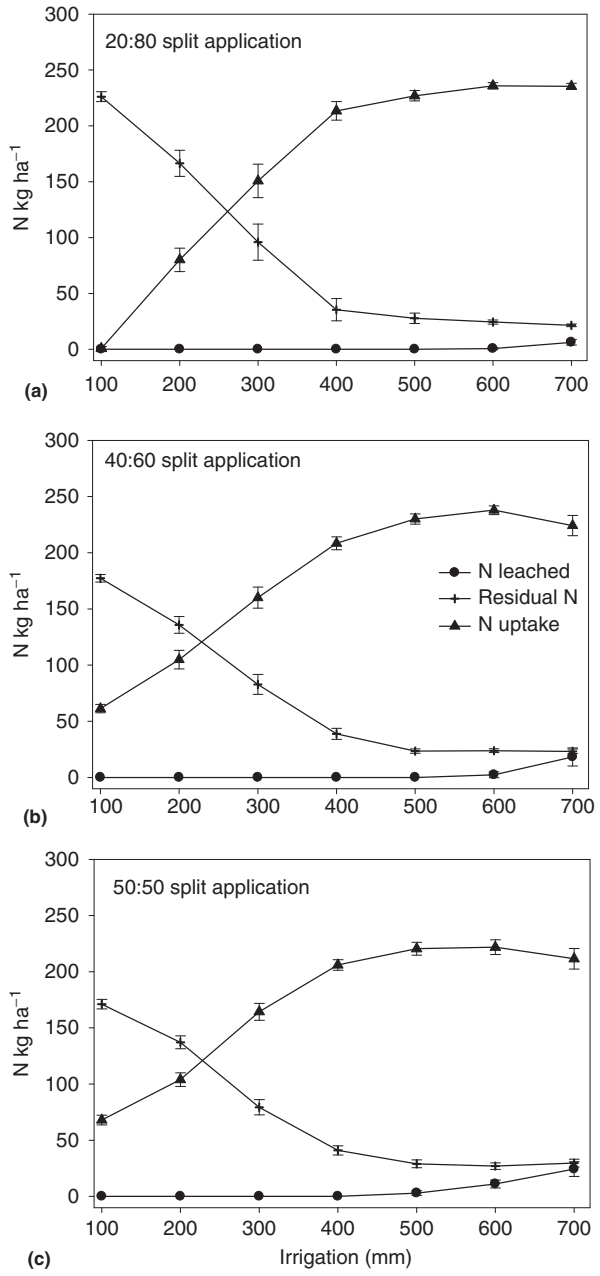


Figure 11 Model-generated N balance components at different levels of water application for corn averaged over 90 years of weather data at Akron, CO, for each scenario of water distribution between growth stages corresponding to the data in **Figure 10** (22 June as the cutoff date differentiating between the growth stages). Again, the vertical bars indicate one standard deviation around the mean values. V, vegetative growth stage; R, reproductive growth stage. Reproduced with permission from Saseendran, S.A., Ahuja, L.R., Nielsen, D.C., Trout, T., Ma, L., 2008. Use of crop simulation models to evaluate limited irrigation management options for corn in a semiarid environment. Water Resources Research 44, W00E02. doi:10.1029/2007WR006181.

be significantly reduced by practicing no-till. By dividing the United States to five regions (**Table 1**), Del Grosso *et al.* (2005) simulated N_2O emission for each region and for each major crop with DAYCENT model and using the EF from the IPCC (**Figure 17**). The biggest GHG emission was from the Central Region that had the biggest area and more fertilizer applications. Results also showed higher N_2O emission from corn and soybean fields compared to cotton, alfalfa, and wheat. Current management practices (1991–2000) produced much more N_2O than pre-1940 management (1921–30) or native vegetation (1591–1600) (**Figure 17**). However, conversion into no-tillage could mitigate 20% of agricultural GHG emissions in the United States (Del Grosso *et al.*, 2005). In a later study at the global scale, they found that nitrification inhibitors led to 10% reduction in N losses, but when combined with no-till, it resulted in 50% reduction in GHG emissions and 7% increase in crop yield (Del Grosso *et al.*, 2009). In California's Central Valley, the model results showed that organic practices had the greatest potential for soil GHG flux reduction, followed by cover cropping and conservation tillage (De Gryze *et al.*, 2010). In another similar simulation study (De Gryze *et al.*, 2011), the results showed that combining various mitigation practices (conservation tillage, winter cover cropping, manure application, and reduced N fertilizer input) led to larger reductions in GHG emissions than the sum of the reductions from individual practices. The combination of winter cover cropping with manure application was particularly efficient in reducing GHG emissions.

These model applications showed complex effects of these various alternative farming management practices across different climate and soil conditions. Process-based models showed great potential for quantifying these complex effects of alternative management on GHG emissions across different soil and climate conditions. However, we need a better understanding of the underlying factors that cause these variations across soils, climates, and management; and identify strategies for mitigation under those conditions. There is a particular need to quantify GHG emissions due to nitrification and denitrification processes. In general, the soil–water–crop management practices that increase crop biomass growth and generate higher carbon residue can potentially increase soil carbon storage to counteract the CO_2 and CHG buildup in the atmosphere (Smith *et al.*, 2007).

Climate-Change Effects on Environment and Crop Production

The likely doubling of atmospheric CO_2 will cause considerable global warming within the twenty-first century. This will very likely increase droughts, heat waves, and floods, and very likely affect agriculture through changes in plant growth rates, evapotranspiration (ET), plant–water relations, plant litter composition, and nitrogen demands (Morgan *et al.*, 2004; Long *et al.*, 2006). The effect of climate change on agriculture at any location will depend on the current climate, soil–plant interactions, the magnitude of change and responses of the crops, and location-specific management. Numerous modeling studies have been conducted to evaluate climate-change effects on crop production in different regions of the globe (Hillel and Rosenzweig, 2011, 2012). Free-air CO_2 enrichment (FACE) experiments, combined more recently with temperature treatment, provide direct evidence of climate-change

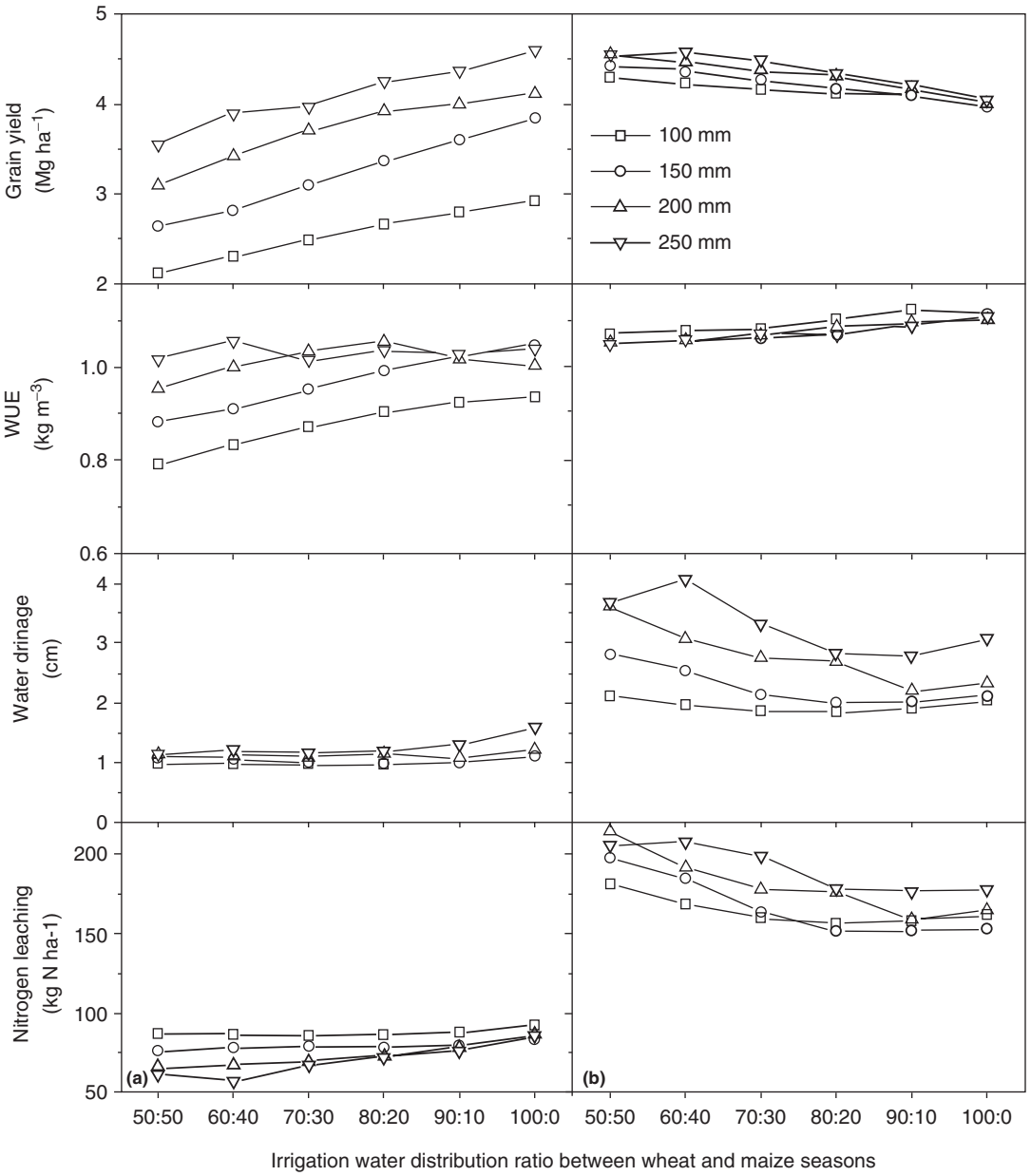


Figure 12 Grain yield, water-use efficiency (WUE), water drainage, and N leaching for wheat (a) and maize (b) seasons at the four limited available water levels (100 mm, –□–; 150 mm, –○–; 200 mm, –△–; 250 mm, –▽–), split between wheat and maize seasons at various ratios. Simulations were made with RZWQM2 from 1961 to 1999. Water was applied at selected growth stages for each crop. Reproduced with permission from Fang, Q.X., Ma, L., Yu, Q., *et al.*, 2010. Irrigation strategies to improve the water use efficiency of wheat-maize double cropping systems in North China Plain. Agricultural Water Management 97, 1165–1174.

effects on crop production in the short term (Kimball *et al.*, 1999, 2002).

Evaluating Future Climate-Change Effects on Crop Production in Specific Regions

Using RZWQM2, Ko *et al.* (2010) were able to simulate the effect of elevated CO_2 on spring wheat growth under various water and N levels from 1992 to 1997 for the FACE study in Maricopa, AZ, USA. With projected CO_2 concentration of 550 ppm in the year 2050 and projected weather from 16 general circulation models (GCMs), they found that the beneficial effects of elevated CO_2 on crop growth were counterbalanced by temperature increase for most of the GCM-projected scenarios. However, precipitation had little effect on crop growth due to smaller projected changes. In a later study to evaluate climate-change impact on dryland crop rotations of wheat–fallow, wheat–corn–fallow, and wheat–corn–millet in the Central Great Plains, USA, Ko *et al.* (2012) found that wheat yield decreased under the projected climate-change scenarios, but not significantly. However, corn and millet

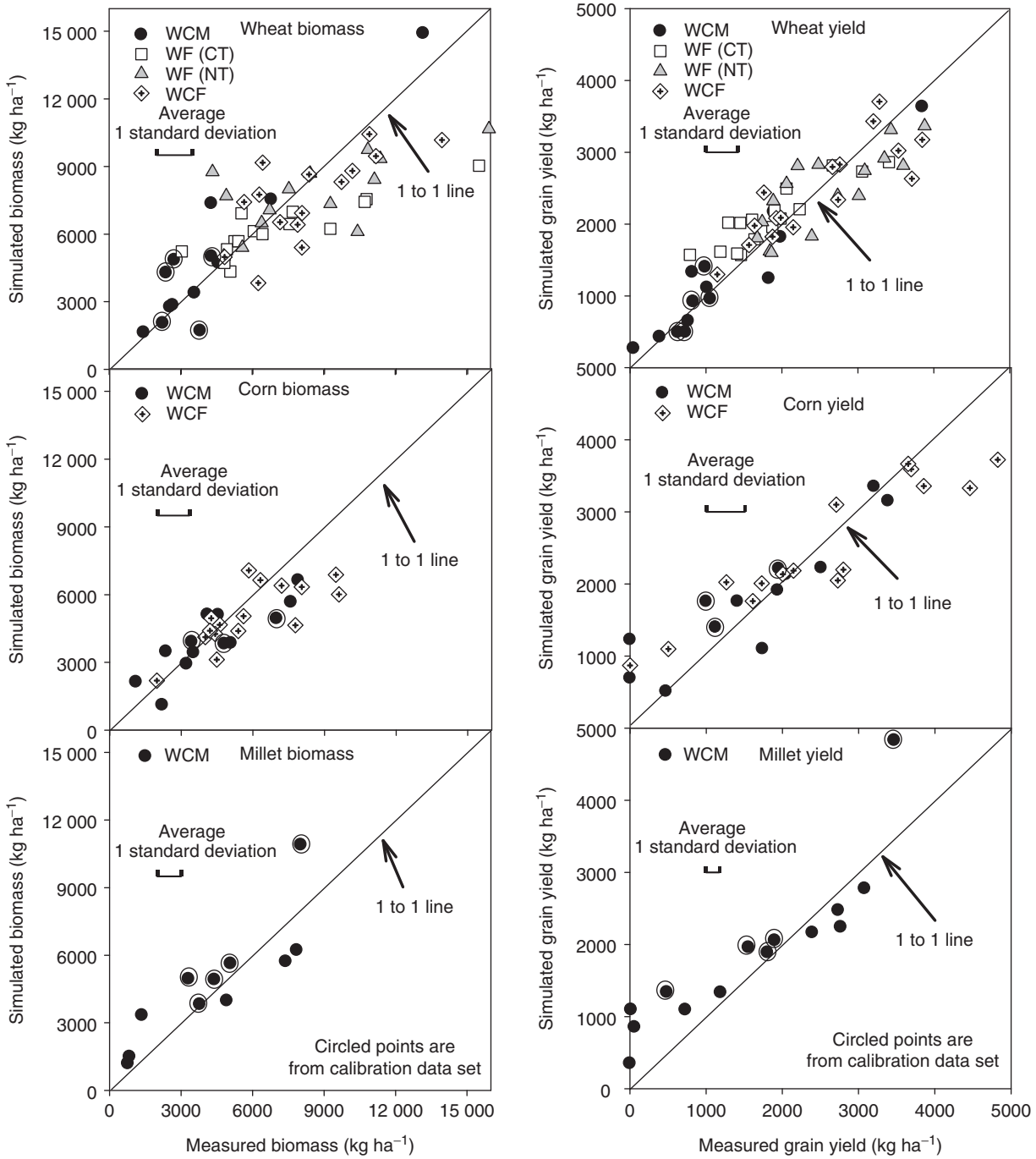


Figure 13 RZWQM modeling of 17–18 years data for biomass and grain yield for wheat, corn, and millet crops from four different rotations at Akron, CO, USA. WCM, wheat–corn–millet; WF, wheat–fallow; and WCF, wheat–corn–fallow. Reproduced with permission from Saseendran, S.A., Nielsen, D.C., Ma, L., Ahuja, L.R., Vigil, M.F., 2010. Simulating alternative dryland rotational cropping systems in the central Great Plains with RZWQM2. Agronomy Journal 102, 1521–1534.

yields decreased significantly, so did the transpiration. Overall, the projected negative effects of rising temperature on crop production dominated over any positive impacts of atmospheric CO_2 increases in these dryland cropping systems (Ko *et al.*, 2012). A similar conclusion was drawn by Islam *et al.* (2012) with irrigated corn, who found that the yield decrease was linearly related to the shortening of the growing period caused by increased temperature.

Chavas *et al.* (2009) examined the potential climate-change impacts on the productivity of canola, corn, potato, rice, and winter wheat in Eastern China. The historical baseline (1961–90) climate and climate change obtained from the

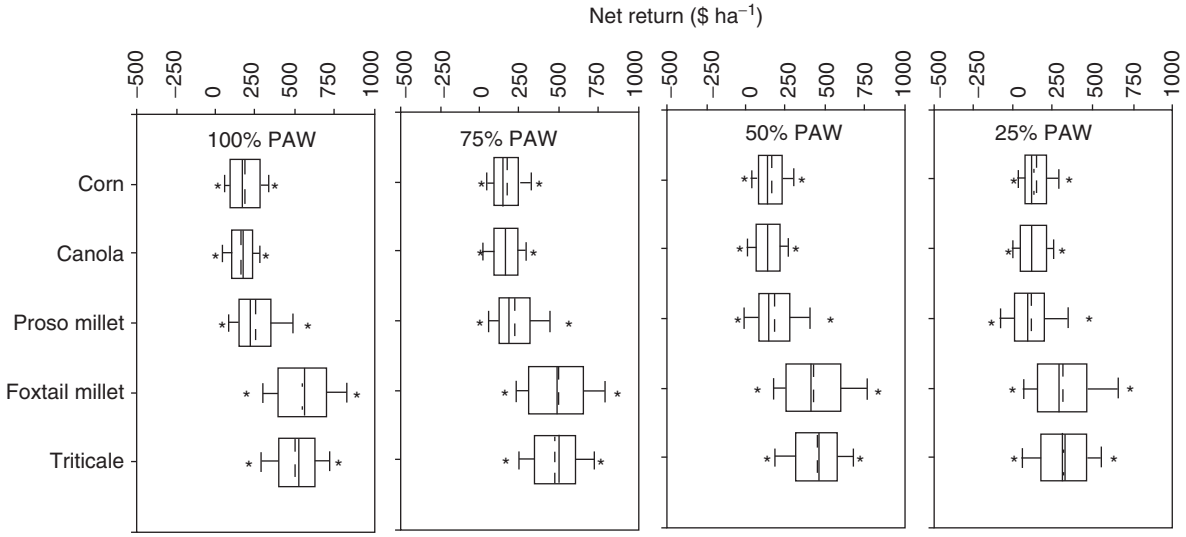


Figure 14 Validated RZWQM2 with long-term weather data generated this graph of Net Return for five summer crops (corn, canola, proso millet, foxtail millet, and triticale), as a guide for summer crop selection in a wheat–summer crop–fallow rotation in Colorado and the Central Great Plains, based on100, 75, 50, and 100% plant available water (PAW) at planting. Reproduced with permission from Saseendran, S.A., Nielsen, D.C., Ahuja, L.R., Ma, L., Lyon, D.J., 2013. Simulated yield and profitability of five potential crops for intensifying the dryland wheat-fallow production system. Agricultural Water Management 116, 175–192.

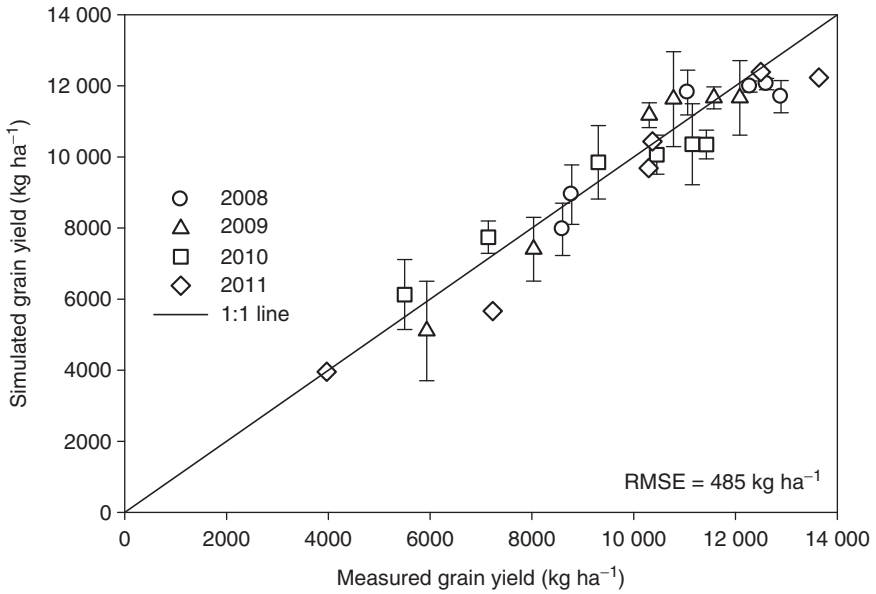


Figure 15 Comparisons of simulated and measured corn grain yields in the limited irrigation trials conducted at Greeley, CO, from 2008 to 2010. RMSE, root mean square error. Reproduced with permission from Saseendran, S.A., Nielsen, D.C., Ahuja, L.R., Ma, L., Lyon, D.J., 2013. Simulated yield and profitability of five potential crops for intensifying the dryland wheat-fallow production system. Agricultural Water Management 116, 175–192.

International Centre for Theoretical Physics RegCM3 regional climate model for future (2071–2100) periods under A2 emission scenario conditions of the Intergovernmental Panel on Climate Change, Special Report on Emission Scenario (Intergovernmental Panel on Climate Change (IPCC), 2007) were used as input for the environmental policy integrated climate agroecosystem simulation model. Results have indicated that in key present-day crop production zones, corn and winter wheat yields may increase substantially, potato yields decline substantially, canola yields remain relatively constant, and rice yields may decrease inland and increase toward the coast. Mo *et al.* (2009) used the vegetation interface processes model to evaluate responses of winter wheat–summer maize double-cropping system in the NCP to future climate scenarios of twenty-first century projected by the HadCM3 GCM under A2 and B1 emission scenarios. Results have indicated that the winter wheat yield will significantly increase with a maximum increase of 19% occurring under the A2 emission scenario

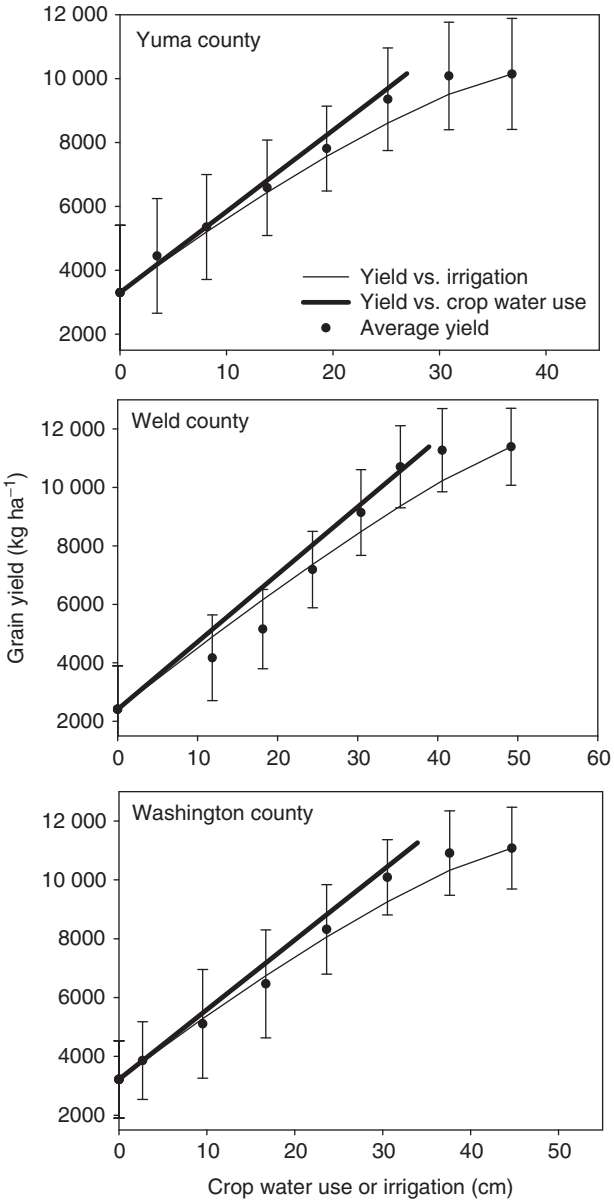


Figure 16 RZWQM with long-term weather data was used to generate these corn water production functions for three Colorado counties for use in the Colorado Water Optimizer to guide deficit irrigation and crops to irrigate. Reproduced with permission from Saseendran, S.A., Nielsen, D.C., Ahuja, L.R., Ma, L., Lyon, D.J., 2013. Simulated yield and profitability of five potential crops for intensifying the dryland wheat-fallow production system. Agricultural Water Management 116, 175–192.

Table 1 Regional Characteristics of DAYCENT simulations for the US

Major regions	*Minor regions*	*Crop simulated*	*Crop area simulated (Mha)*
Northeast	WI, MI, NY, VT, NH, ME, RI, CT, MA, NJ, and DE	Hay, corn, and soybean	7.2
Central	PA, WV, KY, TN, OH, IN, IL, IA, MO, and MN	Corn, soybean, and hay	47
Southeast	VA, MD, NC, SC, GA, FL, AL, MS, LA, and AR	Corn, soybean, hay, rice, and cotton	11
Southwest	OK, TX, NM, AZ, UT, NV, and CA	Corn, soybean, hay, rice, cotton, wheat, and sorghum	18.6
Northwest	KS, NE, SD, ND, CO, WY, MT, ID, OR, and WA	Corn, soybean, hay, wheat, and barley	39.4

Abbreviations: DAYCENT, DAY CENTURY.

Source: Reproduced with permission from Del Grosso, S.J., Mosier, A.R., Parton, W.J., Ojima, D.S., 2005. DAYCENT model analysis of past and contemporary soil N_2O and net greenhouse gas flux for major crops in the USA. Soil and Tillage Research 83, 9–24.

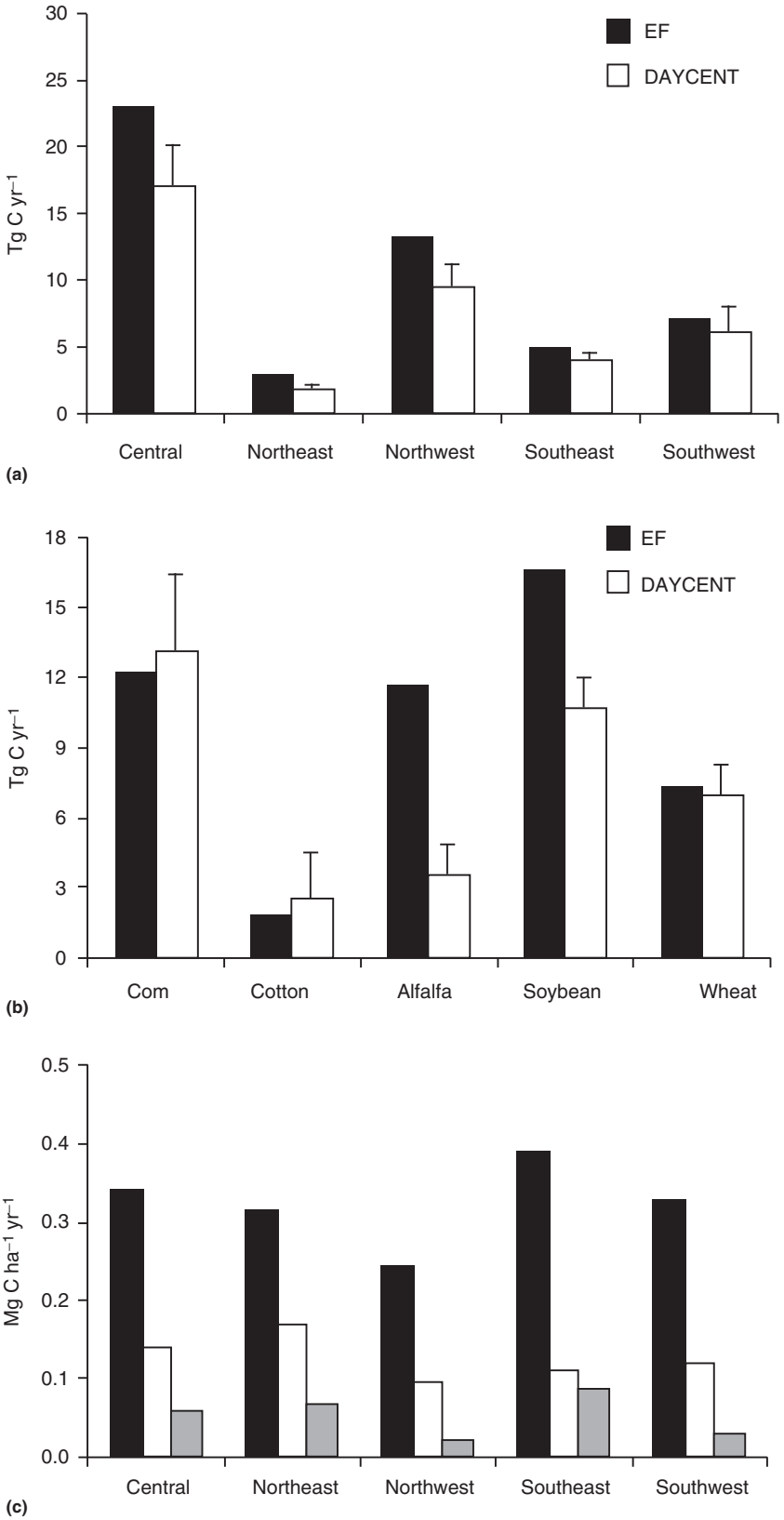


Figure 17 Simulated total N_2O with IPCC emission factor (EF) and DAYCENT model for (a) five regions in the United States, (b) five major crops in the United States, and (c) three management systems (from left to right, current management, pre-1940 management, and native vegetation). Results are 10-year mean and standard deviation in units of CO_2-C equivalents. Reproduced with permission from Del Grosso, S.J., Mosier, A.R., Parton, W.J., Ojima, D.S., 2005. DAYCENT model analysis of past and contemporary soil N_2O and net greenhouse gas flux for major crops in the USA. Soil And Tillage Research 83, 9–24.

during the 2070s, whereas under B1 emission scenario the maximum increase will be 13% during the 2060s. Comparatively, summer maize yield will gently decline by 15% and 12% under A2 and B1 emission scenarios, respectively. As ET is expected to increase by approximately 10% after the 2050s, a lower WUE (with relative changes of more than 25%) under both the scenarios were simulated for the 2090s. Climate-change effects on crop production also depend on soil water and soil N status. Daccache *et al.* (2011) simulated the potato crop under climate change for emissions scenarios A1FI and B1 for the 2050s, including CO_2 fertilization effects, with the SUBSTOR-Potato model included within the DSSAT. The yields showed only marginal increases of 3–6% due to the CO_2 effect because of limitations in nitrogen availability. In contrast, future potential yields, without restrictions in water or N, increased by 13–16%.

However, the predicted climate-change effects depend on the location, GCM scenarios used, and crop growth model. As there is large uncertainty associated with the GCM projected climate-change scenarios, it is very difficult to compare two climate-change studies in the literature. To overcome this uncertainty, the use of multimodel ensembles is better to project future climate. In a recent study of irrigated corn in the Great Plains of the USA, Islam *et al.* (2012) used an ensemble of 112 bias corrected and spatially disaggregated GCM projections at 1/8° spatial resolution for the period 1950–2099 and then ran the RZWQM2 model for the prediction of corn production in future climates. Simulation using the RZWQM2 model with the ensembles showed decreases in irrigated corn yield during 2020, 2050, and 2080 with changes in temperature. As shown in Figure 18, the changes in temperature (T) resulted in the same probability distribution curve as that of with changes in both temperature and precipitation (T + P; one overlapping the other in the figure.). Similarly, changes in precipitation (P) resulted in the probability distribution curves similar to that of the baseline (base) probability distribution curve. Thus, the changes in precipitation had no effect on yield because with full irrigation, 100% consumptive use demand was met by irrigation. When CO_2 fertilization effect (T + P + CO_2) was considered, there was less reduction in yield (Figure 18).

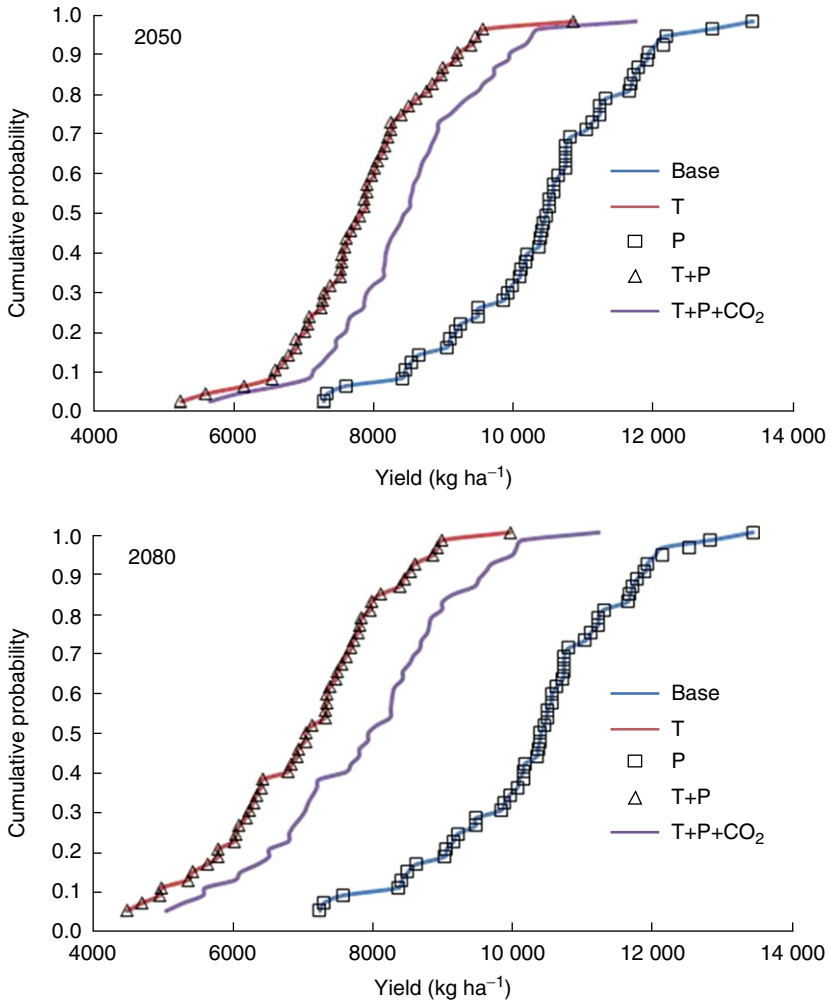


Figure 18 Cumulative distribution function (CDF) of corn yield in response to changes in temperature (T), precipitation (P), and CO_2 in future years over the baseline years for S1 (for an ensemble of 112 projections) scenario, at Greeley, CO, USA. Reproduced with permission from Islam, A., Ahuja, L.R., Garcia, L.A., *et al.*, 2012. Modeling the impacts of climate change on irrigated corn production in the Central Great Plains. Agricultural Water Management 110, 94–108.

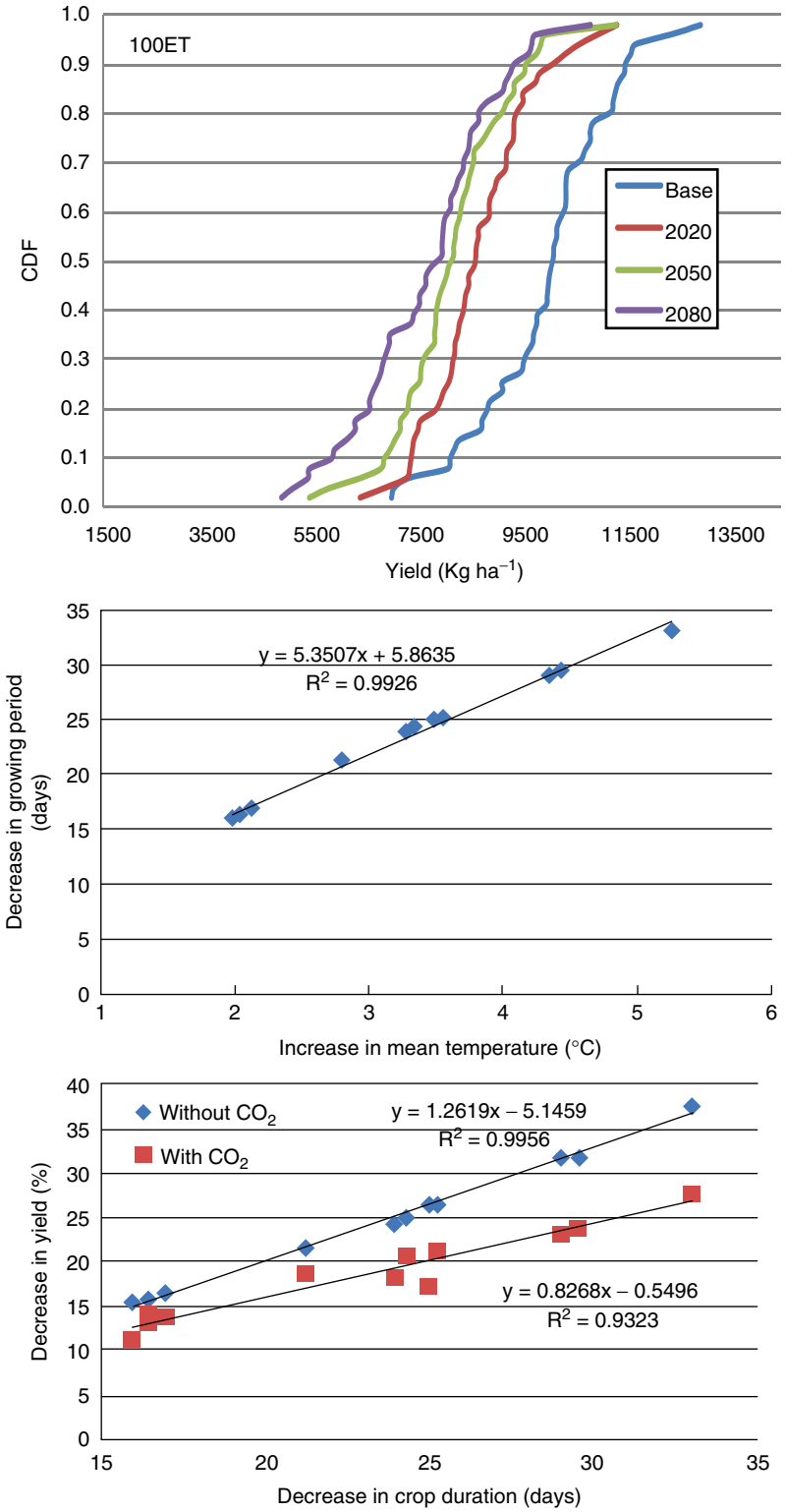


Figure 19 Effect of climate change on the cumulative distribution function (CDF) of fully irrigated corn yield (top); relationship between crop maturity duration with increase in temperature in all scenarios (middle); and relationship between mean decrease in crop yield with decrease in duration (bottom). Reproduced with permission from Islam, A., Ahuja, L.R., Garcia, L.A., *et al.*, 2012. Modeling the impacts of climate change on irrigated corn production in the Central Great Plains. Agricultural Water Management 110, 94–108.

Figure 19 shows climate-change effects on the probability distribution (cumulative distribution function (CDF), stemming from interannual variability) of fully irrigated corn production in CO, USA (Islam *et al.*, 2012). The yield decreased in future years. Additional simulation study also revealed that the relative decrease in corn yield due to climate change was smaller under deficit irrigation than under full irrigation. Simulated yield decreases were closely related to reduction in maturity duration of the crop, and the yield was inversely related to the number of days with maximum temperatures above the upper optimum for corn (32° C) (Figure 19). These results indicated that higher temperatures speed up crop maturity and may also directly decrease growth.

Exploring Adaptations to Climate Change

Models are also being used to study adaptations to climate change through cultivar changes and management practices. Using the APSIM model, Bassu *et al.* (2011) simulated a wheat variety with triticale traits and showed that some of the triticale traits increased wheat yield in the future climate-change scenarios. Gouache *et al.* (2012) studied impacts of heat stress during grain filling of wheat under climate change by coupling downscaled weather scenarios from the Action de Recherche Petite Echelle Grande Echelle climate model with a modified version of the ARCWHEAT phenology model. They also explored the effects of different agronomic solutions: earlier sowing, use of earlier cultivars, and improved genetic tolerance to heat stress. Adaptation through earlier sowing dates proved to be the least efficient. The use of earlier heading cultivars was somewhat efficient, and should be sufficient for the near future. Tolerance to heat stress appeared to be the most promising adaptation strategy.

Climate-Change Effects on Water Resources

Climate-change effects on water resources have gained more attention in the past decades with numerous publications in the literature using GCM-projected weather conditions. It is commonly agreed that climate change will result in more frequent droughts and extreme storm events (Green *et al.*, 2011). In a study at a large Eastern Mediterranean karst spring, Hartmann *et al.* (2012) combined different GCM models and five hydrological models to study climate-change effects on water availability and found that in the near future (2021–51) no conclusive results could be drawn. However, in the more distant remote future (2068–98), all the model combinations predicted a 15–30% decrease of water availability in the region of study. Wang *et al.* (2012) used the SWAT model coupled with climate models with high (A2) and lower greenhouse emission scenarios to study the monthly streamflow in Northwest China, and found that streamflow increased by 0.1–6.1% in the 2020s, 2050s, and 2080s. However, Khoi and Suetsugi (2012) simulated decrease in streamflow ranging from 3.1 to 16.7% in Vietnam. Coupling a spatial hydrometeorological model with GCM-derived climate-change scenarios, MacDonald *et al.* (2012) found that, although the average maximum snow water equivalent may not change under future climate conditions, the timing of spring snowmelt onset is likely to move up and leave a dry summer under future climate scenarios. The differences among various climate-change studies were due to differences in GCMs and emission scenarios, and due to the fact that climate-change effects are region specific (Bennett *et al.*, 2012).

Climate change is likely to result in hydrologic conditions and extremes that will be different from those for which the existing projects were designed. The potential climatic impacts may have significant ramifications for decision making regarding water allocation and management that are likely to be made in the coming decades. Tanaka *et al.* (2006) applied the integrated economic engineering optimization model California Value Integrated Network with two climate warming and a historical climate scenario for studying the impacts of climate and population change on the physical and economic performance of California's intertied water supply system. Simulation results showed that adaptation of California's water supply system would require large changes in the operation of California's large groundwater storage capacity, significant transfers of water among water users, and some adoption of new technologies. Payne *et al.* (2004) used variable infiltration capacity hydrological model and Columbia River Simulation Model along with Pacific Climate Model and RCM scenario to assess the potential effects of climate change on the hydrology and water resources of the Columbia River basin and to evaluate alternative reservoir operating policies designed to mitigate reservoir system performance losses. Simulation results showed that temperature changes dominated the simulated hydrologic effects by reducing winter snow accumulation, thus shifting summer streamflow to the winter. Combination of earlier reservoir refill with greater storage allocations for in-stream flow targets mitigated some of the negative impacts to flow, but only with significant losses in hydropower production.

Conclusions

Achieving environmental protection and food security are two somewhat conflicting goals in agriculture. With increasing demand on food due to escalating population, the society requires high yield from farmland, which calls for high N, water, and pesticide inputs. The latter will definitely increase the risk of environmental pollution. The key to this complex issue is to balance and optimize and assess risks, impacts, and tradeoffs. Agricultural system models have the unique capability to provide a balanced solution to this dilemma. This article has demonstrated some promising examples of model applications in the areas of water and N management, and climate-change effects on crop production. These applications can be extended to other environmental and food security issues, such as pesticides and phosphorus in runoff and soil erosion.

See also: Climate Change: Agricultural Mitigation. Climate Change: Cropping System Changes and Adaptations. Climate Change, Society, and Agriculture: An Economic and Policy Perspective. Plant Abiotic Stress: Water. Simulation Modeling: Applications in

Cropping Systems. Soil Greenhouse Gas Emissions and Their Mitigation

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Computer Modeling: Policy Analysis and Simulation

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Glossary

Cumulative distribution function (CDF) Probability distribution with the possible value for the random value sorted from minimum to maximum.

Multivariate distribution A probability distribution with more than one random variable and they are related linearly (or nonlinearly) to each other so that their correlation is not zero.

Probability density function A schedule of probabilities associated with alternative values of a random variable, for example, a histogram or a bell-shaped curve.

Standard normal deviate (SND) A normally distributed random variable with mean zero and standard deviation of one.

Stochastic dominance A quantitative method for ranking risky alternatives.

Stochastic efficiency A quantitative method for ranking risky alternatives.

Stochastic variables Random variables.

Uniform standard deviate A random variable uniformly distributed between zero and one.

Univariate distribution A single random variable.

Introduction

Simulation has existed since man first started thinking through alternative ways for doing things. Thinking logically through solutions to problems is the most fundamental form of simulation. The modern computer greatly advanced simulation by allowing us to use machines to rapidly crunch through many different scenarios and provide summaries of the possible outcomes. Until the advent of the microcomputer, simulation models were relegated to universities and large corporations that had access to mainframe computers and programmers who developed simulation models using complex languages. With the introduction of Microsoft Excel spreadsheets, the simulation world has changed and anyone can now develop and utilize the power of simulation. Excel has become the language that businesses and researchers use to organize and process data. Simulation add-ins to Excel made the art of simulation more accessible to the business world, to students, and to researchers.

The purpose of this article is to introduce simulation as a tool for analyzing data and making probabilistic forecasts of variables that are not published or have risk about their forecasts. It is assumed that the reader is familiar with Microsoft Excel as this is fast becoming the language for developing simulation models and addressing risk in decision making.

Decision making in business and agriculture implies that management has a choice among alternative actions. The alternative actions could be different combinations of crops to produce, alternative production systems for crops or livestock, or different marketing or financial strategies for an agribusiness. If the decisions are to be made in a risk-free setting, the manager can easily determine which strategy is the best – the one with the greatest economic return. When decisions are made in a risky environment, the manager cannot use such a simple rule because the economic return for each alternative is a probability distribution of returns rather than a single value. One approach to decision making under risk is to simulate alternative strategies to estimate the distribution for each alternatives' return and then base the decision on these simulated distributions.

The purpose of simulation is to 'estimate the shapes of probability distributions for variables we cannot observe,' such as: profits, costs, or prices so the decision maker can make better decisions. The presence of risk complicates decision making and simulation is the best tool for analyzing the impacts of risk on key output variables (KOVs) of interest. Simulation produces hundreds of possible outcomes instead of a few discrete scenarios and the results show not only what could happen, but how likely each outcome is. Simulation makes creating graphs easier for different outcomes and the corresponding chances of occurrence.

In its most general form, simulation is simply the forecast of a KOV as a function of one or more exogenous variables or

$$\hat{Y} = a + b * X \qquad [1]$$

In this case Y is a function of X scaled by the parameter 'b' with the position on the number scale correction equal to parameter 'a,' and there is no risk. Because there is no risk, eqn [1] is a deterministic simulation model. A stochastic (or Monte Carlo) simulation model includes risk on one or more endogenous variables or risk added to the end of the equation as:

$$\tilde{Y} = a + b * X + \tilde{e} \qquad [2]$$

In eqn [2] the dependent variable is now a risky forecast with the addition of a probability distribution ($\tilde{e}$). The $\tilde{e}$ represents the risk for forecasting the $\hat{Y}$ and is based on the error term from econometrically estimating the equation to forecast the deterministic $\hat{Y}$. We can write eqn [2] in a more graphical sense by substituting a diagram of the probability distribution for risk in place of the $\tilde{e}$ or:

$$\tilde{Y} = a + b * X + \boxed{\text{⌒}} \qquad [3]$$

To simulate $\tilde{Y}$, a simulation software package randomly samples the probability distribution for $\tilde{e}$ many times (iterations)

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and each time it adds the stochastic value for $\tilde{e}$ to the deterministic part of $\tilde{Y}$, which is $a+b*X$. After each iteration, the $\tilde{Y}$ value is recorded and after many hundreds of iterations the values for $\tilde{Y}$ provide an estimate of the shape of the empirical probability distribution for $\tilde{Y}$. By recalling, estimating the shape of the empirical distribution for $\tilde{Y}$ is the objective of simulation.

Most simulation models are much more complex than eqn [2]. The equations frequently have more than one exogenous variable, the exogenous variables themselves may be stochastic in addition to the stochastic error term, and there may be hundreds of equations necessary to define the system being modeled.

Steps to Build a Simulation Model

All simulation models have the following parts: (1) input data to define the system being simulated and the control variables, (2) historical data for the stochastic variables, (3) parameter estimation for the stochastic variables and simulated stochastic variables, (4) equations to calculate intermediate variables, and (5) equations to calculate the KOVs.

The pyramid in Figure 1 provides a paradigm for planning a simulation model. The analyst must start at the top of the pyramid by defining the KOVs to be calculated and provided to the decision maker. For an investment model the KOVs could include: net present value (NPV), present value of ending net worth (PVENW), annual net cash income (NCI), annual ending cash reserves (ECR), probability of economic success, probability of increasing real net worth, annual rate of return on investment (ROI), debt to asset ratio (D/A), etc. For a biological model the KOVs could be crop yield, rate of gain for livestock, or number of replacement heifers needed to maintain a herd size without purchasing cows 90% of the time. The simulation model will estimate the data necessary to calculate the empirical probability distributions (PDFs) for each of the KOVs and to calculate probabilities for the KOVs reaching targeted values.

Once the KOVs are known, the next step is to determine the reports that are needed to calculate the KOVs. For an investment model the reports are: an Income Statement, Cash Flow Statement, and a Balance Sheet. All of the KOVs can be taken from these reports or easily calculated from variables in the reports. The next step is to write the equations for all of the variables in the reports and the variables necessary to calculate variables in the reports. For example, the Income Statement has receipts for each enterprise. So the model must have an equation to calculate receipts for each enterprise as follows:

$$\text{Receipts for Enterprise}_{ij} = \text{Price}_{ij} * \text{Yield}_{ij} * \text{Acres}_{ij} \qquad [4]$$

where i represents year and j represents the enterprise (crops or livestock).

In the process of writing the equations to calculate all of the variables in the model, the analyst should identify exogenous variables, management control variables, and stochastic variables. In eqn [4], Acres_{ij} is a control variable if the model is to investigate the profitability for alternative crop mixes. Other control variables that affect the profitability of a business are: terms for initial and new debts, initial and projected asset values, available resources (machinery complement, acres owned and leased, etc.), enterprises for the business (crops grown, livestock raised), input requirements and costs for enterprises (e.g., quantity of fertilizer, seed, herbicides, labor, fuel, or for a livestock model the inputs are hay, protein, and supplements fed per head of livestock). The list of exogenous variables will depend on the system being modeled and the degree of detail for the model.

Stochastic variables are identified in the process of writing the equations for the model. Stochastic variables are the variables the decision maker cannot forecast with accuracy or are control variables. In eqn [4], the prices and yields for the crop are obviously stochastic as the decision maker cannot control prices and yields as these variables are determined by markets and weather. A detailed model may include prices for outputs (e.g., individual crops and livestock) and each input (e.g., seed, fertilizer, chemicals, labor, utilities, livestock feed ingredients, etc.) as stochastic variables. In addition to these types of stochastic variables, the error terms for all econometric equations (such as $\tilde{e}$ in eqn [2]) should be included as a stochastic variable. During this step of model building, the analyst should assemble the historical data for the stochastic variables and the variables to be forecasted using econometric equations.

The steps to build the simulation model in Figure 2 are essentially a reversal of the steps in Figure 1; this time we start at the bottom of the pyramid. The first step is to estimate the parameters to define the PDFs for the stochastic variables. Depending on the simulation software available this can be an easy or a complex task. Parameter estimation for stochastic variables is very important to simulation modeling and is covered in-depth in the next section.

Once the parameters to simulate the stochastic variables are developed, the next step is to simulate the random variables and validate that they indeed reproduce the historical PDFs for the random variables. This step is often ignored by simulation modelers but it is crucial to prove the usefulness of the completed model. Validation tests for testing the stochastic variables start with the Student-t test to ensure that the simulated means statistically equals their historical (or intended) means. The second test is an F test which is used for testing if the

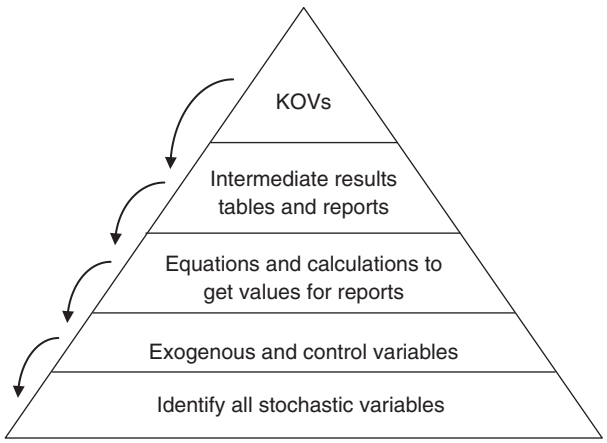


Figure 1 Steps for designing a simulation model. KOVs, key output variables.

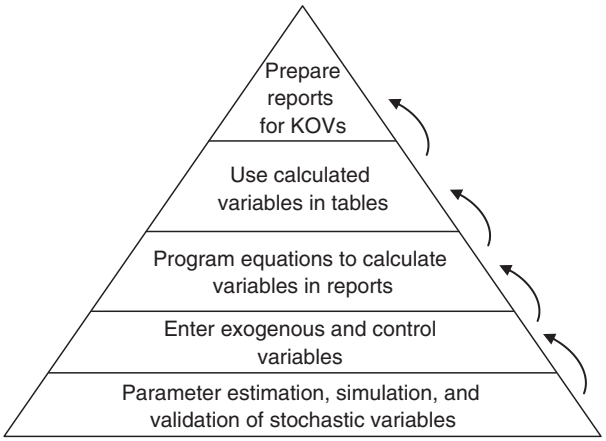


Figure 2 Steps for building a simulation model.

variance for the simulated variable statistically equals the variance historical variability over a period used to estimate parameters for the distribution. If the stochastic variables are correlated then the Box's M Test should be used to test the covariance of the simulated variables against the historical covariance and the Hoteling's T test should be used to test the historical mean vector of the stochastic variables against their simulated mean vector. A complete homogeneity test can be used to simultaneously test the mean vectors and the covariance matrices. After validating the simulated random values for the stochastic variables they can be used in the model. Without detailed validation one is just perpetuating the old argument against simulation: garbage in and garbage out (GIGO).

The stochastic variables are used with the exogenous variables and control variables to program the equations in the model to calculate the intermediate variables. Econometric equations that use stochastic error terms are programmed at this point in the model; however, most of the equations in a simulation model are identities and are easily programmed. It is recommended that the individual equations be kept simple so they can be easily verified rather than programming long equations with many parts and conditions. An Excel worksheet has more number of cells for equations than you will ever need and so there is no need to minimize the number of cells used. Use one cell for each equation and program the equations in a logical order so that the calculations flow from one step to the next down the Excel worksheet. For example, the logical flow of equations for a farm investment model is to use five equations to calculate production, variable costs of production, total production costs, receipts, and profit in the following order:

$$Production_i = \text{Acres}_i * Yield_i \quad [5]$$

$$Variable\ Costs_i = \text{Variable Costs per Unit}_i * Production_i \quad [6]$$

$$Total\ Costs_i = Variable\ Costs_i + \text{Fixed Costs}_i \text{ per Acre} * \text{Acres}_i \quad [7]$$

$$Receipts_i = Price_i * Production_i \quad [8]$$

$$Profit_i = Receipts_i - Total\ Costs_i \quad [9]$$

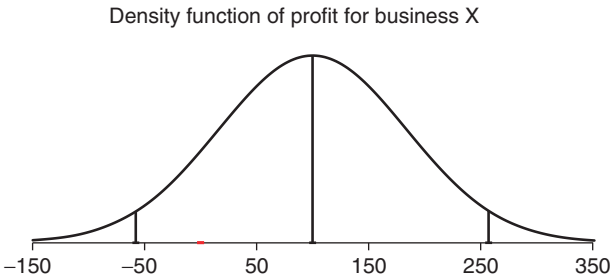


Figure 3 Probability density function for a KOV of profit.

where all variables in italics become stochastic variables because they are functions of the random variables that are in bold.

The stochastic variables for the model are prices and yields but by including them in eqns [5] and [8] it makes all of the other variables stochastic as well. It is through this process that the simulation model is able to forecast the probability distribution for profit. Note that the exogenous variables in the model are acres, variable costs per unit, and fixed costs. The exogenous variables are control variables set by the analyst and can be used for testing alternative scenarios.

The next step in model building is to assemble the calculated variables into reports and tables that are useful for summarizing the model's results. The receipts and expenses for a business model logically are summarized in an income statement which is followed by a cash flow statement and a balance sheet. An example of these summary tables is provided in the Appendix.

The final step in programming a simulation model is to develop reports using the KOVs. Reports can include tables with the summary statistics (means, standard deviation, coefficient of variation, minimum, and maximum) for all of the KOVs, and charts of the KOVs. Probability density charts are very useful as they show that the KOVs are stochastic (Figure 3). Cumulative distribution charts are frequently more useful as we can read the probabilities of alternative outcomes directly from the chart, for example, the probability that the KOV is less than zero is 10% (Figure 4). The two figures depict the results for the same output variable but the CDF is easier to interpret.

Model verification of the completed simulation model must be undertaken as soon as the model is completed. Verification is the process used to test that every equation in the model is functioning as intended. This means that testing each equation to ensure that its independent variables come from the appropriate cells in the worksheet, i.e., that crop production is actually calculated using the cells that have acres and yields for the correct crop and that the model does not multiply sorghum yield and wheat acres. Each equation must be checked to ensure that the variables are using the correct time period (months, years, etc.) and that the equations are not using crossing periods, i.e., yields in 2013 are used to calculate production in 2013. After verifying all equations it is recommended that a series of verification tests be used to further verify the model's ability to forecast the system being analyzed.



Figure 4 Cumulative distribution function (CDF) for a KOV of profit.

Simulating the model using historical data as the starting point and comparing the forecasts to history is a place to start in the verification process. It is recommended that the analyst compare the model results to historical records of the KOVs and published results for other models. This may be difficult if the model is analyzing investments in proposed businesses or business plans that have not been tried. In these cases a Touring Test is appropriate. A Touring Test for a model involves defining a standard scenario, running the model, recording the outcomes, and having experts review the inputs and the outputs. Reviews by experts will help identify inconsistencies in the model's results. For example, a misplaced sign on a coefficient can make demand upward sloping or supply downward sloping, both of which can be detected in a Touring Test.

Parameter Estimation for Stochastic Variables

The random variables are what make the simulation model a stochastic model. To simulate the random variables one must know what distributions they come from, their variability, and their position on the number scale. The parameters for a stochastic variable define the variability and position on the number scale from plus and minus infinity. Parameters to define random variables are estimated from their historical data. A basic understanding of random numbers and probability distribution is necessary to estimate the parameters for stochastic variables.

We start with the simplest of random variables, the uniform distribution as it is used to simulate all random variables. The most general form of the uniform distribution is the Uniform Standard Distribution (USD) which is written as USD~$U(0,1)$. The parameters for the USD are a minimum of zero and a maximum of one. A value drawn at random from a USD can be used to simulate any distribution through the inverse transform method. For example, if $\tilde{Y}$ is a uniform random number distributed over the range of 10–20 (i.e., $\tilde{Y}$~$U(10,20)$) we simulate $\tilde{Y}$ as follows:

$$\text{USD} = \text{UNIFORM}(0,1) \text{ or } \text{RAND}(0,1)$$

$$\text{depending on the simulation add-in} \qquad [10]$$

$$\tilde{Y} = \text{minimum} + (\text{maximum} - \text{minimum}) * \text{USD} \text{ or}$$

$$\tilde{Y} = 10 + (20 - 10) * \text{USD} \qquad [11]$$

Because the USD is always between zero and one, $\tilde{Y}$ has to lie between 10 and 20 on the number line and there is an equal probability that $\tilde{Y}$ will be in the interval of 12 and 14 or 16 and 18. The uniform distribution itself is not used to simulate a random variable unless the shape of the distribution is completely unknown and we only know the minimum and maximum.

The most popular distribution for simulating random variables is the normal distribution because it is easy to estimate the parameters. For that reason many modelers take the easy route and just assume the random variables are distributed normal. Before making this assumption, tests for normality should be applied to the random variables. The parameters for the normal distribution are its mean and standard deviation and we denote that a random variable $\tilde{Y}$ is distributed normal as: $\tilde{Y}$~N(mean, standard deviation). A normal distribution can be simulated with the following equation:

$$\tilde{Y} = \text{Mean} + \text{Standard Deviation} * \text{SND} \qquad [12]$$

where SND = NORMSINV(USD) and USD is defined in eqn [10]. In this equation SND is the standard normal deviate which has a normal distribution with a mean of zero and a standard deviation of one. NORMSINV is an Excel function to convert a USD into a standard normal deviate.

The normal distribution's parameters, mean and standard deviation, can be calculated with any statistical software or calculated directly in Excel.

To estimate parameters for a normally distributed random variable, all that is needed is the historical data for the random variable. To use the historical data to define a random variable, one must first remove the systematic risk before estimating the parameters for the probability distribution. With agricultural data, and particularly with yields and prices, there is frequently a trend or seasonality and cycles which must be removed before attempting to estimate parameters for a random variable. The trend can easily be removed by fitting an ordinary least squares (OLS) regression to the historical data and letting the

unexplained residuals from the regression be the risk to be simulated as the stochastic component to $\tilde{Y}$. In eqn [13] a trend regression is fit to the historical variable and the stochastic residuals are calculated in eqn [14]:

$$\hat{Y} = a + b * T \quad [13]$$

where T is a variable that increments by 1 as 1, 2, 3, … or 2000, 2001, 2002,

$$\tilde{e} = Y - \hat{Y} \quad [14]$$

The $a+b*T$ part of eqn [13] is the deterministic component in eqn [2] and $\tilde{e}$ is the stochastic component of eqn [2] that no longer has a systematic trend. Another way to say this is that $\tilde{e}$ represents the risk about the trend or the OLS forecast and in simulation it represents the risk about the forecasted mean or $\hat{Y}$. If the random variable $\tilde{Y}$ has a structural relationship to other variables, then a more complete OLS equation that includes all of the independent variables must be used to calculate the $\tilde{e}$ series. The residuals should be tested for normality and if they are normally distributed then $\tilde{Y}$ can be simulated as a normally distributed random variable using eqn [15]:

$$\tilde{Y} = \hat{Y} + (\text{Standard Deviation for } \tilde{e} * \text{SND}) \quad [15]$$

A caution in using the normal distribution is that if the mean or $\hat{Y}$ assumed for the simulation in eqn [12] or [15] is greater than the historical data, the simulated variables will have less relative risk than the historical data and *vice versa* if the mean or $\hat{Y}$ is less than the historical mean.

Many other parametric distributions can be used to simulate random variables in stochastic models. The most frequently used parametric distributions are beta, gamma, log normal, Weibull, and exponential. Estimating parameters for these distributions is more complicated and requires special software such as those found in Simetar© and Best Fit©. Whatever parametric distribution is used, you must first remove the systematic variability to identify the actual risk in the stochastic variable before estimating the parameters for the appropriate (or assumed) distribution.

When insufficient data are available to estimate the parameters for a parametric distribution, one can use a nonparametric distribution. The triangle distribution is used frequently because it is easily parameterized with only three values: minimum, mean, and maximum. The triangle distribution has a significant problem in that it never returns the exact minimum or maximum. If one solicits the extreme values by asking for a minimum or maximum that one might expect 1 year in 10 (or 10% of the time), then the triangle will greatly underestimate the frequency of the tails for the distribution. Understating the risk in the tails is extremely problematic as the outcomes in the tails are critical to providing an accurate estimate of the risk associated with a decision.

The empirical distribution is a nonparametric distribution that is similar to simulating a histogram of the random variable with interpolation between the points. The empirical has a finite minimum and maximum and it exactly matches the shape of the distribution as observed in the historical data. The best way to simulate an empirical distribution is to convert the residuals from trend (or structural OLS model, or mean) into fractional deviates and simulate these deviates as an empirical distribution or as

$$S_i = \text{Sorted}(\tilde{e}_i / \hat{Y}_i) \quad [16]$$

$$\tilde{Y} = \hat{Y}_i * (1 + \text{EMP}(S, F(x), \text{USD})) \quad [17]$$

The $F(x)$ term represents the cumulative probabilities for the sorted deviates about the trend or mean forecasts. During simulation the USD is used in the inverse transform formula to simulate a random deviate which is added to one and multiplied by the forecasted Y value. If $\hat{Y}$ is equal to the historical mean, the resulting random values are distributed identical to the historical data without bias from assuming a probability distribution for the random variable. Even if $\hat{Y}$ is different from the historical mean, the simulated values will have the same coefficient of variation as the historical data so that relative risk is maintained as the mean increases or decreases over time.

When a stochastic model has more than one random variable, one must consider the possibility that the random variables are correlated or that causality may exist between or among the variables. When two random variables are positively correlated and the correlation is ignored, the mean for the product of these random variables ($\tilde{Y}_3 = \tilde{Y}_1 * \tilde{Y}_2$) will be biased and its variance will be understated. The variance is overstated if the two random variables are negatively correlated. So if correlation between and among the random variables is present, one must account for it and use a multivariate probability distribution rather than individual distributions for each random variable.

Multivariate normal distributions have been used in simulation models for many years. Clements *et al.* (1971) first demonstrated its use in an agricultural simulation model. Multivariate non-normal (MVNN) distribution was introduced by Richardson and Condra (1981) and their approach was expanded on by Richardson *et al.* (2000). The MVNN approach is described here as it includes the multivariate normal as a special case. The parameters for a MVNN distribution are the correlation matrix of the residuals plus the parameters for the individual random variables' distributions (normal, beta, gamma, empirical, etc.). A vector of J correlated uniform standard deviates (CUSDs) is simulated using the square root of the correlation matrix and a vector of independent standard normal deviates (ISNDs) to simulate a MVNN distribution with J variables:

$$\text{CUSD}_{[J\text{x}1]} = \text{NORMSDIST}(\sqrt{(P_{[J\text{x}J]}} * \text{ISDN}_{[J\text{x}1]}) \quad [18]$$

where $\sqrt{(P_{[J\text{x}J]})}$ is the square root of the correlation matrix and NORMSDIST is the error function in EXCEL to convert SNDs into USDs.

The CUSDs are used in the inverse transform equation to simulate each of the J random variables, as in eqn [18]. Simulation add-ins for Excel, such as Simetar©, include functions that simulate the CUSD vector in one step so that including correlation for multivariate distributions is quite simple. Validation of random variables simulated using a multivariate distribution requires the use of the multivariate validation tests described in the Section Steps to Build a Simulation Model.

Recent research in the area of simulation has promoted the use of copulas to incorporate causal relationships between and among random variables. The procedure described in eqn [18] is a normal copula. The Clayton and Frank copulas can be simulated in Simetar© using eqn [18] by replacing the correlation matrix ($P_{[IxJ]}$) with a Kendall's Tau concordance matrix. Validation of a multivariate distribution simulated using a copula is more difficult and is not covered here.

Applying Simulation Models

Simulating a single scenario is useful, but what simulation models were meant to do was to simulate multiple scenarios so that decision makers can compare the outcomes for making better choices. Multiple scenarios can easily be defined using alternative values for the decision maker's base values of the control variables. Each scenario in a simulation is unique because it is based on a different set of assumptions for the exogenous variables.

Examples of decision problems that are suitable for simulation as scenarios are: comparing insurance options for yields, revenue, weather, etc.; farm program participation options; crop mixes and enterprise selection, such as adding or dropping a livestock enterprise on a farm, machinery replacement by purchasing or leasing; increasing or decreasing acreage to a farm; marketing strategies, such as contracting, selling at different times of the year, hedging, or options; and portfolio analysis using stocks and bonds.

The different simulation add-ins for Excel allow for scenario analysis in different ways. Be sure the add-in you use forces the random variables to use exactly the same USDs for the random variables across all scenarios. This will cause the scenarios to all face the same risk and ensure that the KOV results are only different because of the values of the control variables assumed for the scenarios. Otherwise, differences in the KOVs are due to different risks and the different values assumed for the scenario variables, and the results are not useful.

After simulating multiple scenarios the analyst must help the decision maker decide which is the best scenario. This is the area of ranking risky scenarios and is covered in the next section.

Ranking Risky Alternatives

The results from simulating multiple scenarios are multiple empirical distributions for each KOV. Usually the decision maker will focus on one KOV for ranking risky alternatives. For annual models the KOV of choice is likely to be NCI, ECR, or production. For a multiple-year planning horizon model, the KOV should be one that converts the stream of annual returns into present dollars such as NPV as indicated in eqn [19]:

$$\begin{aligned}\text{NPV} = &-\text{Beginning Net Worth}\\ &+\sum(\text{Cash Withdrawals}_i)/(1+r)^i\\ &+\text{Ending Net Worth}/(1+r)^I \qquad [19]\end{aligned}$$

where r is the discount rate and i represents the years simulated $i = 1, 2, 3, \ldots, I$.

To rank the multiple KOVs developed by the simulation model, we can rely on several techniques, such as: means, mean variance, stochastic dominance, stochastic efficiency, and StopLight charts with target probabilities. For a complete comparison of these and other risk ranking strategies see Richardson and Outlaw (2008). Ranking risky alternatives based on the simulated means is only useful if the decision maker is risk neutral, which is likely not the case.

Mean variance ranking is easy to use and helps identify the scenario with the greatest mean return and the least variance, but can lead to indifferences between scenarios that are not resolvable. See Robison and Berry (1980) for a more complete description of mean variance analysis.

Stochastic dominance is a very useful method for ranking risky alternatives. Three types of stochastic dominance techniques are well defined for ranking risky alternatives: first degree, second degree, and generalized stochastic dominance. First-degree stochastic dominance can be used to rank risky alternatives when the empirical CDFs for the alternatives do not cross. A rational decision maker will prefer the alternative associate with the scenario furthest to the right in **Figure 5**. The right-most scenario (NPV 2) is preferred over the fourth scenario (NPV-4) because it offers the most income for the least risk at each point along the CDF. However, first-degree stochastic dominance cannot rank the other scenarios as their CDFs cross.

Second-degree stochastic dominance measures the differences between the CDFs and arrives at a ranking based on the sum of the area that is greater for the distribution that is further to the right. In the case of **Figure 5**, second-degree stochastic dominance ranks scenario 1 over 2 and 4, and it ranks scenario 3 over 2 and 4, but is unable to rank scenario 1 versus 3. Generalized stochastic dominance ranking of the four scenarios considers the decision maker's utility function and degree of absolute risk aversion and ranks scenario 3 as the most preferred. A disadvantage of using generalized stochastic dominance is that the procedure requires that one knows the decision maker's absolute risk-aversion coefficient. See Meyer (1977) for a mathematical description of generalized stochastic dominance.

Another risk ranking procedure, which uses the decision maker's utility function, is stochastic efficiency but it does not require the decision maker's risk-aversion coefficient. Stochastic efficiency assumes a utility function and ranks the risky alternative over a range of possible risk-aversion levels which are set wide enough to include the relative risk aversion for the decision maker. The results of ranking the risky alternatives depicted in **Figure 5** are presented in **Figure 6** using stochastic efficiency. Stochastic efficiency assumes decision makers prefer more to less and calculates the certainty equivalence (CE) for each risky alternative at many different levels of risk aversion ranging from risk neutral to extremely risk averse. The decision maker chooses the risky alternative that has the highest CE at their relative risk-aversion level. For the risky alternatives in **Figure 6**, all decision makers who are risk averse choose scenario 3. The risk-aversion coefficients in **Figure 6** are: 0, neutral; 1.0, normal; 2.0, moderate; 3.0, somewhat; and 4.0, extremely risk averse, based on the nomenclature proposed by Anderson and Dillon (1992). For a more complete description of stochastic efficiency see Hardaker *et al.* (2004).

The easiest risk ranking methodology, which takes into consideration the complete empirical distributions for the

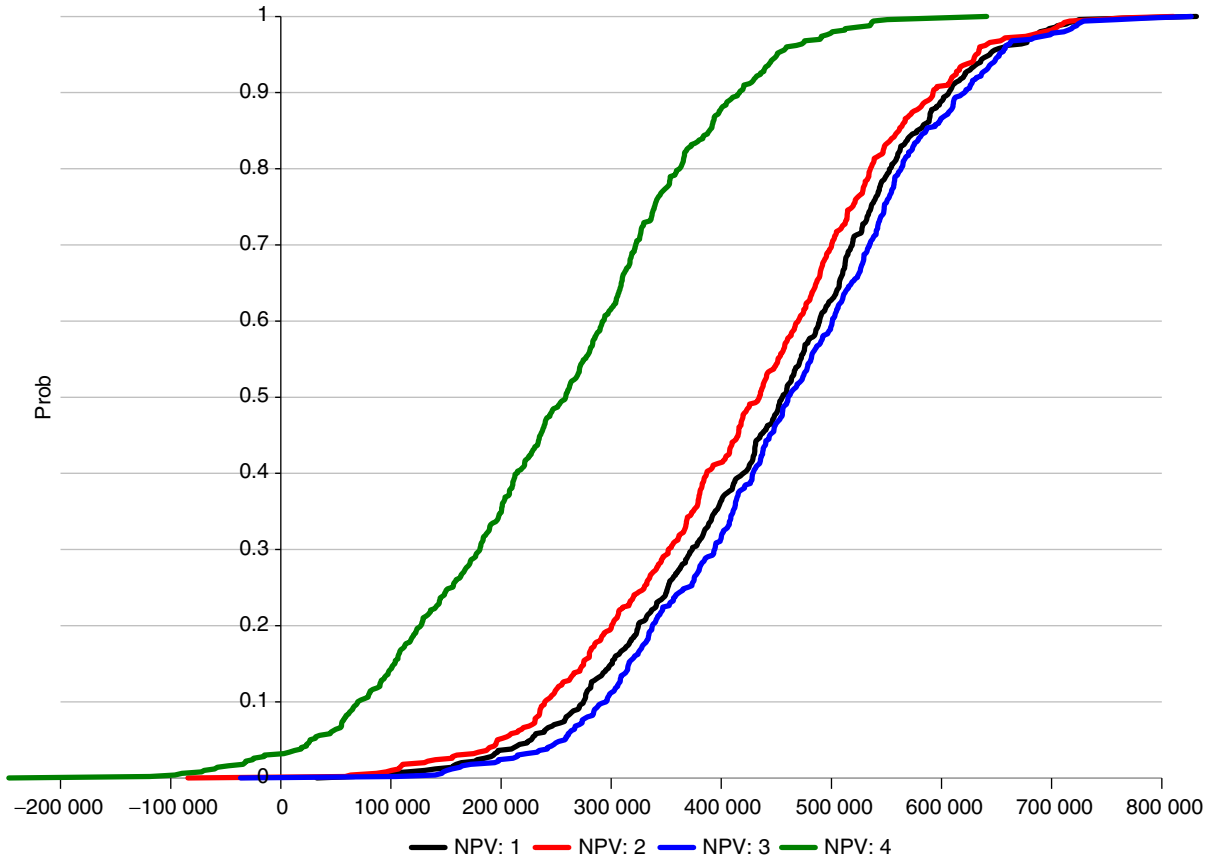


Figure 5 CDFs of NPV for four scenarios. NPV, net present value.

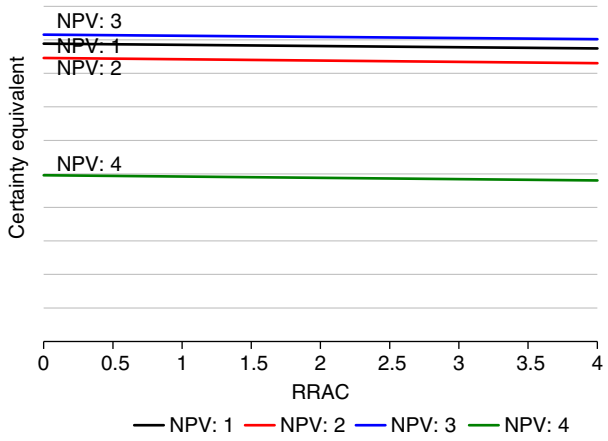


Figure 6 Ranking risky alternatives using stochastic efficiency.

KOV, is the StopLight chart for the probabilities of achieving target values for the KOV. The decision maker provides target values for the KOV and the chart presents the probabilities for exceeding the upper target in green and the probabilities for being less than the lower target in red. Green is good and red is bad is the criteria for ranking the risky alternatives. Based on the chart it is easy to see why risky alternative 3 was selected by stochastic efficiency and generalized stochastic dominance. This method of ranking is very easy to explain to decision makers, particularly if they are not trained in economics or statistics (Figure 7).

The risk ranking methods presented here require complex mathematical calculations that are beyond the capabilities of most simulation packages. See the references cited for more details on the mathematical presentations of the methods.

Selection of a Simulation Add-In for Excel

Excel is an excellent vehicle for a simulation model and a simulation add-in is the motor that makes the model run. Excel provides the basic formulas for programming a stochastic simulation model, i.e., addition, subtraction, multiplication, division, and fundamental statistical tools for calculating means, standard deviation, and sums. Excel also includes a powerful set of graphics capabilities that allows users to develop graphs that are useful for presenting the results for stochastic simulation models. Excel has many other useful statistical functions that can be used by more advanced simulation modelers, but they are not designed for researchers who are just starting in the field of stochastic simulation.

As with many things in life, when starting on a new trek it is good to seek the best advice and help possible. In the case of simulation this means using an Excel add-in that is designed to support development of stochastic simulation models. The leading simulation add-ins are: Simetar©, @Risk©, and Crystal

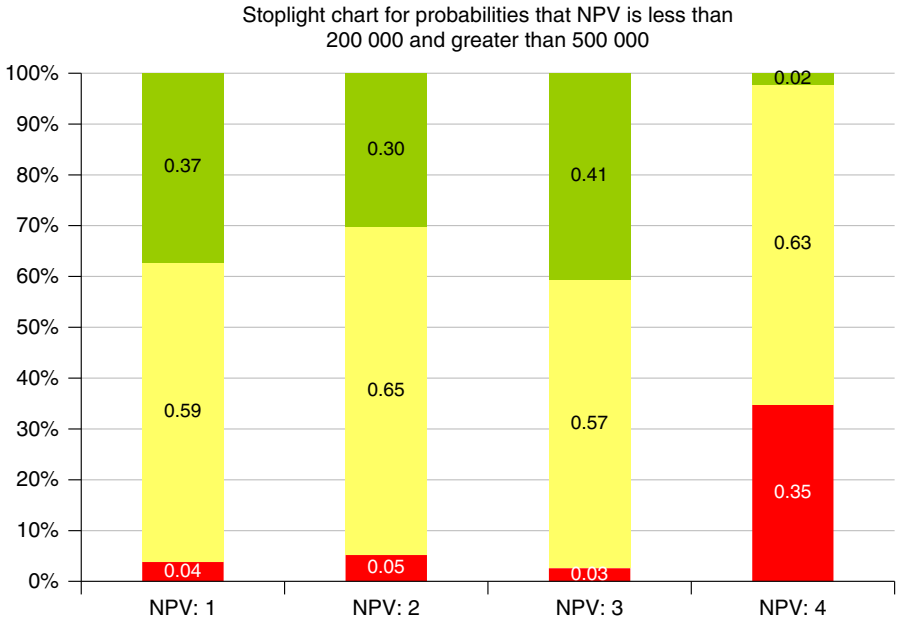


Figure 7 StopLight chart for ranking risky alternatives.

Ball©. All three have been on the market for some time and have their faults and positive features. More information on the three add-ins is available on their web sites.

In selecting a simulation add-in for Excel, the author recommends to seek out a package that meets your needs and is easy (preferable intuitive) to use based on your mode of working. The following is a checklist of features to look for in selecting a simulation add-in for Excel:

- Pseudorandom number generator: user-defined seed to start the random number generator at the same place each time so that every time a model is run it can return the same stochastic results.
- A nondegenerative random number generator: test the random number generator by simulating 100 000 or more USDs to make sure that the last 1000 are indeed distributed $U(0,1)$.
- Random numbers simulated with a Latin hypercube procedure: the alternative sampling procedure is a Monte Carlo procedure, which tends to under- and oversample the USD and thus force one to simulate an obscenely large number of iterations to achieve stable stochastic distributions. Owing to a more efficient sampling procedure the Latin hypercube can generate stable stochastic distributions with less than 2000 iterations instead of tens of thousands with a Monte Carlo procedure.
- Large number of available probability distributions: analysts need not be limited to a small number of probability distributions from which to simulate random variables. The more distributions included in the software, the better.
- Multivariate distribution capabilities: for reasons described above, the add-in must have the capability to simulate correlated USDs so that the model can simulate multivariate distributions without variance bias.
- Copulas to simulate concordance between random variables: when random variables are related in a nonlinear fashion, the model must have the capability to simulate their concordance.
- Regression and forecasting options included in the package: it is more accurate and efficient to estimate OLS coefficients and residuals in the simulation packages than to do it in a second Excel add-in. In addition, forecasting packages such as times series, exponential smoothing, seasonal indices, and moving averages are frequently needed in simulation to estimate the residuals about the forecast for a stochastic variable and to forecast means for the random variables.
- Parameter estimation capabilities for parametric and nonparametric distributions: parameter estimation for other than the uniform and normal distributions requires the use of method of moments or maximum likelihood estimators. These parameter estimation procedures are beyond the capabilities of most simulation modelers so they need to be included in the simulation add-in.
- Statistical tests for validating simulated variables: until the random variables generated by a simulation model are validated, the model should not be used for decision making. Student-t and F or Chi-square tests as well as multivariate validation tests must be included in the add-in for ease of validating the stochastic variables.
- Risk ranking tools: stochastic dominance, stochastic efficiency, and StopLight charts are essential features in a simulation add-in if the modeler wants to help the decision maker select the best scenario.
- Graphing capabilities that complement Excel: specialized charts such as PDFs, CDFs, and Fan Graphs are helpful to display the shapes of the simulated KOVs and for testing the model.

- Ease of specifying and running multiple scenarios: simulation is about comparing risky alternatives so the add-in must provide a transparent and easy-to-use method for simulating multiple scenarios with exactly the same risk from one scenario to the next.
- Simulated values are summarized in a separate worksheet updated after each simulation: this feature allows Excel to automatically update summary tables and risk ranking charts developed by the user after each simulation.

Getting Started with Stochastic Simulation

The way to get started building and using stochastic simulation models is to start with a small model that has two random variables and two or three control variables. Such a model is described in eqns [5]–[9]. Obtain a 10–20-year series of prices and yields for a crop and assume these random variables are independent. Use accepted budgets for the marginal costs to harvest and haul the production and assume all other production costs are fixed costs per acre. Simulate the model for 1 year and plot the probability distribution for profit. Next, change the control variables and re-simulate the model. Next, make acre and fixed costs control variables for a five scenario analysis. Graph the CDFs of profit for the five scenarios to determine the effects of changing these variables.

After becoming comfortable with simulating the model for 1 year, expand it to simulate for 5 or 10 years. First, this involves forecasting mean yields and prices for each year in the planning horizon. Next, it requires a separate random value for each year. The new random variables all have to be validated to ensure that the simulated means for each year equal their assumed means. Because the model is now a multiple-year model, include an income statement, a cash flow, and a balance sheet so the NPV can be calculated as the KOV. Expand the KOVs to include annual NCI, annual ending cash (EC), and the probability that these variables will be positive each year. Next, run five scenarios using alternative acres, fixed costs, and mean yields. Rank the five risky scenarios.

To the final model, change the stochastic procedure to simulate the annual prices and yields as a multivariate empirical probability distribution. Compare the simulated annual NCIs for the model with independent random variables to the model with correlated random variables. Rank the five scenarios to see if the rankings change. Have fun.

Examples of Applying Simulation to Agriculture

Four examples of applying simulation to problems in agriculture are presented in this section. The first example is a summary of a policy analysis conducted by the Agricultural and Food Policy Center (AFPC) at Texas A&M University in 2012 at the request of the US Congress, House Agriculture Committee. The second example is the results of an investment analysis to demonstrate the use of simulation for analyzing a business before investing. The third example is a simple study to demonstrate how simulation can be used to analyze alternative insurance options for a farmer. The last example is a summary of an analysis of alternative technologies and how they could potentially improve the economic and nutritional sustainability of small holder farmers in a developing country.

Each example is presented using the following format: describe the problem to be analyzed, describe the model used and the stochastic variables, summarize the results, and present the charts and tables used to present the results to the decision makers. The full reports for the first three examples are available on request from the author. The fourth example has not been published; however, the simulation model will be made available for free from the author.

Farm Policy Analysis

In 2012, the House and Senate Agriculture Committees in the US Congress were busy formulating a new farm bill. Both Committees had formulated a bill and the AFPC was asked to conduct a risk-based analysis of the two farm bills (Outlaw *et al.*, 2012). The full report is available on the AFPC website at http://www.afpc.tamu.edu/pubs/0/578/wp%202012-03%20-%20to%20post%20to%20web.pdf. The two farm bills were very complex with several options in each bill. The AFPC was requested to conduct a farm-level economic analysis using the Farm Level Income and Policy Simulation Model (FLIPSIM) developed by Richardson and Nixon (1986).

FLIPSIM is a Monte Carlo simulation model for simulating the economic impacts of alternative farm programs and income tax policies on the economic viability of representative crop, dairy, and beef cattle farms (Richardson and Nixon, 1986). The model was initially completed in 1980 and has been expanded and enhanced continuously since then. The model has been used to advise the US Congress on every farm bill since 1983 and is widely cited, based on the more than 14 900 hits on a Google search of 'FLIPSIM-model.' The model can be summarized simply as a multiyear simulation of a farm business with stochastic production and product prices. The model includes farm policy formulas and income tax regulations so that it is able to simulate a farm under alternative policy scenarios. For the example summarized here, the policy options considered by the US Congress were added to the model and 65 representative crop farms were simulated for 5 years.

Scenarios Analyzed

Both the US Congress, Senate and House Farm Bills discussed previously were analyzed using the representative farms for the following scenarios:

- Senate Farm Bill assuming individual-level coverage selected in the Acreage Risk Coverage (ARC) program along with Supplemental Coverage Option (SCO) analyzed with the Food and Agricultural Policy Research Institute's (FAPRI) January 2012 Baseline projections of sector-level prices.
- Senate Farm Bill assuming county-level coverage selected in the ARC program along with SCO analyzed with FAPRI sector-level prices.
- House Farm Bill assuming Revenue Loss Coverage (RLC) selected and analyzed with FAPRI sector-level prices.

- House Farm Bill assuming Price Loss Coverage (PLC) along with SCO and analyzed with FAPRI sector-level prices.
- Stacked Income Protection Plan (STAX) for cotton was assumed to be in place for all farms growing cotton under both the House and Senate Farm Bills.

Simulation Results

Results were presented in terms of which types of farms preferred which farm program option. For example, the results for ranking the Senate bill are summarized in Table 1 in terms of the number of representative farms that preferred individual versus county-level coverage in the Senate bill. Based on the simulated net cash farm incomes (NCFI) for the farms, the majority of crop farmers would prefer the county yield option.

Figure 8 comes from the study and graphically portrays which farms would prefer the House bill and which would prefer the Senate bill. Icons for the types of crops and their locations were used to summarize the results graphically, in addition to using colors to indicate bill preference. Preferences were based on NCFI from simulating the alternative scenarios. The reports demonstrate that complex results can be presented in easy-to-understand graphics and tables for decision makers.

Table 1 Number of representative farms that would prefer individual versus county-level coverage based on NCFI in the Senate ARC Farm Bill package assuming FAPRI-projected prices

	Individual coverage	*County coverage*
Total by Preference[a]	22	40
Feedgrain/Oilseed	7	16
Wheat	3	8
Cotton	8	6
Rice	4	10

[a]Two farms, the small Texas southern plains cotton farm TXSP2500 and the Arkansas cotton farm ARNC5000, are 100% cotton and would only be enrolled in STAX. Therefore, there would be no difference between the alternatives.
Abbreviations: ARC, Acreage Risk Coverage; FAPRI, Food and Agricultural Policy Research Institute; NCFI, net cash farm incomes.

Investment Analysis

Investment analyses are a natural application of Monte Carlo simulation because investments always have risk and usually the investor is analyzing a business that does not exist but is being considered. For example, an investment in a new restaurant, or a new ethanol plant, or even a new feed store all have risks. Simulation is a systematic way to include risks from many different sources and to analyze the probability of the business being an economic success. The model for an investment decision is very straightforward; all it needs is the information to fill in an income statement, a cash flow statement, and a balance sheet for 5–10 years. (See the Appendix for a sample income statement, cash flow statement, and

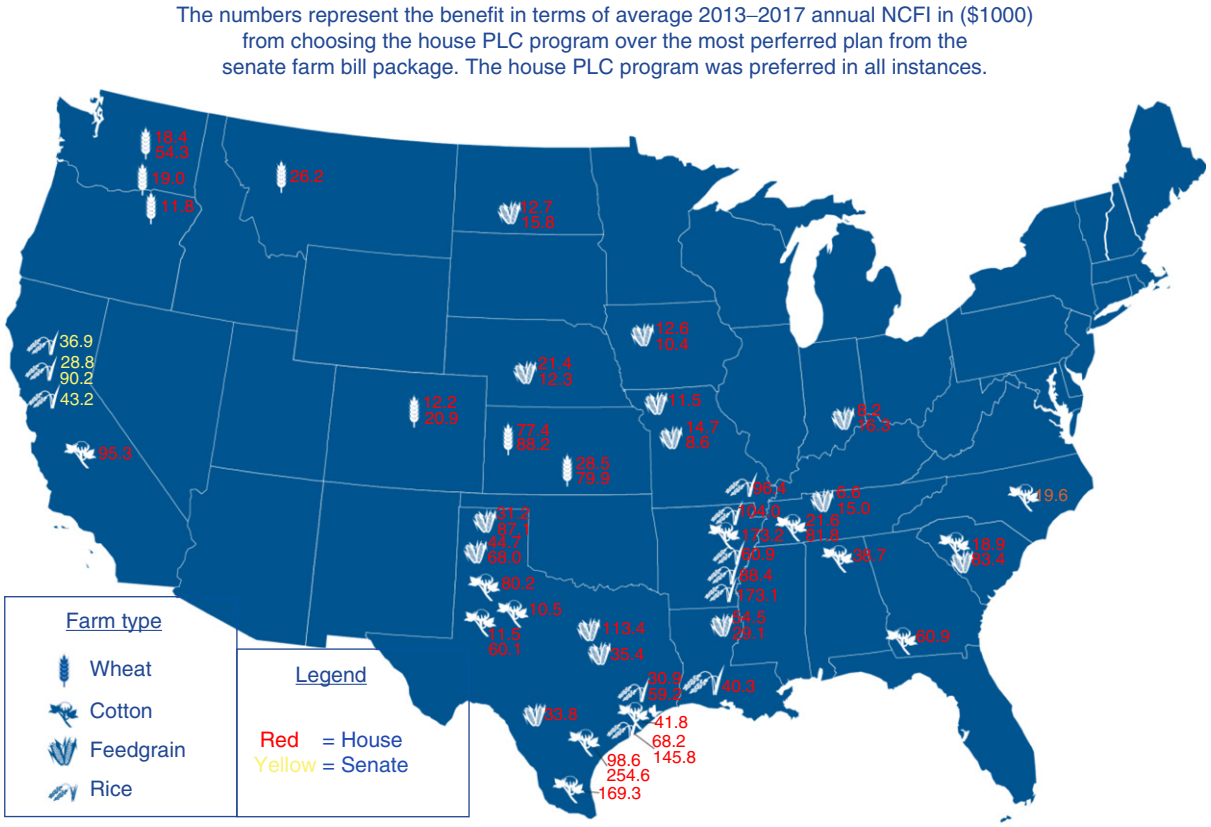


Figure 8 Results indicating the representative farm's preference for the House over the Senate safety net package.

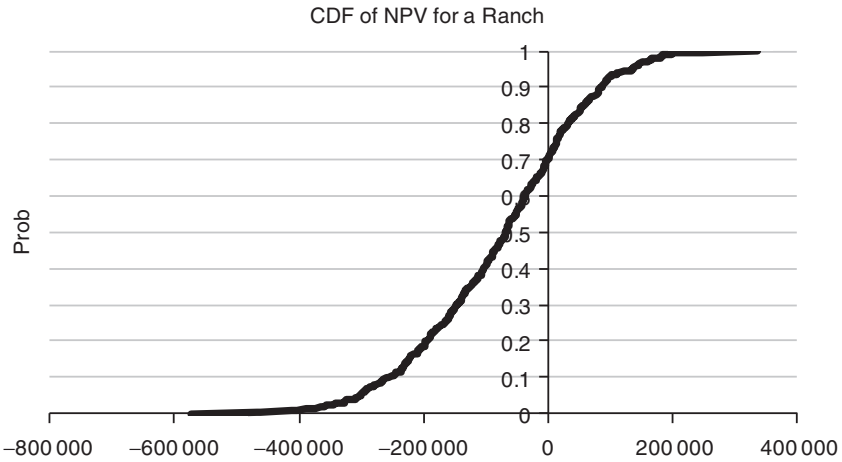


Figure 9 CDF of NPV for a ranch investment to demonstrate the probability of economic success.

balance sheet that would make up the majority of the equations for an investment model.) The stochastic variables are often a bit more challenging as they are distributions for prices of outputs, volume of sales, and costs of inputs or services provided.

The first investment simulation model developed by the author was for an ice plant (Richardson and Mapp, 1976). It was an early application for simulation of investments to appear in the agricultural economics literature and was the first to report a probability of economic success and a probabilistic cash flow. The probability of success was defined to be the probability of NPV being positive. The logic behind probability of success is that if NPV is positive, the investment generates a return greater than the discount rate, which is the investor's opportunity cost of capital. The investor in this case was concerned about the probability that cash flow from the business would be large enough to provide a minimum cash withdrawal, so the probability of positive cash flows was used by the decision maker for evaluating the investment.

A simple investment decision model is presented in this section to demonstrate how simulation can be used to evaluate a risky investment. The investment is a beef cattle ranch that has been in operation and the owner is considering selling the ranch and investing in a business that has an internal rate of return of 5%, so the discount rate is 10% for the problem. The ranch runs 500 mother cows and has an initial herd of 90 replacement heifers and 25 bulls. The ranch raises its own replacements by keeping 43% of the heifers each year. Risks on the ranch include: prices for cattle (culled cows, heifer calves, steer calves, culled replacement heifers, and culled bulls); price for surplus hay; and prices for buying deficit hay and soybean meal. Production risks include: hay yields, calving rate; death rates for calves, replacement heifers; and sale weights for heifers, steers, and culled replacement heifers.

The ranch has an initial net worth of $4.4 million and an expected NPV of minus $47 000. The probability of success from the stochastic analysis is 29% which can be read from the CDF for NPV in Figure 9. The summary statistics from simulating the ranch for 7 years are summarized in Table 2. The probability of NCFI being negative grows over the planning horizon as does the probability that EC is negative. Needless to say, the ranch as managed today is not a profitable investment. A deterministic analysis shows a positive NCFI and EC for the first 4 years and a slightly negative NPV. Without the stochastic analysis an investor would not know what a bad investment the ranch would make. A copy of the ranch investment model can be obtained from the author on request.

Insurance Analysis

Each year, crop farmers face with the problem of deciding whether to purchase crop insurance or not, and if they purchase an insurance, then what level of coverage to purchase. Crop insurance is quite complicated because it comes in many different levels of yield protection and the cost is associated with the level of coverage elected, and the premium subsidy decreases as the level of coverage increases. By definition, crop yields are risky, otherwise farmers would not be interested in purchasing insurance against low yields. In addition to crop yield insurance, farmers can also purchase a revenue insurance policy that insures against low yields and low prices.

A farm simulation model can be used to analyze the economic benefits of purchasing different levels of crop insurance. The model can be a simple model that just compares the economic returns for different insurance programs by simulating stochastic yields and indemnities and comparing the indemnities to the premiums for alternative policies. Or a complete farm simulation model can be used that has stochastic prices and yields for all crops and uses an income statement, cash flow statement, and balance sheet to show the economic consequences of alternative insurance policies on the economic viability of the farm. If a whole farm simulation model is available (see the Appendix), it is a simple task to add the formulas to calculate premiums and indemnities for crop insurance. The alternative policies being considered are simply programmed as scenarios and the model is run once for each insurance policy.

The results for simulating five alternative crop insurance options for a farm growing three crops are presented in this section. The NPV CDFs for the five insurance options are

Table 2 Summary of economic results from simulating the investment opportunity

	NPV	*PV ending net worth*
Mean	(77 462)	4 165 828
StDev	133 646	131 643
CV	(173)	3
Min	(574 180)	3 678 634
Max	338 152	4 571 859

	NCFI 1	*NCFI 2*	*NCFI 3*	*NCFI 4*	*NCFI 5*	*NCFI 6*	*NCFI 7*
Mean	58 031	61 271	48 916	24 893	(15 953)	(55 028)	(101 906)
StDev	55 649	54 481	54 497	57 743	51 520	53 380	52 041
CV	96	89	111	232	(323)	(97)	(51)
Min	(84 133)	(70 730)	(90 462)	(179 039)	(170 604)	(201 765)	(237 800)
Max	260 081	192 390	200 285	186 790	131 123	89 865	51 242
P(NCFI < 0)	5%	14%	30%	48%	73%	93%	100%

	EC 1	*EC 2*	*EC 3*	*EC 4*	*EC 5*	*EC 6*	*EC 7*
Mean	82 031	68 848	42 683	2 515	(77 482)	(198 781)	(369 909)
StDev	45 324	62 784	79 948	100 278	115 424	138 797	163 072
CV	55	91	187	3 988	(149)	(70)	(44)
Min	(50 043)	(140 261)	(209 254)	(320 486)	(447 128)	(666 364)	(949 746)
Max	213 127	215 082	254 661	268 987	206 268	151 167	129 618
P(EC < 0)	16%	15%	21%	34%	59%	84%	98%

Abbreviation: EC, ending cash.

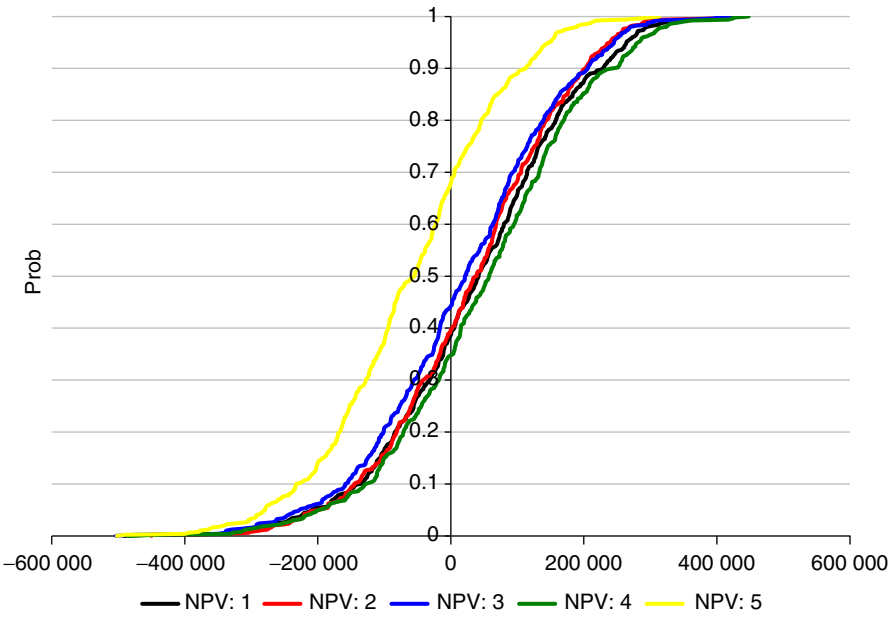


Figure 10 CDFs of NPV for five crop insurance options on a crop farm.

summarized in Figure 10. Scenario 5 is a no insurance option and is clearly the least preferred option. The CDFs for the insurance options cross, so that one cannot easily identify the best policy option for the farm. Stochastic efficiency was used to rank the risky alternatives for a range of relative risk-aversion levels that would likely fit the decision maker. The range of risk aversion was from risk neutral (relative risk aversion coefficient (RRAC) equal zero) to extremely risk averse (RRAC equal 4.0) in Figure 11. The power utility function was assumed for the analysis because the KOV used to compare the risky alternatives was NPV and it was calculated over a 5-year planning horizon. Based on the Stochastic efficiency analysis, the insurance policy associated with NPV-4 was the most preferred by all risk-averse decision makers because the certainty equivalents were greatest for this scenario across all RRACs.

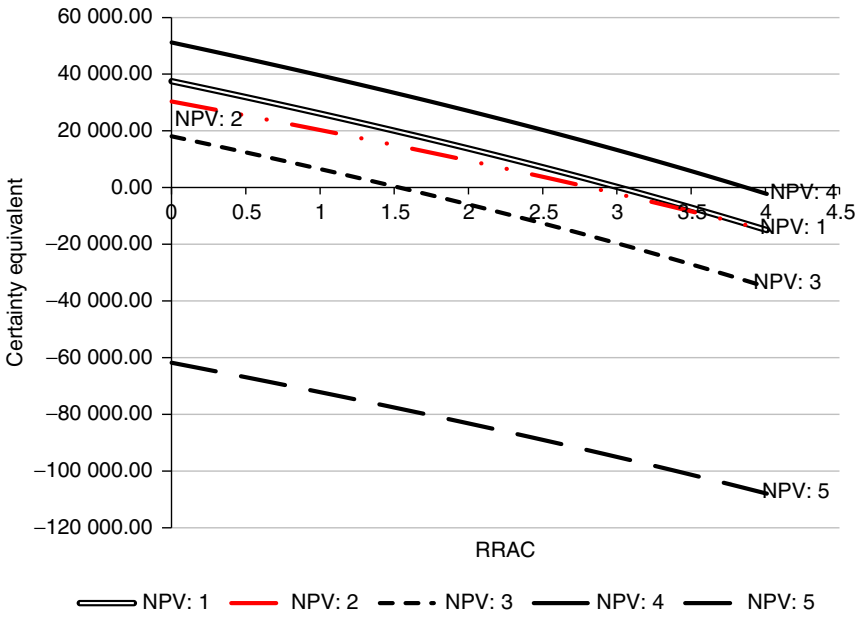


Figure 11 Stochastic efficiency rankings of five alternative crop insurance policies for a crop farm.

Technology Assessment

Technology assessment is another application of Monte Carlo simulation. In the case of technology assessment the task is two-fold: (a) prove that the technology is better than the existing technology and (b) calculating the value of the technology to the adopter so that the technology can be priced to extract the maximum rent to the technology owner. Technology assessments using simulation are not common in agriculture but can easily be done using simulation because technology is often introduced to reduce risk and reduce costs of production. If a technology is designed to reduce risk, then simulation that explicitly incorporates risk is the appropriate tool for assessing the benefits of the technology. Examples of risk-reducing technologies are: irrigation, drought-tolerant plant varieties, salt-tolerant crops, GMO crops, fertilization, and pest-control chemicals.

The example used here to demonstrate a simulation model to assess alternative technologies was developed at Texas A&M University for assessing the benefits of alternative technologies for small holder farms in developing countries. The economics model is part of the Integrated Data Support System which includes SWAT and APEX, which are biological models. APEX is a daily plant growth model capable of simulating a crop under alternative technologies using 30 years of weather data. The resulting output is 30 years of yields for a crop with an assumed technology/cultivation system. APEX's 30 years of yields are used to estimate probability distributions of yields for the base and alternative technologies that are used in the economics model.

The economics model, FARMSIM, simulates a small holder farm for 5 years using stochastic yields for the technologies being analyzed and stochastic prices for crops and livestock. Stochastic crop yields affect the quantity of feedstocks and pasture conditions for the livestock to the extent that forage from the crops are fed to livestock and pasture conditions are stochastic based on weather variability. Family consumption is restricted to raised crops and livestock products plus nutrients purchased using available cash. If cash is limited and raised nutrients are not available, the farm family suffers nutrient deficiencies. The KOVs in the FARMSIM model include the normal variables for NPV, NCFI, ending cash, and nutrient consumption for six nutrients. So, the FARMSIM model can show the economic and nutritional benefits of technology adoption for a family.

The results from simulating a small holder farm in Ethiopia are summarized in this section. The two technologies analyzed are: (a) use of irrigation and fertilizer and (b) use of irrigation plus adoption of fertilizer and improved seed varieties. A StopLight chart in Figure 12 shows the probabilities that the farm would have a cash flow shortage. There is a 34% chance of ending cash being less than 20 000 Birr in the Baseline and a zero chance of low ending cash under the two irrigation scenarios. Under the Baseline, the family's average daily consumption of energy is less than a minimum 11% of the time (Figure 13). This probability drops to zero for the alternative technologies due to increased production of food.

The value of the alternative technologies can be estimated using a risk ranking method called risk premiums. A risk premium is the difference in the certainty equivalents for the Baseline and an alternative technology. The certainty equivalents are calculated assuming a power utility function for all RRACs between risk neutral and extremely risk averse in Figure 14. The value of the irrigation and fertilizer technology is slightly over 30 000 Birr and by adding improved seed, the value of the technology is approximately 42 000 Birr over a 5-year planning horizon or almost 9000 Birr per year. The risk premiums are constant across the risk-aversion levels so that all risk-averse farmers would benefit equally from adoption of the two technologies.

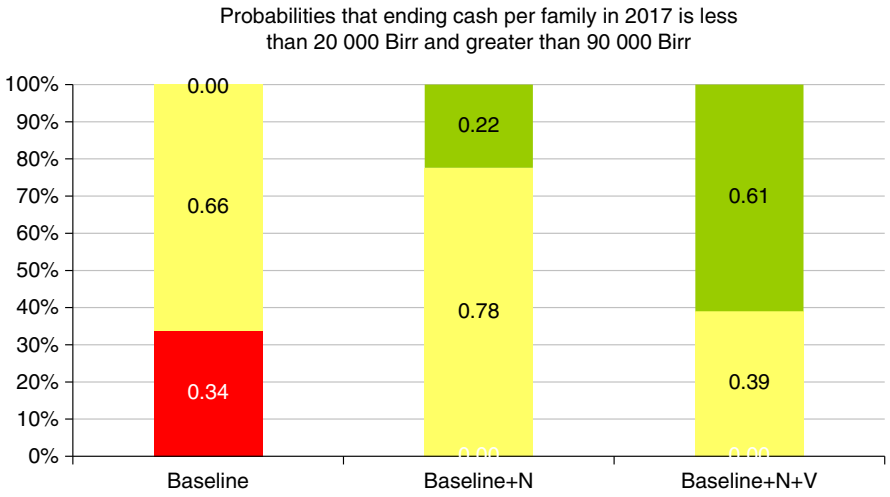


Figure 12 StopLight chart for comparing ending cash reserves under the base and two alternative technologies for a small holder farm in Ethiopia. Birr (Ethiopian Birr – Currency). N indicates the addition of fertilizer to its optimal level and V indicates the addition of improved seed technology through selective breeding for varieties adapted to the local conditions.

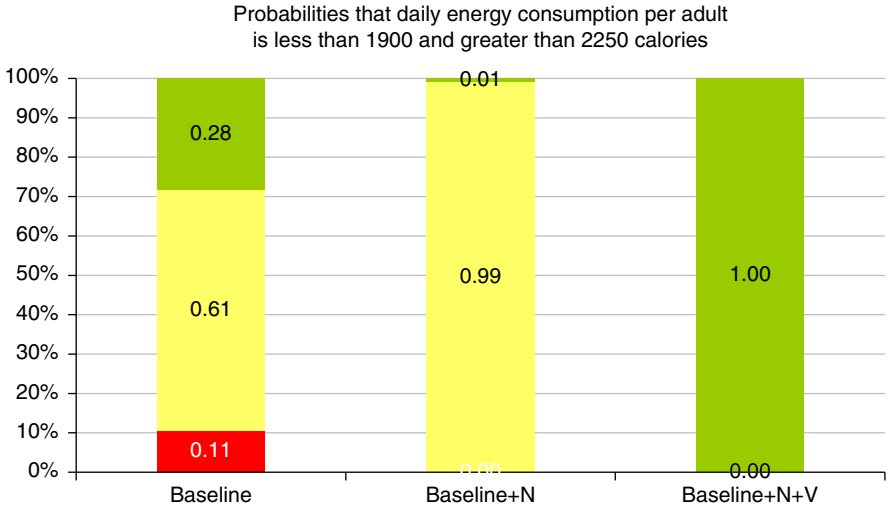


Figure 13 StopLight chart for comparing average daily consumption of energy for an adult equivalent assuming the base technology and two alternative technologies for a small holder farm in Ethiopia. N indicates the addition of fertilizer to its optimal level and V indicates the addition of improved seed technology through selective breeding for varieties adapted to the local conditions.

When simulating alternative technologies as demonstrated here, the risk premiums can be used to estimate the break point for pricing the technology. In the example shown in Figure 14, the value of the improved seed variety is approximately 6.3 Birr per hectare per year as the difference between the two risk premiums is 11 000 Birr (42 000–31 000) over 5 years and the amount of land the technology was applied to was 350 ha. Thus, a seed company wishing to value their improved seed could price the seed variety at some level less than 6.3 Birr and the producer would be better off than not adopting the improved seed.

Summary

Simulation is best suited for quantifying 'what if' questions and comparing probable outcomes for alternative actions. The brief description and examples of simulation analyses presented in this article should serve as a starting point for students and researchers interested in applying simulation to agricultural and natural resource issues. As demonstrated in this article, the introduction of risk into a simulation model is quite easily done and can be easily added to existing simulation models.

Agricultural and natural resource issues are particularly suitable for analysis with Monte Carlo simulation because of the strong influence of weather and price risks on agriculture. If one ignores risk in analyzing agricultural and natural resource issues, decision makers do not have a complete picture of the base situation or the projected consequences of actions they may undertake. Many decision makers are surprised when the outcomes they observe are different from the projections. Simply including risk in simulation models used for analyzing alternatives and making projection so that one can provide

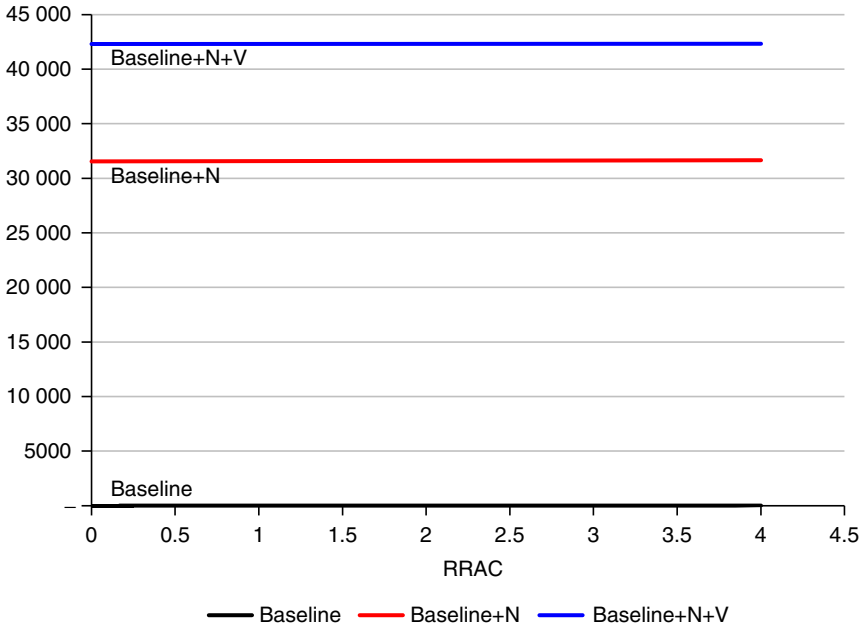


Figure 14 Value of technology for a risk-averse decision maker.

confidence intervals about the projections would help reduce the problem. Remember that, "point projections are always wrong, and projections presented in terms of a mean and a confidence interval are seldom wrong." Monte Carlo simulation is the tool for developing projections with confidence intervals.

See also: Agricultural Finance. Farm Management. Markets and Prices

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Appendix

Sample pro forma financial tables for a simulation model

Income statement	*2007*	*2008*	*2009*	*2010*	*2011*
Receipts					
Corn market receipts	376 393	327 837	347 442	457 512	489 057
SB market receipts	159 369	177 957	177 294	203 825	196 145
Corn indemnity	–	–	–	–	–
SB indemnity	–	–	–	–	–
Total receipts	535 762	505 794	524 736	661 337	685 202
Expenses					
Corn variable cost	140 250	146 842	149 823	151 875	153 622
SB variable cost	38 500	40 310	41 128	41 691	42 171
Corn harvest cost	53 366	45 460	51 587	68 979	76 926
SB harvest cost	6 606	6 913	7 196	8 122	8 712
Crop insurance premium	–	–	–	–	–
Land rent	142 500	145 357	147 962	150 562	153 330
Fixed costs	63 360	66 338	67 685	68 612	69 401
Operating interest	21 718	22 674	24 293	25 864	26 847
Land debt interest	34 702	33 627	32 470	31 227	29 891
Carryover debt interest	–	–	1 236	7 250	4 448
Total expense	501 003	507 519	523 379	554 182	565 347
Net cash farm income	34 760	(1 725)	1 357	107 155	119 855

Cash flow statement	*2007*	*2008*	*2009*	*2010*	*2011*
Beginning cash January 1st	65 000	44 764	–	–	–
Net cash income	34 760	(1 725)	1 357	107 155	119 855
Interest earned	1 950	1 343	–	–	–
Cash inflows	101 710	44 382	1 357	107 155	119 855
Land debt payments	14 344	15 419	16 576	17 819	19 156
Repay deficit loans	–	–	11 840	68 660	41 768
Family living	40 000	40 802	41 533	42 263	43 040
Family living bonus	1 738	–	68	5 358	5 993
Income taxes	864	–	–	14 823	19 141
Cash outflows	56 946	56 221	70 017	148 922	129 097
Ending cash December 31st	44 764	(11 840)	(68 660)	(41 768)	(9 242)

Balance sheet	*2007*	*2008*	*2009*	*2010*	*2011*
Cash December 31st	44 764	–	–	–	–
Land December 31st	1 050 000	1 102 500	1 157 625	1 215 506	1 276 282
Total assets	1 094 764	1 102 500	1 157 625	1 215 506	1 276 282
Land debt	448 355	432 936	416 360	398 541	379 385
Cash flow deficits	–	11 840	68 660	41 768	9 242
Total liabilities	448 355	444 775	485 020	440 308	388 627
Net worth	646 409	657 725	672 605	775 198	887 655

Consumer-Oriented New Product Development

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Introduction

For most companies, the introduction of successful new products is critical to the achievement of the short- and long-term corporate strategic goals of profitability, growth, and continuity. As an illustration, more than 25% of the current retail food sales in the US have been reported to consist of products introduced within the past 5 years (Hughes, 1994). Similarly, US marketing managers indicated that they expect 40% of the company profit made in 5 years' time would come from products not currently on the market (Booz *et al.*, 1982). Within the well-established product-market expansion matrix for growth (Ansoff, 1957), new product development (NPD) is identified as one of the important growth strategies of the firm.

Despite the fact that successful NPD is crucial to profitability and growth ambitions, the actual success rates of new product introductions are fairly disappointing. Although there is a lack of reliable data on actual success and failure rates, reported failure rates are ranging anywhere between 40% (e.g., Barczak *et al.*, 2009) and as high as 90% (e.g., Gourville, 2006). One reason for this lack of insight into actual success and failure rates stems from how success rates are being defined (Castellion and Markham, 2013). Success rates have been expressed as the percentage of commercialized new products that not only meet their marketing (e.g., market share and profit contribution) objectives, but also relative to the number of initial ideas that have entered the NPD selection process. Research on the 2003 the Product Development and Management Association best practices study (Barczak *et al.*, 2009) suggests that approximately 15% of the new product ideas and approximately 60% of the new products actually introduced into the market place make it to a commercial success in the market.

Whatever the exact metric and the exact percentage be, failure rates of new product introduction are an important concern to academics and practitioners alike, as new product introductions require substantial up-front investments that are not necessarily recouped from the new product's financial returns.

Bottom-line, NPD is an activity that is both necessary in light of market turbulence, but at the same time quite uncertain and risky in terms of potential failure. Not surprisingly, the NPD process has received a lot of attention in the marketing and management literatures (see Hart, 1996 for an overview).

New Product Development

NPD is an important activity within firms because of market turbulence; products do not have an infinite life. Rather, they go through a so-called product life cycle (PLC), which a company needs to anticipate to ensure that new products are added to the product portfolio to timely replace products that are nearing the end of their PLC. Also, NPD is identified as one of the basic growth strategies of companies.

Why New Product Development is Important

New product development as growth strategy

Early research by Ansoff (1957) suggested that growth strategies can be classified as to whether they use new or existing products and whether they address new or existing markets. Next to penetration strategy (increasing market share of existing products in current markets) and market development strategy (entering new markets with existing products), new product strategy involves developing new products for present markets and also plays a key role in the so-called diversification strategies where the company develops new products to enter new markets. Without new products, companies cannot grow over time as their existing products would gradually get 'outdated' against changing consumer needs and wants and new generations of products introduced by competitors.

Market turbulence

The need for NPD essentially arises from market turbulence on both the demand and the supply side (Van Trijp and Steenkamp, 2005). Consumer needs are subject to change over time, as are the specific ways in which consumers seek to satisfy these needs through the purchase and consumption of specific products ('demand'). Such changes may occur as a result of demographic, socio-economic, and cultural changes in society.

Turbulence also occurs at the supply side of the market. Changes in the political and legal environment trigger NPD through new requirements from (food) laws and regulations (e.g., increased minimal levels of animal welfare). Changes in the economic environment, such as increased or reduced purchasing power of consumers, will trigger innovation and development of new products that will deliver similar consumer benefits, but at a lower cost. Business strategies in terms of internal resources and business objectives also trigger innovation and predetermine in which categories and directions such innovation is to be found. Importantly, breakthroughs in (food) technology may provide new and unprecedented opportunities to both deliver new product-related benefits to the consumer and deliver existing benefits more effectively and efficiently. Finally, much of innovation activity is triggered by changes in the competitive environment, as new products introduced by competitors may change consumers' value perception of existing products in the market place. Together these developments create a highly dynamic context in which companies operate and compete for consumer loyalty.

The concept of product life cycle

A useful framework to think about the need for NPD is that of PLC. The concept of PLC implies that products, in terms of their sales and profits to the company, go through a four stage process (see Figure 1). At the introduction stage, sales are limited, costs per customer are high, and profit to the company tends to be negative as the necessary up-front investments in the new product cannot (yet) be recouped from sales and margins. At the introduction stage the clientele base for the new product primarily comes from the so-called innovator customers. At the growth stage of the PLC sales are rising not just among the segment of innovators, but also by attracting the so-called early adopters within the consumer population. At this stage of the PLC, companies attempt to increase their market share. Once a solid market share has been achieved, successful new products enter the maturity stage where profits increase and are managed. At this stage, the clientele base is expanded to include middle adopters, seriously reducing the costs per customer. But inevitably most products at some point reach a decline stage, where sales are declining because new products have already been introduced that more effectively or efficiently meet the (changing) consumer demand.

The importance of successful new product development

The concept of PLC nicely illustrates the importance of successful NPD. NPD activity requires substantial upfront investments which need to be recouped from the new product's performance in the market place. However, as is evident from Figure 1, it takes time before the product will take off, and generate sufficient margin and profit to compensate for the upfront investments. As a result, and in light of NPD failure rates, successful new products not only need to earn back their own investment costs, but also of those new products that fail to become successful. Next to the financial conditions, success in NPD also has an impact on the image of the company, as it makes the company more attractive to investors, but also helps to attract and retain creative employees. Successful NPD may help the firm to develop a learning curve on how to effectively synergize between the different functional departments of marketing, engineering, management, and production as well as sales. As an outcome of successful NPD, the firm may be able to create the so-called first mover barriers, for example, through patents that preempt competition from other companies trying to do the same thing.

Different Degrees of Innovativeness

New products introduced in the market place may differ considerably in their levels of newness, each with their own challenges and potential. Several classifications for innovativeness have been proposed, such as that between continuous (innovations with minimal impact on behavioral patterns of consumers), dynamically continuous (products with a higher degree of newness, but that still relate to products currently in use), and discontinuous innovations that violate some of the essential perceptions and habits and aim at creating new behavioral patterns on the part of the consumer (e.g., Gatignon and Robertson, 1991). A well-known classification from a company perspective is that of Booz *et al.* (1982), based on newness to the market and newness to the company, resulting in six categories.

At low levels of innovativeness, the category of 'cost reductions' involves new products that provide similar performance at lower cost, and the category of 'improvements and revisions of existing products,' similarly provide limited levels of newness in that they concern improved performance or greater perceived value with the aim to directly replace existing products. At medium levels of innovativeness, 'repositionings' also hold a limited level of innovativeness, as they are existing products that are repositioned to target new markets or market segments. 'Additions to existing product lines' carry a higher level of innovativeness in that these new products are designed to supplement existing product lines. They typically come as new flavors, new packaging (sizes), and the like. At the higher end of innovativeness, 'new product lines' bring a higher level of newness to the firm, but not necessarily to the market as such. New products aim to allow the company to enter an established market for the first time, and 'new-to-the-world products' are products that are so innovative that they actually

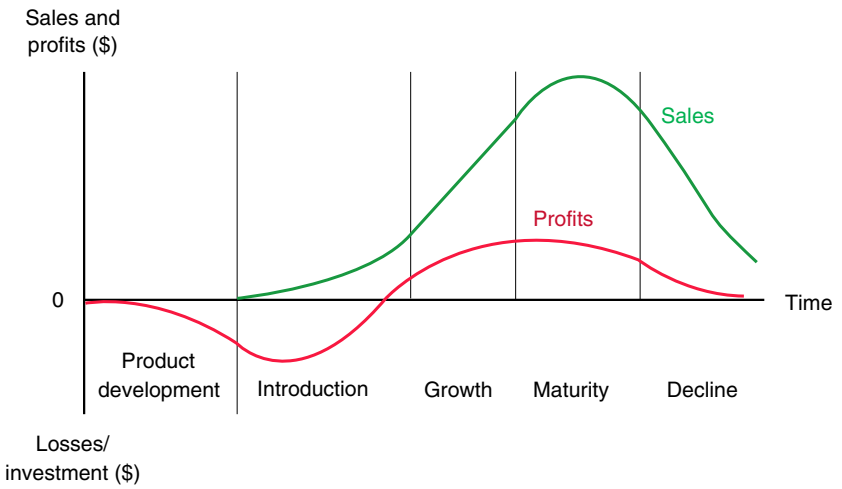


Figure 1 The product life cycle.

create a new market (Booz *et al.*, 1982). The vast majority of new products introduced in the market place involve improvements, additions to existing lines and product lines that are new to the company but not necessarily to the market. Importantly, the really innovative and new to the world products make up less than 10% of all NPD activity (e.g., Costa and Jongen, 2006), and the contribution of both this category and the new product lines category seem to be decreasing over time (Barczak *et al.*, 2009). Although there are no reliable figures for the level of innovativeness in food specifically, the situation in foods is unlikely to be very different. Food is seen as a traditional category with limited real breakthrough innovation.

Success and Failure Factors in New Product Development

There has been a lot of research into the success and failure factors of NPD. Much of this research is generic in nature with only a limited number of studies focusing specifically on NPD success factors in food (see Stewart-Knox and Mitchell, 2003; Kristensen *et al.*, 1998 for exceptions). Research on success and failure factors has essentially progressed along three dominant approaches.

Team performance approaches

Early work on the NPD process has focused on the use of structured processes for innovation management such as the stage-gate process. This line of research, popularized by Cooper and Kleinschmidt (1995), has taken NPD teams and their performance as the unit of analysis. For a wide variety of NPD teams, information has been collected on whether and how different steps in the stage-gate process were executed and at which level. This detailed information was then related to the NPD projects' market success, to identify crucial activities and performance that could differentiate the successful from unsuccessful projects. Based on this analysis, Cooper (1999) summarized the 'invisible success factors in product innovation' as follows:

- solid up-front homework – to define the product and justify the project;
- voice of the customer – a slave-like dedication to the market and customer inputs throughout the project;
- product advantage – differentiated, unique benefits, superior value for the customer;
- sharp, stable, and early product definition – before development begins;
- a well-planned, adequately resourced, and proficiently executed launch;
- tough go/kill decision points or gates – funnels, not tunnels;
- accountable, dedicated, supported cross-functional teams with strong leaders;
- an international orientation – international teams, multi country market research, and global or 'glocal' products.

Meta-analyses across scientific studies

A second approach takes the drivers of new product performance beyond team performance and process competencies, and uses scientific research publications as a basis. Through the so-called meta-analysis, consistency in reported relationships across different academic studies is extracted as a basis of strength of evidence for drivers of the NPD process. Henard and Szymanski (2001) differentiate between four broad clusters of drivers of NPD success, namely product-related factors (characteristics of the new product in terms of newness, sophistication, and product advantage), process-related factors (a structured NPD approach and proficiency in the various disciplines that need to be integrated for successful NPD), strategy-related factors (such as resourcing and cross-functional synergies), and market-related factors (such as competitive intensity and market potential). From these findings, Henard and Szymanski (2001) identified a more limited set of drivers that together account for no less than 59% of the explanation of innovation success. These factors are:

- product advantage (product related);
- product innovativeness (product related);
- marketing synergy (strategy related);
- technological synergy (strategy related);
- structured approach (process related);
- market orientation (process related);
- cross-functional integration (process related);
- competitive response intensity (market related).

A more recent update on Henard and Szymanski's (2001) meta-analysis (Evanschinsky *et al.*, 2012) confirms many of these success factors, but with smaller effect sizes and emphasizes the importance of culture as a moderator to the process, with generally weaker effect sizes for individualistic countries and stronger effects for risk-aversive countries. Product advantage, together with market orientation, comes out as the strongest determinants together with many process-related factors.

Monitoring of specific new products and their (marketing) context

A final approach zooms in more on the new product itself and the marketing context in which it is being positioned in the market place. For example taken by Steenkamp and Gielens (2003) and later extended to an international context (Gielens and Steenkamp, 2007). In this approach, 239 new product introductions in the consumer packaged goods sector were followed during 12 months period for their uptake in a household panel ($N=3687$). This approach takes four groups of determinants: marketing strategy (including relative newness and price), marketing communication (such as advertising and promotions), as well as product category-related factors (such as number of brands in the category, type of category, and advertising intensity in the category). Because the unit of analysis is household/consumer trial of the new product, this study also includes consumer characteristics (level of innovativeness and socio-demographics) as a determinant of new product success. Results on product-related factors are largely in line with those from other approaches, and confirm that the uptake of new products may differ between different consumer segments on the basis of their innovativeness as would be predicted from the product-lifecyle framework.

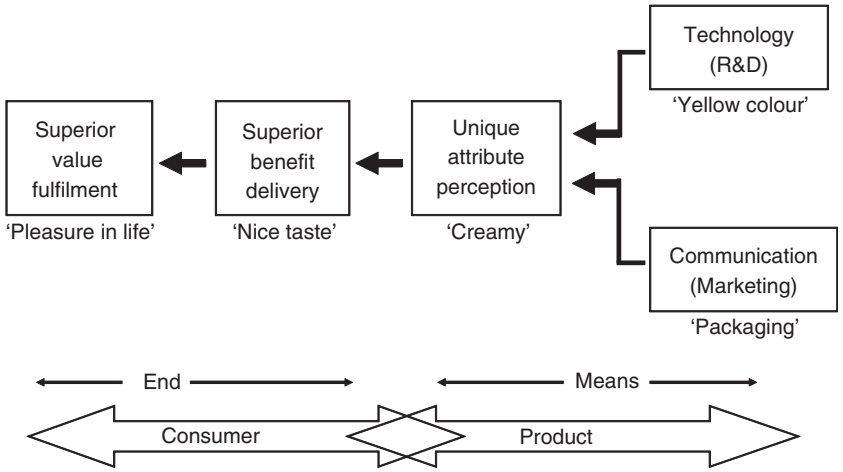


Figure 2 Products as a means to an end. Adapted from Van Trijp, J.C.M., Steenkamp, J.E.B.M., 2005. Consumer-oriented new product development: Principles and practice. In: Jongen, W.M.F., Meulenberg, M.T.G. (Eds.), Innovation in Agri-Food Systems: Product Quality and Consumer Acceptance. Wageningen: Wageningen Academic Press, pp. 87–124.

Integration of Success and Failure Factors

Although these three lines of research each take slightly different perspectives, they converge to a large degree, namely, that new products are more likely to be successful in the market place if:

- the product delivers something meaningful which is perceived of value by the consumer;
- in a way that is distinctive from competitive product offerings;
- the innovation is closely aligned to the capabilities of the company in that it synergizes between the marketing and technology competencies;
- the new product is brought forward through a well-designed and well-executed NPD process that is receiving sufficient support within the culture of the organization (market orientation).

Together these identified drivers of successful NPD form the basis of consumer-oriented NPD.

Consumer-Oriented New Product Development

The Essence of Consumer-Oriented New Product Development

Authors define consumer-oriented NPD as the challenge to the company to "optimally exploit and synergize its technological and marketing capabilities to deliver a distinctive product that is aligned to consumer needs and wants, with the aim to generate product trial and ultimately product loyalty" (cf. Van Trijp and Steenkamp, 2005). The latter addition is particularly important to the context of food and other the so-called fast moving consumer goods. Different from durable consumer goods, fast moving consumer goods are purchased and consumed (and hence re-purchased) on a regular basis. For such products the (product) quality experiences at the moment of consumption are critically important as they form the basis for the consumer decision to repurchase the product at a later stage.

New products as a means to an end

A key determinant of NPD success is the degree of fit between the new product and consumer needs (Grunert *et al.*, 1997). A useful framework to think of consumer-oriented NPD is that of means-end chain analysis (Gutman, 1982). Building on Lancaster's (1966) new consumer theory, means-end chain analysis assumes that consumers do not value products per se, but rather for the benefits that these products are believed to deliver on consumption. **Figure 2** illustrates this means-end chain perspective for a hypothetical case of mayonnaise. Technology can be exploited to change the color of the mayonnaise and marketing can be used to design an appropriate packaging (say glass jar). Consumers will interpret (perceive) these product features (say yellow color) by inferring attribute perceptions (e.g., 'the mayonnaise is creamy,' because consumers may infer that the yellow color comes from egg yolk which is believed to contribute to the creaminess of the mayonnaise). Such inferences in the form of attribute perception of the product may be relevant to the consumer, because he/she believes that creamy mayonnaises have better taste (hence superior benefit delivery). And finally, superior taste as a product benefit may, in the consumer's eyes, contribute to higher eating pleasure contributing to overall pleasure in life (superior value fulfillment).

Identifying these relevant links between product knowledge and consumers' self knowledge is central to means-end chain analysis and allows to understand why certain products are valued higher than others (Grunert, 2010; Gutman, 1997; Walker and Olson, 1991).

The process of linking product perception to consumers' value perceptions can be approached from different perspectives, sometimes referred to as different generations of innovation models (Berkhout and Van der Duin, 2007). A first generation of innovation, known as the 'technology push' model, started at the new technology side: new products were designed from technological opportunity and tested against

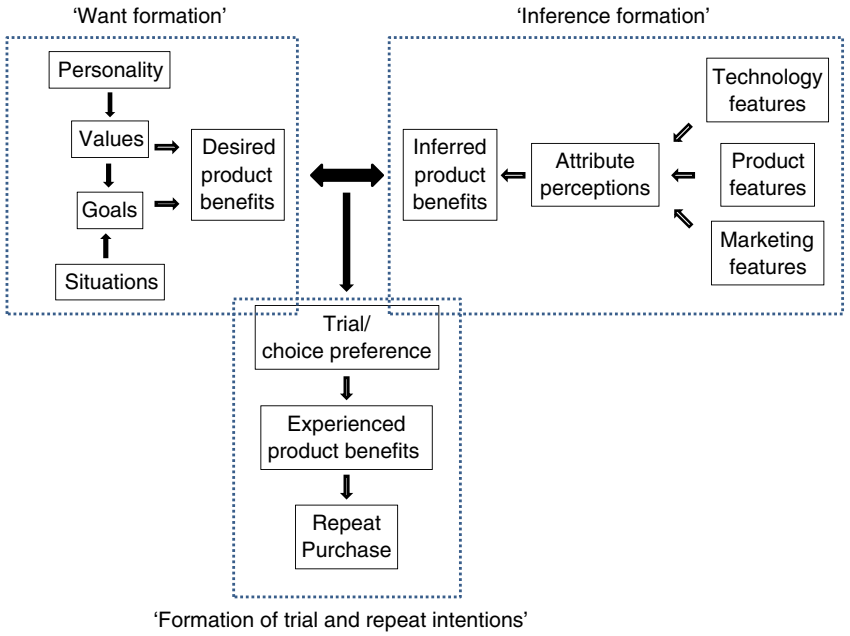


Figure 3 A simplified framework of how consumers decide on new products.

consumer perception and preference. The second generation started at the consumer side, also known as the 'market pull' model: if consumer needs and wants were understood, these could be reverse engineered into an optimal product design. The third generation, and also in line with consumer-oriented NPD as authors propose, attempts to find a more balanced input from both the consumer and technology sides throughout the process. This 'new' generation of innovation models takes consumer understanding as an integral part at all stages of a well-designed stage-gate process.

How Consumers Make Product Choice Decisions

Central to consumer-oriented NPD is the understanding of consumer behavior as the target of NPD success, next to technology and marketing understanding as a means to deliver a valued product proposition. Figure 3 illustrates a simplified representation on how consumer decision-making comes about as a function of three components: want formation, inference formation, and formation of trial and repeat purchases.

The architecture of the model is based on a simple marketing idea: consumers buy products not for their own sake, but because they think the product has characteristics that lead to desired benefits (Lancaster, 1966). This perceived match between wants and perception leads to preference and trial choice which, if delivering the promised benefits on consumption, will lead to repeat purchases. If the experience with the product after the first trial is positive, that is, the (new) product lives up to the consumer's expectations, the consumer may want to buy the product again.

The model has three major components: want formation, inference formation, and formation of trial and repeat intentions. Want formation deals with which benefits a consumer would like to obtain from a product at any moment in time, and this will be determined by both enduring personal (e.g., values) and situational factors (e.g., goals). Inference formation deals with how the consumer forms expectations about which attributes the product has and which benefits these attributes are believed to bring about for him/her inferred from available cues. Finally, formation of intentions for trial and repeat deals with how the comparison of wanted and inferred benefits leads, in comparison to the price of the product, to an intention to make a first-time purchase of the product, and how the subsequent experience with the product will affect intentions to keep on buying the product or not.

Consumers' want formation

The benefits that a consumer expects from a product are determined by both enduring and situational factors. Enduring factors are related to the consumers' values. Human values have been defined as "concepts or beliefs about desirable end states or behaviors that transcend specific situations, guide the selection or evaluation of behavior and events, and are ordered by relative importance" (Schwartz, 1992). Values are a popular and useful concept in the explanation of consumer wants, because they represent the ultimate human motivators with regard to a range of behaviors, including the purchase of products and services, and because there is a solid body of knowledge in social psychology on value types and their measurement. Various typologies of universal human values have been proposed, of which the one that has received most empirical support is the value domain model proposed by Schwartz (Schwartz, 1992; Schwartz and Bilsky, 1987). Schwartz proposes that human values can be grouped into 10 domains: power, achievement, hedonism, stimulation, self-direction, universalism, benevolence, conformity, tradition, and security, which can be grouped in a circular representation spanned by the axes of individualistic versus collective values, and conservative versus change-oriented values. The value domains are universal in the sense that they apply to all

human beings, but people will differ in the relative weight they attach to these values. Values have been used widely to explain consumer choices (e.g., Beatty *et al.*, 1985; Kahle, 1986; Kamakura and Mazzon, 1991), but their main advantage, namely that they are stable across situations and time, is also a disadvantage: abstract values, while often related to specific product choices, are relatively weak predictors of such specific behaviors, which are influenced by a host of other likewise more specific factors. Values provide the enduring motivational aspects of consumer wants, but to explain consumer choice, they will usually have to be supplemented by other factors taking into account situational factors.

Goals have a higher degree of specificity than values, and they have a situational component. When buying food, a consumer can have a goal of pleasing the family, of rewarding himself, of losing weight, or a host of other things. A goal of pleasing the family will be linked to underlying values, like benevolence and security, but will also have a situational component, as pleasing the family is not relevant, for example, when buying food in the canteen of one's workplace. Several goals can and mostly will be salient with regard to any particular food choice, and they can be in conflict with each other, such as when a goal of losing weight conflicts with a goal of rewarding oneself with a pleasurable experience. Developing products that solve goal conflicts is one important avenue to pursue in NPD in the food sector.

People differ in which goals are usually dominant when they choose food, and instruments have been developed to measure these differences and segment consumers accordingly. The food-related lifestyle approach has been a popular approach to this end (Brunsø *et al.*, 2004; Grunert *et al.*, 2001). Food-related lifestyle designates different ways in which people use food to attain life values and leads to generic consumer types that differ with regard to dominant goals and ways of shopping, meal preparation, and eating. The generic types identified are the uninvolved consumers, who are really not very interested in food, the careless consumers, who emphasize novelty and convenience, the conservative consumer, who puts priority on traditional meals and generally uses eating to establish a sense of security, the adventurous consumer, with an emphasis on social and innovative goals in preparing and eating meals, and finally the rational consumer, who has a reasoned approach to food choice and values healthfulness highly. This instrument has been popular in Europe and has even been applied in China (Grunert *et al.*, 2011).

Goals thus point at desired benefits that the consumer wants to get out of the product to be bought. Desired benefits can be many things, but from social dilemma theory (Van Lange *et al.* (2013) and Construal Level Theory (CTL) (Trope *et al.*, 2007), it is suggested that they can meaningfully be classified as to whether they deliver benefit to the self or to others, and whether they deliver direct gratification or delayed gratification (e.g., Van Trijp and Fischer, 2011). Directly gratifying self-oriented benefits include the sensory properties of the food, its convenience, and its price. Self-oriented delayed benefits include the health value of products. Other-directed benefits with relatively direct reinforcement value include motivations of local production to stimulate regional economic development and animal welfare motivations. Delayed, other-directed benefits include sustainability considerations and the impact of new food technologies on the environment and impact on society.

Research from the CTL tradition suggests that self-oriented benefits that deliver instantaneous gratification ('feasibilities') are more likely to be driving forces in situations of low psychological construal (such as the choice situation), whereas preferences for other-directed benefits with delayed gratification (the 'good intentions') take priority in situations of high psychological distance (such as in survey situations). Thus, identifying desired benefits in any particular situation is a methodologically challenging task.

Consumers' inference formation

To infer whether any of the available products matches the desired product benefits, the consumer makes inferences about the available options in the product assortment. This is the process of inference making and benefit perception (Kardes *et al.*, 2004). Based on the characteristics of the product as delivered by its features, description, and positioning, consumers will extract attribute perceptions from which expectations are formed, in a means-end framework, regarding the benefits that the product will deliver. Such benefit inferences carry a degree of uncertainty. In many instances these inferences can build on product associations that are learned from previous experience. Product benefits for which this is possible are known as experience qualities of the product (e.g., Steenkamp, 1990). If a product has delivered good taste, convenience in use and other benefits that are directly perceivable on consumption, this will strengthen the expectation on the next consumption occasion. For many product qualities, the so-called credence qualities (Darbi and Kerny, 1973), such learning from experience is however not possible. For example, to what extent a product delivers health, sustainability, or animal welfare, cannot be verified from personal experience, not even after normal consumption. Yet, consumers form beliefs about such credence qualities through two important psychological processes, known as informational and inferential belief formation (Fishbein and Ajzen, 1975). In information belief formation, consumers make inferences from information provided by relevant and authoritative others, such as through the use of labels, claims on the packaging, and recommendations from, for example, consumer organizations. In inferential belief formation, consumers use their own rules of thumb in what they believe are informative relationships. As a result, packaging cues such as color (say green) may trigger inferences about credence quality attributes such as that the product is probably natural and sustainable. Inferential belief formation based on the so-called quality signals or quality cues (Grunert, 2005) constitute an important consumer strategy when the benefits expected from the product are unknown, and when previous experience is of no help.

The way in which consumers make inferences from quality cues will not necessarily lead to 'correct' inferences in the sense that they will correctly predict the benefits that the product will deliver. For example, consumers are known to use color and fat content of meat as an indicator of taste and tenderness (Brunsø *et al.*, 2005) and organic production as an indicator of superior taste of vegetables (Padel and Foster, 2005). Both of these inferences are, from an objective point of view, at least questionable. Consumers' ability to make such inferences will

depend on their level of knowledge and competence with regard to the product (Selnes and Troye, 1989). When asking consumers which information about a piece of meat they believe to be predictive of taste and tenderness, many consumers believe that information about breed, age of animal, and slaughtering date are predictive of these qualities. But few consumers feel confident in using them, i.e., making the right inferences based on this type of information, because they are not meat experts. Thus, consumers end up making inferences based on cues with which they feel confident, like color of meat and visible fat content, even though they may be aware of the fact that these characteristics are not always highly predictive of taste and tenderness. Such inferences can be deliberate, but often they will be done in a semiconscious, almost automatic way.

Inference processes are getting more complex as new products carry more and more information. A new product that comes on the market will have a brand name, carry nutritional information, may have quality marks and sustainability labels, and carry nutrition and/or health claims. This information may be supplemented by soft claims like the product being natural or good for you, and all this will be embedded in packaging that makes use of colors, pictures, and various stylistic elements. It is the complete array of this, together with the context in which the product is displayed and promoted, that forms the basis for consumer inferences.

The way in which consumers make inferences about product benefits from available cues is based on consumers' product knowledge. When combine consumers' product knowledge, i.e., knowledge about how to infer product benefits from an array of cues, with consumers' knowledge about themselves, i.e., with knowledge about how product benefits will help them attain their goals and values, a complete means-end chain is obtained, as shown in Figure 2. A means-end chain is thus a device to show how consumers become motivated to buy a product based on the combination of knowledge about the product and knowledge about oneself.

Formation of trial and repeat intentions

The extent to which the product benefits that consumers infer from a new product will have matches with the benefits that they desire will be related to the consumer's willingness to try the product, i.e., buy it for the first time. However, the perception of benefits will lead to purchase only when the benefits are perceived as high enough for the consumer to be willing to pay the price demanded in the shop. Measuring willingness to pay and how willingness to pay depends on product characteristics is an established research area in agricultural economics and marketing, and a range of methods is available to this purpose (e.g., Miller *et al.*, 2011). In determining willingness to pay, consumers will try to find points of comparison. Consumers may be familiar with average prices in the product category of which the new product is a member, and will then usually use these as a benchmark. If the new product has an above-average price within the category, willingness to pay will depend on whether the expected benefits clearly exceed the benefits of those products that are already on the market. For a product with a high degree of innovativeness, categorization into an established category may be more difficult and reference prices hence also more difficult to base a judgment on, but consumers will in most cases try to find some point of comparison based on previous experience that allows them to come up with a judgment on the price of the product.

After a product has been bought once, the consumer will have an experience with the product, and this experience will have an important influence on whether the consumer wants to buy the product again. Because, as already noted in the Section Consumers' inference formation, only some benefits that a consumer may expect from a food product can in fact be experienced, mostly taste and convenience, authors may tend to conclude that the decision on whether to buy the product again will depend mainly on the experience with these particular benefits. To a large extent, this is true: a product with a bad taste will not usually be bought again, in spite of other benefits in terms of healthfulness and sustainability. Also, there is evidence that the relative weight of those benefits that indeed can be experienced increases after the purchase at the expense of those that cannot be experienced. In other words, after consumption, taste plays a bigger role in the evaluation of the product compared to healthfulness, than before the purchase. However, the mechanisms at work are more complicated. When a range of competing products do not differ a lot in terms of taste and other benefits that can be experienced, the more intangible benefits will play a larger role, also when it comes to repeat purchases. Inferences in the prepurchase phase and perceptions in the consumption phase may influence one another, such as when a consumer believes that an organically produced product indeed has a better taste than competing products with an identical sensory profile, simply because this is what was expected and the experience is assimilated toward the expectation. Also, during preparation and consumption, new cues may arise that can strengthen or weaken the consumer's perception of the presence of benefits that cannot be experienced. For example, the consumer may think that the feel of the packaging is not very sustainable, or that the taste of the product indicates that it may after all not be very healthy.

The sensory experience with the product, together with convenience, are therefore still decisive for whether a trial purchase of a new product turns into a repeat purchase. But this is mainly a factor that can prevent a repeat purchase, if the product clearly disappoints in terms of taste and convenience compared to competing products. An acceptable taste may not be enough to encourage repeat purchase in an era where new food products are increasingly positioned in terms of intangible benefits like healthfulness, sustainability, naturalness, and authenticity. These benefits being intangible, not amenable to experience, implies that food manufactures need to ensure that the belief in these benefits is kept alive in the mind of consumers throughout repeat purchases, to prevent that these benefits are, over time, crowded out in the mind of the consumer by the more tangible benefits.

Integrative Approaches to Consumer-Oriented New Product Development

The consumer decision-making process, described in the Section How Consumers Make Product Choice Decisions, forms the heart of consumer-oriented NPD, where the aim is to design new products (product and technology features) and to

position these in the market place (marketing features) in a way that they are aligned with consumer-desired benefits in a distinctive way, such that trial (from product quality expectations) and repeat purchase (from experienced product quality) is induced.

This is a challenging task that requires close interaction between the technological and marketing/consumer science capabilities within the company. Market orientation plays a crucial role in this process.

Market orientation

The importance of market orientation as a driver of company performance and success in the market place is one of the best established findings within the marketing literature (see Kirca *et al.*, 2005 for a review). Market orientation involves the organizational norms and values to behave consistent with market orientation, as evidenced in closely monitoring customers and competitors with a focus on inter-functional coordination within the company (Narver and Slater, 1990). The behavioral perspective on market orientation (e.g., Kohli and Jaworski, 1990) emphasizes the activities of generation of information about customers and the market place, the dissemination of this information across different functional disciplines within the company, and use of this information as a basis for a coordinated and responsive marketing approach and market offering. Market orientation enhances a company's performance through a higher level of innovativeness, which serves as a basis for customer loyalty and perceived product quality delivered to the market place (Kirca *et al.*, 2005). Market orientation has both a responsive (aligning with existing consumer needs and wants) and a proactive (addressing latent and emerging consumer needs) component to it (Narver *et al.*, 2004), and hence forms a strong basis for NPD.

Quality function deployment as an overarching framework

Dissemination of customer information across the functional disciplines, and particularly between the marketing and technology departments, is crucial to designing an optimal response in the form of new product introductions. However, such effective communication between the marketing and technology disciplines within the company is often poorly developed (Atuahene and Evangelista, 2000) and a source of NPD failure (Souder and Chakrabarti, 1978).

Quality function deployment (QFD) has been proposed in the early 1970s as a highly structured planning tool to make explicit the 'translation' process of relating consumer and customer inputs to technical design parameters and product requirements. QFD has been applied in many different industries (Hofmeister, 1991), including the food industry (e.g., Costa *et al.*, 2001). QFD consists of four modules of which the first one, the so-called House of Quality, has most relevance for consumer-oriented NPD (e.g., Hauser and Clausing, 1988), as it specifically focuses on the translation of consumer choice criteria into (technical and marketing) product design parameters. **Figure 4** provides a simplified version of the House of Quality.

The House of Quality structure integrates the key questions that form the heart of NPD as will be outlined below, referring to numbering in **Figure 4**.

1. What are the product characteristics desired by the consumer? This 'box' refers to the identification of the key needs and desires that drive consumer choices in the product category. It includes those desires that are necessary to meet and surpass competition and those on which the new product will have improved or unique delivery. Marketing and consumer research are the key tools for identifying the consumer needs and desires as well as their

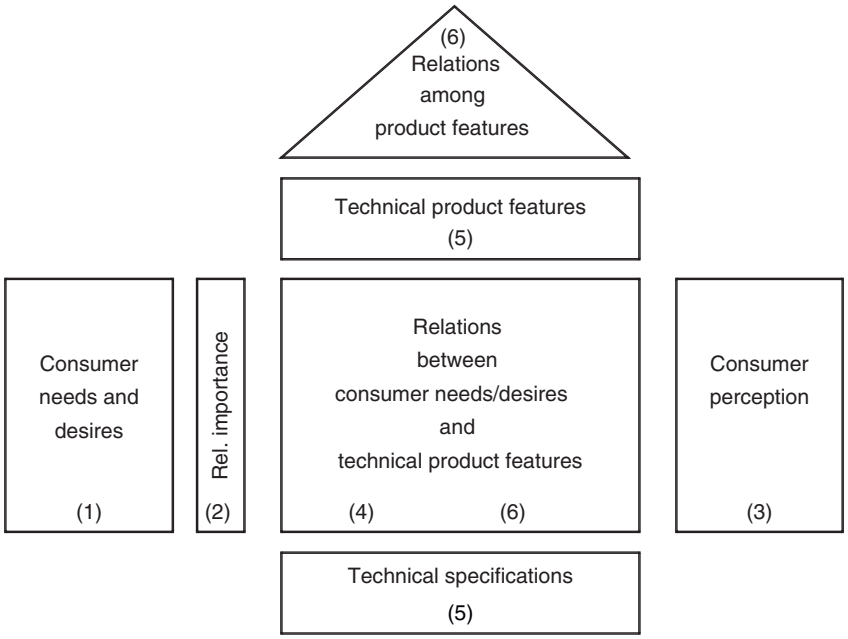


Figure 4 The House of Quality within Quality Function Deployment. Adapted from Van Trijp, J.C.M., Steenkamp, J.E.B.M., 2005. Consumer-oriented new product development: Principles and practice. In: Jongen, W.M.F., Meulenberg, M.T.G. (Eds.), Innovation in Agri-Food Systems: Product Quality and Consumer Acceptance. Wageningen: Wageningen Academic Press, pp. 87–124.

hierarchical nesting. Several techniques are available for this purpose (see Griffin and Hauser, 1993 for an overview), including exploratory qualitative techniques such as in-depth interviews and focus groups as well as more structured approaches such as Kelly's Repertory Grid and Free Elicitation (see Steenkamp and Van Trijp, 1997). A particularly useful technique for revealing the hierarchical nesting of need levels within the means-end chain paradigm is that of laddering (Reynolds and Gutman, 1988).

2. How important are each of the product characteristics to the consumer? Box 2 recognizes that some needs may be more important than others in driving consumer choice within the targeted product category. Identification of attribute important is a crucial step in QFD as any company will prefer to spend its limited resources where they matter most to the customer. Attribute importance is a complex and not always well-defined concept, for which a number of measurement methodologies are available (Van Ittersum *et al.*, 2007). An important distinction needs to be made between attributes that are important in an absolute sense and those that are determinant in consumer choice behavior, as some attributes are a 'conditio sine qua non.'
3. Will adjustments on a consumer attribute lead to competitive advantage? This box addresses the issues of whether changes introduced through the new product will be recognized by the consumer as a competitive edge vis-à-vis competing products already in the market place. Marketing and consumer research are conducted here in the form of the so-called quantitative perceptual mapping techniques (Urban and Hauser, 1993; Steenkamp *et al.*, 1994; Steenkamp and Van Trijp, 1996b). Perceptual mapping research identifies how the consumer perceived product alternatives on key attributes.
4. What are the implications for technical adjustments to the product? The so-called relationship matrix forms the heart of the House of Quality in that it links "what the product is aimed to deliver" (the marketing opportunity) to "how this can be realized" (the product design) in the form of engineering characteristics of the new product. At this stage, relationships are established on how product design features affect consumer perceptions and need satisfaction, and if so how strong these relationships are. Typically these relationships are not of a one-to-one nature, as multiple engineering characteristics combine and interact into a consumer perception of the product. Also, and particularly in the food domain, these engineering characteristics are not orthogonal implying that they cannot necessarily be manipulated independently of each other. These correlations between the engineering characteristics are reflected in the 'roof' of the House of Quality. A statistical implication of the dependence between engineering characteristics is that complex multivariate statistical methods are required for the translation process from marketing opportunity to new product design as reflected, for example, in the Quality Guidance model (Steenkamp and Van Trijp, 1996a).
5. Do consumer attributes have physico-chemical counterparts? Once the relationships have been established, profiling a selection of potential new product alternatives in terms of their engineering characteristics is an integral part of the analysis. Together with insights into the consumer perceptions, this provides highly diagnostic information. For example, a situation may occur where two products show differences in consumer perception (box 3) but not in terms of engineering characteristics. In such case, the new product design needs to be complemented with marketing communication and positioning to realize the desired product image and to gain competitive advantage in the market place.
6. What is the effect of technical adjustments on other consumer attributes? As a final step, this box brings into the picture to what extent technical improvements on one consumer attributes may go at the expense of consumer perception and delivery on other relevant consumer attributes. This step is often overlooked because of some degree of product myopia. For example, reducing the salt levels in a soup will improve the healthfulness of the product, but at the same time may also negatively impact on the (perceived) taste of the product. Such trade offs need to be carefully considered in the process of new food product development.

In summary, QFD provides a highly structured framework for identifying the relevant relationships in the process of translating new product opportunity to product design. However, the structured nature is both a strength and a weakness. Particularly in the food context the product characteristics and design features often interact in highly complex ways and can rarely be manipulated independent of one another. This may partly explain, why QFD has been influential in the food sectors as a thought process, but not as an actual practice. Nevertheless, QFD has served as an important source of inspiration to food-specific quality perception models as a basis for new food product development, such as the Quality Guidance Model (Steenkamp and Van Trijp, 1996a) and the Total Food Quality Model (Grunert *et al.*, 1996).

Structured Approaches to New Product Development

NPD success strongly benefits from the adoption and execution of highly structured innovation processes, with continuous feedback on (anticipated) consumer response. Most innovation projects follow the general NPD stage-gate process, consisting of a number of phases after every of which a go-no-go decision is made on the basis of relevant feedback from the market place.

The New Product Development Stage-Gate Process Model

Structured approaches to NPD conceive it as consisting of a number of phases or stages (Trott, 2008), although the exact number and the naming of the stages differs. Authors follow Van Kleef *et al.* (2005), who distinguish between the stages of opportunity identification, development, optimization, and launch. Structured processes as particularly important as they identify the critical steps in moving from initial idea conception all the way through to the actual 'product as marketed' being launched into the market place. Up-front investment costs to the company increase from the left to the right of the

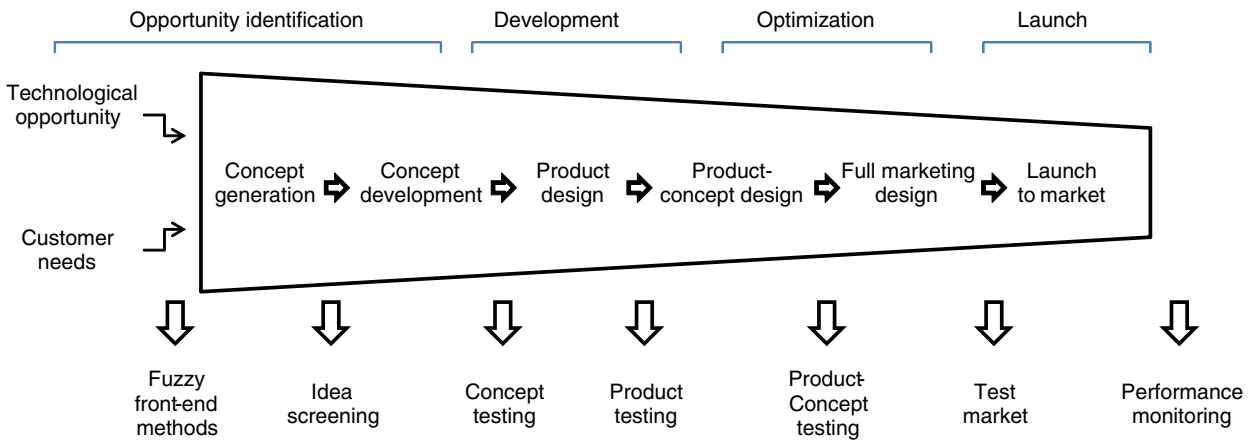


Figure 5 The formal stage-gate process to NPD.

stage-gate process and hence also the (financial) risk to the company. This is why 'gates' are introduced in the process at which the feasibility of the new product, in different stages of development, is critically assessed and reviewed. Crucial stages in the process, where costs increase sharply are the actual development process (i.e., product design), the full marketing development, and the market launch stage.

Figure 5 represents the stage-gate process, including the activities and the critical gates which are implemented through consumer/market testing. First, new market opportunities have to be identified from both understanding of consumer and customer needs as well as new technological opportunities. From this, new product ideas are being developed and screened for their potential to the company, including their technical and economic feasibility. From this insight, product concepts are being developed which essentially reflect a very concise description in consumer terminology of the product's core benefit proposition: "the unique benefits that the product is to provide to customers as well as those benefits required to meet and surpass competition" (Urban and Hauser, 1993, p. 164). If the results from concept testing are promising, the new product may actually be designed; first as a product prototype and later in combination with its intended positioning in the market place (product-concept design). If product and product-concepts tests with customers and consumers yield positive results, the marketing mix of the product may be further developed, including the packaging and the advertising materials. In some specific situations, the product may then be tested in a test market (either real or experimental) as a basis for the final product launch into the market place.

Consumer research for the stage-gate process

Consumer research methodology for most of the gates in the stage-gate process is well developed and documented, particularly for the design and optimization stages (e.g., Ozer, 1999; Kaul and Rao, 1995; MacFie, 2007), with the aim to screen out new product ideas, concepts, and prototypes that may be unsuccessful in the market place. However, increasingly it is being recognized that NPD effectiveness and efficiency relies as much on 'screening-in' promising ideas and opportunities upfront (known as the 'fuzzy front end of innovation') as it does on 'screening-out' options during later phases.

Consumer input at the fuzzy front end has been challenged by some authors on the argument that many existing consumer research techniques are better equipped for measuring consumer response to presented new product ideas (i.e., product screening) rather than for using consumers as a source of new idea generation (Eliashberg *et al.*, 1997). Mainstream consumers are seen as a poor source of inspiration and creativity, because of their 'status-quo bias,' through which their thinking is heavily restricted by their current experiences (e.g., Lilien *et al.*, 2002). Yet, all research on NPD success indicates that 'bringing the voice of the customer upfront' already in the fuzzy front-end of NPD is an important success factor. Selection of market and consumer research methodologies at the fuzzy front end of NPD is hence crucially important, and a variety of research methods are available to enhance actionability without limiting creativity (Van Kleef *et al.*, 2005).

Consumer acceptance of new products

More generic research on consumer acceptance of innovations and new products largely originates from the early work by Rogers (1995). Rogers identified five the so-called innovation characteristics, perceived product attributes of an innovation, which affect the rate of adoption of new product innovations. These innovation characteristics are as follows:

- relative advantage: the degree to which the innovation is perceived as better than the product it replaces;
- complexity: the degree to which an innovation is perceived as difficult to understand and use;
- compatibility: the degree to which an innovation is perceived as being consistent with the existing values, past experiences, and needs of potential adopters;
- trialability: the degree to which an innovation may be experimented with on a limited basis;
- observability: the degree to which the results of an innovation are visible to others.

All five factors are highly relevant to the acceptance of new food products and particularly the first two factors have become central to the research tradition of Technology Acceptance Models (e.g., Venkatesh *et al.*, 2003), where they have be

relabeled as 'Usefulness' and 'Ease of Use.' This research confirms that innovation are more likely to be accepted and adopted by end user, if they add value over and above the products currently in use, and are easy to understand and use.

However, in the specific case of new food products, aspects of compatibility play an important role too, next to relative advantage and (low levels of) complexity. A first reason why compatibility is important in new food product acceptance is that new (an unknown) technologies applied to foods, which are actually ingested into the human body, are often approached with reluctance on the part of the consumer (Siegrist, 2008; Ronteltap *et al.*, 2007). This is not because of product performance-related inferences but because of socio-political attitudes that consumers hold with the technology (Frewer *et al.*, 2004; Scholderer and Frewer, 2003). Importantly also, food behaviors have a strong cultural and habitual component to them, which makes consumers reluctant to accept new products that require adjustment in existing food routines (e.g., Van Trijp and Van Kleef, 2008). Hence for new food products (e.g., Rozin, 1976), generating consumer acceptance may even be more challenging than for products outside the food domain (Szymanski *et al.*, 2007).

Concluding Remarks

As started off this article by stating that NPD is a necessary yet high risk activity for the firm. However, throughout this article it has been argued that this risk can, at least to some extent be managed. Authors provided evidence that consumer relevance of the product advantage and market orientation throughout the process are key identified factors for NPD process. Authors developed a simplified model of how consumers make decisions regarding (new) product decisions, and used this as a basis for consumer-oriented NPD. Incorporating this consumer perspective throughout a structured and well-executed NPD process enhances the changes of NPD success.

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Critical Tracking Events Approach to Food Traceability

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Glossary

Case of illness An individual person who acquires a disease or illness associated with an epidemiologically significant exposure.
Critical Tracking Event A physical point in the food supply chain where an operator identifies a minimum set of event data to systematically collect, typically consisting of three basic data items: unique location/Event ID, unique Item ID, and date/time.
Food supply chain A sequence of processes involved in the production and distribution of food.
Global Trade Identification Number (GTIN) An identifier for trade items used to lookup product information in a database or between databases.
Hazard analysis critical control points A systematic preventive approach to food safety and allergenic, chemical, and biological hazards in production processes that can cause the finished product to be unsafe as well as designs measurements to reduce these risks to a safe level.
Key data element A set of data, defined by a food operator, associated with a Critical Tracking Event.
Product case It is typically the smallest logistic unit in consumer supply chain; a cardboard box or container holding individual consumer units for sale in a retail setting.
Universal Product Code (UPC) A barcode symbology used to track trade items in stores.

Introduction

Foodborne outbreaks represent a significant burden of illness in the United States and internationally causing significant morbidity and mortality (Scallan *et al.*, 2011; Kuchenmüller *et al.*, 2009). Although the majority of these illnesses are of an unknown etiology, a significant number are associated with commercially distributed foods. As the complexity and speed of the food supply increases, private industry, government regulators, and public health officials have been challenged in tracing potentially implicated foods during and after foodborne illness outbreaks. Notable examples include outbreaks associated with spinach, peanut butter, shell eggs, fresh produce, and pet food (Wendel, 2009; Medus *et al.*, 2009; Cavallaro *et al.*, 2011; Braden, 2006; Anonymous, 2010).

As a result of these outbreaks, improved recordkeeping and traceability requirements were included in the landmark passage of the Food Safety Modernization Act in January of 2011. This Act specifically required the Food and Drug Administration to establish pilot projects to explore and evaluate methods to rapidly and effectively identify recipients of food to prevent or control a foodborne illness outbreak.

Surprisingly to many, the primary goal of food traceability is not food safety. The primary goal of food traceability is to improve investigational efficiency. Specifically, the goal of improving food traceability is to improve the speed of investigations as well as the accuracy of results. Therefore, the problem of food traceability requires a mindset that is first rooted in logistics rather than food safety. Certainly, achieving improvements in food traceability will more likely result in fewer cases of foodborne illness, reduction in the amounts of otherwise wholesome foods discarded, as well as added protection of industry segments and/or product brands from erroneous implication in outbreaks. Also, increasing the number of successful outbreak investigations will lead to more opportunities to learn from mistakes, resulting in accelerated improvements to food safety throughout the supply chain. Therefore, increased food safety is a likely but indirect benefit of improvements in logistic performance related to food traceability.

Although the link between food traceability and food safety exists, there are a few layers of activity, action, and investment required to better secure that linkage. Historically, the food industry and the FDA have tended to view food traceability exclusively through the prism of food safety rather than logistics and that may have slowed innovation and adoption of effective food traceability solutions. Food safety tends to involve conditions of handling, processing, and production as opposed to movement of products through the supply chain. Specifically, food safety is a quality function, whereas food traceability is a logistic one. Although safety is always a concern with food, logistics involves a different perspective, different skill sets, and different tools than production-oriented quality control and assurance.

Currently Accepted Concepts for Food Traceability

Based on current regulatory requirements to maintain one-forward-one-back (OFOB) traceability documentation (Anonymous, 2002), most supply chain participants are comfortable with the concepts of 'internal' and 'external' traceability. However, traceability requires that linkages through each operation are maintained, so these definitions of 'internal' and 'external' are not particularly useful in trying to comprehend the problem and possible solutions. Some operators argue that this definition is necessary to protect internal proprietary information, but authors will show this to be unfounded. By focusing on solving 'external' traceability at the expense of 'internal' traceability, effective traceability solutions

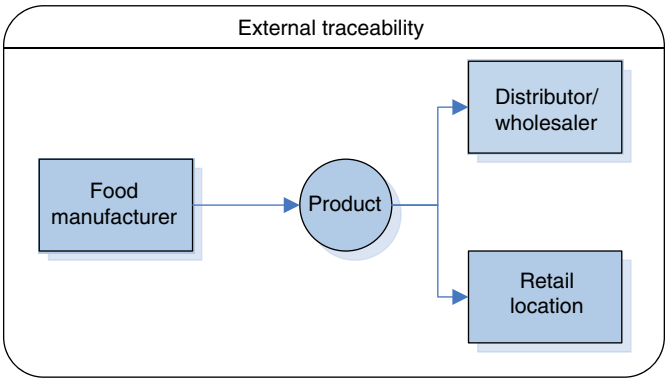


Figure 1 Example of external traceability. A food manufacturer produces a product and tracks the distribution of that product to a distribution and retail location.

remain elusive. Therefore, the hope to eliminate the notions of 'external' and 'internal' traceability in favor of the more comprehensive concept of Critical Tracking Events (CTEs) that are applicable throughout the supply chain while offering greater efficiency as well as data security.

The Old Concept of 'External Traceability'

Transactions between growers, processors, distributors, shippers, brokers, and brand owners (Figure 1) represent external traceability and all segments of the supply chain must participate for such a traceability system to be effective. Missing data slow or stymie investigations. External traceability is largely in practice today throughout the supply chain because companies naturally maintain records of shipments received from suppliers and shipped to customers for the regular business practices of invoicing and payment.

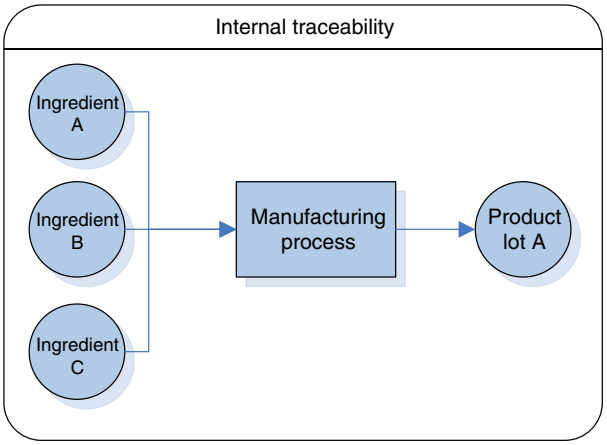


Figure 2 Example of internal traceability. A food manufacturer produces a product from three ingredients. These inputs are recorded and related to Lot A of the finished product.

The Old Concept of 'Internal Traceability'

Internal traceability (Figure 2) requires that food processors or distributors track internal inputs that change the identity or configuration of the product they are selling. For food manufacturing, internal traceability may require that all lot code or batch information for the ingredients (grain, corn syrup, flavorings, vitamins, etc.) that are used be recorded and stored. For a distributor, internal traceability may require that multiple data elements be recorded if cases of product from varying lots are used to create a pallet (or an equivalent logistic unit).

What is sometimes referred to as 'internal traceability' is not actually traceability, but rather good manufacturing practice. There is no doubt that these data are useful to outbreak investigations, but they are not needed in any investigation until they are actually needed by investigators, due to implication of the specific operator in a specific outbreak. In other words, investigators should only need these data from operators implicated as a likely source of contamination. Forcing investigators to dig into these records of each supply chain operator, whether implicated or not, wastes precious time of both investigators and operators, which not only jeopardizes the entire investigation, but also frustrates everyone involved with lots of tedious and expensive work, and relying on these data for routine traceability is unwieldy and unnecessary. Better approaches are needed to more quickly identify the most likely sources of contamination in order to avoid wasting precious time and money of operators who should be excluded from an investigation.

An Example Investigation

Traceability, in order to protect public health, should encompass all aspects of the food system, starting at the point of harvest and continuing to retailers. Animal feed, as well as food packaging, should also be included in a robust food chain traceability system.

Numerous foodborne outbreaks over the past several years have demonstrated the importance and need for rapid traceability of food products sold to consumers. More rapid traceability can aid and clarify foodborne illness investigations by aligning product distribution data with epidemiological exposure data. These investigations could be completed more rapidly and with a greater degree of accuracy if current data

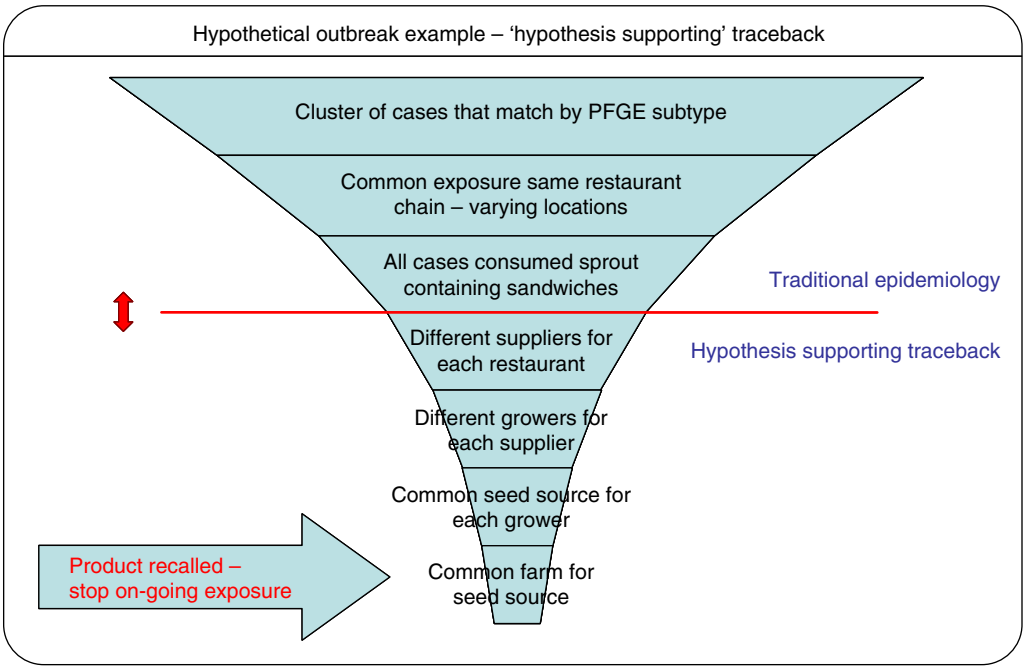


Figure 3 Conceptual diagram of a 'hypothesis supporting' traceback investigation. PFGE, pulse field gel electrophoresis.

requirements and collection practices for food traceability were better defined and aligned across the food supply chain.

Figure 3 shows a cluster of illnesses matching a pulse field gel electrophoresis subtype identified by epidemiologists at a state health department. Owing to the difficulty and cost of traceback investigations, significant clusters of illness must be identified before an investigation commencing. Once the cluster has been identified, epidemiologists interview specific cases and try to determine commonality such as dining at operations of the same restaurant chain. Further investigation finds that all cases consumed some type of sprout-containing sandwich at each restaurant location, but the source of the sprouts remains unclear.

Although the epidemiological investigation may identify a plausible source, the regulatory investigator must trace the likely exposure to a point of convergence or commonality in the supply chain in order to identify the 'source' of the outbreak.

Continuing with the example, once an outbreak vehicle is identified, the epidemiological investigation ends with the possible recommendation that persons not consume sprout-containing sandwiches at these locations. The traceback investigation is an extension of the epidemiological investigation and it serves two purposes:

1. It supports the epidemiological associations by confirming that temporal and physical distribution of suspect products could adequately match the case exposures, and
2. It further characterizes the source of the outbreak, thereby increasing the likelihood of a meaningful intervention to protect public health.

In Figure 3, this concept is demonstrated when the investigation moves from the information generated in the epidemiological interviews to the information collected by a food regulatory agency based on record collection and in-field investigations. An investigation of the invoices and bills-of-lading from each restaurant location where a case of illness was reported shows that each restaurant received their sprouts from a different supplier. Further investigation of the records from the suppliers shows that they received their sprouts from a number of different growers. A review of the grow logs, seed sources, and invoices at each of the sprout grower locations shows that all of the seed in implicated time frame would have come from a single seed-supply company. A review of the lot codes for the implicated seeds shows that a common lot-code of seed was used at each grower in the implicated time frame and further investigation shows that the lot-code corresponds to a single farm that produced all of the questionable seed.

It is not until all of these data are collected and analyzed that a truly meaningful public health intervention, in the form of seed and sprout recalls and a market withdrawal of the implicated lot-code, can be made. As might be imagined, such an investigation is complicated and time- and resource-intensive. Outbreaks often subside before investigators are able to pinpoint a cause resulting in wasted time and effort of both doing the investigating and those being investigated.

Traceforward Investigations

Traceforward, sometime called 'tracking,' is the capability to find a product based on specific criteria while it is handled along each point of the supply chain. This is a critical feature of any traceability system because companies must be able to identify and locate their products within the supply chain in order to withdraw or recall them whenever necessary. Once a food item or ingredient has been associated with illness, improving forward traceability through the channels of

distribution can prevent further consumer exposure and additional cases of illness. Additionally, labeling on consumer packaging for manufactured foods with information containing lot or batch codes will allow consumers to easily identify products in their homes that may be associated with a recall or outbreak.

Limitations of Current Systems, Technology, and Thinking

Improving investigatory efficiency requires knowledge of the process of investigation, supply chain logistics, food handling and production, as well as associated technological developments in these areas. However, recent efforts have focused on testing existing food traceability practices and/or augmenting these practices with not-well-understood emerging technologies such as radio frequency identification (RFID) in the hope that they might offer a 'silver bullet'-style solution. Efforts have also been made to coordinate use of specific data elements throughout the supply chain but with limited success (e.g., Produce Traceability Initiative), because there simply can never be a one-size-fits-all solution for such a large, complex, and dynamic web of supply chains. What is needed is a more general framework that can be applied to a variety of situations. The authors believe that this framework is offered by the concept of 'CTEs.'

One-Forward-One-Back

Currently, food traceability revolves around the concept of OFOB, which is often also referred to as 'one-up and one-down.' This approach is popular because it does not require operators to do anything other than to maintain customary business records that virtually all responsible operators already maintain without the additional consideration of food traceability. The concept of OFOB requires that each operator be able to determine, within a reasonable amount of time and typically within 24 h, the identities and locations of immediate suppliers and customers. Production records, purchase orders, sales orders and invoices, as well as shipping and receiving records substantially satisfy the basic food traceability requirements of OFOB. From the perspective of the operator, OFOB 'works' and requires little if any additional investment other than what might normally enhance business productivity in terms of improving efficiency of data storage and retrieval. Without even considering traceability, responsible operators already maintain a variety of important business process records such as payroll, production, receiving, shipping, sales orders, invoices, purchase orders, inventory, and quality-control data. As mentioned, most of these data are only useful to food outbreak investigators after likely sources of contamination have been identified.

Indeed, OFOB does work, but the problem is that it is slow, inefficient, and often ineffective for investigators, resulting in too many unsolved outbreaks, implication of incorrect products, unnecessary damage to industries and brands, and waste of enormous quantities of otherwise wholesome foods. A better understanding of the investigative and recall processes helps to expose why OFOB is more likely to be incapable of substantially improving food traceability accuracy and speed regardless of capital investments made. The information contained in business process records simply cannot be collated and analyzed quickly enough by investigators to quickly reconstruct the supply chain and identify points of convergence.

The investigative and recall process generally begins with epidemiological evidence of an outbreak. As illnesses are being reported, epidemiologists must wait to identify genetically related 'clusters' of multiple-reported illnesses before commencing the investigation. Once one or more clusters are deemed to be sufficiently promising to pursue, investigators attempt to discover the most likely foods and/or ingredient suspects and their most immediate source (e.g., package, store, restaurant, etc.). Typically, multiple foods and/or ingredients are suspects and multiple simultaneous traceback investigations must be initiated.

For each suspect, investigators seek to learn the immediate source of the suspect product (i.e., one back). Requests for information are made from suppliers in order to identify subsequent suppliers. In this manner, investigators follow the trail backward until the source of the outbreak is identified by multiple traces converging on a particular item and/or location or the trail simply 'goes cold' (Miller, 2012).

Points of convergence provide investigators with the greatest degree of confidence in identifying potential sources of outbreaks. Once one or more points of convergence are identified, sampling and testing may or may not confirm the cause and a decision must be made whether or not to recall suspected product as well as define the scope of the recall. Then the OFOB process works in reverse in order to identify and remove implicated product from the supply chain.

The problem with OFOB is that it is slow and inefficient. OFOB is slow because investigators must work their way backward one supply chain node at a time and each node may use the customary 24 h to provide data that identify the next node in the chain. It is inefficient because investigators must simultaneously pursue suspect foods and ingredients that are not a cause of the problem and this not only wastes precious time for investigators, but it also wastes time of all operators who receive requests for such data. As time is spent, people may continue to consume contaminated food, illnesses mount, and the likelihood of confirming the correct source of the outbreak diminishes.

Anything done under the guise of improving food traceability performance, particularly with respect to government regulation, should have the potential to significantly reduce the time required to identify points of convergence in the supply chain. Doing anything else will not do much to improve food traceability performance but will add substantial costs to operators, which must be passed onto consumers in the form of higher food prices. Imprudent regulations also raise the barrier to entry into commerce, thus depressing innovative start-ups and job creation in the food industry.

Limitations of Lot or Batch Numbers for Traceability

The role of the 'lot number' or 'batch number' serves as a significant example to illustrate the consequences and

challenges of applying production-oriented concepts to food traceability. Most production workers are food safety oriented. When food safety is in question, workers tend to focus on lot/batch numbers in order to understand the scope of the problem because the lot/batch denotes product that was produced or treated under similar conditions using related inputs. Lot numbers are critical when the source of contamination is identified, but because they tend to be operator specific and meaningful only to a given operator within the supply chain, lot numbers are not particularly useful to traceback investigations until a specific operator's facility is implicated. Indeed, each operator has different definitions of lots and batches and food products often become ingredients to other food products making it difficult to recreate paths through the supply chain using lot/batch codes. However, once investigators pinpoint an operator as a likely source of contamination, that operator's specific lot/batch codes as well as all other related information such as payroll (who was working that day), storage room temperatures, cleaning records, etc. all become critically important to investigators. Therefore, although food production and food safety workers often passionately argue for using lot/batch codes as a central component of food traceability, it should now be clear that lot/batch codes are less than ideal for solving the logistic food traceability problem. To be clear, the authors are not arguing for elimination of the use of lot/batch codes for the purposes of production management. They recognize that these data are critically important to food traceability investigations but only when investigations lead to a specific food production operation.

Even if not used as a basis for traceability, lot/batch codes will continue to play a pivotal role in outbreak investigations once points of convergence or the source of tainted food is otherwise identified. Lot/batch codes will serve as the key data element ('KDE') for subsequent trace-forward investigations and recalls. However, it should be clear that this KDE need only exist at the operator in a form convenient to the operator.

Implementation of the CTE framework requires minimal and highly abstracted data (data that are meaningless to observers who are not authorized to access secured, related data) to be collected in a format that can ultimately be accessible electronically. Proprietary production data, such as lot/batch codes, need not be immediately accessible electronically because the goal is to quickly find the source(s) of convergence and/or contamination. Once convergence is identified in the supply chain, thorough investigations will require review of all pertinent documentation in all formats. The goal is to quickly focus the investigation, not to burden every operator with unnecessary data collection and associated restrictions on data formatting.

The notion of unique identification codes has tended to stir up passionate debates and resistance among operators, but this may be due to a lack of understanding how such codes can greatly simplify the traceability process. Unjustified opposition to the use of unique identification codes has led to an unending debate over the 'ideal' universal set of KDEs that might serve the same purpose as unique identification codes (McEntire and Bhatt, 2013). Perhaps the only thing that has been concluded from all of that effort is that there is no universal set of KDEs that will work for all operators in all situations.

Logistic Event-Based Approach to Traceability – Critical Tracking Events

The logistics perspective simplifies the supply chain into a series of events through which food-containing 'units' pass. Units may be shipping containers, pallets, cases, or individual items. Therefore, advancing food traceability requires a decision as to resolution; what is the smallest and most useful unit to be tracked in the supply chain? Because consumers typically purchase individual items in some form of retail setting, it is more likely that the smallest unit received by retailers would be an aggregate of individual units, and the most common aggregation of individual units is the shipping case (typically a corrugated box containing a set number of individual items). Therefore, advancing food traceability will, at least, require some means of uniquely identifying cases. As many individual cases may represent the same lot, there is an associated need for operators to maintain data relationships between production lots and traceability case identifiers.

It follows that advancements in food traceability require collection and maintenance of data and data relationships. This exposes the need for involving expertise in relational data collection, storage, and retrieval for advancing food traceability. Unfortunately, as the topic of food traceability has been viewed primarily as a food safety issue, people with expertise in food safety rather than logistics and distributed relational data have played a primary role in drafting regulatory guidelines that appear to lack sufficient expertise for flexibility, scalability, adaptability, efficiency, and interconnectivity that will be necessary to achieve the goal of food traceability while offering opportunities for adding as yet unforeseen value in the marketplace. Ultimately, a successful global food traceability system will need all of these attributes to grow organically and improve over time.

Current Frameworks and Standards

Worldwide standards and frameworks exist to better facilitate traceability throughout the supply chain. These organizations seek to define data standards so that data are collected in a uniform format and can be more easily shared between trading partners and other entities in the supply chain. In many cases, specific standards have outlived their usefulness and now represent an impediment to advancement. Ideally, enforcement of standards should be avoided wherever possible in order to leave as many avenues for future improvements as possible. Therefore, to the extent possible, conformance with standards should not be required, but rather encouraged and/or provided as examples of modern best practices.

The Critical Tracking Events Framework

These realizations have led to development of a new framework concept for food traceability that offers opportunities to build on past food traceability efforts, tools, and technologies into an easily understandable and universally applicable approach. This framework concept is known as CTEs (Welt and Blanchfield, 2012; McEntire, 2009). The CTE framework

provides a basis for flexibility, scalability, adaptability, efficiency, and interconnectivity with little requirement for enforcing specific standards on any operator. CTE promises to do for food traceability what hazard analysis critical control point (HACCP) has done for food safety. The key concept is that each operator knows their operation best and operators are in the best position to identify those events that are critical to the overall goal of food traceability. The CTE concept simplifies the large, complex, and seemingly intractable problem into a local and familiar series of events that are deemed critical to tracking items through an operation. Each operator properly identifies their own CTEs and commits to collecting a minimum set of event data for each CTE, typically consisting of a three basic data items including unique location/event ID (e.g., Receiving Door #2 at a given physical address), unique item ID, and date/time stamp. Each operator would collect event data from all of their CTEs and store them as they see fit in secure databases that may be accessed for query by properly authorized personnel. This simple structure leads directly to the possibility of authorized investigators being capable of generating reports showing locations, dates, and times, throughout the entire supply chain, of suspect food items and ingredients, virtually instantaneously and with minimal intrusion and bother to operators. When multiple traceback queries expose points of convergence in the supply chain, investigators can then focus their attention on the broader process and handling data of the implicated operator in order to attempt to identify the source of contamination.

As with HACCP, the CTE framework does not prescribe any particular method or technology for doing so. Operators are free to choose the methods and/or technologies that best suit their purposes. The beauty of the CTE framework is that it is simple, flexible, scalable, secure, and efficient and does not require immediate universal participation in order to benefit from the system. As operators adopt the CTE concept into their operations, the food supply chains will become increasingly traceable. Additionally, modern distributed data networks preclude any requirement for pushing or uploading CTE data to any central repository, government, database, or authority. The CTE concept permits operators to maintain ownership and control of their own CTE data. As unique traceability codes can only be linked to proprietary production-related data such a lot/batch codes, CTE offers a level of security through data abstraction. This means that unique traceability codes have no inherent meaning. They simply point to a richer set of meaningful data in properly secured databases. Table 1 depicts the conceptual relationship between HACCP and CTE.

Table 1 Comparison of hazard analysis and critical control points (HACCP) and critical tracking events (CTEs)

HACCP	*CTEs (product tracing)*
Conduct a hazard analysis	Identify products and product inputs to be traced
Identify critical control points	Identify CTEs
Determine critical limits	Determine key data elements
Establish monitoring procedures	Establish data collection procedure
Establish corrective actions	Establish data storage procedures
Establish verification procedures	Conduct mock tracebacks
Ensure recordkeeping	Maintain a written record of the product-tracing plan

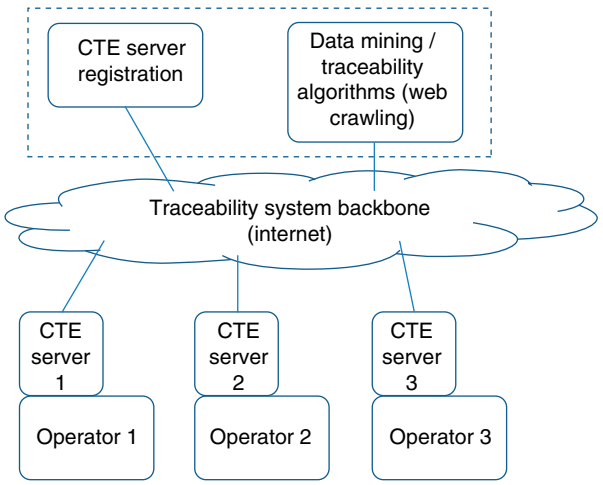


Figure 4 The CTE framework permits operators to control their own data while making them available for rapid traceback investigations without exposing proprietary data.

Data Security

Generally, supply chain participants do not wish to expose proprietary data to competitors and most prefer to not be put in a position that requires trust of government agencies and/or third parties to secure such data on their behalf. It is, therefore, unlikely that the vision of a central data repository controlled and/or accessible by FDA or another government entity, to which all food traceability data must be pushed, represents a sound solution. A similar effort was envisioned in the 2000s by the USDA to create a national database with all farm premise locations and animal movement data to a centralized database to be used in animal disease outbreaks. Resistance from industry and trade associations quickly derailed this effort (Pendell *et al.*, 2010). In contrast, although CTE does not prescribe a particular solution for data handling, the CTE framework invites development of modern, massively distributed, and highly abstracted and secure data-handling methods. These modern approaches to data handling provide for operator ownership and complete control over their own data. Data abstraction provides inherent top-level security in that exposed codes do not expose meaningful information. Ideally, traceability codes should simply point to meaningful data within secured databases that can be physically and logically distributed and only accessible to properly authorized personnel with proper permissions from data owners.

Briefly, an example of a CTE distributed data approach involves collection and storage of CTE data at the physical location/address of the events. Operators would maintain a database on their own site or contract with a third party to host their data in much the same way that many operators contract with third parties to host their web presence or to handle critical and proprietary payroll functions (Figure 4).

Event data would be stored in an operator-owned and -controlled database which is secure. By securely connecting

these data servers to the internet/cloud, investigators could use modern and increasingly advanced querying and data-mining tools with appropriate authentication and permissions and determine which events suspect items traversed. In this manner, investigators will be able to rapidly identify paths of different suspect products through the supply chain with minimal interruption to operators. Rapid identification of points of convergence would permit timely and focused investigations as well as targeted recalls resulting in fewer illnesses and deaths, reduced food waste, and less overall damage to industries and brands.

Categorization of Critical Tracking Events

The supply chain can be divided into four categories of CTEs, namely terminal, transfer, aggregation/disaggregation, and commingling (Table 2).

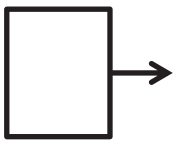
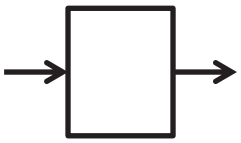
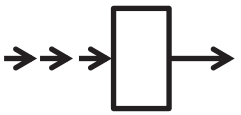
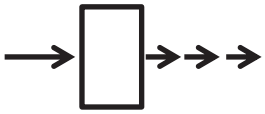
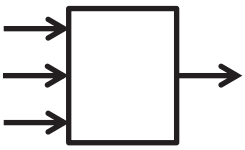
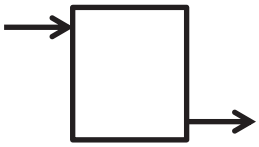
Terminal Critical Tracking Events

By definition, terminal CTEs exist on the boundary of the supply chain. Products enter and exit the traceable supply chain through terminal events. Specific situations always vary and it is the role of the operator to determine how internal linkages are made between CTE data and their actual operation. For example, consider an operation where produce is harvested from a particular field on a particular day. Harvested produce is collected in bulk and delivered by truck to an operation involving cooling, washing, sorting/grading, and packing. To do this, the operator may use the point where packed cases emerge from the operation to initiate supply chain traceability. This terminal event need not be at the field of harvest so long as the operator's records are capable of leading investigators to the source field should that be necessary in the future. The terminal CTE defines entry of this food product into the supply chain. Again, the CTE could be associated with more internal data elements if the operator so chooses such as harvest worker, environmental temperature, sampling results, and/or other relevant production data items. However, for the terminal CTE, the KDEs are simply identification data to define 'what, where, and when.'

Aggregation/Disaggregation Critical Tracking Events

Following the terminal CTE (which in this example occurred at the case level as product sorted and packaged), the

Table 2 Four categories of critical tracking events (CTEs); terminal, transfers, aggregations/disaggregations, and commingling

CTEs category	*Description*	*Diagram of inputs and outputs at event type*
Terminals	1. Creation, origination 2. Disposition	
Transfers	1. Shipping 2. Receiving	
Aggregation/disaggregation	1. Item ↔case 2. Cases ↔ pallet 3. Pallet ↔ container, trunk, etc. 4. Container ↔ ship, rail, etc.	 
Commingling	1. Blend 2. Formulate 3. Bulk commingling 4. Rework	 

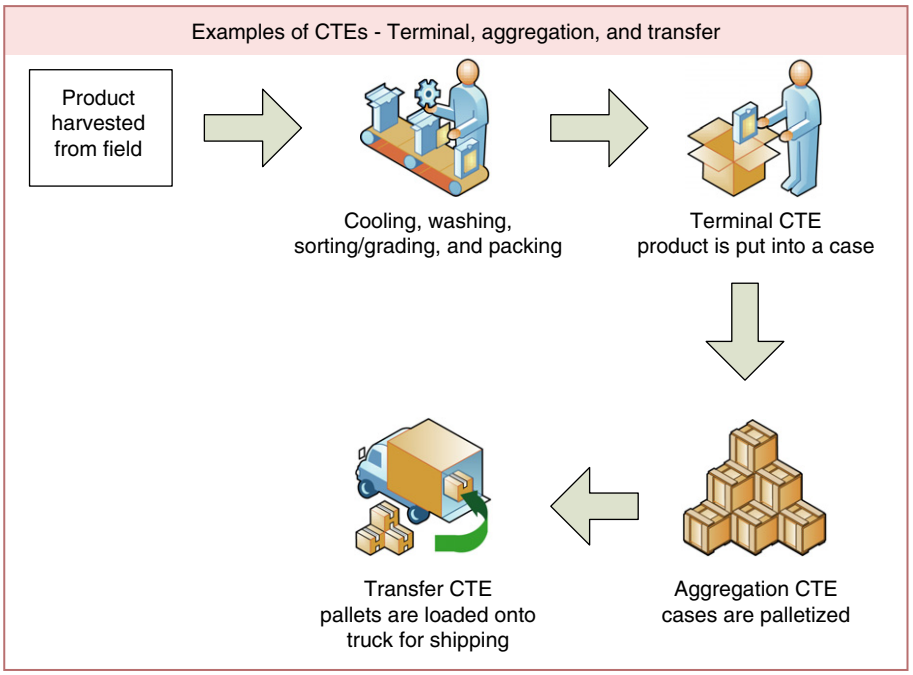


Figure 5 Example of CTEs in a simplified produce-packing facility (terminal, aggregation, and transfer CTEs).

packinghouse has identified an aggregation CTE in their process. As cases of product are palletized, an aggregation CTE exists and captures data identifying which cases comprise an individual pallet.

When pallets are broken down, the process works in reverse in that one incoming object (pallet) results in many outgoing objects (cases).

Transfer Critical Tracking Events

For the hypothetical produce harvester, a transfer (shipping/receiving) CTE is created when pallets of product are loaded onto a truck for shipment.

Commingling Critical Tracking Events

Commingling is usually an irreversible process where items from multiple sources of the same item and/or different items are blended together to create a new product. Comingling CTEs are typically characterized by many inputs and one output (Figure 5).

Lot-Coding Considerations Using Critical Tracking Events

Continuing with the produce-harvesting example, the operator must answer the 'what?' question. In other words, 'what is this item that is being introduced to the supply chain?' First explore why lot numbers are not a good choice for answering this question. The operator is free to define a 'lot' in a manner that makes most sense to the operation. Perhaps a shift's worth of production, a partial shift, one or more bulk truckloads, etc. Whatever the operator uses, it is highly likely that any given lot will be subsequently subdivided down the supply chain and those operators will have their own definitions for their own lots that make sense to their own operations. Clearly, the term 'lot' is more of an idea than a universally defined term. Although this alone should provide a sufficient argument against the choice of lot numbers as the core data for traceability, at least two additional arguments might be made against use of lot numbers. First, lot numbers are currently elusive when dealing with an unpackaged food or an ingredient. Lot codes are often inconsistent and change meaning throughout the supply chain and therefore represent limited utility when conducting a traceback. Lot codes are generally more useful when conducting a recall and therefore targeting specific production units in the supply chain. When the source of an outbreak or point of convergence is identified, investigators and operators need to know the size of the lot or lots associated with the implicated product in order to commence the subsequent investigative process and initiate the recalling of food. Using CTEs, until the source or point of convergence is identified, investigators have no need for every operator's definition of their own lots. They simply need an effective means to find points of convergence. Another issue with using lot numbers is that they tend to unnecessarily expose intelligence about production volumes and inventory turnover to competitors and customers and present food defense risks. This may or may not be deemed important to any given operator, but operators should be free to choose whether or not they wish to expose those data without being forced to do so by regulation. Therefore, although lot numbers currently are critical to the investigative process, lot numbers do not represent an ideal means for tracing items through the supply chain. Implementation of the CTE concept throughout the supply chain will obviate the need for investigators to focus primarily on lot code information as a proxy for internal traceability because case level traceability may be more widely available.

Critical Tracking Event Codes

CTE traceability codes (Table 3 below) answer the 'what?' question and should simply permit unique identification of an item in the supply chain. This means that the code need not provide rich information about the item, but rather the ability to distinguish one item from another in the supply chain. For example, it is now common to use electronic identification to pay tolls on highways. Drivers are issued a device that contains a unique code. The code itself does not contain any descriptive information about the driver or the driver's automobile. Knowledge of the code would not allow someone to know the driver's height, weight, or hair or eye color. The code is simply a number that, when applied to the right database, is able to locate the driver's database record for billing. Although it is more likely that descriptive information about the driver exists in the database, only properly authorized personnel may access it.

The example of automated toll collection applies directly to the CTE framework. The toll collection history shows only the data necessary to identify the item/car and its path in space and time ('What?,' 'Where?,' and 'When?'). For food traceability, this is actually all that is required during the first traceback step of an investigation. For traceability purposes, it does not matter whether the item was cheddar cheese or shredded cheese or even cheese. Only a record of which CTEs handled that item with a particular unique traceability code and when ('What?,' 'Where?,' and 'When?') is needed. It is often forgotten that the operator associated with the terminal creation CTE for any item could, if asked, provide all of the necessary information associated with the creation of the item and its introduction to the supply chain (provided they properly associate these data with the terminal CTE). The purpose of the traceability codes is to efficiently direct investigators to the operator if associated product might be implicated in an outbreak. Therefore, the best code to be used for traceability has at least the following traits:

1. Globally unique.
2. Least amount of data/bits as possible and practical.
3. Simple to print, write, and/or encode.
4. Simple to read.
5. Contains no 'meaningful' information about the product or operator (i.e., does not carry decodable information such as Julian date, etc.)

Technology Considerations and Platforms

There are a variety of coding options available that provide reasonable guarantees of uniqueness. One option that has received considerable attention was developed as a consequence of advances in RFID technology is the electronic product code (EPC). Through standardization efforts, the EPC is widely referred to as a serialized global trade identification number (sGTIN). The GTIN has been in use for a long time and is most recognizable as the Universal Product Code (UPC) printed on most food packages (Figure 6).

As with the lot number, the GTIN or UPC code does not identify a specific item, but rather a type of product in general. The sGTIN is a simple modification that adds a serial number to the GTIN to provide unique identification of items in the supply chain. GTIN codes and therefore sGTIN codes are managed globally through GS1, a non-profit international standards organization, on a subscription basis. Although GS1 is widely recognized and respected, there may be reason for an operator to wish to use another coding system now or in the future. The CTE framework simply requires uniqueness while the code exists within the supply chain. Therefore, the only practical limitation on coding systems is ensuring that others in the supply chain can also read codes. It is worth noting that the GTIN was established before development of modern computing technologies and practices. GTIN and sGTIN codes inherently deliver meaningful data within the code, such as manufacturer identification. Serialized code data may also provide insight into production volumes and rates. Exposing such data may or may not be desirable to operators, especially when exposing such information is not necessary under the CTE food traceability framework. Therefore, the authors recommend that operators consider alternative coding schemes that simply satisfy the basic CTE requirements.

Contrary to an apparently common tendency to seek enforcement of compliance with data standards and structures, readability is the only important requirement for achieving



Figure 6 Universal Product Code (UPC) code including company prefix, item reference number, and mathematically calculated check digit.

Table 3 Examples of traceability codes: The codes are represented by the Unique IDs created for each combination of CTE type, name, and location

Critical tracking events type	*Name*	*Location*	*Unique ID*
Terminal creation	Procedure case packer	Washing/sorting/packaging machine	XYZ123
Aggregation – Palletizing	Produce palletizer	End of conveyor	ABC321
Transfer – Shipping	Shipping dock door 2	Shipping dock door 2	DEF456

CTE-based traceability. Standardized data formats may offer some limited benefits, but as long as trading partners are capable of reading codes of other trading partners, whether similar in structure to their own or not, CTE-based traceability can be accomplished. There is no technical reason that all supply chain participants use similar identifying data types or structures. Modern computer applications are very well suited for generating unique identification codes. Therefore, many readily available options exist for generating unique identification codes under the CTE framework.

With the ability to assign unique identification codes to items in the supply chain, the authors turn their attention to the question 'Where?' and 'When?' Each CTE represents a repetitive event that occurs at a specific location. At worst, the location can be defined by the physical address of the operator. At best, it can be defined by the specific location within the operation where the event takes place, such as a piece of processing equipment or warehouse shelf. The event is often defined by a particular machine that is bolted to the production floor. Extending the prior produce-harvesting example (Figure 5), the terminal creation event might occur on the output side of the cooling/washing/sorting/packing operation where cases emerge on a take-away conveyor before being palletized. The operator could choose to apply preprinted and coded labels (manually or automatically), directly print codes on cases, print and then apply labels to cases, etc. However, if codes are applied, it is possible to uniquely identify the location of the event as well as capture a date–time stamp for each occurrence.

Again, GS1 offers a data standard for uniquely identifying locations known as the global location number; however, any unique identification number chosen to describe the CTE location is sufficient to achieve CTE-based traceability.

As an operator identifies, instruments, and documents CTEs within the operation, it becomes clearer how proprietary data remain secure while meaningless identification codes are used to point to rich sets of data within operators' secure organizations.

For the simple example of the harvest operation (Figure 5), three CTEs are identified, including a terminal CTE (creation), an aggregation CTE (palletization), and a transfer CTE (shipping). The operator's proprietary records would describe these CTEs perhaps as shown in Table 3.

The CTE event record for the terminal creation CTE using unique item code '789' would be as shown in Table 4.

Similarly, the aggregation-palletizing CTE would record '789' being associated with the specific pallet. The shipping CTE would record the pallet being shipped. When the product arrived at the next operator, their receiving CTE would record arrival of the pallet. When the pallet is broken apart, the case identified as '789' would be recorded as being removed from the pallet, etc. There is no need to attempt to predict the path of the item through the supply chain because each operator records CTE data themselves.

Table 4 Example of Terminal Creation critical tracking event showing the creation of an event record that records When' related to the creation of a product

Where?	*What?*	*When?*
XYZ123	789	January 31, 2013/13:50:23

Ultimately, consumers might purchase sandwiches made with produce from Case '789.' Other cases from the same production lot would have more likely arrived at many other retailers. Using the unique case identifiers, investigators should be able to query the distributed CTE food traceability system essentially asking, "Which CTEs handled Case '789'?" The few CTEs that actually handled the item could alert operators that an affirmative response to an investigative query must be made. At this point, the operator can provide either a quick "Yes, we handled Case '789'" or a more robust response with all dates, times such as "Yes, we saw the item at (CTE location XYZ123) on (Date/Time)."

The dataset compiled from all CTEs will provide a relatively immediate physical and temporal mapping of the item through the supply chain allowing investigators to quickly visualize the path and timing of multiple suspect items through the supply chain. In many situations, the CTE framework is even capable of jumping over missing nodes, which means that the traceability system will be immediately useful and improve over time as individual operators come online with their CTE data. The CTE framework is capable of satisfying the objective to quickly focus investigator attention on points of convergence, rather than working backward, serially through the cumbersome OFOB process with associated delays at each stop (Figure 7).

Modern interconnectivity of computer networks via the Internet as well as cloud-based storage and computing permit relational databases to exist virtually anywhere. Availability of this highly distributed global data infrastructure obviates the notion of a large central food traceability database. Small-scale operators could still capture these data by hand, if need be, or by the ubiquitous smart phone with appropriate applications.

The CTE food traceability framework fits well with the modern notion of highly distributed data while promoting additional benefits of operators maintaining ownership and control of their data as well as the associated data security that ownership and control affords.

Distributed versus Centralized Data

Although the CTE framework does not necessarily prescribe use of distributed data versus centralized data, it is easy to recognize the benefits of the distributed model over a centralized model. A centralized model requires that all supply chain participants conform to the central data model as well as central interface protocols. Operators would need to push data to the central database in a timely manner. As all operators would be expected to interact with the central database, necessary changes over time would be extremely difficult to implement. Therefore, central databases tend to be inflexible and not easily scalable and therefore become quickly obsolete. However, the distributed model permits operators to maintain ownership and control of their own data. Simple interfaces permit investigators to make infrequent queries of data and operators are capable of controlling the scope and manner of responses. Operators maintain and upgrade their systems as appropriate without interfering with the rest of the supply chain in much the same

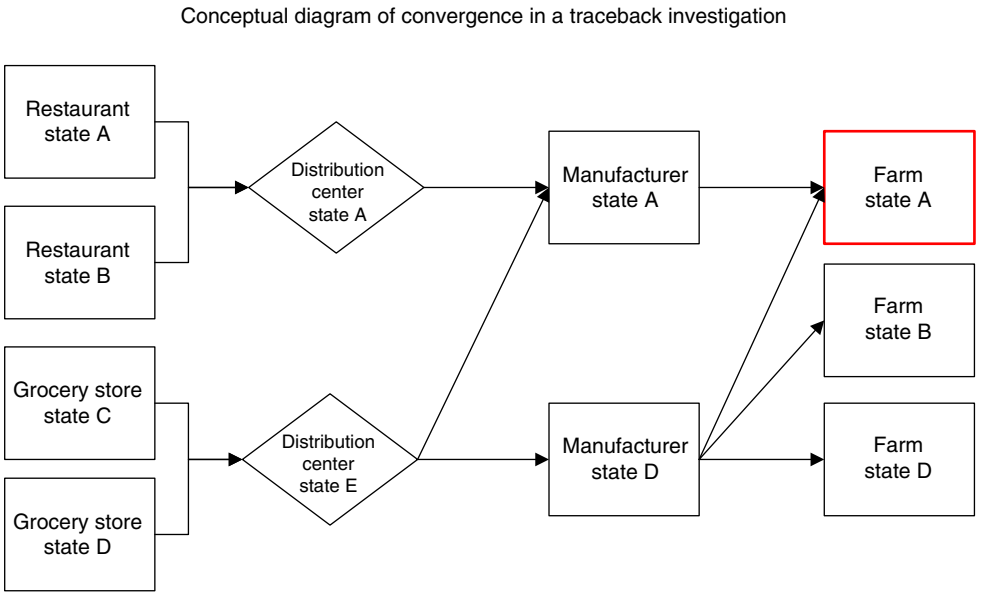


Figure 7 Simple conceptual diagram of traceback investigation. In this investigation, product is traced back to a point of convergence at Farm A.

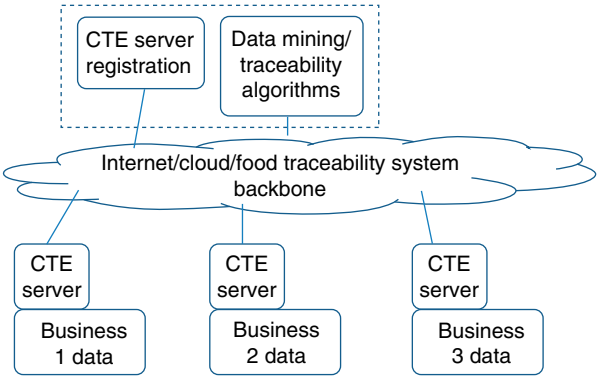


Figure 8 Conceptual diagram of CTE Traceability backbone. CTEs can be identified by leveraging cloud-based search algorithms and distributed databases. Unique traceability IDs would be identified by leveraging cloud-based search algorithms and distributed databases. Convergence in the supply chain is quickly identified.

way that companies can upgrade their own websites without interfering with the rest of the Internet. In contrast to the central database model, the distributed data model is flexible and scalable. Leveraging the modern distributed data infrastructure will permit rapid and independent expansion and utilization of CTE-based food traceability (Figure 8).

Conclusion

Past outbreaks have demonstrated the need for more rapid and accurate food traceability. Using existing standards and technologies, and adopting the CTE concept of traceability, would allow industry and regulators to intervene in outbreaks and prevent additional cases of foodborne illness. CTE allows for more targeted food recalls, potentially limiting the amount of unaffected food that would need to be recalled and destroyed. In turn, better traceability based on the CTE framework will result in increased public confidence in the food supply because implicated or adulterated food would be rapidly identified and removed from sale.

See also: Agribusiness Organization and Management. Food Chain: Farm to Market. Food Labeling. Food Law. Food Packaging. Food Security: Development Strategies. Food Security: Food Defense and Biosecurity. Food Security, Market Processes, and the Role of Government Policy. Food Security: Postharvest Losses. Global Food Supply Chains. Government Agricultural Policy, United States. Regulatory Conventions and Institutions that Govern Global Agricultural Trade

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www.producetraceability.org
Produce Traceability Initiative.

Crop Insurance

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Glossary

Actuarially fair Means that premiums on policies equal the expected payments from the policy.
Adverse selection Occurs because of asymmetric information. After insurance premiums are set, potential insurance purchases evaluate premiums. Individuals with more risk will purchase crop insurance and those with less risk will not purchase insurance.
Moral hazard Occurs after an insurance policy is purchased when purchasers take on more risk with the policy than they would without the policy.
Multiperil Crop insurance covers all yield losses that are naturally occurring.
Premium The costs of insurance.

Introduction

Crop insurance is a contractual agreement between a farmer and an insurer under which the farmer pays a premium to the insurer and the insurer agrees to make insurance payments contingent on events occurring in the future that trigger losses as defined in the crop insurance contract. Crop insurance payments are intended to reduce risk by making payments when a farm is under financial stress. Under better than average outcomes, a farmer pays a premium but does not receive a payment, so the intended net effect of insurance is to reduce the range of possible outcomes that farmers can experience.

Most insurance markets are regulated to assure that insurance companies can make the insurance payments stipulated in insurance contracts. Conceivably, this regulatory function could be the only governmental involvement in crop insurance. In the United States, however, the federal government is much more heavily involved in crop insurance. The federal government determines the specifications of federal crop insurance contracts that are sold to farmers, sets premiums that farmers pay on crop insurance policies, subsidizes the costs of premiums and program delivery, and acts as a reinsurer to crop insurance companies offering crop insurance contracts. It is thus important to understand the role of the federal government in crop insurance markets and how crop insurance differs from other more common forms of insurance. Although each country is unique, many countries are involved in crop insurance and face many of the same issues as in the United States, as noted in the final section of this article.

In the materials that follow, features of the crop insurance market are delineated first by types of crop insurance products available to farmers. Then the history of the involvement of government in crop insurance is discussed, with particular emphasis given to increases in subsidies that have occurred through time. Finally, major issues that have caused difficulties and concerns in crop insurance delivery are outlined and described, along with implications for performance of crop insurance.

Types of Crop Insurance

The various crop insurance products are described roughly in their order of introduction into the US market, progressing from single-peril insurance to multiperil insurance, and then to index insurance. Within multiperil insurance there are two major types depending on whether the yield or revenue associated with the crop is insured. Within the division of revenue insurance, there is a further distinction based on the possibility that the insured amount or guarantee value can increase if prices increase. Finally, index insurance is described with the major types being area insurance plans or group plans and weather event insurance.

Single-peril insurance products provide insurance against a specific named peril, such as hail or wind snap. Hail is by far the most widely used single-peril crop insurance. Hail insurance makes payments when hail occurs and causes sufficient damage to result in an insurance claim. The judgment of damage is made by an insurance adjuster who inspects the affected crop and generally indicates that yields are expected to be reduced by a specific percentage (e.g., the hail event caused a reduction in yield of 30%). After subtracting the deductible, a claim is paid on the basis of a dollar value of protection set in the crop insurance policy. Other than through regulatory oversight, hail insurance policies are not part of a government program and are not federally subsidized, nor reinsured. Hail insurance policies are offered through private companies, and gains or losses are accrued to the private entities backing the insurance. Aiding the development of this private market is the fact that hail events tend to impact small geographical areas with little correlations across areas. These types of losses allow crop insurance companies to diversify risks.

In contrast to single-peril insurance, multiperil yield insurance provides payments for any yield loss resulting from natural causes. Because yield insurance protects against all naturally occurring causes of loss, yield insurance provides superior risk protection to single-peril insurances. Yield insurance contracts are typically implemented by first determining a guaranteed yield. The guaranteed yield is, in turn, determined as the product of an expected yield and a coverage level. The expected yield typically is based on historical yields, sometimes adjusted to reflect changes in farming technologies. The coverage level is a percentage of the expected value, usually restricted to be less than one so as to provide a deductible. Typical coverage levels ranges from 50% to 85%. Payments are then made if the actual yield experienced is less than the guaranteed yield. To illustrate, suppose a farmer with an

expected yield of 160 bushels per acre elects a 75% coverage level. The guaranteed yield is 120 bushels per acre (160×0.75). If actual yield falls below 120 bushels per acre, insurance payments will occur. Payments typically equal the yield shortfall times the indemnified price per bushel shortfall. The price is determined before the realization of yield. In the United States, the federal policy proving yield insurance is called yield protection (YP).

Revenue insurance provides protection against losses of expected revenue. Typically, expected revenue is measured through the uses of prices based on futures contracts, which serve as a measure of the price expected at a future date. A projected price based on futures prices is set before planting and is used to establish the revenue guarantee. A harvest price is determined near the typical time of harvest and is then used to determine available revenue. This revenue is then compared with the revenue guarantee to determine whether an insurance payment will occur. To illustrate, suppose a farmer has a revenue protection policy with an expected yield of 160 bushels per acre and a projected price of US$6.00 determined in this case as the average futures price for the upcoming December corn futures price during the month of February. Given a 75% coverage level, the revenue product will have a US$720 (160 expected yield $\times$ US$6.00 projected price $\times$ 0.75 coverage level). At harvest, actual revenue is measured as actual yield times harvest price. In this case, suppose the farmer had a 100 bushel yield and the harvest price is determined to be US $7.00, yielding revenue of US$700. A payment is made equal to the difference between the revenue guaranteed and actual revenue, or US$20 (US$720 revenue guarantee – US$700 actual revenue). In the United States, the federal policy that provides protection against revenue losses is termed revenue protection with harvest price exclusion (RP-HPE).

Revenue insurance is also available under which the guaranteed revenue is based on the higher of the projected or harvest prices, known as revenue protection (RP). In essence, the guaranteed revenue under RP resets using the harvest price if the harvest price is above the projected price. RP insurance will make the same insurance payment as RP-HPE if the harvest price is below the projected price. However, when the harvest price is above the projected price, RP insurance will pay more than RP-HPE. Continuing with the example above, a farmer with a 160 bushel expected yield, a US$6.00 projected price, a US$7.00 harvest price, and a 100 bushel yield would have revenue guaranteed at US$7.00 $\times$ 160 $\times$ 75% or US$840. RP insurance would make a payment of US$140, or US$120 more than RP-HPE because the indemnity price increased to the larger of harvest or projected price.

The Federal Crop Insurance Corporation (FCIC) offers all three types of farm-level crop insurance in most counties with significant crop production, across a wide range of coverage options. In locations where all three of these multiperil products are offered for a single crop, RP tends to be the most popular. For example, 73% of the corn acres were insured with RP in 2012, 3% with RP-HPE, and 10% with YP (Risk Management Agency, 2012). Revenue policies generally have been shown to provide superior risk protection compared with yield policies, likely accounting for the higher use of revenue insurances. The guarantee increase allowed in RP is useful for farmers who hedge compared with the use of YP or RP-HPE. In cases of yield declines, which are often widespread, prices often increase, leading to hedging losses and the guarantee increase provision of RP is intended to offset these losses and allows farmers to make pricing decisions before harvest if conditions warrant.

In contrast to multiperil products, index insurance products do not insure a particular event on a farm, but rather they provide payments when an index falls below a threshold. For index insurance to provide risk protection, the index has to be highly correlated to losses on a farm. Index insurance products potentially have a number of advantages over multiple peril crop insurance products. First, index insurance does not require measurement of yields from an individual farm, the determination of which can be a costly error-prone activity. Moreover, index insurance reduces the possibilities of moral hazard and fraud, because a farmer cannot influence the value of the index.

Within the United States, the most prevalent type of index insurance is provided in the form of area insurance or group plans. These plans typically make payments based on county yield or revenue. Group risk plan (GRP) is a county-level insurance that makes payments when a county's yield falls below a guaranteed level, usually determined as a coverage election times an average or expected yield. Group risk income plan (GRIP) is a county-level insurance product that makes payments when county revenues fall below a county revenue guarantee. GRP is similar to YP based on a county yield and GRIP is similar in concept to a county-level RP policy. Both GRP and GRIP are federally subsidized products. Use of these products has been confined mainly to the Midwest, and in the Midwest they represent a low portion of policies. In Illinois, for example, GRP and GRIP accounted for 0.4% and 5.3%, respectively, of corn acres insured in 2012 (Risk Management Agency, 2012).

Weather indexes are another form of index insurances that make payments based on measures of weather events, such as temperature or rainfall at specific locations, like weather reporting stations. Various forms of weather insurances exist, including policies that make payments when: (1) rainfall is below a specified level during a specified time interval, (2) some combination of low rainfall and high temperatures occur in a specified range, and (3) 'early' frost occurs. Rating of index products is relatively straightforward as plentiful historical data exist from which the likelihood and severity of potential payments can be assessed. Typically, weather insurance products are free from moral hazard and adverse selection concerns, as the purchaser cannot affect the index with their own behavior. However, developing weather insurance policies that follow yields closely enough to substitute for direct farm-level insurance is still problematic in many cases. Weather insurance is currently offered privately in the United States. Weather insurance products have been attempted in developing countries in efforts to provide basic levels of production insurance, often before the development of the infrastructure and data needed to support specific farm-level contracts.

History of Involvement of Federal Government in Multiperil Crop Insurance

Several attempts to offer multiperil crop insurance were made by private crop insurance companies in early parts of the

twentieth century. In 1917, for example, private insurers offered policies in North Dakota, South Dakota, and Montana, but the companies suffered large losses due to a drought and did not continue offering insurance (Valgren, 1922). Other companies offering multiperil insurance policies were also not successful (Gardner and Kramer, 1986). Partially explaining these failures is the correlated nature of crop insurance losses, making it difficult for a company solely dependent on crop insurance to diversify risks from crop insurance policies. A similar situation exists in other markets where there is government participation, including flood insurance and certain forms of disaster insurance where relatedness of loss experience renders private insurance difficult to offer.

The 1930s saw several major droughts across large portions of the Midwest, perhaps providing impetus for governmental involvement in crop insurance. Federal involvement in crop insurance began with the passage of the Crop Insurance Act of 1934. Soon thereafter, the FCIC was formed to act as fiduciary entity for crop insurance and crop insurance policies were offered to farmers through governmental agencies. The goal when setting premiums was to determine actuarially fair premiums such that premiums equaled the expected payments from crop insurance. In principle, the government could act as a risk-neutral agency to facilitate the formation of a mutual insurance fund that paid out losses from broadly distributed premiums that equaled each other over time. Initially, farmers paid the entire premium for policies, and the delivery of crop insurance was subsidized. However, the early history of crop insurance can be characterized as having poor actuarial performance, with actual indemnities paid out of the crop insurance programs exceeding premiums paid in. Various attempts were then made at improving rate setting, meeting with some success during the 1950s. However, participation in crop insurance remained low and was concentrated in areas where farming risks were highest.

In the 1970s, the US Congress passed legislation that created standing disaster assistance programs (Gardner and Kramer, 1986). These programs were popular with farmers, as farmers did not have to pay to participate in the programs. However, the existence of both disaster assistance and federally sponsored crop insurance raised a number of issues. A disaster assistance program provided much the same protection as crop insurance, hence there was some concern that disaster assistance would substitute for or crowd out crop insurance. The policy position that emerged was that if participation in crop insurance could be induced to occur at high levels, disaster assistance programs could be replaced by crop insurance, which has more desirable distributional features and better aligns risk reduction with actual needs.

Congress then passed the Federal Crop Insurance Act of 1980, which replaced the standing disaster assistance programs with subsidized crop insurance (Glauber, 2004). A goal of the subsidy structure was to induce participation of at least 50% of eligible acres through the payment of a portion of the premium in the form of risk subsidies. As a result, farmers pay only a portion of the total premium, and the remainder is paid by the federal government. Moreover, the delivery of crop insurance was transferred to private companies, with the hope that profit incentives would encourage private companies to aggressively sell insurance. In addition to selling and servicing crop insurance products, the private companies participate in a portion of the underwriting gain or losses associated with the policies. However, even with subsidized insurance and private company delivery, participation in crop insurance remained low through much of the 1980s. When a widespread drought hit the Midwest in 1988, only 25% of eligible acres were insured (Chite, 1988). Low participation, along with political pressure, led to the passage of ad hoc disaster assistance programs again in both 1987 and 1988.

Efforts continued to encourage participation in crop insurance. Congress passed the Federal Crop Insurance Act of 1994, which increased premium subsidies (Glauber, 2004). During the 1990s, revenue and area insurance products were introduced. Before this point, all federal products had been yield insurance products. Revenue insurance proved to be popular and through time became the dominant share of federal policies. Congress increased premium subsidy rates with passage of the Agricultural Risk Protection Act of 2000 (Glauber, 2004). Finally, the 2008 farm bill also increased premium subsidies for enterprise units, a particular manner of insuring that combines all acres in one crop in one insurable unit to encourage insurance in a form more related to actual farm operation revenue needs.

These efforts have resulted in dramatically increased usage of crop insurance. In 1991, only 101 million acres were insured (see **Table 1**). Since 1990, acres insured have increased in most of the years, reaching 282 million acres in 2012. Total premiums paid into the program have also increased from US $836 million in 1990 to more than US$11 billion in 2012 (see **Table 1**). At the same time that total premiums have increased,

Table 1 Acres insured, total premium paid, and precent of premium subsidized, United States, 1990–2012

Year	*Net acres insured*	*Total premiums*	*Premium subsidized (%)*
1990	101 360 754	US$836 468 229	26
1991	82 351 639	737 041 249	26
1992	83 104 417	758 785 010	26
1993	83 707 606	755 677 234	26
1994	99 638 441	949 391 928	27
1995	220 510 627	1 543 349 837	58
1996	204 863 837	1 838 559 196	53
1997	182 188 943	1 775 367 833	51
1998	181 881 122	1 877 064 224	50
1999	196 918 128	2 310 132 781	60
2000	206 466 664	2 540 163 689	53
2001	211 328 990	2 961 847 611	60
2002	214 864 551	2 915 944 057	60
2003	217 409 022	3 431 359 362	60
2004	221 019 863	4 186 132 552	59
2005	245 856 440	3 949 230 060	59
2006	242 074 457	4 579 348 909	59
2007	271 647 215	6 562 350 708	58
2008	272 271 550	9 851 159 116	58
2009	264 763 798	8 949 427 876	61
2010	256 149 551	7 594 174 309	62
2011	265 729 829	11 960 605 833	62
2012	282 377 256	11 080 197 770	63

Source: Risk Management Agency, 2012. United States Department of Agriculture. Summary of Business. Available at: http://www.rma.usda.gov/data/sob.html (accessed 15.01.14).

the federal government's share of total premiums has increased as well. In 1990, 26% of the total premiums were paid by the federal government. In 2012, 63% were paid by the federal government (see Table 1).

The current size of the crop insurance program may have accomplished a major policy goal: replacing disaster assistance programs with crop insurance. Since passage of the Federal Crop Insurance Act of 1980 that eliminated the standing disaster assistance program, Congress has implemented ad hoc disaster assistance programs throughout the 1980s, 1990s, and 2000s. In 2012, however, there was major drought that impacted much of the Midwest and Great Plains, yet no ad hoc disaster assistance program was passed. A major reason given for no disaster assistance program was the size and coverage of the crop insurance program.

Structure of the US Multiperil Crop Insurance Industry

Participants in the crop insurance channel can be delineated into the following five primary groups: farmers, crop insurance agents, crop insurance companies, reinsurance companies, and the federal government (see Figure 1).

Farmers and share-rent landowners first purchase crop insurance. As indicated earlier, farmers pay a portion of the premium associated with crop insurance and receive indemnity payments when insurable losses occur. Crop insurance agents provide information to farmers, help to make product and coverage decisions, and service the policies they sell. Servicing activities include compiling of yield histories needed for the crop insurance policies, collecting acreage information from the farmer, and managing processes associated with getting insurance in place. Insurance indemnity claims are initiated by farmers through their crop insurance agents, although the claim adjustment process is handled by adjusters who are by regulation independent of the agents. Some crop insurance agents are employed by a crop insurance company, whereas many others act as independent agents who sell polices through more than one company.

Crop insurance companies own and service the crop insurance policies and interact with The Risk Management Agency (RMA) in initiating policy coverage and maintaining appropriate records. Crop insurance companies, in turn, receive premiums associated with policies and are responsible for managing the claims adjustment process. In addition, crop insurance companies are subject to underwriting gains and losses associated with crop insurance policies; however, crop insurance companies do not bear all the risks associated with the polices. Much of the risk is borne by the federal government, and private agreements with reinsurance companies also are used by the crop insurance companies to manage risk.

The federal government is heavily involved in the US crop insurance industry on almost every level. Day-to-day management of crop insurance programs and provisions is provided through the RMA, an agency of the US Department of Agriculture. RMA determines the types of polices that will be offered with subsidies from the US government and develops the ratings structures underlying each policy. RMA maintains all data associated with policies and provisions and losses and yield records, across all companies. All companies must offer the same basic policy at the same costs. Thus, for a farmer, the price and terms of a federally subsidized multiperil policy will not vary with the crop insurance company it is purchased from, nor by the crop insurance agent from whom it is purchased.

Reinsurance of crop insurance policies is also accomplished through the FCIC, a wholly owned government corporation. The sharing of underwriting gains and losses is detailed in a loss-sharing arrangement called the Standard Reinsurance Agreement (SRA), in which all crop insurance companies must participate in order to sell crop insurance. All companies are subject to identical term, and hence the 'Standard' label in the SRA. The SRA determines how gains and losses are shared between the federal government and crop insurance

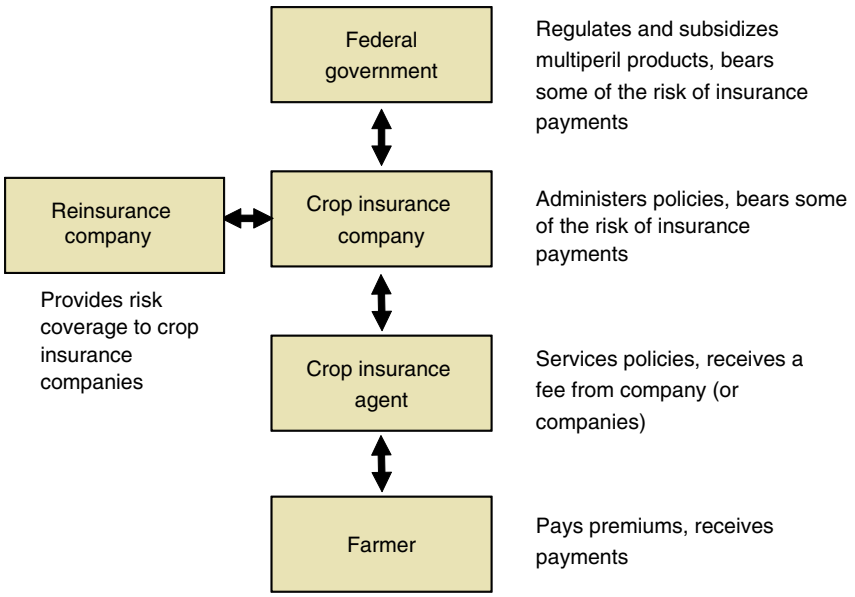


Figure 1 Participants in federal crop insurance.

companies and is periodically renegotiated to maintain performance targets through time. The negotiations around the SRA can be very controversial, as crop insurance companies and the federal government are often at direct odds about the terms of the agreement. Crop insurance companies prefer to retain a higher share of the gains and a lower share of losses, whereas the federal government wants to provide incentives for greatest coverage at lowest net cost. As policy terms and premium determination are set outside a company's control, the terms of the SRA have a large impact on the ultimate financial performance of crop insurance for companies.

Under the terms of the SRA, two funds of policies exist in each state into which each policy may be committed. These are termed (1) assigned risk fund and (2) commercial fund (Risk Management Agency, 2013b). Within specified limits, a crop insurance company must place each policy into either an assigned risk or a commercial fund before determining the loss experience of the policy. Risk sharing differs dramatically across these pools with the ability to retain exposure to policy risk greater within the commercial fund.

For polices placed in the assigned risk fund, the companies cede 80% of the premiums to the federal government. On this ceded premium, the crop insurance company does not receive any gains or losses regardless of the outcome of the underlying policy. On the 20% of retained premium, gains and losses are shared on the basis of a prescribed schedule, with the majority share accruing to the FCIC. To illustrate, suppose that the loss ratio, or indemnity payments divided by premiums, equaled 1.5 at a state level. In this case, losses are 50% greater than premium, and for each dollar of premium, an additional US $0.50 has to be paid, resulting in a loss of equal magnitude. Under the Assigned Risk fund, at this level of loss ratio, the company will have a US$0.04 loss, whereas the FCIC will bear US$0.46 of the loss. As shown in Table 2, the losses increase as loss ratios increase, but not proportionately with loss levels. The company's losses go up with loss ratio to US$0.08 for a 2.5 loss ratio, US$0.11 for a 3.5 loss ratio, US$0.14 for a 4.5 loss ratio, and losses are then capped at US$0.15 for a 5.5 and higher loss ratios.

For policies placed in the commercial fund, the company can retain between 35% and 100% of the total premium in 5% increments. The amount of premium to retain is a company's decision. In the commercial fund, a company bears more of the risk associated with losses. For example, if the loss ratio were 1.5, the company has US$.30 of loss per US$1 of retained premium and the FCIC has US$0.20, if in the commercial fund in Group 1 states (Illinois, Indiana, Iowa, Minnesota, and Nebraska) compared with US$0.04 for the assigned risk fund (see Table 2). If it were in Group 2 or other states, the shares are reversed and the company would lose US$0.20, whereas the government would pay the excess US$0.30. As loss rates increase, the losses borne by the company increase, but the government's share increases faster with maximum losses capped at US$0.88 in the commercial fund in Group 1 states and at US$0.61 in Group 2 states. If there are gains instead, the SRA also determines the split in the excess premium. For example, if the loss ratio is 0.65, then there is a US$0.35 gain per dollar of premium. Under the SRA, the company would receive 26.25 cents and the government would receive 8.75 cents if in the Commercial fund in Group 1 states. In the Assigned Risk fund, the company would receive only 7.89 cents instead and the government would retain the remainder of the gain. The full schedule of losses and gains is prescribed in the SRA and thus a reason that the SRA is so vigorously negotiated.

Intent of the differential loss sharing schedules is to incent crop insurance companies to identify and place their riskier polices in the assigned risk fund. This strategic placement of policies will tend to cause the crop insurance company to have a lower proportion of losses and a higher proportion of gains (Coble *et al.*, 2007) than random assignment or if there were only one average schedule. As discussed in the following section, the fund allocation decisions are also an important determinant of the effective crop insurance subsidy.

Subsidies for US Multiperil Crop Insurance Policies

There are three types of subsidies involved in the US multiperil insurance market: (1) risk, (2) administrative and operating subsidies, and (3) shared underwriting losses.

Risk subsidies directly reduce the farmers' costs of purchasing crop insurance. When setting rates, RMA attempts to determine total premiums so that total premiums roughly equal expected payments from crop insurance policies, thus resulting in actuarially fair premiums, on average. Because

Table 2 Loss sharing for different funds under the 2012 Standard Reinsurance Agreement, dollars of loss per dollar of retained premium

Loss ratio	*Total loss*	*Assigned risk*		*Commercial fund group 1 states*[a]		*Commercial fund other states*	
		Insurance company	*FCIC*	*Insurance company*	*FCIC*	*Insurance company*	*FCIC*
		Per US$1 premium		*Per US$1 premium*		*Per US$1 premium*	
1.5	0.50	0.04	0.46	0.30	0.20	0.20	0.30
2.5	1.50	0.08	1.42	0.65	0.85	0.38	1.12
3.5	2.50	0.11	2.39	0.74	1.76	0.47	2.03
4.5	3.50	0.14	3.36	0.83	2.67	0.57	2.93
5.5	4.50	0.15	4.35	0.88	3.62	0.61	3.89
6.5	5.50	0.15	5.35	0.88	4.62	0.61	4.89

[a]Includes Illinois, Indiana, Iowa, Minnesota, and Nebraska.

Abbreviation: FCIC, the Federal Crop Insurance Corporation.

Source: Risk Management Agency, 2013. U.S. Department of Agriculture, Standard Reinsurance Agreement.

farmers have private information and can likely assess their own risks to determine whether they are more or less risky than average, if all policies were sold at the actuarially fair value, disproportionate participation would be expected by riskier farmers. Partly in response to the difficulty in developing perfectly accurate individual rates, the risk subsidy encourages participation by reducing the costs paid directly by the farmers through these risk subsidies. The percentage of the total premium that is subsidized is set in legislation by Congress. Table 3 shows the current subsidy levels for multiperil products, delineated by type of unit and coverage level. The major determinations are whether the insured unit is an enterprise unit or not. Enterprise units refer to all of one crop in a county and require certain other restrictions to be met before this unit can be used. Alternatively, the crop might be insured in basic or optional units. A basic unit is all of one crop in a county under the same ownership structure. One basic unit exists for all owned and cash-rented farmland, with additional units for each share-rent landlord and by each fraction at risk. Optional units divide basic units based on township sections.

Table 3 Risk subsidies on multiperil insurances

Coverage level (%)	*Unit*	
	Basic optional	*Enterprise (%)*
	Total premiums (%)	
50	67	80
55	64	80
60	64	80
65	59	80
70	59	80
75	55	77
80	48	68
85	38	53

As shown in Table 3, risk subsidies range from 67% of total premium at a 50% coverage level down to 38% at an 85% coverage level. This schedule was set by the Agricultural Risk Protection Act of 2000 and will continue until Congress again modifies subsidies. Enterprise subsidies are higher, ranging from 80% of total premium at a 50% coverage level down to 35% at an 85% coverage level. Before 2008, enterprise units had the same subsidy levels as basic and optional units. The 2008 farm bill included increases in the subsidy rates for enterprise units to encourage aggregated coverage. The intent of the differing subsidy rates, to some degree, is to provide a similar dollar-valued subsidy per acre across all options, with lower subsidy rates against higher valued insurance and vice versa. Both dollar levels and percentages of premium paid in the form of risk subsidies have been increasing over time. For the 2003 cropping year, risk subsidies were US$2 billion. For the 2012 cropping year, risk subsidies were estimated at US $6.9 billion in the United States. These subsidies were larger than the remaining subsidies.

The second type of subsidy is administrative and operating (A&O) expense subsidies. As total premiums do not include cover costs of delivery and total premium, A&O subsidies are designed to provide crop insurance companies funds needed for delivery of the product. A&O subsidies are stated as a percentage of total premiums. Percentages are set within the SRA and vary somewhat with product. The A&O subsidy on most insurance products is 18.5% of net booked premium. For the 2012 cropping year, A&O subsidies are estimated to be approximately US$1.4 billion.

Underwriting subsidies potentially occur when total premiums are greater than total indemnity payments. The SRA determines the relative shares of the gains or losses between the federal government and crop insurance companies. Table 4 shows historical loss experience to federal crop insurance in the United States from 2002 to 2012. The table shows gross premium, which includes farmer-paid

Table 4 Premiums, indemnities, and gains (losses) from Federal Crop Insurance

Year	*Gross premium*	*Gross indemnity*	*Underwriting gain or loss*		
			Gross[a]	*Insurance company*[b]	*The Federal Crop Insurance Corporation*[c]
			Million dollars		
2002	2 909	4 058	(1149)	(47)	(1102)
2003	3 434	3 259	175	377	(202)
2004	4 185	3 290	895	691	204
2005	3 945	2 341	1604	915	689
2006	4 709	3 551	1158	821	337
2007	6 547	3 465	3082	1571	1511
2008	9 833	8 422	1411	1094	317
2009	8 950	5 214	3736	2298	1438
2010	7 595	4 253	3342	1916	1426
2011	11 967	10 838	1129	1663	(534)
2012	11 112	17 361	(6249)	(1312)	(4937)
Total	75 186	66 052	9134	9987	(853)

[a]Equals gross premium minus gross indemnity.
[b]Insurance companies' share of gain.
[c]Equals gross gain – insurance company's gain. Represents Federal Crop Insurance Corporation share of gains.
Source: Risk Management Agency, 2013b. United States Department of Agriculture. Reinsurance Reports Online. Available at: http://www.rma.usda.gov/tools/reinsurance.html (accessed 15.01.14).

premiums and risk subsidies. Gross indemnities are subtracted from gross premium to arrive at gross underwriting gains. As can be seen in Table 4, there were gross underwriting gains in all but two years wherein losses were US$1.1 billion in 2002 and losses were US$6.2 billion in 2012. Unprecedented losses in 2012 resulted from a major drought that impacted the Midwest and Great Plains. Over the 11-year period, underwriting gains totaled US$9.1 billion. As a result of the reinsurance agreement, insurance companies have received a larger portion of gains than the federal government. For the entire 11-year period, insurance companies have US$9.9 billion of gain, whereas the FCIC experienced a US$.9 billion loss, providing additional profits to crop insurance companies. Over this time period, crop insurance companies have received an average of US$830 million per year in underwriting gains.

Issues Associated with Crop Insurance

Crop insurance has all the problems associated with any other form of privately offered insurance: ratings difficulties, adverse selection, and moral hazard. As crop insurance is also publically subsidized, it faces policies concerns, including the perennial question of why to subsidize crop insurance in the first place. The following four subsections cover issues associated with crop insurance beginning with ratings issues and moving to more public policy concerns. This progression of issues is not without overlap, as many of the issues are intertwined with one another.

Rating Difficulties and Adverse Selection

Determining the proper rates and premiums for multiperil crop insurance has proven to be a challenge, as evidenced by the poor actuarial performance of crop insurance during much of the twentieth century. Inherent within this difficulty is deriving loss exposure measures that accurately reflect risks for policies under differing productivities and locations. The RMA uses a loss cost approach for determining yield rates, which relies on previous experience from crop insurance policies to determine rates for current policies. Typically, experience from a county is aggregated to arrive at rates for county. This approach has some desirable characteristics but also faces two basic problems: first, the loss cost approach is based on the ability for historic loss rates to accurately proxy future loss experiences. In agriculture, technologies are changing continually, causing yields from farms to generally increase and to change relative to weather and input decisions. Hence, previous loss experience may not totally capture yield variability in the future (Skees and Reed, 1986). Second, land quality varies considerably even within county. Hence, determining rates for a diversity of farmland that exists may be problematic, if not fully reflected in historic yields within a policy record.

These difficulties in ratemaking can lead to adverse selection (Skees and Reed, 1986). Adverse selection occurs when the individuals being insured know more about their risks than the entity setting the rates. Those individuals who know that they are more risky will be more likely to purchase crop insurance than those who know that they have less risk. Adverse selection results in a group of policies that are more risky than reflected in the ratings procedure. Adverse selection likely contributes to poor actuarial performance of multiperil crop insurance but likely more so in the past when participation rates were much lower. Research suggests that rating methodologies have resulted in unequal actuarial performance, with relatively less risky crops and regions having lower losses than implied by the rates (Woodard *et al.*, 2012).

Responses to adverse selection are continuously being undertaken to improve rate making and design-specific risk indicators. Adverse selection also provides impetus for area and other index insurance products, as these are typically easier to rate accurately and face less adverse selection issues (Miranda, 1991). Area insurance products, however, typically do not provide as much risk protection as farm-level polices, as county yields are not perfectly correlated with farm yields.

Systemic Risk

Insurance markets work best when losses across policies are independent and uncorrelated in space or time. Uncorrelated losses allow crop insurance companies to diversify risks and increase the predictability of losses within a time period. Insurance payments become more variable and extreme across time with more highly correlated insurance payments. Correlated losses also result in the need for crop insurance companies to hold more capital to cover potential crop insurance payments. In extreme cases, highly correlated losses can result in the financial failure of an insurance company even if policy premiums are set properly because capital did not exist to cover intermediately large losses.

Crop insurance losses are positively correlated across locations in a given crop year because weather is highly influential on loss experience and because revenue insurance will all be impacted by the same price changes. When severe droughts occur, as happened in the Midwest in 1988 and 2012, crop insurance payments will be large and underwriting losses will occur.

The nature of the systemic risk in agricultural production has been given as one reason for federal involvement in crop insurance. The federal government can act as a reinsurer against the systemic risk that is destabilizing to the private crop insurance companies and not face the same liquidity or capital constraints that individual companies might. Reinsurance through the SRA is one way of providing this protection. Other methods have been proposed, including the use of area yield plans to backstop crop insurance companies (Miranda and Glauber, 1997). In this case, the federal government provides subsidies and payments on area yield insurance, with the remaining farm losses not covered by area insurance to be less positively correlated and more manageable from a private company perspective.

Crop Insurance Impacts on Farmer's Decisions: Moral Hazard, Input Use, and Acreage Decisions

Purchasing crop insurance may result in impacts on other farmer's decisions, with those changes sometimes undesirable, or having effects that are specific to individual interests. Moral hazard is a prime concern within crop insurance, as moral

hazard occurs when a farmer takes more risk in the presence of crop insurance than would be taken without crop insurance. A farmer would take these risks because crop insurance may partially or totally offset losses from adverse events, thereby reducing losses from the risky activity while potential profits still remain. This additional risk taking can cause loss experience to be larger than anticipated for when crop insurance rates were determined. One way of countering moral hazard is to have a deductible so that first losses are born by the insured. Crop insurance usually has a deductible based on incomplete available coverage. For example, if maximum coverage is 85% of expected revenue, then the implied deductible is 15%. For multiperil crop policies, RMA also requires that good farming practices be followed, meaning that production methods must be used that allows the crop to make normal progress to maturity and produce at least the production guarantee (Risk Management Agency, 2013a). Certainly, what constitutes good farming practices can be difficult to define and monitor on an individual producer basis.

Of prime interest is whether the presence of crop insurance influences farmers' chemical use. This interest results because chemical use may impact the environment. Moral hazard arguments could be made to suggest that chemical use that is protective in nature, such as use of insecticides and fungicides, may decrease with crop insurance usage. However, the exact nature of crop insurance impacts on chemical use depends on the nature of the production function (Horowitz and Lichtenberg, 1993). Some studies find that crop insurance increases chemical use (Horowitz and Lichtenberg, 1993), whereas others find that crop insurance reduces chemical use (Smith and Goodwin, 1996). In some cases, perhaps the majority, crop insurance impacts on chemical use will be small. At this point it is not possible to unequivocally state the impacts on chemical usage of crop insurance.

Crop insurance may also impact acreage decisions. Acreage impacts generally would not be viewed as a case of moral hazard, but acreage impacts may be a general concern of public policy. Subsidized crop insurance may increase the attractiveness of the subsidized crop relative to crops that have no insurance. This effect could come from substitution of insured crops with crops without insurance (Nelson and Loehmann, 1987). Studies that have examined crop insurance impacts on acreage generally have found modest impacts (Wu, 1999; Goodwin *et al.*, 2004). For example, Goodwin *et al.* (2004) found that a 30% decrease in premiums result in a 1% increase in Midwest corn acres and 1% increase in northern plains barley production.

Farmer's Demand for Crop Insurance and Subsidies

Theories of demand suggest that risk-averse farmers will purchase crop insurance that is priced in an actuarially fair manner. Because actuarially fair insurance has total premiums equal to expected payments, farmers can purchase insurance that reduces risks without any reduction in expected returns, but instead simply trades off some higher for some lower revenue outcomes resulting in more stability. As a goal of RMA is to price insurance such that policies are actuarially fair, theory would suggest that many farmers would purchase federally subsidized crop insurance even without subsidy.

However, participation in federal crop insurance has not occurred without significant subsidies to premiums. Legislation in 1980, 1994, 2000, and 2008 increased subsidies, resulting in higher participation in each case. Studies suggest that increases in crop insurance subsidies result in a relatively small increase in crop insurance participation (Goodwin, 1993). In 2012, federal subsidies amounted to 62% of total premium (see **Table 3**), meaning that farmers pay 38% of total premium. At that level, insurance purchases should result in farmers receiving net gains from crop insurance purchases.

However, a number of reasons can be given for the relatively low demand for crop insurance in the absence of subsidy. Many of those reasons revolve around development of average ratings across heterogeneous producers. Total premiums are priced to an average level of risk and those farms with below average risk will pay relatively more for the risk reductions offered by the crop insurance product. Hence, farmers with below-average risk will not purchase crop insurance without significant subsidies. Another reason may be that the farmers have other options for risk management, including the production of multiple crops, use of pricing hedging tools, and holding financial reserves.

Use of subsidies then leads to the question: Why subsidize crop insurance? Assuming that crop insurance is priced in an actuarially fair manner, farmers in aggregate receive income transfers from crop insurance in addition to the risk protection offered from the crop insurance policies. This then leads to the question of why taxpayers should provide income subsidies to farmers. This is a continuing debate. Usual reasons given for subsidies include the systematic nature of agricultural losses, leading to the need for government involvement. Use of crop insurance may also have other societal benefits, such as assuring a more reliable food supply. Also, governments are involved in the subsidy of many insurance products, including flood, bank deposit, unemployment, and disability insurances. For a variety of reasons, private solutions in insurance markets may not be publicly desirable. In any case, debate on governmental involvement in crop insurance likely will continue.

Crop Insurance Outside the United States

This article has focused on use of crop insurance in the United States. Crop insurance has been used extensively in many countries around the world, including Brazil, Costa Rica, India, Japan, Mexico, and the Philippines (Hazell, 1992). When crop insurance is subsidized, a remarkably consistent set of issues arise from those of the United States' case, including (1) low participation in crop insurance occurs; (2) adverse selection, moral hazard, and other ratings problems arise; and (3) crop insurance losses are systematic in nature.

A problem that presents larger issues outside the United States is in measuring yields. Farms in developing countries are often small, lacking the means for accurately measuring yields. Moreover, histories of farm yields that can be used to determine yield risk do not exist. Both of these issues then lead to problems implementing crop insurance in developing countries. This has led to more of a reliance on weather-based

insurances and area-based contracts in developing crop insurance contracts in developing countries (Skees *et al.*, 1999). Of course, use of weather or index contracts introduces issues of correlation between the index on which crop insurance is based and actual yield. Whether or not these contracts will be successful is an open question.

Summary

Crop insurance provides important risk management protection to farmers. Over time, this risk management protection has been provided with heavy government involvement, including standardization and rating of products, pricing crop insurance policies, and reinsurance of crop insurance companies. Issues common to all insurance markets occur in crop insurance, and issues related to the systemic risk further complicate the provision through private markets alone. It has unique features that reset each year with annual prices of the underlying insured commodities and due to the single-price feature across participants and delivery channels. The degree of subsidy involved in its provision seems to be a key point of contention, but this issue should also be viewed in the context of the political environment that includes considerations of ad hoc disaster assistance and its use to motivate other desirable policy outcomes as well. In any case, it has become the primary cornerstone for many farmers' risk management activities and has also become one of the main features of farm program legislation debate. It is expected that crop insurance markets and products will continue to become more sophisticated through time and that innovations will continue, but some form of public participation will also continue for the foreseeable future due to the underlying nature of crop revenue risk.

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Crop Pollination

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Glossary

Biotic-pollination When pollen is delivered to stigmas by animal vectors such as insects.
Cross-pollination The transfer of pollen from an anther of the flower of one plant to a stigma of the flower of another plant.
Pollination The main mode of sexual reproduction in plants, which occurs when the transfer of pollen (male) from the anther of a flower to a stigma (female) results in fertilization which produces seeds and, in some cases, fruits.
Pollination dependency A measure of the level of impact that animal pollination has on the productivity of a particular (crop) plant species.
Self-pollination The transfer of pollen from an anther to a stigma of the same flower.
Wind-pollination When pollen is transported by wind, this is also called anemophily.

Introduction

Pollination is the main mode of sexual reproduction in plants, which occurs when the transfer of pollen (male) from the anther of a flower to a stigma (female) results in fertilization which produces seeds and, in some cases, fruits. Pollination is, therefore, an important input in the production of the marketable goods of many crops and can have a substantial impact on production. Pollination by animals in particular is a vital component in global agricultural economies by increasing crop productivity and profits. However, some of the main animal pollinators, such as bees, hoverflies, and butterflies, are in a state of long-term decline in some regions of the world, thereby threatening the stability and security of this ecosystem service. This article presents a brief overview of the main modes of pollination in globally important crops, highlighting the yield and economic benefits of animal pollination in particular. The main drivers of animal pollination service declines are then reviewed along with possible measures to mitigate these declines.

Modes of Pollination

Within crops there are several widely observed modes of pollination. Self-pollination whereby flowers of the plant are capable of fertilizing themselves is the most simplistic and often occurs in plants such as peas with enclosed flowers. However, most crops require pollen transfer between different flowers to successfully fertilize or benefit from external agents increasing their rate of self-pollination. In many crops pollen grains are light enough to be transferred effectively by wind with some crops, such as wheat, relying largely on wind pollination to successfully pollinate. Approximately 75% of globally important crops benefit from biotic pollination whereby animals transfer pollen between flowers or increase the rate of self-fertilization that occurs (Klein *et al.*, 2007). In some crops, biotic pollination by particular animals is essential to the production of marketable output. This is especially important to crops where the pollen is too heavy or sticky to move via the wind (e.g., almond *Prunus dulcis*), where there are separate male and female flowers (e.g., kiwifruit) and where pollen must come from a different cultivar (pollinizer) to produce fruit (e.g., rabbiteye blueberries, *Vaccinium virgatum*) (Free, 1993). Biotic pollination is usually performed by bees and flies, many of which have evolved to feed exclusively on floral pollen and nectar, but butterflies, beetles, birds, bats, and even some terrestrial mammals (e.g., palm squirrel; Chakravarthy and Thyagaraj, 2012) can provide pollination services to commercial crops (Klein *et al.*, 2007).

Globally, domesticated honeybees (*Apis* spp.) are widely utilized to provide pollination services to a wide variety of crops, particularly in large-scale systems (e.g., rapeseed) where abundant pollinators are required. However, some studies have demonstrated that honeybees are not always the most effective pollinators of crops, either by collecting nectar from flowers without contacting the anthers (e.g., apples, *Malus domestica*; Thompson and Goodall, 2001), displaying foraging preference for noncrop plants over some crops or simply finding some unattractive (e.g., pears, Stern *et al.*, 2004). Another widely observed group of pollinators are bumblebees (*Bombus* spp.), which are effective pollinators of many small fruits (e.g., raspberries, *Rubus idaeus*; Willmer *et al.*, 1994) and are widely domesticated to provide pollination services to crops that honeybees cannot effectively pollinate (e.g., tomatoes, *Solanum lycopersicum*; Banda and Paxton, 1991). Other pollinators have also been domesticated to provide more specialist pollination services to certain crops. These include alfalfa leafcutter bees (*Megachile rotundata*) that are used to pollinate alfalfa and mason bees (*Osmia* spp.), which have recently been domesticated to provide pollination services to some fruit crops (Bosch and Kemp, 2002).

Although domesticated pollinators can be readily managed to provide pollination services to a wide range of crops, pollination services by wild insects are increasingly thought to be important to crop production even in intensive cropping systems, such as muskmelon (*Cucumis melo*) production in Pennsylvania, USA (Winfree *et al.*, 2008). In many tropical countries feral honeybees, stingless bees (*Meliponina* sp.), and solitary bees are important contributors to crop pollination in

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small holder systems. Other plants have more specialized pollination systems, such as figs (*Ficuscarica*) which are exclusively pollinated by fig wasps (*Blastophaga scripta*), which have evolved in parallel to the tree (Free, 1993). Many species of flies can also act as effective pollinators, notably *Cecidomyiid* spp., and *Ceratopogonid* midges that are the primary pollinators of cocoa, and hoverflies such as *Eristalis tenax* (Klein *et al.*, 2007). Ants are also known to be effective pollinators of a few tropical crops, such as mango (*Mangifera indica*; Carvalheiro *et al.*, 2010). In some rare circumstances where high value crops are grown beyond their native range, such as cherimoya (*Annona squamosa*) grown in Spain, there are no suitable insect pollinators available, necessitating that producers employ labor-intensive artificial pollination methods (Gonzalez *et al.*, 2006). Artificial pollination is usually accomplished by directly applying pollen to floral stigmas by hand using brushes (Pinillos and Cuevas, 2008); however, recent engineering advances have resulted in cost-effective pollen sprays for use in small orchards (Sakomoto *et al.*, 2009).

Benefits of Pollination

It is estimated that 75% of globally important crops benefit from biotic pollination in various ways, from directly increased yields to greater crop quality or other agronomic benefits (Klein *et al.*, 2007). Most overtly, biotic pollination directly increases fruit seed set in many crops compared with other modes of pollination alone (e.g., pears, *Pyrus communis*; Nyeki and Stolesz, 2003), resulting in greater overall production. This is especially important to crops that cannot self-pollinate, many of which require biotic pollination to effectively transfer pollen between neighboring plants (Free, 1993). Similarly, in many crops, biotic pollination produces fruits with greater weight compared with those produced by wind and self-pollination alone, increasing the total market output per hectare. Recent studies have demonstrated that pollination by insects can increase the proportion of marketable oil content in rapeseed (*Brassica napus*; Bommarco *et al.*, 2012). Biotic pollination can also increase the speed and synchronization of fruit maturity, resulting in easier, more efficient harvesting (e.g., linseed, *Linum usitatissimum*; Williams *et al.*, 1991). In some highly productive crops, such as sweet peppers (*Capsicum annum*) grown in glasshouses, this increased maturity can even result in additional harvests per year (Shipp *et al.*, 1994).

Beyond direct increases in output, biotic pollination can also significantly improve fruit quality in certain crops. For instance in strawberries (*Fragaria* × *ananassa*), pollination of all anthers by insects is required to produce fruit of an acceptable shape (Chagnon *et al.*, 1993). Besides economically significant quality factors, biotic pollination can improve the nutrient content (e.g., apples; *M. domestica*; Volz *et al.*, 1996), and taste quality (e.g., tomatoes, *S. lycopersicum*; Hogendoorn *et al.*, 2010) in some crops. Biotic pollination can also provide more long-term agronomic benefits to crop producers. By transferring pollen between different plants, crop pollination can reduce inbreeding effects within crops, which may help improve disease resistance (Free, 1993) and reduce crop abortion rate (e.g., almond, *P. dulcis*; Martinez-Garcia *et al.*, 2012). A study on persimmon (*Diospyros kaki*) tree productivity found that trees receiving ample pollination from insects also grew at a quicker rate, probably because the plant was forced to increase its nutrient uptake to support greater yields (George *et al.*, 1995).

Although pollination can benefit many plants, it is possible that biotic pollination may negatively impact productivity in some crops. For instance, if excessively pollinated, crop trees may become overburdened with fruits, requiring costly thinning by hand or chemical induction to prevent damage to the tree or excessive nutrient use. In other crops, notably pineapples and some varieties of citrus fruit (*Citrus* sp.) and cucumber (*Cucumis sativus*), biotic pollination can result in seed production which can leave the product unmarketable (Free, 1993). As most noncrop flowering plants also benefit from biotic pollination (Ollerton *et al.*, 2011), the prevalence of abundant pollinators can also encourage the propagation of many weeds.

Crop Dependency on Biotic Pollination

Although biotic pollination can have significant benefits to crop productivity, most crop plants will produce some marketable output through self and wind pollination alone. Nonetheless biotic pollination is often essential to produce profitable outputs in many crops (e.g., blackcurrants, *Ribes nigrum*; Denisow, 2004). This section presents an overview of the total yield benefits of pollination to different crop types (**Table 1**), highlighting the general trends and exceptions within each group.

Fruit Crops

As a group, the majority of fruit crops are dependent on pollination to produce marketable yields. Several tree fruit crops, notably apple (*M. domestica*), plum (*Prunus domestica*), and figs (*Ficus carica*), are largely self-incompatible and very highly dependent on animal pollinators to transfer pollen between flowers from different trees. Yields of most other tree fruits, including avocado, peach, pear, plum, and sour cherry, can increase by 500–900% by animal pollinators transferring pollen between plants and flowers as wind pollination is often insufficient to successfully transfer enough pollen. By contrast, the benefits of biotic pollination to persimmon trees (*D. kaki*) can vary substantially with some varieties being able to set fruit entirely through self and wind pollination, whereas other cultivars can double yields with ample biotic pollination (George *et al.*, 1995; Free, 1993). Citrus fruits (*Citrus* sp.) also vary in their need for biotic pollination; although some species, such as mandarin produce more and larger fruits when cross-pollinated by insects (Schneider *et al.*, 2009), varieties of other citrus crops can set more desirable seedless fruits with parthenocarpy, making biotic pollination largely undesirable (Free, 1993).

Small fruits largely benefit from biotic pollination to more moderate extents than other fruits as many are self-compatible, have small, light pollen grains, require fewer grains per stigma to fertilize, and produce multiple anthers per flower allowing them to set fruit even if not all stigmas are fertilized.

Table 1 Benefits of biotic pollination to selected globally significant crops

Crop	*Benefits of biotic pollination*	*Approximate yield lost without biotic pollination (%)*[a]	*Effective pollinators*[b]
Almond	Higher nut set	65	Honeybees, mason bees
Apple	Greater fruit set and weight, higher nutrient content	65	Mason bees, Honeybees
Buckwheat	Greater seed set	65	Honeybees
Citrus fruits	Increased fruit weight (some varieties)	5	Honeybees
Cocoa	Greater number of pods, greater pod weight	95	Midges
Coffee	Higher bean set and weight, fewer misshapen beans	25	Honeybees, stingless bees
Faba bean	Increased seed set and weight	25	Long-tongued bumblebees
Mango	Increased fruit set	65	Honeybees, stingless bees
Raspberry	Increase druplet number, fruit set, and weight	25	Bumblebees, honeybees
Rapeseed	Higher oil content, greater pod set, and weight	25	Honeybees
Seed cotton	Increased boll number, seed weight, and lint weight	25	Honeybees
Soybean	Increased pod set and weight	25	Bumblebees, honeybees
Strawberry	Greater fruit weight, less malformed fruit	25	Bumblebees, honeybees, mason bees, *Andrena* sp.
Sunflower	Higher seed set, greater oil content per seed	25	Honeybees, solitary bees
Tomato	Greater fruit weight, enhanced taste	25	Bumblebees

[a]Adapted from Gallai, N., Vaissière, B.E., 2009. Guidelines for the economic value of pollination services at a national scale. Available at: http://www.internationalpollinatorsinitiative.org/uploads/POLL%20VALUE%20NATIONAL%20MANUAL.pdf

[b]Adapted from Klein, A.M., Vaissiere, B.E., Cane, J.H., *et al.* 2007. Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society B – Biological Sciences 274 (1608), 303–313.

Nonetheless, visits by insects are often required to produce crops of marketable quality, particularly in strawberry (*Fragaria* × *ananassa*) which will set malformed, unmarketable fruit if only partially pollinated (Chagnon *et al.*, 1993). Biotic pollination is also important to increase fruit set in currants sufficiently to produce profitable output, despite their often strong degree of self-compatibility (Denisow, 2004). Blueberries and cranberries (*Vaccinium* spp.) benefit substantially from cross-pollination between different cultivars, increasing their fruit set and weight significantly over self-pollination. In temperate regions, bumblebees (*Bombus* sp.) are widely observed to be the most effective pollinators of most small fruits (Delaplane and Mayer, 2000). The only significant small fruit crop that does not benefit from pollination is grape (*Vitis vinifera*), which is highly self-compatible and readily pollinated by wind alone (Free, 1993).

Kiwifruit (*Actinidia deliciosa*) in particular, which has separate male and female plants, is highly reliant on insect visitors, usually honeybees and bumblebees to transfer pollen between plants of the two sexes. Several other fruit crops are highly self-incompatible or benefit substantially from cross-pollination, such as passion fruit (*Passiflora edulis*) and mango (*M. indica*), both of which produce significantly heavier fruits when cross-pollinated by insects (Bos *et al.*, 2007; Carvalheiro *et al.*, 2011). Commercial triploid banana (*Musa acuminata*) cultivars by contrast are often sterile and naturally produce fruit without any influence from biotic pollination (Free, 1993).

Vegetable Crops

Many of the most common vegetable crops, such as carrot, brassica, and onion do not benefit from insect pollination services to produce marketable output; however, pollination is often important to ensure ample seed set when breeding. Yields of most fruiting vegetables benefit significantly from biotic pollination. In most cucurbits (*Curcurbita pepo* – pumpkins, squash, zucchini, etc.), melons (*C. melo*), and watermelons (*Citrulus lanatus*), plants produce separate male and female plants that require pollen transfer from male to female flowers to produce fruits. These crops are highly dependent on biotic pollination which is typically provided by honeybees, wild solitary bees or, in North and South America, by squash bees, which have evolved to specialize on cucurbits (Klein *et al.*, 2007). Tomatoes (*S. lycopersicum*) and eggplants (*Solanam melongena*) by contrast are self-compatible but benefit moderately from biotic pollination when larger bodied bees vibrate their flowers in order to gather pollen, which is naturally sticky and heavy, dislodging additional pollen onto the stigma (Gemmill-Herren and Ochieng, 2008). Honeybees are too small to perform this kind of pollination ('buzz pollination'), so most commercial pollination is performed by bumblebees such as *Bombus impatiens*, particularly in enclosed glasshouse systems where honeybees are difficult to manage (Delaplane and Mayer, 2000). Although managed bumblebees are widely used in glasshouse systems, pollination by vibrating wands is still practiced in Australia where bumblebees cannot be introduced, although efforts persist to commercially domesticate a suitable native pollinator. Stingless bees, (*Meliponini*), though small, have been shown to be effective buzz pollinators for a number of tropical vegetable cropping systems (Slaa *et al.*, 2006).

Edible Oil and Proteinaceous Crops

Edible oil crops are a wide range of usually unrelated crops produced for oils extracted from their fruits and seeds. Many of these crops, notably seed cotton (*Gossypium* sp.), coconut (*Cocos nucifera*), sunflower (*Helianthus annuus*), and rapeseed (*B. napus*/*B. rapa*) are among the most widely grown crops

globally (FAO, 2013). Sunflowers have one of the two pollination systems, in most oil producing cultivars the flower switches between the male and female phases, whereas in hybrid production, specifically bred male and female lines are planted within the same field. Both benefit from insect visitation to optimize pollen transfer to female plants (Free, 1993). Rapeseed and canola are highly self-compatible and readily set pods with wind and self-pollination; however, their high nectar concentration makes them attractive to insects which can increase pollen transfer, thereby increasing the total marketable yield by 20% (Bommarco *et al.*, 2012). Rapeseed is attractive to a wide diversity of pollinating insects and although wild insects can be significant, managed honeybees are thought to provide a more reliable and stable service to larger fields (Rader *et al.*, 2009 but see Rader *et al.*, 2011; Woodcock *et al.*, 2013). Pollination in coconut, which has separate male and female flowers, produces similar increases in yield through greater drupe set (Meléndez-Ramírez *et al.*, 2004). Some edible oil crops gain very little benefit from pollination, such as linseed (*L. usitatissimum*) (Williams *et al.*, 1991), whereas olive (*Olea europaea*), is entirely wind pollinated (Klein *et al.*, 2007) and some, specially bred cultivars of rapeseed can also set ample yield from wind pollination alone (Free, 1993). In seed cotton, biotic pollination benefits production of both utilized outputs, resulting in a 20% increase in total seed weight and a 16% increase in lint production (Rhodes, 2002).

Stimulant Crops

Both the major stimulant crops, cocoa (*Theobroma cacao*) and coffee (*Coffea arabica* and *C. canephora*), benefit from biotic cross-pollination between plants to produce good quality yields. In cocoa, although bees have been observed to provide pollination services in some regions, the majority of pollination services are provided by midges (*Cecido myiid* and *Ceratopogonid* spp.). Both species of coffee benefit from insect visitation, however, despite their lighter pollen grains; *C. canephora* is thought to be slightly more dependent on insect pollination than *C. arabica* due to greater self-incompatibility (Free, 1993; Klein *et al.*, 2003). Field studies have indicated that pollination produces both greater bean set and weight by ~20% and reduces the occurrence of misshapen pea berries by 27% (Ricketts *et al.*, 2004; Klein *et al.*, 2003).

Nut Crops

Yields of most nut crops benefit to a great extent from biotic pollination, often by increasing the total number of nuts produced, as is seen in almond (Klein *et al.*, 2012). Brazil nuts (*Bertholletia excelsa*) in particular are highly dependent on pollination by larger bodied bees (e.g., carpenter bees, *Xylocopa* sp.) to produce marketable produce (Cavalcante *et al.*, 2012; Klein *et al.*, 2007). Although chestnut (*Castanea sativa*) is mostly wind pollinated, as a self-incompatible crop, insect visitation can still result in economically significant increases in crop yield (Free, 1993). Of the most widely grown nut crops (Klein *et al.*, 2007) only walnuts (*Juglans* sp.) and some cultivars of peanuts (*Arachis hypogaea*) are known to produce nuts completely by self and wind pollination.

Pulse Crops

Several pulse crops, notably soybean (*Glycine max*) and faba bean (*Vicia faba*), are often primarily self-pollinated due to their tightly enclosed flowers which place the anthers in direct contact with the stigma. Pollination of soybeans by Africanized honeybees has been observed to increase yields by 50% under experimental conditions, with bee-pollinated flowers producing more and heavier pods than enclosed plants (Chiari *et al.*, 2005). In faba beans, cross-pollination by insects has also been demonstrated to improve both yield and disease resistance (Suso, 2012). By contrast, biotic pollination has no effect on the yields of peas (*Pisum sativum*), lentils (*Lens esculenta*), and chickpeas (*Cicer arietinum*) and very little in cowpea (*Vigna unguiculata*). Other pulses such as runner beans (*Phaseolus coccineus*) have more open flowers that directly benefit from biotic pollination (Łabuda, 2010).

Spice Crops

Among the crops grown for condiment or spice products are several species of the plant family *Umbelliferae*, notably fennel (*Foeniculum vulgare*), caraway (*Carum carvi*), and coriander (*Coriandrum sativum*), which are characterized by numerous small flowers with each flower producing multiple seeds. Visitation of these flowers by foraging insects helps transfer pollen among the many flowers, resulting in substantial increases in seed set (Free, 1993). Owing to the arrangement of its anthers making self-pollination impossible, vanilla (*Vanilla planifolia*) relies entirely on biotic pollination for pod set, although in many regions this must be done via hand pollination (Free, 1993).

Cereal Crops

Most arable grain crops, including the global staples of wheat, rice, and maize do not benefit from biotic pollination, instead relying entirely on self and wind pollination to produce seeds (Klein *et al.*, 2007). The only exception is the pseudocereal Buckwheat (*Fagopyrum esculentum*), which is self-incompatible and benefits greatly from insect pollination to set seed (Taki *et al.*, 2011).

Root and Tuber Crops

The marketable components of vegetables grown for the roots and tubers, such as potato (*Solanum tuberosum*) and cassava (*Manihot esculenta*) are not known to benefit from insect pollination (Klein *et al.*, 2007). As potato tubers propagate vegetatively, most commercial varieties of potato have a reduced ability to flower and breeders do not select for traits that make the flower attractive to pollinators. Although insects are capable of pollinating these flowers, pollination in many of these plants is done by hand to ensure genetic purity.

Sugar Crops

Although visited by several insects, sugar beet (*Beta vulgaris*) is not known to benefit from biotic pollination as their flowers are highly self-compatible and effectively pollinated by self

Table 2 Economic value of pollination services to global regions

Region	*Total value of crop production (€bn)*	*Value of pollination services (€bn)*	*Pollination services as a % of total value*	*Regional % of global pollination service value*
Africa	137.5	11.9	9	8
Asia	881	88.1	10	58
Europe	216.7	22	10	14
North America	176.8	17.9	10	12
South America	187.7	11.6	6	8
Oceania	18.8	1.3	7	1
Total	1618.5	152.8	9.5	

Source: Adapted from Gallai, N., Vaissière, B.E., 2009. Guidelines for the economic value of pollination services at a national scale. Available at: http://www.internationalpollinatorsinitiative.org/uploads/POLL%20VALUE%20NATIONAL%20MANUAL.pdf

and wind pollination alone (Free, 1993). As a grass, sugar cane (*Saccharum officinarum*) is entirely pollinated by wind.

Other Crops

Apart from edible crops, yields of several important plants grown for commercial seed production benefit to a great extent from insect pollination, often by specialist insects. Lucerne seed (*Medicago sativa*) yields, in particular, are heavily dependent on insect pollination by specialist alfalfa leafcutter bees (*M. rotundata*), which are better able to access the nectaries and pollen of lucerne flowers (Delaplane and Mayer, 2000). Similarly, several species of clover (*Trifolium* sp.) are widely bred for planting as nitrogen fixing cover crops or hay and require insect visitation to effectively cross-pollinate. Red clovers (*Trifolium pratense*), among other species, have long, deep flowers that cannot be accessed by most short-tongued bees and instead require longer-tongued species such as the bumblebee *Bombus hortorum* (Bommarco *et al.* 2011).

Economic Valuation of Crop Pollination

It is widely recognized that the benefits of pollination services to yields carry considerable economic value, particularly as insect-pollinated crops are on average significantly more valuable per ton than other crops (Gallai *et al.*, 2009). Quantifying these benefits can play an important role in decision making and illustrating the impacts of changes in service availability (e.g., Ricketts *et al.*, 2004). Although a range of methods have been developed to estimate the economic value of pollination services, the most common is the dependence ratio method that estimates value based on the proportion of crop production lost in the absence of pollination services at a field (e.g., Olschewski *et al.*, 2006) and market scale (e.g., Losey and Vaughn, 2006). On the basis of this method, the global economic value of biotic pollination to crop production in 2005 was estimated at €153bn in enhanced production alone (Gallai *et al.*, 2009). Notably this estimate does not include the benefits to vegetable seed production and crops not traded on monetary markets, such as subsistence growing and plants used by traditional people (Ashworth *et al.*, 2009). More than half (58%) of this value originates from Asia (**Table 2**), in particular China and India, although valuation hotspots can be found in Brazil, Western USA, and several parts of Japan (Lautenbach *et al.*, 2012; Gallai *et al.*, 2009). In some developing nations, pollination-driven production can form a substantial proportion of national agricultural Gross Domestic Product (GDP) such as in Ghana where cocoa production forms a major component of both agricultural and total national GDP. As such pollination services, valued at US$788m formed ~0.5% of total national GDP, substantially higher than in other more developed nations (Ngo *et al.*, 2012) (**Figure 1**).

The value of pollination services as estimated by various sources (Gallai *et al.*, 2009; Losey and Vaughn, 2006; Smith *et al.*, 2011; Jian-Dong and Wen-Feng, 2011; Brading *et al.*, 2009; Gallai and Vaissière, 2009) was converted into US$ and divided by total national GDP (current US$) using the data from World Bank (2012).

Within crop groups, these economic benefits are particularly high for fruit crops and fruiting vegetables which encompass ~66% of global pollination service value (**Table 3**) due to their high market prices and high dependence on pollination to produce an optimal yield, and within edible oilseeds due to the high global volume of the crops grown (Gallai *et al.*, 2009).

The economic benefits of added crop productivity also vary in scale and form between different stakeholders; for producers, increased production and market quality can increase profits per hectare substantially (Kasina *et al.*, 2009; Winfree *et al.*, 2011). This can be especially valuable to producers in lower income countries, where agriculture often forms a more important component of local economies (Lautenbach *et al.*, 2012). Consumers by contrast benefit from reduced prices as a result of added production. Globally, the total value of this price reduction is estimated to be between €153bn and €422bn, greater than the value of additional produce itself (Gallai *et al.*, 2009).

Beyond these direct production benefits, animal pollination services also provide significant value to producers in costs avoided. In the absence of sufficient animal pollination services, producers often utilize labor-intensive artificial pollination using paintbrushes (e.g., Partap and Ya, 2012), vibrating wands (e.g., Hogendoorn *et al.*, 2010), or sprays (e.g., Sakomoto *et al.*, 2009), which can substantially increase producer costs. For instance, Allsopp *et al.* (2008) estimated that the total costs of replacing pollination services to tree fruit crops in South Africa's Western Cape region is at between

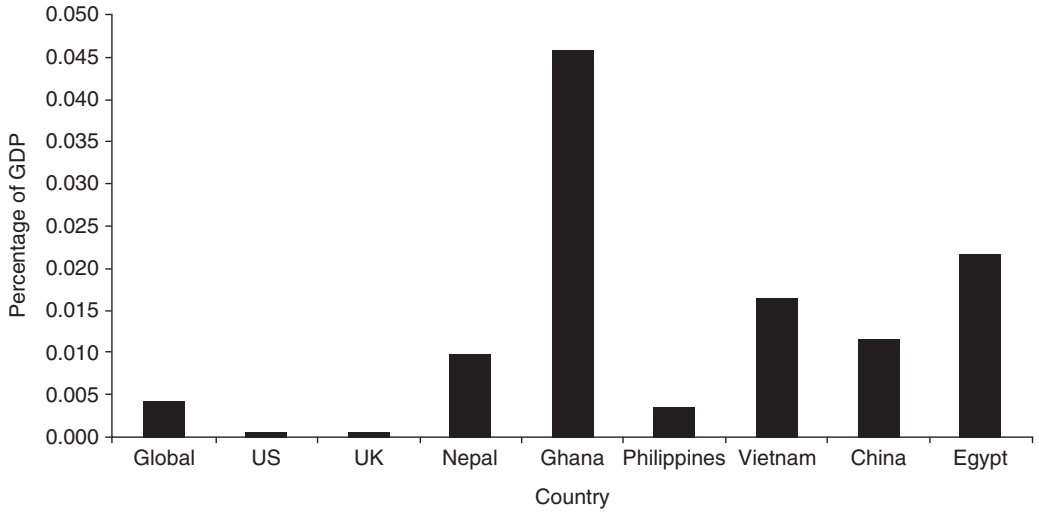


Figure 1 Proportion of total national GDP arising from insect-pollinated crops for selected countries and global average. Compiled by H. Ngo from FAO data.

Table 3 Economic value of pollination services to crop groups

Crop group	*Total value of crop production (€bn)*	*Value of pollination services (€bn)*	*Pollination services as a % of total value*	*Regional % of global pollination service value*
Vegetables	418	51	12	33
Fruits	219	50	23	33
Edible oil crops	240	39	16	25
Stimulants	19	7	39	5
Nuts	13	4	31	3
Pulses	24.1	1	4	1
Spices	7	0.2	3	0.1
Cereals	312	0	0	0
Sugar crops	268	0	0	0
Roots and tubers	98	0	0	0
Total	1618.5	152.8	9.5	

Source: Adapted from Gallai, N., Vaissière, B.E., 2009. Guidelines for the economic value of pollination services at a national scale. Available at: http://www.internationalpollinatorsinitiative.org/uploads/POLL%20VALUE%20NATIONAL%20MANUAL.pdf

$77m and $433m (US) annually. Furthermore artificial pollination may not be viable for all crops, such as raspberry where hand pollination produces lower quality fruits compared with insect pollination (Kempler *et al.*, 2002). Pollination services provided by wild animals can also reduce the need to hire managed honeybees for crop pollination. For example, hiring additional honeybees to replace pollination services provided by wild pollinators in the watermelon plantations in New Jersey would cost producers an estimated $200 000, effectively doubling the expenditure on managed pollination services (Winfree *et al.*, 2011).

In addition to these economic benefits, production added by pollination services has a substantial impact on human diets. Globally, animal-pollinated crops form 35% of the total crop production (Klein *et al.*, 2007) and a loss of pollination services would result in a reduction of total crop production by 3–8% even if highly pollinator-dependent crops were replaced with pollinator-independent ones (Aizan *et al.*, 2009). Although the majority of crop-based calories and protein in the human diet derive from pollinator-independent crops, animal-pollinated crops are the main sources of vegetable fats and several major micronutrients. Consequently, ~41% of vitamin A, 20% of vitamin C, 32% of carotenoids, and 20% of fluorides in global diets are thought to derive from production added by insect pollination (Eilers *et al.*, 2011).

Threats to Pollination Services

Many of the benefits of biotic pollination are directly tied to the abundance and diversity of pollinating animals, with shortfalls linked to localized yield losses (Bommarco *et al.*, 2011), limitations (Groeneveld *et al.*, 2010), and instability (Garibaldi *et al.*, 2011a), despite growing global yields (Aizen *et al.*, 2008). In recent decades, although global honeybee stocks have increased (Aizen and Harder, 2009), there have been widely reported declines in the number of managed

honeybees in many western countries (Potts *et al.*, 2010a; van Engelsdorp and Meixner, 2010) and many wild pollinators have suffered observed declines across the world (Potts *et al.*, 2010b). Contrary to these declines in available pollinators there has been a 300% rise in the global area of insect-pollinated crops (Aizen and Harder, 2009); and insect-pollinated crops have become increasingly important to the agricultural economies of many developed and developing countries (Lautenbach *et al.*, 2012). Furthermore, horticultural crops, many of which are insect pollinated, form ~20% of agricultural exports from the developing world, twice that of cereals and further crop diversification in developing nations is increasingly regarded as an effective means of alleviating poverty (Lumpkin *et al.*, 2006). Unlike the historical increase in cereal production, this expansion of production in the developing world has come primarily from increases in the area cropped, not from yield increases.

Declines in wild pollinators have been primarily driven by the loss, degradation, and fragmentation of seminatural habitat within agricultural landscapes as large monocultures have replaced numerous small fields, leaving many pollinating insects with little forage or nesting resources (Feon *et al.*, 2010). Although mass flowering crops can provide highly abundant forage for some pollinating insects (Westphal *et al.*, 2003), these resources are not available for much of the flying season and can, over several years, increase competition for later season resources with other species (Diekötter *et al.*, 2010). These effects are exacerbated by high applications of herbicides and fertilizers, which can significantly alter plant communities by changing the soil composition or by killing plants (Henle *et al.*, 2008; Carvalheiro *et al.*, 2011). Consequently, it is widely observed that pollination services to crops often decline substantially with greater distance to the seminatural habitat (Garibaldi *et al.*, 2011b) and less diverse habitat within the wider landscape (e.g., Klein *et al.*, 2012; Taki *et al.*, 2011).

Within managed honeybees, which are less sensitive to habitat loss than wild pollinators (Winfree *et al.*, 2010), declines are primarily thought to be driven by the spread of parasites and pests, in particular the mite *Varroa destructor* which can directly spread many diseases and viruses to afflicted bees (van Engelsdorp and Meixner, 2010). Several of these viruses have been suggested as possible causes of widely observed colony collapse disorders within North America (Cox-Foster *et al.*, 2007), although the exact cause remains as yet unidentified. The fungi *Nosema* sp. and foulbrood (e.g., *Melissococcus plutonius*) also represent significant pressures on honeybee colonies by reducing breeding success and killing many honeybee brood if left unchecked (van Engelsdorp and Meixner, 2010). The prevalence of disease within wild bees is less well understood; however, several studies have demonstrated that diseases can spill over from managed to wild populations and even between different species, further increasing pressures on wild populations (Meeus *et al.*, 2011; Otterstatter and Thomson, 2011). The rising costs of treating these diseases, coupled with falling honey prices and poor availability of effective *Varroa* treatments in some countries (e.g., UK; Formato *et al.*, 2010) have driven sharp declines in the number of beekeepers in many countries (Potts *et al.*, 2010b).

Wider use of insecticides across the world is also thought to have negatively affected both wild pollinators and managed honeybees by causing direct mortality (Scott-Dupree *et al.*, 2009) or reducing breeding success (Lu *et al.*, 2012), metabolic efficiency (Hawthorne and Dively, 2011), or foraging efficiency (Yang *et al.*, 2008). These impacts are further exaggerated by exposure to multiple pesticides (Gill *et al.*, 2012). Recent research has supported this concern by demonstrating reduced pollination services in landscapes with greater chemical inputs (Brittan *et al.*, 2010). In some regions, such as parts of China, extreme pesticide use has completely eradicated native pollinators and deterred beekeepers from placing their hives in affected areas, forcing producers to resort to labor-intensive hand pollination or switch to pollinator-independent crops (Partap and Ya, 2012). Climate change may also play a role in the declines of pollinating insects by driving the spread of new pests, such as the Asiatic hornet in Europe, where native honeybees have no defenses (Marris *et al.*, 2011) or by disrupting plant-pollinator phenological networks (Schweiger *et al.*, 2010). Outbreeding between imported honeybee hives and local strains could potentially cause the loss of desirable local traits (Jaffe *et al.*, 2010). Finally, the introduction of managed pollinators into an area may also increase resource competition with native wild pollinators (Goulson and Sparrow, 2009 but see Garibaldi *et al.*, 2013).

Management of Pollination Services

Despite widely observed declines in pollinators, there are a number of ways that producers can manage their operations to enhance or stabilize pollination service provision. Foremost, managed pollinators can be brought in to provide concentrated pollination services to crops particularly to large-scale fields or orchards, where services from wild pollinators alone may be too unstable. Honeybees in particular are effective pollinators of many open-grown crops globally although several other species have been domesticated for pollination service provision in particular crops or cropping systems. Large numbers of honeybees are particularly important for pollination in almond plantations in California, USA (Klein *et al.*, 2012) and in large-scale systems where high numbers of visitors are required (Rader *et al.*, 2009; Isaacs and Kirk, 2010). In some crops that are less attractive to honeybees (e.g., pears) or which honeybees may not visit legitimately (e.g., apples), careful management such as introducing some hives later than others can result in greater overall pollination services by slowing the rate of nectar robbing behavior and increasing competition (Stern *et al.*, 2001, 2004).

Although honeybees are highly numerous and will forage on most crop plants, other managed pollinators are more effective service providers in some crops or production systems. Bumblebees (*Bombus* sp.) have been observed to be more effective pollinators of several soft fruit crops (Isaacs and Kirk, 2010; Denisow, 2004; Stubbs and Drummond, 1997; Willmer *et al.*, 1994) and forage earlier in the day and at lower temperatures than honeybees, increasing their efficiency further in cooler climates (Isaacs and Kirk, 2010). Long-tongued bumblebees are widely observed to be the

primary pollinators of several deep flowered crops, notably faba beans (Aouar-Sadli *et al.*, 2008; Benachour *et al.*, 2007) and red clover (Bommarco *et al.*, 2012). With their smaller colony sizes, bumblebees are less vulnerable to overheating and resource depletion when confined in enclosed systems than honeybees (Delaplane and Mayer, 2000), making them ideal glasshouse pollinators and highly effective on several crops such as tomatoes (Banda and Paxton, 1991), strawberry (Ji-Larn *et al.*, 2006), and sweet pepper (Ercan and Onus, 2003).

Some solitary bee species have also been domesticated to provide more specialist pollination services to certain crops. Mason bees (*Osmia* sp.) in particular, have been demonstrated to be several times more effective per individual than honeybees in apples, almonds (Vicens and Bosch, 2000a,b), blueberries (Stubbs and Drummond, 1997), and sweet cherries (Bosch *et al.*, 2006). Mason bees are primarily bought as cocoons and incubated at different temperatures to ensure emergence in time with peak crop flowering (Sheffield *et al.*, 2008a); however, it is possible that introduced individuals may find or enhance wild populations if careful management to provide suitable nesting sites and postcrop forage is provided (Stubbs and Drummond, 2001; Sheffield *et al.*, 2008b). For instance, Sheffield *et al.* (2008b) found that sowing late flowering bigleaf lupins (*Lupinus polyphyllus*) in Nova Scotia apple orchards significantly increased breeding success of *Osmia lignaria* introduced to provide pollination. Another domesticated solitary bee is the alfalfa leafcutter bee (*M. rotundata*), which has been domesticated primarily to pollinate lucerne, its preferred forage, but can also effectively pollinate other crops such as blueberry (Stubbs and Drummond, 1997).

Although managed pollinators can provide ample pollination services to crops, in many cropping systems, wild insects are often as or more important service providers (Winfree *et al.*, 2008; Garibaldi *et al.*, 2011b; Holzschuh *et al.*, 2012; Garibaldi *et al.*, 2013). In some crops, notably strawberries (Chagnon *et al.*, 1993) and sunflowers (Carvalheiro *et al.*, 2011; Greenleaf and Kremen, 2006) a mix of wild pollinators and managed honeybees has been demonstrated to provide the highest yields as the two groups provide complementary pollination of the same flowers. Diverse wild pollinator communities often provide insurance against losses of key service providers as the remaining species become more able to exploit crop resources (Winfree *et al.*, 2010; Klein *et al.*, 2012) and produce more stable crop yields between years (Garibaldi *et al.*, 2011b). Recent studies have also demonstrated that honeybees are largely incapable of fully substituting for losses of wild insect pollination services in most crop systems, intensive or small holder (Garibaldi *et al.*, 2013). Furthermore, diverse pollinator communities allow producers to grow more diverse crops within their holdings or between years as part of rotations by providing an array of pollinators with different foraging habits and preferences.

There are a number of ways that producers can manage their holding to maintain and encourage healthy wild pollinator populations. Foremost, providing natural habitat in close proximity to crops can provide foraging and nesting resources to wild insects when crops are not in bloom. Morandin and Winston (2006), for instance, recommend that ~30% of the surrounding landscape is left uncultivated to optimize pollination services to mass flowering crops. Ricketts *et al.* (2008) also demonstrate that pollination services fall substantially at distances of more than 1000 m from a seminatural habitat. Where maintaining large sections of habitat is not possible or practical, including fallow land as part of crop rotations has been demonstrated to encourage pollinators even in intensive landscapes (Kuussaari *et al.*, 2011). Alternatively, many plants used as unharvested cover crops, such as red clover, can add forage diversity to the landscape. Pollinators can also be encouraged within fields by planting diverse nectar flower margins or tussocky grasses at the edge of crops left untreated by pesticides (Pywell *et al.*, 2011; Potts *et al.*, 2009; Lye *et al.*, 2009). In several developed nations many of these practices are subsidized as part of national agri-environmental schemes, providing an added incentive to adopt these practices (Kleijn *et al.*, 2006), and can provide additional on-farm benefits such as soil quality maintenance and erosion control (Wratten *et al.*, 2012). A recent study in South Africa has also demonstrated that allowing flowering weeds to remain in sunflower fields enhanced pollination service benefits by a greater extent than the negative effects of the weeds themselves and produced a more even pollination throughout the field (Carvalheiro *et al.*, 2011). Reducing herbicide use and grazing intensity on grasslands can also help promote pollinator diversity by allowing more diverse flower communities to establish (Hatfield and LeBuhn, 2007; Scheper and Kleijn, 2011).

Conclusion

As the global population continues to grow and demand for food production increases, the areas of flowering crops needed to meet this demand will continue to expand and so will the reliance on pollination services. Pollinators provide a wide range of production, economic, and health benefits and they will need to be increasingly considered as a legitimate agricultural input contributing to food security.

See also: Biodiversity and Ecosystem Services in Agroecosystems. Forage Crops. Land Use: Management for Biodiversity and Conservation. Medicinal Crops. Natural Capital, Ecological Infrastructure, and Ecosystem Services in Agroecosystems. Spices and Aromatics. Tree Fruits and Nuts

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D

Dairy Animals

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Glossary

Age at first calving The age from the date of birth to date of first calving.
Breed A group of animals related by descent and having similar appearance, behavior, and most of the other characteristics.
Crossbreeding The mating of animals of different breeds. Crossbreeding is followed for breeding animals for milk and meat production. In India, zebu nondescript cows are crossed with exotic breeds, like Holstein Friesian, Brown Swiss, and Jersey bulls or their semen, to enhance the milk production potential of the progeny.
305-days milk yield Milk yield produced up to 305 days of lactation.
Dry period The period from the date of dry to the date of next calving.
Gestation period The period from the date of conception to the date of calving.
Lactation length The period from the date of calving to the date of dry.
Lactation milk yield Total milk yield produced by a cow or a buffalo in complete lactation.
Service period The period from the date of calving to the date of conception.
Species A group of individuals that have certain common characteristics, which distinguish them from other group of individuals and are capable of interbreeding and producing fertile offspring.

Cattle

Animals belonging to the phylum Chordata (backbone animals), class Mammalia (milk giving), order Artiodactyla (even toed and hoofed), suborder Ruminatia (cud-chewing), family Bovidae (hollow unbranched horn), and genus *Bos* (ruminant quadrupeds) are cattle.

Cattle can be broadly classified into dairy and beef cattle. Dairy cattle are cows (adult females) that are bred for their ability to produce milk. Beef cattle are bred for meat production.

Zoological Classification of Cattle

Table 1 shows the zoological classification of cattle.

Domestication of Cattle

Time: 6000–6500 years BC.
Location: Old World.
Reason: Religious.
How: Aurochs.

Number of chromosome pairs of cattle: 30.

Body Weights

Body weight in cattle ranges from 25–45 kg at birth to 464–653 kg at maturity.

Common Terms Related to Cattle

Terms related to cattle that are commonly used are given in Table 2.

Utility

Milk, meat, draught, manure, and hide.

Table 1 Zoological classification of cattle

Kingdom	Animalia
Phylum	Chordata (backbone animals)
Class	Mammalia (milk-giving)
Order	Artiodactyla (even toed and hoofed)
Suborder	Ruminatia (cud-chewing)
Family	Bovidae (hollow unbranched horn)
Genus	*Bos* (ruminant quadrupeds)
Species	1. *Bos indicus* (humped cattle)
	2. *Bos taurus* (without any hump)

Important Breeds of Cattle

Although there are approximately 800 cattle breeds around the globe, a few important cattle can be studied by classifying them as *Bos indicus* and *Bos taurus*. Historically, there was little distinction between dairy and beef cattle, with the same stock often being used for both meat and milk production, but now cattle are bred specifically for meat or milk purpose.

Dairy cows generally are of the species *B. taurus*. A few important *taurus* breeds are listed in Table 3. Cows of *B. indicus* species, also known as zebu cattle, are known for their sturdy nature, disease resistance, draught ability, and adaptation to high temperature. Moreover, a few breeds of zebu cattle are good milkers. According to the Food and Agriculture Organization Manual entitled 'Zebu Cattle of India and Pakistan' (1953), Indian cattle breeds are grouped into six categories as given in Table 4. The meat of adult cattle is known as beef and cattle raised for meat production are beef cattle. A few important beef cattle breeds are listed in Table 5.

In India, zebu nondescript cows are crossed with exotic breeds, like Holstein Friesian, Brown Swiss, and Jersey bulls or their semen, to enhance the milk production potential in the progeny. A few important crossbred cattle are listed in Table 6.

Depending on the cattle species, breed, and region of location of an animal, age of puberty differs. Accordingly, breeding or artificial insemination of heifers is usually done around 13 months of age in *taurus* breeds in temperate regions, whereas it is done around 25–30 months of age in *zebu*. A cow's gestation period is approximately 9 months. Average ranges for some economic traits in Indian cattle are given in Table 7.

Jersey

Origin: This breed was developed from the island of Jersey in the English Channel off the coast of France.

Distinguishing characters:

- Jersey is one of the oldest dairy breeds, having been reported by authorities as being purebred for nearly six centuries.
- The color in Jerseys may vary from a very light gray or mouse color to a very dark fawn or a shade that is almost black. Both the bulls and females are commonly darker around the hips and around the head and shoulders than on the body.

Table 2 Common terms related to cattle

Common name of animal	*Male*	*Female*	*Young*	*Group*	*Act of mating*	*Gestation/pregnancy period*	*Name of giving birth*
Dairy cattle	Bull	Cow/heifer	Calf	Herd/drove	Serving	9 months	Calve

Table 3 List of *Bos taurus* dairy cattle breeds

S. No.	*Name of the breed*	*Native breed*	*Specific region*	*Remarks*
1	Brown Swiss	Switzerland	–	Dairy breed
2	Holstein Friesian	Holland	Province of North Holland and West Friesland	Dairy breed
3	Jersey	British Isles	Island of Jersey	Dairy breed
4	Guernsey	Guernsey	British Channel Island of Guernsey	Dairy breed
5	Ayrshire	Scotland	Scotland	Dairy breed

Table 4 Different breed groups of Indian cattle breeds

Group	*Particulars*	*Name of breeds*
First	Lyre-horned gray cattle with white foreheads, prominent orbital arches, and faces with flat or dished profiles	Kankrej, Malvi, Kherigarh, and Tharparkar
Second	Shorthorned, white or light gray with coffin-shaped skull, orbital arches, and faces with convex profiles	Hariana, Ongole, Mewati, Nagauri, Rathi, Krishna Valley, and Gaolao
Third	Heavy body build, pendulous dewlap and sheath, prominent forehead, spotted red or white, or various sheds of red and white	Gir, Red Sindhi, Sahiwal, Deoni, Nimari, and Dangi
Fourth	Mysore-type cattle. Forehead is prominent and the horns emerge from the top of the poll fairly close together in upward and backward direction	Amritmahal, Hallikar, Kangayam, Khillari, Alambadi, and Bargur
Fifth	Heterogeneous mixture – small, black, red, or dun cattle often with large patches and white markings. Found in Himalayan region and rugged terrain	Ponwar and Siri
Sixth	Those animals that cannot fit in any of the five groups	Dhanni (Pakistan)

Source: Reproduced from Banerjee, G.C., 2010. A Textbook of Animal Husbandry, eigth ed. New Delhi: Oxford and IBH publishing Co. Pvt. Ltd.

- Age at first calving: 26–30 months.
- Milk yield: 5000–8000 kg.

Holstein Friesian

Origin: This breed originated in Holland.

Distinguishing characters:

- Holsteins are large, stylish animals with color patterns of black and white or red and white.
- Holstein heifers can be bred at 15 months of age, when they weigh approximately 800 lb. It is desirable to have Holstein females calve for the first time between 24 and 27 months of age.
- Milk yield: 7200–9000 kg.
- This is by far the best diary breed among exotic cattle regarding milk yield. On an average, it gives 25 l of milk per day, whereas a crossbreed Holstein Friesian cow gives 10–15 l of milk per day.
- It can perform well in coastal and delta areas.

Red Sindhi

- Home tract of Red Sindhi breed of cattle is Sindh province (Karachi and Hyderabad) in present Pakistan. Portion of Sindh called Kohistan is real breeding tract of this breed.
- Mainly available in Punjab, Haryana, Karnataka, Tamil Nadu, Kerala, and Odisha.
- Milk production in institutional herds ranges from 1250 to 1800 kg per lactation (Indian Council of Agricultural Research, 2008; Banerjee, 2010).

Sahiwal

- Breeding tract is Montgomery district of Pakistan, which is now known as Sahiwal district.
- In India, pedigree herds found in Punjab, Haryana, Uttar Pradesh, Delhi, Bihar, and Madhya Pradesh.
- First lactation milk yield ranges from 1597 to 2125 kg (Indian Council of Agricultural Research, 2008).

Gir

- Mainly found in the Gir forest areas of south Kathiawar in Gujarat (India).
- Also found in Maharashtra and adjacent Rajasthan.
- Milk yield ranges from 1250 to 1800 kg.

Deoni

- Mainly found in western parts of Andhra Pradesh in India.
- Cows are good milk producers and bullocks are good for work.

Table 5 List of beef cattle breeds

S. No.	*Name of the breed*	*Native breed*
1	Angus	Scotland
2	Nellore	India

Table 6 List of crossbred cattle in India

Name	*Inheritance*		*Place*
	Bos indicus *(cows)*	Bos taurus *(bull)*	
Taylor	Local cows	Ayrshire	Patna (Bihar)
Jersind	Kankrej, Gir, Hariana, Sahiwal, and Red Sindhi	Holstein Friesian, Brown-Swiss, Jersey, and Guernsey	Allahabad (Uttar Pradesh)
Karan Swiss	Sahiwal and Red Sindhi	Brown-Swiss	NDRI, Karnal (Haryana)
Karan Fries	Tharparkar	Holstein Friesian	NDRI, Karnal (Haryana)
Sunandini	Local nondescript	Brown-Swiss	Kerala
Frieswal	Sahiwal	Holstein Friesian	Military Dairy Farm

Abbreviation: NDRI, National Dairy Research Institute.

Table 7 Averages range for some economic traits in Indian cattle

Breeds	*Age at first calving (months)*	*First calving interval (days)*	*First service period (days)*	*First lactation milk yield (kg)*	*First lactation length (days)*
Hariana	41–49	434–523	136–303	730–1170	257–315
Sahiwal	38–48	418–473	136–189	1597–2125	228–330
Tharparkar	39–53	418–474	130–183	1326–2139	268–317
Red Sindhi	39–49	436–562	152–158	1312–1694	284–345
Gir	44–61	456–541	135–259	1125–1859	230–394
Ongole	36–42	529–637	210–241	658–999	279
Deoni	47–55	456–472	173–192	818–1041	282–302

Source: Reproduced from Indian Council of Agricultural Research, 2008. Handbook of Animal Husbandry. New Delhi: Indian Council of Agricultural Research.

Hariana

- The native tract of this breed is Haryana state in India. Mainly found in Hisar, Rohtak, and Gurgaon district of Haryana, Delhi, Uttar Pradesh, and western parts of Madhya Pradesh.
- The average milk yield is between 600 and 800 kg per lactation.
- Most popular dual-purpose breed of cattle in Indo-Gangetic plains. Bullocks are powerful for road transport and rapid plowing (Indian Council of Agricultural Research, 2008).

Tharparkar

- Tharparkar breed of cattle belongs to Tharparkar district in Sindh province in Pakistan.
- Also found in Jodhpur and Jaisalmer district of Rajasthan in India.
- First lactation milk yield ranges from 1326 to 2139 kg.

Kankrej

- Native of this breed is southeast of Rann of Kutch in Gujarat.
- Bullocks are fast, active, and strong. Good for plow and cart purpose.

Kangayam

- Also known by other names of Kanganad and Kongu, although the name Kangayam is well known. These cattle are bred in the southern and southeastern area of the Erode district of Tamil Nadu in India.
- Best suited for plowing and transport. Withstands hardy conditions.

Amritmahal

- Mainly found in Karnataka.
- Best suitable for plowing and transport.

Hallikar

- Mainly found in Tumkur, Hassan, and Mysore districts of Karnataka.
- Bullocks are strong, well spirited, quick, and steady in field as well as on road.

Umblacherry

Origin: Tanjore district in Tamil Nadu.

Distinguishing characters:

- This breed has similar characters as Kangayam.
- Bulls are used for plowing in Tanjore delta area.
- Calves are red in color when born and become gray in color after 6 months of age.
- Cows are poor milker with average milk yield of 300 kg per lactation.
- Male animals are good for hard work.

Cow Nutrition

Average rates of daily feeding of concentrates and green and dry fodder assumed for different stages of life of cattle are given in Table 8.

Heifer

Heifer is a young female cow before she has had her first calf. Heifers are selected on the basis of progeny testing, i.e., the potential of the sire and milk production of the dam, their proper growth, good health, and freeness from any genetic abnormality.

Bull

Bulls contribute 50% of the inheritance to the next generation. Most of the genetic improvement in a population comes through proper bull selection. It is not very practicable to have intense selection of the females for breeding, i.e., almost all the heifers will have to be reared and used for breeding in a situation where age at first calving and calving interval are not optimum. Hence, most care is to be given for bull selection.

Cattle Breeding

The following points describe the different aspects of scientific breeding of cattle and buffaloes.

- Reproduction is an important consideration in the economics of cattle production. In the absence of regular breeding and calving at the appropriate time, cattle rearing will not be profitable. A healthy calf each year is the usual goal. This is possible only by increasing the reproductive efficiency of the animals.
- Successful reproduction encompasses the ability to mate, the capacity to conceive and to nourish the embryo, and deliver the viable young ones at the end of a normal gestation period. In fact, interruption in this chain of events

Table 8 Average rates of daily feeding of concentrates and green and dry fodder assumed for different age groups of cattle

Cattle		*Concentrate (kg)*	*Green fodder (kg)*	*Dry fodder (kg)*
Crossbred (milch)		2.75	20.0	6.00
Females >3 years of age	Improved cows (milch)	1.20	10.00	6.00
	Other milch cows and not calved even once	0.125	3.5	3.16
Males >3 years of age		0.17	4.96	5.65
Males <3 years of age	Crossbred (young stock)	1.50	10.00	2.00
	Other young stock	0.016	1.58	1.47

Source: Reproduced from Banerjee, G.C., 2010. A Textbook of Animal Husbandry, eigth ed. New Delhi: Oxford and IBH publishing Co. Pvt. Ltd.

leads to failure of the cow to conceive, the death of the embryo, or premature delivery of the fetus.

- Mating – The reproductive efficiency is a complex phenomenon controlled by both genetic and nongenetic factors, the nongenetic factors being climate, nutrition, and level of management. The reproductive efficiency varies not only between species and breeds but also among the animals within the same breed. Even the best feeding and management cannot coax performance beyond the genetic limit of an inferior animal. Improving the genetic merits of livestock populations is important at all levels of management. A sound breeding program is a necessary part of the total animal production system.
- Factors affecting breeding efficiency of cattle are as follows:
  1. Number of ova – The first limitation on the breeding efficiency of fertility of an animal is the number of functional ova released during each cycle of ovulation. Ovulation is the process of shedding ovum from the Graafian follicle. In the case of cow, usually a single ovum is capable of undergoing fertilization only for a period of 5–10 h. Therefore, the time of mating in relation to ovulation is important for effective fertilization.
  2. Percentage of fertilization – The second limitation is fertilization of ova. Failure to fertilize may result from several causes. The spermatozoa may be few or low in vitality. The service may be either too early or too late so that the sperms and eggs do not meet at the right moment to result in fertilization.
  3. Embryonic death – From the time of fertilization till birth, embryonic mortality may occur due to a variety of reasons. Hormone deficiency or imbalance may cause failure of implantation of fertilized ova, which die subsequently. Death may occur as a result of lethal genes for which the embryos are homozygous. Other causes may be accidents in development, overcrowding in the uterus, insufficient nutrition, or infections in tile uterus.
  4. Age of first pregnancy – Breeding efficiency may be seriously lowered by increasing the age of first breeding. Females bred at a lower age are more likely to appear stunted during the first lactation, but their mature size is affected little by their having been bred early.
  5. Frequency of pregnancy – The breeding efficiency can be greatly enhanced by lowering the interval between successive pregnancies. The wise general policy is to breed for the first time at an early age and to rebreed at almost the earliest opportunity after each pregnancy. In this way, the lifetime efficiency is increased. Cows can be rebred in 9–12 weeks after parturition.
  6. Longevity – The length of life of the parent is an important part of breeding efficiency because the return over feed cost is greater in increased length of life. Also, it affects the possibility of improving the breed. The longer the life of the parents, the smaller the percentage of cows needed for replacement every year.
- Management practices to improve breeding efficiency of cattle are listed below:
  1. Keep accurate breeding records of dates of heat, service, and parturition. Use records in predicting the dates of heat and observe the females carefully for heat.
  2. Breed cows near the end of heat period.
  3. Have females with abnormal discharges examined and treated by a veterinarian.
  4. Call a veterinarian to examine females not settled after three services.
  5. Get the females checked for pregnancy at the proper time after breeding.
  6. Buy replacements only from healthy herds and test them before putting them in your herd.
  7. Have the females give birth in isolation, preferably in a parturition room and clean up and sterilize the area once parturition is over.
  8. Follow a program of disease prevention, test, and vaccination for diseases affecting reproduction and vaccinate the animals against such diseases.
  9. Practice a general sanitation program.
  10. Supply adequate nutrition.
  11. Employ the correct technique.
  12. Provide suitable shelter management.
  13. Detect silent or mild heat by using a teaser bull.

Cattle Population

According to the FAOSTAT in the year 2010, there were 1428.7 million cattle stock. Among those with approximately 210.2 million cattle stock, India is the country with the largest cattle population, contributing approximately 14.7% to the world, followed by Brazil (209.5 million), the United States (93.9 million), and China (83.8 million).

Housing Systems

In the UK, there are three main options available for housing dairy cattle.

- Cubicles
- Straw (loose) yards
- Kennels.

Cubicles and straw yards are most commonly used in Great Britain. There are advantages and disadvantages to both housing systems. Both systems can work equally well with regard to cow welfare and productivity, with much of the variation caused by management decisions and actions.

An efficient management of cattle will be incomplete without a well-planned and adequate housing of cattle. Improper planning in the arrangement of animal housing may result in additional labor charges and curtail the profit of the owner. During erection of a house for dairy cattle, care should be taken to provide comfortable accommodation to an individual cow. Also important are (1) proper sanitation, (2) durability, (3) arrangements for the production of clean milk under convenient and economic conditions, etc.

Location of dairy buildings

The points to be considered before starting construction of dairy buildings are as follows:

1. Topography and drainage: To offer a good slope for rainfall and drainage for the wastes to avoid stagnation within dairy building, construction should be at a higher elevation. A leveled area requires less site preparation and

thus lesser cost of building. Low lands and depressions and proximity to places of bad odor should be avoided.
2. Soil type: Fertile soil should be spared for cultivation. Foundation soils, as far as possible, should not be too dehydrated or desiccated. Such a soil is susceptible to considerable swelling during rainy season and exhibits numerous cracks and fissures.
3. Exposure to the sun and protection from wind: A dairy building should be located to a maximum exposure to the sun in the north and minimum exposure to the sun in the south and should have protection from prevailing strong wind currents, whether hot or cold. Buildings should be placed in a way that direct sunlight can reach the platforms, gutters, and mangers in the cattle shed. As far as possible, the long axis of the dairy barns should be set in the north–south direction to have the maximum benefit of the sun.
4. Accessibility: Easy accessibility to the buildings is always desirable. A cattle shed should be situated by the side of the main road, preferably at a distance of approximately 100 m.
5. Durability and attractiveness: It is always attractive when the buildings open up to a scenic view and add to the grandeur of the scenery. Along with this, durability of the structure is obviously an important criterion in building a dairy.
6. Water supply: Abundant supply of fresh, clean, and soft water should be available at a cheap rate.
7. Surroundings: Areas infested with wild animals and dacoits should be avoided. Narrow gates, high manger curbs, loose hinges, protruding nails, smooth-finished floor in the areas where the cows move, and other such hazards should be eliminated.
8. Labor: Honest, economic, and regular supply of labor should be available.
9. Marketing: Dairy buildings should only be in those areas from where the owner can sell his products profitably and regularly. They should be in a position to satisfy the needs of the farm within no time and at reasonable price.
10. Electricity: Electricity is the most important sanitary method of lighting a dairy. As a modern dairy always handles electric equipment that is economical, it is desirable to have an adequate supply of electricity.
11. Facilities, labor, and food: Feed storages facilities such as hay stacks, silo and manure pits should be quite near to the cattle barn for most efficient utilization of labour.
Some important features of feed stores are:

- Feed storages should be located near the center of the cow barn.
- Milk house should be located almost at the center of the barn.
- Center cross alley should be well designed with reference to feed storage, the stall area, and the milk house (Banerjee, 2010).

Types of housing

In India except in some organized dairy farms- owned by government, co-operatives or military- the prevalent practice is to tie the cows with rope on a Katcha floor. It is quite easy to understand that unless cattle are provided with good housing facilities, the animals will move too far in or out of the standing space, defecating all around and even causing trampling and wasting of feed by stepping into the mangers. The animals will be exposed to extreme weather conditions, all leading to bad health and lower production (Banerjee, 2010).

There are wide varieties of conditions, ranging from close confinement to little restrictions except at milking time, where dairy cattle may be successfully housed. However, two types of dairy barns are in general use at the present time.

1. The loose housing barn in combination with some type of milking barn or parlor.
2. The conventional dairy barn.

Loose housing system

It is a system where animals are kept loose except at the time of milking and treatment. The system is most economical. Some features of loose housing system are as follows.

- Cost of construction is significantly lower than the conventional type.
- It is possible to make further expansion without change.
- Facilitates easy detection of animal in heat.
- Animals feel free and therefore prove more profitable with even minimum grazing.
- Animals get optimum exercise, which is extremely important for their better health.
- Overall, better management can be rendered.

Cattle shed

The entire shed should be surrounded by a boundary wall of 5 ft height from three sides and manger, etc. on one side. The feeding area should be provided with 2–2.5 ft of manger space per cow. All along the manger, there shall be a 10-in.-wide water trough to provide clean drinking water. The water trough thus constructed will also minimize the loss of fodders during feeding. Near the manger, under the roofed house, 5-foot-wide floor should be paved with bricks having a little slope.

Shed for calves

On one side of the main cattle shed there should be a fully covered shed of 10×15 sq ft area to accommodate young calves. Such sheds with suitable partitioning may also serve as calving pen under adverse climatic conditions. Beyond this covered area, there should be a 20×10 sq ft open area having boundary wall so that calves may move there freely. In this way, both calf and cattle sheds will need in all a 50×50 sq ft area for 20 adult cows and followers. If one has limited resources, they can build ordinary, Katcha/semikatcha (mud/semimud) boundary walls; however, feeding and water trough should be cemented ones.

Conventional dairy barn

The conventional dairy barns are comparatively costly and are now becoming less popular day by day. However, by this system, cattle are more protected from adverse climatic condition.

The following barns are generally needed for proper housing of different classes:

- Dairy stock in the farm
- Cow houses or sheds

- Calving box
- Isolation box
- Sheds for young stocks
- Bull or bullock sheds.

Cow sheds

Cow sheds can be arranged in a single row if the number of cows is less – say, less than 10 – and in a double row if the herd is a large one. Ordinarily, not more than 80–100 cows should be placed in one building. In double-row housing, the stable should be so arranged that the cows face out (tail-to-tail system) or face in (head-to-head system) as preferred.

Advantages of tail-to-tail system:

- Under the average conditions, 125–150 man-hours of labor are required per cow per year. Study of time: Time motion studies in dairies showed that 40% of the expended time is spent in front of the cow, 25% in other parts of the barn and the milk house, and 60% of the time is spent behind the cows. Time spent at the back of the cows is four times more than the time spent in front of them.
- In cleaning and milking the cows the wide middle alley is of great advantage.
- Lesser danger of spread of diseases from animal to animal.
- Cows can always get more fresh air from outside.
- The head milkman can inspect a greater number of milkmen while milking. This is possible because milkmen will be milking on both sides of the gowala.
- Any sort of minor disease or any change in the hindquarters of the animals can be detected quickly and even automatically.

Advantages of head-to-head system:

- Cows make a better showing for visitors when heads are together.
- Cows feel easier to get into their stalls.
- Sunrays shine in the gutter where they are needed the most.
- Feeding cows is easier; both rows can be fed without back tracking.
- It is better for narrow barns.

Floor

The inside floor of the barn should be of some impervious material that can be easily kept clean and dry and is not slippery. Paving with bricks can also serve one's purpose. Grooved cement concrete floor is still better. The surface of the cowshed should be laid with a gradient of 1–1 14 in. from manger to excreta channel. An overall floor space of 65–70 sq ft per adult cow should be satisfactory.

Walls

The inside of the walls should have a smooth hard finish of cement, which will not allow any lodgment of dust and moisture. Corners should be round. For plains, dwarf walls, approximately 4–5 ft in height, and roofs supported by masonry work or iron pillars are best or more suitable. The open space in between supporting pillars serves for light and air circulation.

Roof

Roof of the barn may be of asbestos sheet or tiles. Corrugated iron sheets have the disadvantage of making extreme fluctuations in the inside temperature of the barn in different seasons. However, iron sheets with aluminum-painted tops to reflect sunrays and bottoms provided with wooden-insulated ceilings can also achieve the objective. A height of 8 ft at the sides and 15 ft at the ridge is sufficient to give the necessary air space to the cows. An adult cow requires at least approximately 800 cubic ft of air space under tropical conditions. To make ventilation more effective, continuous ridge ventilation is considered most desirable.

Manger

Cement concrete continuous manger with removable partitions is the best from the point of view of durability and cleanliness. A height of 1 ft to 4 in. for a high-front manger and 6–9 in. for a low-front manger is considered sufficient. Low-front mangers are more comfortable for cattle, but high-front mangers prevent feed wastage. The height at the back of the manger should be kept at 2 ft to 6–3 in. An overall width of 2–2.5 ft is sufficient for a good manger.

Alleys

The central walk should have a width of 5–6 ft exclusive of gutters when cows face out and 4–5 ft when they face in. The feed alley, in case of a face out system, should be 4 ft wide, and the central walk should show a slope of 1 in. from the center toward the two gutters running parallel to each other, thus forming a crown at the center.

Manure gutter

The manure gutter should be wide enough to hold all dung without getting blocked and be easy to clean. Suitable dimensions are 2 in. width with a cross-fall of 1 in. away from standing. The gutter should have a gradient of 1 in. for every 10 ft length. This will permit a free flow of liquid excreta.

Doors

The doors of a single-range cowshed should be 5 in. wide with a height of 7 ft, and for double-row shed the width should not be less than 8 in. to 9 ft. All doors of the barn should lie flat against the external wall when fully open.

Calving boxes

Allowing cows to calve in the milking cowshed is highly undesirable and objectionable. It leads to unsanitary conditions in milk production and spread of disease, like contagious abortion in the herd. Special accommodation in the form of loose boxes enclosed from all sides and with a door should be furnished to all parturient cows. It should have an area of approximately 100–150 sq ft. With ample soft bedding, it should be provided with sufficient ventilation through windows and ridge vent.

Isolation boxes

Animals suffering from infectious disease must be segregated soon from the rest of the herd. Loose boxes of approximately 150 sq ft are very suitable for this purpose. They should be situated at some distance from the other barns. Every isolation

box should be self-contained and should have separate connection to the drainage disposal system.

Sheds for young stocks

Calves should never be accommodated with adults in the cowshed. The calf house must have provision for daylight ventilation and proper drainage. Damp and ill-drained floors cause respiratory trouble in calves to which they are susceptible. For an efficient management and housing, the young stock should be divided into three groups, viz., young calves (aged up to one year), bull calves (the male calves over one year) and the female calves (above one year). Each group should be sheltered in a separate calf house or calf shed. As far as possible, the shed for the young calves should be quite close to the cow shed. Each calf shed should have an open paddock or exercise yard. An area of 100 sq ft per head for a stock of 10 calves and an increase of 50 sq ft for every additional calf will make a good paddock. It is useful to classify the calves below 1 year into three age groups, viz., calves below the age of 3 months, 3–6-month-old calves, and those more than 6 months of age, for a better allocation of the resting area. An overall covered space of:

1. 20–25 sq ft per calf below the age of 3 months,
2. 25–30 sq ft per calf from the age of 3–6 months,
3. 30–40 sq ft per calf from the age of 6–12 months and more, and
4. 40–45 sq ft for every calf above 1 year. Provision of water troughs inside each calf shed and exercise yard should never be neglected.

Bull or bullock shed

Safety and ease in handling a comfortable shed, protection from weather, and a provision for exercise are the key points while planning accommodation for bulls or bullocks. A bull should never be kept in confinement, particularly on hard floors. Such a confinement without adequate exercise leads to overgrowth of the hoofs creating difficulty in mounting and loss in the breeding power of the bull. A loose box with rough cement concrete floor approximately 15×10 ft in dimensions having an adequate arrangement of light and ventilation and an entrance 4 ft in width and 7 ft in height will make a comfortable housing for a bull. The shed should have a manger and a water trough.

If possible, the arrangement should be such that water and feed can be served without actually entering the bull house. The bull should have a free access to an exercise yard provided with a strong fence or a boundary wall of approximately 2 ft height, i.e., too high for the bull to jump over. From the bull yard, the bull should be able to view the other animals of the herd so that it does not feel isolated (Banerjee, 2010).

Cattle Milk Production

Although India was the largest milk-producing country in the world with respect to overall milk production from livestock by the year 2010, cow milk production was highest in the United States (87.5 million tons) followed by India (50.3 million tons), China (36.0 million tons), and Brazil (31.7 million tons).

Cow Meat Production

As cow is a motherly figure and worshipped as mother according to the Hindu religion, cow slaughter is banned in parts of India and remains a contentious issue in states where it is legal. In the year 2010, cow meat production was 64 275 698 ton.

Diseases in Cattle

Performance of cattle in the form of milk, meat, or hide production or reproduction is affected by a number of diseases that may be caused by bacteria, virus, or protozoa or may be due metabolic cause and nutritional deficiencies. A few important diseases of cattle are anthrax, black quarter, bovine abortions, bovine mastitis, cow pox, foot-and-mouth disease, hemorrhagic septicemia, leptospirosis, rinderpest, vibrionic abortion, and metabolic disorders.

Anthrax

- Anthrax is an acute, infectious febrile disease of virtually all animals and man. It is caused by *Bacillus anthracis*.

Symptoms:

- The disease may occur in a peracute, acute, or subacute form. In the first form, the animal dies suddenly, rarely showing any symptoms.
- In acute and subacute forms, there may be high rise in body temperature and signs of intense pain.

Black quarter (black leg)

The disease is common in areas with moderate rainfall and where dry-crop cultivation is common. Young animals in the prime of condition and 6 months to 3 years of age are affected more than others. Outbreaks generally occur with the onset of rains. True black quarter is caused by *Clostridium chauvoei*. Fever with redness of eye and hot painful swelling in the affected leg are some of the observed symptoms. A crepitating sound is heard on pressing the affected part of muscle. Death may occur in severe cases within 1–2 days.

Symptoms:

- The disease usually occurs in an acute form; affected animals die within 24–48 h of the onset of symptoms.
- There is high fever with a hot, tense, painful swelling, usually in one of the quarters, more often a hindquarter; however, such swelling may also occur in the other quarter before death. The swelling becomes cold and painless and crepitates on pressure due to the presence of gas in it.

Prevention and control:

- To prevent the spread of infection and contamination of the soil with spores of the causal organisms, carcasses of animals dead of black quarter should be either buried deep and covered over with lime or cremated.
- Administration of penicillin in repeated doses may be effective if injected before muscle damage has been caused.
- Use of black quarter vaccine protects animals against the disease for approximately a year. Animals should be

vaccinated with this approximately 3–1 month before the onset of rain.

Foot-and-mouth disease

- The food-and-mouth disease is a highly communicable disease affecting cloven-footed animals. It is characterized by fever and formation of vesicles and blisters in the mouth, udder, teats, and on the skin between the toes and above the hoofs.
- Animals recovered from the disease present a characteristically rough coat and deformation of the hoof.
- The disease spreads by direct contact or indirectly through infected water, manure, hay, and pastures.
- It is also conveyed by cattle attendants. It is known to spread through recovered animals, field rats, porcupines, and birds.
- Foot-and-mouth disease occurs in a relatively mild form in India and is seldom fatal. It occurs practically all the year round.

Symptoms:

- Fever with 104–105 °F temperature.
- Profuse salivation ropes of stringy saliva hangs from mouth.
- Vesicles appear in the mouth and in the interdigital space.
- Lameness observed.
- Crossbred cattle are highly susceptible to it.

Control and prevention:

- Heavy milch animals and exotic breeds of cattle bred for milk should be protected regularly.
- It is advisable to carry out two vaccinations at an interval of 6 months followed by an annual vaccination program.
- Isolation and segregation of sick animals. It should be informed immediately to the veterinary doctor.
- Disinfection of animal sheds with bleaching powder or phenol.
- Attendants and equipment for sick animals should be ideally separate.
- The equipment should be thoroughly sanitized.
- Proper disposal of leftover feed by the animal.
- Proper disposal of carcasses.
- Control of flies.

Hemorrhagic septicemia

This acute septicemic disease of cattle and buffaloes is widely prevalent in India. It occurs generally in low-lying areas periodically inundated by rainwater and in areas where irrigation facilities have developed. The causal organism, *Pasteurella multocida*, is a small Gram-negative coccobacillus, commonly called bipolar organism on account of the intensity with which it stains at the poles. Redness of eye and lancination along with fever; severe dyspnea; hot painful swelling at head, jowl region, or brisket region are observed. In severe cases sudden death may occur due to high fever and severe dyspnea.

Symptoms:

- The disease generally runs an acute course. Cattle and buffaloes often develop a highly septicemic condition and die within the course of approximately 24 h of infection.
- Affected animals show a high rise in body temperature.
- The lesions comprise hemorrhagic spots in the lymph nodes, on the serous membranes, and in other organs, including the inner lining of the heart; however, spleen is normal in size.
- The entire gut is highly inflamed and intensely red with bloody contents.

Treatment and prevention:

- Early cases of the disease are amenable to treatment with sulfonamides, notably sulfadimidine coupled with antibiotics, such as penicillin, but on account of the short course of the disease and its termination in sudden death, animals are seldom available in good time for treatment.
- Vaccination with the improved type of adjuvant vaccine, carried out approximately a month before the onset of rains, will protect the animals against the attack of the disease for approximately 1 year. In endemic areas, such vaccination should be carried out every year.

Bovine mastitis

- This disease is characterized by inflammation of the udder, resulting in changes in the udder tissue and its secretion.
- Infectious mastitis results from infection with one or more of the many organisms associated with cattle in all countries where dairy industry is well developed, and the disease is of great economic importance to milk producers.
- Clinically, the disease may be recognized as acute, subacute, or chronic, and these forms may depend on the type of the causal organism concerned. It may be accompanied by systemic disturbance, with a rise in body temperature of the affected animal and other febrile symptoms, but usually it occurs in the form of a localized involvement of the udder, with a progressive damage to the udder tissue.
- The milk is affected both in quality and quantity, and as a result of permanent impairment of the function of one or more quarters, milk production may cease altogether. Both cows and female buffaloes suffer from the disease.

Leptospirosis

Leptospirosis occurs in animals and humans in almost all parts of the world. Serological evidence indicates the prevalence of leptospires among domesticated animals in different parts of the country. The damage done to animal industry results from the death of animals in the acute stage of illness; stillbirth; abortion; stunning; decrease in weight (loss of meat); reduced milk production; and unthriftiness.

Causes and pathogenesis:

The causative organisms of leptospirosis belong to the genus *Leptospira*.

Symptoms:

- In cattle, it is an acute, often fatal, disease characterized by hemorrhage, hemoglobinuria, and icterus.
- Nonfatal infections are often characterized by fever, anemia, abortions, sterility, decreased lactation, and mastitis.

Rinderpest

- Rinderpest is the most destructive of the virus diseases of cloven-footed animals, such as cattle, buffaloes, sheep, goats, pigs, and wild ruminants. Its control was a major issue until recently all over the world.
- Organized efforts over half a century have brought about a total eradication of the disease in the western hemisphere.
- The disease still persists in Asian countries.
- The virus is found notably in the saliva, discharge from the eyes and the nostrils, and in the urine and feces.
- It is present in the circulating blood during the febrile stage and is later concentrated in different organs, especially in the spleen, lymph nodes, and liver. Outside the animal body, the virus is rapidly destroyed by direct sunlight and disinfectants. Cold preserves the virus.
- The virus is usually spread by contaminated feed and water.
- Rise in temperature up to 104–107 °F. Lacrimation and redness of the eyes.
- Foul odor from the mouth. Discrete necrotic foci develop in the buccal mucosa, inside lip, and on the tongue. Bloody mucoid diarrhea is noticed.

Vibrionic abortion of cattle

- This is a widely prevalent form of abortion in some countries and the causal organism is *Vibrio fetus*.
- The disease resembles *Brucella abortus* infection but is less severe in form. It is generally transmitted during natural service or artificial insemination with semen from infected bulls.

Diagnosis:

- Diagnosis is made by examination of uterine exudate and stomach contents of the fetus.
- The disease is usually self-limiting; infected animals develop active immunity after one abortion.

However, hygienic measures should be taken to prevent spread of the infection.

Table 9 Zoological classification of buffalo

Kingdom	Animalia
Phylum	Chordata (backbone animals)
Class	Mammalia (milk-giving)
Order	Artiodactyla (even toed and hoofed)
Suborder	Ruminatia (cud-chewing)
Family	Bovidae (hollow unbranched horn)
Genus	*Bubalus* (ruminant quadrupeds)
Species	1. *Bubalus bubalis* (all types of domestic river buffalo) 2. *Bubalus carabanesis* (swamp)

Metabolic diseases

Milk fever

- Milk fever, also known as parturient hypocalcemia and parturient paresis, is a disease that has assumed considerable importance with the development of heavy milking cows.
- Decrease in the levels of ionized calcium in tissue fluids is basically the cause of the disease.
- In all adult cows there is a fall in serum calcium level with the onset of lactation at calving.
- The disease usually occurs in 5–10 year old cows, and is chiefly caused by a sudden decrease in blood-calcium level, generally within 48 h after calving.

Symptoms:

- In classical cases, hypocalcemia is the cause of clinical symptoms. Hypophosphatemia and variations in the concentration of serum magnesium may play some subsidiary role.
- The clinical symptoms develop usually in 1–3 days after calving. They are characterized by loss of appetite, constipation, and restlessness, but there is no rise in temperature.

Buffalo

Animal belonging to the phylum Chordata (backbone animals), class Mammalia (milk giving), order Artiodactyla (even toed and hoofed), suborder Ruminatia (cud-chewing), family *Bovidae* (hollow unbranched horn), and genus *Bubalus* (ruminant quadrupeds) is buffalo.

Zoological Classification

Table 9 explains the zoological classification of buffalo.

Domestication

Time: 2500–2100 BC.

Number of Chromosome Pairs

Bubalus bubalis: 25.
Bubalus carabanesis: 24.

Common Terms Related to Buffalo

Terms related to buffalo that are commonly used are given in Table 10.

Table 10 Common terms related to buffalo

Common name of animal	*Male*	*Female*	*Young*	*Act of mating*	*Group*	*Gestation/pregnancy period*	*Name of giving birth*
Buffalo	Buffalo bull	Female-buffalo/buffalo cow	Calf	Serving	Herd	10 months	Calve

Utility

Milk, meat, draught, and manure.

Domestication

It has been suggested that buffaloes were in service of humans as early as 2500–2100 BC. The domesticated buffaloes can be classified into two main categories, i.e., (1) The swamp buffalo (chromosomes, $2n=48$) and (2) The river buffalo (chromosomes, $2n=50$). They belong to the same species, *B. bubalis*, but have very different habits. The former is more or less permanent inhabitant of marsh lands, where it wallows in mud and feeds on coarse marsh grass, and is found principally in Malaya, Singapore, the Philippines, Thailand, Indonesia, southern China, and other counties in the Far East. In the Philippines and some other countries, it is known as the Carabao and in Malaysia as the Kerban. The river type is the one found throughout India, Pakistan, Bangladesh, Nepal, and Sri Lanka. These are primarily milch animals (Banerjee, 2010). Water buffaloes were domesticated in India approximately 5000 years ago and in China approximately 4000 years ago. Two types are recognized on the basis of morphological and behavioral criteria – the river buffalo of the Indian subcontinent and further west to the Balkans and Italy and the swamp buffalo, found from Assam in the west through Southeast Asia to the Yangtze valley in China in the east.

Breeds

In India there are 13 well-defined breeds with standard qualities and with specific physical characters that differentiate them unmistakably from other types as may be found in various states of the country. On the basis of regions, the well-defined buffalo breeds are listed in Table 11.

Out of all these breeds, six breeds, viz., Murrah, Nili-Ravi, Jaffarabadi, Bhadawari, Surti, and Mehsana are high-quality milch breeds of the country and they all come from the northern and western parts of the country comprising the states of Punjab, Rajasthan, and Gujarat. The breeds of central and western parts are noted as draught purpose due to the fact that they have swamp as well as river characteristics.

Murrah

Home tract stretches around the southern parts of Haryana comprising the districts of Rohtak, Jind, Hisar, Jhajhar, Fatehabad, and Gurgaon and the Union Territory of Delhi. However, this breed has spread to almost all parts of the country and is either being bred in pure form or being used as improver breed for grading up local buffaloes. Murrah breed has even found an important place in the livestock industry of many developing countries like Bulgaria, the Philippines, Malaysia, Thailand, China, Indonesia, Bangladesh, Nepal, the former USSR, Myanmar, Vietnam, Brazil, and Sri Lanka. Milk yield varies from place to place depending on the management practices and environmental conditions under which animals are reared. Large herds have shown average yields as 1800 kg.

Housing – In the breeding tract, these buffaloes are kept in a mixed type of housing system. The buffaloes are tied to a tree or a pole in the open, but shelter is provided during extreme weather conditions. Houses are well ventilated and mostly made up of *pucca* (solid) walls with *katcha* (mud) floor.

Feeding – Animals are mostly stall fed. Berseem, oat, and mustard are the green fodders fed in Rabi season and pearl millet, sorghum, and cluster bean in Kharif season. In lean season, Murrah animals are maintained on wheat and pulse straws in conjunction with oilcakes and other concentrates. Mostly, women are engaged in buffalo rearing (80%), and all the activities pertaining to feeding, milking, cleaning, etc. are looked after by them. Calves are not weaned. Very few farmers rear bulls exclusively for breeding purpose. Natural service is mostly practiced in field.

Nili-Ravi

Nili and Ravi were two different breeds long before, but due to the passage of time and with intensive crossbreeding, the two breeds converted into a single breed named Nili-Ravi. Nili-Ravi buffaloes are found in almost all the districts, with major concentration in Amritsar, Gurdaspur, and Ferozepur districts of Punjab in India and in Lahore, Sheikhupura, Faizabad, Okora, Sahiwal, Multan, Bohawalpur, and Bahwalnagar districts of Punjab in Pakistan. However, due to good dairy characteristics of this breed in Pakistan, Nili-Ravi buffaloes are found in whole of Pakistan with major concentration in buffalo colony at Karachi. The average lactation yield in Nili-Ravi buffaloes range from 1688–2317 kg.

Banni, Kalahandi, and Chilika are newly registered buffalo breeds in India.

Banni

Home tract of this breed is Bhuj, Nakhatrana, Anjar, Bhaahau, Lakhpat, Rapar, and Khavdatalukas in Gujarat in India. Animals are heavily built with typical double and vertical coiling of the horn. Average age at first calving is approximately

Table 11 Breeds of buffalo in India

Murrah group	*Gujarat group*	*Uttar Pradesh group*	*Central India group*	*South India group*
1. Murrah	1. Surti	1. Bharawari	1. Nagapuri	1. Toda
2. Nili-Ravi	2. Jaffarbadi	2. Tarai	2. Pandharapuri	2. South Kanara
3. Kundi	3. Mehsana		3. Manda	
4. Godavari			4. Jerangi	
			5. Kalhandi	
			6. Sambalpuri	

Source: Reproduced from Banerjee, G.C., 2010. A Textbook of Animal Husbandry, eigth ed. New Delhi: Oxford and IBH publishing Co. Pvt. Ltd.

40 months and average lactation milk yield is approximately 2857 kg in field conditions.

Kalahandi

Kalahandi buffaloes are dual type; they are used both for milk and draught purpose in Kalahandi and Rayagada districts of Odisha. Animals are medium sized; have long, strong, and half-circled horns with broad base; and are excellent in heat and drought tolerance.

Heat Tolerance

Although buffaloes are found in greatest numbers in the tropics, they have poor heat resistance and suffer real distress if worked during the heat of the day or if they are left to stand in the direct rays of the sun for long periods. Access to water or shade is essential for the well-being of buffaloes. It is customary to rest working buffaloes for several hours in the middle of the day and to allow them to wallow at that time and again in the early evening when the day's work is over. It is thus to be noted that sudden changes of temperature, especially the effect of cold winds and drought, may be extremely harmful to this species. Heat-regulating mechanism of buffaloes in comparison with cattle is less efficient. The difference may be due in part to the heavy coat of the cow preventing wetting of the skin but more probably to the fact that the thyroid–adrenal mechanism is less efficient in buffaloes (Banerjee, 2010).

Wallowing

It means rolling or floundering in mud or in water. The river breeds of Indian subcontinent prefer the clear water of streams and pools, bunching close together, but the swamp buffalo of China and southeast Asia likes to wallow in slime and mudhole, accommodating one animal or very few animals only. It is seldom that buffaloes are found in areas where there is no easy access to water. Although wallowing is not absolutely necessary for buffaloes to maintain themselves, they apparently wallow for two main reasons: to regulate body temperature and to control parasites. Moreover, there is no definite pattern of wallowing (Banerjee, 2010).

Buffalo's Nutrition

Average rates of daily feeding of concentrates and green and dry fodder assumed for different stages of life of buffalo are given in Table 12.

Buffalo Milk Production

In the year 2010, 92.51 million tons of buffalo milk was produced in the world. Buffalo milk production was the highest in India (62.40 million tons) followed by Pakistan (22.28 million tons).

Buffalo Meat Production

In the year 2010, buffalo meat production was 3 499 857 tons.

Goat

Animal belonging to the phylum Chordata (backbone animals), class Mammalia (milk-giving), order Artiodactyla (even toed and hoofed), suborder Ruminatia (cud-chewing), family Bovidae (hollow unbranched horn), and genus *Capra* is goat.

Zoological Classification of Goat

Table 13 explains the zoological classification of goat.

Domestication of Goat

Time: 9000–7000 BC.

Number of chromosome pairs of goat: 30 (*Capra hircus*)

Body Weights

Body weight in goat ranges from 2.5–3.5 kg at birth to 26–102 kg at maturity.

Table 13 Zoological classification of goat

Kingdom	Animalia
Phylum	Chordata (backbone animals)
Class	Mammalia (milk-giving)
Order	Artiodactyla (even toed and hoofed)
Suborder	Ruminatia (cud-chewing)
Family	Bovidae (hollow unbranched horn)
Genus	*Capra*
Species	*Capra hircus* (True goat including Bezoar)
	Capra falconeri (Markhor)
	Capra ibex
	Capra caucasica (Caucasian tur)
	Capra pyrenaica (Spanish ibex)

Table 12 Average rates of daily feeding of concentrates and green and dry fodder assumed for different age groups of buffalo

Age group buffalo		*Concentrate (kg)*	*Green fodder (kg)*	*Dry fodder (kg)*
Females more than 3 years of age	Improved buffalo	1.50	10.00	6.00
	Other milch buffalo and not calved even once	0.41	5.72	5.08
Males more than 3 years of age		0.109	6.51	5.43
Males less than 3 years of age		0.01	1.59	1.64

Source: Reproduced from Banerjee, G.C., 2010. A Textbook of Animal Husbandry, eigth ed. New Delhi: Oxford and IBH publishing Co. Pvt. Ltd.

Table 14 Common terms related to goat

Common name of animal	*Male*	*Female*	*Young*	*Group*	*Act of mating*	*Gestation/pregnancy period*	*Name of giving birth*
Goat	Buck	Nanny	Kid	Trip	Serving	148–156 days	Kidding

Common Terms Related to Goat

Terms related to goat that are commonly used are given in Table 14.

Utility

Milk, meat, fiber, manure, and hide.

Important Breeds of Goat

There are more than 100 breeds of goat around the world. These breeds could be grouped according to their utility, i.e., milk, meat, and fiber.

Dairy goats

Alpine

Alpine goats are known for their very good milking ability. They are multicolored and have no set markings. They have erect ears, horns, and have a dish face. The breed originated in the French Alps. Mature animals weigh approximately 61 kg or 125 lbs and are approximately 0.8 m or 30 in. tall at the shoulder. Alpine goats can range in color from white or gray to brown and black. Alpine goats are heavy milkers; the milk can be made into butter, cheese, soap, ice cream, or any other dairy product that cow's milk can produce. They are most often used for commercial milking. The French-alpine is also referred to as the Alpine Dairy goat and registration papers for this dairy goat use both designations, which are synonymous. These are hardy, adaptable animals that thrive in any climate while maintaining good health and excellent production. Alpine goats' milk has an average butterfat of approximately 3.5%. The face is straight.

Alpine colors are described by using the following terms:

- Cou Blanc – (coo blanc) literally 'white neck' – white front quarters and black hindquarters with black or gray markings on the head.
- Cou Clair – (coo clair) literally 'clear neck' – front quarters are tan, saffron, off-white, or shading to gray with black hindquarters.
- Cou Noir – (coo nwah) literally 'black neck' – black front quarters and white hindquarters. Sundgau – (sundgow) black with white markings, such as underbody, facial stripes, etc. Pied – spotted or mottled.
- Chamoisee – (shamwahzay) brown or bay – characteristic markings are black face, dorsal stripe, feet and legs and sometimes a martingale running over the withers and down to the chest. Spelling for male is chamoise. Two-tone Chamoisee – light front quarters with brown or gray hindquarters. This is not a coublanc or couclair, as these terms are reserved for animals with black hindquarters.
- Broken Chamoisee – a solid chamoisee broken with another color by being banded or splashed, etc. Any variation in the above patterns broken with white should be described as a broken pattern, such as a broken coublanc (Briggs and Briggs, 1980; American Dairy Goat Association, n.d.).

Anglo-Nubians

These goats were developed in England by crossing British goats with bucks of African and Indian origin. The Anglo-Nubian is an all-purpose goat, useful for meat, milk, and hide production. It is not a heavy milk producer but its milk has a high average butterfat content (between 4% and 5%). As it is best suited, of the dairy goat breeds, to hot conditions, the Anglo-Nubian has been used in grading up programs in many tropical countries to increase the milk and meat production of local breeds. The Anglo-Nubian is a relatively large, proud, and graceful dairy goat. It is named after Nubia, in northeastern Africa. The original goats imported from Africa, Arabia, and India were long legged, hardy goats that had some characteristics desired by goat breeders in England. English breeders crossed these imported bucks on the common short-haired does of England before 1895 to develop the Anglo-Nubian goat. In the United States, the breed is usually spoken of as the Nubian. The Anglo-Nubian is regarded as an aristocratic-appearing goat and has very long, pendulous ears that hang close to the head. It carries a decidedly Roman nose and is always short haired. Any solid or parti-colored coat is permitted in the Anglo-Nubian, but black, red, or tan are the most common colors, any of which may be carried on combination with white. Usually there is shorter hair on the Anglo-Nubian males, particularly along the back and on the thigh, than is commonly found on the Swiss breeds. Its udder is capacious but is sometimes more pendulous than that of the Swiss breeds. A mature doe should stand at least 30 in. at the withers and weigh 135 lbs or more, whereas the males should stand at least 35 in. at the withers and weigh at least 175 lbs. It usually gives less milk than the Swiss breeds but produces a milk of higher butterfat content. The head is the distinctive breed characteristic, with the facial profile between the eyes and the muzzle being strongly convex. The ears are long (extending at least 1 in. beyond the muzzle when held flat along the face), wide, and pendulous. They lie close to the head at the temple and flare slightly out and well forward at the rounded tip, forming a 'bell' shape. The ears are not thick, with the cartilage well defined. The hair is short, fine, and glossy (Briggs and Briggs, 1980; Mason, 1988; Meat and Livestock Australia, 1989; American Dairy Goat Association, n.d.).

Meat goats

Black Bengal

The Black Bengal goat is a breed of goat found in West Bengal, Bihar, and Odisha regions of northeastern India and

throughout Bangladesh. This breed is usually colored black, but it is also found in brown white or gray. The Black Bengal goat is small in size. Its body structure is tight. Its horns are small and legs are short. Adult male goat weights approximately 25–30 kg and female 20–25 kg. It is poor in milk production. It is very popular in Bangladesh because of its very low demand of food and very high reproduction rate. The Black Bengal goats gain sexual maturity very early. The female goat conceives twice a year and gives birth to 2–3 baby goats every time. This breed can adapt to any environment easily and its disease-preventive ability is very high. It produces high-quality meat and skin. This breed plays a very important role in reducing unemployment and poverty from Bangladesh (Mason, 1996).

Fiber goat

Angora

The Angora goat originated in the district of Angora in Asia Minor. The Angora dates back before early Biblical history. Mention is made of the use of mohair at the time of Moses, which would fix the record of the Angora sometime between 1571 and 1451 BC, according to the Angora Goat Mohair Industry publication from the United States Department of Agriculture. Mohair became a valuable product in commerce early in the nineteenth century. To increase the supply of mohair available for export to the European countries, the Turks crossed the Angora goat with common stock to increase the poundage of salable hair. Probably there was no effort to keep the original Angora separate, and the general increase in size and vigor of the goats in the Angora area was, undoubtedly, partially the result of this infusion of other blood. Angora stock was distributed to different countries, and a pair of Angoras was imported to Europe by Charles V around 1554.

Mohair production – The most valuable characteristic of the Angora as compared with other goats is the value of the mohair that is clipped. The average goat in the US shears approximately 5.3 lbs of mohair per shearing and is usually sheared twice a year. They produce a fiber with a staple length between 12 and 15 cm. The mohair is very similar to wool in chemical composition but differs from wool in that it has a much smoother surface and very thin, smooth scale. Consequently, mohair lacks the felting properties of wool. Mohair is very similar to coarse wool in the size of fiber. It is a strong fiber that is elastic, has considerable luster, and takes dye very well. Mohair has been considered very valuable as an upholstering material for the making of plushes and other covering materials where strength, beauty, and durability are desired (Briggs, 1969; Select Genes Ltd., 1675; Meat and Livestock Australia, 1989).

Systems of goat production

The systems in which people keep goats differ from country to country. There are three main systems of production, viz., (1) extensive grazing, (2) sedentary family herds, and (3) intensive commercial production.

Housing management

- Goats are housed in stalls or loose boxes. For efficient production in dairy goats, the animals must be provided with good health and comfort. The house should protect goats from the sun, rain, and cold nights. One need not have expensive house for the goats. Instead, locally available material can be used. A mature goat requires $1.5 \times 1.0\ m^2$ floor space. To protect the goats from cold air, especially at night and rainy days, a wall of at least 1.5 m or 4.2 ft height should be built. If the floor is made of clay or earth, it should be compact, as far as possible, and there should be a gradual slope toward one corner of the house. If the floor is made of wood, it should be elevated and slated with just at least 0.5–0.75 in. space in between to facilitate easy escape of manure and urine.
- Bucks should be housed far away from the dairy goat shed. This will help in avoiding goat's smell in the milk. Kids up to 2 weeks of age should be kept with the does.
- The stalls may be arranged in two rows, with a passage between them. The recommended dimensions on each stall should be 0.75 m wide and 1.05 m long. The length of the shed will depend on the number of milch goats kept. There should be portions between stalls made of brick, stone, or iron tubing. Sometimes a small milk room is constructed at one end of the milch goat shed, especially in breeding farms.
- The methods commonly used to control the goats are herding, tethering, and fencing. Control methods help to prevent the loss of goats by theft, attacks from wild animals, or by the goats wandering off. Also, they limit the amount of feed that goats have access to at any time and prevent damage to crops.

Feeds and Feeding

Feed represents the highest item of expenses in raising goats; hence, it is very necessary to understand the principles of feeding in order to feed goats economically. A nutrient is a substance that aids in support of life. Goats require nutrients for growth, body maintenance, pregnancy or reproduction, and milk production. Nutrients required in the goat's feed are energy, protein, minerals, vitamins, and water.

Goat is a ruminant, but its feeding is quite dissimilar from that of sheep and cows. For its size, a goat can consume substantially more feed than cow or sheep, which can be 6.5–11% of its body weight in dry matter compared with 2.5–3.0% in case of cattle and sheep. This means that goats can satisfy their maintenance and production requirement on good fodder and pasture grass.

- Concentrates: These are low in crude fiber and high in digestible nutrients. Concentrates low in protein are maize, rice, sorghum, bran, molasses, etc., whereas protein-rich concentrates are groundnut cake, cottonseed cake, soyabean meal, etc.
- Roughage: These are high in crude fiber but low in digestible nutrients, such as sorghum fodder, bajra fodder, rice and wheat straw, grasses like paragrass and young pasture grasses, silage, and dry hay.
- Feed additives: There are chemicals that are added to feed for growth promotion or for disease prevention, for example, antibiotics aureomycin, and terramycin.
- Minerals: Salt, oyster shell, lime stone, bone meal, wood ash, etc. supply minerals to goat's body.

- Vitamins: Dietary requirements of goats are simple because feeds that they consume mostly supply their necessary requirements.
- Local ingredients used in goat feed: These high-energy ingredients are rich in fat and proteins. Maize, sorghum, wheat bran, rice bran, groundnut cake, cottonseed cake, by-products of legumes, molasses, etc. are important goat feed.

Feeding the goat

Goats are fed differently depending on whether they are dry, pregnant, lactating, breeding, buck, or baby goat.

- Feeding the dry doe – Feed well during the pregnancy as the unborn babies gain more weight during the last week of pregnancy. The pregnant doe should be in good flesh and weight before giving birth. Nutritious grasses and legumes are sufficient to support the doe. If the pregnant doe looks thin then give approximately 0.5–1 kg of concentrate mixture.
- Feeding the doe about to kid – 3–5 days before giving birth, give pregnant doe approximately 250–500 g of concentrate. Then 1–2 days before kidding, replace this concentrate ration with just maize, bran, wheat bran, or rice bran. The bran is known for its laxative property and will help to clean the stomach. Clean stomach will assist the doe in easy kidding.
- Feeding the milking doe – Milk does should be given as much quality grasses and legumes as they can consume. Concentrate grams for every liter of milk should be given and fresh water and mineral lick-brick should be provided to the does frequently.
- Feeding the bucks – Bucks used for breeding should be fed properly. When not used for breeding, feed a buck at least 500 g of concentrate mixture plus green grass and legume, like lucerne. See that the does do not become fat, aggressive, and sterile. During breeding period, increase its ration from 500 g to 1 kg.
- Feeding young kids – The object should be not to fatten them up but rather provide them enough nutrients for growth and maintenance. Sufficient space for exercise plus abundant quality grass and legumes are important for yearlings. Feed 500 g of concentrate every day.
- Feeding the baby goats – Keep the kids with the mother for the first 2–3 days. This will ensure sufficient intake of colostrum needed for their good health. From the 3rd or 4th day, allow the kid to be with the mother only during the day. Continue this up to 4–5 months, i.e., till they are weaned. You can feed the kid with the help of a bottle. For this you must separate the kid from the doe after the 3rd or 4th day of its birth. Take care to keep the milk warm around 103–105 °F. Keep the nipple and bottle clean after each feeding.

Goat's Population

In the year 2011, there were 875.53 million goats in the world.

Goat Milk Production

Aggregate (official, semiofficial, or estimated data) of 15.85 million tons goat milk was produced throughout the world in the year 2011.

Goat Meat Production

In the year 2011, world's aggregate goat meat production was 5 114 494 tons.

Goatskin Production

Aggregate 1 138 100 tons goatskin was produced throughout the world in the year 2011.

Sheep

Animal belonging to the phylum Chordata (backbone animals), class Mammalia (milk giving), order Artiodactyla (even toed and hoofed), suborder Ruminatia (cud-chewing), family Bovidae (hollow unbranched horn), and genus *Ovis* is sheep.

Zoological Classification of Sheep

Table 15 explains the zoological classification of sheep.

Domestication of Sheep

An archeological site in Iran produced a statuette of a wooled sheep, which suggests that selection for woolly sheep had begun to occur more than 6000 years ago. The common features of today's sheep already appeared in Mesopotamian and Babylonian art and books by 3000 BC.

Number of chromosome pairs of sheep: 54 (*Ovis aries*).

Body Weights

Body weight in sheep ranges from 2.0–4.0 kg at birth to 34–80 kg at maturity.

Common Terms Related to Sheep

Terms related to sheep that are commonly used are given in Table 16.

Utility

Milk, meat, fleece, manure, and hide.

Important Breeds of Sheep

Selection for wool type, flocking instinct, and other economically important traits over the centuries has resulted in more than 200 distinct breeds of sheep occurring worldwide.

Table 15 Zoological classification of sheep

Kingdom	Animalia
Phylum	Chordata (backbone animals)
Class	Mammalia (milk-giving)
Order	Artiodactyla (even toed and hoofed)
Suborder	Ruminatia (cud-chewing)
Family	Bovidae (hollow unbranched horn)
Genus	*Ovis*
Species	*Ovis aries* (sheep)

Table 16 Common terms related to sheep

Common name of animal	*Male*	*Female*	*Young*	*Group*	*Act of mating*	*Gestation/pregnancy period*	*Name of giving birth*
Sheep	Buck/ram	Ewe/dam	Lamb	Flock	Tupping	148–156 days	Lambing

Modern breeding schemes have also resulted in an increasing number of composite or synthetic breeds that are the result of a crossing of two or more established breeds.

Sheep can be grouped into two breed groups as hair-sheep breeds and Merino sheep types.

Hair-sheep breeds – Africana, Barbado, Barbados Blackbelly, Blackhead Persian, Brazilian Somali, Damara, Dorper, Katahdin, Masai, Morada Nova, Pelibuey, Rabo Largo, Sahel type, Somali, St. Croix (Virgin Island White), Touabire, Uda, West African Dwarf, and Wiltshire Horn.

Merino sheep types – Booroola Merino, Delaine Merino, Fonthill Merino, German Mutton Merino, Medium-Wool Merino, Merinolandschaf, Poll Merino, South African Merino, South African Mutton Merino, and Strong Wool Merino.

Sheep Population

In the year 2011, there were 1 043 712 633 sheep in the world.

Sheep Milk Production

Aggregate (official, semiofficial, or estimated data) of 9.26 million tons sheep milk was produced throughout the world in the year 2011.

Sheep Meat Production

In the year 2011, world's aggregate sheep meat production was 7 911 505 tons.

Sheeepskin Production

Aggregate 1 741 333 tons sheepskin was produced throughout the world in the year 2011.

Wool Production

1 985 797 tons of wool (greasy) was produced throughout the world in the year 2011.

See also: Breeding: Animals. Detection and Causes of Bovine Mastitis with Emphasis on *Staphylococcus aureus*. Domestication of Animals

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Detection and Causes of Bovine Mastitis with Emphasis on *Staphylococcus aureus*

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Glossary

Bovine Cattle or closely related ruminants.
Enterotoxins Toxins elaborated by some strains of *Staphylococcus aureus* that may cause gastrointestinal signs (vomiting, diarrhea, etc.) when ingested by a person.
Mastitis Inflammation of the mammary gland, usually caused by microorganisms infecting the gland.
Methicillin-resistant *Staphylococcus aureus* Bacterium that is resistant to the antibiotic methicillin, and that can cause serious infections in man and animals.
Pathogenic Disease producing.
Staphylococcus aureus Bacterium that causes mastitis in cattle and other diseases in a number of species.

General Summary of Mastitis

Bovine mastitis is the leading cause of economic losses in the dairy industry worldwide, primarily due to a decrease in the quantity and quality of milk. Expenses associated with the treatment of mastitis, such as use of antimicrobials and the requirement of discarding the milk from treated cows during the withhold period, cause additional economic losses to dairy farmers (Barkema *et al.*, 2009). Annual mastitis losses in the United States are estimated at more than US$2 billion by the National Mastitis Council (Hogan *et al.*, 2011). Mastitis also negatively impacts cow health and reproductive performance.

Mastitis is almost always caused by the entry of pathogenic bacteria through the opening at the end of the teat, the teat duct, causing inflammation of the mammary glands (Schalm *et al.*, 1971, p. 1). Bovine mastitis can be caused by a wide variety of pathogenic microorganisms. Some mastitis specialists divide mastitis microorganisms into major or minor pathogens, relative to the degree of inflammation and seriousness of the signs they cause. Major pathogens are those that produce more serious disease and inflammation. Minor mastitis-causing microorganisms cause only a slight amount of irritation and uncommonly produce clinical mastitis.

Microorganisms that most mastitis specialists consider as major pathogens include, among others:

- *Staphylococcus aureus*
- *Streptococcus* spp. (*Streptococcus agalactiae*, *Streptococcus dysgalactiae*, *Streptococcus uberis*, etc.)
- *Trueperella pyogenes* (formerly *Arcanobacterium pyogenes*)
- *Mycoplasma* spp.
- *Escherichia coli*
- *Klebsiella* spp.

Minor mastitis-causing pathogens are commonly considered to include:

- Various species of coagulase-negative *Staphylococcus* spp.
- *Corynebacterium* spp.

Many of these mastitis-causing pathogens and other possible mastitis-causing microorganisms can be present in the dairy environment and can pose a threat to dairy cows. Therefore, mastitis control strategies have been developed to control and minimize the risk of mastitis on a dairy farm. The most commonly recognized mastitis control program consists of a five-point program to control mastitis pathogens on a dairy farm. In this program, suggested measures recommended to control a pathogen such as *S. aureus* include establishing proper milking techniques for prevention of new infections, using individual towels for udder cleaning, and postmilking teat disinfection. Two measures for elimination of intramammary infections include using antimicrobial therapy or culling of the cow, depending on the severity of the case (Bramley and Dodd, 1984; Sommerhäuser *et al.*, 2003).

In accordance with this recommended mastitis control program, mastitis is the main reason for use of antimicrobials, particularly antibiotics, in the dairy industry. As a result of extensive use of antimicrobials in both human and veterinary medicine, the emergence of antimicrobial-resistant organisms has become an important public health concern. Early detection of mastitis is becoming more important in order to minimize the use of antimicrobials in mastitis cases. This may limit the damage to the mammary glands caused by the infectious agent, as well as increase the success of treatment.

Mastitis cases are classified as subclinical, clinical, or chronic. Subclinical mastitis can be the early stage of a mastitis case and there are no visible changes in the milk or the cow's mammary gland. Diagnosis of mastitis at the subclinical stage may significantly improve treatment success and limit damage to the mammary glands. In clinical mastitis cases, there is inflammation and damage in the mammary glands and the udder is often swollen. Chronic mastitis is the persistence of the infectious agent in the udder, often at the subclinical stage. In contagious mastitis, measures such as segregation of the cow and intramammary antibiotic treatment of the udder may limit the spread of infectious agents to other cows.

Mastitis Detection Tests

Timely detection of a mastitis case may significantly improve the success of treatment and limit the losses associated with mastitis. Therefore, in the dairy industry there are several

methods that are used for early detection of mastitis. A dairy farm could implement one or more of the following detection tests, depending on the particular farm's management decisions.

1. *Determination of total somatic cell counts in milk*: Enumeration of somatic cells in milk and evaluation relative to critical thresholds is used in the diagnosis of bovine mastitis. In the course of mastitis, the presence of pathogenic organisms in the gland triggers an immune response from dairy cows, producing increases in the number of somatic cells in milk (Olechnowicz and Jaśkowski, 2012; Jayarao *et al.*, 2004; Lievaart *et al.*, 2007; Pantoja *et al.*, 2009). Previous studies characterizing differential milk somatic cell profiles of healthy cows reported varying percentages of each cell type. However, the reports agreed on the specific cell types present in milk (Pilla *et al.*, 2012; Schwarz *et al.*, 2011; Koess and Hamann, 2008; Merle *et al.*, 2007; Sarikaya *et al.*, 2006; Dosogne *et al.*, 2003; Rivas *et al.*, 2001; Leitner *et al.*, 2000). Cells present in cow milk include polymorphonuclear leukocytes, lymphocytes, and macrophages. On infection of the mammary glands, dramatic increases in milk cells occur by transfer of white blood cells from blood to the mammary glands (Kelly *et al.*, 2000; Olechnowicz and Jaśkowski, 2012). The primary cells that transfer from the blood stream are the polymorphonuclear leukocytes, and their level increases up to 90% of the total somatic cells (Olechnowicz and Jaśkowski, 2012). This increase in milk total somatic cell numbers during intramammary infection is commonly used as a diagnostic and quality evaluation tool in the dairy industry. It was previously reported that the increased somatic cell numbers in milk cause changes in milk composition, especially reductions in lactose, fat, and casein content (Kelly *et al.*, 2000; Lindmark-Mānsson *et al.*, 2006). Although determination of total somatic cell count provides useful information in determining possible presence of a mastitis case, further characterization of the infectious agent may be required to implement effective treatment of the mastitis case.
2. *California mastitis test* (*CMT*): The CMT is a very widely used onsite test in the dairy industry. This test was developed to estimate the total somatic cell count by using an anionic detergent (Schalm *et al.*, 1971, p. 12). The detergent is mixed with the milk sample and the milk thickens if the somatic cell count of the sample is high. Mastitis is diagnosed by qualitative scoring of the thickening of the milk sample. The test is commonly used because it is a simple, inexpensive test and does not require extensive training of the personnel. However, this test is quite subjective as the evaluation of the change is analyzed by personnel and also further characterization of the possible mastitis case may need to be implemented to select the effective treatment.
3. *Measurement of electrical conductivity of milk*: Mastitis, i.e., inflammation of the mammary glands, causes changes in the composition of milk. As a result of transfer of white blood cells from bloodstream to the mammary glands, the concentrations of Na^+ and Cl^- increase and lactose and K^+ decrease in milk (Kitchen, 1981; Oshima, 1977; Nielen *et al.*, 1992). This changed concentration of Na^+, Cl^-, and K^+ produces increases in the electrical conductivity of mastitic milk (Kitchen, 1981; Nielen *et al.*, 1992). Using available tools for measuring electrical conductivity, the potential occurrence of intramammary infection can be detected. However, similar to above mentioned methods, measurement of electrical conductivity only provides information about the presence of mastitis but not about the specific infectious agent. Therefore, further characterization is required to select the effective intervention for treatment.
4. *Standard microbiological culturing of milk samples*: Standard microbiological culturing of milk samples is widely accepted as the 'gold standard' for diagnosis of intramammary infections in the dairy industry. This method involves enrichment of the pathogenic organism from the aseptically collected milk sample from the infected quarter. As this method enables identification of the specific agent that causes the mastitis case, it is possible to employ the most effective treatment method. Although this method enables specific identification of a mastitis case, it is used less commonly for routine screening of a dairy herd as it requires highly trained personnel, it takes time to grow organisms (at least 24 h), and the samples are prone to contamination during aseptic collection. In addition, there are reported mastitis cases in which microbiological cultures give negative results. Reasons for false negative results include, among others, special growth requirement of some mastitis-causing organisms (e.g., *Mycoplasma* spp.), the state of the mastitis-causing organism (e.g., organism might be in viable-but-nonculturable state), and instances where the inflammatory reaction is still present but the microbes have been cleared.
5. *Application of real-time polymerase chain reaction* (*RT-PCR*): With the advancement of molecular diagnostic techniques, commercial diagnostic kits using RT-PCR have become available for detection of mastitis pathogens. This method enables detection of species-specific regions of the deoxyribonucleic acid (DNA) of pathogenic organisms, yielding a highly sensitive and specific tool for detection of a mastitis case. Previous studies reported high accuracy of this method compared to bacterial culture method (Koskinen *et al.*, 2010). The biggest disadvantage of this method is that the test needs to be conducted using highly technical equipment by trained personnel. In addition, although the commercial kit is able to detect majority of mastitis-causing organisms, if mastitis is caused by an uncommon organism this method would give false negative results.

Methicillin-Resistant *Staphylococcus aureus*, Prevalence in Dairy Industry, and Food Safety Implications of *Staphylococcus aureus* in Milk

Antimicrobials such as penicillin and cephalosporins are used in the dairy industry for treatment or prevention of mastitis and other diseases caused by bacterial organisms. The multistate surveillance report issued by US Department of Agriculture National Animal Health Monitoring system indicated that mastitis was the most common disease in the dairy industry associated with antibiotic use in 2007 and 2002 (in 2007 16.4% and in 2002 15.0% of cows were treated for mastitis) (**Figure 1**; USDA APHIS, 2008). The primary

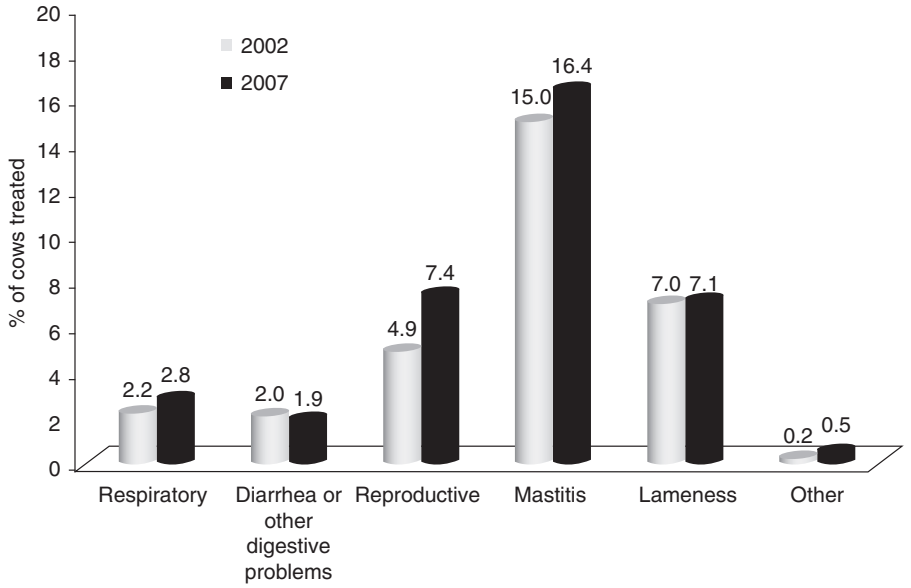


Figure 1 Use of antibiotics at dairy farms in the United States during the previous 12 months of 2002 and 2007. Reproduced from United States Department of Agriculture, Animal Plant Health Inspection Service National Animal Health Monitoring System (USDA APHIS, 2008). Antibiotic use on U.S. dairy operations, 2002 and 2007. Available at: http://www.aphis.usda.gov/animal_health/nahms/dairy/downloads/dairy07/Dairy07_is_AntibioticUse.pdf (accessed 05.05.13).

antibiotic class used for mastitis treatment was cephalosporins (53.2% in 2007 and 36.8% in 2002), followed by lincosamide (19.4%) in 2007 and noncephalosporin beta-lactams (33.8%) in 2002 (**Figure 2**; USDA APHIS, 2008). In addition to treatment, use of antimicrobials as a mastitis preventive measure during the nonlactating period improves the health and productivity of dairy cows, and reduces mastitis incidence. Therefore, some dairy farms use 'dry cow' therapy, in which approved antimicrobials are administered to all quarters of all cows in the herd at the end of lactation (dry-off) (Oliver and Murinda, 2012). It is known that extensive use of antimicrobials serves as a selective pressure for antimicrobial-resistant strains of bacteria (Piddock, 1996). Epidemiological studies on *S. aureus* have revealed that a limited number of isolates persisted in individual herds. These genotypes may have developed necessary resistance or virulence mechanisms, or other properties, that allowed them to persist in cows on specific dairy farms (Anderson and Lyman, 2006; Matthews *et al.*, 1994; Sommerhäuser *et al.*, 2003). The antimicrobials used in veterinary medicine often differ from the antimicrobials used in human medicine. However, the development of resistance to a certain group of antimicrobials could lead to cross-resistance of an organism to other antimicrobials, including those possibly used in human medicine (Piddock, 1996). Therefore, the prevalence of antimicrobial-resistant microorganisms in farm animals and their environment is considered by some to be an important public health consideration. In this respect, one report from an organization focused on the dairy industry and milk quality has concluded that "Scientific evidence does not support a widespread emerging resistance among mastitis pathogens to antibacterial drugs" (Erskine *et al.*, 2004).

Staphylococcus aureus is a Gram-positive bacterium that is considered as one of the major mastitis-causing pathogens. *Staphylococcus aureus* is commonly associated with subclinical, clinical, or chronic mastitis in the dairy industry (Barkema *et al.*, 2009). As *S. aureus* has the ability to spread within and among cows during milking, it is considered as a contagious udder pathogen (Barkema *et al.*, 2009; Capurro *et al.*, 2010). Therefore, accurate and reliable detection of *S. aureus* is crucial for control of the organism in a dairy herd. In routine clinical testing, *S. aureus* is usually differentiated from other less pathogenic members of the *Staphylococcus* genus by its hemolytic and coagulase activities (Boerlin *et al.*, 2003). Although previous studies characterizing the antimicrobial susceptibility of mastitis-associated *S. aureus* isolates reported low number of antimicrobial-resistant *S. aureus*, some level of antimicrobial resistance has been observed (Erskine *et al.*, 2002; Owens and Watts, 1988; Anderson *et al.*, 2006).

Staphylococcus aureus isolates that phenotypically possess resistance to methicillin and related beta-lactam antibiotics are classified as methicillin-resistant *Staphylococcus aureus* (MRSA) (Shore *et al.*, 2011). Since first reported in 1961 in England (Jevons, 1961), MRSA has become a major public health concern as a significant antibiotic resistant pathogen in hospitals, primarily through nosocomial infections (Aquino *et al.*, 2012; Shore *et al.*, 2011). MRSA isolates are often resistant to other drugs (multidrug resistant) as well and this results in increased treatment time and costs, as well as higher hospitalization rates (Haran *et al.*, 2012; Cosgrove, 2006; Noskin *et al.*, 2005). Parallel to its significance in human medicine, awareness of MRSA is increasing in veterinary medicine because of its zoonotic potential (Shore *et al.*, 2011). The first MRSA strain from a dairy cow was isolated in 1972 (Devriese *et al.*, 1972). Although since then there are reports of sporadic MRSA isolation from mastitis cases in dairy cattle, the prevalence of MRSA is typically very, very low among *S. aureus* isolates from bovine mastitis cases (Ferreira *et al.*, 2012; Fessler

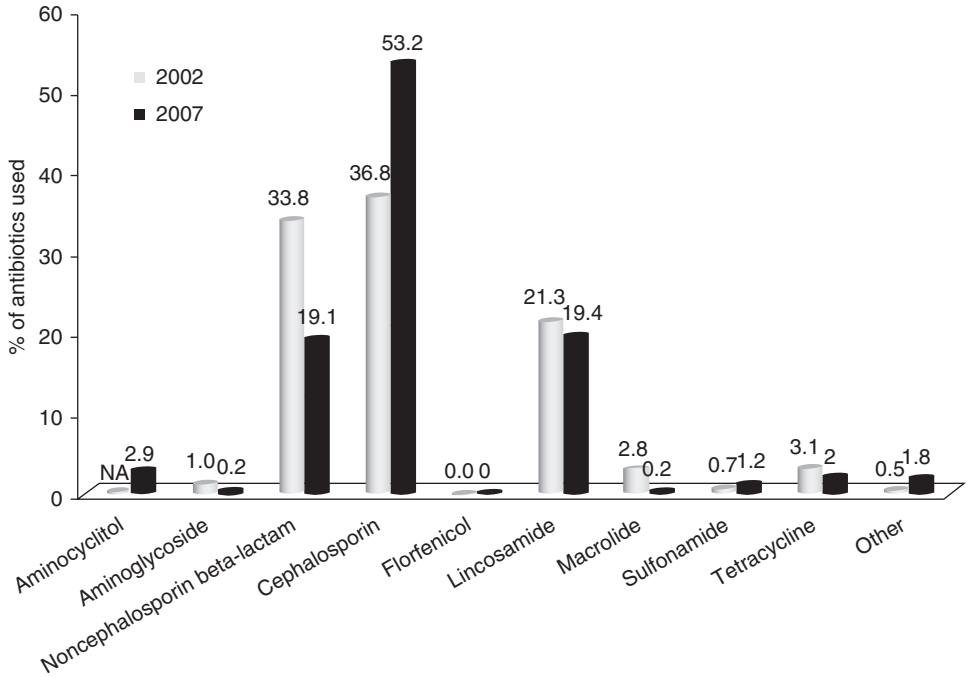


Figure 2 Percentage of primary antibiotic used for treatment of cows during the previous 12 months of 2002 and 2007. Reproduced from the data presented in USDA APHIS United States Department of Agriculture, Animal Plant Health Inspection Service National Animal Health Monitoring System, 2008. Antibiotic use on U.S. dairy operations, 2002 and 2007. Available at: http://www.aphis.usda.gov/animal_health/nahms/dairy/downloads/dairy07/Dairy07_is_AntibioticUse.pdf (accessed 05.05.13).

et al., 2010; Huber *et al.*, 2009; Juhász-Kaszanyitzky *et al.*, 2007; Vanderhaeghen *et al.*, 2010; Weese, 2010). Two recent surveys found no MRSA in bulk tank milk samples in the United States, but there are reported MRSA isolations from dairy in other parts of the world (Ferreira *et al.*, 2012; Virgin *et al.*, 2009). Some MRSA isolates found in livestock are referred as 'livestock-associated MRSA' (LA-MRSA). Some authors report that these MRSA isolates do not commonly colonize in human hosts (Köck *et al.*, 2013). However, there are reports of LA-MRSA passing the species barrier and colonizing the nasopharynx of pig farmers and veterinarians (Cuny *et al.*, 2009; Köck *et al.*, 2012; Köck *et al.*, 2013; Wulf *et al.*, 2008). LA-MRSA isolates are usually colonized in pigs and the reports of dairy isolates of MRSA can be from small-scale, multispecies farm environments. This suggests that the MRSA isolates can be transmitted from other farm animals to dairy cattle.

In the majority of MRSA isolates, resistance is the result of harboring the *mecA* gene that encodes altered penicillin binding protein (PBP2a or PBP2′). This protein has low affinity for beta-lactam antimicrobials (such as cephalosporins, etc.) (Weese, 2010). A large mobile genetic element, the staphylococcal cassette chromosome *mec* (SCCmec), carries the *mecA* gene along with a set of recombinase genes (*ccrA*, *ccrB*, or *ccrC*) for restriction and integration into the host chromosome (Graveland *et al.*, 2011). This SCCmec can be localized on a specific site in the chromosome of a methicillin-susceptible *S. aureus*. Recently, MRSA isolates that are lacking the *mecA* gene have also been reported (Shore *et al.*, 2011; García-Álvarez *et al.*, 2011).

Food Safety Implications of *Staphylococcus aureus* in Milk

Staphylococcus aureus is considered as a foodborne pathogen because it can produce heat-stable enterotoxins during its growth in foods and these enterotoxins can cause food poisoning in humans and animals (Marrack and Kappler, 1990). It is estimated that annually approximately 241 000 persons in the United States experience food poisoning due to staphylococcal enterotoxins (Doyle *et al.*, 2012; Scallan *et al.*, 2011). The food poisoning associated with staphylococcal enterotoxin occurs very shortly after ingestion of the causative food (can start within 3 h of ingestion) and includes signs of abdominal pain, nausea, and vomiting. Dairy foods are among the food categories that are responsible for food poisoning cases associated with staphylococcal enterotoxins (2.1% of the reported 573 outbreaks in the United States between 1998–2010) (Doyle *et al.*, 2012). One of the largest staphylococcal intoxication cases occurred in Japan in 2000 and was associated with low fat milk and more than 13 000 cases were reported (Asao *et al.*, 2003; Doyle *et al.*, 2012). Another staphylococcal intoxication outbreak occurred in 2007 in Paraguay. This outbreak affected approximately 400 individuals and was associated with ultrapasteurized milk product (Doyle *et al.*, 2012). Pasteurization of milk is a common practice in the dairy industry, and pasteurization would result in viable *S. aureus* being eliminated from the product. However, the staphylococcal enterotoxins would resist destruction by the high temperatures of pasteurization and would be present in the final food product. Therefore, staphylococcal

enterotoxins pose a food safety concern as in the foodborne staphylococcal intoxication outbreak in Paraguay in 2007.

The prevalence of MRSA in the dairy industry is low. However, MRSA is a potential food safety concern for dairy products that are made from unpasteurized milk. As of 2012, it was reported that there was no report of MRSA cases associated with a dairy food contaminated with the organism (Doyle *et al.*, 2012). At the time of this writing, only two cases of foodborne MRSA outbreaks were reported, both of which were associated with contamination of food materials by the food handlers (Jones *et al.*, 2002; Kluytmans *et al.*, 1995).

See also: Dairy Animals. Food Chain: Farm to Market. Food Microbiology

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Determining Functional Properties and Sources of Recently Identified Bioactive Food Components: Oligosaccharides, Glycolipids, Glycoproteins, and Peptides

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Glossary

Gangliosides Glycolipids with negatively charged glycans containing one or more sialic acid residues.
Glycoconjugate Molecule in which one or more glycan units are covalently linked to a noncarbohydrate entity (e.g., protein or lipid).
Glycolipids Lipids with one or more glycans attached.
Glycoprotein Protein with one or more covalently bound glycans.
Mass spectrometry Analytical technique that measures the charge-to-mass-ratios of molecules.
Oligosaccharides Carbohydrates consisting of between 2 and 20 monosaccharides, linear or branched connected by either an α- or β-glycosidic linkages. May also be referred to as glycans, especially when attached to other noncarbohydrate structures like proteins and lipids.
Peptide A fragment of a protein released by enzymatic cleavage.
Prebiotics Selectively fermented ingredients that allow specific changes, both in the composition and activity in the gastrointestinal microbiome that confers benefits on host's well-being and health.
Recovery The amount of pure extracted compounds that can be recovered from a matrix.
Whey Liquid part of milk that separates from the curds during cheese-making.

Guiding Agriculture, Food, and Nutrition Sciences to Improve the Sustainability and Health Value of the Food Supply System

During the twentieth century, nutrition science advanced by identifying and characterizing nutrients essential for growth and development. At the same time, food production and processing advanced largely as commodity-driven enterprises benefiting from engineering and science techniques that enabled unprecedented economies of scale. Food fortification and enrichment efforts in developed countries have since eliminated many nutritional deficiencies that previously plagued humanity. These efforts, combined with population-based approaches also had the unfortunate consequence of begetting an era of overnutrition, obesity, and increased environmental degradation. These economies of scale also produce waste at unprecedented levels. The food and beverage industries alone produce approximately 3.5 billion tons of agricultural residues yearly in the world (John, 2009). Designing systems that deliver individually appropriate food and nutrition solutions through efficient utilization of renewable resources will be a hallmark of industrial development in the new millennium.

Currently, most organic waste streams have potential for reutilization, as they contain components valuable for health improvement. Recent evidence suggests that many of the same biomolecules in food processing waste streams that contribute to environmental damage, are also biologically active, health-promoting molecules (Wijngaard *et al.*, 2012). Till date, these 'waste' streams remain relatively untapped resources waiting to be exploited for valuable, healthy components, with concomitant mitigation of environmental damage.

Advances in high-throughput analytical methods, novel scale-up processing methods, and 'big data' information systems, provide a platform of technologies on which agriculture, food, and nutrition sciences can address these large-scale environmental and societal health problems. Biology and biochemical sciences are proceeding rapidly in the identification of structure-interaction-function relationships that bring to light precise molecular targets and biochemical mechanisms underlying various health and disease processes and endpoints. Identifying these mechanisms of health and disease processes provides biomolecular intervention targets. At the same time, the molecular decomposition of food commodities and processing streams is producing libraries of source materials for bioactive chemicals, and the underlying biological and processing conditions that give rise to their formation.

Figure 1 illustrates a life-cycle diagram for the development of new functional ingredients. First (1) desired optimal physiologic conditions are identified, and associated with related biological processes and biochemical pathways, leading to the development (2) of health targets. Provisioning of health targets enables (3), the identification of potential bioactive mediators. Lab separation techniques can deconstruct foods and their processing effluents to reveal classes of contained bioactive molecules (4). Utilizing advanced instrumentation and analysis techniques, these classes of molecules can then be further characterized and quantified (5) to the molecular level. Lab-scale quantities of these molecules can be made available (6) for *in vitro* and *in vivo* experiments that validate target and molecule selection choices. Quantitation of these molecules within foods and food byproducts (7) permits the development of pilot-scale separation techniques. When these techniques are scaled up to industrial levels (8), they can be leveraged to reduce pollution in food processing effluents while providing functional ingredients for new food products (9) for population health improvement.

The remainder of this article follows four classes of bioactive molecules through case studies along the functional food

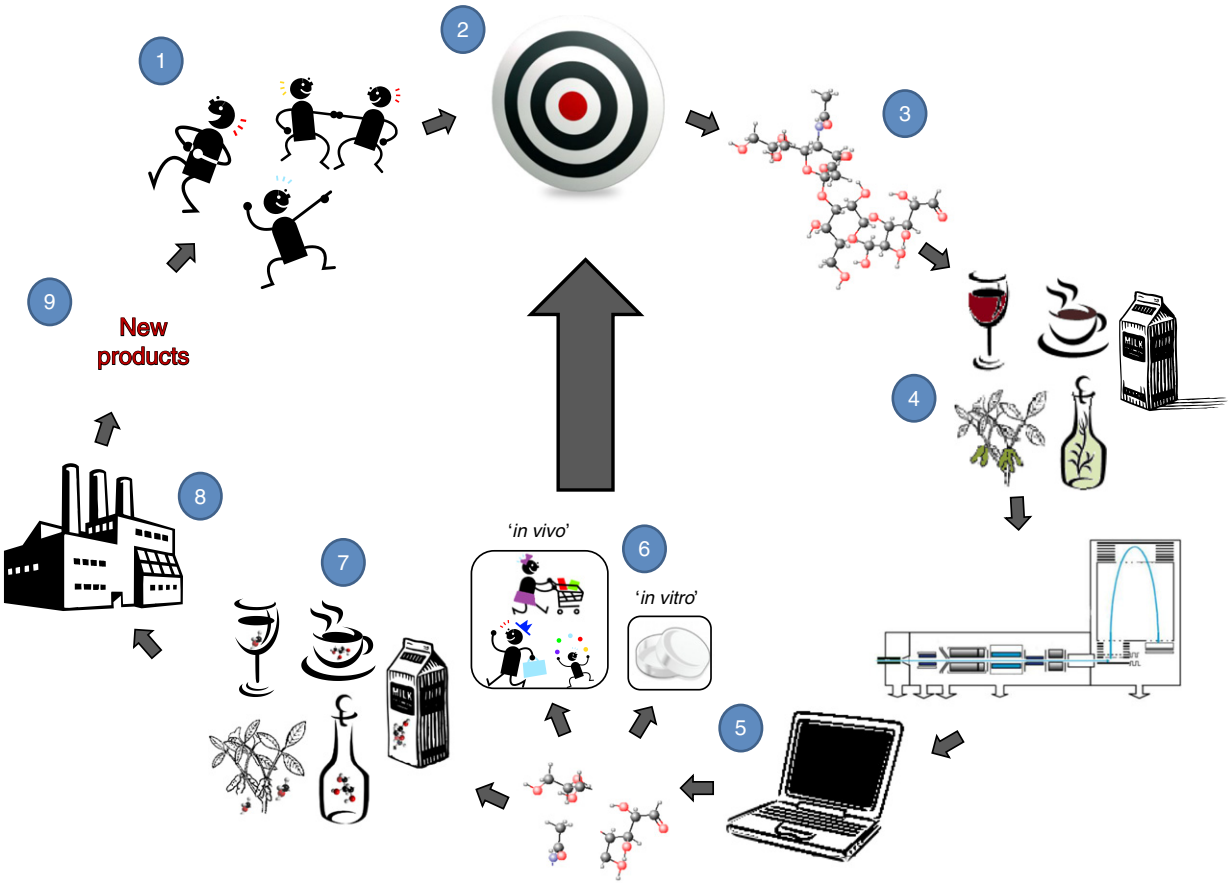


Figure 1 Functional ingredient development life cycle: (1) desired optimal physiological conditions are identified and associated with related biological processes and biochemical pathways; (2) development of health targets; (3) provisioning of health targets enables the identification of potential bioactive mediators; (4) lab separation techniques can deconstruct foods and their processing effluents to reveal classes of contained bioactive molecules; (5) utilizing advanced instrumentation and analysis techniques, these classes of molecules can then be further characterized and quantified to the molecular level; (6) lab-scale quantities of these molecules can be made available for *in vitro* and *in vivo* experiments that validate target and molecule selection choices; (7) quantitation of these molecules within foods and food by products permits the development of pilot-scale separation techniques; (8) when these techniques are scaled up to industrial levels, they can be leveraged to reduce pollution in food processing effluents while providing functional ingredients for new food products; and (9) population health improvement.

development life cycle. Beginning with health and food target endpoints, the reader then progresses through scientific and engineering components of functional bioactive molecule identification and recovery from foods and food processing effluents, to arrive at the exploration and validation of effects these molecules have in individuals, and their potential manipulation to enhance future product development.

Bioactive Molecules versus Nutrients

Nutrients are defined as molecules that are essential for human health. Bioactive or functional molecules have not been shown to be essential for human health, but have the capacity to modulate biological processes that confer health. In this article, 'bioactive' and 'functional' refer to these health-improving molecular properties. Many nonnutrient, bioactive constituents of animal, edible plant, and edible fungi foods have been investigated and annotated for functional molecules with positive health benefits when ingested. Databases that record evidence of health-promoting effects, especially in relation to chronic disease prevention and amelioration, are under development (Gry *et al.*, 2007; Holden *et al.*, 2005; Møller *et al.*, 2007; Rothwell *et al.*, 2012). Integration of assembled bioactivity information with individual genomic and physiologic measurements holds great potential for the development of individually appropriate foods and diets for personalized health improvement interventions.

Health Targets and Model Foods

Functional molecules act on many different physiological systems through a wide variety of biological mechanisms, ranging from substrates for commensal bacterial growth to binding toxins in the blood stream. Defining desirable health traits, and analyzing the biological processes, molecular mechanisms, and molecules necessary for desired health outcomes is an important first step in bioguided processing for bioactive ingredients. As food processors begin the process of

deconstructing the bioactive components of their food waste streams, they may also be guided by knowledge about bioactive composition of similar foods. This section examines the human gut microbiota as an example case for health intervention with bioactive ingredients. It also examines human milk as an example case for modeling known bioactive functionalities of a food and its components. These combined model cases guide the development of scientific and engineering methods mentioned in the case study for bioguided processing in the next section.

Case Study, Health Target: Human Gut Microbiota

Substantial evidence now demonstrates that the intestinal microbiota, the complex mixture of microorganisms that live inside the human intestinal lumen, is an important determinant of health. The intestinal microbiota is essential for the development and function of gut mucosal and systemic immune cells. Imbalances in gut microbiota have been linked to infection, allergic disease, inflammatory bowel disease, and metabolic disease (Abt and Artis, 2009; Albenberg *et al.*, 2012). Intestinal microbiota is also directly linked to immune cell homeostasis (Kalliomaki and Isolauri, 2003). The human microbiota consists of 10–100 trillion microorganisms, representing at least 10-fold more cells than that exist in the entire human body (Proctor, 2011). Metagenomic analysis, the quantitation of all genes from all organisms within an environmental sample, reveals that within the human colon alone, there are 150 times more genes from bacteria than from our own human cells (Qin *et al.*, 2010). These microbes occur in a variety of bacterial population mixtures across individuals, between and within mammalian populations; conferring diverse phenotypic traits in all mammals, including humans. Populations of commensal bacteria are necessary for healthy gut and immune function. Commensal bacteria in the gut can provide a physical barrier that displaces pathogens from receptor binding sites on epithelial surfaces. Commensal microbes also compete for available nutrients with noncommensal microbes. In addition, many commensal bacteria secrete antimicrobial agents that protect the host against pathogens and promote immune system development (Hornef *et al.*, 2002). Establishment of a health-promoting and stable microbiota contributes to both short- and long-term human health. The gastrointestinal microbiota have, therefore, become an important area of study as a health intervention target for functional foods and bioactive molecules.

Recent metagenomic studies have confirmed that bifidobacteria, a genus of bacteria found in human intestinal lumen, are especially enriched in the intestines of healthy breast-fed infants versus formula-fed infants (Yatsunenko *et al.*, 2012). It is now well-established that bifidobacteria can contribute to the prevention and treatment of many animal and human gastrointestinal disorders, such as necrotizing enterocolitis, inflammatory bowel disease, and other colonic transit disorders (Culligan *et al.*, 2009). One specific species, *Bifidobacterium longum*, has been shown to modulate intermediate biomarkers of colon cancer, as well as reduce tumor outcomes (Challa *et al.*, 1997; Reddy and Rivenson, 1993; Rowland *et al.*, 1998; Singh *et al.*, 1997). Because of these conferred health benefits, *Bifidobacterium longum* is considered a probiotic. 'Probiotics' have been defined as "live microorganisms that when administered in adequate amounts confer a health benefit on the host" (Sanders, 2000).

Case Study, Model Food: Human Milk

Whereas probiotics alter the bacterial populations directly, prebiotics help shape the composition of the intestinal microbiota by selectively nourishing commensal bacterial populations. Prebiotics are defined as "selectively fermented ingredients that allow specific changes, both in the composition and/or activity in the gastrointestinal microbiome that confers benefits upon host well-being and health" (Manning and Gibson, 2004). Probiotics and prebiotics are widely used to improve and maintain health (Rastall and Maitin, 2002). Breast milk, the sole source of nourishment for newborns, has been under intense selective pressure over millions of years of evolution to meet the infant's needs to grow and survive (German *et al.*, 2002; Zivkovic *et al.*, 2011). Mother's milk plays a crucial role in directing and educating the infant's immune, metabolic, and microbial systems, enhancing nutrient absorption and delivery, and conferring multiple means of protection between the maternal mammary epithelia and the infant gastrointestinal system. The third most abundant compounds in human milk after lactose and lipids is a class of carbohydrates known as oligosaccharides. Oligosaccharides are chains of monosaccharides between 3 and 20 sugar units in length. Human milk oligosaccharides (HMOs) are indigestible by infants because their secretory enzymes are incapable of cleaving these complex sugars into small enough units to be absorbed through intestinal epithelia. A convincing body of evidence now supports the hypothesis that HMOs are prebiotics that promote the growth of beneficial bacteria, such as bifidobacteria, normally found in the intestine of breast-fed infants (Donovan *et al.*, 2012; LoCascio *et al.*, 2010). HMOs exist as free-floating entities, and may also be conjugated with proteins and lipids. When oligosaccharides are conjugated with proteins, they are sometimes referred to as glycans. In addition to providing selective nourishment to commensal bacteria like *Bifidobacterium longum*, HMOs existing both freely and as glycans attached to proteins and lipids prevent the binding of pathogens to intestinal cells, thereby preventing infections (Coppa *et al.*, 2006; Crane *et al.*, 1994; Morrow *et al.*, 2005; Newburg *et al.*, 2005; Strömqvist *et al.*, 1995).

The molecular deconstruction of mother's milk, and annotation of its effects on infant biology, provides a rich model replete with molecules, as well as molecular and biological mechanisms, through which milk's varied individual and ensemble components confer health (German *et al.*, 2002). Understanding how the components of milk interact for health-improving biological processes is driving the development of new food products. Clinical trials are beginning to show that these products are capable of stimulating and strengthening various health outcomes in infants, immunocompromised elderly, and individuals in the population at large (Sullivan *et al.*, 2010).

Mining Functional Molecules from Food Processing Side-Streams: Promoting Environmental Sustainability While Sourcing Molecules for Health Targets

Environmental sustainability aims to promote long-lasting engineered systems capable of supporting human well-being while having a neutral or positive impact on the surrounding natural environmental systems. Industrial waste streams (often referred to as 'side streams,' 'by-products,' or 'industrial streams') are residual materials resulting from industrial and agricultural operations to create a primary product. Many agricultural and food processing waste streams contain high levels of organic materials that can act as energy sources for aerobic microorganisms. When these streams are released into the environment, microorganisms bloom and create an increased requirement for oxygen in their environment. This phenomenon is referred to as biological oxygen demand or biochemical oxygen demand (BOD). When BOD increases, there is less oxygen in the water for fish and other aquatic organisms to obtain the oxygen they need to live.

The concept of utilizing excess waste from agricultural residues to produce energy or food products is not new. Food makers and engineers have long been exploring suitable technologies to reduce the pollution associated with agricultural wastes by creating novel uses for side stream components. Many processed meat and cheese products are themselves made from byproducts resulting from food processing. More recent is the development of engineering methods to capture bioactive molecules from processing side-streams. Bioguided processing refers to the development of food processing methodologies that preserve the biological functionality of selected components while reducing the environmental impact (often by reducing BOD) of streams (Ward *et al.*, 2004). Bioguided processing capitalizes on recent advancements in high-throughput analytical technologies, combined with novel separation methods, for the characterization and recovery of functional molecules from waste streams.

Table 1 shows some examples of by-products from the food industry including: dairy soybean, wine, coffee, and olive oil side streams. Many functional compounds could potentially be extracted from these side streams. Examples of compounds include oligosaccharides, glycolipids, glycoproteins, and peptides.

Case Study, Sustainable Bioguided Processing I: Scientific Mining of Cheese Whey for Functional Molecules

Many applications await the isolation and characterization of nondigestible oligosaccharides that mimic the protective properties of HMOs. Currently, however, no commercial source of HMO-like compounds (glycans with high levels of sialylation and fucosylation) exist. As a result, the food industry supplements products with simpler inexpensive glycan alternatives. Infant formula manufacturers currently use prebiotic molecules derived enzymatically from the trans-galactosidation of lactose (such as galactooligosaccharides) and fructo-oligosaccharides derived from plant inulin (Jenkins *et al.*, 1999). Although these oligosaccharides mimic the prebiotic effects of human milk to a certain degree, they are structurally and compositionally different from HMOs and lack some HMO biological functions.

Table 1 Example of five commodities and the side streams they generate

Main product	*Side streams*
Cheese	Whey
Soybean	Soybean processing waste (fiber-rich spent solids)
Wine	Wine processing waste (wine-grape residues and pomace)
Coffee	Residues from coffee processing (spent grounds)
Olive oil	Olive oil wastewaters

Whey is the liquid part of milk that separates from the solid curds during cheese-making and was traditionally considered a waste product; it, therefore, serves as an excellent example of a biological waste stream that was only recently shown to contain functional molecules. Cheese whey has been viewed as a secondary product from cheese production for centuries. Recently, cheese whey from cow's milk, also known as bovine whey, was shown to contain complex milk oligosaccharides (Barile *et al.*, 2009). These bovine milk oligosaccharides (BMOs), decorated with fucose and sialic acid, respectively, are structurally and compositionally analogous to HMOs, and confer many of the same health outcomes (Aldredge *et al.*, 2013). Bovine whey also contains bioactive glycolipids, glycoproteins, and peptides similar to those found in human milk (Smithers, 2008). In addition to being inexpensive and available in large quantities, whey is an attractive model source of bioactive molecules because removal of these molecules greatly reduces the pollution index of whey, making cheese processing more sustainable. Because bovine whey is considered 'generally regarded as safe (GRAS),' it presents a unique source for food-grade BMOs and other bioactive molecules. Owing to the wide variety of cheeses and dairy side-streams available, researchers must characterize and quantify the varied processing streams relative to bioactive components, and thus commercial and bioguided remediation potential.

Although varying according to cheese processing methods, approximately 9 l of whey are produced from 10 l of bovine milk during cheese making. More than 400 000 metric tons per year are being generated worldwide by dairy processors. Global demand for cheese is fueling massive growth in cheese production, with more whey generated every year (U.S. Export 5 Year Trend, 2013). The type of cheese manufactured and the processing technologies employed for cheese production determine the type and composition of the resulting bovine whey. Within the cheese manufacturing process, perhaps the most profound determinant of whey composition is the method used for casein precipitation. Typically, whey consists primarily of water (93% of the volume), lactose, proteins, minerals, and vitamins (Walzem *et al.*, 2002). Whey contains almost 50% of all solids present in whole milk (Marwaha and Kennedy, 1988). Only 50% of whey is currently further processed into various food and feed products (Baldasso *et al.*, 2011). Dairy processors are facing the problem of surplus whey disposal and reutilization, posing serious economic and environmental problems. High BOD of whey poses major problems for waste water treatment, and a substantial cost for treatment plants (Marwaha and Kennedy, 1988). Similarly,

whey waste negatively alters the physical and chemical structure of soil, and a prolonged exposure can cause a decreased crop yield, limiting possibilities for irrigation with whey. Untreated whole liquid whey is used as an animal feed, particularly for pigs, although transport of liquid whey over any distance is both difficult and expensive (Schingoethe, 1976). The amount of whey that can be incorporated into animal diets is trivial compared to the volumes that need to be absorbed (Schingoethe, 1976). Therefore, greater utilization of whey components is desirable to avoid these economic and environmental costs. Recent advances in technology now allow the separation of protein and lactose (Scott and Krishnapillai, 2012).

Ultrafiltration is a type of filtration that uses hydrostatic pressure to force liquid through a filter fine enough to retain colloidal particles and high molecular weight molecules. Though ultrafiltration systems have been in commercial use for approximately 30 years, dairy processors have been slow to adopt these systems for whey processing because of a high price of implementation and difficulties with large-scale membrane processing, including membrane fouling (Cuartas-Uribe *et al.*, 2009). The major technological breakthrough in the commercial production of whey proteins was the development of scalable ultrafiltration systems that yielded nondenatured whey protein concentrates (WPC). WPC and whey protein isolates (WPI)were developed in the late 1990s and produced mostly by membrane filtration (Morr and Ha, 1993). To obtain WPI, whey is passed through a membrane filter (ultrafiltration) which, because of the structure of its pores, retains the macromolecules while letting the water containing the dissolved smaller molecules pass through. This process allows whey proteins to be separated from lactose, minerals, and other components. Ultrafiltration produces two fractions: retentate (containing all retained molecules) and permeate (containing molecules that permeate through the membrane). The final protein-enriched retentate can be dried to a powder in a spray drying tower. The permeate fraction can likewise be dried to make permeate powder. A profitable process for utilization of whey permeate compounds is still lacking. More research and development is required to maximize whey utilization. Discovery of functional proteins such as lactoferrin in WPC sparked growth in the whey protein market (Smithers, 2008). Although manufacturers are increasingly taking advantage of the bioactive benefits of whey when designing new products, the full health-enhancing potential of whey and whey components is still underdeveloped. Concentration of whey proteins in the retentate leaves behind 'waste' streams in the permeate that often contain functional components like BMO and bioactive peptides.

Component characterization and quantification

The basis of all food formulations is the ability to accurately measure the structures and the absolute amounts of the functional molecules present. Side-streams for bioguided processing requires similar molecular characterization because handling, storage, and production processes may have huge impact on the composition and bioactivity, resulting in an altered material compared to the original substrate. Therefore, the first step in valorization, the process by which value is added to a process or product, is the complete characterization and quantitation of all bioactive components in processing byproducts and side streams. Recently, detailed knowledge of waste composition has grown steadily and is essential to the assessment of all basic applications. Measurement of the overall composition of products, including water content, carbohydrates, proteins, and fats is simple and can be performed by all food industries as part of their routine analysis. Greater analytical expertise and advanced instrumentation and data analysis software are required for the unambiguous characterization of complex chemicals in waste sources. Functional compounds such oligosaccharides, glycolipids, glycoproteins, and peptides, are found in relatively low concentrations, and are extremely heterogeneous and complex in nature. Identification and detailed characterization of these compounds, therefore, demand specific analytical expertise. Even small differences in structure can cause significant differences in function, so structural characterization is essential to accurately distinguish molecular function. To identify their biological functions through *in vitro* and *in vivo* studies, it is necessary to measure those molecules with accurate and sensitive methods.

Many of milk's functional molecules could not be discovered until the right concordance of novel separation and analytical technologies were developed and applied. Many health-promoting components still await discovery due to technical challenges in their identification, isolation, and testing. As analytical technologies advance in sophistication and accuracy, new functional milk molecules are being discovered.

In whole milk, many components mask the analytical signal of others, so some components cannot be detected. Because milk is such a complex mixture, its compartments need to be separated, and then fractioned into molecular classes. Modern analytics allow for the discovery and characterization of hundreds of novel milk compounds with high resolution and high accuracy. Liquid chromatography (LC) paired with electrospray ionization allows the separation of peptides, glycans, and glycolipids for improved mass spectrometric detection. Target proteins and glycoproteins can now be purified from intact milk or other dairy streams by chromatography in order to better characterize these proteins for new bioactivities. The combination of advanced analytics with the new engineering capabilities will allow for high molecular resolution and separation techniques that can be scaled up to semiindustrial and industrial scale for translation of lab-based discoveries.

Many technological breakthroughs have made discovery of new milk molecules possible. These advances include improved separation science, high-resolution detection instrumentation, bioinformatic toolsets (like proteomic software), and genomics (as a tool to guide proteomics). Currently, toolsets exist for the detection of a wide array of free milk oligosaccharides (glycomics), milk lipids (lipidomics), proteins (proteomics), and naturally occurring peptides in milk (peptidomics).

Chemical characteristics: oligosaccharides, glycolipids, glycoproteins, and peptides

Chemical characteristics of oligosaccharides

Milk oligosaccharides can have diverse and complicated structures even though they commonly share a lactose core

consisting of a glucose and a galactose linked via a β 1,4-linkage (Kunz *et al.*, 2000). These oligosaccharides are produced in the mammary gland where several monosaccharides are added to a lactose core by action of specific enzymes called glycosyltransferases (Urashima and Taufik, 2010). These glycosyltransferases elongate the core by repetitive attachment of galactose (Gal) and *N*-acetylglucosamine (GlcNAc) in β-glycosidic linkage, which are further decorated by multiple resides of sialic acid and fucose (Kunz *et al.*, 2000). Neutral oligosaccharides are composed of glucose and galactose (lactose core) extensively elongated by β1-3 or β1-6 linkages to lactosamine units, and further decorated with fucose residues in terminal positions connected with α1-2,3,4 possible linkages. Acidic oligosaccharides can contain all these monosaccharides in addition to one or more molecules of *N*-acetyl-neuraminic acid (also known as sialic acid) connected with α2-3,6 linkages. The possible arrangement of monosaccharide combinations and linkages results in a structurally complex array of linear and branched oligosaccharide structures. In particular, the structural elements fucose and sialic acid appear to be crucial to the ability of oligosaccharides to act as bioactive components. These five monosaccharides (glucose, galactose, *N*-acetyl-glucosamine, fucose, and sialic acid) are linked in various ways through at least 12 α- and β-glycosidic linkages. The most abundant oligosaccharides in human milk are fucosylated, whereas sialylation is more abundant than fucosylation in bovine milk and cheese whey (Morrow *et al.*, 2005).

Chemical characteristics of glycolipids

Nearly all glycolipids in vertebrates are glycosphingolipids. The glycolipids are composed of two parts: ceramide lipid portion and carbohydrate moiety. The ceramide is formed by attachment of a fatty acid in amide linkage to the long-chain amino alcohol sphingoid base. Ceramide structures vary in length, hydroxylation, and saturation of both the sphingoid base and fatty acid moieties, resulting in lipid structural diversity that imparts the presentation of the attached glycan at membrane surfaces.

In the complex glycolipids, the glucose moiety in head group is typically substituted with β-linked galactose on the C-4 hydroxyl of glucose, to give lactosylceramide. Further the glycans are extended by the addition of different monosaccharides.

Glycolipids are subclassified as neutral (no charged sugars or ionic groups), sialylated (having one or more sialic acid residues), or sulfated according to the carbohydrate moieties. Traditionally, all sialylated glycolipids are known as 'gangliosides.' The most abundant human and bovine neutral glycolipids are lactosylceramide, glucosylceramide, and galactosylceramide (Newburg and Chaturvedi, 1992). GM3(NeuAcα2-3 Galβ1-4Glcβ-Cer) and GD3 (NeuAcα2-8NeuAcα2-3 Galβ1-4Glcβ-Cer) are the major gangliosdes in bovine milk and whey buttermilk (Lee *et al.*, 2011; Rueda, 2007).

Chemical characteristics of glycoproteins

Protein glycosylation, a common posttranslational modification, plays a key role in structural conformation and resultant bioactivity of proteins (Marth and Grewal, 2008; Shental-Bechor and Levy, 2009). This posttranslational modification is involved in various intra- and intercellular processes including adhesion and trafficking (Ohtsubo and Marth, 2006). During biosynthesis, many milk proteins are posttranslationally modified. Milk glycoproteins are present in the whey fraction (lactoferrin), the casein micelle (κ-casein), and also in milk fat globule membrane (lactotransferrin, clusterin, mucin1, and butyrophilin) (Picariello *et al.*, 2008; Charlwood *et al.*, 2002). The common classes of glycans are primarily defined according to the nature of the linkage to the protein. Glycans can be linked to the protein through O-glycosidic or N-glycosidic bonds. N-glycans are the most widespread modification in human and bovine milk proteins.

Chemical characteristics of glycoproteins: N-glycans

N-glycans are attached, via *N*-acetylglucosamines, to the Asparagine residues of proteins in the specific amino acid sequence that is Asn-X-Ser/Thr (where X can be any amino acid except proline). The N-glycan core is composed of 2 *N*-acetylglucosamines (GlcNAc) and 3 mannoses (Man). The N-glycan core is assembled in the endoplasmic reticulum of the cell and then the glycan is elongated by other monosaccharides via the action of enzymes, which determines the degree of branching and the type of linkage (Aebi *et al.*, 2010). Elongation with sialic acid and fucose increases the diversity and complexity of the N-glycan structure (Ohtsubo and Marth, 2006). N-glycans share a common pentasaccharide core region and can be generally divided into three main classes; oligomannose (or high mannose), complex type, and hybrid type. Glycan function varies based on the glycan composition and the site of attachment, and this diversity is involved in the functional activity of a protein.

Chemical characteristics of glycoproteins: O-glycans

O-glycans are frequently linked to the polypeptide via *N*-acetlygalactosamine (GalNAc) to a hydroxyl group of a serine or threonine residue and can be extended into a variety of different structural core classes. Casein glycomacropeptide or GMP is the prototype O-glycan found in cheese whey: it is a casein-derived peptide that is also present in human milk and may contain up to five different types of O-linked oligosaccharides chains (usually sialylated glycans) (Minkiewicz *et al.*, 1996).

Chemical characteristics of peptides

Peptides are chains of amino acids resulting from the cleavage of larger proteins. In milk, these peptides contain all 20 amino acids. Whether these peptides have complex three-dimensional structures remains unknown. The average length of naturally occurring peptides in whey is 13.3 amino acid residues long with a range between 7 and 25. The average peptide mass is 1502.728 Da (range 687.346–2925.334) (Dallas *et al.*, 2013a,b).

Basic lab-scale separation methods

Basic lab-scale separation methods of oligosaccharides

The basic goal of separating oligosaccharides as a biomolecule class from complex matrices including milk has been developed successfully in the microscale as a standard aspect of analysis. Extraction is a crucial step in the characterization and quantification of all milk bioactives by mass spectrometry.

To characterize the oligosaccharides in milk accurately, it is of great importance that the oligosaccharides are isolated from the other milk components such as lipids, proteins, and small peptides. This is currently done by employing physical methods such as a combination of centrifugation and liquid/liquid extraction and solid-phase extraction (Ninonuevo *et al.*, 2006). All these methods are used in sequence to separate the oligosaccharides based on their unique chemical properties, for example, when using reversed phase solid-phase extraction, the hydrophobic lipids and proteins are bound by the C8 silica cartridge, whereas the hydrophilic oligosaccharides are free to pass through the column undisturbed (Barile *et al.*, 2010). A further extraction step involves the purification and concentration of the oligosaccharides by employing graphitized carbon cartridges that allow for the removal of salts, mono- and disaccharides, and remaining proteins while achieving a nearly complete recovery of the oligosaccharides. The specific mechanism of interaction between the complex carbohydrates and graphitized carbon is poorly understood, has not been completely elucidated yet, and assumed to involve both absorption and hydrophobic interaction (Packer *et al.*, 1998). Retained oligosaccharides can be divided into acidic and neutral fractions, hence their properties, and are further analyzed by accurate mass spectrometry. Unfortunately, it is currently impossible to obtain enough quantities of oligosaccharides in laboratory to support prebiotic and other functional studies.

Basic lab-scale separation methods of glycolipids

The analytical methods used for glycolipids require several purification steps. Because of their amphipathic nature, it is currently not possible to purify and measure total glycolipids using a single method. The liquid–liquid solvent system requires a polar and a nonpolar component, and neutral and anionic glycolipids are often fractionated and analyzed separately (Ledeen and Yu, 1982; Merrill *et al.*, 2005).

The general procedure includes separating milk cream by centrifugation. Further separation is then achieved by liquid/liquid extraction based on the relative solubilities in polar and nonpolar solvents. Highly polar glycolipids, such gangliosides, are further enriched on reverse phase solid-phase extraction cartridges. Nonpolar glycolipids are usually fractionated on normal phase chromatography.

Basic lab-scale separation methods of glycoproteins

To isolate glycoproteins, all lipids and caseins have to be removed by centrifugation (to eliminate the cream) and by acid treatment (to precipitate the caseins). Owing to the low concentration of glycoprotein in bovine milk, the resulting whey needs to be significantly concentrated. Glycoproteins can be isolated from other whey proteins by separation methods like ion exchange and affinity chromatography, resulting in very high purity (Barboza *et al.*, 2012; Law and Reiter, 1977). Chromatographic methods allow separation of glycoproteins based on their amino acid sequence or glycan composition (Kletter *et al.*, 2013). For example, lectin immobilized on beads can be used to recover lactoferrin through binding of specific protein-linked glycans (e.g., the lectin called concanavalin A binds α-linked mannose and terminal glucose). These techniques achieve high purity isolation of the protein of interest from complex mixtures like milk and whey. However, for single protein isolation, each step of the chromatographic needs to be optimized for each glycoprotein. The quality of the purified fraction can be monitored by gel electrophoresis and mass spectrometry. The identification of the protein can be validated by Western blot and peptide mass fingerprinting. Novel protocols are being developed to achieve site-specific analysis of milk glycoproteins (Nwosu *et al.*, 2012, 2011). These methods involve using aspecific proteases to digest the proteins into short glycopeptide chains whose structural elucidation is accomplished by using accurate mass and tandem mass spectrometry.

Basic lab-scale separation methods of glycoproteins, N-glycan purification

To identify the glycans, they can be released by a chemical method or the use of a commercial enzyme, peptide-*N*-glycosidase F (PNGase F), which cleaves between the Asparagine residue and the first *N*-acetylglucosamine of the N-glycan core. One of the advantages of the enzymatic method is the release of a large variety of glycans, except those containing a fucose α (1–3) linked to the terminal *N*-acetylglucosamine residue of the N-glycan core. PNGase F is not able to cleave the linkage between the first *N*-acetylglucosamine and the asparagine residue due to steric hindrance. Glycans can be released from the protein in solution or from the Coomassie-stained gel band that contained the glycoprotein (Rendić *et al.*, 2007). Specific exoglycosidases can also be used to get more information about the N-glycan structure. The deglycosylated protein can be eliminated by ethanol purification and the released carbohydrates can be purified by graphitized carbon chromatography and analyzed by sensitive methods like mass spectrometry.

Basic lab-scale separation methods of peptides

Peptidomic analysis of milk's naturally occurring peptides is now possible only through a confluence of novel preparative isolation, analytical separation, analytical detection, and computational techniques. Milk peptides can be isolated by first removing cream by centrifugation, then removing the large proteins via acid precipitation, and finally by removing the salts, lactose, and oligosaccharides by preparative nonpolar (C18) solid-phase extraction (SPE).

Analytical instrumentation and molecular characterization

High-throughput strategies have recently been developed that enable the annotation of the molecular milk components by using advanced analytic tools like mass spectrometry. The advantage of the mass spectrometer is that in many cases it can provide unambiguous identification. Mass spectrometry has emerged as an invaluable technique with a wide array of applications, including food analysis. Its use in waste stream composition analysis is burgeoning. Not only does it yield structural information from the molecule under investigation, but it also provides the molecular weight of the analyte. This is, in most cases, the single most important and discriminating piece of information available because it reduces the number of possible identities of the analyte. Another advantage of mass spectrometry is its sensitivity. Chemical species identification can be obtained from subfemtomole amounts of analyte. Mass spectrometry can also provide quantitative information if appropriate standards are used.

Liquid chromatography separations – A closer look

The combination of chromatographic techniques, such as the high pressure liquid chromatography (HPLC) microchip, with mass spectrometry reduces the time of analysis and generates more detailed information by separating molecules before they reach the detector. Employing LC in conjunction with mass spectrometry can identify molecules with identical composition but different structures, and therefore, different biological activities. A recent review published in the *Journal of Chromatography A* detailed the astonishing increase in the number of papers, more than 300 per year, that utilize HPLC–mass spectrometry for food analysis (Di Stefano *et al.*, 2012). A 50-fold increase since 1991 makes HPLC–mass spectrometry the fastest growing analytical technique for food analysis (Di Stefano *et al.*, 2012).

Commercially available HPLC chip devices with integrated enrichment and separation columns packed with graphitized carbon allow isomer-level separation of glycans. (Ninonuevo *et al.*, 2006, p. 200; Niñonuevo and Lebrilla, 2009) When these microchips are coupled with high performance mass spectrometry, such as the high accuracy time-of-flight (TOF) mass analyzer, all isomers can be rapidly analyzed in a precise and reproducible manner (Niñonuevo *et al.*, 2005, 2007; Tao *et al.*, 2009; Wu *et al.*, 2010a,b).

Mass spectrometry – A closer look

Mass spectrometric platforms are capable of detecting more compounds in a single run than other traditional analytical tools. With small molecules, this high precision measurement can lead to a single compositional possibility. A variety of mass spectrometers can be employed for detection of functional milk components (e.g., TOF, Fourier transform ion cyclotron resonance (FTICR)). These mass analyzers have high resolution and are highly sensitive. Mass spectrometers possess several components: (1) a sample inlet that introduces samples into the mass spectrometer, (2) an ion source that generates gas phase ions from analytes, (3) a mass analyzer that separates ions based on their mass-to-charge ratio (m/z), (4) a detector that monitors the ion current and converts it into a signal, (5) a computer and data system that coordinates the functions of the instrument components and records and stores the data, and (6) a vacuum system that removes molecules, thereby providing a collision-free path for the ions from the ion source to the detector. In tandem mass spectrometry, neutral gas molecules are added to the ion path, causing collisions that result in molecular fragmentation.

Ionization techniques

A variety of ionization techniques are used for mass spectrometry. Two soft ionization methods – matrix-assisted laser desorption ionization (MALDI) and electrospray ionization (ESI) – have led to an enormous increase in the utility of mass spectrometry for biological macromolecules such as proteins and glycans.

Mass analyzers

High mass accuracy and resolution mass analyzers, such as TOF and Fourier transform ion cyclotron resonance (FTICR) analyzers are often used for mass profiling. Ions of interest can be isolated and fragmented for identification. LC-MS/MS analysis with a triple quadrupole mass spectrometer in multiple reaction monitoring (MRM) mode provides excellent quantitation (when used with internal standards) due to its high accuracy. MRM provides a highly selective and sensitive determination of a compound of interest in a mixture.

Molecular characterizations of oligosaccharides

Identifying and quantifying milk oligosaccharide structures has been a major challenge. Functional studies previously involved either a limited number of structures or little to no structural information. Recently, methods for the comprehensive analysis of milk glycans has evolved, involving advanced separations methods and high performance mass spectrometry (Leoz *et al.*, 2013; Strum *et al.*, 2012; Wu *et al.*, 2012). The developments of new analytical techniques have significantly improved our knowledge about the structures of milk oligosaccharides (Pfenninger *et al.*, 2002). Bovine milk is potentially an excellent source of commercially viable HMO mimetics. Until recently, the analysis of oligosaccharides from bovine milk was hindered by the lack of effective analytical tools. Recently, the lower abundant oligosaccharides from bovine milk were characterized and shown to contain complex structures similar to HMO (Barile *et al.*, 2010; Hua *et al.*, 2012; Wickramasinghe *et al.*, 2011). There are 40 unique BMO in bovine colostrum, including 24 acidic structures containing sialic acid, and 16 neutral oligosaccharide structures containing glucose, galactose, and *N*-acetylglucosamine (Tao *et al.*, 2009). The identified oligosaccharides in bovine colostrum include several structures identical to neutral and acidic HMO, including LNnT (lacto-*N*-neo-tetraose), LNnH (lacto-*N*-neo-hexaose), 3′-SL (3′sialylactose), and 6′-SL (6′sialylactose). Recently, the bovine glycome was established for several dairy breeds (Barile *et al.*, 2009; Sundekilde *et al.*, 2012; Tao *et al.*, 2008). Recent analysis of bovine dairy streams by accurate mass spectrometry has revealed the presence of previously unknown complex fucosylated and sialylated oligosaccharides, analogous in composition and structure to the ones found only in human milk (Aldredge *et al.*, 2013). This discovery has led to the hypothesis that these specific oligosaccharides can be isolated from dairy streams, individually characterized for structure, and reconstituted into a pool of protective oligosaccharides that mimic the activities observed for human milk.

Advances in mass spectrometry have enabled identification and determination of milk oligosaccharides at the molecular level as well as provided detailed information about their specific utilization by intestinal bacteria; sequencing of the whole genome allowed a new level of understanding of the specific prebiotic activity (LoCascio *et al.*, 2010; Sela *et al.*, 2012; Wu *et al.*, 2010a,b). Analysis of oligosaccharides from bovine milk has been hindered by the lack of effective analytical tools to analyze complex carbohydrate structures present in low concentrations. The development of analytical tools such as microchip LC combined with high-performance mass spectrometry allowed significant progress in the examination of oligosaccharides in bovine milk and milk from other mammals (Tao *et al.*, 2011, 2010, 2009, 2008).

Molecular characterizations of glycolipids

The first survey profiling for glycolipids is often exploratory, thus called an 'untargeted' approach. Milk glycolipids have been identified using MALDI mass spectrometry (Bode *et al.*, 2004; Lee *et al.*, 2011). High resolution mass analyzers, such as FTICR, provide rapid identification of these molecules. A number of differences between bovine milk and human milk have been observed. Major bovine and human milk gangliosides are GD3 and GM3; whereas, the ion intensities of ganglioside species are different. Identification of gangliosides relies on tandem MS to confirm the compositional and structural assignments.

Upfront chromatographic separation of a glycolipid and phospholipid mixture makes it possible to detect more ions by minimizing ion suppression and ultimately increases sensitivity (He *et al.*, 2007; Lee *et al.*, 2012). LC-tandem mass spectrometry (MS/MS) analysis in multiple reaction monitoring (MRM) mode has become an effective technique for highly specific and accurate quantitation of glycolipids, especially when present in low abundance (Lee *et al.*, 2013; Sorensen, 2006; Zhang *et al.*, 2012). This technique could be used to quantitate the exact amounts of glycolipids in dairy products and side streams (Lee *et al.*, 2013).

Unlike free milk oligosaccharides, glycoconjugates are more complicated due to the respective protein or lipid moieties. Glycolipids are heterogeneous in their properties due to variation in the fatty acid or sphingosine structure of the ceramide lipid component as well as the diversity of the oligosaccharide. For example, glycolipids composed of ceramides with short fatty-acid side chains and large oligosaccharide chains will be much more soluble in polar solvents than glycolipids composed of ceramides with long fatty-acid side chains and short oligosaccharide chains. Therefore, the classical analytical methods use multiple chromatographic analyses along with extensive sample preparation. Moreover, the analytical methods fail to describe in precise details both the lipid and glycan moieties simultaneously. The method often requires huge amount of samples, which impedes the functional studies for those low abundant molecules.

Molecular characterizations of glycoproteins

Glycosylation of proteins is a complex posttranslational modification with high diversity of possible structures. Some biomolecules, including protein and nucleic acid, can be easily sequenced but the elongated branches and diversity of N-glycan isomers complicates their unambiguous characterization. Enumeration of each fully described glycoprotein chemical species remains a significant scientific challenge. Isomer separation and identification are important steps for glycan characterization. Identifying site occupancy on the protein, of each varied glycoform is also necessary for complete glycoprotein characterization. Furthermore, the concentration of ruminant glycoproteins is low in milk. Bovine milk lactoferrin concentration is ten times lower than human milk. Glycoprotein characterization requires the use of highly sensitive and specific instruments. Rapid profiling of glycans can be obtained by MALDI-TOF-MS (Hansen *et al.*, 2010). MALDI-TOF has been successfully used in a large number of studies to characterize N-linked glycans (Finke *et al.*, 1999; Niñonuevo and Lebrilla, 2009). Biological samples like milk and serum typically contain a mixture of neutral and sialylated glycans. Neutral glycans are typically analyzed in presence of sodium, as $[M+Na]^+$ in the positive mode and sialylated glycans are typically analyzed as $[M\text{-}H]^-$ in the negative mode (Harvey, 2006). Biological samples typically contain a mixture of neutral and sialylated glycans. Accurate analysis of sialylated glycans is difficult because the sialic acids can be lost during the ionization process (Hansen *et al.*, 2010; Harvey, 2006). MALDI-TOF-MS provides the accurate mass and the relative abundance of glycans in the sample. Studies on the milk N-glycome reveal 51 different compositions for bovine milk and 38 for human milk with notable abundance differences of fucosylated and sialylated glycans between the 2 species (Nwosu *et al.*, 2012).

Molecular characterizations of peptides

Peptides can be ionized without in-source fragmentation by MALDI and ESI. These soft ionization techniques were required for the analysis of proteins and protein components. Mass analyzers that can be used for peptide analysis include TOF, Orbitrap, triple quad, and FTICR. LC is typically applied for peptide detection. Increased LC separation simplifies detection by decreasing ion supression and providing isobar separation for clear tandem fragmentation.

Once isolated, peptides can be separated with a C18 analytical column and detected by a mass analyzer. Even low ppm precision intact mass measurement is not enough to identify the exact peptide sequence. Therefore, compounds can be sequentially isolated and fragmented. The fragment spectra can be analyzed for components of the peptide to provide evidence for which possible sequence is correct. As the mass spectrometer typically produces thousands of tandem spectra in an hour run, data must be processed via automated software. Data can be exported and the fragment spectra analyzed with proteomic software such as X!Tandem. A search for a aspecific enzymatic cleavage patterns must be performed. To narrow the possible peptide sequences, a milk protein-specific library can be employed as the basis for the search rather than the usual complete human proteome. Peptides identified from automated analyses can be compiled as libraries of known peptides with mass, retention time, and a unique identity. These libraries can then be applied back to the mass spectrometer runs of the sample for peak volume extraction. Peak volumes can be compared between identical peptides across different sample sets.

Data analysis software

Mass spectrometry data includes mass and peak intensities. Mass combined with retention time from LC separation can be used to identify molecules. Tandem mass spectra can provide further evidence for identification. Compound structure can be elucidated from empirical formula calculations and the vast amounts of accurate mass data generated by these precision instruments. Data analysis software simplifies aggregation of large amounts of data and eases its interpretation. Using data analysis software (e.g., Agilent MassHunter Qualitative Analysis software), discrete molecular entities defined by the combination of retention time and mass are generated. Highly accurate measured masses of the different molecular species combined with their isotopic patterns and collisionally

induced dissociation (CID) fragments are additionally used for empirical formula calculation and structure elucidation. Relative quantities of each molecule can be also derived.

Analytical instrumentation and molecular characterization: Molecular libraries and structural information resources for molecular identification

Construction and application of mass and retention time-based molecular libraries allows streamlined, high-throughput identification of molecules. Once molecules are identified, they can be compiled into libraries. With software, these libraries can be used to search the chromatograms for previously identified molecules based on accurate mass and retention time. Application of a molecular library within spectral analysis software (such as Agilent MassHunter) allows fast matching of ions with the library and computational extraction of each compound's abundance. These libraries typically include the mass, retention time, and identity of the compound. More sophisticated libraries such as Agilent Personal Compound Database Library also employ representative MS/MS spectra for each compound to increase the certainty of the match. For these libraries, the MS/MS spectra of the unidentified compound must match, within a margin of error, the peaks in the reference spectra. These libraries allow high-speed molecular evaluation of samples from milk and dairy streams.

Mass and retention time-based libraries have been created for more than 80 HMOs (Wu *et al.*, 2010a,b). Aldredge has recently assembled a BMOs library (Aldredge *et al.*, 2013). More than 50 oligosaccharides have been identified including several novel fucosylated oligosaccharides. The construction and use of these libraries enable automated identification of these oligosaccharides. Application of the BMO library facilitates identification of oligosaccharides in commercial dairy streams.

Current structural libraries for glycolipids are limited in size. Partial tandem mass spectra libraries for glycolipids are available from LipidMaps (Dennis *et al.*, 2005; Fahy *et al.*, 2007). Dallas recently published a library of endogenous human milk peptides (Dallas *et al.*, 2013a,b). Hua and Kronewitter have established, for mice and humans, respectively, libraries of N-linked glycans (Hua *et al.*, 2013; Kronewitter *et al.*, 2009). These libraries of structural identification are based on accurate mass, reproducible retention time, and effective isomer separation. This approach obviates the need for continued *de novo* structural elucidation by providing researchers with look-up identification mechanisms. These spectral libraries additionally provide a resource against which bioactive molecules isolated from clinical trial specimens (e.g., feces, urine, and serum) can be matched, thereby advancing the field of molecular diagnostics.

Scaling Up: PILOT and Industrial Scale Extraction of Functional Compounds from Food Matrices and Processing Effluents

Chemical and biosynthesis methods for production of functional compounds are often cost prohibitive. Yet pilot-scale production methods are necessary to produce functional molecules in sufficient quantities for evaluation in functional assays, as well as tolerance and efficacy clinical trials. Lack of affordable, commercially feasible, large-scale methods for bioactive molecule production has hindered progress in knowledge that could be gained from *in vivo* and *in vitro* functional tests. Food matrices and food processing effluent streams are a rich source of bioactive compounds with potential for highly efficient industrial-scale extraction and production (Agyei and Danquah, 2011). Many food sources, such as milk, eggs, soybeans, fish, corn, wheat, and many others, contain naturally occurring functional compounds – or can release functional compounds when subjected to specific processing conditions such as enzymatic hydrolysis and microbial fermentation (Korhonen *et al.*, 1998; Korhonen and Pihlanto, 2006). While seeking out molecules for their biofunctional properties like antithrombotic, antihypertensive, immunomodulatory, antioxidant, antimicrobial, to name a few, bioactive molecule extraction from food matrices also requires extensive knowledge of intrinsic molecular physical–functional properties like solubility, foaming, and gelling, among others (Agyei and Danquah, 2011; De Moura *et al.*, 2011a; Hernández-Ledesma *et al.*, 2011; Kinsella, 1979). Consideration of bioactive molecule physical–functional properties determines, in large part, the best methods and technologies to use for their extraction and production.

Effects of Processing Conditions on Extraction, Recovery, and Functionality of Extracted Compounds

Maximizing extraction efficiency of target compounds while preserving their bioactivty is essential to improving the economic viability of any bioactive compound extraction procedure. High yields may result in poor bioactive functionality under suboptimal conditions. Alternate methods of extraction yield products with varied chemical structures and biological functionalities. The form in which the target compound is released from its matrix is also a factor in final recovery yield and functionality (De Moura *et al.*, 2011a,b; Clydesdale, 2005).

Because composition, structure, and functionality of food compounds can be significantly affected by processing conditions (Jung *et al.*, 2012; Kinsella, 1979; Korhonen *et al.*, 1998; De Moura *et al.*, 2011a), the methods used to produce, extract, and recover functional molecules from food must be carefully considered. Processing conditions such as heating, shear, pH, enzyme treatment, and solvent-ratio can exert major effects on physical–chemical and bioactive properties of food compounds. Although the impact of food processing conditions on proteins and peptides from various sources have been extensively reported in the literature (De Moura *et al.*, 2011a,c; Korhonen *et al.*, 1998), less information is available regarding other classes of bioactive compounds such as oligosaccharides, glycolipids, and glycoproteins. These functional molecules have only recently begun to be fully characterized. Determining the impacts of processing conditions on the structure and function of bioactive compounds is essential. Consideration of postextraction storage conditions on bioactive molecule stability is similarly important, and is an emerging area of investigation.

Challenges for Stream Fractionation and Enrichment of Functional Molecules

The quest for alternative sources – The human milk oligosaccharides example

The limited supply of HMOs precludes their use as an industrial source for large-scale production of prebiotics. Researchers are currently investigating alternative sources of complex oligosaccharides in sufficient quantity for *in vitro* and clinical studies. Various chemical and biological synthesis strategies have attempted to produce glycans with bioactivities mimicking those of HMOs. Currently, much simpler structures, including inulin, fructo-oligosaccharides, and galacto-oligosaccharides are commercially available and have been tested in clinical trials. These simple structures are either extracted from plants or obtained by β-galactosidase-catalysed conversion of lactose. These glycans stimulate the growth of intestinal bacteria, but they do not selectively stimulate the growth of commensal bacteria to the exclusion of undesired bacteria (Ninonuevo and Bode, 2008). These oligosaccharides are nonselective because their simple structures mean that only a limited number of bacterial glycosidases are required for their degradation. Solid-phase oligosaccharide synthesis is useful to synthesize small amounts of simple oligosaccharides for use as standards in analyses (Tolborg *et al.*, 2002), but production of large quantities needed for human trials is currently economically prohibitive.

Commercial-scale sources of complex oligosaccharides that more closely mimic the structures and functions of HMOs are needed for clinical trials to determine their bioactivities, efficacy, and tolerability in humans. As structures of oligosaccharides from a variety of potential sources are identified and quantitated, new sources and methods for their recovery will emerge.

Current status of dairy industrial processing techniques for functional molecules

In addition to the scientific challenges around identification and quantitation, commercial extraction of functional molecules from milk has largely been limited by lack of economically feasible large-scale isolation technologies and methods. Yet industrial adoption of larger-scale methods for isolation of functional bovine milk components could lead to improved infant formulas or other therapeutic applications. Current processes to fractionate and purify functional molecules (including oligosaccharides, glycolipids, glycoproteins, and peptides) from dairy sources at laboratory-scale include cream separation, reverse phase, ion-exchange, and affinity chromatography, gel and capillary electrophoresis, selective precipitation, and membrane filtration. Low productivity, large effluent production, product degradation, and operational complexity have stalled commercial adoption of many laboratory fractionation/enrichment methods.

Membrane filtration is used most frequently by industry for the fractionation and enrichment of proteins-, peptides-, and oligosaccharides fractions (De Moura *et al.*, 2011b; Korhonen and Pihlanto, 2003; Martinez-Ferez *et al.*, 2006; Zydney, 1998). Membrane technology has also been widely used for isolation and fractionation of whey proteins in the dairy industry since the early 1970s (Cheryan, 1998; Pouliot, 2008). Stepwise filtrations using different pore size membranes have been used to separate numerous milk components according to their size (Ramchandran and Vasiljevic, 2013). Membrane-based separations can be effectively and economically implemented at large scale, which is necessary for most industrial applications (Zydney, 1998). Membrane microfiltration is often used in dairy applications to remove milk fat (Maubois, 2011). Microfiltration is also used to filter bacteria enabling the production of milks with extended shelf life (Elwell and Barbano, 2006). Ultrafiltration has been used to recover and fractionate whey proteins and casein micelles from milk, and the combination of ultra- and nanofiltration has been used to recover oligosaccharides (Cheryan, 1998; Goulas *et al.*, 2003; Zydney, 1998). Application of membrane separation technology in the dairy industry improves existing processing lines. The possibility of recovering previously lost compounds with specific and known bioactivity enables development of new products while reducing pollution, thereby enhancing process efficiency, profitability, and environmental stewardship (Rosenberg, 1995).

Purification of extracted functional molecules is an essential component of downstream processing. The high cost of some solid-phase extraction techniques has hindered the scale-up of LC for large-scale molecular purification. Ongoing innovations are helping to make these techniques economically feasible in the near future (Scoma *et al.*, 2012). Attempts to improve the feasibility of large-scale chromatography through regeneration and reuse of both solid-phase materials and solvents are ongoing and will be critical to enable future scale-up of this technique (Scoma *et al.*, 2012). Scientific advances that promote the creation and production of safe and easy to handle columns, optimized for high throughput yet capable of utilizing different resins, all at a broad range of scale, will surely propel the bioprocessing fields and industries forward.

Case Study, Sustainable Bioguided Processing II: Pilot-Scale Extraction of Functional Molecules from Cheese Whey

Once known as a major pollutant of waterways, bovine cheese whey is now recognized as a pool of valuable bioactive compounds. Increasingly, knowledge of whey bioactive compounds is transforming whey from a pollutant and source of inexpensive animal feed to a source of functional compounds that can increase the health and personalization values of foods and ingredients.

Although WPC and WPI are the two major industrial processing recoveries of whey (Ramchandran and Vasiljevic, 2013), it is now known that use of high temperatures within these traditional whey processing methods has been linked to reduced product functionality, opening up the opportunities to use membrane technology as a more forgiving processing method (Marcelo and Rizvi, 2008). Whey processing filtration techniques currently includes microfiltration for fat and microorganism removal as a pretreatment of whey for the manufacture of WPC and WPI; ultrafiltration to recover and fractionate whey proteins; and nanofiltration and reverse osmosis to concentrate and demineralize whey and whey permeates (Ramchandran and Vasiljevic, 2013).

The production of WPC by membrane filtration leaves behind a permeate that contains oligosaccharides and naturally occurring peptides. Currently, this fraction is mainly utilized as a source of lactose or disposed by the manufacturer, so this current waste stream holds great potential for dairy industry recovery of functional molecules. A general schematic for possible future industrial-scale applications for isolation and fractionation of functional milk molecules such as oligosaccharides, glycoproteins, and glycolipids and from bovine milk is presented in **Figure 2**. After pasteurization, residual lipids are separated from whey by centrifugation in a cream separator (Cheryan, 1998) (1). Once the lipids are removed, skim whey is further subdivided (2) by a 10 kDa membrane to capture whey proteins. After the proteins are removed, lactose is hydrolyzed (3) into glucose and galactose to prevent capture of lactose in the nanofiltration membrane. Nanofiltration (4) of the lactose-hydrolyzed whey permeate yields a solution with oligosaccharides, peptides, and some mineral salts in the retentate while glucose, galactose, and most mineral salts pass through the membrane into the permeate. This clean permeate solution can be used as fermentation and growth media. Lipids can potentially be further fractionated from cream to obtain a selective enrichment in glycolipids. Solvent extraction (5) can be used to fractionate acidic glycolipids from neutral lipids (Svennerholm and Fredman, 1980). Further purification of glycolipids can be achieved with reverse-phase chromatography. Reverse phase chromatography can also be employed at large-scale to remove other components from the glycolipids and generate enough purified glycolipids for *in vitro* studies. Whey proteins are not all glycosylated so additional steps of fractionation are necessary if increased purity is desired. Proteins can be precipitated (6) by adding ethanol; ion exchange chromatography and lectin-affinity chromatography can be used to recover glycosylated proteins (Saito *et al.*, 1991). Oligosaccharides in the nanofiltration retentate are further purified (7) from

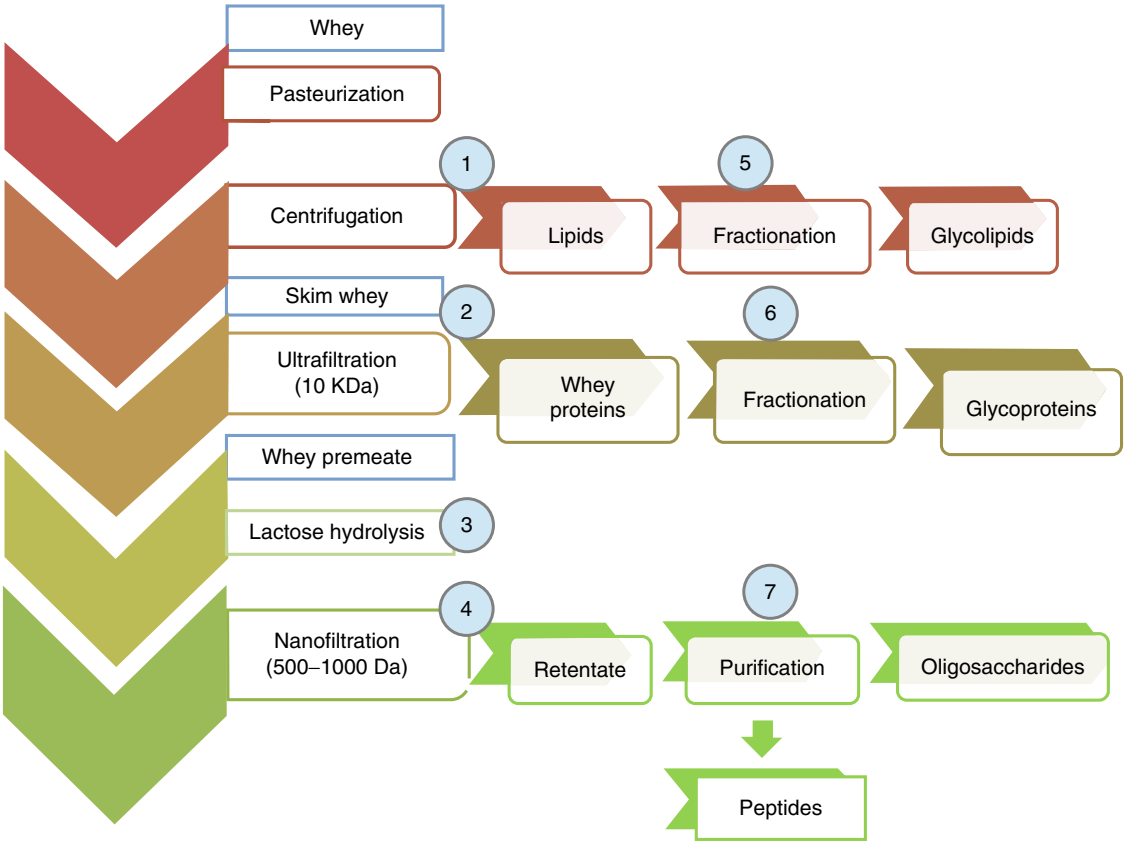


Figure 2 Processing the workflow for whey bioactive component extraction. (1) After pasteurization, residual lipids are separated from whey by centrifugation in a cream separator. (2) Once the lipids are removed, skim whey is further subdivided by a 10 kDa membrane to capture whey proteins. (3) After the proteins are removed, lactose is hydrolyzed into glucose and galactose to prevent capture of lactose in the nanofiltration membrane. (4) Nanofiltration of the lactose-hydrolyzed whey permeate yields a solution with oligosaccharides, peptides, and some mineral salts in the retentate while glucose, galactose, and most mineral salts pass through the membrane into the permeate. This clean permeate solution can be used as fermentation and growth media. Lipids can potentially be further fractionated from cream to obtain a selective enrichment in glycolipids. (5) Solvent extraction can be used to fractionate acidic glycolipids from neutral lipids. Further purification of glycolipids can be achieved with reverse-phase chromatography. Reverse-phase chromatography can also be employed at large-scale to remove other components from the glycolipids and generate enough purified glycolipids for *in vitro* studies. Whey proteins are not all glycosylated so additional steps of fractionation are necessary if increased purity is desired. (6) Proteins can be precipitated by adding ethanol; ion exchange chromatography, and lectin-affinity chromatography can be used to recover glycosylated proteins. (7) Oligosaccharides in the nanofiltration retentate are further purified from monovalent salts and monosaccharides resulting from lactose hydrolysis by applying continuous or batch diafiltration.

monovalent salts and monosaccharides resulting from lactose hydrolysis by applying continuous or batch diafiltration (Goulas *et al.*, 2002).

Improvements in separation technology

Although ultrafiltration has been extensively used to concentrate proteins, its use as a fractionation technique for proteins of similar size has been hindered by low selective separation.

Diafiltration, the addition of water to wash microsolutes from the retentate, increases the purity of macromolecules retained in the retentate. Development of multistage, continuous operations using robust membrane systems, alternate membrane configurations, and diafiltration have contributed to the recent success of this technology in the dairy industry (Cheryan, 1998). Glycoproteins from whey protein concentrate can be isolated from the whey or casein protein fractions at industrial scale by traditional chromatography techniques. The application of positively charged membranes to separate proteins from cheese whey improved fractionation selectivity by more than 600% when compared with uncharged membranes (Bhushan and Etzel, 2009). Charged membranes show promise in fractionating proteins with similar size but different isoelectric points at specific pH and ionic strength (Arunkumar and Etzel, 2013; Bhushan and Etzel, 2009). This exciting area of research holds promise for advancements in membrane life-time, efficacy of ligands based on processing time, and resistance to cleaning procedures. All of these processing variables will help determine economic feasibility for future industrial adoption.

When higher levels of purification are required, industrial-scale application of ion-exchange chromatography could be the best choice, for example, for lactoferrin isolation (Law and Reiter, 1977).

The major challenge of oligosaccharides purification from cheese whey is enriching the oligosaccharide fraction while reducing the content of lactose and other simple sugars that lack selective prebiotic activity. Lactose removal is important for oligosaccharide bioactivity studies because, due to its predominance in whey, it can confound functional studies on the biological activity of oligosaccharides. Among the small-scale processes to produce oligosaccharide-rich fractions reported in the literature, an inexpensive and scalable approach to recover biologically active oligosaccharides from milk was developed (Sarney *et al.*, 2000). Sarney and colleagues have investigated the use of combined lactose enzymatic hydrolysis with a two-step filtration (ultra- and nanofiltration), followed by diafiltration in order to remove the monosaccharides and residual lactose. This approach enabled a significant enrichment of the retentate in oligosaccharides: more than 50% of goat milk's free oligosaccharides were recovered.

Examining the Health Benefits of Cheese Whey Components

Whey contains several classes of bioactive molecules. In addition to previously mentioned oligosaccharides, whey contains bioactive glycolipids, glycoproteins, and peptides. Glycolipids are lipid molecules that are decorated with sugar residues. Similarly, glycoproteins differ from regular proteins because of the oligosaccharide residues that form a coat around specific regions of the protein. This glycan coat differentiates glycolipids and glycoproteins from their nonglycosylated molecular brethren in terms of their bioactivity, as well as the methods scientists must use to detect, isolate, characterize, and quantify these molecules. Free floating peptides found in whey also exhibit important health conferring bioactive properties, and require special isolation and quantitation methods to accurately associate their unique structures with bioactivities.

Health benefits of oligosaccharides

In addition to guiding the development of the human intestinal microbiota, by promoting growth of commensal organisms and protecting infants from a variety of pathogenic and inflammatory conditions, HMOs provide myriad functions including modulating the immune system, enhancing cognitive development, and providing protection from toxins and pathogenic diseases (Kunz *et al.*, 2000; Newburg, 2001; Newburg *et al.*, 2004; Reinhardt *et al.*, 2009).

The ability of HMOs to support the competitive overgrowth of protective *Bifidobacterium infantis* within the intestine is at the core of its value to infants. Bifidobacterial colonization of the gut protects the infant by lowering the pH and reducing accessibility via spatial inhibition (Urashima and Taufik, 2010). Furthermore, bifidobacteria are protective because they are involved in fighting infections caused by bacterial pathogens (Sakata *et al.*, 2005; Thibault *et al.*, 2004). Consequently, a bifidobacteria-dominated microflora may decrease the risk of gastrointestinal diseases. Additionally, evidence suggests that the presence of beneficial intestinal microbiota during the first few weeks of life is important for the development of the immune system (Eiwegger *et al.*, 2004; Martino *et al.*, 2008; Sudo *et al.*, 1997). The proposed mechanism for this immune support is that specific bacteria interact with immune cells in the intestines, increasing cytokine and antibody production (reviewed by Seifert and Watzl, 2007). Lower levels of *Bifidobacterium* species during the neonatal period are associated with increased risk for allergic diseases (Björkstén *et al.*, 2001; Kalliomäki *et al.*, 2001; Sepp *et al.*, 1997). From a genomic prospective, bifidobacteria represent a remarkable example of coevolution because they contain a cassette of genes encoding glycosidases capable of metabolizing HMOs (Sela and Mills, 2010). Mammalian evolution likely selected for this specific group of bacteria based on the genes required to degrade complex oligosaccharides.

Approximately 200 oligosaccharides have been identified, of which nearly 100 are now fully characterized structurally (Tao *et al.*, 2011, 2010; Wu *et al.*, 2010a,b). Linking the precise complex structural characterization of each of these carbohydrates with their multitude of biological functions is an area of ongoing investigation.

In addition to stimulating beneficial microflora, HMOs also inhibit pathogenic bacteria in the gut. Recent research suggests that breastfed infants of mothers who produce specific HMO are protected against diarrhea (Morrow *et al.*, 2004). HMO containing fucose and sialic acid share common structural motifs with glycans on the infant's intestinal epithelia known to be receptors for pathogens. Such structures imply that their presence in milk provides a defensive strategy by acting as decoys to prevent binding of pathogens to

epithelial cells, thereby protecting infants from disease (Newburg *et al.*, 2005). Oligosaccharides containing α1,2-linked fucose (Newburg, 2009; Newburg *et al.*, 2005) or terminal NeuAcα2,3 Gal residues (Bouchara *et al.*, 1997; Stins *et al.*, 1994) block specific pathogens from binding to the intestinal epithelium.

The ability to metabolize HMO is not exclusively restricted to bifidobacteria. *Bacteroides fragilis* and *Bacteroides vulgatus* also exhibit *in vitro* growth on HMO (Marcobal *et al.*, 2011). Interestingly, the ratio of Bacteroidetes to Firmicutes has been associated with the prevention of obesity (Jumpertz *et al.*, 2011; Turnbaugh *et al.*, 2009). Firmicutes dominate over Bacteroidetes and Actinobacteria in the gut of obese children and adults (Armougom *et al.*, 2009); and the proportions of Firmicutes and Bacteroidetes are significantly greater in obese compared with normal weight adults (Abdallah Ismail *et al.*, 2011). Children maintaining a normal weight have greater populations of bacteria from the phylum Actinobacteria, especially bifidobacteria, in infancy compared with children becoming overweight (Kalliomäki *et al.*, 2008). An increasing number of studies report strong correlations between altered microbial composition and development of metabolic diseases and obesity (LoCascio *et al.*, 2010; Serban, 2011). These investigations suggest that anomalous development of the microbiota early in life may be associated with metabolic dysregulation later on; therefore, manipulation of the gut microbiome by prebiotic supplementation in childhood may be an effective way to improve human health. Using prebiotics to modulate the microbiota is a novel research direction for treatment of obesity.

Because oligosaccharides were discovered in whey permeate only recently, most of the *in vitro* research on oligosaccharides to date has been performed with small amounts of oligosaccharides isolated from human milk at the lab scale (LoCascio *et al.*, 2010; Ward *et al.*, 2006). Investigating the catabolism and fermentation of HMO by bifidobacteria has revealed that some strains of bifidobacteria have unique capabilities, and thus preference for consumption of specific oligosaccharides (LoCascio *et al.*, 2010). Additionally, the presence of sialic acid and fucose in terminal positions act as a shield, thus rendering HMOs inaccessible to intestinal bacteria that do not possess the necessary enzymes (glycosyl hydrolases) (Marcobal *et al.*, 2010).

Genomic analysis of *Bifidobacterium infantis* and *Bifidobacterium bifidum* – two related strains that grow well on HMO – revealed distinctive gene clusters that are specifically induced during growth on HMO (Sela *et al.*, 2011; Sela and Mills, 2010). *In vitro* studies with cell-lines demonstrated that HMOs enhance bifidobacteria persistence in the gut by improving the integrity of intestinal barrier function via regulation of tight junction proteins (Chichlowski *et al.*, 2012).

Recent research also demonstrates that in a mouse model, sugar-specific consumption by bifidobacteria, as well as bacterial production of acetic acid, improves intestinal barrier function (Fukuda *et al.*, 2011).

Antiadhesive activity of free HMO has been described for *Vibrio cholera* (Coppa *et al.*, 2006), *Salmonella fyris* (Coppa *et al.*, 2006), enteropathogenic (Coppa *et al.*, 2006) and enterotoxigenic (Morrow *et al.*, 2005), *Escherichia coli*, *Streptococcus pneumonia* (Andersson *et al.*, 1986), and caliciviruses (Morrow *et al.*, 2005). Because HMOs are excreted in urine of breast-fed infants, it is likely that small amounts of oligosaccharides are absorbed intact from the gastrointestinal tract and end up in the systemic circulation (Obermeier *et al.*, 1999; Rudloff *et al.*, 1996); thus pathogen inhibition by oligosaccharides may occur at parts of the body other than the intestines. Similar to HMOs, BMOs have been shown *in vitro* to block adhesion to target cells, of seven enterotoxigenic *E. coli* strains isolated from diarrheal calves (Shabana *et al.*, 2013; Shabana *et al.*, 2013) and *Neisseria meningitides* (which causes meningitis and septicemia) (Hakkarainen *et al.*, 2005). Furthermore, 3′-Sialyllactose (NeuAc(α2–3)Gal(β1–4)Glc) – a major constituent of both BMO and HMO – inhibits the binding of *Helicobacter pylori* to human duodenal cancer cells (Simon *et al.*, 1997, p. 199).

Milk oligosaccharides have also been shown to have antiviral actions. Some HMO bind to the dendritic cell-specific ICAM3-grabbing integrin (DC-SIGN) and block adhesion of HIV-1 by its gp120 protein (Hong *et al.*, 2009). Binding of gp120 to DC-SIGN is essential for the virus to enter the dendritic cell, from where it is passed to T cells (Hong *et al.*, 2009). The oligosaccharide blocking of DC-SIGN binding sites may be partially responsible for the low risk of HIV-1 transmission through breastfeeding (Hong *et al.*, 2009).

Clinical studies on the oligosaccharides' potential to modulate the gut flora, to affect different gastrointestinal activities and to influence inflammatory processes are still lacking, as the large amounts of milk oligosaccharides needed are not available yet. Implementation of these activities resulted in the first human trial conducted using purified BMO extracted from cheese whey (ClinicalTrials.gov Protocol Record 264294). The bifidogenic effect of human milk has been recently shown both by characterization of oligosaccharides in breast-fed infant feces and by the study of intestinal microflora. Several studies demonstrate that oligosaccharides withstand the pH of the stomach and resist enzymatic digestion in the gastrointestinal tract (Boehm and Stahl, 2007; Gopal and Gill, 2000). Some HMOs are absorbed and then excreted into the urine intact, implying that inhibition of intestinal and urinary pathogens by HMOs is quite likely in breast-fed infants (Chaturvedi *et al.*, 2001). Breast-fed infants compared to formula-fed infants are at a lower risk of gastrointestinal disease, respiratory disease, and other infectious diseases, and have chances of a better development of their gastrointestinal tracts and immune systems (Lawrence and Pane, 2007; Newburg, 2005; Pabst *et al.*, 1997). The studies purport that milk bioactive molecules are likely to be beneficial for human health not only in a short-term manner, but throughout life.

Health benefits of glycolipids

Glycolipids are ubiquitous components of animal cells and are abundant in the apical membrane of the epithelial cells of the intestinal tracts (Simons and van Meer, 1988). The acquisition of glycolipids through the diet may be an important contributor to health because of their interactions with bacteria. Glycolipids are found in milk fat and can also be extracted from whey cream and whey buttermilk (Lee *et al.*, 2013). Moreover, glycolipids may have an important role in the promotion of intestinal immunity development (Rueda, 2007).

Glycolipids are thought to play an important role in cell self-recognition (Yamakawa and Nagai, 1978). They are also the site at which many pathogens bind and attack human cells (Fantini *et al.*, 2000; Otnaess *et al.*, 1983). When milk fat globules are secreted, they are completely coated with the cellular bilayer membranes of the epithelial cells of the mammary gland. As a result, milk and particularly the milk fat membrane is considered to be rich in glycolipids. However, the specific benefits of glycolipids are unclear, and their role in milk continues to be a subject of research.

Ingestion of milk glycolipids may contribute to the prevention of infection and immunity (Rueda, 2007). Glycolipids act as pathogen decoys, which compete for pathogen binding sites and block pathogens from binding to their host cell receptors in the mucosa (Idota and Kawakami, 1995). The binding of the different bacterial pathogens to their ganglioside receptors is structure-specific. Human milk gangliosides inhibit the growth of *E. coli* and *V. cholera* enterotoxins (Otnaess *et al.*, 1983). Milk gangliosides are also known to inhibit the adhesion of *E. coli* to human intestinal carcinoma cells. Another notable aspect is the ability of gangliosides to modulate the development or behavior of cells of the immune system. Recent research also reported a specific effect of GM3 and GD3 on dendritic cell maturation suggesting a role for these milk glycolipids (especially ganglioside GD3) in modulating the process of oral tolerance during the first stages of life (Brønnum *et al.*, 2005).

Along with milk oligosaccharides and glycoproteins, glycolipids act as prebiotics. Ganglioside-supplemented infant formula has been reported to modify the intestinal ecology of preterm newborns, increasing the bifidobacteria content and lowering that of *E. coli* (Rueda *et al.*, 1998). In addition, the influence of dietary gangliosides on several parameters related to the development of the intestinal immune system, such as cytokine and intestinal IgA production, has also been described in animal models (Vazquez *et al.*, 2001). Animal studies demonstrate that inflamed intestinal mucosa has fewer gangliosides than healthy intestinal mucosa (Park *et al.*, 2007). Accelerated catabolism of gangliosides in the intestine increases proinflammatory signaling, inflammatory markers, and susceptibility to pathogens. Dietary gangliosides are able to replace the mucosal gangliosides that are progressively degraded in inflammatory conditions (Miklavcic *et al.*, 2012). Restoring proper ganglioside abundance and function in the intestine could resolve inflammation, increase resistance to infection, and improve gut integrity to induce remission of conditions like necrotizing enterocolitis, inflammatory bowel diseases, and Crohn's disease (Miklavcic *et al.*, 2012). Most of the clinical studies used glycolipids from whole animal organs (i.e., brain); however, the biological issues associated with extracts of brain tissue from any source preclude its use in routine food applications without exhaustive safety testing. Bovine colostrum contains high levels of gangliosides and is, therefore, an ideal source to extract pure gangliosides that are analogous in structure to the gangliosides present in the intestinal mucosa (Lee *et al.*, 2013).

Health benefits of glycoproteins

The most abundant whey proteins are β-lactoglobulin and α-lactalbumin, representing approximately 70% of the total protein content of whey. However, whey also contains low abundance glycosylated proteins like lactoferrin and lactoperoxidase that display interesting bioactive properties. Several authors have demonstrated an array of glycoproteins bioactivities including antioxidant, antibacterial and antiviral action, as well as immunomodulation, which contribute to the increased populations of commensal organisms in intestinal microbiota (Legrand *et al.*, 2005; Lonnerdal and Iyer, 1995; Orsi, 2004; Seganti *et al.*, 2004). Lactoferrin appears to protect the intestinal cells against viral or bacterial gastroenteritis. Lactoferrin can target immune cells, including lymphocytes and macrophages and has the apparent ability to modify their function (Ward *et al.*, 2002). This glycoprotein may also be implicated in the inhibition of proinflammatory biomolecules such as cytokines (Sanchez *et al.*, 1992).

The ability of glycoproteins to behave as simple prebiotics is well-documented; however, precise determination of functional components (protein and the glycan) relative to enrichment of specific bacterial populations remains a topic of inquiry. Glycan structure determination offers another dimension for characterizing the relationship between structure and function of the protein. Characterizing and quantifying the relative contributions of varied functions of glycosylation on individual milk and whey proteins remains a significant challenge.

For example, bovine lactoferrin, a multifunctional glycoprotein in milk, contains four N-glycosylation sites, whereas human lactoferrin contains only two sites. *In vitro* studies show that lactoferrin absorbs iron, inhibits bacterial growth, and enhances the growth of commensal bacteria (Sanchez *et al.*, 1992). As glycosylation of human lactoferrin varies significantly within human lactation (Marcobal *et al.*, 2011), association of glycosylated molecular species with consumption of specific bacteria remains unknown.

The first step of microbial infection *in vivo* is the interaction of glycan from the epithelial surface of the host with bacterial adhesin that will bind the glycoproteins present at the cell surface. Recent studies support the hypothesis that glycans linked to milk protein may help protect against microbial attacks (Farnaud and Evans, 2003). Emerging evidence shows that protein-linked glycans protect intestinal mucosa by inhibiting the attachment pathogens, thereby protecting infants from gastrointestinal infection. By inhibiting bacterial growth and attachment to the epithelial cells, lactoferrin has been shown to exhibit antimicrobial activity against, *E. coli*, *Listeria monocytogenes*, *S. pneumonia* (Murdock and Matthews, 2002; Yekta *et al.*, 2010). Lactoferrin's antimicrobial activity has been shown to be related to the amino acid chain (Farnaud and Evans, 2003), but a role for the carbohydrate chain can be speculated. Lactoferrin can also exhibit a protection against bacteria due to its iron binding capability. The protein limits bacterial growth by making iron unavailable. Other mechanisms are involved in the antimicrobial activity of lactoferrin, including binding to bacterial and mammalian cell receptors to block the adhesion of pathogens (Valenti and Antonini, 2005). However, not all mechanisms have been well elucidated, including the role of the glycan part in protein function.

Recent *in vitro* studies indeed revealed that the glycan part of human lactoferrin decreases *Salmonella* infections of

cultured human intestinal epithelial cells (Caco-2 cells) (Barboza *et al.*, 2012). *Salmonella* is one of the most common pathogens infecting humans. It appears that specific monosaccharides such as fucose may play a specific role in inhibition of epithelial adhesion of this pathogen. Senkovich proposed the structure of a human lactoferrin complex with pneumococcal surface protein A, as one possible microbial defense mechanism (Senkovich *et al.*, 2007). Mucin 1 and 4 (known milk proteins) inhibit the binding of enteric bacteria to intestinal epithelial cells FHs 74 Int (derived from normal human fetal intestine) and Caco-2 (derived from human colon adenocarcinoma; Liu *et al.*, 2012). Whey glycoproteins may therefore represent a therapeutic source against infant infection caused by *Salmonella* as well as other pathogens.

Infant supplementation with bovine lactoferrin revealed a decrease of digestive tract infection and chronic infection caused by *Giarda* species in infants (Ochoa *et al.*, 2008, King *et al.*, 2007).

Health benefits of peptides

A large number of milk peptides produced by *in vitro* proteolysis have been found to be functional beyond their simple nutrient provision as amino acids (Dallas *et al.*, 2012). Activities of milk peptides include immunomodulation (Jørgensen *et al.*, 2010; Migliore-Samour *et al.*, 1989), opioid-like activity (Brantl, 1984; Kampa *et al.*, 1996), antimicrobial action (Aniansson *et al.*, 1990; Liepke *et al.*, 2001; Strömqvist *et al.*, 1995), and probiotic action (Azuma *et al.*, 1984, p. 198; Bezkorovainy *et al.*, 1979; Liepke *et al.*, 2002). These peptide fragments are not functional when constrained in the context of intact milk proteins (Schanbacher *et al.*, 1997). Site-specific proteolysis releases these enjoined fragments. The best described example is the *in vitro* digestion of human lactoferrin protein: the gastric digestion of this molecule operated by the enzyme pepsin peptide fragment lactoferricin that has potent and specific bactericidal properties (Bellamy *et al.*, 1992). Most of these peptides are not naturally occurring – they were produced by *in vitro* digestion, some with the goal of recreating peptides that would be produced in digestion.

There is currently no clinical research on naturally occurring peptides from human or bovine milk. However, peptides produced by *in vitro* digestions of several milk proteins (mostly the caseins) have been analyzed in a few *in vivo* models. The ensemble of naturally occurring peptides in human milk inhibits growth of *E. coli* and *Staphylococcus aureus* in plate-based radial diffusion assays (Dallas *et al.*, 2013a,b). This article represents the only study of the *in vitro* actions of naturally occurring milk peptides. A large body of work, however, exists on the *in vitro* actions of *in vitro* digested products from purified milk proteins (largely the caseins). These studies have shown a variety of *in vitro* actions including antimicrobial (Liepke *et al.*, 2002, 2001), immunomodulatory (Jørgensen *et al.*, 2010; Migliore-Samour *et al.*, 1989), and opioid agonist/antagonist actions (Brantl, 1984; Kampa *et al.*, 1996). For example, *in vitro* digests of purified human milk lactoferrin promote the growth of bifidobacteria (Liepke *et al.*, 2002). This function further supports the glycan-based prebiotic effects of milk. However, it is not known whether the effectiveness and selectivity is enhanced when these peptides are glycosylated. Bovine lactoferrin hydrolysates produced by pepsin digestion were shown to protect against foodborne pathogens, such as *Salmonella*, *E. coli*, *L. monocytogenes*, and *St. aureus*, in an *in vitro* assay (Murdock and Matthews, 2002). Both human and bovine lactoferricin have been shown to have activity against the human papillomavirus, a known risk factor for cervical cancer (Mistry *et al.*, 2007). These peptides may affect the gut, intestinal epithelium, and the immune system, but the required *in vivo* studies have not yet been carried out.

Effective separation from bovine milk processing streams of the aforementioned biomolecules, combined with evidence of their health benefits, is leading to new classes of bioactive food ingredients. Current research suggests that concentrating certain bioactives from whey permeate can be a cost-effective process for the valorization of whey permeate into high quality, profitable novel dairy ingredients. Given the massive quantities of bovine dairy streams available for capture worldwide, large-scale production is possible with current technologies. Although bioactives in whey are less abundant than in breast milk, existing manufacturing capabilities based on membrane filtration and chromatography will make it possible to isolate these components in enough quantities to carry on the needed studies for clinical validation. These lines of research set the stage to enhance and improve existing prebiotics by translating the evolutionarily linked beneficial association between human milk and their associated beneficial bifidobacteria.

Conclusion and Future Directions

For many years bovine milk was considered a nonviable source for human milk-like glycans because they were thought to be simpler than human milk. The study of glycosylation on protein and lipids was hindered by inherent complexity and low abundance. Low abundant bioactive molecule discovery and recovery is now made possible by modern chemical analytical techniques like mass spectrometry. These high-tech methods provide windows through which compounds can be discovered, characterized, and quantified. Bovine whey provides a model for the ways in which many food processing streams can be interrogated and mined. With massive amounts of agricultural byproducts available worldwide, the process of identification, extraction, and delivery of health-promoting bioactive molecules from these streams hold great promise for the future of food process engineering. Assembly of the molecular fingerprints bioactive compounds into food- and organism-specific spectral libraries is hastening the process by which new compounds can be identified. As libraries are built, bioactive molecules are identified and isolated, and their efficacy and tolerance proved out through clinical and laboratory testing, the process of building knowledge bases about bioactive molecule sources and appropriate uses are further enabled.

Databases of bioactivity are being developed, but standardized infrastructures for annotation, integration, query, and reporting on aggregate knowledge about bioactive chemicals, their food sources, physical properties, bioactive mechanisms, and efficacy/tolerance in individuals

remain to be built. Building semantically integrated on- and off ramps for access to data within each knowledge domain along the food-to-health information superhighway has the potential to collapse the bioactive ingredient development life cycle, propelling related fields forward. Collapsing the food ingredient product development life-cycle effectuates quicker delivery of innovative food products for personalized health improvement. Utilizing such information stores in bioguided analysis and design of agriculture and food processing side streams can transform waste into value-added products, reduce disposal costs, lower the environmental impact of these waste streams, and improve the health of the population.

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See also: Consumer-Oriented New Product Development. Energy and Greenhouse Gases Footprint of Food Processing. Food Engineering. Food Safety: Food Analysis Technologies/Techniques. Investments in and the Economic Returns to Agricultural and Food R&D Worldwide. Virtual Water and Water Footprint of Food Production and Processing. Vitamins and Food-Derived Biofactors

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Domestication of Animals

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Introduction: What is Domestication?

The subjugation of fire, the invention of the plow, and the domestication of animals would seem to be the springboard for the rapid explosion of civilization that started nearly 10 000 years ago. However of the three, only the last one involves a collaborator. In the development of tools, like the fire and the plow, our species can claim almost all the credit; but the domestication of animals? That takes a willing collaborator. The process, some might say the 'invention,' of domestication would fail to succeed unless there was benefit to both the people involved and the animals asked to join our community. A topic of endless fascination and speculation, the domestication of animals will always be of interest. It is a process and force for the coevolution of species, a force that continues to shape life on this planet.

However as the plow is considered as an important invention (Pryor, 1985), an obvious question arises. If we wish to till the earth, where does the strength come to do so? And that is where the need to consider the entry of domesticated animals; a source of power and strength, a component of work. As will be seen, though there are a myriad of uses for animals today, such as food, clothing, entertainment, research, and companionship, ancient societies did not domesticate animals for what might be thought to have been their most obvious purpose – food. It is doubtful that our ancestors began this process by thinking: "perhaps we can make yogurt," and then domesticated cattle, horses, and sheep to meet that desire. Instead domestication seems to have moved from initial desires for power and entertainment, perhaps even an element of "can I do this," to all the impacts we see today (Bulliet, 2005). Indeed, as seen during the investigation of the first domesticated animal, the dog, there may have been no goal at all, just a gradual process that was not deliberate or of any conceived direction (Clutton-Brock, 1995).

Herein is outlined this fascinating journey, covering the 'when' of domestication, the 'where,' the 'how many times' and when possible the 'how' it was done, or the 'why' was this undertaken. Then considered are the impact of this important invention, the impact on the animals, and of course the impact on us. Ideally, in this article, there will be a meaningful blend of general principles and specific examples.

Where to begin? Perhaps, it is best to start this journey with a definition to provide a concrete identity of the topic that is explored. The most comprehensive definition is that of Price (Price, 1999): A domestic animal is one that is bred in captivity for purposes of economic profit to a human community that maintains mastery of breeding, territory, and food supply. A fundamental component of this concept is one of genetic change. Domesticated animals are different from their wild ancestors. The human control of breeding has made it so. At the heart of this distinction is the human construct of breed. Therein lies the key distinction between domesticated animals and tamed or captive ones. Animals we domesticate are the ones we control, and in that control we choose parents and mates with a direction in mind. Over the course of time, that continued pressure of selection gradually but measurably changes the animal and its genome. This is the essence of animal breeding, and it is a key distinction in the creation of domesticated animals.

Though this definition is comprehensive in its description of the animal, a final element that may be missing is the recognition that this process involves mutual change. One is reminded almost every day that the animals have changed, just look at the distance between wolves and dogs. However, what is often overlooked is how we are different from our agricultural ancestors. Domestication changed us, and continues to change us. Seeing this as a process of coevolution is critical to our understanding. The *Homo sapiens* of 12 000 years ago are not the *Homo sapiens* of today. Moreover, a sliver of that difference can be traced to our evolving relationship with the animals we brought along with us on this journey. The aspects as to how and why this happened is considered now.

Species of Domesticated Animals

Though clearly an important and fascinating question, no one who has ever thought about the 'when and where' of domestication should expect a definitive concrete answer. How could there be? This process was not only undocumented by our ancestors but it is also not a yes/no process. Domestication, and the acceptance of animals as partners in our lives and survival, has been a gradual process. A little more each day, a little closer each year, a bit more dependent as a society advances. It is not unlike asking 'when and where did modern humans begin.'

Nevertheless, there are some tell-tale signals of where and when this process began. For the evidence, both genetic and archeological data point to the same general time regardless of location; the end of the last ice age, some 12 000 years ago. Throughout this article, the unit of time has been kept consistent, regardless of the measure used in any original article cited. That unit, BP, for Before the Present, is typically a measure based on radiocarbon dating, using AD 1950 as the base year of calculation. In source articles, readers may find the notation of BC, for Before Christ, or the now preferred BCE, for Before the Common Era. There are yet other authors who define events with terms such as the 'fourth millennium BC.' Using the author's notation above, the author using this phrase would be referring to a time period from 4000–3000 years BC, or from 5950–4950 years BP.

The accumulation of evidence from three broad geographic regions is considered: the Near East, the Far East, and Mesoamerica, extending as far south as present day Peru. This oversimplified description includes the domestication of cereal grains in the Near East dating to 9000 years BP, the domestication of maize in the Tehuachan Valley of present day Mexico

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more than 5000 years BP, and rice cultivation in the Far East some 7000 years BP (Bar-Yosef, 2012; Harris, 2012).

Realizing this represents a considerable swath of time, it is nevertheless interesting to address the comparative simultaneity of agricultural development across the ancient world. Why did agriculture begin at this time? Did the idea travel? Did people in one area suggest this process to their neighbors and 'bring' domestication with them? Or did indigenous people arrive at this invention on their own? Anthropologists now seem to prefer the last alternative (Bellwood and Oxenham, 2008; Cauvin and Watkins, 1994) that as the climate change of the ending Pleistocene era advanced, the rapidly changing biology surrounding human communities almost 'pointed' to humans exploiting this bounty. Still, the transition from nomadism and the hunter/gatherer to sedentism and farming was hardly revolutionary (Lewin, 1988). The process was slow, with fits and starts, failures and limited success along the way. Nevertheless, eventually a transition was made, a transition from which turning back to the past life of hunting and gathering was not possible. Moreover, once that line had been irrevocably crossed, the long process of identifying, subduing, taming, and eventually domesticating animals began.

The list of domesticated animals is remarkably short. Although the list of candidates would appear impossibly long, the table of species that made the transition from wild to human dominated is limited. Among the large herbivorous mammals one would list sheep, goats, cattle, horses, pigs, camels, llamas, donkeys, water buffalo, and yaks. Other large herbivores that are considered domesticated are mithans, bali cattle, and reindeer. Among the birds that have been domesticated, the authors list chickens, ducks, geese, and turkeys. A handful of other animals that are considered domesticated would be dogs and cats, rabbits, mice and rats, and other rodents useful in laboratory work, and a small assortment of aquatic species useful as a food resource like trout, salmon, and catfish. In constructing this list, it is worth considering the earlier definition, along with an assessment of genetic change. In the end, domestication is about human needs and human goals. That is why, ultimately, the line between tame/captive and domesticated, though gray and blurry in some places, rests on the notion of 'breed.' Domesticated animals are constructed around the notion of breed, a population of animals with distinguishable, heritable characteristics.

Why then, is this list so short? Why are so few species called into service by human societies? This topic has been addressed by many authors (Budiansky, 1999; Diamond, 1997) and many competing ideas have been put forward as potential explanations (Anderson, 1998; Darwin, 1900; Sauer, 1969; Trut *et al.*, 2009). Nevertheless, a consensus is building around the exploitation of neoteny as the 'fuel' that drives the domestication process (Trut *et al.*, 2009). Neoteny is the expression of juvenile traits in adults of any species, essentially the juvenilization of the individual. In the context of animal domestication, the critical component of the process would be the exploitation of variation, especially genetic variation, in neotenic traits (e.g., food begging, reduced fear in confronting foreign species) expressed in older, more adult, individuals. To be able to approach, tame, and control undomesticated animals, these neotenic characteristics of behavior and anatomy would be part of any human's unconscious selection decisions. A series of now classic experiments in the fox demonstrated that selection for juvenile behavior traits produced correlated changes in the physiology and morphology of these now domesticated foxes (Trut *et al.*, 2009). Among the changes observed include floppy ears, curly tails, large eyes, shortened forehead, and a shortened muzzle. This exploitation of the variation in neoteny is now considered to play a similar role in the domestication of the dog (Wayne, 2001) and by extension to the other major species of domesticated animals, including livestock (Clutton-Brock, 1999; Driscoll *et al.*, 2009; Price, 1999).

So to answer, why these animals; apparently these are species that satisfy two essential requirements. They are species that offer some special benefit for human survival, and second, they possess the biological (including genetic) variation in neoteny permitting them to be manipulated and eventually domesticated by our human ancestors. It is thus a two-way street, we have the desire/need and the animal gives rise to the capacity to meet this need.

It is indeed an interesting marriage, one with a unique evolutionary history; a history with three dominant articles. The first article, the longest, is one spanning hundreds of thousands of years under the forces of natural selection imposed by evolution. This is an article where animals and humans led distinct lives, intersecting across the environments they both inhabited and the potential to relate as predator and prey. The second article, no more than several thousand years, spans the transition from wild to domesticated. This article is where the marriage began, and in which it has spent the most time. We are presently in the final, third article spanning little more than a handful of decades. However, it is in this article where we witness the intensive breeding and management practices inherent in modern animal agriculture. It has been in this most recent article that humans have exerted their most powerful pressure and in many ways tying our destiny to theirs. It is now examined what special characteristics are required to make it to this select group of species that has moved from the wild to a state of ownership by a human partner.

Common Principles of Domesticated Animals

A natural question to pose, having grasped the fundamental benefits and challenges of domestication, is to identify what characteristics of a species, beyond exploitable variation in neoteny, can lead to successful domestication. For after all, though there are thousands of potential candidates for domestication, only a relative handful can be included within the confines of the opening definition. "Though many have been called, few have been chosen." There are many candidate species, even to this day. Any list would have to include the American bison, any of the several species of zebra that still roam the African plains, even the elephant, might make lists of suitable candidates. Nevertheless moving these and other species, from candidate to an animal under complete human mastery, remains elusive if not impossible. What is it about the special species where we succeed in imposing our control that makes this process workable?

Diamond, among many others, has listed general criteria that appear to be helpful to the domestication process (Diamond, 1997; Jensen, 2002; Mignon-Grasteau *et al.*, 2005; Price, 1999). Though this list is hardly exhaustive, and exceptions can be identified throughout, this list can be helpful in providing a focal point for discussion. The areas to consider include diet, growth and development rate, captive breeding, disposition, tendency to panic, and social structure. Each of them will be considered individually.

Flexible Diet

The key component of this distinctive principle is competition with humans for food resources. Though there are exceptions (and dogs and cats are perhaps the most obvious), most domesticated animals do not compete directly with human beings for their nutritive needs. Indeed, one of the beneficial attributes of cattle, sheep, and goats is that as ruminants they complement human diets rather than compete (Pond *et al.*, 2005). It is not known whether at the time of domestication, or today, these livestock species are notable for their consumption of byproduct feeds. In the well-established agricultural systems of the developing agriculturalists of the Tigris–Euphrates river basin (Peters *et al.*, 2005), sheep and goats provided a much valued complement to the dry-land grain farming of this society. Put simply: humans ate the seeds, the animals ate the stalks, providing meat, milk, fiber, and manure in the process (Harris, 2012). Together, a viable and sustainable food production system was implemented, and indeed lasts to this day.

Dogs and cats are, of course, an exception, both animals being carnivores and thus more directly competing with their human owners for food resources. Of course, in the case of cats, it is their diet of vermin that makes them so valuable to human agricultural societies (Driscoll *et al.*, 2007). Protection of seed stores from the infestation of mice and rats makes the cat a valuable, if in theory competitive, companion. Dogs on the contrary provide no such simple niche explanation. Instead this closest of human–animal bonds needs more to explain it than simple dietary complementarity.

Contrasting the dog–human relationship with newly domesticated aquatic species like trout, catfish, and salmon are precisely the challenge this topic addresses (Wurts, 2000). The long-term sustainability of salmon culture, a top of the food chain aquatic predator, surely calls into question the wisdom of domestication. Regardless of the species-specific comments, it is clear that as a general principle, the diet of the potential domesticate is clearly among the first questions a would-be domesticator must address.

Growth/Developmental Rate

In today's agricultural economy, a market hog is expected to reach 100 kg of live body weight by 20 weeks of age. A market broiler can make it to 5 lbs by 7 weeks after hatching (Field and Taylor, 2012). Of course, the first domesticated ancestors of these animals did not grow at such accelerated rates. Nevertheless, domesticating elephants, or redwoods, is not a strategy for sustainable success in a society living in 12-month annual cycles. Domesticates must have the capacity for rapid developmental change; the capacity to move from young to economically advantageous in a relatively short time span. The species we raise today, like those cited above, surely satisfy this need. A similar mindset must have been present in our domesticating ancestors. The fruits of their labor, whether to develop a powerful animal 'machine' or to efficiently produce a desired resource, had to be a factor in their 'cost/benefit calculations,' however crude those calculations might have been by our standards today. Though by no means paramount, the notion of near-term return on investment had to have been a component of their 'domestication calculus.'

Human-Directed Breeding

This topic, the human control of breeding decisions of animals raised in human communities, hardly needs emphasis in the discussion for this concept is firmly embedded in the earlier definition of domestication. However, human control over breeding must be paramount in the domestication process. Without the control of which animals are entitled to become parents of the next generation, what is indeed the point of domestication? As one might expect, most species do not willingly forswear this control. The few species that have been domesticated seem to have several common attributes to their reproductive strategies, strategies that are now considered.

The first is promiscuous mating. This refers to the lack of an elaborate (or in some cases even a rudimentary) mating ritual. A more pedestrian means of describing this concept is to say that the animal must 'breed in captivity.' And that is true enough. However, the point to emphasize is one more broadly based. It does a human society no good if animals will 'breed in captivity' but not the precise male and female combinations we desire. That is why the term of promiscuous mating is much preferred, a mating strategy in which females will accept any male that the breeders determine is suitable to meet their objectives. Ultimately, if one is to realize the full potential of animal domestication, human mastery of breeding is essential. This control is among the chief impediments one confronts in taking the first steps to shift a species from its wild state to one of domestication (Zohary *et al.*, 1998).

It may be interesting to speculate overcoming this challenge with the modern tools available for reproductive manipulation. That is, with a more thorough understanding of the physiology of reproduction in a species of interest, it might be feasible to control reproduction in the laboratory, not in the field, pen, or cage. Such options were not available to our ancestors. However, the future of animal domestication may find that the tools of biotechnology can open doors that are closed today. Regardless, the challenge still remains of identifying who gets to be a parent and who does not. That fundamental decision is the key to domestication; our principal power and our principal challenge.

Suitable Disposition

First, do no harm. If taken for granted, the conceit that domestication of wild animals was considered by our ancestors to enhance their survival in a harsh world, then domesticating

animals that would not harm them would seem obvious. Nonetheless, some of the species that are considered hallmarks of the domestication process (e.g., cattle and horses) are capable of considerable harm to their human handlers, including mortally wounding humans who stray just a bit too close to their boundaries. Yet, of course, these animals do have a disposition that can be managed, a disposition flexible enough to be shaped by experience and familiarity with humans (Price, 1984). This is not likely to be said of grizzly bears, the North American bison, or the hippopotamus of Central and Southern Africa. In other words, unpredictable aggressive behavior is likely a character our ancestors considered as they eliminated candidates for domestication. Though perhaps tame as juveniles, needlessly aggressive adults should be easy to eliminate from our list of suitable candidates for domestication. Indeed, it is the plasticity, or lack thereof, of aggressive behavior over the course of an animal's lifetime that is instructive. Juveniles are often easily handled, regardless of their eventual adult disposition. However, fully grown adults, often several times the body weight of their putative human 'masters,' cannot be permitted unexpected violent outbursts. It is that unexpected, unanticipated aggression of a large adult that would seem to be the primary source for their elimination from domestication.

Tendency to Panic

Perhaps not as obvious a characteristic as an aggressive disposition, animals suitable as domesticates must certainly have a demeanor free of panic. Animals prone to flee, and flee quickly, from approaching threats are a safety hazard to themselves and their handlers. Imagine a Grant's gazelle, an ungulate capable of fast acceleration to speeds in excess of 45 mph, forced into an enclosure (Heglund and Taylor, 1988). Sheep and goats deal with threats in a far different manner than these speed-oriented mammals, and their suitability for domestication is evident. This speed, coupled with the associated temperament of nervousness, of the hyperawareness of threats makes such animals unlikely candidates for domestication. Not that attempts have not been made. Rather, one can see and explain the seeds for the universal failure of these attempts.

Social Structure

It is evident in our language; the plural for sheep and cattle are the same as the singular. These successful examples of domestication demonstrate that animals that live in large groups, with a prevailing social structure, have an increased likelihood of being shaped by humans from wild to domesticated animals (Price, 1984, 1999). How conspecifics interact with one another, especially in systems of a dominance/submissive hierarchy can play an important role in the success of domestication. That is because humans can insert themselves in the social hierarchy, a mechanism to force the transition from wild to domesticate.

Like so many other conditions, this 'requirement' of domestication is not apparent in all species that have been successfully domesticated. However it is the dominant paradigm. Cattle, sheep, goats, and horses are all familiar living in large, often gregarious, social structures, where dominance and submission play important roles in the social fabric of the group and individual. However as in any other of the conditions of domestication described in this list, such a 'requirement' can be violated. One need only think of the domesticated cat. These animals are often found as solitary predators, yet have become one of the more ubiquitous of domesticated animals. Thus, the list is more an outline of the general principles than a rigid inventory of hard and fast requirements. However a stable social structure, where individuals know their place and behave accordingly, is a useful tool for humans to have seized on. By manipulating these animals to see us as part of their social environment increases the probability that these animals can be transitioned from wild independent creatures to animals willing to tolerate our control of their food, territory, and breeding.

Domestication is about control; and this crude outline of the principles common to domesticated species (i.e., breeding in captivity, flexibility of diet, avoidance of panic, and a fluid yet stable social structure) provides the 'grease' on the gears of this domestication machine. Though not exhaustive, and certainly not part of a necessary and sufficient test of domestication, these concepts help understand and evaluate what our ancestors had to contend with and the thoughts and plans that must have danced in their heads.

The Where, When, and How of Domestication

Marshaling the Evidence of Animal Domestication

How do we know what we know? Not an unreasonable question. With regard to the process of domestication, what appears simple on the surface becomes more challenging, considering the nature of the information that is sought. As the process of domestication began so long ago, with so little formal documentation, piecing together the evidence of how this important process progressed is as challenging as it is fascinating. So as one take on this important topic, asking why did domestication occur and how might it have progressed, one need also to address questions such as how to measure and detect progress? The detection of evidence for domestication has two major points of attack: archeology and genetics (Bradley, 2006; Zeder, 2006a; Zeder *et al.*, 2006a, b). In either case, whether archeologic or genetic, the goal is to identify the markers of this process. Such markers should be objective measures that can be agreed as stably and consistently evaluated. Of course, as one considers such markers one must assess their suitability to change with the varying stages of the domestication process. Any markers that are considered seriously must be the ones that can distinguish wild animals from domesticates, natural processes from directed, evidence of human intervention in an animal's life cycle. Attempts have been made to study those areas; those elements most likely shaped by human intervention are behavioral changes in the transition from wild to domesticated animals, morphological and/or subsequent genetic changes brought about by this transformation. The combined story, unlocked by both archeologists and geneticists, form the basis of all that is

documented in this article. Each area is considered for its information content in 'decoding' the process of animal domestication.

Archeological evidence for domestication

As the process of domestication is considered, and the path it most likely followed, the components most likely to have been selected first are behavioral (Zeder, 2006a). Any pressure our ancestors brought to bear on changing wild animals into domesticates would have been on behavioral characteristics to exploit. Changing or manipulating the morphology and genes would surely take more time and concentration of effort. However exploiting behavioral variation is a natural beginning, behaviors including social structures and hierarchy, sexual and developmental precocity, tolerance of humans and of potential confinement, and components of panic and reduced aggression to perceived threats (Clutton-Brock, 1999). As domestication proceeded, humans would have, consciously or unconsciously, selected for adaptable elements, adaptable to human interests in reduced aggressiveness, submission to various environmental stimuli, and limitations or to various contributions to sexual and mating behaviors (Hemmer, 1990; Kruska, 1988). However in any of these considerations, documenting these changes is near impossible. Such behavioral adaptations do not leave a hard 'footprint' to be uncovered in the present as the domestication process is being documented. Some evidence does exist to this day, as reviewed in the article of Price (Price, 1984). However unlike other measures of change, behavioral adaptation is a marker that is too variable to assess and too plastic to serve as evidence of domestication's advance. We see it today, but have no way to tell when or where it first distinguished itself from any wild ancestor.

However as domestication proceeded, across time and generations, the morphological and changes induced by human control become measurable. In the case of morphological changes, archeologists have a variety of markers to assess as evidence of the progress of animal domestication. Most prominent among them are the changes in body size, often accompanied by reduced brain/cranial size (Hemmer, 1990; Kruska, 1988). The assessment of collected bones and teeth offer data that can be confidently measured and, usually, reliably dated. An obvious application of using bone samples as markers of domestication could simply be the discovery of the samples outside the natural range of the wild ancestor (Horwitz, 2003; Vigne *et al.*, 2005). Additional observations are also available in the measurement of teeth and bones, such as alterations in composition, microscopic changes in structure, or patterns of wear and disease. Astute observation of putative domestic remains, contrasted with similar measures in verifiable wild remains often serve as evidence for the archeological assessment of the progress in the process of domestication at a given site. One of the more commonly considered, though not always reliable, techniques is the contrast of demographic patterns in remains, usually measured as variation in age and gender composition in populations of wild and domesticated animals. The thought underlying this technique is that the gender/age mix of hunted animals is expected to be different from the distribution in captive versus farmed animals (Vigne, 2008). Though common, this technique is not without its critics (Zeder, 2006c), but nevertheless serves as a helpful measure of the process of domestication, reflecting the gradual transition the animals (and the people) took from wild to herded.

Though likely to have occurred later in the domestication process, archeologists can also make use of the physical remains of settlements that have been built or invented by their human inhabitants. That is, the remnants of animal corrals, pens, and other physical structures intended for animal confinement. Samples of animal manure, feed residues or hoof prints, and the ability to date them, can also serve as reliable signposts of this process (Olsen, 2006), including the discovery of the tools of animal husbandry (e.g., bits for horse bridle, sheep crooks). This assessment also includes detection of food processing equipment (e.g., butter churns) or the residues of animal food products in discovered storage vessels (e.g., yogurt from mare's milk) (Dudd and Evershed, 1998; Outram *et al.*, 2009). Taken across this spectrum, archeologists have been able to generate a rich tapestry of data to support the time, place, and progress of animal domestication.

Genetic evidence for domestication

Complementing, and indeed building on, the extensive body of archeological data is an ever expanding body of genetic data to augment one's understanding of the process of domestication (Dobney and Larson, 2006). As with the archeological data, the first steps along the path of domestication cannot be detected as distinct from the existing natural genetic variation in wild species. However, as the process of domestication advances a recognizable 'footprint' of its impact is left in the genome of our domesticated animals. Moreover, as can be seen, this process also left an impact on our own genome and our evolution as a species. First, the genetic evidence in animals is considered.

As can be seen throughout this article, the bulk of the genetic information assembled is used to shed light on the number and geographic location of domestication events, along with assisting in placing these events in time. Most of the genetic evidence derives from the analysis of neutral (or nearly so) genetic markers and noncoding sections of the genome. Though a few studies (Bradley, 2006; Emshwiller, 2006; Zeder *et al.*, 2006b) have tried to identify the 'genes for domestication,' most of the genetic research conducted to examine the evidence for domestication has concentrated on genetic information as a measure of the process, not of the effect a gene may have on the trait of domestication itself. Although, like any other measure of animal performance, a research aim could be to identify the actual genes that our ancestors exploited to create domesticates. That is, the identification of those genetic variants that create and distinguish the 'new' domesticated species from their wild counterparts.

Most genetic studies of animal domestication make use of mitochondrial DNA (mtDNA). There are obvious advantages in choosing this part of the genome. The most obvious is the relatively rapid rate of mutation of this component in comparison to that of nuclear DNA. Given that domestication began, in geologic terms, a relatively short time ago, this rapidly evolving genetic material provides a powerful resource to evaluate the when and where of animal domestication. For the species we most commonly study (e.g., cattle, goats, and

sheep) the matrilineal inheritance (Griffiths *et al.*, 2004) of mtDNA provides exceptional insight into the domestication process.

There are also investigations that make use of the mammalian male Y-chromosome variation (Götherström *et al.*, 2005; Wheeler *et al.*, 2006), a source of genetic material of patrilineal inheritance that evolves more slowly than mtDNA. One can also find the occasional use of microsatellite DNA from noncoding regions of the genome in some reports (Luikart *et al.*, 2006; Parker *et al.*, 2004). Put simply, all of the genome has found its way into answering questions regarding the domestication process. The preponderance of mtDNA-based reports should not preclude our consideration of other information. However, as stated, this material provides distinctive advantages as attempt is made to assess the time and place of ancient events.

Perhaps the most exciting advance in technology to come forward in the past few years has been the analysis of ancient DNA (aDNA). The vast majority of results discussed in this article are derived from taking tissue samples and extracting DNA from animals alive today, and asking "what processes are likely to have occurred in the past to deliver the genomic variation we see today?" This is a question common to population geneticists regardless of the species, attempting to evaluate the past from the data of the present through our understanding of the forces of mutation, selection, migration, and finite population size. In this way attempt has been made to delve, from sequence variation today, into the forces that have shaped this variation and how such variation contradicts or supports one's views on the domestication process. The advance of technology has also allowed to evaluate the DNA of animals long deceased. Given the ability of the bone to 'preserve' DNA, museum samples of wild animals and their possibly domesticated descendants from generations in the past can now contribute to the genetic analysis of domestication (Fernandez *et al.*, 2005; Leonard *et al.*, 2002; Troy *et al.*, 2001; Vila *et al.*, 2001). This capacity to look back directly provides an extraordinary means of examining the shifting progress of domestication. So though our story on the domestication of animals seems, today, reasonably complete, the likelihood of new ground being broken in the coming years increases every day.

The Major Species of Domesticated Animals

To tell the story of animal domestication, one might hope to organize it as one would a newspaper article. That is, to outline the where, when, and how of the process as distinct, almost independent, subtopics. However on further reflection and investigation, one quickly sees the naiveté of such an approach. The study of this important process is an interrelated story, one that involves all the basic questions simultaneously. Any such article would follow these topics based on a myriad of scientific facts and marshaling of facts. This complexity in documentation of this important story is seen in some of the recent conferences, and the ensuing publications that address this fascinating process. 'Documenting Domestication' (Zeder *et al.*, 2006a) tries to cover this immense area of investigation by considering a two by two table; where plants and animals comprise one main descriptor and archeology and genetics comprise the second. Though it is not possible to cover the comprehensive nature of that volume in this work, attempt is made to consider both the archeological and the genetic data that relate to animal domestication. It is a broad topic, but one that can be distilled into several broad, understandable, and interrelated themes.

For example, consider the potential archeological evidence. Study in this area follows one of the three major trajectories: (1) the study of human settlements and patterns therein, (2) the examination of food residues, especially the analysis of organic residues on cooking and storage artifacts, and (3) the examination of human, animal, and plant remains at these settlements. From this variety of information the simple questions of where, when, and how can be addressed. It is easy to see that the question of where is quite easily addressed, if only by the location of the studied settlement. The question of when can also be discussed, these remains often providing mechanisms of dating that are well understood, verifiable, and repeatable. However archeological discovery has a more challenging objective when asked to address the 'how.'

In a similar fashion, the understanding of genetics can be put to use to also assess the simple questions of where, when, and how. This is especially true with the explosion of molecular genetic information and based on the understanding of the mathematics of molecular evolution. With these tools it is possible to evaluate quite precisely the 'when,' for the processes of evolution and the forces that alter gene frequency are sufficiently understood. These molecular tools also help one understand and unlock elements of the 'how,' for one can trace the footprint of genes across populations to assess migration and breeding patterns that might have occurred generations ago to arrive at the results seen in today's domesticated animals. Though the genes have a hard time telling the 'where,' there is some information that can be extracted on the patterns of animal movement. In short, archeology and genetics combine as powerful tools in the investigation of the domestication process; one clearly informs the other.

How Did Animal Domestication Proceed?

As outlined earlier, and surely is obvious, the people who began the process of domestication did not document their work. Nor could they have, not if expected that documentation to have been covered in the span of several generations. The process of domestication was anything but rapid. This pace reflects both the challenges of the task, and what some might suggest as the reluctance to take on such a project (Diamond, 1997).

To illustrate the potential time span, as well as the detective work used today to uncover the work of the past, the archeological site of Tel Abu Hureya (Budiansky, 1999) is examined. Tel Abu Hureya was a village of continuous human settlement from 11 000 to 7000 years BP in the northern reaches of modern Syria on the banks of the Euphrates River. Archeologists have been able to recover tens of thousands of bone fragments, enough to tell a very interesting, and what is believed to be a typical, story for the advancement of agriculture and the domestication of animals.

At the beginning of this settlement (approximately 11 000 years BP) there is no substantive evidence of an organized food production system (i.e., agriculture). The people of this settlement appear no different from other hunter–gatherer cultures. Even after the domestication of cereal grains, which seems to date to approximately 9500 years BP in this settlement, hunting played a prominent role. The great majority of bone fragments from this time period are of gazelles, with fewer than 10% being the bones of sheep and goats (Saña Segui *et al.*, 1999).

With a more sophisticated analysis, archeologists have provided some fascinating insights into the dietary habits of these people. The sheep and goat bones dated between 11 000 and 8500 years BP show no decisive evidence of belonging to a domesticated animal. However by 8500 years BP an interesting pattern can be uncovered. The milk teeth of young gazelles, an animal that to this day remains hunted and undomesticated, fell into one of the two groups: those with virtually no wear (i.e., newborns) and those with substantial wear (i.e., yearlings) with no teeth discovered between these two mutually exclusive classes (Saña Segui *et al.*, 1999). The conclusion to be drawn: these animals were hunted, killed in the late spring as part of their migration through Tel Abu Hureya. However, the teeth of sheep and goats tell a qualitatively different story.

By 8500 years BP there are sufficient goat and sheep teeth in the sample to quantify patterns of tooth wear. Unlike the two classes of gazelle teeth, sheep and goat teeth show patterns of continuous wear. That is, animals were killed throughout the year, suggesting domestication, and are at the very least, a pattern of close, communal living. The point to sustain is the long time period and gradual transition from hunter to farmer. Indeed, the people of Tel Abu Hureya clearly demonstrate the coexistence of grain farming and animal hunting, coupled with a gradual change to domesticated animals (Bar-Oz *et al.*, 2011; Saña Segui *et al.*, 1999).

This story of the slow adoption of agriculture and the domestication of animals is played out repeatedly, including the advance of this process in Europe and other sites of human expansion (Pinhasi *et al.*, 2005). The driving element of this process appears to be the availability of species with which to work and the pressure of population growth among the societies taking this step (Childe, 1942). Nevertheless, the outline of the domestication story from Tel Abu Hureya leaves us with one abiding conclusion: that domestication is not a moment, but a process, a process that was repeated in many places, at many times, with a variety of species. These facts lead us to ask, what has this process wrought? What have we done to the animals in our care, and indeed to ourselves, as we traveled this path of interdependence?

Impacts of Animal Domestication

Impacts on the Animals

As outlined at the beginning of this article, the purpose of domestication is to demonstrate mastery over an animal's food supply, access to territory, and breeding practices. Within that broad sweep of control, the implication is that this control is done for a reason, with a purpose in mind. In the case of Neolithic people, the mechanism driving any such change might have been poorly understood, but a direction for this change must surely have been present. Today, it is rather thought that the mechanisms of change are understood much better. And indeed we do. However our goals are not fundamentally different from those of our Neolithic ancestors. We wish to shape animals to our own needs, to our own vision of their purpose. And so we have. Though a thorough treatment of all these areas of change is not possible in the space of this article, some of the more important among them are identified. Having set approximately, some 10 000 years ago, to reshape a handful of the world's animal species to our needs and ends, what have we accomplished?

Changes in body size

One of the most common observations of animals, certainly in the initial generations of domestication, is a reduction in body size. The reason for this result may vary from species to species, but the general trend is apparent in the archeological record (Zeder, 2012). One could speculate that a poor, or limited, food supply may lead to reduced growth. However, over the longer term, human handlers may have unconsciously or even consciously selected for smaller, more juvenile easier to manage animals. In the long term, however, this general observation may not fit in all cases. Certainly there are breeds of dog, turkey, or horse that exceed the mature size of their wild ancestor (Field and Taylor, 2012). In these instances, one can surely see the hand of motivated animal breeders, individuals with a clear goal in mind and the steadfast desire to reach that goal.

Modifications of appearance

Absent bones and other physical evidence can span centuries, but are limited in comparisons of appearances between wild and domesticated animals by those occasional cases where the wild ancestor survives. That is, one can see the dramatic changes in coat color and hair quality between dogs and gray wolves. One can directly observe the changes through this direct comparison. Indeed, in the circumstance of comparing dogs and wolves some of the changes have been so great that it is challenging to see the remnants of a wolf in many of the breeds of dog today (Larson *et al.*, 2012). However, the study is no longer limited by direct visual comparison for some of these 'softer' traits. As seen, through the sequencing of ancient DNA, the wild horse coat colors were quite different from the patterns and colors seen today. Animals with little chance of survival in the past can now be protected and encouraged to reproduce.

One can also note the reduction in size (or presence) of horns. In the wild, horns can play a valuable role in defending oneself from predators or in securing food, territory, or mates from conspecifics. As domesticates, horns are a threat to their human handlers and to other animals in the flock or herd. This is another simple example of how domestication modifies the external appearance and functionality of the animals in our care (Zeder, 2012).

One might think of this as the 'price' an animal pays for submitting to the domestication process in the first place. Traditional views of domestication made the process seem to be one of human instigation and human domination.

However the process is now thought to be more of a 'two-way street;' where humans hope to take advantage of this captive resource and the animals 'submit' to the capture, finding this a path to increased access to resources (food, water, and territory) and eventual survival (Budiansky, 1999). Perhaps this exploitation, and selection, for an animal's willingness to live within the confines set by humans is the greatest impact we have had on their morphology, behavior, and appearance (Udell *et al.*, 2010). In our mutual goal, to enhance 'both' our survival strategies, we have shaped each other into a species that was not there at the outset. Neither of us has left the process, which continues still, as we began.

Dramatic physiological changes

No discussion of the impact of domestication on the animals would make sense without a mention of the dramatic changes we have made in the anatomy and physiology of these creatures. No hen, in the wild, would need (or be capable) to lay 250 eggs in a production year; although that is precisely what a commercial laying hen can do in the production and laying facilities we manage today. And what cow would produce more than 11 300 kg of milk in a 10-month lactation? Broiler-type chickens can reach 2.2 kg by 7 weeks of age, and do so on as little as 4 kg of feed. The alteration of the physiology of these animals is staggering (Field and Taylor, 2012); and the changes in many instances have not slowed down.

In virtually every instance of animal domestication, a list of species could be drafted and could distinguish one or more contributions these animals make to human survival and quality of life. Moreover, in nearly every element of such a list one could delineate an exaggerated component of their wild ancestor that humans have exploited to their own needs. Whether it is growth rate, fecundity, fertility, lactation, or components of behavior, the animals in our charge have moved dramatically from the homeostatic midpoint where they were placed by natural selection. Humans have remodeled and overhauled these species, often with discernible negative consequences (Mcgreevy and Nicholas, 1999); and this sweeping set of changes did not occur in a vacuum. Not only have the animals changed, so have we.

Impacts on People

In the end, the whole purpose of this article is to describe the impact of the process of domestication on our view of animals, one another, and how this process has influenced our past as it guides our future. The domestication of plants and animals coincided with and facilitated our transition from small bands of hunters and gatherers into the complex technological society we have become today. As a result, trying to assess the impact of animal domestication on humans is as simple as saying: 'everything.' Although such brevity is hardly informative, it surely contains a kernel of truth. All that we are, and all that we are to become, can be traced to the capture, taming, and eventual subjugation of our fellow animal species. Nevertheless, one can, and should, take some time and space to illustrate this sweeping conclusion with a few examples.

No example may be more powerful in demonstrating the impact of animal domestication on people than the origin stories of some of our oldest cultures. For example, it is in the Vedas, the originating sacred texts of Hinduism where cattle, sheep, horses, and goats play important roles in the creation of the world and of humanity (Koslowski, 2001). Sheep play a fundamental role in the imagery of Judaism and early Christianity. In these examples, one can see that the domestication of animals was not only a technical achievement, but is also imbued with a fundamental contribution to the origin stories of our societies. Apparently, the domestication of animals was so important that these societies viewed their very origin as inextricably linked to the animals in their care and on whose performance their survival was invested (Anderson, 1998; Bulliet, 2005). Therefore, it was that for much of our society's history we viewed the domestication of plants and animals as an unalloyed good. It was this process that has led us to our advancing technology and science, to expand our political and legal organization, and have led us to a comfortable, and civilized, way of life. How could the domestication of animals be anything but a cherished and valuable step on our path to success and personal fulfillment? However that view was to change.

With the advancing discoveries of archeologists and anthropologists, a more nuanced view of the impact of domestication began to take hold. Indeed, by 1987 an article by Jared Diamond could easily proclaim, in the popular science press, that agriculture was "the worst mistake of the human race" (Diamond, 1987). How did this transformation of ideas take place? What in the historical record forced us to move from viewing domestication, and thus agriculture, as an unaltered good to a process suspected of exacerbating the worst of our darker angels (Weisdorf, 2005)?

In broadly described terms, we more clearly see the impact of domestication on our food production as having led to several changes in our societal structure and our biology: an increased exposure to infectious agents, the development of technology, the creation of political organizations and structures, the advent of writing and a change in the natural selection pressures on human evolution. Several of these topics are dealt with in vivid detail in Prof. Diamond's Pulitzer Prize winning book, Guns, Germs, and Steel (Diamond, 1997). In that text, expanding on his earlier article on the 'mistake' of agriculture, Diamond outlines the impact that domestication of large mammals had on human beings and our social/governmental arrangements. To cover this briefly, humans spent hundreds of thousands of years living as hunter/gatherers, consuming a diverse diet of plants and animals. However with the development of domestication, humans became less nomadic and less dependent on gathered foodstuffs. The usually more abundant food supply, at least initially, of domestication led to an expansion of the population, and with it the attendant need to coexist and cooperate across family boundaries to clans and tribes, and eventually to the growth of nation states. Thus, do we see a line connecting the domestication of animals with the growth of government, and with it the growth of class distinctions. And it is in the growth of class, whether determined on economic, political, gender, or ethnic lines, that anthropologists have transitioned to a more balanced and complex view of the domestication of plants and animals (Price, 1995; Zeder, 2006b).

As with other components of this article, addressing the impact of animal domestication on our species would take shelves of books. Here attempt is made only to highlight a few areas of interest and impact; and in that light expect to see some of what this complex invention has done to change our societies, our view of ourselves, as well as how this process has impacted our own biology. In any of the examples that might be considered, it is usually observed that the impact is balanced, and in many ways nuanced by our present economic and political circumstances. That there has been an impact is not for debate. The interpretation of that impact, for 'good' or for 'bad,' may depend on the place from which one takes their view. For example, it is clear that the growth in food supply provided by domestication and agriculture eventually lead to increases in population size and concomitant changes in political arrangements. One need only reflect on the imagery sculpted into Tutankhamun's sarcophagus. In one hand the pharaoh holds a grain flail and in the other hand a sheep crook. Symbols of sustenance and government authority, their origins are deeply embedded in the domestication of plants and animals. How we choose to view that control, as the generous husbandry of a protective shepherd or the onerous treatment under a subordinating ruler may say more about our views of government than our views on the invention of domestication. Consider another example of how domestication of an animal species changed the organization of human society; consider the example of the horse.

Much of what one thinks of the impact of the domestication process, and its impact, relies on varying degrees of speculation. After all, early domesticators did not provide a written record of their successes, failures, or insights. However there are footprints of this process and that has moved our understanding forward. However, there are instances, rare perhaps, where first person, or nearly so, accounts of the impact of the domestication process has been witnessed and if not completely recorded, more recently observed. Such an example would come from the impact of the domestication of the horse, and of horseback riding on a culture previously without this technology. Specifically, one can consider the introduction of horses to the native people of the North American plains.

Though horses evolved on the North American continent, they were extinct by the time Europeans arrived. Why horses were extinct is the subject of some debate (Grayson, 2007) (i.e., a natural extinction or hunted to extinction), but extinct they were. However by the late-seventeenth century, in the Southwestern United States, horses were reintroduced by European colonists. This relatively recent acquisition of horses, especially the impact of horseback riding, has been, all things considered for events occurring between 1680 and 1750 AD, reasonably well documented (Ewers, 1955). As a result, one can visualize the primary and secondary effects that the use of domesticated animals had on early societies. In the instance of horses, there are several obvious uses to which this animal can be put: a new food resource, a power source for bulk transport including long-distance transport of people and goods, a mount for the purpose of hunting other species of wild animal (e.g., bison) and, if necessary, a mount for war against neighboring bands and tribes. In each of these uses, there are obvious and documented outcomes. Chief among them would be a tool to make life on the grassland plains more sustainable and reliable (Catlin, 1973). This, in turn, would lead to an increase in population size for the established social group and an opportunity for accumulation of wealth. Moreover, that accumulation can lead to differentiation of social class and all the attendant consequences such distinctions bring (Ewers, 1955).

The use of horses in the transportation of goods, including the use of this animal as a mount, dramatically increases the territory exploitable by the horse-adopting societies (Krader, 1955). Of course, an expansion of territory simultaneously expands trade and wealth distribution, leads to the development of new community social structures, and any concomitant conflict over the resources provided and exploited by this territorial expansion. Moreover, any conflict over territorial resources will certainly place a decided advantage in the military power provided by horse-mounted warriors (Lauwerier and Hessing, 1992).

This drama has been played out in many locations in North and South America as a result of the colonization of these continents by horse-owning Europeans. Projecting these outcomes and observations to the first societies of the Eurasian steppes is obvious (Levine, 1999). As horse domestication proceeded, and evolved into horseback riding, the fundamental interaction of communities changed dramatically, sometimes peacefully and at other times erupting into open conflict. Interestingly, that conflict has its remnants in the games of today. The national sport of Afghanistan, buzkashi, originated with their horseback riding ancestors with all the attendant maneuver and strategy of mounted cavalry.

This is just one example of how horses impacted the development of early-adopting societies. What we see is how this new invention facilitated actions, emotions, and desires already existent in these groups. Like any invention, the domestication of animals has intended and unintended consequences, both of which played important roles in the evolution of the human communities that adopted this technology.

Beyond the social impacts of domestication, it is also worth considering, if only briefly, the biological impacts of domestication on our fitness and survival. Though the exploitation of plants and animals as a stable food source may have led to an initial expansion of population size, archeological evidence from sites around the globe tell a consistent story of changes in lifespan, stature, nutritional deficiencies, and increased rates of infectious disease (Goodman *et al.*, 1984; Rathbun, 1984). The list of maladies afflicting societies that chose the path of agriculture quite naturally leads one to ask why, "what were they thinking?" Reviewing the paleopathology of early agricultural communities reveals a picture of a society 'pushed' into agriculture, rather than a society 'pulling' itself to a new paradigm. What the archeological record reveals, time after time, site after site, is that the adoption of agriculture extended over a considerable frame of time, interrupted by fits and starts of cultivation and a return to hunting/gathering.

The record of human survival, measured in bone lengths, age of death, and evidence of pathology tell a story of reduced health and longevity in societies engaged in early adoption of agriculture (Armelagos *et al.*, 2005). Though animals can be a

source of agricultural power, and of high-quality protein, this does not seem to have translated to all members of the community. The archeological record suggests that food diversity was reduced, workload and labor increased, and in the case of animals, exposure to new infectious agents all contributed to a dramatically altered quality of life (Armelagos *et al.*, 2005; Diamond, 1997).

This consistent story of the hardships of the domestication process calls into question the 'why' of continuation. One can only speculate, but this long process seems to support the claim, that once a society embarks on the journey to cultivation of their food, there is no retreat to their former model of gathering wild plants and hunting wild animals. For, as these communities transformed their environment so as to be suitable for farming, they simultaneously removed their opportunity to return. Their lot with agriculture had been cast. Cultivation of selected plants required some modification, even destruction, of the natural habitat of other plants and hunted animals. Once changed, the objects of their hunting and gathering had disappeared. It seems a very inauspicious way to begin the journey to today's technologically advanced globally connected society. Nevertheless the record of the past, held in our stories (Koslowski, 2001) and the remnants of pathology in our ancestor's remains, points to an impact of animal domestication that is often free of any obvious benefit beyond simply crossing the hurdles of daily survival. The growth of zoonotic disease alone is enough to question any lasting benefit from the domestication of animals (Armelagos *et al.*, 2005).

The legacy of the impact of zoonotic disease is seen in so many places, in our politics and language. As Prof. Diamond extensively documents (Diamond, 1997), the transmission of disease from animal-owning Europeans to nonanimal-owning North and South American natives changed the maps of the New World. To list only a few examples, the milk, hair, and skin of domesticated animals transmit anthrax, Q fever, brucellosis, and tuberculosis. Add to that partial list food poisoning, parasitic infections, and other water borne diseases, and the common problems of animal agriculture today that must surely have devastated early societies setting out to adopt this technology. Our language still reflects this tie to our domesticated animals. Preventive medicine for many infectious diseases includes the use of vaccines, a word with its roots in *vaca*, Latin for cow.

This association of disease prevention and our domesticated animals derives from the discovery of the British physician Edward Jenner, who observed that people who worked with cattle did not contract smallpox. As is known now, people who worked with cattle were no doubt exposed to cowpox, a disease with far less severe symptoms than smallpox but one that apparently bestows immunity from this dreaded zoonotic scourge. The term vaccination, used by Jenner, means 'from cows,' and so it is that the process of animal domestication, beyond providing the power behind early agriculture or a reliable source of food and fiber, also altered elements of our biological adaptation to the environment. Altering our lifespan, changing our height and exposing us to unfamiliar pathogens has each left its mark on our history as a species. However, the domestication of animals has also altered, and indeed driven, our evolution as a species. Though the time span since the domestication of cattle is relatively short (between 7000 and 8000 years), there has been a demonstrable change in our genome, as evidenced by the recent work on lactase persistence in human populations associated with adult milk consumption (Tishkoff *et al.*, 2006).

Like all mammals, human infants use milk as their sole source of nutrients, gradually taking on solid food until weaning. During infancy, with rare exception, lactose, a disaccharide of glucose and galactose, is broken into its two simple sugars by the enzyme lactase-phlorizin hydrolase (LPH) in the small intestine (Swallow, 2003). The capacity to activate LPH and digest lactose typically declines after weaning. However, some individuals maintain this capacity into adulthood, a trait called 'lactase persistence.' Lactase persistence is a dominant Mendelian trait. The fascinating element of this trait, however, is the changing frequency of this dominant allele from one human population to the next. That is, nonpastoralist populations in Asia and Africa have a very low frequency of this allele; approximately 1% in China and between 5% and 20% in West Africa (Durham, 1992; Swallow, 2003). However in populations that rely on milk as a food source into adulthood, populations with the practice of keeping cows, the allele for lactase persistence jumps to more than 90% in places like Denmark and Sweden (Durham, 1992; Swallow, 2003). Other populations and ethnic groups in Africa, with a culture of cattle and milk consumption into adulthood also carry the persistence allele in high frequency (Tishkoff *et al.*, 2006). What we see demonstrated here is the presence of a very strong selective sweep, one that has dramatically altered human evolution in a relatively short span of time. Domestication of animals has not just changed how we live and how we eat, it has fundamentally altered our very biology.

Conclusion

For most of our time as a species, whenever that may have begun, human beings lived in ways little different from our animal relatives and neighbors. However eventually we began to live in groups and social settings where we began to feel different, feeling distinct, and separate from the other animals. Eventually that feeling would change, and as human social groups evolved we began to question our relationship to, and with, the animals around us. That feeling of distinction finally brought us to the task of changing some of these animals to fit our needs and expectations; to move them from wild animals to our now close domestic 'partners.' What the future will hold for our mutual relationship can only be guessed. What remains certain is the importance this process has played in our lives and culture.

See also: Beef Cattle. Biosecurity and Equine Infectious Diseases. Breeding: Animals. Dairy Animals. Domestication of Plants. Food Security, Market Processes, and the Role of Government Policy. Human Nutrition: Malnutrition and Diet. Poultry and Avian Diseases. Social Justice: Preservation of Cultures in Traditional Agriculture. Swine Diseases and Disorders

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Domestication of Plants

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Glossary

Archaeobotany The identification and analysis of botanical remains found in archeological investigations. The remains can be subdivided into macroremains (identifiable to the naked eye) and microremains (require the use of a microscope). Among macroremains are seeds and pods. Microremains include pollen grains and subcellular structures like starch grains and phytoliths (silica deposit inside plant cells). The shape of microremains can be diagnostic of the identity of the plant material. The conservation of archaeobotanical remains can be favored by certain environmental conditions (like dryness or excess water).

Centers of agricultural origins Agriculture started in multiple locations in the world some 10 000 years ago. These locations (where crop domestications took place) are distributed in some 10 areas generally between 30° northern latitude and southern latitude. They tend to occur in areas with higher levels of biodiversity.

Domestication Evolutionary process driven by natural and human (whether conscious or unconscious) selection applied to wild plants or animals and leading to adaptation to cultivation and consumption or utilization. Domestication can be complete, whereby organisms become entirely dependent on humans for their continued existence or can be partial or incipient, whereby they still reproduce independently of human intervention.

Domestication syndrome A set of morphological, biochemical, and physiological traits that distinguishes domesticated plants or animals from their wild progenitor. These traits depend on the life history (annual vs. perennial) and reproductive system (outcrossing, selfing, and vegetative reproduction). Traits affected include dispersal of propagules (e.g., seed shattering and pod dehiscence), seed dormancy, growth habit, diversity of harvested parts (size, shape, and color), flowering response to environmental cues (temperature and day length), organoleptic qualities (taste, texture, and toxicity), and any other traits affecting harvested product use (e.g., fiber quality).

Molecular markers Markers are traits with a simple inheritance (like Mendel's characters). Molecular markers are based directly or indirectly on deoxyribonucleic acid (DNA) sequence variation. Indirect molecular markers are proteins, such as isozymes (enzymes of the basic metabolism, which can be distinguished by their electric charge) and seed proteins (which can be distinguished by their size). Direct molecular markers include RFLP, RAPD, AFLP, etc. markers (which can be distinguished by the DNA fragment sizes). Increasingly, the actual DNA sequence is used to distinguish among individuals and trace back their ancestry.

Quantitative trait loci Locus controlling a quantitative trait that differs from a Mendelian trait (or marker locus: see Molecular marker) in that it does not exhibit clear-cut segregation classes because the trait is controlled by more than one gene or is subject to environmental effects or a combination of the two. These are often measured traits (e.g., yield and seed weight) or counts (number of seeds or days to flowering). Because of the lack of segregation classes, the inheritance is analyzed by correlating markers with the expression of the trait in segregation populations resulting from the cross between two contrasting parents.

Taphonomy The science of fossilization. It studies the factors that favor or hinder the formation of fossils.

Introduction

The evolutionary lineage leading to the modern human species (*Homo sapiens*) has been marked by several key inventions, such as the development of increasingly sophisticated tools (Stout, 2011), the mastery of fire (Alperson-Afil and Goren-Inbar, 2010; Berna *et al.*, 2012; Twomey, 2013), the acquisition of writing (Houston, 2004), and the current digital revolution. Among these inventions is agriculture or the transition from hunting-gathering (HG) to the cultivation of crops and tending of animals. This transition initiated a change that cannot be overestimated in all aspects of life on the earth, including the biological and physical environment and, obviously, also the way of life of humans. It is, therefore, not surprising that this transition has been called the Neolithic Revolution.

The signs of the changes brought about by the momentous introduction of agriculture are numerous. For example, many famous 'natural' landscapes on the earth are actually agricultural landscapes: the rice terraces of Yunnan in China, the rolling, cypress-studded lands of Tuscany in Italy, and the big-sky, luminous plains of the Palouse in Northwest United States. Thirty-eight percent of total land area is now devoted to agriculture, making it currently the single most important land use. For example, forests (most of which are subjected to some type of anthropic exploitation) only account for 30% of the land area (FAO, Land use database).

Among the changes that were more or less concurrent with the origination of agriculture were sedentism (as opposed to nomadism) and the appearance of villages and ultimately cities, the introduction of ceramics, the transformation of more egalitarian societies into more hierarchical ones, a stronger division of labor by the addition of nonfood production related occupations, and, later on, the introduction of writing. The actual sequence and order of these technologies is still being disputed and may diverge in different regions where

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agriculture was initiated. Ultimately, the transition from HG to agriculture was a precursor and a necessary condition for the eventual appearance of civilizations. The sequence of events subsequent to the initial transition to agriculture is beyond the scope of this article but is the subject of intensive, long-term studies (e.g., Maisels, 1993; Price and Bar-Yosef, 2010; Kuzmin *et al.*, 2011). As stated by Diamond (1997), "plant and animal domestication meant much more food and hence much denser populations. The resulting food surpluses … were a prerequisite for the development of settled, politically centralized, socially stratified, economically complex, technologically innovative societies."

Agriculture has been for some time and is still the main source of food, fiber, and feed for humanity. So far, it has been able to keep up with the tremendous growth in population. It has been estimated that the total human population at the time of the Neolithic Revolution was approximately 6 million people (Livi-Bacci, 2012), which now amounts to 7 billion (World Population Clock, US Census Bureau), with a nearly certain prospect of a further increase of 2 billion by 2050 (United Nations, Department of Economic and Social Affairs). The current hunger episodes are not due to insufficient production but other factors affecting food security (FAO, The State of Food Insecurity). Nevertheless, the dominance of agriculture as a human activity has come at an ecological price, which includes habitat destruction, reduction in biodiversity both of natural and agricultural ecosystems, widespread contamination with chemicals of agricultural origins, such as fertilizers and pesticides, and a significant part of the emissions of greenhouse gases.

It is in this broader context that domestication of crop plants (and farm animals) has operated, not only as a component of the adaptive process to which cultivation (or captive rearing) has subjected them by humans but also more broadly as part of the Neolithic Revolution that included the transition from HG to agriculture.

The Concept of Domestication and the Domestication Syndrome

Domestication is, in essence, an evolutionary process of selection for adaptation to changed environmental conditions, as plants are not only consumed but also actively cultivated. Cultivation is a necessary condition for domestication to take place. The selective forces that act on plant populations in the original natural environments are to a great extent different from those in the subsequent cultivated environments. In natural environments, strong intra- and interspecific competition exists among plants for light, water, and soil nutrients. In contrast, agroecosystems are characterized by less competition, even in well-known, diverse arrangements like agroforestry (Leakey, 1998; Perfecto and Vandermeer, 2010) and gardens (e.g., Ban and Coomes, 2004; Buchmann, 2009). This reduced competition is then converted into higher productivity for harvested organs (e.g., grain, leaves, roots, etc.) through modified partitioning of photosynthates and a higher harvest index (ratio of harvested biomass to total biomass).

A second major difference between natural and cultivated environments is the need for developing a more efficient production system, in terms of biomass per unit of surface and time. The overall goal has been to increase the harvested biomass although decreasing the total effort necessary to harvest this biomass. Hence, several traits have been selected to achieve this goal. These traits include: (1) loss of seed dormancy, which led to more uniform stands at planting; (2) a more compact growth habit, with reduced branching and shorter branches, which reduces intraspecific competition and makes harvest more synchronous; (3) a tendency for reproduction to evolve from outcrossing to inbreeding to vegetative propagation, which makes reproduction less dependent on abiotic and biotic factors; and (4) reduced or loss of seed shattering, which limits grain losses at harvest.

Third, humans also exert an important selective role not only as farmers but also as consumers of their production, irrespective of whether it is for food, feed, or fiber. A key aspect here is the attraction of humans for novelties, such as new seed and fruit colors or shapes, which has led to the striking morphological diversity in some crops, such as developmental differences in cabbages (*Brassica* spp.: red cabbage, Brussels sprouts, cauliflower, etc.); seed color, size, and shapes in certain legumes (*Phaseolus* sp. and *Vigna* sp.); and fruit size, shape, texture, and color in the Rosaceae (e.g., apple: *Malus* sp.; pear: *Pyrus* sp.; and cherry and plum: *Prunus* sp.). Generally, domestication has led to an increase in the size of the harvested organs, irrespective of whether they are roots, leaves, fruits, or grains. Increases in size can sometimes by remarkable as they can reach a $10x$–$20x$ difference between wild and domesticated types. Plants generally contain toxic substances that fulfill several functions like protection against diseases or pests. During domestication, the concentration of these compounds has generally decreased in all or at least part of the domesticated gene pool, as shown, for example, by the reduction in cyanogenic glucosides in cassava (Bradbury *et al.*, 2013) or lima bean (Vanderborght, 1979).

The existence of these sets of correlated traits that are characteristic of domesticated plants and show some degree of consistency among different, even unrelated, crops led Hammer (1984) to call them 'domestication syndromes.' Such syndromes are generally applicable to more strongly domesticated plants; however, there are sometimes important differences among crop plants, depending on their life history and reproductive mode (Harlan *et al.*, 1973; Smartt, 1990; Ladizinsky, 1998; Hancock, 2004; McKey *et al.*, 2010, 2012). Perennial plants, such as fruit and nut trees or vines, often show more limited differences between wild and domesticated types because of their extended juvenile phase, long life cycle, high gene flow levels, and potential for vegetative reproduction (Miller and Gross, 2011). For example, the main domestication trait in grape vine is the evolution from a diecious (separate male and female individuals) reproduction to an autogamous reproduction, made possible by hermaphroditic flowers (with both male and female reproductive organs). This change is controlled by a single locus (Battilana *et al.*, 2013). Thus, in general the domestication syndrome of perennial crops consists of fewer differences between wild progenitor and domesticated descendant (Pickersgill, 2007). The expression of constituent traits is also often limited. For a given crop, there may be different domestication syndromes, depending on the local production circumstances. For example,

one could envision a different domestication syndrome for maize grown for grain (as is currently the case) or for its vegetative matter as feedstock for biofuels. The latter could involve a more branched plant type that increases the production of stems and leaves rather than grain. Meyer *et al.* (2012) provided an extensive overview of the broad range of traits characterizing domesticated plants. Dempewolf *et al.* (2008) provided a discussion on the level of domestication.

Finally, the constituent traits of the domestication syndrome are often deleterious in the wild. For example, more compact growth habits and loss of spontaneous seed shattering reduce the fitness in natural environments because they limit competitiveness with the surrounding vegetation and reproductive ability, respectively. Although they are selected against in the wild, the opposite is true in agricultural environments.

Where Did Domestications Take Place?

The domestication of crops, as an invention, is embedded in the origins of agriculture. The transition from HG to agriculture has taken place in multiple regions of the earth, remarkably at about the same time approximately 12 000–10 000 years ago in the aftermath of the last (Wurm) ice age. The actual causes for this transition are poorly understood and therefore both the location and timing of the transitions can only be investigated empirically using a combination of information from different fields, each with their strengths and weaknesses.

The main fields contributing knowledge about the origins of agriculture have traditionally been archeology, biology, linguistics, and history as proposed by de Candolle (1882) in the nineteenth century. Since then, a broad range of scientific fields have been applied to solve the puzzle of agricultural origins. Archaeobotany seeks to describe archeological remains of crop plants and their wild progenitors from Neolithic sites. Of particular interest is the transition in the archeological record from cultivation of wild plants (predomestication cultivation) to the cultivation of actual domesticates. Some key traits have been identified, mainly pertaining to seed shattering in cereals, such as wheat and barley (Hillman and Davies, 1990; Tanno and Willcox, 2006; Fuller and Allaby, 2009). An additional advantage of archeobotanical remains is that they can be dated by ^{14}C accelerator mass spectrometry, which allows direct dating of the remains rather than indirect stratigraphic dating previously practiced with ^{14}C dating (Smith, 1989, 1997; Kaplan and Lynch, 1999; Benz, 2001; Pinhasi *et al.*, 2005). A disadvantage of archeobotanical approaches is that they are limited to the available archeological sites, which may not be representative of the geographic distribution of early agriculture and in many regions are limited in number.

Genetic evidence is based primarily on the study of contemporary wild and domesticated populations of plants. An important element is to determine the identity of the wild ancestor of each crop. This has been accomplished for most crops, first through artificial hybridizations that determine the viability and fertility of progenies between crops and putative wild ancestors (Harlan and de Wet, 1971). Because domestication took place only 10 000–12 000 years ago at most, there has been limited differentiation between a crop plant and its wild ancestor, one expects normal viability and fertility in their cross in most cases, with the exception of polyploid series, such as wheat. In the latter crops, crosses involving different ploidy levels usually do not yield viable or fertile progenies in spite of the close genetic relationship expected from ancestor–descendant relationship.

Additional analyses involving molecular markers can then refine the identity of the crop ancestor. All molecular markers are ultimately based on deoxyribonucleic acid (DNA) sequences, irrespective of whether they are proteins, such as enzymes (allozymes) and seed storage proteins, or DNA sequences themselves. Because of advances in DNA sequencing technologies, plant populations are increasingly being characterized by sequencing directly (genotyping by sequencing) (Doebley, 1992; Gepts, 1993; Burke *et al.*, 2007; Gross and Olsen, 2010; Olsen and Wendel, 2013). These analyses, akin to paternity tests, reveal a minimum number of domestications and in some cases also a more defined putative region of domestication within the overall distribution area of the wild ancestral form. Recent examples of this capability include the identification of putative domestication areas for crops in the Mesoamerican center of agricultural origins, such as maize (*Zea mays*; Matsuoka *et al.*, 2002), common bean (*Phaseolus vulgaris*; Kwak *et al.*, 2009), and pepper (*Capsicum annuum*; Loaiza-Figueroa *et al.*, 1989), in different areas of the Mexican territory. This polycentric process of assembly of cropping systems in the Mesoamerican center is mirrored in other centers of agricultural origins like Southwest Asia ('Fertile Crescent') and China (Fuller *et al.*, 2012; Riehl *et al.*, 2013; Cohen, 2011; d'Alpoim Guedes, 2011).

Two potential confounding factors operate when attempting to determine an area of domestication. First, gene flow both within the domesticated types and between domesticated and wild types can obscure the local relatedness relationships. For example, maize (*Z. mays* var. *mays*) was domesticated from lowland teosinte (*Z. mays* var. *parviglumis*), but the close relationship between domesticated maize and highland teosinte (*Z. mays* var. *mexicana*) is due to gene flow (van Heerwaarden *et al.*, 2011). Common bean, a predominantly self-pollinated species, nevertheless shows evidence of low but detectable levels of gene flow between wild and domesticated types (Papa and Gepts, 2003; Papa *et al.*, 2005, 2007; Payró de la Cruz *et al.*, 2005; Zizumbo-Villarreal *et al.*, 2005).

Second, there is possibility that the distribution of the wild relative has changed since the initial domestication process. Contemporary wild progenitors are the immediate descendants of the wild types that were domesticated and genetically closest to the original types that were domesticated. They are, therefore, the plant material of choice when studying domestication (Ross-Ibarra *et al.*, 2007). Existing climate models combined with species distribution models may be used to retrospectively estimate the original distribution of the putative ancestral type.

Occasionally, genetic analyses target ancient DNA contained in archeobotanical remains (Jaenicke-Després *et al.*, 2003; Roullier *et al.*, 2013). Although these experiments represent a laboratory tour de force to obtain data from degraded

DNA, their scope is generally limited, however, by the small sample size of the analyses so far, thus limiting the inferences that can be made. Linguistic analyses also contribute to the determination of the area of domestication. The existence of words designating a crop, its product, or tools related to the crop, in native languages provide an additional indication of the importance of the crop. More recently, paleobiolinguistics has reconstructed words in precursors of modern languages (protolanguages), dated them based on lexical similarity, and located the homeland center based on lexical diversity (e.g., common bean, Brown, 2006; cassava, Brown *et al.*, 2013b; and pepper, Brown *et al.*, 2013a). A question associated with the linguistic approach – and other approaches as well – is the antiquity of the evidence it can uncover.

Based on these analyses, **Figure 1** shows a sample of crop domestication origins. Several of these centers of origin are fairly well circumscribed, such as the Mesoamerican, Southwest Asian, and Chinese centers. Others cover a much broader territory, such as the South American, African, and Southeast Asian centers. In all cases, however, recent archeobotanical and genetic data suggest that individual crops were domesticated in different areas within each of these centers (Fuller *et al.*, 2012; Riehl *et al.*, 2013; Cohen, 2011; d'Alpoim Guedes, 2011; Clement *et al.*, 2010; Piperno and Pearsall, 1998; Piperno, 2011). For example, maize and common bean were domesticated in different watersheds in western Mexico but were eventually united postdomestication into the milpa ('three sisters') cropping system with squash (Matsuoka *et al.*, 2002; Kwak *et al.*, 2009; Zizumbo-Villareal and Colunga GarcíaMarín, 2010; Zizumbo-Villarreal *et al.*, 2012). Einkorn, durum, and bread wheat were domesticated in different areas of the Fertile Crescent or adjacent regions (Riehl *et al.*, 2013, Willcox, 2013). Barley was domesticated not only in the Fertile Crescent but also further east in Central Asia (Morrell and Clegg, 2007) and Tibet (Dai *et al.*, 2012). In China, there may be at least two domestication areas (Bettinger *et al.*, 2010; Cohen, 2011), one primarily in the Yellow River basin, where millets (broomcorn millet (*Panicum miliaceum*) and foxtail millet (*Setaria italica*)) were domesticated, and the Yangtze River basin, where Asian rice (*Oryza sativa*) was domesticated.

This geographic analysis can be complemented with an ecological analysis through the identification of the major biomes in which crops originated (Harlan, 1992). A biome is a major terrestrial environment characterized by its overall climate (mainly temperature and rainfall), vegetation, and fauna. Some 10 biomes have been described, including tundra, taiga (evergreen coniferous forest), temperate deciduous forest, grasslands (prairie or steppe), deserts, Mediterranean or chaparral, tropical savanna, tropical deciduous forest, and tropical evergreen forest. For each of these biomes, one can

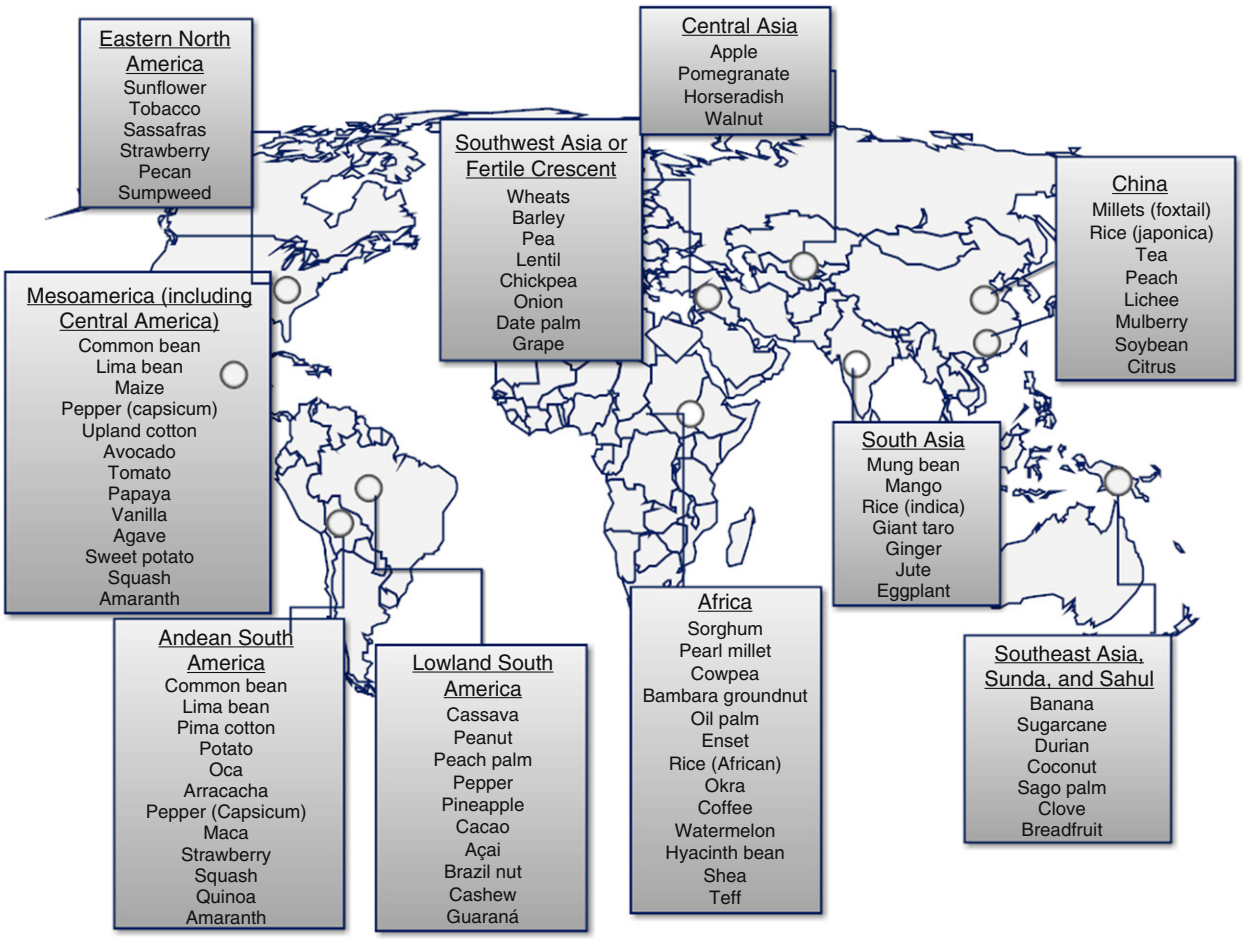


Figure 1 Selected centers of agricultural origins and their respective crops.

then assess to what extent they have played a role in the origins of agriculture and crop domestication. Such an analysis reveals that several crops originated in two biomes, the Mediterranean and tropical savanna biomes. Among crops domesticated in the Mediterranean biome are those from the Fertile Crescent, such as wheat, barley, lentil, chickpea, and pea. Crops domesticated in the savanna biome (and adjacent dry tropical forest) include crops such as maize, common bean, rice, cassava, and peanut. These two biomes share the characteristic of a long dry season, whether during the summer for the former or the winter for the latter (monsoon-type of climate). The dry season may have been an impetus toward cultivation because of the increased need to develop a store of food, irrespective of whether they are grain or roots.

Domestications are not exclusive to the Mediterranean or tropical dry savanna and forest biomes. Other environments have contributed crops as well, such as highland environments (e.g., coffee in the Ethiopian plateau; several root crops, including potato in the Andes Mountains). Coastal areas have contributed coconut, beets and more recently sugarbeets, and cotton. Temperate forest may have contributed fruits and nuts, such as apples, pear, cherry, and walnut. Tropical rain forests were most likely the home of sugarcane, banana and plantain, mango, and cacao.

Centers of domestication tend to occur in areas of higher biodiversity or biodiversity hotspots (Gepts, 2008). Thus, actual or prospective farmers have been opportunistic in recognizing potential crop plants by domesticating them from local biodiversity, wherever they were located. In this regard, it is perhaps not surprising that certain species or groups of related species have been domesticated multiple times. For example, there are five domesticated *Phaseolus* bean species, two of which – common bean and lima bean (*Phaseolus lunatus*) – have been domesticated twice, in Mesoamerica and in the Andes (Gepts, 1998; Serrano-Serrano *et al.*, 2012; Andueza-Noh *et al.*, 2013). Three other domesticated *Phaseolus* species – runner bean (*Phaseolus coccineus*), year bean (*Phaseolus dumosus*), and tepary bean (*Phaseolus acutifolius*) – were domesticated in ecologically different environment (Freytag and Debouck, 2002), reflecting a possible choice on the part of farmers to select different domesticates rather than adapt a single domesticate to a broad range of environments. Other examples are *Capsicum* species (five species domesticated in different areas of Mexico, Central America, and South America; Pickersgill, 2007), cotton (four species domesticated, two in the Old World and two in the New World; Wendel *et al.*, 2009), and wheat (three species domesticated in and around the Fertile Crescent; Willcox, 2013).

When and How Quickly Did Domestication Take Place?

One of the remarkable observations concerning the origins of agriculture is that most origins trace back to a similar period, approximately 11 500–8 000 BP (Price and Bar-Yosef, 2011 and other articles in the same special issue). This period coincides with the end of the last Ice Age. This may suggest that climate change may have played a role in the transition from HG to agriculture, either because the warming temperatures may have been more favorable for cultivation or may have increased the length of dry seasons. In addition, a climatic singularity may have played a role. It has also been suggested that there was an increase in CO_2, which may have stimulated plant growth around that time (Sage, 1995), or that the climatic conditions became more stable thereby facilitating selection for adaptation during the domestication process (Richerson *et al.*, 2001). However, alternative explanations can be offered. For example, the different groups of humans initiating the practice of agriculture did so because they had reach similar levels of cultural development, including knowledge of food plants and their respective harvest and processing methods. An additional feature of this transition is that climate change did not proceed linearly toward a warmer and drier state. Following an initial, brief warming after the last age, there was a reversion – the Younger Dryas – when cold and dry conditions returned from the preceding warmer/wetter Bølling–Allerød interstadial between the Pleistocene and Holocene eras. The Younger Dryas lasted approximately from 13 000 to 11 500 BP years (Balter, 2010). It is thought to have been one of the factors leading hunter-gatherers to start cultivating plants, not only in the Fertile Crescent (but for opinions to the contrary, see, e.g., Willcox *et al.*, 2008), but also to varying degrees in other areas involved in the origins of agriculture (Bar-Yosef, 2011).

Although there is some variation in the earliest dates for each of the centers of origin, there is also great variation in the abundance of archeological sites among centers. The Fertile Crescent is generally considered to be the most intensively studied center of agricultural origins. One is more likely to find older when the number of sites increases. Another factor influencing the antiquity of archeobotanical remains is the nature of the remains. Macroremains (e.g., whole seeds) are generally less likely to survive undamaged for a long time. Hence, they will generally be younger than microremains (e.g., phytoliths or starch grains). For example, the oldest remains for common bean and maize are starch grains (Piperno and Dillehay, 2008; Piperno *et al.*, 2009). Thus, when comparing the domestication age of different crops, the type of remain and the taphonomic parameters that affect their survival should be taken into account (Allison and Bottjer, 2011).

The duration of the process of domestication has only recently drawn attention, in part because of the recent discovery of sites that harbor a mix of wild and presumably domesticated remains, principally in the Fertile Crescent and China (Fuller *et al.*, 2009, 2012). Two traits have been studied principally: seed shattering (in cereals only) and seed size (in cereals and other crops). Seed shattering in cereals takes place because of the presence of a brittle inflorescence axis (also called rachis). A brittle rachis can be recognized because of the smooth break area where the seed developed on the rachis, in contrast with the rough breakage area caused by mechanical threshing to release seeds from the nonbrittle rachis. Because of the qualitative nature of the trait (presence or absence of abscission scar) and the clear segregation classes, there are no environmental effects on the trait and therefore limited ambiguities in determining the domesticated status of the remains (aside from potential developmental differences). Thus, this anatomical diagnostic trait makes it possible to follow the progress toward full domestication ($\sim$100% of remains in the

domesticated category) in any given archeological site. For seed weight, one or more of the dimensions of the seed are measured. Based on observations on contemporary wild and domesticated seeds, one can determine a threshold beyond which a seed can be considered domesticated as opposed to a wild-type seed. A complicating factor here is that seed size is influenced by environmental conditions (Johannsen, 1909; Harper *et al.*, 1970; Motto *et al.*, 1978). An increase in seed size can, therefore, not be considered automatically as a result of an ongoing domestication process (i.e., a genetic change due to selection) but could also represent an improvement in growing conditions. For example, reduced population densities in wild stands (because of previous harvests) may lead to larger seeds, as does cultivation, even in the absence of selection during domestication. An increase in seed size can potentially be taken as evidence for domestication, but only with the necessary caution.

Several approaches have been followed to estimate the duration of domestication. Empirical approaches involving harvesting of contemporary wild populations of cereals – einkorn wheat (*Triticum monococcum*), emmer wheat (*Triticum dicoccum*), and barley (*Hordeum vulgare*) – as well as mathematical modeling of the frequency of mutant (nonshattering) alleles have shown that with the appropriate harvest method (e.g., use of sickles) could proceed quickly (from 20–30 to 300 generations) (Hillman and Davies, 1990). Factors considered in the modeling experiments were the level of selection intensity and self-pollination, with stronger selection and higher inbreeding levels accelerating the pace of domestication. Thus, it would appear on the face of these experiments that there would be no genetic impediments to a rapid domestication once mutations were present in the wild populations.

Molecular analysis of DNA sequence variation has also provided estimates of the length of the domestication bottleneck. In maize, when taking a domestication duration of at most 2800 years (Eyre-Walker *et al.*, 1998), the bottleneck size was estimated at 3500 individuals.

In soybean, a domestication bottleneck of 3000 year was posited for a founding population of 6000 individuals (Guo *et al.*, 2010), whereas in rice the founding population was only 1500 for a similar duration (Zhu *et al.*, 2007). These estimates are ambiguous, however, because the bottleneck severity depends on both population size and duration of the bottleneck. Thus, estimates of the duration of the bottleneck are dependent on the size of the population of the wild progenitor during the domestication process, which is essentially unknown.

One should also take into account several considerations that can slow down the speed of domestication. First, the source of variation for domestication alleles may determine how quickly domestication could proceed, namely, whether variation originated in existing variation in the wild progenitor populations ('standing variation') or if it originated in *de novo* mutations. Standing variation may have led to faster domestication than reliance on *de novo* mutations; however, it remains to be determined how strong a barrier the appearance of mutations would be, given the large population sizes observed for some wild relatives. Observations in a wide range of organisms and traits have shown that selection for adaptation relies on both standing variation and *de novo* mutations (Durand *et al.*, 2010; Peter *et al.*, 2012; Fu and Akey, 2013; Studer *et al.*, 2011). Second, the modeling experiments assume constant, nonzero selection levels in each generation, which may not have been the case, given that at least in its initial phase, agricultural production may have been a supplementary source of food rather than a mainstay. In some years, there may not have been any cultivation at all and therefore no selection leading potentially to domestication. Third, domestication in most cases is based on multiple traits, which have to be recombined into a single evolutionary lineage. Even if selection for individual domestication traits was taking place in different lineages, ultimately these individual traits needed to be combined through outcrossing among lineages and recombination in the progenies. Aside from the likely chance encounter of lineages, outcrossing (especially in autogamous species) and the concomitant recombination will almost certainly have slowed down, although not prevented the domestication process. Fourth, hybridizations between the wild ancestor and the incipient domestication, a likely occurrence if the two types were sympatric, would have also slowed down domestication by diluting the frequency of domestication alleles and decreasing the expression of the traits they control, given their generally recessive nature (Ladizinsky, 1985).

These considerations, as well as archeobotanical observations, have led to the current proposal that domestication was a drawn-out process taking place over several millennia, generally approximately 2000–3000 years (Allaby *et al.*, 2008; Fuller *et al.*, 2012). This proposal is based on several observations. There is a relationship between the frequency of domesticated phenotypes (e.g., seed size and nonbrittleness) and their age over several sites in the Fertile Crescent and China (Fuller, 2007): the younger the site, the higher the frequency of domesticated archeobotanical remains. Concomitantly, there is an increase in the frequency of seeds of the so-called arable weeds that accompany crop cultivation (Colledge and Conolly, 2010). Finally, the amounts of stored grains also increased around this time and have been deemed to be too large to originate in mere gatherings of wild seeds.

In turn, these new arguments need to be considered with caution. The development of a timeline for domestication based on different archeological sites (e.g., Tanno and Willcox, 2006) introduces a confounding factor, namely, the differential rate of spread or adoption of agriculture. Thus, differences in the percentage of domesticated remains among locations may not reflect the degree of advancement of the domestication process but rather the differential spread or the earlier or later adoption of cultivation of plants. In addition, the presence of weeds may not necessarily indicate the presence of cultivation. The main characteristic of these weeds is their adaptation to disturbed conditions and their ability to colonize these environments. Although plowed fields are disturbed environments, they are not the only anthropogenic environments. Terrains with intensely harvested wild populations or the surroundings of villages could also be a source of arable weed seeds. Thus, the mere presence of these plants does not necessarily indicate cultivation and may lead to an overestimate of the duration of the domestication process. Large amounts of grains in storage likewise is not indicative of harvest from cultivated plots. Several experiments or observations on the production of wild stands of plants, whether

annuals or perennials, suggest high levels of productivity in natural stand of crop wild relatives (CWR) (Harlan, 1967; Hillman and Davies, 1990). The proposed extended predomestication cultivation also needs to be reconciled with a potential push–pull situation related to the cultivation and harvest of wild plants. Cultivation of a wild plant that is unadapted to cultural practices, including planting and harvesting, may not lead to expected yields needed to complement harvests from wild plant gathering. Abbo *et al.* (2011, 2013) showed how harvests of wild pea are very variable and low across location and years, making cultivation for a substantial number of years less likely unless key mutations would be present in these populations to increase yield, such as mutations for reduced seed dormancy after planting and limited pod dehiscence at maturity. However, once this type of mutation is present, domestication could proceed more rapidly as suggested by Tzarfati *et al.* (2013), who showed how the nonbrittleness and free-threshing mutations in emmer wheat (*Triticum turgidum*) reduced threshing time by 30% and 85%, respectively, thus providing an incentive for cultivation of these variants. An important limiting factor may, therefore, be the frequency of mutations pertaining to domestication syndrome traits in wild progenitor populations, combined with gene flow and recombination rates of these different mutations into a single evolutionary lineage.

Overall, the actual duration of the domestication process is still a controversial topic. Although it is probably longer than what the analysis of individual traits suggests, claims for a long predomestication cultivation phase need to be examined with caution and the actual length should be determined more precisely.

A Common Feature among Domestications: Reduction of Genetic Diversity at the Genome Level

A general feature of domestication is the reduction of genetic diversity in the domesticated gene pool compared with the gene pool of the wild progenitor. The amount of reduction depends on the species, its reproductive system, and the molecular marker system used. In general, outcrossing species show a smaller reduction compared with selfing species (e.g., maize: 83% nucleotide diversity retained in domesticated gene pool, Hufford *et al.*, 2012, 2013; rice: 60–65%, Caicedo *et al.*, 2007, or 35%, Zhu *et al.*, 2007; common bean: ~40% each in Andean and Mesoamerican domestications, Bitocchi *et al.*, 2013; soybean: ~60%, Lam *et al.*, 2010). Vegetatively propagated crops also tend to maintain high levels of genetic diversity as illustrated by grape and apple (95% retention of diversity, Myles *et al.*, 2011; Cornille *et al.*, 2013). Techniques of propagation of specific phenotypic variants, such as grafting or cuttings, as well as the role of major genes in the genetic control of individual traits, and the presence of a juvenility period and the long production period in vine or tree crops could have strongly reduced genetic diversity. Nevertheless, gene flow from local wild populations, small-scale propagation, local adaptation to environmental conditions, and consumer preferences could act to maintain high levels of diversity (Cornille *et al.*, 2013).

Domestication has also affected multilocus association as measured by linkage disequilibrium (LD), the nonrandom association of gametes. The nonrandomness can arise from close linkage, in which case LD can be used to map loci controlling phenotypic traits. LD, however, is also induced by other factors, such as population structure induced by geographic isolation, genetic bottlenecks, and reduced recombination. For example, in common bean, which consists of two geographically separated taxa (Andean vs. Mesoamerican), there is much higher LD in a sample including the two taxa (95% of locus pairs in LD) than in separate Andean and Mesoamerican samples (~70%; Kwak and Gepts, 2009). In general, LD increases as a consequence of domestication (e.g., maize: Wright *et al.*, 2005; Hufford *et al.*, 2012; rice: Zhu *et al.*, 2007; soybean: Hyten *et al.*, 2007; sunflower: Kolkman *et al.*, 2007; common bean: Kwak and Gepts, 2009; Rossi *et al.*, 2009; foxtail millet: Wang *et al.*, 2010).

The Genetic and Molecular Basis of the Domestication Syndrome

Although crops and their wild progenitors belong to the same biological species and their divergence was initiated only some 10 000 years ago, they generally show marked morphological and physiological differentiation as a result of the selection for adaptation to human cultivation and consumption for food and nonfood uses. The genetic basis for this profound change resulting in crop plants as are known today has only relatively recently been elucidated. Initially, genetic analyses were conducted on individual traits. The general conclusion was twofold, namely, that most domesticated traits were controlled by recessive alleles at one or two genes, suggesting loss of function mutations (Ladizinsky, 1985). Such studies were generally limited, however, by the lack of information on the location of these genes within plant genomes and their potential linkage. The ability to develop linkage maps with molecular markers of sufficient density and distribution in the crop genome, together with the development of segregating populations resulting from crosses between carefully selected wild and domesticated genotypes, remedied this situation and provided a more complete picture (including linkage information) on the inheritance of the domestication syndrome.

Results from these analyses have led to a series of general conclusions about the architecture of the genetic control of the domestication syndromes across a broad range of crops, mostly annual, herbaceous plants (Gepts, 2004). A first conclusion is that often major, Mendelian genes or quantitative trait loci (QTLs) control individual traits, in addition to genes or QTLs of smaller effect. This observation confirms the single-trait analyses. Second, the phenotypic variation is often mainly due to genetic rather than environmental effects, suggesting high heritability. The first two observations suggest a simple genetic control, which would have facilitated and speeded up selection during the first stages of domestication. Third, in many crops, a subset of the genes controlling the domestication syndrome are linked, at least loosely, on a limited number of chromosomes. The latter situation may have been an advantage in situation where hybridizations take place, either between wild and domesticated types or among

incipient domesticates in the early phases of domestication when lineages with different elements of the domestication syndrome were recombined. Linkage made recovery of parts of the hybridization syndrome easier, although not preventing assembly of the domestication syndrome because of repulsion linkage.

With the availability of very large numbers of markers, such as microsatellite or simple-sequence repeats, genome-wide association studies (GWAS) have been made possible among nonpedigreed individuals. In contrast with QTL analyses, which are conducted in the segregating progeny of crosses between parents, GWAS are conducted among individuals of a species, which are presumed to be unrelated. After removing the potentially confounding effect of population structure, which could lead to false positives, any association between marker and a phenotypic trait could be attributed to linkage. In this way, the different genes controlling the domestication syndrome can be placed on the crop linkage map. An example of this approach is provided by association of certain genes, such as the photoreceptor gene *PHYC* and flowering time in pearl millet and changes in frequency of alleles at this locus in a 27-year period corresponding to aridity in Western Africa (Saïdou *et al.*, 2009; Vigouroux *et al.*, 2011). Another example is the identification of the *INTERMEDIUM-C* gene responsible for the 6-rowed variants in barley (*H. vulgare*) (Ramsay *et al.*, 2011).

The introduction of next-generation sequencing has made sequencing more efficient and cheaper. Hence, sequencing of multiple genotypes has also been made possible, allowing sequence comparisons on a genome-wide basis and a larger sample of genotypes. Comparisons between wild and domesticated types identify potential genome regions that have been targets of selection during the domestication process. An interesting feature of this approach is that it does not require prior knowledge or assumptions about traits under selection. In contrast with QTL and GWAS approaches, which require phenotypic variation (top-down approaches; Ross-Ibarra *et al.*, 2007), the resequencing approach is a bottom-up approach that relies on molecular population genetic arguments, such as allele frequencies differences. For example, a sharp reduction in nucleotide variation in certain areas of the genome in domesticated types compared with wild types suggests selection on phenotypes controlled by one or more genes in this region (also known as a selective sweep). Genetic drift associated with domestication would lower genetic diversity across the entire genome during and after domestication, whereas selection will be confined to those regions of the genome that contain traits under selection. The size of the region is negatively correlated with the level of recombination but positively correlated with the selection intensity. An example of this approach is the identification of a selective sweep around the waxy (wx) locus in rice. The wx locus is involved in starch metabolism in rice grains; in particular, it is responsible for the stickiness of rice grains and was selected during or after domestication in *japonica* rice (Olsen *et al.*, 2006).

In sunflower, a genome-wide study identified 36 genes showing evidence of selection during and after domestication (Chapman *et al.*, 2008). Many of the genes involved were involved in amino acid metabolism and protein catabolism (as in maize; Wright *et al.*, 2005) and were located in the same regions as previously identified QTLs for the sunflower domestication syndrome. The timing of selection could be presumably narrowed down to the initial domestication process per se or the subsequent improvement stage by distinguishing within the domesticated group between the so-called primitive (or landrace) varieties and varieties improved by selective breeding. Hufford *et al.* (2012) conducted a genome-wide resequencing in wild, landrace, and improved maize entries. Among their findings were the existence of stronger selection during the actual domestication phase than in the subsequent improvement phase. An additional observation is the existence of potential introgression from a wild relative (*Z. mays* var. *mexicana*), which is not the progenitor of maize but contributed nevertheless alleles that are potentially instrumental in adaptation to higher altitudes (van Heerwaarden *et al.*, 2011). Furthermore, several regions were identified that showed evidence of selective sweeps, representing some 1–2% of the maize gene set. Some of these genes map near QTLs that had been identified previously. As a note of caution, the separation between domestication and improvement genes may not always be clear-cut, and in some cases, such as color or shape, variants may involve arbitrary decisions as to the timing of the appearance of these variants. In addition, some domestication genes (identified as such by their absence in the wild progenitor gene pool) are not distributed across the entire domestication gene pool but characterize only a subset of the gene pool, suggesting that there is no clear dichotomy between these two classes of genes.

Concurrent with these studies, many genes controlling important domestication traits, whether they are considered domestication or improvement traits, have been isolated using map-based cloning of QTLs or a candidate gene approach, based on sequence information of genes controlling similar phenotypes in other species (Paterson *et al.*, 1995; Lenser and Theyßen, 2013). Doebley *et al.* (2006), Gross and Olsen (2010), and Olsen and Wendel (2013) presented recent overviews of genes that have been isolated. The majority of these genes are transcriptional regulators, such as the *tb1* gene in maize (conditioning the single-stem, nonbranched plant type of domesticated maize; Wang *et al.*, 1999); however, a significant proportion codes for structural genes like enzymes, such as the waxy locus (not only in rice but also in broomcorn millet and maize) and the *BADH2* gene (for rice fragrance). The types of mutations involved are diverse and include nucleotide substitutions (leading to premature stop codons or amino acid substitutions), insertions or deletions (indels), transposon insertions, or *cis*-regulatory changes (the latter outside the gene, such as is the case for the *tb1* locus controlled by an enhancer-like transposon insertion some 65 kbp upstream of the gene). In most cases, a single causative mutation can be identified. An exception to this pattern is the *PvTFL1y* gene, which is responsible for the determinate growth pattern in common bean, in which a retrotransposon insertion, synonymous substitutions, nonsynonymous substitutions, indels, a putative intron-splicing failure, and a deletion of the entire locus, all lead to loss of function, consistent with the recessive nature of the determinate phenotype (Repinski *et al.*, 2012; Kwak *et al.*, 2012). This observation suggests that the determinate trait has been selected multiple times, underscoring the importance of earliness and compact growth habit in crop cultivation.

In general, therefore, the extensive sequence data available from wild and domesticated types of major crop plants and related genetic and genomic approaches have provided a trove of information about several important features of the domestication process, including the genetic structure of the domesticated gene pool in relation to its progenitor gene pool, the effect of domestication on genetic diversity, evidence for selection, and the nature of the genes underlying domestication phenotypes.

Implications of Domestication Studies for Crop Improvement, Distributed Breeding, Redomestication, and Neodomestication

Although domestication analyses are integral part of broader studies on the origins of agriculture, results of these have important practical applications in three major areas. First, they provide essential information for conservation of genetic resources. In most, if not all, crops, improved cultivars contain less diversity than landraces (varieties selected and grown by farmers in a subsistence agriculture context) and markedly less than wild progenitors and other wild relatives because of the genetic bottleneck and selective effect that have operated during domestication and dissemination and improvement subsequent to domestication. It is hard to overestimate the importance of the diversity contained in landraces and CWR for continued improvement of crops. Yet, this diversity is also being severely threatened by a number of interconnected factors, such as habitat destruction and climate change. Both *in situ* (in farmers' fields and natural vegetation) and *ex situ* (in gene banks, botanical gardens, and other collections) approaches are being used to conserve this diversity (Gepts, 2006), but a more intensive characterization is urgently needed, at the molecular (McCouch *et al.*, 2013) and phenotypic (Furbank and Tester, 2011; Andrade-Sánchez *et al.*, 2013) levels. More basic research on plant function, especially gene interactions as well as gene–environment interactions (e.g., Mochida and Shinozaki, 2011), are required to increase the use of this genetic diversity. An additional finding – the existence of selective sweeps – has also profound impacts on breeding, because it suggests that, in addition to beneficial effects, some genes may have been introduced that have deleterious effects but are in coupling phase with the introgressed beneficial genes, a possible explanation for linkage drag. Identification of these deleterious genes and recombinants between them and beneficial genes would represent a significant progress in the introgression of genetic diversity of the exotic germplasm represented by landraces and CWR.

Domestication is not just a process that occurred at the transition from HG to agriculture. To the extent that this process involves an active and conscious selection process, it has also been operative in subsequent phases of crop evolution during the different dissemination steps to other growing regions, especially those outside the centers of origin. Current breeding efforts aiming to produce improved cultivars through selective breeding can also be construed as a step in the domestication process. During these different domestication steps, farmers have played a significant role in maintaining existing but also selecting new diversity appearing in their fields, leading to domesticated gene pools with high levels of phenotypic diversity up until the nineteenth century and beginning of the twentieth century (e.g., von Martens, 1860; Tracy, 1907; Freeman, 1912; Hedrick, 1931). Although genetic diversity in domesticated gene pools has decreased in the latter part of the tewntieth century and early twenty-first century, farmers continue to play an important role in maintaining crop genetic diversity (e.g., beans: Payró de la Cruz *et al.*, 2005; Zizumbo-Villarreal *et al.*, 2005; Worthington *et al.*, 2012; cassava: Elias *et al.*, 2001; Pujol *et al.*, 2005; pearl millet: Couturon *et al.*, 2003; Lakis *et al.*, 2011; and sorghum: Alvarez *et al.*, 2005; Barnaud *et al.*, 2008) through their knowledge of adaptation to local conditions and consumer preferences. Through their seed systems, farmers can control levels of genetic diversity, the genetic composition of their fields, and in- and outflows of diversity in their fields, including wild relatives and improved varieties.

It is this ability of farmers to recognize useful genetic variation and to assemble their own seed stock as part of the capital of their farms (Soleri *et al.*, 2002) that has led to successful efforts of participatory breeding generally involving farmers and villages in subsistence agriculture settings (e.g., maize: Smith *et al.*, 2001; barley: Ceccarelli *et al.*, 2000, 2003; common bean: Asfaw *et al.*, 2012; and agroforestry: Leakey, 2012). These participatory activities are particularly significant because they lead to a decentralized or distributed type of breeding in contrast with the current prevalent model, which is primarily centralized in public agricultural experiment stations or seed companies. Distributed breeding (by analogy with computing) may give a boost to genetic improvement by addressing local needs of farmers dictated by the needs of local adaptation and consumer preferences for individual crops. As proposed by Leakey and Asaah (2013), domestication has more than production benefits; it can have social, economic, and environmental benefits when it is applied to the entire spectrum of plants. This process includes not only continued domestication of existing crops but also incipient domestication of locally adapted, underutilized, and often perennial tree crops (for agroforestry purposes). In turn, these improved crops can play diverse roles, for example, in mitigating environmental degradation, creating new income opportunities, and promoting local employment and commerce related to food and tree products (Leakey and Asaah, 2013). This local focus of plant domestication may get a further boost in the response to climate change. The inherent uncertainty associated with climate change (e.g., Thornton *et al.*, 2009) will make it difficult to institute breeding programs with broad adaptation. Hence, to make agroecosystems more resilient, the response should be local and should combine a broad variety of responses, genetic and nongenetic, as proposed by Kiers *et al.* (2008) and Clough *et al.* (2011).

Finally, domestication is and will be playing a role in redomestication and neodomestication of plants. For example, some crops may be repurposed for an entirely different objective than the one they were first domesticated for. Maize was initially a food crop before it became an important feed crop and was also used for industrial purposes. Using maize as a feedstock for alcohol fuel production should decrease the emphasis on seed production but increase the emphasis on

vegetative matter (stems and leaves) production, essentially leading to maize varieties with reduced seed harvest index, reversing the millennia-long trend toward a higher seed harvest index. It has often been observed that domesticated plants constitute a very small fraction (<0.01%) of the total number of plant species (approximately 300 000 species; Mora *et al.*, 2011). Even if not all of plant species can be domesticated (for a variety of reasons), it seems likely that additional species can be domesticated to satisfy the needs of humanity. The experience acquired with domestication of existing crops should help one conduct deliberate and conscious neodomestication of additional plants; conversely, one does not know why so few plants have been domesticated so far. The concept of domestication potential needs to be explored further to assess which plants could be domesticated with greater ease. Further basic research in plant domestication is, therefore, needed to better understand the domestication process and the process of transition from HG to agriculture in general. These studies, although ostensibly turned toward the past, have an important practical role in the future of humanity and its well-being.

See also: Agroforestry: Complex Multistrata Agriculture. Agroforestry: Participatory Domestication of Trees. Biodiversity: Conserving Biodiversity in Agroecosystems. Breeding: Plants, Modern. Climate Change: Agricultural Mitigation. Climate Change and Plant Disease. Climate Change: Cropping System Changes and Adaptations. Climate Change, Society, and Agriculture: An Economic and Policy Perspective. Cloning: Plants – Micropropagation/Tissue Culture. Domestication of Animals. Food Security, Market Processes, and the Role of Government Policy. Food Security: Yield Gap. From Foraging to Agriculture. Genebanks: Past, Present, and Optimistic Future. Genomics: Plant Genetic Improvement. Intellectual Property in Agriculture. Plant Cloning: Macropropagation

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http://www.census.gov/main/www/popclock.html
World Population Clock, US Census Bureau.

Dust Pollution from Agriculture

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Glossary

Dust Fine particulate matter, usually with an aerodynamic diameter of ≤10 μm.
Emission factor Amount of particulate matter emitted per unit of a specific activity.
PM2.5 Particulate matter having an aerodynamic diameter of ≤2.5 μm.
PM10 Particulate matter having an aerodynamic diameter of ≤10 μm.
TSP Total suspended particulate matter.

Dust as a Nuisance, Pollutant, and Natural Resource

Dust is often visualized as particles that are carried great distances by the wind or that reflect light and seemly shimmer when suspended in the atmosphere. Dust also casts a dull appearance or haze on otherwise bright and clean surfaces. These particles are considered by some to be a nuisance because they can mask the true appearance of a surface and require work to restore the original appearance of the surface or they can irritate our eyes or pulmonary airway. To others, dust is a valuable natural resource because it is important in the formation of raindrops and soils. The poet Robert Frost may have envisioned dust as a valued resource when he composed the following verse to the poem A Peck of Gold in 1928:

> "All the dust the wind blew high
> Appeared like gold in the sunset sky,
> But I was one of the children told
> Some of the dust was really gold."

Although this poem was written before the North American Dust Bowl of the 1930s and societal interest in natural resource conservation, farmers and land managers have long recognized dust as being the most precious of materials (gold) which comprise soils and sustain life.

Early explorers were acutely aware of the adverse effects of dust on humans. For example, Meriwether Lewis of the Lewis and Clark Expedition (Moulton, 1991) noted "… soar eyes seem to be a universal complaint among those people; I have no doubt but the fine sand of these plains and river contribute much to this disorder" while traveling along the Columbia River in the United States Pacific Northwest in 1806. Governor-in-Chief George Simpson (1826) of the Hudson Bay Company noted "This district of country is subject to very high winds which, sweeping over the sands, raise such a cloud of dust as renders it dangerous, or even impossible, to leave the house …" while traveling near Walla Walla, Washington in 1826. Little did these explorers realize that this windblown dust was the parent material from which soils formed on the Palouse, one of the most productive wheat-producing regions in the world located on the eastern edge of the Columbia Plateau along the border of modern day Idaho and Washington. Since that time, human activities undertaken to support a growing population have expanded sources from which dust is emitted into the atmosphere or exacerbated conditions that cause dust to be emitted into the atmosphere. As a result of these activities and a greater awareness of public health, nations began to adopt laws in the mid-twentieth century to protect the health and welfare of its citizens. For example, the Clean Air Act of 1971 required the United States Environmental Protection Agency (USEPA) to establish National Ambient Air Quality Standards for Particulate Matter. Air Quality Standards were established for suspended particles having a nominal diameter of ≤45 μm, but more recent legislation has set standards for regulating much smaller particles suspended in the atmosphere.

In this article, dust is defined more specifically as particles with an aerodynamic diameter ≤10 μm. This definition conforms to criteria used to describe particulate matter as a pollutant. Particulate matter having an aerodynamic diameter ≤2.5 μm (PM2.5) and ≤10 μm (PM10) are both regulated as pollutants. Many nations have created laws and established air-quality standards for regulating dust concentrations in the atmosphere. These air-quality standards were developed to protect citizens from the adverse effects of being exposed to dust. This article will, in part, review air-quality standards established by many nations throughout the world and describe techniques that are employed to measure dust concentrations in the atmosphere.

Sources that contribute to the dust load in the atmosphere can be classified as either point or nonpoint sources. Point sources emit dust into the atmosphere from a specific source or location, whereas nonpoint sources emit dust into the atmosphere from diffuse or widespread areas. Perhaps, the biggest nonpoint source of atmospheric dust is the Saharan Desert. Warren *et al.* (2007) suggested that the Bodélé Depression, located along the southern edge of the Saharan Desert, is the dustiest place on Earth. Dust storms in the Bodélé Depression occur approximately 100 days per year. Other major nonpoint sources of dust include wildfires, wood or debris burning, construction and mining sites, unpaved roads, and motor vehicles. Major point sources of atmospheric dust include foundries, paper mills, refineries, and power plants. Agricultural activities also contribute to the dust load in the atmosphere. This is, perhaps, best evidenced by long-term records which indicate a rise in atmospheric dust

concentrations after the introduction of European farming practices in the Pacific Northwest United States (Busacca *et al.*, 1998) and southeastern Australia (McGowan *et al.*, 2010).

This article focuses on agricultural sources of dust and, where possible, strategies to control dust emissions from these sources. Although the goal of developing strategies is to reduce emissions to achieve compliance with air-quality standards, these strategies must also be sustainable to ensure a viable agricultural industry.

Environmental Regulations

Many nations around the world have adopted air-quality standards to protect the health and welfare of its citizens against the adverse effects of air pollution. The World Health Organization, which has representation from 194 nations, has adopted a constitution that set guidelines on air pollutants including atmospheric dust. The guidelines established by the Organization recommend the respective daily PM2.5 and PM10 concentrations not exceed 25 and 50 $\mu g\ m^{-3}$ and the respective annual PM2.5 and PM10 concentrations not exceed 10 and 20 $\mu g\ m^{-3}$ (World Health Organization, 2005).

There is no clear and unequivocal evidence that associates adverse health effects of people to exposure to specific concentrations of particulate matter in the atmosphere. This lack of evidence is, in part, due to the variability among people in their response to exposure to particulate matter. As a result, nations have adopted guidelines or air-quality standards on the basis of availability of resources and risk assessment. Air-quality standards adopted by individual nations may, therefore, be more relaxed or more stringent than World Health Organization guidelines. The European Union, for example, has adopted a daily PM10 Air Quality Standard of 50 $\mu g\ m^{-3}$ that should not be exceeded more than 35 days per year (European Commission, 2011). The European Union has not set a daily air-quality standard for PM2.5, but has adopted an annual PM2.5 and PM10 Air Quality Standard of, respectively, 25 and 40 $\mu g\ m^{-3}$. Similarly, Australia and New Zealand have adopted a daily PM10 Standard of 50 $\mu g\ m^{-3}$, that is, respectively, not to be exceeded more than 5 and 1 day per year. The United States has adopted a daily PM2.5 Air Quality Standard of 35 $\mu g\ m^{-3}$ that should not exceed the 98th percentile averaged over 3 years and a daily PM10 Air Quality Standard of 150 $\mu g\ m^{-3}$ that should not be exceeded more than 1 day per year averaged over 3 years. Although annual concentrations of PM10 are not regulated, the United States has adopted an annual PM2.5 Air Quality Standard of 15 $\mu g\ m^{-3}$. Chile, Costa Rica, and Mexico have adopted a daily PM10 Air Quality Standard similar to the United States (not to exceed 150 $\mu g\ m^{-3}$).

New air-quality standards for particulate matter were established by China in 2012. Before this time, no air quality standard had been established for PM2.5. The new air-quality standards, which are to be implemented by residential, industrial, and rural areas across China by 2016, include a respective daily PM2.5 and PM10 concentration not to exceed 75 and 150 $\mu g\ m^{-3}$ and a respective annual PM2.5 and PM10 concentration not to exceed 35 and 70 $\mu g\ m^{-3}$.

Many communities across the world fail or have failed to comply with air-quality standards for particulate matter. Emission of particulate matter from point and nonpoint sources can contribute to the dust load and exceedance of PM2.5 and PM10 Air Quality Standards. To achieve compliance, the relative contribution of sources to overall emissions is important in devising an abatement program. For this reason, emission factors have been established to identify the relative contribution of sources to the overall dust load. Emission factors are defined as the amount of particulate matter emitted per unit of specific activity and are used to document emission inventories in Australia (http://www.npi.gov.au/), Canada (http://www.ec.gc.ca/inrp-npri/), Europe (http://www.eea.europa.eu/publications/emep-eea-emission-inventory-guidebook-2009), and the United States (http://www.epa.gov/ttn/chief/).

Techniques to Measure Dust in the Atmosphere

Dust in the atmosphere can be characterized by mass, number of particles, or size of particles using active and passive sensors. Active sensors rely on artificial aspiration to draw particles into the sensor whereas passive sensors use natural ventilation to guide particles into the sensor. Active sensors are seldom isokinetic and, thus, tend to underestimate or overestimate the mass or concentration of particles in the atmosphere. Passive sensors are dependent on wind to draw particles into the sensor and, therefore, are impractical for characterizing particles under stagnant atmospheric conditions. Although several active and passive sensors are highlighted in this section, other sensors have been developed or are commercially available to characterize atmospheric dust.

Active sensors characterize particles in the atmosphere using optical detectors, β-attenuation analyzers, and filters. The DataRAM, DustTrak, E-sampler, and Grimm Environmental Dust Monitor characterize particles using optical detectors. These detectors measure the scattering or absorption of light passing through a column of air with the amount of scattering or absorption being proportional to concentration of dust in the column of air. These sensors can be programmed to measure near real-time mass or particle characteristics, including PM10. Beta-attenuation analyzers measure the intensity of β-rays passing through dust, which is generally collected on a filter. A reduction in intensity is due to absorption of β-rays by dust on an otherwise clean filter. The Tapered Element Oscillating Microbalance (TEOM) is a common instrument used to measure near real-time PM2.5 or PM10 concentration. The TEOM (**Figure 1**) aspirates the sediment-laden air, captures the particles on a filter affixed to the end of an oscillating element, and periodically measures the oscillating frequency of that element to ascertain either PM2.5 or PM10 concentration. Both the β-attenuation analyzer and TEOM are approved devices for measuring PM10 concentration in many nations including China, the United Kingdom, and the United States. Sensors that rely on filters to extract particles from an airstream are typically classified by the volume of air moving through the sensor. Both the low-volume and high-volume sampler aspirate air at a known rate through a preweighed hydrophobic filter. The change in weight of the filter over time provides a time-integrated measure of dust in suspension. The high volume sampler (**Figure 1**) is the most



Figure 1 A Tapered Element Oscillating Microbalance (TEOM) and three High Volume samplers for measuring PM10 concentration on the leeward side of an erodible field. The inlet to the TEOM (foreground) is located above the silver enclosure (door to the enclosure is open) whereas the inlets to the High Volume samplers (behind and to the left of the TEOM) are protected by a windshield and positioned at 1, 3, and 5 m above the soil surface.

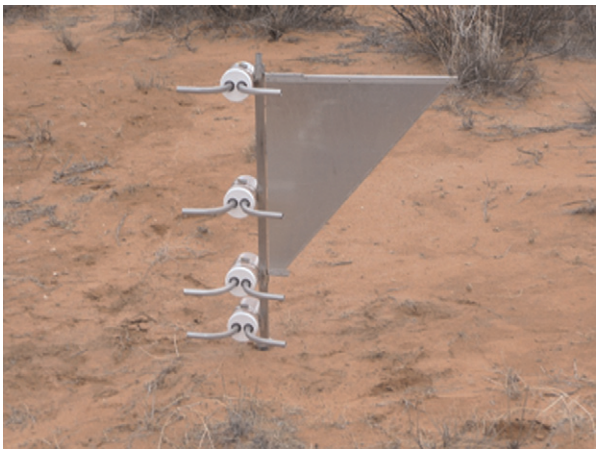


Figure 2 A profile of Modified Wilson and Cooke sensors used to trap windblown sediment. The mast to the right of the sensors maintains their alignment into the wind. Photo courtesy of Dr. R. Scott Van Pelt, Big Spring, TX, USA.

common instrument employed by regulatory agencies throughout the world for measuring PM10 concentration.

Passive sensors include the Modified Wilson and Cooke (MWAC) (Wilson and Cooke, 1980), Big Spring Number Eight (BSNE) (Fryrear, 1986), and Wedge Dust Flux Gauge (WDFG) (Hall *et al.*, 1994). These sensors manually collect airborne sediment during high wind events and are typically inspected and cleaned after each event. Another passive sensor, the Suspended Sediment Trap (SUSTRA), weighs the collected sediment for automated real-time characterization of particles (Janssen and Tetzlaff, 1991). The most widely used passive sensors include the MWAC (**Figure 2**) and the BSNE (**Figure 3**). Passive sensors vary in sampling efficiencies (percentage of sediment trapped inside the sensor to that entering the sensor) due to differences in design characteristics of the sensors. For example, the sampling efficiency of the MWAC,



Figure 3 A profile of Big Spring Number Eight sensors used to trap windblown sediment. The fins (rectangular objects to the left) maintain alignment of the sensors into the wind. The airstream enters through the rectangular opening on the windward face and exits through the wedge-shaped screen on the top of the sensor.

BSNE, WDFG, and SUSTRA sensors, respectively, vary from 90%, 40%, 22%, to 15% when trapping particles $\leq$63 μm in diameter at a wind speed of 5 m s^{-1} (Goossens and Offer, 2000). Particle size and wind speed can dramatically affect the sampling efficiency with efficiencies typically being higher when trapping larger particles or trapping particles at lower wind speeds (Goossens *et al.*, 2000; Sharratt and Feng, 2009). Sharratt and Feng (2009) observed the BSNE sensor trapped PM10 with greater efficiency at lower wind speeds with an efficiency of approximately 15% and 30% when exposed to respective wind speeds of 8 and 3 m s^{-1}.

Sources of Agricultural Dust

Dust can be generated by a multitude of activities within the agricultural industry. These activities might include traveling on unpaved roads, using an internal combustion engine, stockpiling manure, transporting feed or fiber from the field to market, feeding livestock, cleaning pens or machines, aerial spraying, and welding. This article focuses attention on two main sources of agricultural dust that pollute the atmosphere, namely, agricultural facilities and lands. Dust emitted from agricultural facilities occurs primarily from enclosures that confine livestock and store or process raw materials into feed, fiber, food, and fuel. These facilities are regulated as point sources because activities that generate dust are confined to enclosures or buildings often occupied by workers. Dust emitted from agricultural lands result primarily from natural events (e.g., high wind event) and farming operations (e.g., harvesting crops).

Agricultural Facilities

Agricultural facilities, or primarily those enclosures that confine livestock and store or process raw materials into feed, fiber, food, and fuel, can contribute to the dust load in the atmosphere. These facilities generate dust from grinding, shearing, and pulverizing raw products; dander, hair, or feather shedding from animals; or vegetative particles from crop processing, storage, and transfer. Dust emitted from these facilities can be controlled through management practices that involve filtration, design, and husbandry.

The primary risks associated with dust generated by agricultural facilities include explosions, respiratory impairment of humans or animals, nuisance (including associated odors) to neighbors, and reduced visibility (together with its associated traffic hazards). Explosions require confined spaces, threshold concentrations of entrained, flammable dusts, and an ignition source. Therefore, explosions are of concern in grain elevators, feed mills, and similar structures and facilities. Respiratory impairment of livestock and poultry in confined facilities may result in economically significant reductions in productivity or increases in maintenance costs. Exposure to dust in these facilities has more wide-ranging effects on humans, from reduced occupational productivity to impaired health. Agricultural dust as a nuisance can cause interferences in the use or enjoyment of property by neighbors whereas reduced visibilities caused by dust can be a safety hazard and detract from the enjoyment of particularly scenic areas.

Our focus will be on livestock facilities and grain storage and processing facilities that are major sources of agricultural dust.

Livestock facilities

The worldwide production of animal protein and its coproducts involve a nearly infinite spectrum of management systems. At one extreme, animals are free to roam across expansive and largely nonconfined areas. For example, cattle, sheep, and goats may be free to move within a rangeland or pasture, whereas swine and poultry may be free to roam an entire building and adjacent outdoor areas unconstrained by individual cages or pens. In these nonconfined facilities, animal excreta may be reincorporated into the landscape by natural processes or may be collected and stored for fuel or fertilizer. Dust generated from these nonconfined or open-lot facilities may originate from both animal activity as well as natural processes (erosion of the native landscape).

At the other extreme, animals live in confined or concentrated facilities. Animals in these facilities are stocked more densely in space and, in the case of poultry or veal calves, raised in cages or small hutches. Confined beef operations may be either sheltered (under roof) or nonsheltered (open lot without roof) feedyards. Feedyards may have paved or earthen surfaces and be stocked at densities such that no vegetation can be maintained on the surface. Dairy operations may use open-lot facilities similar to beef feedyards, full confinement facilities like poultry buildings, or some intermediate form such as a free-stall barn with both sheltered and nonsheltered areas accessible to the herd. Swine are generally confined within roofed facilities, with animals being segregated according to developmental stage. In confined facilities, animal excrement is periodically collected to avoid accumulation on the pen surface, which would otherwise impose stress on the animals or the broader environment. Dust from confined facilities can typically be distinguished from dust originating from the broader landscape. In the case of open-lot facilities, dust emissions are strongly modulated by weather, especially precipitation and wind speed. In contrast, dust emissions from under-roof facilities tend to be modulated more indirectly by air temperature and humidity as those variables affect mechanical ventilation rates. Some roofed facilities may be passively or naturally ventilated (instead of mechanically ventilated), in which case, dust emissions are relatively unaffected by precipitation but result primarily from the natural ventilation provided by the wind.

Our focus of discussion will be on dust emitted from confined livestock facilities.

Beef feedyards

Beef cattle are increasingly fed in confinement worldwide to capture economies of scale, increase the rate at which retail beef can be brought to market, and access markets for higher-grade beef cuts as compared with animals grazing pasture or rangeland. The United States is the leading producer of cattle for slaughter, but Australia, Canada, Argentina, Brazil, and Mexico also have significant cattle-feeding industries. Developing countries in Asia, Africa, and South America are witnessing rapid growth in the beef sector as long-term disposable income rises. Although it is possible to feed cattle in confinement in temperate and high rainfall areas, feeding systems in those areas tend to be under roof to reduce the amount of rainfall-driven wastewater that must be managed, controlled, and disposed. As a result, open-lot cattle feeding facilities tend to be more prominent in semiarid to arid climates such as the Great Plains and Southwest regions of the United States, the Prairie Provinces in Canada, and areas of Australia west of the Great Dividing Range in Queensland, New South Wales, and Victoria.

The primary prerequisite for the development of a growing cattle sector is the availability of feed grains either from local farming or imported by rail, ship, or truck. Feed grains are the primary component in fed-cattle diets. In some regions, depending on grain markets and the scale of food-processing or biofuel-processing industries nearby, the concentrate (or energy and protein fraction) in fed-cattle diets may be provided by byproducts such as processed root vegetables (e.g., potatoes and beets) or spent grains (e.g., distillers grains and sweet bran). Dust emitted from cattle feedyards is derived primarily from manure excreted by the animals, therefore the type of feed provided to confined-beef cattle is thought to influence emission rates, airborne concentrations, and particle-size characteristics of dust.

Although the cattle are in confinement, excreted manure is deposited on the pen surface and the feed apron (which may be earthen or paved). As the manure dries and is subjected to the animals' hoof action, it becomes part of the pen surface either as a well-compacted manure–soil matrix or as a noncompacted layer of material dominated by manure solids. Under dry conditions, any mechanical disturbance of the noncompacted manure layer – whether by wind scouring, animal hoof action, or operation of heavy machinery, will

generate dust particles and entrain them in the air. This dust, known as fugitive dust or dust emitted from a diffuse or nonpoint source, consists primarily of dried manure particles but will also include soil and waste feed particles, animal dander, exhaust from light vehicles and heavy machinery, dust from unpaved roads, and hair.

Fugitive dust emitted from a feedyard surface tends to be dominated by relatively coarse particles. The median aerodynamic diameter of fugitive dust from feedyards is in the range of 15–25 μm. Sweeten *et al.* (1988) reported that the ratio of PM10 to total suspended particulate (TSP) in fugitive feedyard dust, as measured by high volume samplers, is in the range of 0.19–0.40. Less is known about the relative abundance of fine particles (PM2.5) in feedyard dust, but recent measurements suggest that the PM2.5/TSP ratio is on the order of 0.05. Rainfall events reduce coarse-particle emissions to a greater extent than fine-particle emissions such that both the PM10/TSP and PM2.5/TSP ratios increase temporarily following precipitation but return to original levels within days thereafter.

Fugitive dust emissions from cattle feedyards are usually expressed as emission fluxes (mass per unit of pen area per unit time) or emission factors (mass per animal unit per unit time). These quantities are difficult to measure directly and are usually estimated by measuring dust concentrations both upwind and downwind of the source area. The measured dust concentrations are then input to a dispersion model to infer the emission flux that would have been required to generate the difference in measured concentrations. This indirect approach yields estimates of emission fluxes and emission factors that vary over an order of magnitude as shown in **Table 1**. The high uncertainty in values in **Table 1** may be expected given the differences in climate, feedyard management practices, feed composition, aerosol monitor performance, and dispersion-modeling algorithms across all studies.

Concentrations of fugitive dust in the air downwind of beef feedyards vary diurnally and seasonally depending on emission flux, topography, atmospheric stability, particle-size distribution, and the distance downwind from the source. Because these emissions occur at ground level, increasing atmospheric stability – associated with nighttime, dense daytime cloud cover, or atmospheric inversions – tends to favor higher ground-level concentrations. Even a short-term inversion may have a dramatic influence on ground-level PM concentrations, especially when the inversion coincides with periods of increased animal activity and depleted surface moisture. Under those conditions, which are quite commonly observed near sunset in semiarid and arid climates, short-term (5 min to 1 h) concentrations of fugitive dust may increase 10–15 times higher than the 24-hour average concentration (**Figure 4**). Although the absolute values of those evening peak concentrations vary up to 2 orders of magnitude from day to day, the diurnal pattern (especially in the summer) is remarkably consistent.

To the extent that wind scouring is responsible for emissions from pen surfaces, wind speed, pen-surface moisture content, and stocking density will all be important factors in determining emission fluxes and predicting downwind concentrations. The mechanisms involved in these emissions will be closely analogous to those at play in wind erosion. To date, however, wind-driven emissions of dust from cattle feedyards remain a relatively unexplored research domain.

Dairy cattle

Half of the world's dairy production occurs in the European Union, India, and the United States. Dairy operations employ either low-density pasture systems or high-density feeding systems, or a hybrid of the two, depending principally on climate. Fugitive dust from dairy production is associated primarily with high-density systems in which the animals are housed on nonvegetated or minimally vegetated open lots or in free-stall barns with outdoor exercise areas. Superficially, open lots and exercise areas on dairies resemble cattle feedyards, in that pen surfaces begin as exposed mineral soil and evolve into soil–manure mixtures that are partially compacted in place by animal activity. These surfaces are susceptible to dust emissions as noncompacted manure dries and is aerosolized by hoof action, wind scouring, or machinery operations. Dust emission processes from confinement dairies, therefore, are fundamentally similar to those of beef feedyards. Factors that control emissions, however, can differ between beef and dairy operations. First, beef animals tend to be younger, smaller, and more active than lactating cows. This leads to differences in behavior and associated hoof action and moisture-excretion rates. Second, dairy pens are temporarily emptied once or twice daily as lactating cows are moved to the

Table 1 Published emission factors and/or fluxes of fugitive particulate matter from open-lot beef cattle feedyards

Citation	*Study location*	*Emission flux*[a] *(kg ha^{-1} d^{-1})*			*Emission factor*[b] *(g per head d^{-1})*		
		PM2.5	*PM10*	*Total suspended particulate (TSP)*	*PM2.5*	*PM10*	*TSP*
Peters and Blackwood (1977)	California (USA)	6	29	114	14	70	280
Parnell *et al.* (1999)	Texas (USA)	0.6–0.8	3–4	11–15	1.4–1.8	7–9	28–36
Flocchini *et al.* (2001)	California (USA)	1.5–6	8–31	33–122	4–15	20–75	80–300
Wanjura *et al.* (2004)	Texas (USA)	1.5	8	31	4	19	76
Lange *et al.* (2007)	Texas (USA)	0.3–0.5	2–3	7–10	0.8–1.2	4–6	16–24
McGinn *et al.* (2010)	Australia	3–5	13–25	51–98	6–12	31–60	124–240
Bonifacio *et al.* (2012)	Kansas (USA)	2–3	11–16	44–64	5–6	27–30	108–120

[a]Emission fluxes in this table are computed from the published emission factors on the basis of a nominal animal spacing of 14 m^2 per head. PM2.5 and PM10 are assumed to be 5% and 25% of TSP, respectively.

[b]When primary data sources for these columns were provided on an animal unit basis, we have converted them to a per-head basis by assuming a nominal mean live weight of 454 kg per head.

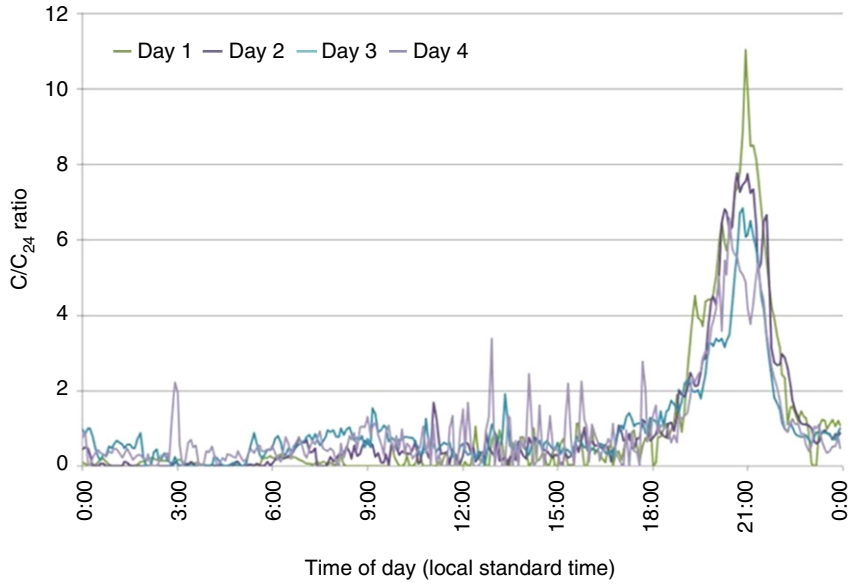


Figure 4 Typical daily variation of summertime mass concentrations (5-min averages) of fugitive PM10 downwind of a cattle feedyard in the south-central United States, normalized to the 24-h average PM10 concentration.

milking facility. Pens may then be groomed in the absence of livestock. In contrast, feedyard pens are emptied only when the cattle are being reimplanted or shipped to slaughter. Machinery operations for pen-surface maintenance on a beef feedyard must occur either when the animals are in the pen or after the cattle are shipped and the pen is empty. Third, harrowing the pen surface several times a week is commonplace in open-lot dairies. The primary reason for harrowing the pen surface in dairies is to maintain animal comfort, health, and milk production by giving the cows a softer surface on which to rest. Harrowing is not a common practice in beef feedyards except where needed to distribute bedding materials evenly across the surface. Fourth, the spatial density at which pens are stocked with animals differs widely between beef feedyards and open-lot dairies. Depending on climate, breed, topography, surface hydrology, and other factors, the average pen area allocated to a single dairy animal may be 1.5–3 times that allocated to a single beef animal. This difference in space allocation affects: the pen surface's susceptibility to wind scouring; flux of excreted and evaporated moisture; the nature and intensity of social interactions between animals; and the distribution, compaction, and rate of accumulation of manure solids. These characteristics influence dust emissions.

In addition to the differences associated with pen surfaces, patterns of truck traffic differ markedly on dairies as compared with feedyards. Depending on the size of the milk-storage tank at a dairy and the size and productivity of the dairy's milking herd, milk tankers may drive in and out 5 to 10 times per day at relatively consistent intervals. This results in periodic emissions of road dust. By contrast, comparable heavy traffic on beef feedyards involves fewer trucks and more episodic ingress and egress.

Dust concentrations downwind of open-lot dairies follow similar daily patterns to those of beef feedyards (Figure 5). As with feedyards, a pronounced evening peak in ground-level PM10 concentrations appears to be associated with temporary, regional inversions that begin shortly before sundown and persist for 4–6 hours. Notably, the ratio of the peak concentration to the 24-hour average concentration appears to be consistently lower downwind of an open-lot dairy than downwind of a cattle feedyard. This observation presumably reflects the combined effect of the major differences, outlined above, between the two types of livestock systems.

As with beef feedyards, estimates of PM2.5 and PM10 emission rates and fluxes from dairy operations vary widely (Table 2). Published research on fugitive dust emissions from open-lot dairies is much scarcer than that from beef feedyards; therefore, the uncertainties in emission estimates in Table 2 are at least as great as for beef feedyards.

Sheep and goats

Small ruminants, predominantly sheep and goats, were among the first livestock to be domesticated for food and fiber. The primary agricultural products of these animals are milk and milk products, meat, wool, mohair, and cashmere. Sheep and goats, because they are ruminants and highly adaptable, are also raised to control invasive plants.

Domesticated sheep are primarily raised in China, Australia, India, Iran, Sudan, New Zealand, and the United Kingdom. The United States is responsible for less than 1% of the world's sheep production, with the top five sheep-producing states (Texas, California, Wyoming, Colorado, and South Dakota) being semiarid and coinciding partly with North America's cattle-feeding regions. World goat production is centered in Asia and Africa with more than half the production coming from China and India. India, Bangladesh, and the Sudan dominate world production of goat milk. Goat meat production is centered in China and India, with all other nations together contributing approximately 51%. Mohair production is now centered in South Africa, with Turkey, Australia, and New Zealand having important mohair industries.

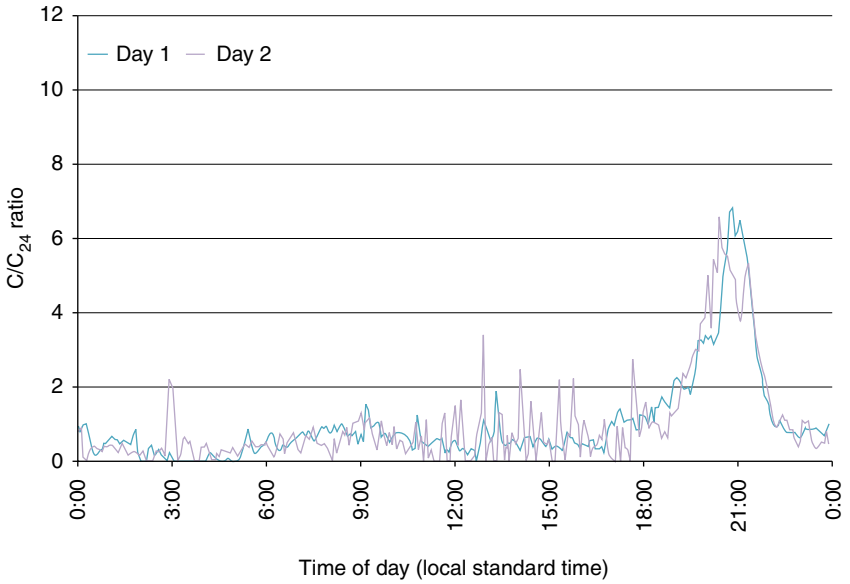


Figure 5 Typical daily variation of summertime mass concentrations (5-min averages) of fugitive PM10 downwind of a large, open-lot dairy in the southwestern United States, normalized to the 24-h average PM10 concentration.

Table 2 Published or adopted emission factors and/or fluxes of fugitive particulate matter from various dairy-housing systems

Citation	*Configuration/study location*	*Emission flux*[a] *(kg ha^{-1} d^{-1})*			*Emission factor*[b] *(g per head d^{-1})*		
		PM2.5	*PM10*	*TSP*	*PM2.5*	*PM10*	*TSP*
USDA (2000)	Open-lot	0.2	1.1	4.3	0.8	4	16
Goodrich *et al.* (2002, 2003)	Free-stall, Texas	0.1–0.4	0.6–1.9	2.2–7	0.4–1.4	2–7	8–27
NAEI (2010)	Full confinement, UK	0.02	0.1	0.4	0.1	0.4	1.6
Countess Environmental (2006)[c]	Synthesis of data	0.1	0.8	1.7	0.3	3	6.5

[a]Emission fluxes in this table were computed from published emission factors on the basis of a nominal animal spacing of 37.2 m^2 per head. PM2.5 and PM10 are assumed to be 5% and 25% of TSP, respectively, except where noted.

[b]When primary data sources for these columns were provided on an animal unit basis, we have converted to a per-head basis on the assumption of standard Holstein cows having a nominal live weight of 636 kg per head.

[c]PM2.5 and PM10 emission factors were determined on the basis of the California Air Resources Board guidance that assumes PM10 and PM2.5 are 48% and 5.3% of TSP, respectively.

Most of the sheep and goats raised around the world are pastured, with sheep preferring grasslands and goats being raised in more woody or brushy rangelands. Animals raised for milk may be confined near the milking parlor during the winter months. Sheep and goats raised for meat or fiber typically live on pasture or range, but meat animals may be finished on grain-based diets to achieve desirable meat qualities. Nonvegetated sheep and goat feedlots are common in the United States and Australia and have many similarities to cattle feedyards and, to a lesser extent, open-lot dairies. As with the beef and open-lot dairy operations, dust emissions and downwind concentrations from sheep and goat feedlots are driven by regional climate, short-term weather phenomena, feeding and pen-surface management, and patterns of animal activity. However, researchers have not examined emission rates of fugitive dust from sheep and goat feedlots. Fully confined (i.e., in buildings or under roof) sheep and goat production does have a substantial presence in Europe, and limited research there has provided some estimates of emission rates and concentrations of dust associated with total-confinement facilities. Aarnink *et al.* (2012) reported annual emissions of TSP at 69 g per head, PM10 at 22 g per head, and PM2.5 at 1 g per head from goat houses in the Netherlands. Dust emissions were largely attributed to the straw used for bedding inside the houses and, to a lesser extent, dry fecal material resuspended in air by animal activity. Papanastasiou *et al.* (2011) reported that PM10 and PM2.5 concentrations inside sheep houses in Greece varied inversely with ventilation rate, but they measured neither outdoor concentrations nor emission rates through the ventilation system.

Swine and poultry

Swine, poultry meat, and eggs are produced at respective annual rates of 110, 87, and 68 million metric tons worldwide, as compared with beef (62 million tons), mutton/lamb (14 million tons), and milk (671 million tons) (UNFAO, 2009). As nonruminants, pigs and poultry cannot be raised on grass or

other forages. Therefore, pork, poultry meat, and eggs are produced predominantly in a wide range of confinement systems. Swine and poultry facilities may be fully or quasi-confined, roofed or open-lot, actively or passively ventilated, and on earthen or paved surfaces. Quasi-confined facilities allow animals to move liberally around a relatively large and partial-outdoor environment, but are fed in specified locations. Examples of quasi-confined facilities include free-range areas for poultry and hoop barns for swine. By contrast, fully confined facilities are essentially designed to optimize the animals' stocking density and to control their environment for economic productivity. Although there is some trend toward quasi-confined facilities for the sake of animal-welfare considerations, the majority of swine, poultry meat, and eggs is produced under roof with controlled or semicontrolled indoor environments. As a result, most of the dust emitted from swine or poultry houses originates as an indoor air pollutant that poses health and productivity risks to both the animals and the workers. Where natural wind currents are insufficient to maintain acceptable indoor air quality, forced ventilation, and attentive dust-management practices in swine (Pedersen *et al.*, 2000) and poultry houses are essential. Among all of the world's major livestock-production systems, swine and poultry houses have been the most extensively studied with respect to dust concentrations, characteristics, and emissions.

Swine

China accounts for nearly one-half, whereas the European Union accounts for 20% and the United States and Brazil together account for 10% of the world's swine production (USDA, 2012). Swine production generally involves the use of confined facilities with houses having paved or earthen floors, natural or artificial lighting, and passive or forced ventilation. Moreover, different growth stages of the animals may be raised in different housing types to ensure that animals in the growth stages most vulnerable to health impairment or productivity loss (sows, baby pigs, and breeding boars) are subjected to the least environmental stress. As a result, the sources, mechanisms, and characteristics of dust produced in swine houses may be meaningfully stratified by animal growth stage. For example, one recent study found that dust from a growing-finishing house, in which slaughter pigs were fed on a concrete, partially slatted floor, was composed primarily of feed, feces, and skin particles. In contrast, dust was largely composed of straw fragments when finishing houses used straw for bedding material (Aarnink *et al.*, 2004). Reflecting the diversity in swine-production systems, Haeussermann *et al.* (2008) developed a mathematical model to predict PM10 emissions from swine facilities that accounted for variations in stocking rate, animal liveweight, animal growth stage, and characteristics of the housing system.

The rate at which dust is emitted from swine houses is governed by the indoor dust concentration and the ventilation rate, both of which vary strongly with time. Estimating emissions from houses with forced-air ventilation systems involves continuously measuring the flow rate of air through the exhaust fans and synchronized monitoring of indoor dust concentrations at the fan intake (Hinz and Linke, 1998a). Emissions from passively ventilated houses are more difficult to measure and are characterized by greater uncertainty, as airflow patterns (directions and flow rates) are highly variable. In a study at a swine finishing house, Hinz and Linke (1998b) found total dust concentrations as high as 5000 $\mu g\ m^{-3}$ during the daytime when animal activity was high and as high as 2000 $\mu g\ m^{-3}$ during the nighttime hours. Emission rates of inhalable dust (nominally PM10) from swine houses in northern Europe ranged from 121 to 1364 $mg\ h^{-1}$ per 500 kg of animal liveweight in the house, suggesting that dust-emission rates scale approximately with each facility's animal capacity (Takai *et al.*, 1998).

Poultry

Eggs, broiler chickens, turkeys, and other poultry products are important sources of animal protein throughout the world. The United States leads global production of broiler meat (20%), with China, Brazil, and the European Union together producing another 40%. The United States also produces more than half of the world's turkey meat, followed by the European Union, Brazil, and Canada (Pedersen *et al.*, 2000). Of the approximately one trillion eggs produced globally per year, China produces approximately half and the United States another 10%. India, Japan, European Union, Mexico, and Russia round out the top seven egg-producing regions.

Broiler and turkey houses are typically designed to raise the birds on bedding materials (e.g., sawdust, wood shavings, and crop residues) that optimize meat quality and growth rates while absorbing excreta. Dust from poultry raised for meat is composed of feather fragments, crystals from dried urine, feed and feces particles, bedding fragments, and microorganisms (Aarnink *et al.*, 2004). Layer houses, by contrast, seldom have bedding; excreta are collected and removed frequently or even continuously. Animals in layer houses are raised in cages, or stacks of cages, that facilitate egg removal. As a result, dust from broiler and turkey houses differs from that of layer houses, both in composition and emission rates (Seedorf *et al.*, 1998; Takai *et al.*, 1998).

As with swine facilities, dust emissions from broiler houses tend to scale with the total liveweight housed in a single building (Hinz and Linke, 1998b). In northern Europe, researchers (Takai *et al.*, 1998) found that inhalable dust (nominally PM10) concentrations in caged-layer and broiler houses ranged from 750 to 1640 and 3830 to 10 360 $\mu g\ m^{-3}$, respectively, with emission rates ranging from 398 to 872 and 1856 to 6218 $mg\ h^{-1}$, respectively, per 500 kg of animal liveweight in the houses.

Processing and storage facilities

Dust generated in facilities that process or store raw materials for manufacturing feed, food, fiber, or fuel is of particular concern to the occupational safety and welfare of workers within these facilities. Explosions and fires at grain-storage facilities are not uncommon and can result in death of occupants; such an explosion killed six workers at a facility in Atchison, Kansas in 2011. The health of occupants can also be impaired by inhaling dust within or near these facilities. Dust generated at grain-processing facilities can be even more hazardous than storage facilities because processing involves grinding grain into fine particles. Agricultural processing and storage facilities that are major sources of dust include cotton gins, grain elevators, and feed mills.

Cotton gins

Cotton is a natural fiber derived from the fruit, or boll, of the woody plant. Cotton requires a long growing season with abundant sunshine; thus, it is grown throughout the desert, temperate, and tropical climates of the world. Most of the cotton produced worldwide comes from Asia (i.e., China, India, Pakistan), Brazil, Australia, Turkey, and the United States. In the United States, major cotton-growing states include California, Georgia, Mississippi, and Texas. Together, China and India are responsible for more than half of the world's cotton production.

The mature cotton boll consists of three main parts, namely the seed, lint, and burr. The seed is high in protein and oil and is embedded within and attached to the lint; the lint consists of fibers used to manufacture fabrics. Modern cotton harvesting is highly automated and is accomplished with either a cotton picker or cotton stripper. Cotton pickers are designed to mimic the selective action of manual harvesting and may pass through a field more than once. Cotton strippers move more quickly through the field and strip nearly all of the bolls from the plant leaving behind the main stalk and larger stems. The raw products obtained from these two harvesters differ primarily in terms of the relative amounts of mature versus immature lint and the amount of nonlint material in the harvested bulk.

Cotton ginning is essentially a two-stage mechanical process of removing gin trash (stems, burrs, soil, and other debris) from cotton bolls and separating the cotton fibers from the seed. The modern cotton gin originated in the late eighteenth century but has become a highly sophisticated, multistage, high-throughput operation that yields compressed lint bales weighing 200–225 kg. Cotton gins now consist of many specialized, mechanical processes (**Figure 6**). The conveyors in a cotton gin are pneumatic, using air flow at high speed to move the materials from point to point. Along the way, debris, lint, and seeds must be removed from the various air streams with the conveying air ultimately exhausted to the outside.

Dust emissions from cotton gins originate from the exhaust of conveying systems within the gin enclosure. The dust consists of soil particles, insect fragments, and fragments of lint, leaves, stems, and other plant parts. Each of the specialized, mechanical processes within a gin produces a characteristic type of dust. Moreover, the manner in which the cotton is harvest (i.e., picker vs. stripper) strongly influences the load on each stage of the ginning process. Stripper-harvested cotton may generate 6–7 times as much trash during the ginning process as picker-harvested cotton (USEPA, 1995).

As with most agricultural dusts, cotton gin dust is composed of both organic (plant-derived) and mineral (soil derived) particles. Most of the dust generated by cotton ginning, therefore, is relatively coarse with aerodynamic diameters exceeding 10 μm. The ratio of PM10 to TSP varies slightly between processes, but is typically between 0.25 and 0.5. In addition to the parent materials, dust associated with cotton-gin exhaust may also contain traces of chemical residues, including pesticides and harvest aids (defoliants).

As implied by **Figure 6**, estimates of the total dust emissions from cotton gins are assembled from individual process emissions. As shown in **Table 3**, emissions are typically calculated from an emission factor for each process (mass of particles per bale of cotton produced) multiplied by the gin's throughput (bales per unit of time). Modern, high-capacity gins can process 1500 bales per day.

Concentrations of dust at ground level downwind of cotton gins depend on the efficiency of the control systems (cyclones and screens); the elevation of the exhaust points; the flow velocities, orientation, and temperatures of the exhaust streams; and atmospheric conditions. Every cotton gin is unique, but ground-level concentrations of PM10 and TSP have been measured over the past several decades. Recently, Hughs *et al.* (2008) measured respective daily PM2.5 and PM10 concentrations of 0.02–0.92 and 5–40 $\mu g\, m^{-3}$ downwind of a gin in the southwestern United States.

Grain elevators and feed mills

Grain-storage and grain-processing facilities are found across a wide range of sizes, configurations, and capacities throughout the world. For example, individual farmers may have on-site bunkers and silos for grain storage. Local farmers' cooperatives typically have one or more storage elevators, sometimes known as country elevators, to facilitate grain marketing for their members. Animal-feeding operations may also use bunkers and silos to store and mills to process grains and other components into animal feed. Flour mills, bread factories, breweries, and other grain-processing industries may maintain on-site storage of grains to ensure adequate production capacity. Regional transfer facilities in larger towns and cities will aggregate grain from surrounding country elevators into numerous, large elevators for long-distance transport by rail or tractor-trailer. Terminals and processing facilities along major waterways or harbors will have sizeable elevators and mills to store and process a wide range of grains for import/export markets. At all scales, however, the dust associated with loading, unloading, transferring, storing, and processing grain has significant implications for human safety, human health, and environmental air quality.

Grain dust, which is rich in organic carbon, is highly flammable and can detonate or deflagrate, with catastrophic results in fatalities, injuries, and loss of property. The risk of grain-dust explosions is present when the suspended dust concentration exceeds the minimum explosive concentration (MEC), dusty air is confined within an enclosed space, adequate oxygen is available to support combustion, and an ignition source (e.g., static electricity, electrical shorts or loose connections, unsealed motors, pilot lights, failing bearings between metal parts, and cigarettes) is present (Jones, 2011). Particles of grain dust are intrinsically flammable, but their explosive risk increases as particle size decreases. The MEC of grain dusts may be as low as 45–50 $g\, m^{-3}$, with optimum explosive concentrations between 100 and 150 $g\, m^{-3}$ (Gillis, 1985).

Occupational health is at risk when grain-storage or grain-processing workers do not wear adequate respiratory protection. Grain dusts may include soil particles, fragments of plant tissues and grains, insect fragments, mold spores, fungi, bacteria, viruses, and other biological aerosols. Even when biological aerosols are noninfectious, they may contain nonviable or dead organisms whose cellular components (e.g., endotoxins, lipopolysaccharides, and peptidoglycans) may be toxic to humans, with either chronic or acute health effects

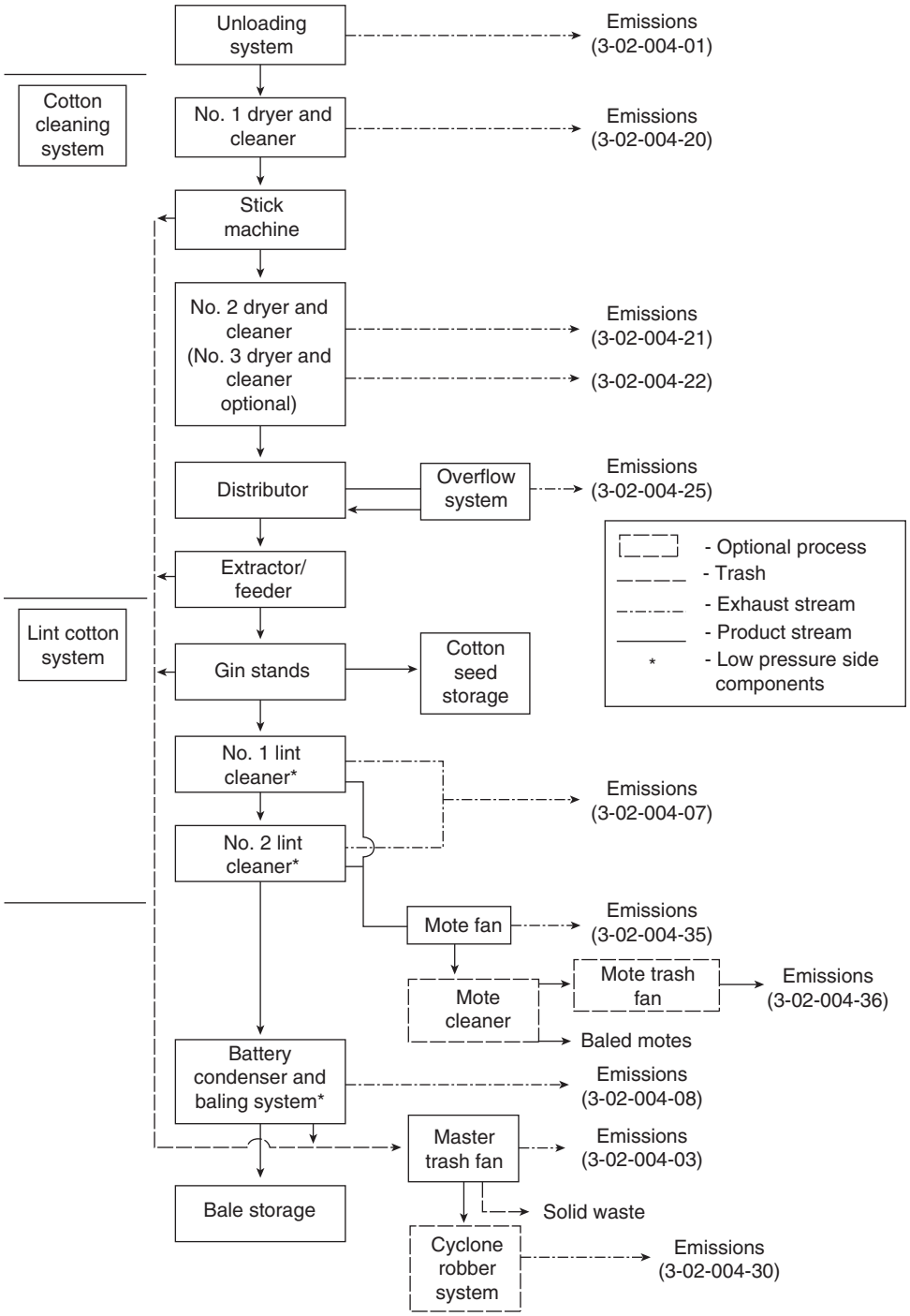


Figure 6 Schematic of a modern cotton gin showing the numerous discrete processes that generate dust emissions (USEPA, 1995). Numbers in parentheses are Source Classification Codes used by the USEPA to categorize operations that emit particulate matter.

(Schwartz *et al.*, 1995). Environmental air quality may also be a concern for neighboring residences and communities, especially for susceptible persons including the young, elderly, asthmatics, or those with weak or compromised immune function. In general, grain dust from elevators and feed mills is a class of air pollutants subject to governmental regulatory standards.

Emission rates from elevators and mills are generally computed using emission factors or process-weight tables and, similar to cotton gins, each discrete process within an elevator or mill will have its own emission factor (**Figure 7**). For example, the emission factor for grain cleaning in elevators or grain crushing in feed mills is at least twice that of receiving grain at either facility (**Table 4**). In addition, each

Table 3 Emission factors for modern cotton gins with high-efficiency cyclone controls on the exhaust streams (USEPA, 1995)

Source	*TSP (kg bale^{-1})*	*PM10 (kg bale^{-1})*	*PM10/TSP ratio*
Unloading fan	0.132	0.055	0.41
#1 Dryer/cleaner	0.164	0.005	0.03
#2 Dryer/cleaner	0.109	0.042	0.39
#3 Dryer/cleaner	0.043	0.015	0.35
Overflow fan	0.032	0.012	0.37
Lint cleaners:			
• with high-efficiency cyclones	0.264	0.109	0.41
• with screen drums or cages	0.500	–	–
Cyclone robber	0.082	0.024	0.29
Mote fan	0.127	0.059	0.46
Mote trash fan	0.035	0.010	0.27
Battery condenser:			
• with high-efficiency cyclones	0.018	0.006	0.36
• with screen drums or cages	0.077	–	–
Master trash fan	0.245	0.034	0.14
Grand total	1.828	0.370	0.30

type of grain has its own intrinsic dustiness, which may vary with moisture content, harvest method, or other management factors (USEPA, 2003). In principle, then, there could be a unique emission factor for each permutation of grain type, grain condition, harvest method, and elevator or mill process.

Agricultural Lands

Agricultural lands, primarily in the arid and semiarid regions of the world, contribute to the dust load in the atmosphere. The lack of precipitation in these regions impairs crop production and generally results in dry and poorly structured soils, both of which affect dust emissions from agricultural lands. Dust is emitted into the atmosphere from agricultural lands as a result of natural events and farming operations. Although natural events cannot be controlled or regulated, management practices or farming operations imposed on these lands can dramatically influence dust emissions.

Natural events

High winds, volcanic eruptions, and wildfires are natural events that can affect atmospheric PM10 concentrations. High-wind events are of particular relevance to agriculture. Dust emitted into the atmosphere as a result of high winds eroding agricultural lands (**Figure 8**) constitutes 10% of the atmospheric dust load worldwide (Tegen *et al.*, 2004). Windblown dust has contributed to exceedance of national PM10 air-quality standards in China, Europe, and the United States (Liu *et al.*, 2011; Escudero *et al.*, 2007; Sharratt and Lauer, 2006). Long-range transport of PM10 from eroding agricultural land has also contributed to exceedance of PM10 air-quality standards. For example, transport from agricultural lands in the Ukraine have resulted in exceedance of the European Union air quality standard for PM10 (daily concentration not to exceed 50 μg m^{-3}) in Slovakia, the Czech Republic, Poland, and Germany (Birmili *et al.*, 2008) whereas transport from agricultural lands in Africa has contributed to exceedance of the European Union PM10 air-quality standard in Spain (Escudero *et al.*, 2007). Although intercontinental transport of dust has not contributed to the exceedance of PM10 Standards in the United States, erosion of agricultural lands in China (Wang *et al.*, 2004) has contributed to a rise in PM10 concentrations in the Pacific Northwest of greater than 100 μg m^{-3} (Husar *et al.*, 2001). In the United States, windblown dust generated from agricultural lands has contributed to exceedance of the PM10 Air Quality Standard in Arizona (Fields *et al.*, 2001), California (Chow and Watson, 2001), and Washington (Sharratt and Lauer, 2006).

Very few studies have examined the emission of PM2.5 or PM10 from agricultural lands during high-wind events (**Table 5**). Sharratt *et al.* (2007) measured a PM10 concentration of greater than 8500 μg m^{-3} above an eroding agricultural field during a high-wind event in eastern Washington. More recent field data collected in eastern Washington indicate that PM10 concentration and vertical flux can exceed those in **Table 5**. For example, PM10 concentration and vertical flux, respectively, exceeded 70 000 μg m^{-3} and 10 000 μg m^{-2} s^{-1} above an eroding agricultural field during a high-wind event on 3 September 2009 (**Figure 9**). The daily PM10 concentration at a 2 m height during this high-wind event was 1735 μg m^{-3}. Others have measured concentrations and fluxes of fine particles above eroding agricultural fields, but these measurements have been limited to particles either smaller or larger than 10 μm in diameter. For example, Gillette *et al.* (1972) observed a vertical flux of PM6 (particles with aerodynamic diameters ≤6 μm) of 1 μg m^{-2} s^{-1} over an eroding field before sowing wheat in Nebraska. Gillette (1977) observed a vertical flux of PM20 (particles with geometric diameters of <20 μm) of 10 to 5×10^{5} μg m^{-2} s^{-1} above eroding sands, loamy sands, sandy loams, and clays in Texas. Gomes *et al.* (2003) have reported vertical fluxes of PM20 of respectively 66 and 302 μg m^{-2} s^{-1} over eroding agricultural fields in Spain and Niger.

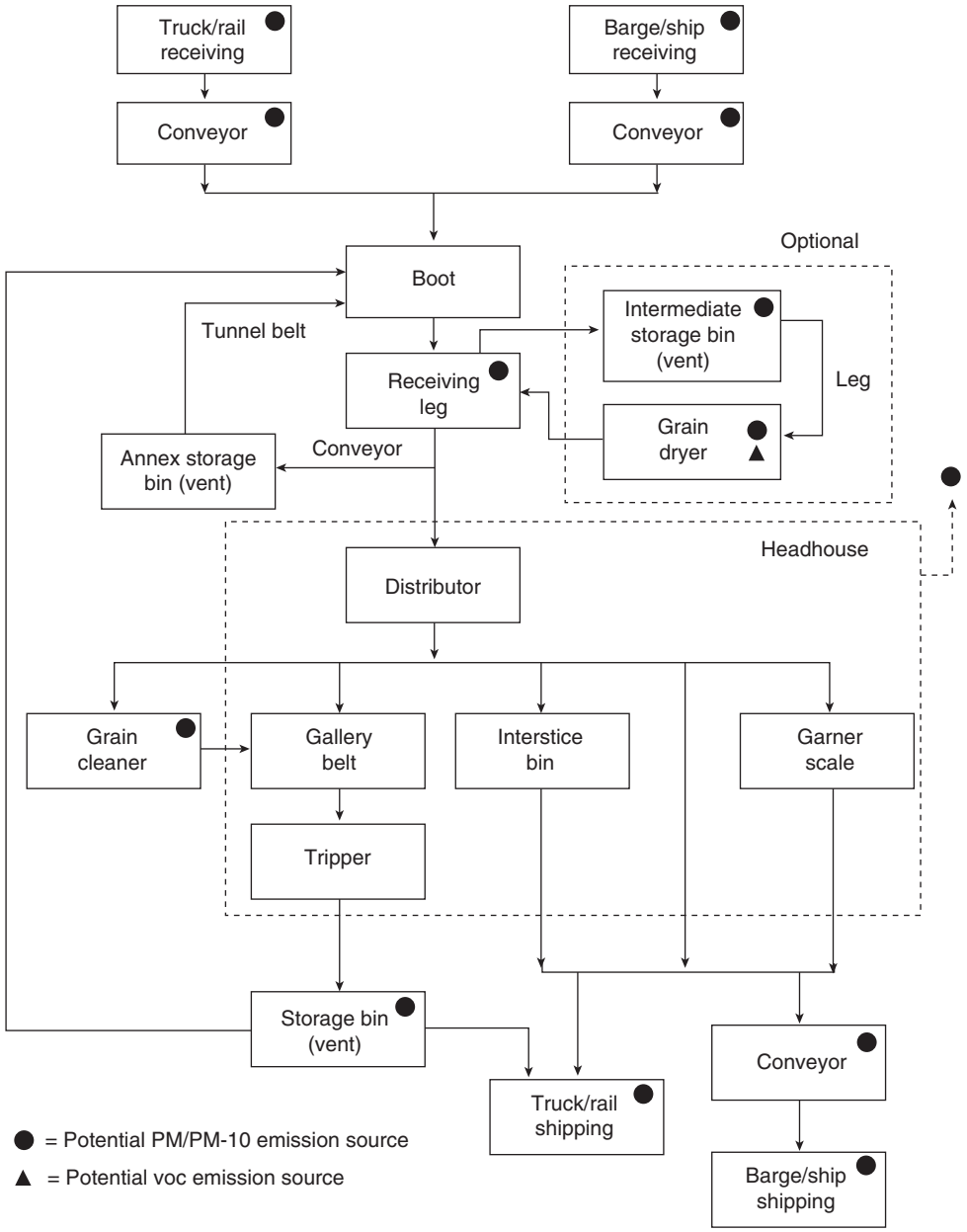


Figure 7 Schematic of emissions sources in a grain elevator (USEPA, 2003). VOC, volatile organic compound.

Table 4 Example emission factors for processes within grain elevators and feed mills in the United States (USEPA, 2003)

Process	*TSP emission factor (g mg^{-1})*	*PM10 emission factor (g mg^{-1})*	*PM10/TSP ratio*
Feed mill:			
• Grain receiving	8.5	1.25	0.15
• Hammer mill with cyclone	33.5		
• Feed shipping	1.65	0.4	0.24
Grain elevator:			
• Grain cleaning with cyclone	37.5	9.5	0.25
• Grain receiving, hopper truck	17.5	3.9	0.22
• Grain handling	12.5	3.15	0.25

Two studies have estimated PM10 emissions from agricultural lands during high winds. Saxton *et al.* (2000) estimated PM10 vertical fluxes as high as 300 000 $\mu g\ m^{-2}\ s^{-1}$ from agricultural fields during a design wind storm in some portions of the Columbia Plateau. These estimates, based on an integrated meteorological/chemical transport/PM10 emissions model, were not confirmed in the field. Xuan and Sokolik (2002) estimated an annual PM10 loss across gridded locations in northern China using an empirical model which estimates PM10 loss from surface characteristics and climate. Their analyses suggest that annual PM10 loss can approach 10 $kg\ ha^{-1}$ in agricultural regions.

Geologic material is generally composed of coarser particle matter and, thus, PM2.5 constitutes a small percentage of PM10 emitted from agricultural lands. For example, PM2.5 comprised from 4% to 7% of PM10 that was observed downwind of eroding agricultural lands in the Columbia Plateau region of the Inland Pacific Northwest (Sharratt and Lauer, 2006). Gillette and Walker (1977) measured the size distribution of particulate matter 1.5 m above eroding agricultural soils in Texas and found that PM2.5 comprised from approximately 1% to 4% of PM10.

Best management practices to reduce dust emissions from agricultural soils during high-wind events are similar to those required to control wind erosion. These practices include the use of wind barriers, ridge tillage, tillage operations that enhance surface roughness or cover with crop residue, mulching with vegetation or manure, cover crops, perennial, or multiyear crops, strip cropping, delayed tillage, and sowing when soil moisture is adequate for timely seed germination and emergence. Fields *et al.* (2001) estimated the reduction in emissions during a high-wind event in Arizona for various management practices and found that multiyear crops, residue management, and timing of tillage operations were the best strategies for reducing PM10 emission from cropland.



Figure 8 Dust rising from an isolated cultivated field during an October 2003 high-wind event near Ralston, WA, USA.

Farming operations

Tillage, harvest, seeding, fertilizing, and spraying are routine farming operations that generate dust. Dust generated by agricultural operations is typically characterized by particles with diameters larger than 2.5 μm (Capareda *et al.*, 2004) and, therefore, does not solely contribute to exceedance of the PM2.5 air-quality standard. Dust emitted into the atmosphere as a result of farming operations has contributed to the exceedance of the PM10 air-quality standards in the United States, most notably in California (Chow *et al.*, 1992; Dolislager and Motallebi, 1999). Dust generated by farming operations is the second largest source, with road dust being the largest source, in the San Joaquin Valley of California (Cassel *et al.*, 2003). Air stagnation in the Imperial Valley and San Joaquin Valley during the autumn, winter, and spring trap fine particles in the atmosphere that are emitted during tillage or harvest operations (Chow and Watson, 2001). In northern Europe, high atmospheric dust concentrations in the spring have been linked to tillage activities (Goossens, 2004).

Tillage and harvest operations typically generate a higher proportion of coarse particulate matter (particulates with a diameter 2.5–10 μm) as compared with PM2.5 (Matsumura *et al.*, 2003; Kasumba *et al.*, 2011). Particulates emitted during tillage or land preparation operations are affected by the type of implement, speed of implement, surface characteristics (e.g., roughness and residue cover), soil properties (e.g., type and moisture), and atmospheric conditions. Particulates emitted during harvest, however, tend to be unique to each crop. Some crops require only one harvest operation (e.g., direct combine), whereas the harvest of other crops, such as nut trees, require multiple operations. Each operation can contribute to the particulate load in the atmosphere. Particulates can be emitted during the cutting, swathing, raking, or combining operations of field crops or the shaking, sweeping, and pickup operations of tree crops. For example, the harvest of almonds in California involves shaking the tree to allow the

Table 5 PM10 concentration, vertical flux and loss measured within eroding agricultural fields during a high-wind event. PM10 concentration was measured at various heights above an eroding surface

Citation	*Location*	*Height (m)*	*Concentration ($\mu g\ m^{-3}$)*	*Vertical flux ($\mu g\ m^{-2}\ s^{-1}$)*	*Loss ($kg\ ha^{-1}$)*
Gillette (1974)	Texas			10 000	
Zobeck and VanPelt (2006)	Texas	2	2200	0.48	
Kjelgaard *et al.* (2004)	Washington	3	6500	258	
Sharratt *et al.* (2007)	Washington	5	8535	255	212
Stetler and Saxton (1996)	Washington	1.5	1255	260	

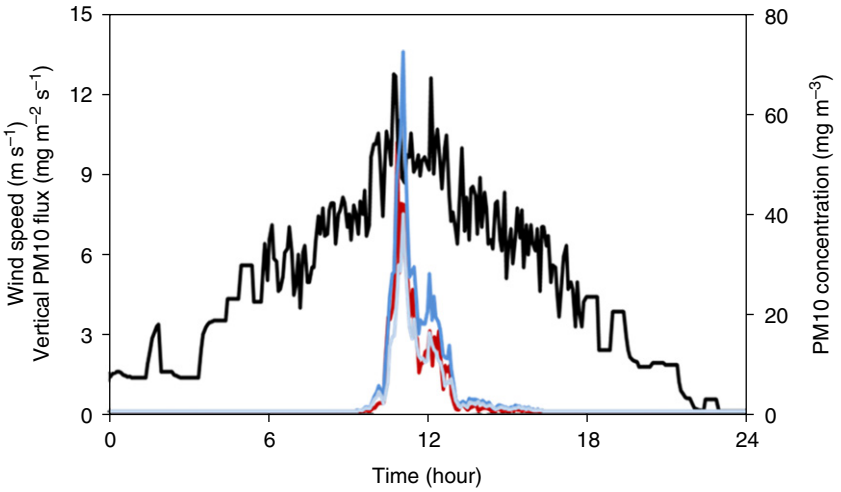


Figure 9 Five-minute averages of wind speed at 2 m (black line), Tapered Element Oscillating Microbalance PM10 concentration at 1 (blue line) and 2 m (light blue line), and vertical PM10 flux (red line) above an eroding agricultural field during a September 2009 high-wind event in eastern Washington.

almonds to fall to the soil surface to air dry, sweeping the almonds on the soil surface into windrows, and picking up the almonds from the soil surface with a machine that separates the almonds from the soil and other debris. Each sequential operation emits one magnitude more PM10 into the atmosphere (Faulkner and Capareda, 2012). PM2.5 and PM10 emission factors for tillage and harvest operations are provided in **Table 6**. The range in emission factors for any operation is likely due to differences in atmospheric conditions (e.g., relative humidity), moisture content of soil, depth of tillage, implement speed through the field during the operation, and methodology used to measure emissions during the operation. Virtually no information is available on PM10 emission factors for seeding, fertilizing, and spraying operations. However, data of Bogman *et al.* (2007) would suggest that the PM10 emission factor for the seeding operation is similar to the plowing or disking operations whereas the PM10 emission factors for fertilizing and spraying operations are an order of magnitude less than the cultivating, disking, and plowing operations.

Exceedance of PM10 air-quality standards due to farming operations have forced local or national government organizations to adopt alternative practices that emit less particulate matter into the atmosphere. For example, exceedance of the PM10 standard in Maricopa County prompted the development of best management practices to reduce dust emissions from agricultural lands in Arizona (State of Arizona, 2008). Best management practices for field crops include using one-pass operations (e.g., apply fertilizer when cultivating or seeding), reduced or no tillage practices, tillage tools that do not invert the soil, and stripper headers rather than traditional headers on combines. Other best management practices include cultivating the soil at lower speeds or when the soil is moist, roughening the soil surface, and minimizing the chopping and spreading of residue from the combine. Best management practices for tree crops include sweeping or pickup of nuts from the soil surface when the surface is moist and using less invasive operations and modified harvest equipment.

Biomass burning

Biomass burning is used throughout the world to control diseases and pests in crops, remove crop residue that otherwise interferes with harvest or seeding operations, and as a fuel source. Biomass burning, however, can contribute to the dust load in the atmosphere. For example, burning wheat and corn residue is a major contributor to high PM2.5 concentrations in Beijing, China (Li *et al.*, 2007; Song *et al.*, 2006), whereas burning sugarcane is the main source of PM2.5 in some Brazilian cities (Lara *et al.*, 2005). Burning biomass generates a higher proportion of PM2.5 as compared with coarser particulate matter. In fact, 93% and 98% of the PM10 liberated from burning respectively wheat straw and corn stover is PM2.5 (Li *et al.*, 2007). In addition, biomass burning can release toxic compounds such as polycyclic aromatic hydrocarbons and phenols. PM2.5 and PM10 emission factors for burning agricultural residues are provided in **Table 7**. The range in emission factors for any crop is likely due to differences in atmospheric conditions (e.g., relative humidity), configuration of residue, or moisture content of residue during the burn.

A greater awareness of biomass burning being a source of atmospheric PM2.5 has prompted government organizations around the world to adopt policies that regulate burning of crop residue. In Washington, for example, agricultural burning has been reduced by half over the past decade and is currently allowed on certain days by those possessing a permit. Violation of this law has resulted in fines that exceed US$20 000. Other methods of handling crop residue are being advocated rather than burning; these include removing residue from the soil surface after harvest, incorporating residue into the soil after harvest, or using no-till seeding technologies and pesticides.

Table 6 PM2.5 and PM10 emission factors for tillage and harvest operations of agricultural crops

Operation	*PM2.5*	*PM10*
	g m^{-2}	
Tillage		
Chisel		0.13[a], 0.25[b]
Cultivate	0.01[c]	0.19[c]
Disk	0.01[c], 0.01–0.11[d]	0.08–0.65[d], 0.08–1.38[e], 0.09[f], 0.13[a], 0.14[c], 0.21[b]
Harrow	0.03[c]	0.08[c]
Land smoothing	0.55[d]	0.12–2.32[e], 0.50–0.65[b], 1.34[d], 1.40[a]
Plow	0.01–0.13[c]	0.12–1.05[c]
Subsoil	0.01–0.12[d]	0.04–0.72[d], 0.51[f], 0.52[a]
Weeding		0.09[a]
Harvest		
Almond		4.58[g]
Shake		0.015[h], 0.042[g], 0.05[b], 1.65[i]
Sweep		0.08[b], 0.20[h], 0.42[g], 1.94[i]
Pickup		0.19[b], 1.07[j], 1.22[h], 3.23[i], 4.12[g]
Corn		0.19[a]
Cotton	0.0002[k]	0.04[h], 0.05[k], 0.11[e], 0.38[a]
Oat		0.65[a]
Potato		0.19[a]
Rice		0.19[a]
Sugar beet		0.19[a]
Wheat		0.65[a]

[a]Countess Environmental (2006).
[b]Flocchini *et al.* (1994).
[c]Hinz and Funk (2007).
[d]Trzepla–Nabaglo *et al.* (2003).
[e]Cassel *et al.* (2003).
[f]Holman *et al.* (2001).
[g]California Air Resources Board (2003).
[h]Ashbaugh *et al.* (1996).
[i]Ashbaugh *et al.* (1997).
[j]Faulkner and Capareda (2012).
[k]Wanjura *et al.* (2008).

Table 7 PM2.5 and PM10 emission factors applicable to burning biomass of agricultural crops

Crop	*PM2.5*	*PM10*
	g kg^{-1}	
Almond	4.1[a], 4.5[b]	4.3[a], 4.8[b]
Apple	4.0[a]	4.2[a]
Barley	7.4[a,b]	7.7[a,b]
Canola	8.5[a]	8.9[a]
Corn	5.0[c], 6.0[b], 11.7[d]	6.2[b], 10.7[c]
Cotton	6.2[c], 8.5[a]	8.9[a],
Kentucky bluegrass	11.6[c], 12.1[e], 29.6[f]	15.8[c]
Oat	10.9[a]	11.4[a]
Olive	8.3[a]	8.9[a]
Rice	2.4[c], 3.2[b], 13.0[g]	3.3[c], 3.5[b], 3.7[h]
Sugarcane	2.2[i], 2.6[j], 4.3[c], 5.0[a]	4.9[c], 5.4[a]
Walnut	4.7[b]	5.0[b]
Wheat	0.8–4.7[e], 3.6[k], 4.0[c], 4.7[g], 5.4[a,b], 7.6[d]	5.7[a,b], 7.0[c]

[a]Air Sciences Inc. (2005).
[b]Jenkins *et al.* (1996).
[c]McCarty (2011).
[d]Li *et al.* (2007).
[e]Dhammapala *et al.* (2006).
[f]Air Sciences Inc. (2004).
[g]Hays *et al.* (2005).
[h]Kadam *et al.* (2000).
[i]Yokelson *et al.* (2008).
[j]de Azeredo Franca *et al.* (2012).
[k]Air Sciences Inc. (2003).

Future Perspectives

The pursuit of clean air will intensify as societies become more urbanized and interest escalates in protecting public health. Air-quality standards are being adopted and revised by many nations around the world. For example, China will fully implement new air-quality standards by 2016. In addition, the USEPA is mandated to review and revise, if appropriate, air-quality standards every 5 years. There is expectation that stricter or tighter PM2.5 and PM10 air-quality standards will be adopted as more evidence associates adverse health effects with exposure to dust. Tighter or more restrictive air-quality standards will necessitate that even greater measures be taken or better practices be implemented to control dust emissions. This will be a challenge for the agricultural industry, particularly in regions where weather affects emissions and profit margins are thin. Meeting this challenge will require the development of more cost-effective practices to control dust emissions from agricultural facilities and lands.

See also: Air: Confined Animal Facilities and Air Quality Issues. Beef Cattle. Dairy Animals. Land Use: Management for Biodiversity and Conservation. Swine Diseases and Disorders. Tree Fruits and Nuts

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ENCYCLOPEDIA OF AGRICULTURE AND FOOD SYSTEMS

VOLUME 3

ENCYCLOPEDIA OF AGRICULTURE AND FOOD SYSTEMS

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The material in the encyclopedia is arranged as a series of articles in alphabetical order.

There are four features to help you easily find the topic you're interested in: an alphabetical contents list, cross-references to other relevant articles within each article, and a full subject index.

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The alphabetical contents list, which appears at the front of each volume, lists the entries in the order that they appear in the encyclopedia. It includes both the volume number and the page number of each entry.

2 Cross-References

Most of the entries in the encyclopedia have been cross-referenced. The cross-references, which appear at the end of an entry as a See also list, serve four different functions:

i. To draw the reader's attention to related material in other entries.
ii. To indicate material that broadens and extends the scope of the article.
iii. To indicate material that covers a topic in more depth.
iv. To direct readers to other articles by the same author(s).

Example

The following list of cross-references appears at the end of the entry Critical Tracking Events Approach to Food Traceability.

> *See also*: Agribusiness Organization and Management. Food Chain: Farm to Market. Food Labeling. Food Law. Food Packaging. Food Security: Development Strategies. Food Security: Food Defense and Biosecurity. Food Security, Market Processes, and the Role of Government Policy. Food Security: Postharvest Losses. Global Food Supply Chains. Government Agricultural Policy, United States. Regulatory Conventions and Institutions that Govern Global Agricultural Trade

3 Index

The index includes page numbers for quick reference to the information you're looking for. The index entries differentiate between references to a whole entry, a part of an entry, and a table or figure.

4 Contributors

At the start of each volume there is list of the authors who contributed to that volume.

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PREFACE

Food is absolutely necessary for human existence, yet for most in wealthy nations it is largely taken for granted because of its abundance. Sufficient food is a concern, however, for about 1 billion of the earth's inhabitants today who often go to bed hungry. Food security in a broad sense is becoming a worry of the future for those who understand the limitations of our earth's ecosystems. Malthusian prophecies have so far been wrong, but there is growing concern that we are rapidly reaching the point where feeding the world's growing and richer population will be at the cost to our environment that is unacceptable. In the next few decades we face the challenge of growing more food, with less water, with less fertilizer on less land – because of the growth of urban areas on prime agriculture land. We also face the largely unknown consequences that global warming will have on agricultural production. During the last century agricultural scientists were able to bring cutting-edge science into traditional agricultural practices and increase food production sufficiently to prevent global food shortages. The hope that new scientific discoveries will provide the means to keep ahead of world food demand is complicated by a growing public discomfort with biotechnology being applied to food production.

The concept of services being provided by the ecosystems of the earth is a fairly recent attempt to understand and place value on functions of natural lands that have historically been assumed to have few limits. In the past, if more food was needed, new lands were converted from forests or steppe lands into farm land and new water systems developed to provide the water needed for agriculture. When human populations were low our activities were largely buffered by the abundance of forest and steppe, but too late, we are beginning to understand that these provisioning services of our ecosystems are being overused and are no longer buffered by the abundance of wild lands and waters. We are rapidly losing our planet's biodiversity, irreplaceable ground water is being unsustainably consumed, and major river systems are being overused and polluted. Our oceans, the last place on the planet that still support our hunter and gathering traditions may not be able to sustain these activities into the future. And, food production and processing activities contribute to the greenhouse gas emissions that are rapidly warming our planet. Agriculture is the single greatest user of the earth's land and water resources. In the concept of ecosystem services, provisioning or providing food for all organisms is one of the services provided by ecosystems. Human population growth has and will continue to overtax the ecosystems we inhabit. The ultimate outcome of this major diversion of nature's resources into provisioning the human species is unknown, but it is critically important for us to understand what we must do to sustain our planet.

The breakthrough discovery about 10 000 years ago that plants and animals could be bred to provide a more abundant and secure food source was the foundation upon which all other human activities were able to flourish. Activities other than finding food now became possible and our diverse cultures were able to develop because of agriculture. Until fairly recently, however, the majority of the population of most nations was still directly involved in producing food. Mechanization of agriculture and continued improvements in genetics, fertilizers, and pesticides made food production very efficient in developed nations. In the United States, the leading nation in value of agricultural exports, less than 2% of the workforce is currently employed in producing food. The United States, however, is alone among the most populous nations of the world in having such a small population employed as farmers. In countries such as China, India, Indonesia, and Nigeria the majority of people are rural and involved in agriculture either directly or indirectly. But, as food production becomes more efficient in these countries, and as wages increase in other sectors, a major shift is occurring from rural to urban occupations. This revolution is potentially as important in affecting our cultures and community structures as was the development of agriculture. Many nations are currently experiencing a very rapid transition from rural to urban living with all of the social and logistic problems associated with such rapid structural changes. While this transition in our social and cultural structures is a broad subject, it does have significant impacts on agriculture and our food systems. To mention just a few, agriculture labor, food transport, food safety, and access to healthy food.

There is genuine concern among agricultural scientists that human populations and changing diets are outpacing our ability to meet the increasing food needs of the planet. In the first iteration by Academic Press in 1994 of the *Encyclopedia of Agricultural Science*, Noble Prize Winner Normal Borlaug wrote in its forward:

> Had the world's 1990 food production been distributed evenly, it would have provided an adequate diet (2350 calories, principally from grains) for 6.2 billion people – nearly one billion more than the actual population. However, had the people in Third World countries attempted to obtain 30% of their calories from animal products – as in the United States, Canada, or European Economic Community countries – a world population of only 2.5 billion people could have been sustained – less than half of the present world population.

The issue raised by Dr. Borlaug is probably the most important challenge we face. Human behavior and the food choices of consumers will determine the outcome of the race between food supply and population. Population control has been advocated for decades, and in some cases has become part of national policy, but the world's population continues to grow. Science breakthroughs cannot solve our food security and environmental quality challenges if consumers reject food that is not traditionally produced. Likewise, if meat products and other inefficiently produced food continue to be in high demand by consumers, there will be increased pressure on our food production systems. As supplies become short, prices rise. While this may be good for farmers, high food prices and food shortages will probably undermine our efforts to preserve the

world's remaining arable land as natural lands. We must change human behavior to solve the problems we face.

Food choices, nutrition, diets, food cultures, water and air quality, GMOs, global warming, food security, and similar topics are daily in the news throughout the world. We are all concerned about these issues, yet with all of the information easily available in the popular media about food there seems to be too little informed discussion on these various topics. In planning the *Encyclopedia of Agriculture and Food Systems* the editorial committee chose to organize the topics primarily by issues, rather than to focus on a traditional topic approach. We organized the issues that would be discussed in the chapters around the broad topics of Agriculture and People, Agriculture and the Environment, Agricultural Products, Plant Health Management, Animal Health Management, and Agriculture and Science. The issues raised in this preface are the ones that we felt needed to be addressed in this encyclopedia.

The associate editors joined me in the development of topics for the encyclopedia and were responsible for working with the authors – they deserve particular recognition. I was fortunate to be joined by a very distinguished group of colleagues who, I hope, are still friends. They spent much more time and effort in bringing this project to completion than any of us anticipated. I want to thank our authors who while overly committed and overworked, fulfilled their commitments to contribute to this work. I have been impressed with the quality of their contributions. The editorial staff of Elsevier have had the professionalism and patience to work with scientists who do not work under the same time and budget constraints that the staff work. I want to particularly thank Kristi Gomez, Donna de Weerd-Wilson, and Simon Holt who, each in succession, oversaw this effort, and I especially thank the project managers, who worked directly with me, and the associate editors, Kate Miklaszewka-Gorczyca, Will Bowden-Green, and Sam Mahfoudh.

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Ecoagriculture: Integrated Landscape Management for People, Food, and Nature

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Glossary

Agricultural biodiversity (agrobiodiversity) The variability among living organisms associated with the cultivation of crops and rearing of animals, and the ecological complexes of which those species are part. This includes diversity within and between species, and of ecosystems.

Agroecosystem An ecological and socioeconomic system, comprising domesticated plants and animals and the people who husband them, intended for the purpose of producing food, fiber, and other agricultural products.

Biological diversity (biodiversity) The variability among living organisms from all sources, including terrestrial, marine, and other aquatic ecosystems and the ecological complexes of which they are part; this includes genetic diversity within species, between species, and of ecosystems (Convention on Biological Diversity or CBD, article 2).

Connectivity A measure of spatial continuity of a vegetative corridor, biological network, or matrix.

Conservation agriculture An agriculture practice that aims to achieve sustainable and profitable agriculture through the application of the three principles: (1) minimal mechanical soil disturbance, (2) permanent soil cover, and (3) crop rotation (based the Food and Agriculture Organization of the United Nations publications).

Corridor A strip of a particular type of land that differs from the adjacent land on both sides. Such corridors may have important ecological functions including conduit, barrier, habitat, and improve 'connectivity.'

Ecoagriculture An approach to the managing landscapes for the simultaneous and synergistic achievement of three sets of outcomes: (1) maintaining, increasing, or improving agricultural production; (2) conserving biodiversity and ecosystem services; and (3) enhancing human livelihoods and well-being. These elements are stitched together by institutions that support multistakeholder collaboration to achieve these outcomes.

Ecosystem services (environmental services) The benefits people obtain from natural and human-modified ecosystems, including provisioning services (goods such as food, fiber, energy, and drinking water), regulation services (beneficial processes, such as climate regulation, pollination, flood control and purification of water, and air), habitat and supporting services (such as gene pool protection) and a range of cultural services (such as aesthetic, spiritual, and cultural values).

Integrated landscape management Long-term collaboration among different groups of land managers and stakeholders to achieve the multiple objectives required from the landscape, including agricultural production, provision of ecosystem services, protection of biodiversity, and local livelihoods, health, and well-being. Stakeholders seek to solve shared problems or capitalize on new opportunities through technical, ecological, market, social, or policy means that reduce trade-offs and strengthen synergies among different landscape objectives.

Landscape A mosaic of natural and human-modified ecosystems, with a characteristic configuration of the topography, vegetation, land use, and settlements that is influenced by the ecological, historical, economic, and cultural processes and activities of the area. Both the mix of land cover and use types that make up the larger mosaic, including agricultural lands, native vegetation, and urban areas (landscape composition); and the spatial arrangement of different land uses and cover types (landscape structure) contribute to the character of a landscape. Depending on the management objectives of the stakeholders, landscape boundaries may be discrete or fuzzy, and may correspond to watershed boundaries, distinct land features, orjurisdictional boundaries, or crosscut such demarcations. Because of the broad range of factors a landscape may encompass areas ranging from 100 to 10 000 square kilometers.

Introduction and Definition

'Ecoagriculture' is an approach to managing landscapes for the simultaneous and synergistic achievement of three sets of outcomes: (1) maintaining, increasing, or improving agricultural production; (2) conserving biodiversity and ecosystem services; and (3) enhancing human livelihoods and well-being. These outcomes are achieved by institutions that support multistakeholder collaboration (McNeely and Scherr, 2003; **Figure 1**).

A 'landscape' is a mosaic of natural and human-modified ecosystems, with a characteristic configuration of topography, vegetation, land use, and settlements that is influenced by the ecological, historical, economic, and cultural processes and activities of the area. Both the mix of land cover and use types that make up the larger mosaic, including agricultural lands, native vegetation, and urban areas (landscape composition); and the spatial arrangement of different land uses and cover types (landscape structure) contribute to the character of a landscape. Depending on the management objectives of the stakeholders, landscape boundaries may be discrete or fuzzy, and may correspond to watershed boundaries, distinct land features, or jurisdictional boundaries, or crosscut such demarcations. Because of the broad range of factors a landscape may encompass areas ranging from 100 to 10 000 square kilometers (McNeely and Scherr, 2003).

'Integrated landscape management' involves long-term collaboration among different groups of land managers and stakeholders to achieve the multiple objectives required from the landscape, including agricultural production; provision of ecosystem services; protection of biodiversity; and local livelihoods, human health, and well-being. Stakeholders seek to solve shared problems or capitalize on new opportunities that reduce trade-offs and strengthen synergies among different landscape objectives. There are many different approaches to integrated landscape management, with varied entry points, processes, and institutional arrangements, but most share features of broad stakeholder participation, negotiation of objectives, strategies, and adaptive management based on shared learning (Landscapes for People, Food and Nature Initiative, 2013).

Ecoagriculture is the application of integrated landscape management in landscapes where agriculture is an important land use. Ecoagriculture involves collaboration among different groups of farmers and other land managers and stakeholders in the landscape to solve shared problems or capitalize on new opportunities. This is achieved through technical, ecological, market, or social means that reduce trade-offs and strengthen synergies among different landscape objectives (illustrated by the landscape shown in **Figure 2**). The term ecoagriculture was first coined by McNeely and Scherr (2001).

Applying the landscape approach in areas of thriving production agriculture faces additional challenges compared to forest or savannah-dominated landscapes where the approach was originally applied. Agriculture-dominated landscapes have dynamic patterns of land use change, as farmers respond to agricultural market incentives. With higher population densities, there is higher pressure on land, vegetation, and water resources, and more complex governance systems. The economic value of land for commercial crops is usually higher than for conservation. Farmers, agribusinesses, and agricultural agencies, long concerned about farmland stewardship to ensure sustainable production, have not been generally held responsible by society for stewardship of watersheds, wild biodiversity, and ecosystem functioning.

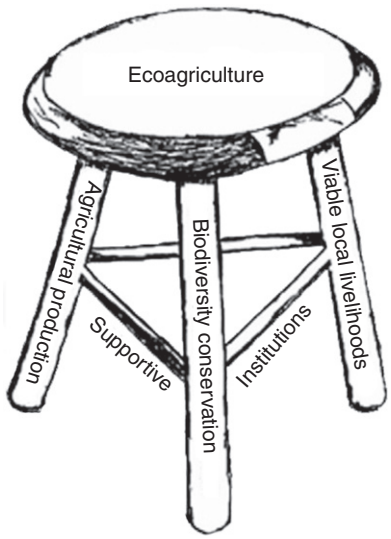


Figure 1 The ecoagriculture 'stool' illustrates the three sets of outcomes for agricultural production, environment, and human well-being in the landscape, and the institutions that support them. Reproduced from Buck, L.E., Milder, J.C., Gavin, T.A., Mukherjee, I., 2006. Understanding ecoagriculture: A framework for measuring landscape performance. EcoAgriculture Discussion Paper No 2. Washington, DC: EcoAgriculture Partners.

Evolution of Landscape Approaches

At the level of individual farms, there are numerous opportunities to increase sustainability and multifunctionality. However, sustainable field practices alone cannot usually provide the full complement of societal benefits expected from rural landscapes. A broader, spatially explicit landscape perspective is needed to address the dynamics, linkages, synergies, and trade-offs among multiple objectives, land units, and stakeholder interests, and to manage or overcome conflicts.

Landscape management concepts emerged in the 1980s with the development of the field of landscape ecology. Forman and Godron produced a seminal book in 1986 on the distribution patterns of landscape elements or ecosystems; the flows of animals, plants, energy, mineral nutrients, and water; and the ecological changes in the landscape over time (Forman and Godron, 1986). Although only marginally concerned with agriculture at first, landscape ecologists developed an analytical framework, tools and science enabling more systematic understanding and management of landscape elements for diverse functions (Dramstad *et al.*, 1996; Forman, 1995). By the 1990s, 'community-based natural resource management' approaches became more popular in the fields of forestry, watershed management and biodiversity conservation, as resource managers sought to accommodate human activities in

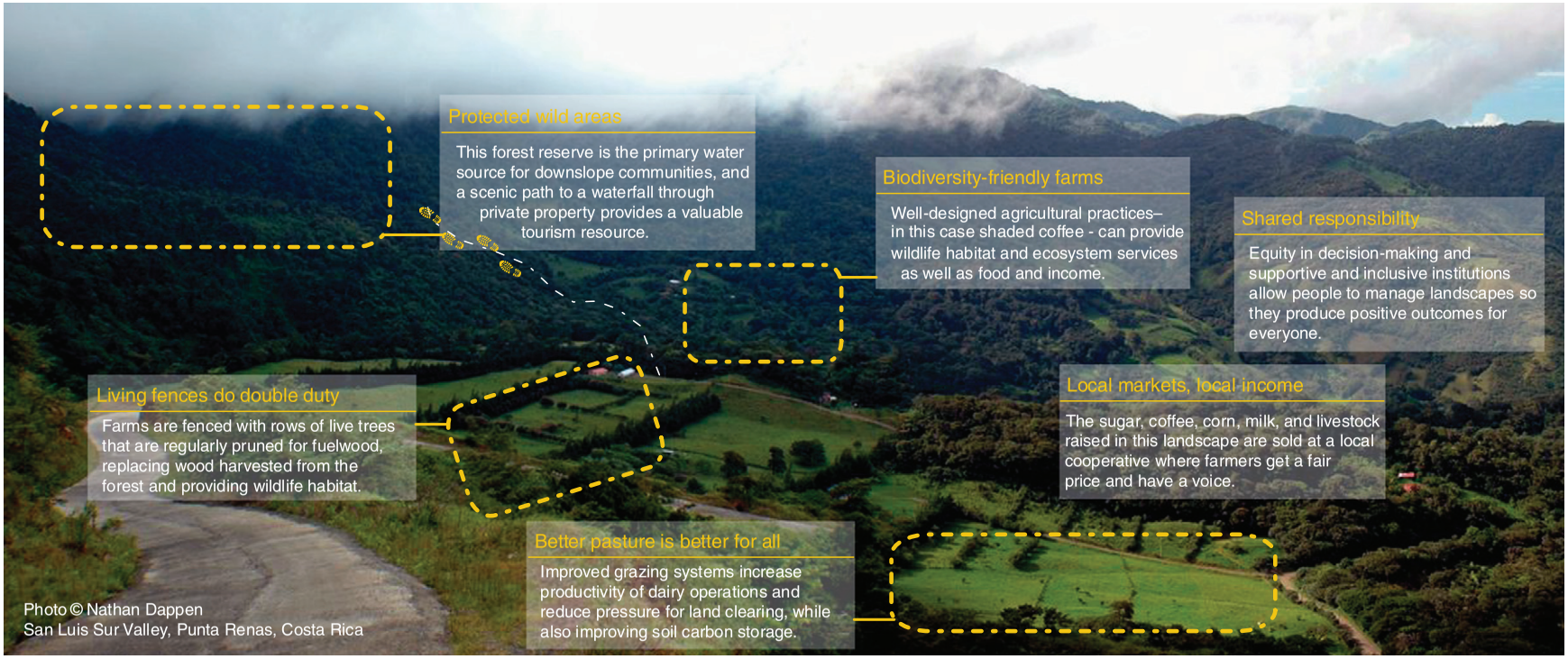


Figure 2 Achieving agricultural production, biodiversity, ecosystem, climate, and livelihood objectives in the San Juan Sur Valley landscape in Puntarenas, Costa Rica through diverse and coordinated land use activities. Photo: Nathan Dappen.

and around important habitats and protected areas. In many cases, these grew into landscape-scale strategies for action (van Noordwijk *et al.*, 2001; Sayer and Campbell, 2001).

Meanwhile, though most agricultural policy and investment still focus on field, farm, and supply chain levels, there is growing interest in landscape management systems that could simultaneously increase food production, ecosystem services, and local livelihoods. The role of healthy ecosystems in supporting and sustaining agricultural productivity is more widely recognized (Jordan *et al.*, 2007; UNEP, 2012). Societal demand for other ecosystem services is growing (Tscharntke *et al.*, 2012); given the geographic dominance of crop and livestock production in global land use, farmlands must clearly play a central role in providing them (Wood *et al.*, 2000). Analysts concerned with large-scale land-based climate change mitigation recognize the need for coordinated action across landscapes to reduce emissions, sequester, and maintain carbon storage across agriculture, forest, and conservation land uses (FAO, 2013; Scherr and Sthapit, 2009).

Varied Entry Points to Landscape Management

Landscape management strategies have emerged throughout the world to deliberately increase synergies and reduce trade-offs among rural livelihood development, agricultural production, and ecosystem conservation, through a variety of entry points.

Environmental organizations have found that spatial configuration of farmed and nonfarmed areas in a landscape is a key factor in conserving biodiversity and ecosystem services. For example, the effectiveness of fragmented protected areas is influenced by how easily wildlife can use and move through the agricultural production areas within the landscape (Blann, 2006). Thus conservation organizations are investing in landscape partnerships with farmers, ranchers, and forest managers. The managers of common property resources, such as forests, grazing lands, inland fisheries, and irrigation water find they require coordination and negotiation among institutions and stakeholders at a broader level.

Farmers, land users, and governments who depend for food security on highly degraded ecosystems are finding that ecosystem restoration can increase agricultural production, assure continued access to key water and forest resources by agricultural communities, and catalyze economic growth. Agribusiness and the food industry have begun to consider landscape management as part of corporate strategies related to risk management, supply chain reliability, regulatory compliance, and public image (Kissinger *et al.*, 2013).

Humanitarian organizations working with food-insecure farming communities have found that reducing vulnerability and increasing long-term resilience often requires action at landscape scale to manage the agricultural and natural resources on which they depend, in ordinary circumstances as well as in crises caused by disaster, famine, conflict, and climate change (Bailey and Buck, 2013). In Ethiopia, for example, the government now widely promotes landscape restoration in the highly degraded watersheds where many of the country's undernourished people reside (**Figure 3**).

These and other groups use a variety of terms for integrated landscape management that reflect their different objectives, perspectives, and initial entry points. For example, water-oriented programs may refer to 'participatory watershed management,' whereas biodiversity-led efforts are 'biological corridors.' Proponents of technological innovation around agroforestry, agroecology, permaculture, and organic agriculture are advancing their work at a landscape scale. Indigenous land managers, drawing on embedded ecological knowledge, are promoting 'indigenous territorial development,' whereas farmer-led collaborative action to restore degraded lands and waters prompted the 'landcare' movement. Scherr and Shames (2012) identified over 80 terms in active use that may be used as analogs to ecoagriculture.

Examples of Ecoagriculture Landscape Initiatives

Three examples documented illustrate the range of contexts and strategies where the ecoagriculture landscape approach is being practiced.



Figure 3 A site in Tigray, Ethiopia, where the Government of Ethiopia and the World Food Programme have restored highly degraded watersheds to achieve food security and climate resilience. Reforestation and revegetation of slopes, soil improvements, and rainwater harvesting for irrigation in microwatersheds have enabled crop intensification and greatly reduced the need for food aid during droughts (Kozar and Scherr, 2013). Photo: Raffaela Kozar.

Farming and Forest Conservation in the Central Highlands of Kenya

The Lari-Kijabe landscape in central Kenya, with one of country's last native forests is valued for its rich biodiversity and cultural heritage and for being an important smallholder agricultural production area and the catchment area for much of the capital city Nairobi's water supply. Almost half of the landscape is forested, much of which is designated important bird habitat. Over the past 15 years the community-based organization Kijabe Environment Volunteers (KENVO) has led a multistakeholder effort to mobilize local farmers and communities to balance agricultural production, livelihood security, and conservation functions by pursuing integrated approaches to forest and agricultural land management. Multisectoral development, education, research, and communication efforts by KENVO have mobilized community members and other stakeholders to restore, enrich, and protect large sections of the forest land; to sustainably intensify agricultural production systems and expand agroforestry, fish-farming, beekeeping, and other integrated practices; and to strategically locate and manage rainwater and surface water catchments to ensure adequate local access without compromising the value of the resource to downstream users (Buck *et al.*, 2011).

Farming with Wildlife in the Skagit River Delta, USA

The Skagit River Delta, approximately 100 km north of Seattle, WA in the northwestern United States harbors some of the most productive soils in the world as well as critical habitat for many wildlife species including migratory shorebirds and salmon. It is an important wintering site on the Pacific Flyway – a major travel route for birds, some of which migrate from Patagonia to Alaska – and provides crucial foraging grounds for over 100 000 shorebirds each year. The landscape also is an important food production area, providing half of the global beet and cabbage seed supply and 75% of the world's spinach. Seeing potential to align interests of conservationists and farmers, The Nature Conservancy initiated the farming for wildlife project to motivate farmers to create habitat for shorebirds on their working farms by performing 'habitat rotations' in addition to crop rotations. Groups of farmers cooperate with wildlife management authorities to create viable units of bird habitat by flooding their fields during migration season, which for more than a century have been drained of water year-round. When migration season is over, farmers drain their fields and return to growing crops. Farming for wildlife demonstrated that wetland rotations on farms can provide wildlife habitat at scale while sustaining and apparently improving soil health, reducing the need for synthetic fertilizer, and providing sufficient economic incentive to scale up the program without external payments. The enjoyment that farmers derive from managing habitat for migrating birds provides further incentive to continue their cooperative efforts (Moslemi, 2011).

Agroforestry for Watershed Protection and Reforestation in Yunnan, China

The 42-square kilometer watershed in Yangliu Township, Baoshan Prefecture in Yunnan province of Southwest China is the site of a bold and successful initiative by the World Agroforestry Center (ICRAF), China and the Baoshan Forestry Bureau to shift the Chinese government's Sloping Lands Conversion Program (SLCP) from a reforestation strategy to an agroforestry strategy that improves the livelihoods of farmers and their communities. The SLCP was created to prevent recurrence of the massive flooding that in 1998 took a tragic toll on human life and displacement, and eliminated or degraded 10 million ha of agricultural land. Its initial strategy was to deliberately take agricultural land and farmers out of production. The ICRAF–Baochan Forestry Bureau partnership launched an alternative approach to reforesting steeply sloping lands in Yunnan province that engaged village leaders in jointly developing agroforestry technologies that would integrate productive and profitable trees into villagers' farms. Building the initiative around indigenous technical knowledge to incorporate nontimber forest products into forest restoration strategies, the partners tapped into deep historical knowledge about managing and trading in medicinal herbs, indigenous tree products, and wild mushrooms of Yunnan. The Baoshan Bureau mobilized coordinated government support from diverse sectors to improve access to technical and social services by villages in the watershed and accelerate income opportunities from farming. Living standards are measurably improving, reforestation rates are rising, and investment is underway to scale up the effort to thousands of more villages in the region (Buck, 2009).

An Ecoagriculture Landscape Approach: Key Elements

Achieving multifunctional agricultural landscapes in the context of diverse and often conflicting land uses and users requires systematic action at different scales. Field experience and research on social, ecological, and production processes in landscapes have taught many lessons (e.g., Milder *et al.*, 2012a; Scherr *et al.*, 2013; Sayer *et al.*, 2013; Laterra *et al.*, 2012).

Five mutually reinforcing components comprise an ecoagriculture landscape approach: (1) agreed landscape objectives; (2) identification of synergies and trade-offs; (3) land use practices that contribute to multiple objectives; (4) markets, policies, and programs that encourage synergies and reduce trade-offs; and (5) institutions that enable collaborative planning, implementation, and monitoring among stakeholders (**Table 1**). These topics are discussed in the Sections Agreement among Stakeholders on Landscape Objectives; Management of Ecological, Social, and Economic Synergies and Trade-offs among Different Land and Resource Uses in the Landscape; Land Use Practices That Contribute to Multiple

Table 1 An ecoagriculture landscape approach: Key elements

1. Agreement among key stakeholders on landscape objectives
2. Management of ecological, social, and economic synergies and trade-offs among different land and resource uses in the landscape
3. Land use practices that contribute to multiple landscape objective
4. Development of supportive markets, policies, and investment
5. Establishment of collaborative processes for multistakeholder governance

Landscape Objectives; Development of Supportive Markets, Policies, and Investment Programs; and Establishment of Collaborative Processes for Multistakeholder Management.

Agreement among Stakeholders on Landscape Objectives

Landscapes reflect the management of resources by diverse stakeholders, who have different values, beliefs, and objectives for land management. Collective action toward ecoagriculture landscapes is commonly motivated by conflict among stakeholders or the inability of certain stakeholders to achieve their goals without aligned action from others. As discussed in the Sections Farming and Forest Conservation in the Central Highlands of Kenya; Farming with Wildlife in the Skagit River Delta, USA; and Agroforestry for Watershed Protection and Reforestation in Yunnan, China, in Kenya, the United States, and China, forest, biodiversity, and watershed conservation objectives initially clashed sharply with farmers' objectives. To be successful, ecoagriculture initiatives must commit to achieve multiple objectives of importance to the diverse stakeholders (**Table 2**). This commitment mobilizes interest, energy, and innovation to find solutions that are 'win-win' or at least reduce trade-offs among objectives.

Various tools and approaches have been developed to help align objectives among stakeholders. These methods foster interaction among people and organizations involved, help them look at the landscape from other perspectives, define their own goals more clearly (rather than preexisting 'positions' and the conventional solutions these assume), envisioning possible futures for their landscape and defining a few key objectives. Examples include participatory mapping, scenario development, and other tools (Stolton and Dudley, 2008; Landscape Measures Resource Center, 2013).

Management of Ecological, Social, and Economic Synergies and Trade-offs among Different Land and Resource Uses in the Landscape

Identifying and understanding beneficial and detrimental interactions among land uses and practices in some parts of the world and addressing them in ways that are acceptable to diverse stakeholders is a key driver in developing ecoagriculture landscapes. Stakeholders seek to modify agricultural practices in ways that protect biodiversity and ecosystem services (e.g., by reducing agrochemical pollution of habitats); to modify protected area management in ways that help farmers increase their production (e.g., pollinators); and to modify resource use and access to benefit local livelihoods and well-being (e.g., clean water).

Water availability is a common protagonist in landscape trade-offs and synergies. The volume and patterns of water flow, storage, and infiltration across a landscape – and thus its availability to and impacts on different water users including freshwater species – is profoundly affected by vegetative cover, physical barriers, storage, abstraction, and drainage on farms and other lands (Boelee, 2013; **Figure 4**). The design and management of irrigation systems, from sourcing to physical distribution systems to rules for water allocation and patterns of drainage, affects the availability and quality of water for agriculture, environmental, and other uses. Farmers and others users can benefit from innovations to link agriculture and water management (Macleod and Haygarth, 2010).

Table 2 Landscapes performance criteria

Conservation Goal: The landscape conserves, maintains, and restores wild biodiversity and ecosystem services
C1: Does the landscape contain an adequate quantity and suitable configuration of natural and seminatural habitat to protect native biodiversity?
C2: Do natural and seminatural habitats in the landscape approximate the composition and structure of the habitats historically found in the landscape?
C3: Are important species within the landscape biologically viable?
C4: Does the landscape provide locally, regionally, and globally important ecosystem services?
C5: Are natural areas and aquatic resources adequately buffered from productive areas and activities?
Production Goal: The landscape provides for sustainable, productive, and ecologically compatible agricultural production systems
P1: Do production systems respond to demand by internal (local) consumers and buyers, and by external buyers?
P2: Are production systems financially viable and can they adapt to changes in input and output markets?
P3: Are production systems resilient to disturbances, both natural and human?
P4: Do production practices have a neutral or positive impact on wild biodiversity and ecosystem services?
P5: Are species and varietal diversity of crops, livestock, fisheries, and forests adequate and maintained?
Livelihood Goal: The landscape sustains or enhances the livelihoods and well-being of all social groups that reside there
L1: Are households and communities able to meet their basic needs while sustaining natural resources?
L2: Is the value of household and community income and assets increasing?
L3: Do households and communities have sustainable and equitable access to critical natural resource stocks and flows?
L4: Are people in the landscape able to adapt to changes in human and nonhuman (plant & animal) population dynamics?
L5: Are households and communities resilient to external shocks, such as flooding, draught, changes in commodity prices, disease epidemics, and others?
Institutions Goal: Institutions are present that enable integrated, ongoing planning, negotiation, implementation, resource mobilization, and capacity-building in support of the goals of integrated landscape management
I1: Is there effective cross-sectoral and cross-boundary planning, monitoring, and decision-making at landscape scale?
I2: Do farmers, producers, and communities have adequate capacities to contribute to effective landscape management?
I3: Do relationships among public and civic institutions support the management of integrated landscapes?
I4: Do markets provide incentives for the management of integrated landscapes?
I5: Do knowledge, norms, and values (culture) support integrated landscape management?

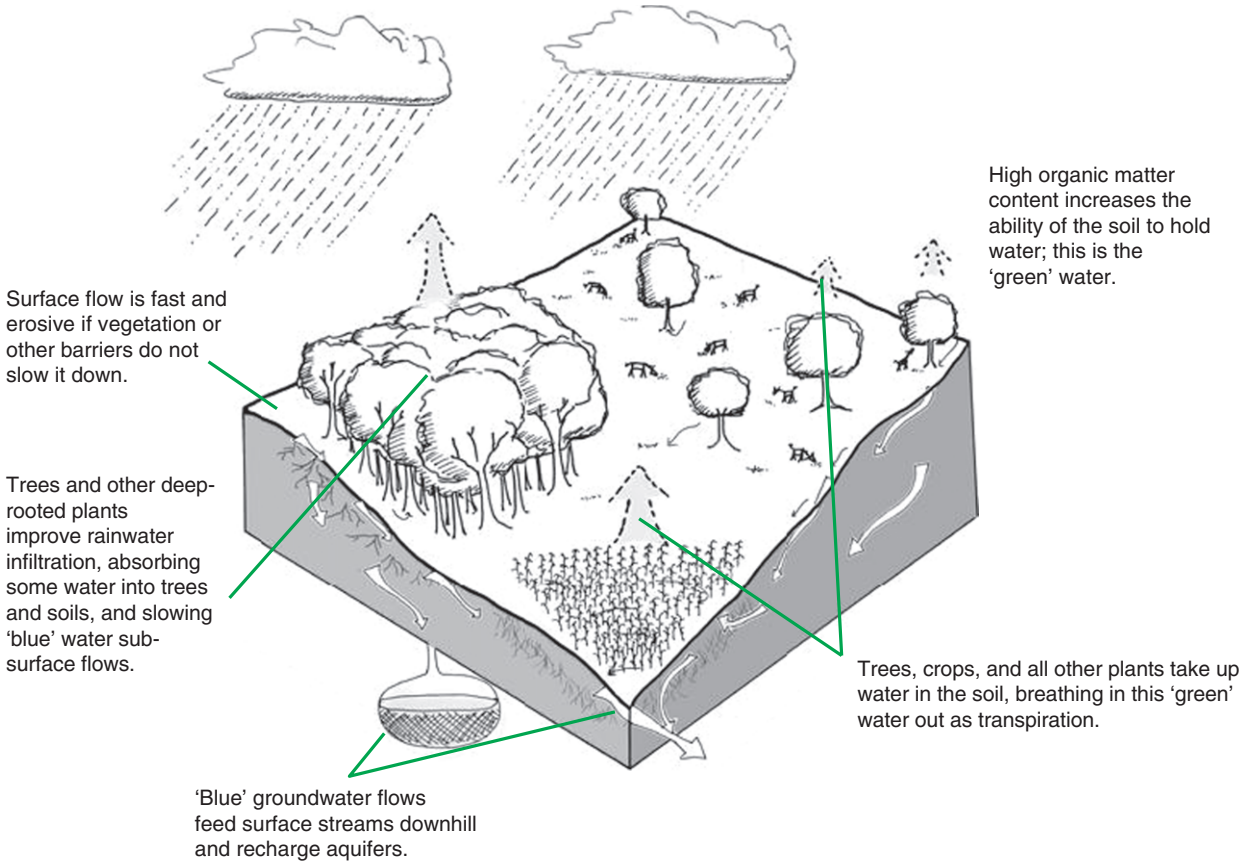


Figure 4 Water resources in a landscape include both 'blue' flows (like rainfall, streams, lakes, and underground aquifers) and 'green' flows (water stored in and moving through soils and the stems and roots of crops, grasses, trees, and other vegetation). By managing soils, vegetation, and the speed and direction of both sets of flows, the total volume of water available can be regulated. Reproduced from Buck, L.E., Scherr, S.J., 2011. Moving ecoagriculture into the mainstream. In: Starke, L. (Ed.), State of the World: Innovations that Nourish the Planet. Washington, DC: The Worldwatch Institute, pp. 15–24.

Managing perceived trade-offs between biodiversity conservation and agricultural production is another common motivator. To sustain wild species populations requires sufficient extent and configuration of natural areas, networks of suitable habitat using the noncultivated areas in and around farm, community lands, and biodiversity-compatible crop and livestock production practices (Burel and Baudry, 2005; Harvey, 2007; McNeely and Scherr, 2003; **Figure 5**). Farming communities should be able to draw some benefit from the presence of natural areas nearby and be protected from negative impacts (McNeely and Scherr, 2003). Where farmers use biodiversity-friendly agricultural practices less protected area may be needed to sustain wildlife populations (Blann, 2006). Additionally, to minimize pressures to expand production area or permit reestablishment of natural cover, it is essential to have compatible agricultural development processes in other parts of the landscape (Shames *et al.*, 2011).

Landscape-scale coordination of land management practices and investments can increase the overall effectiveness and reduce costs of climate change mitigation (Scherr *et al.*, 2013). For example, international and national reducing



Figure 5 Agricultural areas provide critical habitat for wildlife species and landscapes can be managed to enable year-round wildlife access to fresh water and food sources and protected breeding areas, in and around crop, livestock, and forest production. In Bwindi, Uganda, shaded coffee plantations are important habitats for wildlife, such as this chameleon. Photo by Jeff McNeely.

emissions through deforestation and degradation programs are shifting their strategies to a larger landscape frame, explicitly targeting action in the agricultural sector (Shames *et al.*, 2011). Risks to farmers and farming communities from climate change can be mitigated through sustainable land management practices at community as well as farm level (Nkonya *et al.*, 2011).

Stakeholders can also take advantage of the social synergies of diverse land use across the landscape. Certain areas in the landscape may be designated and managed collectively for provision of reserve food, feed, or fuel for years when communities face crop failure or interruption of markets. Differentiation of land cover can help to sustain agrobiodiversity, by maintaining social–ecological dynamics that contribute to species resilience and adaptation. Encouraging seed exchange and on-farm experimentation in interconnected farming communities can increase farmers' access to diverse varieties, knowledge, and new practices (Mijatovic *et al.*, 2013).

Scientific advances in remote sensing, resource monitoring, participatory methods, and spatial analysis are providing new tools and methods to understand spatial interactions – biophysical and socioeconomic – across the landscape (Dushku *et al.*, 2007; O'Farrell and Anderson, 2010). This knowledge can help stakeholders locate and target the most cost-effective activities, investments, and policies across a landscape. In the Lake Victoria Basin of East Africa, for example, remote-sensing methods were used to identify sites in the watershed that were generating the greatest sedimentation from soil erosion, so that investments in soil conservation could be spatially targeted, reducing overall costs to farmers and agency programs (Egoh *et al.*, 2011).

Land Use Practices That Contribute to Multiple Landscape Objectives

The basic building blocks of ecoagriculture landscapes are farming, ranching, forest, and other resource management practices on individual farms and local communities that contribute to multiple landscape objectives. McNeely and Scherr (2003) identified three key strategies that lead to ecosystem-compatible production systems: minimizing pollution; modifying management of soil, water, and vegetation resources in and around productive fields; and using farming systems that mimic components of natural ecosystems, such as species diversity, configuration, and land cover.

Over the past few decades, numerous such systems have been identified by research and farmer innovation (Buck *et al.*, 2007). Some practices incorporate advanced modern technology (e.g., precision agriculture with geopositioning tools); some are based on longstanding tradition and local knowledge (e.g., use of fertilizer trees); some incorporate both (FAO, 2011). These agroecological systems tend to have greater agricultural species and varietal diversity than conventional systems, although coexisting with greater native floral and faunal biodiversity (Delgado *et al.*, 2011; Lal *et al.*, 2011; Perfecto *et al.*, 2009).

Building soil organic matter and soil biota is a common feature. Minimal tillage, crop residue incorporation, and cover cropping practices enhance the organic matter stored in soil, while also supporting biological processes, nutrient, and hydrological cycling (Milder *et al.*, 2011; Hobbs and Govaerts, 2009). Precision methods incorporate modern technologies for fertilizer application, irrigation, land leveling, crop protection, and other agronomic techniques are helping farmers increase yields with fewer inputs and less pollution (Bongiovani and Lowenberg-DeBoer, 2004). Best practices for irrigation, water-harvesting technology, and terrace or contour farming systems contribute to improved water-use efficiency and conservation, while greatly reducing the very high greenhouse gas emissions associated with conventional irrigation systems.

Agroforestry, the intermingling of crops and trees, can address numerous functions. Productive trees and shrubs can provide diverse fruits, nuts, medicines, fuel, timber, nitrogen-fixation services, and animal fodder, whereas their canopy, roots, leaf litter, and other features provide ecosystem services benefits. Farming with perennials that develop root and woody biomass can substitute for an annual tillage regime, provide year-round ground cover, and retain organic matter and water in soil (Glover and Reganold, 2010). Systems of 'evergreen agriculture,' in which crops are produced under a managed canopy of nitrogen-fixing trees, are being adopted in many African countries (Garrity *et al.*, 2010; **Figure 6**).

Improved pasture and grassland management, including rotational grazing, regenerating vegetation, and restoring degraded land, can increase production and increase the landscape's water-holding capacity and habitat value (**Figure 7**). These strategies also contribute to climate mitigation goals through carbon sequestration in deep-rooted vegetation and soils. Converting confined livestock manure into biogas can provide added benefits of an alternative energy source with fewer negative health impacts from cooking, heating, and lighting, and reduced water pollution (Neely and Hatfield, 2007).

Such agroecological systems have been shown to increase agricultural yields, improve livelihoods, and benefit the environment in a wide range of contexts. A recent study assessed 219 peer-reviewed studies for five agroecological intensification systems, containing a total of 426 individual comparisons with conventional or baseline farming systems (Milder *et al.*, 2012b). The review found both yield and ecosystem benefits for precision agriculture and system of rice intensification (an agroecological method for increasing the productivity of irrigated rice by changing the management of plants, soil, water, and nutrients; Uphoff *et al.*, 2011) in nearly all comparisons, and in approximately half of the cases for conservation agriculture, holistic grazing management, and organic agriculture.

Local producers and communities must continuously develop, adopt, and adapt these systems at a scale that will have landscape-wide impacts. Local knowledge-sharing, training, and extension institutions need to be strengthened or developed, so land managers have strategic access to research support and specialized knowledge (Buck and Scherr, 2011).

Development of Supportive Markets, Policies, and Investment Programs

Supportive market institutions, public policies, and investment programs can encourage synergies and reduce trade-offs among the agreed landscape objectives. Widespread adoption



Figure 6 Evergreen agriculture combines annual crops with over-story trees that benefit crop production as well as landscape goals, such as wild biodiversity, soil quality, and water infiltration. Photo by ICRAF.



Figure 7 Intensive rotational grazing systems, such as this one in Washington County, VA, USA, increase meat and milk productivity by increasing feed resources at low cost, while also improving above- and below-ground vegetation with benefits for rainfall infiltration, carbon sequestration, storage, and biodiversity. Photo by Jeff Vanuga.

of multibenefit production systems depends in part on clear financial incentives for farmers, ranchers, and forest managers to do so. In some cases, the profitability (from lower costs, higher yields, or quality) and reduced risks of these systems provide sufficient incentive. But often changes in market institutions are needed as well. Diverse strategies are being used to link market development with landscape approaches (Scherr *et al.*, 2011).

In some cases, markets for new and minor products can incentivize the diversification of production systems. For example, there are now widespread efforts to domesticate indigenous fruit and nut trees that are traditionally and culturally important to produce marketable products. New supply chains, quality standards, and processing methodologies may need to be developed for products that are being sustainably harvested from wetlands or forests to supplement local incomes.

Entire supply chains for some crop and livestock products may need to be restructured. Market signals are needed to incentivize sustainable sourcing. To provide these market

signals, ecostandards, ecocertification, and ecolabeling systems have emerged (Millard, 2007). Whereas organic certification has been dominant, commodity roundtables have developed other certification systems for more sustainable palm oil, soy, biofuels, cocoa, sugar, and more recently for rice and livestock. Numerous other certifications for environmental and social standards have arisen. By 2010, the global market for certified agricultural products was estimated to be over US$64 billion, of which organics accounted for more than US$50 billion. Such markets are projected to grow at 15% annually in the short term (Potts *et al.*, 2014). New models are being developed to make certifications easier for smallholder farmers to use (Blackmore *et al.*, 2012).

Although focused initially on farm-scale impacts, sustainability standards have begun to address landscape-scale impacts. For example, company members of the Consumer Goods Forum, worth almost US$2.8 trillion of processed products, committed in 2010 to help achieve zero net deforestation by 2020, by eliminating from their supply chains all products associated with tropical deforestation (The Consumer Goods Forum, 2010). Landscape labeling approaches are being developed that seek to turn unique landscape qualities into a marketing advantage for diverse products.

Other market mechanisms are being developed to pay farmers and communities directly for using production systems that contribute to ecosystem services, particularly agroecological practices (Kinzig *et al.*, 2011; Lipper and Zilberman, 2009). Already worth billions of dollars, a majority of payments are by public agencies, but increasingly, private companies or conservation groups are paying farmers directly, such as water bottling companies seeking to protect water quality. The design and payment allocation of such systems is increasingly informed by a landscape perspective (Milder *et al.*, 2010). Spatial or ecosystem criteria can be added to develop marketing strategies that target specific ecological niches and social groups in a landscape (Scherr *et al.*, 2011).

Some agribusiness actors are integrating landscape thinking into their supply chain strategies. A recent scoping exercise found 27 international companies that had begun to adopt landscape approaches (Kissinger *et al.*, 2013; **Figure 8**). The most common rationales were mitigating local community and operational risks, including secure access to water and mitigating climate change; value chain efficiency; and voluntary standards compliance. The most common modes of engagement were: value chain interventions that include landscape elements (such as ecocertification, which often requires the identification of high conservation value lands at regional scales); regional producer support programs across communities; and payments for ecosystem services (especially carbon or water finance).

Public policies and programs can be used to establish, develop, and scale up ecoagriculture. Decentralized governance enables local stakeholders to control key planning decisions, incorporating local needs and priorities. Secure systems of use, access rights, and property rights provide farmers and communities the necessary incentive to manage their lands sustainably, and in many landscapes, achieving multiple product and service functions may require reforming land, resource tenure, and access rights (Mwangi *et al.*, 2012; WRI, 2005).

Coordination of policies is required, with mechanisms to encourage regular engagement between agriculture, forest, environment, climate, health, and rural decision-making institutions. Public investment programs must be structured to enable intersectoral funding of activities that have multiple cobenefits (Shames *et al.*, 2012). Financing may also be needed to cover early investments costs at farm or landscape levels. Around the world, countries seeking to support the multifunctionality of agriculture are shifting in the main focus of subsidy programs from production to the social and environmental functions of agriculture. An ecoagriculture lens for development planning can highlight alternative investment strategies, as illustrated for biofuel development (Milder *et al.*, 2008) and agriculture green growth strategies in Tanzania (Milder *et al.*, 2013).

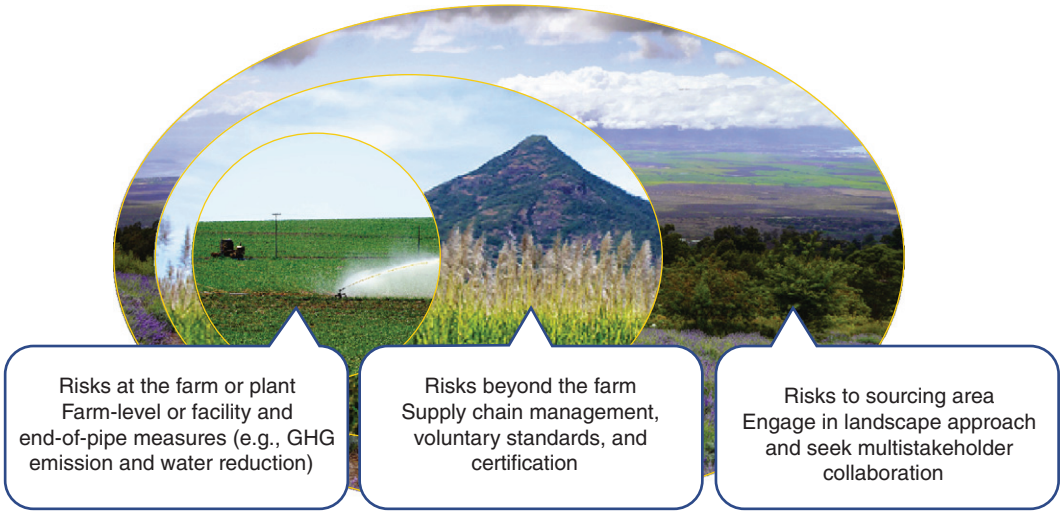


Figure 8 Companies become engaged in landscape approaches when business risks must be managed beyond the farm and supply chain scales. Adapted from Kissinger, G., Brasser, A., Gross, L., 2013. Reducing risk: Landscape approaches to sustainable sourcing. EcoAgriculture Partners for the Landscapes for People, Food and Nature Initiative. Washington, DC: EcoAgriculture Partners.

Establishment of Collaborative Processes for Multistakeholder Management

Further elaboration of the four elements of ecoagriculture (described in the Sections Agreement among Stakeholders on Landscape Objectives; Management of Ecological, Social, and Economic Synergies and Trade-offs among Different Land and Resource Uses in the Landscape; Land Use Practices That Contribute to Multiple Landscape Objectives; and Development of Supportive Markets, Policies, and Investment Programs) requires coordinated decision-making and action by stakeholders from public, private, and civic sectors who bring diverse knowledge and interests to planning and managing integrated landscapes. Such processes serve as a means to develop partnerships, share knowledge, build coalitions, and pool investments.

Landscape management initiatives need to recognize the presence of complex overlapping jurisdictions, and the uneven distribution of decision-making authority among actors with interests in the outcomes. Research points to the benefits of establishing collaborative, adaptive management processes that seek to include a broad spectrum of participants, women and men alike, in thoughtfully designing change strategies that are implemented incrementally, step by step. Such processes are structured to engage actors with diverse perspectives to envision optimal futures and then design innovative interventions, monitor their implementation, observe their effects, and learn from the experience. Through this social learning, viable ways of capturing synergies and reducing trade-offs become apparent, innovations that address the interests of multiple stakeholders become better understood and appreciated, mistakes are made and mitigated, trust is built, and commitments are made to continue working together toward shared goals for the landscape (Sayer *et al.*, 2013; Buck and Scherr, 2009).

Ecoagriculture strategies for building multistakeholder management are explicit about the interests, rights and roles of farmers, pastoralists, fisherfolk, and other producers as well as the agricultural research, extension, finance, and administration actors who support them. Management strategies strive for inclusive and transparent governance, or ways and institutions through which citizens and groups express their interests, exercise their rights and obligations, mediate their differences, and build trust and cooperation (Colfer and Pfund, 2011).

The Landscapes for People, Food and Nature Initiative's reviews of integrated landscape initiatives found an average of 9.4 stakeholder groups representing an average of 3.8 sectors per initiative, whereas in Latin America and the Caribbean an average of 10.5 stakeholder groups are involved representing an average of 4.1 sectors (**Table 3**). More than 83% of initiatives included local farmers or producers association, the most

Table 3 Sectors and stakeholders engaged in integrated landscape management initiatives in Africa, Latin America, and the Caribbean

	Africa	*Latin America and the Caribbean*
Number of integrated landscape initiatives surveyed	87	104
Countries	33	21
Average number of stakeholder groups	9.4	10.5
Most frequently involved stakeholder groups (in more than 70% of initiatives)	Local farmers' or producers' associations (83%), local government leaders (80%), extension officers (71%), and local nongovernmental organizations (NGOs) (71%)	Local farmers' or producers' associations (86%), local government leaders (82%), local NGOs (78%), district-level government offices (75%), local or national research center or university (74%), and state or provincial government offices (71%)
Other stakeholder groups involved (in fewer than 20% of initiatives)	Representatives of landless people groups (13%), In-country agribusiness groups (8%), logging or forest products industry members (5%), Mining, oil or gas industry members (3%), and foreign agribusiness groups (0%)	Representatives of landless people groups (18%), foreign agribusiness groups (7%), logging or forest products industry members (20%), and Mining, oil or gas industry members (7%)
Average number of sectors	3.8	4.1
Most frequently involved sectors (in more than 50% of initiatives)	Natural resources conservation or environment (in 86%), agriculture (in 80%), and forestry (in 57%)	Natural resources conservation or environment (in 89%), agriculture (in 75%), forestry (in 53%), and tourism (in 52%)
Other sectors involved (in fewer than 50% of initiatives)	Livestock (in 49%), education (in 30%), tourism (in 25%), health (18%), roads, transportation or infrastructure (in 16%), and energy (in 14%)	Education (in 47%), livestock (in 39%), health (in 26%), energy (in 16%), and roads, transportation or infrastructure (in 13%)
Percent of initiatives that aimed to form a new coordinating body	53%	50%
Percent of initiatives that reported improved coordination and cooperation among stakeholder groups and sectors	77% among stakeholder groups and 43% among sectors	80% among stakeholder groups and 55% among sectors

Source: Reproduced from Estrada-Carmona *et al.*, 2013 and Milder, J.C., Buck, L.E., Hart, A.K., Scherr, S.J., Shames, S.A., 2013. A Framework for Agriculture Green Growth: Greenprint for Sagcot. Dar es Salaam: SAGCOT (Southern Agricultural Growth Corridor of Tanzania).

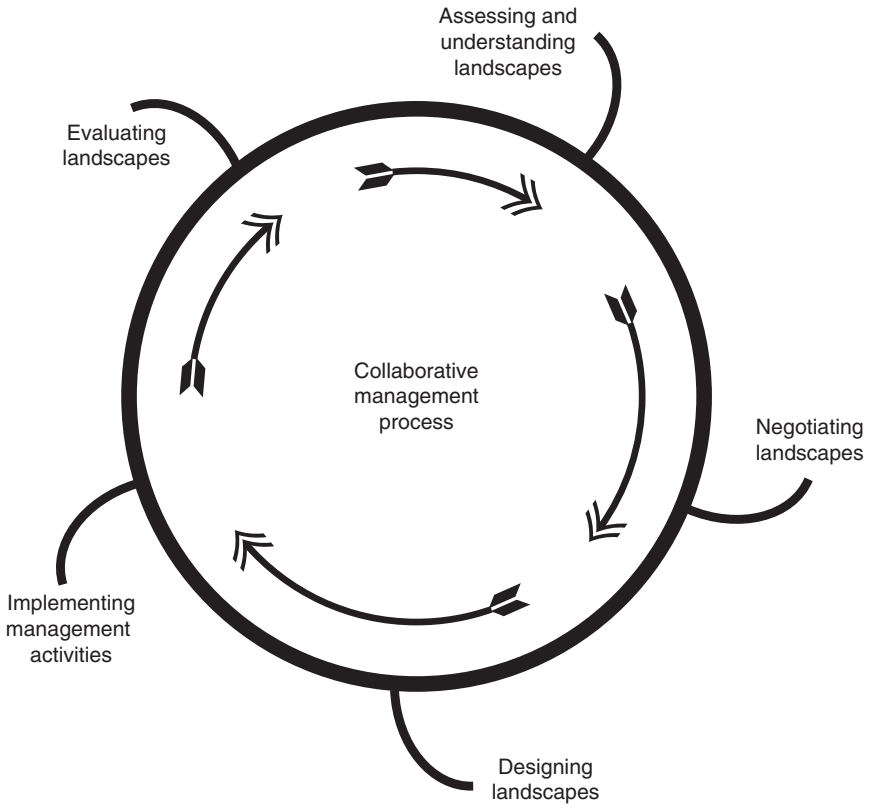


Figure 9 Collaborative processes for integrated landscape management move through typical cycles of adaptive management: Assessment of landscape issues, negotiation over objectives, design of stakeholder actions, implementation, and monitoring, followed by reassessment, and redesign.

common category of stakeholders. Other sectors most frequently involved are natural resources, conservation or environment, forestry, and tourism (Estrada-Carmona *et al.*, 2014).

Colfer *et al.* (2011), who examined landscape governance in numerous tropical countries, found that despite the inherent complexities a dual emphasis on bottom-up and top-down approaches leads to the best chances for long-term success. This dual approach was more viable than prioritizing one approach over the other. Alexandra (2012) stresses the rich learnings from recent experience in bioregional conservation planning, natural resource management, landcare, and water reform as a basis for building capacity for integrated and adaptive resource management. Primmer and Furman (2012) emphasize landscape governance for operationalizing ecosystem services approaches, and stress the importance of moving from sector-based to integrated approaches by deliberately building on governance arrangements that are geared toward sustainability.

In some cases, community-based organizations or farmer groups find they can better meet their goals through collaboration with other stakeholders or sectors and initiate a process of landscape-level learning and negotiation that eventually leads to commonly accepted roles and rules of decision-making (Buck *et al.*, 2010). As primary managers and stewards of land and resources, farmers and communities must be involved in landscape initiatives as stakeholders and partners, not simply as 'beneficiaries' or 'targets.'

Because ecoagriculture landscapes are transformed over a generation or more, not through a single short-term project, collaborative management systems must enable stakeholders to assume long-term perspectives by continuously planning, monitoring, and adapting strategies to address dynamic social, economic, and ecological conditions (**Figure 9**). Leaders must enable their constituents to understand and communicate the multiple benefits that ecoagiculture landscapes stand to generate: including yield improvements, food and energy security, human health, biodiversity conservation, and other ecosystems services, and to make good use of landscape monitoring systems that are being developed to monitor suites of objectives over time (Buck *et al.*, 2006; Kinzig *et al.*, 2011; Landscape Measures Resource Center, 2013; Sachs *et al.*, 2010; Vital Signs, 2013).

Current Scope and Scale of Integrated Landscape Initiatives

In regions with high pressure on land, multifunctional landscapes are increasingly seen to play a crucial role in reducing conflicting claims on land, while meeting societal demands for multiple goods and services from rural landscapes (Brandt and Vejre, 2004; Smith *et al.*, 2010). Landscape approaches involving farmers and agriculture are being applied in agricultural policies and programs, as more communities, governments, and organizations find they cannot meet their needs

and objectives through strategies that focus only on specific sectors like agriculture, forestry, or water.

As shown in **Table 3**, recent surveys have documented over 107 integrated landscape initiatives in Latin America (Estrada-Carmona *et al.*, 2014) and over 85 in Africa (Milder *et al.*, 2014). In Asia and the Middle East, other research has documented 21 longstanding landscape management systems where humans have developed integrated strategies for maintaining agricultural productivity and rich natural ecosystems (Ichikawa, 2012). Many of these are in places where high levels of poverty coincide with critical conservation priorities. Meanwhile, in North America, Europe, Australia, and Japan, many integrated landscape approaches are being developed to meet challenges of water quality, resolve water conflicts, manage commercial agriculture in environmentally sensitive areas, and sustain cultural aspects of rural landscapes (Daugstad *et al.*, 2006; Crossman *et al.*, 2010; Gascoigne *et al.*, 2011; Plieninger and Bieling, 2012). The need to manage landscapes in an integrative way was picked up in the political arena with several comprehensive spatial planning strategies in Europe and a shift toward farm subsidies for practices that support ecosystem services and biodiversity, rather than increasing production (e.g., Dijst *et al.*, 2005; Cairol *et al.*, 2009; Vejre *et al.*, 2010).

Some landscape initiatives are led by farmer or community groups who band together to solve problems that transcend the purview of single organizations. Others have been organized through government initiatives, programs of nongovernmental organizations (NGOs), or new market initiatives. Landscape approaches have been applied by many of the world's leading international organizations, funding agencies, and NGOs dedicated to agriculture, rural development, watershed management, and ecosystem conservation. For instance, in Africa, the continent-wide TerrAfrica program is harnessing several billion dollars in government support and donor funding, with high-level political commitments, to promote sustainable land management at large scale, including through landscape approaches.

Several networks have emerged to help support and share information among landscape initiatives. The Ibero-American Model Forest Network supports 28 landscapes in Latin America, the Caribbean, and Spain (International Model Forest Network, 2010). Landcare International facilitates farmer groups, in Australia, Africa, and Asia, to integrate agricultural production, water, and wildlife management (Catacutan, 2010). The International Partnership for Satoyama Initiative is supporting community-managed landscapes, drawing inspiration from traditional Japanese landscape approaches. The program of Globally Important Agricultural Heritage Systems supports the continued vitality of 19 socioecological landscapes developed by traditional societies, and assists them to meet new challenges (FAO, 2012). The Landscapes for People, Food, and Nature Initiative has set up a knowledge-sharing network for landscape leaders around the world (Landscape strategies are being incorporated into the Convention on Biological Diversity's work on the ecosystem approach in agricultural landscapes (Shames and Scherr, 2009), and United Nations Environment Programme's (UNEP's) work promoting an ecosystem-based approach to food security (Munang *et al.*, 2013). The United Nations (UN) Framework Convention on Climate Change is sponsoring its first Global Landscapes Forum in 2013 .

In Central America, heads of state for eight countries, including the Dominican Republic, have endorsed and are now implementing in 29 landscapes a territorial approach to rural development that supports participatory planning for agriculture, environment, health, human development, and climate change in an integrated way (IICA, 2010). In the West African Sahel, a multinational coalition is working with communities to restore woodlands, protect and enrich agricultural soils, and reduce poverty in landscapes stretching across a belt 7700 km long, from Senegal in the west to Djibouti in the east (World Bank, 2011). The new Global Partnership on Forest and Landscape Restoration is aiming to restore 150 million ha of degraded land, of which 50 million targets agricultural landscapes in the tropics (GPFLR, 2013). The United Nations Development Programme (UNDP), with support from the government of Japan, began in 2011 the UNDP Satoyama Initiative, which is assisting community-based agricultural landscape initiatives in 15 developing countries. The Global Environment Facility is implementing integrated landscape programs with strong agriculture and food security components in focal areas of land degradation, biodiversity, international waters, and climate change (Bakarr *et al.*, 2013).

In 2004, the European Landscape Convention came into effect, a Europe-wide concept centering on the quality of landscape protection, management, and planning and covering the entire territory, not just outstanding landscapes (Council of Europe, 2004). In 2012, a group of African heads of state adopted the Gabarone Declaration, which includes explicit mention of integrated landscape approaches for agriculture, environment, and development (Gaborone Declaration, 2012). In June 2012, participants in the Nairobi International Forum endorsed a Call to Action to promote Landscapes for People, Food, and Nature (Landscapes for People, Food and Nature Initiative, 2012).

Current State of Research on Ecoagriculture Landscape Management

As action on the ground is accelerating, the evidence suggests that ecoagriculture landscape approaches have promising potential to reshape land use at local, national, and global scale. Recent scientific articles are refining conceptual approaches and expectations from integrated landscape management (Menz *et al.*, 2013; Scherr and McNeely, 2008; Cunningham *et al.*, 2013). Authors have stressed a range of interdisciplinary future research needs (Aggarwal *et al.*, 2010; Carpenter *et al.*, 2009; Rounsevell *et al.*, 2012; Sayer *et al.*, 2013; and Veldkamp *et al.*, 2011). Current landscape science covers the understanding, explorations, and acknowledgment of many multidisciplinary issues like the spatial multilevel character of landscape processes and governance systems (Veldkamp *et al.*, 2011), the behavior of individuals and society regarding land management decisions (Matthews *et al.*, 2007), the ways in which people and land are teleconnected to the broader world (Lambin and Meyfroidt, 2011), and the future and past drivers of landscape change (Claessens *et al.*, 2009).

However, there are many remaining challenges to support the mainstreaming of ecoagriculture landscape approaches. The quantitative evidence of impacts of landscape-scale interventions remains weak (EcoAgriculture Partners, 2012). Also needed is a better understanding and evidence of the impact of agricultural practices, level of intensification, and temporal aspects of agricultural systems on a broad range of landscape benefits. Also, new research is needed to better understand the scientific principles and processes underlying ecosystem-friendly farming systems, and ways to improve their management and performance across different spatial and temporal dimensions.

The proliferation of spatial data sources, available online as open-access resources, should allow for better assessment of the condition, use, and changes in resources and functions across the landscape. Paired with appropriate modeling and decision-support tools, data access enables landscape managers and stakeholder groups to evaluate and predict the effects of alternative courses of management actions, select the most suitable approaches, and monitor the impacts (Kok and Veldkamp, 2011; Kenwarda *et al.*, 2011).

Another focus area for research is to gain a better understanding of how local agricultural decision-making takes place in reaction to macro-level economic and price dynamics and to understand the role of incentives and investments to enhance a synergetic supply of benefits from rural landscapes (Bryan, 2013). To support decision-making, landscape science has so far mainly developed methods to describe landscape processes. Normative methods that can prescribe pathways to desired outputs are not yet readily available. Such prescriptive methods are crucial to identify and plan for alternative development pathways.

Several national research programs are advancing landscape systems analysis, such as the Commonwealth Scientific and Industrial Research Organization in Australia, Leibniz Center for Agricultural Landscape Research in Germany, and Cornell University's Ecoagriculture Working Group in the United States. The Consultative Group for International Agricultural Research, focusing on science-for-development, has established a number of Collaborative Research Programs with strong landscape science components. Relevant approaches to research partnerships are being developed (Tomich *et al.*, 2007).

The Landscapes for People, Food, and Nature Initiative is undertaking collaborative scoping studies to synthesize and disseminate the current state of knowledge relevant to practitioners. Generally, however, the practical research base to support ecoagriculture landscape management is still at an early stage. Research priorities for development include generating more systematic evidence on:

- best agricultural and land management practices for implementing ecoagriculture in different (changing) biophysical and social contexts, uncertainties, including evidence about the benefits and costs (initial investments and trade-offs) of integrated landscape approaches;
- underlying field-to-farm-to-landscape processes and interactions, and the functioning of farming and natural resource management systems to realize synergies and reduce trade-offs across a range of benefits and beneficiaries;
- implementation strategies for successful landscape initiatives. Methods for facilitating multistakeholder landscape assessment, setting of desired outputs/vision, planning, negotiation, and monitoring require further development; and
- how policies, incentives, and investment can create an enabling environment for integrated landscape management and for realizing new sources of synergy in rural landscapes.

See also: Agroforestry: Complex Multistrata Agriculture. Agroforestry: Fertilizer Trees. Agroforestry: Fodder Trees. Agroforestry: Hydrological Impacts. Agroforestry: Participatory Domestication of Trees. Biodiversity and Ecosystem Services in Agroecosystems. Biodiversity: Conserving Biodiversity in Agroecosystems. Food Security: Yield Gap. Soil: Nutrient Cycling

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Economics of Natural Resources and Environment in Agriculture

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Glossary

Ambient pollution The amount of a contaminant present in an environmental medium, such as air or water; usually expressed per unit volume. Ambient pollution is the end result of pollution discharges after mixing and natural degradation processes take place.

Depletable resource A substance from which economic benefits are produced but which has a finite supply within a human timescale. For example, most mineral resources are considered depletable, although technological advances and recycling may increase human capacity to exploit them. Radio wave bands, although not material in nature, may also be considered depletable resources, given limitations on the available spectrum.

Economic efficiency The condition under which it is not possible to reallocate resources between uses, either in production or consumption, so as to increase overall value. For priced resources, an economically efficient allocation satisfies the condition that the ratio of incremental benefits from the use of any two resources equals the ratio of their prices.

Economic sustainability The capacity to endure economically, encompassing not only the resources necessary to sustain well-being at levels at least comparable to the present, but also social, cultural, and ecological capacities to adapt as conditions change.

Economic welfare The well-being achieved through enjoyment of goods and services realized through economic activity.

Ecosystem services Resources and processes supplied by ecosystems. Examples include the pollination services provided by insects, degradation services provided by microorganisms feeding on pollutants, and esthetic and genetic preservation services provided by nature reserves.

Externality A consequence of an activity or transaction that imposes costs or benefits on a party without that party's consent. For example, industrial smoke may increase lung discomfort and disease in nearby residents or a conservation area may provide recreational and esthetic benefits to nearby residents without cost.

Point and Nonpoint source pollution Point source pollution emanates from sources that are easily identified and monitored, such as smokestacks or waste discharge pipes. Nonpoint pollution originates from diffuse sources, such as soil particles or fertilizer emanating from land, in contrast to discharges from discrete and easily monitored sources like smokestacks or effluent pipes. The diffusion of sources complicates monitoring, measurement, and assignment of responsibility.

Public good A valuable material or service that satisfies two conditions: (1) nonexcludable – potential beneficiaries cannot effectively be excluded from use and (2) nonrival – one user's enjoyment of the good does not diminish its availability to others. Examples include air quality, national defense, knowledge, and mosquito control.

Renewable resources A substance from which economic benefits are produced and which reproduces or replenishes relatively quickly through natural processes. Examples include wildlife, vegetation, and wind.

Introduction

Until the early 1970s, agricultural policies in developed countries were largely intended to serve policy objectives related to agricultural productivity, farm income, commodity prices, agricultural trade, and rural economic vitality. Environmental externalities and resource degradation associated with agricultural production were generally unrecognized or not considered public policy issues. Natural resource policies relating directly to agriculture were intended to facilitate access to and to protect the quality of land and water resources essential to agricultural production. In the United States, for example, the federal government invested in the development of reservoirs and irrigation systems in the first half of the twentieth century essential to large-scale agricultural development in the arid West. These systems are operated by the Federal Bureau of Reclamation (FBR) and have historically offered water for agriculture at prices that do not cover costs. The United States established the Soil Conservation Service (now the Natural Resource Conservation Service) to administer soil and water conservation programs in the 1930s with the primary objective of protecting agricultural productivity and sustaining agriculturally dependent rural economies. The catalyst for these programs was the 'Dust Bowl' of the 1930s, named for giant dust storms originating from soils disturbed through the conversion of native grasslands to cultivated crop land. Policies directed at inputs or activities that are today considered important determinants of agri-environmental externalities existed, but served other objectives. For example, national insecticide regulation programs initiated with the Federal Insecticide Act of 1910 were to protect farmers from fraud in the insecticide supply chain.

The goals of agricultural resource and environmental policies have shifted significantly since the late 1960s from agricultural production to environmental protection. In the 1960s food was abundant, agriculture was declining in importance as

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a source of income and employment in many countries, the environment was emerging as a major public policy issue, and agricultural practices were recognized to pose significant environmental risks. Harm to fish, wildlife, and human health resulting from pesticides was an early concern and led to policy initiatives to regulate pesticide use for environmental protection. In the United States, for example, the 1972 Federal Environmental Pesticide Control Act, which superseded the 1910 Federal Insecticide Act, made environmental and public health protection the primary objectives of pesticide regulation, and transferred regulatory responsibility from the US Department of Agriculture to the newly created US Environmental Protection Agency. Fertilizers, pesticides, animal wastes, and eroded soils were increasingly recognized as major causes of water pollution in agricultural regions of Europe and North America, leading to initiatives to protect water quality from agricultural production. In the United States, water quality, and subsequently other environmental objectives have largely displaced traditional soil and water conservation objectives in federal agricultural conservation programs; large confined animal enterprises are regulated as industrial polluters. The proenvironmental evolution of resource-oriented policies has also recognized beneficial agricultural impacts. In Europe and North America policies protect agricultural land from urban development to conserve cultural resources and to provide rural amenities. The elevation of the environment in contemporary agricultural policy has also led to some rethinking of traditional proagricultural policies, as some have been recognized as encouraging environmental degradation and inefficiency in the use of scarce natural resources.

This article examines the economic foundations for contemporary analysis of agricultural policies related to natural resources and the environment. It begins with an economic framework for thinking about agriculture's relationship to natural resources and the environment, and then elaborates that framework by introducing pertinent economic concepts. These concepts are applied to various environmental problems and natural resource issues associated with agriculture, including water pollution and use, air quality and climate impacts, biodiversity conservation, and soil quality.

Agricultural Production and the Environment

Traditionally, agricultural production would be described by economists as involving the application of labor, capital, fuel, and material inputs to land to produce conventional agricultural commodities. Land provided space and access to essential natural resources – soils, water, nutrients, and solar energy. The implications of agricultural land scarcity, in both quantity and quality, for the welfare of humans were among the first concerns of Thomas Malthus, David Ricardo, and other early founders of modern economics writing in the early days of The Industrial Revolution. These concerns were allayed by the migration of European populations to new continents, the migration of people from agricultural occupations and locations to urban areas and industrial occupations, and technological change that diminished the land intensity of agricultural production.

Advances in environmental science since the 1960s have led to new conceptions of the relationship between land use, landscapes, the products and productivity of managed and unmanaged ecosystems, and human well-being, and to a new ecological paradigm for conceptualizing these relationships. This paradigm, introduced in the 1990s, views managed and unmanaged ecosystems as providers of ecosystem services. Ecosystem services are benefits that people receive directly or indirectly from ecosystems (Daily, 1997; MEA, 2005). They are broadly classified as provisioning services (e.g., food, fiber, fuel, and water), regulating services (e.g., regulation of floods, drought, land degradation, and disease), supporting services (e.g., soil formation and nutrient cycling), and cultural services (outdoor recreation, esthetics, and nonmaterial benefits). Within this paradigm, agricultural production takes place within agroecosystems that encompass crops, pasture, livestock, other flora and fauna, soils, water, and the atmosphere and their interactions on the land on which agricultural activity takes place and beyond to encompass other systems affected by farming activity. These agroecosystems are contained within and interact with larger landscapes, which include uncultivated land, drainage networks, and wildlife. The emergence of agroecosystems as a typology reflects the profound impact that agricultural activity often has on the structure of the surrounding landscape (Heinz Center, 2003; MEA, 2005). Within the taxonomy of ecosystem services, agroecosystems serve first and foremost to provide 'provisioning services,' which are the food, fiber, and energy products from agricultural enterprises (**Figure 1**). Agroecosystems depend on supporting and regulating ecosystem services for their productivity, and agricultural production activities in turn influence these and cultural services (Power, 2010; Swinton *et al.*, 2007; Zhang *et al.*, 2007).

The environmental consequences of agriculture are influenced by a variety of factors. One is the amount of agricultural activity affecting the environment, and one indicator of this is the amount of land in agriculture. However, there is much more than agricultural land area that is important. Other factors include the characteristics of farming systems (e.g., tillage intensity, chemical use, nutrient management, animal intensity, and crop diversity), characteristics of soils, climate, and topography, the ecological structure of the agricultural landscape, and the types and sensitivity of the environments that are affected by agriculture. These factors are not independent, and in large and highly geologically, topographically, climatically, and ecologically diverse landscapes can vary greatly across space.

The ecosystem services framework can be merged with the economic theory of public goods and externalities to offer a modern conception of agricultural production that is useful for economic and policy analysis (**Figure 2**). Agricultural production involves combining private market goods (labor, capital, fuel, and materials inputs) with nonmarket public or quasi-public goods (ecosystem services) to produce private market goods (commodities – provisioning services). However, agricultural land and production activities also cause or influence the volume and composition of various material flows from farms to the environment (odors, pests, pesticides, nutrients, carbon, runoff, dust, and smoke) that affect environmental public goods (air quality, water quality, nutrient

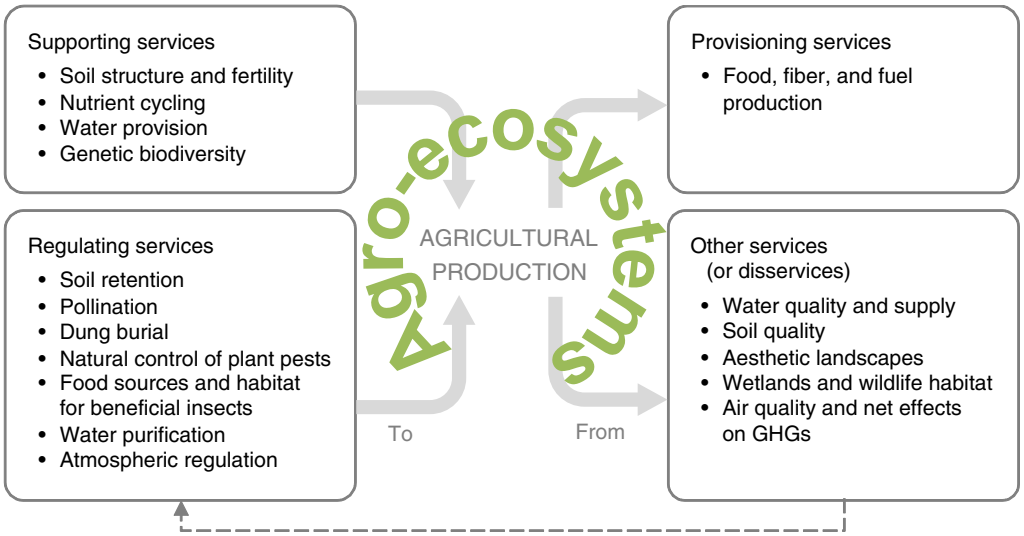


Figure 1 Ecosystem services and disservices to agriculture. Adapted from Zhang, W., Ricketts, T., Kremenc, C., Carney, K., Swinton, S., 2007. Ecosystem services and (disservices) to agriculture. Ecological Economics 64, 253–260, with permission from Penn State's Center for Environmental Informatics.

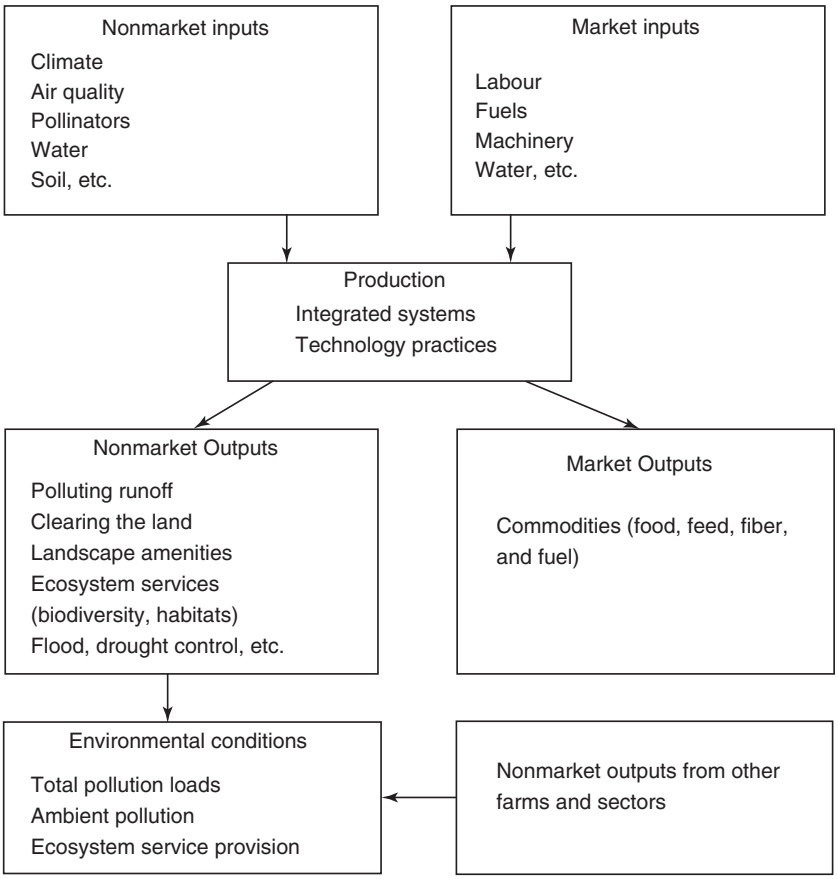


Figure 2 Agricultural production and agri-environmental externalities. Reproduced from Organization for Economic Cooperation and Development (OECD), 2010. Guidelines for Cost-Effective Agri-Environmental Policy Measures. Paris: OECD Publishing and Organization for Economic Cooperation and Development (OECD), 2013. Providing Agri-Environmental Public Goods through Collective Action. Paris: OECD Publishing.

cycles, climate, etc.). Agricultural land and production activities also have nonmaterial flows (sights and sounds) that affect environmental public goods (visual amenities and noise). Being nonexclusive (people cannot be excluded from using them) and nonrival (consumption by one person does not reduce the amount available to others), access to and the quantity of environmental public goods cannot be determined efficiently by private property rights. In consequence, the material and nonmaterial flows affecting these goods are traditionally nonmarket goods. Agricultural production has traditionally had open access to these goods as a presumptive property right (Bromley and Hodge, 1990). The joint production of a public good (or bad) with a market good is a classic source of economic externality (Cornes and Sandler, 1996). Markets provide agricultural producers with prices for traditional market inputs and outputs, but not for jointly produced nonmarket outputs that affect the off-farm environmental conditions. If input and output prices reflect marginal social costs and marginal social value, and if agricultural producers are perfectly competitive profit maximizers, then the expected result without policy intervention is an oversupply of negative environmental externalities and undersupply of beneficial environmental externalities. Economic analysis of agricultural externalities typically proceeds under the assumption that these conditions apply. However, alternative conditions can be important to the nature and economic cost of agricultural externalities. The nature, magnitude, and location of externalities may be influenced by distortions in input and output markets, imperfect information about technologies, and imperfections in property rights for land, water, and other market goods.

An important consideration in the creation of agricultural externalities is the distortion of prices paid and received by farmers as a result of public policies (Just and Antle, 1990; Lichtenberg and Zilberman, 1986). Agricultural production is typically competitive, but agricultural markets are often distorted by public policy interventions. In developed countries, these generally aim to increase farm profits by increasing output prices and reducing input prices for producers. The impact on externalities depends on the effects of price changes on the mix of agricultural outputs, the mix of inputs, the scale and location of production, and the relationship between these factors and agricultural externalities. Policies that generally increase prices received by producers above market prices without imposing restrictions on output will encourage higher production and will increase (decrease) externalities that are positively (negatively) correlated with production. The reverse is true for policies that increase prices by restricting production (e.g., output quotas). Policies that reduce the prices of inputs below their social costs will result in higher input use, and to the extent that lower prices induce higher production, increase (decrease) externalities that are positively (negatively) correlated with the scale of production. Technologies and inputs vary in their effects on the environment, and their utilization varies across commodities. For example, some commodities are more pesticide and nutrient intensive than others. Some farming systems are more tillage intensive than others. Finally, some regions are more ecologically sensitive to agricultural production than others. Accordingly, policies that influence the composition of agricultural output, the location, technologies, and composition of inputs will affect the composition and cost or benefit of agricultural externalities.

The direction of impact of agricultural production on environmental conditions in specific locations depends on the specific practices employed. For example, some agricultural practices are more harmful to air or water quality, biodiversity, or global climate than others. In consequence, changes in agricultural practices can increase or decrease the supply of ecosystem services. An alternative comparison is between agricultural and nonagricultural land uses. Agriculture is generally ecologically disruptive compared with forests or native landscapes. However, urban land uses generally pose a far greater risk to air and water quality, and ecosystem services generally, than agricultural production in the same location. Accordingly agricultural land use can be viewed as increasing the supply of ecosystem service when compared with some alternatives and the opposite when compared with others.

Key Concepts in Environmental and Resource Economics

Efficiency in Markets

A central focus of economics is the efficient allocation of resources to supply goods and services to satisfy the demands of consumers living now and in the future. Natural resources are treated as goods that yield direct consumption benefits (water for human consumption, recreational benefits from the use of land) or as inputs in the production of other goods that are ultimately consumed (crops and forest products). That is, their value is viewed from the perspective of their direct or indirect consumptive utility, or preference satisfaction, for individuals. Economics is sometimes criticized for its focus on consumption. However, it should be borne in mind that this includes the ability of individuals to 'consume' health care, education, and a range of other services and to be able to exercise choice in the use of their time for leisure and recreational pursuits, that is, to have access to the things that many would associate more broadly with the 'quality of life.' Besides, production is not limited to physical goods. It includes services provided by natural resources, such as environmental amenities, that are valued by people. One of the implications of this is that when consumptive resource use in agriculture is consistent with the maintenance of a given ecosystem (often referred to as 'sustainability') there is unlikely to be any conflict between agricultural activities and the provision of ecosystem services, whereas the opposite can be the case.

Much of the emphasis by economists on the interface between agriculture and the environment has been on decision making by individual economic agents on the use of natural resources. This emphasis reflects the focus on individual well-being as the building block of social welfare, and the role of individual decisions in determining agri-environmental outcomes. The supply of goods is conventionally viewed to be determined by decisions made by economic agents (e.g., farmers or ranchers) whose aim is profit maximization. The broader objective of utility maximization has been employed primarily to deal with risk and uncertainty, that is, where there is a difference between expected profit and expected utility

because individuals are not indifferent to risk. It is possible to conceive of agents maximizing a more general utility function that includes a broad range of noneconomic objectives, but a simpler approach involving profit or the expected utility of profit captures the essence of economic decision making and lends itself to determining optimal usage of inputs and outputs (Becker, 1976).

A basic concept in economics is that under appropriate conditions, competitive markets will determine prices for resources, goods, and services that reflect their scarcity and will generate an allocation of resources that is Pareto efficient. Economics also shows that there are many possible Pareto-efficient allocations that could be attained by markets. These would differ in the mix of goods and their distribution among consumers. Ranking alternative Pareto-efficient allocations is equivalent to ranking alternative distributions of income across individuals and generations. Specifically, resource allocation in competitive markets (or indeed under any system for resource allocation) will result in a particular distribution of economic welfare.

A fundamental question in economics is that when does a change in resource allocation improve social welfare. Such a change may involve moving from a resource allocation that is Pareto inefficient to one that is Pareto efficient, or moving from one Pareto-efficient allocation to another. In economics, the assumption is made that a change in resource allocation that increases the welfare of one or more individuals is socially desirable. This is called a Pareto improvement. In such a case, the move would have positive benefits but no costs. No Pareto improvements are possible when an economy is Pareto efficient. Changes in resource allocation that improve the well-being of some but harm others are not Pareto improvements, but may lead to Pareto-efficient allocations. If those who gain could compensate those who lose while leaving both better off, then all could potentially be made better off by the change in resource allocation. In this case, the reallocation is a potential Pareto improvement and would pass a benefit–cost test in determining if the allocation improves economic efficiency. However, judging whether a reallocation that improves the well-being of some while harming others is socially beneficial requires ethical criteria regarding the distribution of income that are outside the realm of economics. Such criteria can be used to define 'social welfare functions' that attach differing weights to the welfare of individuals. This approach has been used, for example, to examine policy choices and their implications for resource allocation in agriculture, where in many countries the welfare of farmers tends to be weighted more highly by policymakers than that of consumers and taxpayers. Defining social welfare functions is challenging and controversial as it is heavily dependent on what value judgments are used to determine whether the welfare of one or some group of individuals is to be weighted more highly than some other individual or group.

A large number of assumptions are involved in applying economic theory to reach the conclusion that a competitive market economy is Pareto efficient. These include access to full or 'perfect' information in making allocation decisions; the existence of well-defined property rights that govern the use of resources, the existence of a sufficient number of buyers and sellers of homogenous goods produced under constant or decreasing returns to scale without barriers to entry and exit in order to preserve competition and prevent monopolization of markets; the existence of perfect factor mobility and absence of transactions costs so that the allocation of resources can respond efficiently to consumptive needs; and an absence of policy-generated distortions. The impact of relaxing these assumptions (e.g., the presence of imperfect competition) on resource allocation and economic welfare has been a major focus of study in economics, as this may provide a justification for corrective action on the part of governments. Despite this, the central tenet remains that the operation of markets in determining what will be produced and consumed is likely to lead to an allocation from which there are no possible win-win alternatives. If the underlying distribution of income is considered fair, then markets can be said to have achieved the highest level of economic welfare for society.

Externalities, Public Goods, and Market Failure

The recognition that private decision making in competitive markets might not lead to a socially optimal allocation of resources dates back to the early part of the twentieth century. The British economist Arthur C. Pigou (1932) is credited with introducing the concept of externalities, whose existence is central to the environmental dimension of agricultural activities. Externalities are sometimes said to result from institutional failure in that they reflect missing markets that result in missing prices. The solution proposed by Pigou was to impose a tax on a negative externality-causing activity and to provide a subsidy for an activity that generates a positive externality. These Pigouvian taxes and subsidies 'internalize' external costs and benefits, that is, ensure that they are taken into account in the decisions of individuals that determine resource allocation. It has also been shown that under certain conditions the use of subsidies and taxes on inputs can achieve equivalent results (Peterson *et al.*, 2002). This is particularly relevant for agriculture as many of its externalities (e.g., pollution resulting from the application of fertilizer to land or agriculture's contribution to maintaining wildlife habitat) are associated with land management practices and the use of inputs and externality outputs may be difficult to observe or measure. Taxes and subsidies are not the only approach that can be used to deal with externalities; measures that establish property rights can also address the issue, as discussed further below following a brief elaboration on the nature of externalities.

A related concept to a positive externality is that of a public good, whose consumption is indivisible or nonrival. It is difficult to charge a price for a public good because it is difficult to exclude individuals from consuming it (because it is nonexclusive). This means that there will be no economic incentive for individuals to supply such goods. Public and quasi-public goods may be provided by virtue of jointness in production with private goods. This is particularly relevant to agriculture, where the use of land in farming may provide both agricultural commodities and ecosystem services. A key issue in this case is whether the economic incentive to produce the private good (food and agricultural products) also leads to a sufficient supply of associated public or quasi-public goods.

Table 1 A taxonomy of some goods associated with land use

	Exclusive	*Nonexclusive*
Rival	Pure private goods: Food and agricultural products	Quasi-public goods: Open access grazing
Nonrival	Quasi-public goods: National parks	Pure public goods: Landscape amenities

Table 1 provides examples of various types of goods that are associated with land use with respect to the two key dimensions: whether they are rival or nonrival and whether they are exclusive or nonexclusive.

Although taxes and subsidies can be used to promote the provision of public and quasi-public goods, this can also be pursued through the creation of property rights – rights of use or ownership that permit a charge to be levied for usage or consumption (Coase, 1960). For example, the goods that are excludable but nonrival (e.g., performances in theaters and cable television) can be provided by markets if the costs of production plus exclusion are less than the revenues that can be obtained from supplying them – these are called club goods (Buchanan, 1965). Another example is the use of markets to allocate polluting emissions among alternative sources. In this case, governments create property rights to pollute, but restrict the amount of pollution that is allowed (Crocker, 1966; Dales, 1968; Goulder, 2013).

The absence of property rights or imperfections in property rights plays a key role in the overexploitation of common-pool resources, such as common grazing land or timber from public forests. For markets to allocate goods efficiently, property rights must be exclusive, enforceable, and transferable. The absence of enforceable exclusive property rights results in the classic problem of open access. The private cost of the exploitation of open access resources by an individual is less than the social cost, resulting in overexploitation (Hardin, 1968). The issue of whether and under what conditions individual members of a collectivity, acting in a self-interested manner will supply public or quasi-public goods has been addressed (e.g., Olson, 1971; Janssen, 2013). There has also been empirical work on this issue. Ostrom (1990), for example, examined how communities manage communal resources, such as land, and identified several key factors conducive to successful collective action:

1. The resource in question must have definable boundaries.
2. There must be a perceived threat to the resource for which it is difficult to find substitutes.
3. There is a community – a small and stable population with a dense social network and social norms that promote conservation.
4. Community-based rules and procedures exist that provide incentives for responsible use of the resource/penalties for overuse.

Intertemporal Allocation

As noted in the Sections Efficiency in Markets and Externalities, Public Goods, and Market Failure, resource management is an important question in economics with attention focusing on the efficient allocation of resources across time and space, the implications of alternative regimes for property rights, market structures, the role of information, and the design of market or nonmarket institutions to correct for market failure. In terms of individual decision making attention focuses on the economic returns from the use of natural resources.

Resources can be classified as expendable, renewable, or depletable depending on the period of adjustment involved in their use (Carlson *et al.*, 1993):

1. Expendable – adjust rapidly such that use in one time period has little effect on availability in subsequent periods.
2. Renewable – self-renewing within a period relevant to economic decision making.
3. Depletable – adjust so slowly that one can meaningfully treat them as being available only once within a period relevant to economic decision making.

Land is a complex resource in that it can yield all three types of resource:

1. Expendable – agricultural crops.
2. Renewable – forests, forest products and fuelwood, livestock and wild animals, flowers and insects, groundwater, and animal populations (providing that use does not cause irreversible changes in potential availability).
3. Nonrenewable – endangered species, top soil, virgin wilderness, and water in some aquifers.

The analysis of decision making for expendable resources has focused on levels of input use in a single production period or over a limited number of periods to maximize profits, for example, how much land to devote to wheat or oilseed production and what quantities of inputs, such as fertilizer and labor to apply to that land.

The focus on depletable and renewable resources has been on the optimal rate of depletion over time. The management problem is typically framed in terms of the maximization of the net present value of the flow of benefits from consumption less the costs of extraction or harvesting over a future time horizon, subject to the dynamics of resource (how the stock evolves over time), initial stock size, a target for the end of the planning horizon (or a limit in the case of an infinite time horizon), a measure of time preference (the discount rate), and other relevant market, price, and technology constraints. In the case of depletable resources, current use irreversibly reduces the resource stock available for future use. In the case of renewable resources, natural processes can result in stock growth for future consumption. In both cases, economically optimal use is achieved when the marginal cost of extraction or harvesting plus the current opportunity cost of extracting the resource (the value foregone by not exploiting the resource) equals the marginal value of consumption (Hanley *et al.*, 2002). The magnitude of the interest rate (the discount rate applied to future economic benefits from the use of the resource) will affect the rate of depletion: a higher rate will accelerate depletion and a lower rate will reduce it. The key role played by the discount rate in the determination of optimal rates of resource depletion has generated much discussion in economics and this is analyzed further below in this section. Economic

efficiency is obtained when the marginal private benefits under a particular time path are equal to the marginal cost of harvesting plus the opportunity cost of the resource.

A key feature that distinguishes renewable from nonrenewable resources is the capacity of renewable resources to be managed to steady states, characterized by a situation in which the resource inventory does not change over time. The steady state that supports the maximum physical use of the resource (harvest) that can be sustained indefinitely is the maximum sustainable yield. However, the economically optimal harvest rate, which takes into account costs associated with the use of a resource, will generally be lower than the maximum physically sustainable yield. The economic optimum depends on interest rates. Increasing extraction costs will tend to lower the current use of the resource, whereas higher interest rates (implying a higher discount rate on future consumption) will tend to increase current usage. The management of the resource over time will also depend on the resource-growth function, that is, how resource inventory is affected by the rate of current usage. In the case of soils, for example, an expansion of productive capacity may be needed to reach a steady state equilibrium if the existing productive capacity of the soil is below the economic optimum. However, as the present value of future opportunity costs associated with current extraction is close to zero if the discount rate is sufficiently high this may dictate exhausting the soil resource (McConnell, 1983; Shortle and Miranowski, 1987). In other words, the fact that soil is a renewable resource does not necessarily imply that it is economically optimal to sustain it (see Section Soil Quality).

The management of natural resources, such as land, may have irreversible outcomes, for example, the conversion of land into alternative uses can create irreversible changes to ecosystems or biodiversity. If, for example, the possibility of increased consumer preferences for the nonagricultural goods associated with land (e.g., ecosystem services) is not taken into account, then current 'overuse' of the land resource may result. This may be viewed as another example of market failure, but one which is more speculative and difficult to address than that resulting from identifiable unpriced externalities, such as the costs imposed on others by soil erosion.

The difference between physical and economic sustainability is clearly an important issue and the key role of the discount rate in determining the optimal economic use of both renewable and nonrenewable resources should be underlined. The use of a discount rate reflects the assumption that individuals place a lower value on events that occur in the future (including consumption) relative to current events. Higher discount rates reduce the present value of future consumption, and dictate that the benefits of using a resource will be realized sooner. The importance of the discount rate in determining the optimal rate of depletion (or conservation) of natural resources inevitably leads to considerations of whether the private discount rate is equivalent to the social discount rate – the rate at which society would discount the future stream of benefits from using a resource (Baumol, 1968). This raises a complex set of issues, not least of which is how the socially optimal rate should be determined. The issue of discounting is particularly controversial in the context of the debate about intergenerational equity, for example, whether it is 'fair' for one generation to use resources so that they are unavailable to future generations or to behave in the management of renewable resources that could reduce the economic welfare of future generations. The importance of discount rates in sustainability analysis is currently most prominently on display in analyses of optimal policies for addressing climate change (Nordhaus, 2007).

Nonmarket Valuation

A central assumption in economics is that individuals are able to place a value on the goods and services they consume. Consumers maximize utility by choosing among such goods and services based on such valuations. When confronted with a set of prices they determine the amounts that they wish to purchase based on tastes, preferences and their income. It is possible to tradeoff quantities of various goods against one another in determining consumption choices and those choices reveal willingness to pay (WTP) for particular goods and services. The problem with many environmental goods is that valuation is not possible because of missing markets. Various approaches have been used to infer values (implicit prices) of unpriced environmental goods and services (Hanley and Barbier, 2009). The most popular approach has been contingent valuation (CV). Other approaches make use of goods that are substitutes for or complements to environmental goods, for example, the use of travel costs to estimate the value placed by users on recreational sites or hedonic pricing – how environmental quality affects local property prices. In this approach, surveys or experiments involving hypothetical choices are used to infer the value that individuals place on environmental goods. An advantage of the approach is that not only can it be used to determine values for goods and services that individuals may actually consume (e.g., clean water or recreational services), but it can also be used to determine values for the nonuse of environmental goods, i.e., existence values – the value that results from knowing that a resource exists (e.g., wilderness areas and endangered species) even though that resource confers no direct consumption benefits.

Stated preference (e.g., CV and choice experiments involving groups of individuals) and revealed preference (e.g., travel cost and hedonic price) valuation methods seek to elicit values through estimates of the WTP to obtain a positive externality, public, quasi-public, or to avoid an externality (e.g., pollution). An alternative approach is to estimate willingness to accept (WTA), that is, the amount an individual would be prepared to receive if prevented from obtaining a good or to accept something undesirable (Venkatachalam, 2004). WTP estimation has been more widely applied than WTA as the former is constrained by an individual's wealth. WTA estimates for some goods may be high in comparison to WTP estimates because of the lack of this constraint.

There is an ongoing debate on CV methodology, particularly on how to improve the accuracy and reliability of estimates obtained. Some economists are highly critical of the ability to derive meaningful values for intangible goods and services through the CV approach, and, in particular, to derive values that reflect prices that consumers would actually be prepared to pay if they were faced with purchasing these goods

and services in a market (Diamond and Hausman, 1994; Hausman, 2012; Horowitz and McConnell, 2002).

Both WTP and WTA assume that it is possible for individuals to value unpriced attributes, whereas this may not always be possible (or acceptable). One class of goods that would fall under the nonacceptability heading is moral goods – goods that are associated with moral values, that is, whose provision is viewed to be morally necessary and not necessarily subject to an economic calculus. Although he does not use the term, the concept of moral goods is implicit in the arguments made by Spash (1997) that moral or ethical values make it difficult to value some environmental goods. As with distributional judgments and judgments of what constitutes fairness or equity, this area is fraught with difficulty as moral values can differ among individuals and this is not generally addressed in economics. To the extent that moral goods can be addressed, economists would probably look for mechanisms to ensure a generally accepted level of provision (e.g., minimum quantity that would be generally accepted by society). It is possible for preferences for higher levels of provision to be reflected through the pricing mechanism. An example here would be water quality. Most individuals would accept that water quality should be such that consumption does not provide a significant risk to health (e.g., through high levels of dangerous contaminants). Beyond that, however, it may well be possible to examine the benefits and costs of supplying water that satisfies higher standards of quality in terms of chemical composition, taste, or other criteria.

Information and Information Asymmetry

As noted in the Section Externalities, Public Goods and Market Failure, taxes and subsidies can be used to address externalities and the provision of public goods. Taxes are rarely used in this context in agriculture for both technical and political reasons. There has been a tendency in wealthy countries to provide incentive payments (subsidies) through agri-environmental programs to pursue environmental objectives in agriculture. Determining the size of payments that will achieve a desired outcome is a problem as a farmer (the agent) will generally possess more information than a policymaker (the principal) about the effect of her/his economic activities and the costs of supplying environmental goods. Such asymmetric information is the central characteristic of the principal–agent problem that has received a lot of attention from economists in analyzing the design of agri-environmental programs (e.g., Shortle and Dunn, 1986; Wu and Babcock, 1996). The problem can result in a number of issues including adverse selection – the tendency for those who are most likely to supply the desired environmental services in any case to want to participate in a program, rather than the poor environmental performers who are the prime targets. Fixed payments may pose particular problems as they may encourage an undersupply of environmental services from producers in areas where it costs more to supply these and an oversupply in other areas. The targeting of payments may be more efficient if a mechanism is used through which producers reveal their costs of provision (or WTA) through an auction process (such as that used in the US Conservation Reserve Program).

The response of producers to incentives under agri-environmental programs is the focus of considerable research (Uthes and Matzdorf, 2013). Some of the issues addressed are the implications of risk and uncertainty for program compliance and environmental outcomes, the role of transactions costs, the amount of monitoring size, and structure of penalties to ensure compliance. The literature in this area suggests that there is a complex interaction between these factors in determining the response of producers to incentives provided through agri-environmental programs.

Agri-Environmental Externalities, Natural Resources, and Public Policy

Table 2 lists some externalities associated with agricultural production, characterizes their economic impacts, and suggests methods that can be used to estimate their economic importance. This list should be considered illustrative. This section elaborates the economic features of selected elements of this list and policy approaches that are used to address these elements.

Agri-Environmental Policies and Programs

In the context of land use and agriculture the issue of missing markets has been central to environmental outcomes from agriculture's use of natural resources. The issue has often been addressed through mechanisms that try to ensure the provision of environmental goods (such as wildlife habitat) and reduce the provision of environmental bads (such as pollution). Some of the very earliest agri-environmental programs were directed toward the control of soil erosion, such as the Dust Bowl in the United States.

The provision of environmental goods in agriculture has been addressed through the following mechanisms:

1. The specification of management practices to be followed as a condition for receiving payments that have non-environmental objectives, primarily income support (cross-compliance).
2. The use of regulations, particularly for the use of animal waste, applied to large livestock operations in order to reduce pollution (regulation).
3. The use of incentive payments to induce producers voluntarily to implement particular environmental practices that reduce negative externalities/increase positive externalities from agricultural production; to enhance the supply of public/quasi-public goods; or to induce producers to convert environmentally sensitive working lands from productive uses into permanent vegetative covers, or to prevent the conversion of environmentally sensitive lands into productive use (agri-environmental programs).

Mechanisms 1 and 3 are based on the use of economic incentives to encourage farmers to adopt appropriate practices. Mechanism 2 will impose an economic cost on farmers but relies on command and control to achieve environmental aims. Economists argue that, other things being equal, if incentive payments are used they should be targeted to specific

Table 2 Inventory of agricultural externalities

Externality	*Environmental impact*	*Economic impacts*	*Valuation method(s)*
Increased stormwater runoff	More variable stream flows	Increased flood damage	Hedonic analysis of property values
	Increased stream erosion	Decreased base flows to support aquatic biota	Cost of insurance and remediation
		Loss of productive soils and acreage	Lost recreational values via travel cost method
			Value of lost agricultural production
Sediment and salts in runoff or irrigation return flows	Clog streams and drainage channels	Higher channel and reservoir maintenance costs	Added costs of maintenance, water treatment, and flood damages
		Higher water treatment costs	
		Increased flood damage	
	Increased turbidity	Altered biotic communities	Species valuation via stated preference methods
		Diminished recreational values	Lost recreational values via travel cost method
		Reduced water amenities	Hedonic property value analysis of changed amenities
	Salinization and accumulation of toxic compounds in water	Diminished usefulness of water	Increased costs of treatment or substitute supplies
		Death, deformity, and reproductive abnormalities in wild and domesticated animals	Lost recreation values via travel cost method
		Human health impairments	Lost wildlife values via stated preference methods
			Human health values via opportunity cost valuation
Pesticides	Chemicals present in drinking water, food, and fish tissue	Increased risks to health of humans and fish/wildlife	Opportunity cost of health impairments
	Disturbances to aquatic ecosystems	Less-productive ecosystems	Lost recreational values via travel cost method
			Nonconsumptive wildlife losses via stated preference methods
Livestock wastes	Increased pathogens	Increased human health risks	Opportunity cost of health impairments
	Other effects similar to fertilizers	Other effects similar to fertilizers	Hedonic property value analysis
	Odors	Decreased amenity and property values	
Climate/atmospheric modification	Change in solar gain	Changes in heating/cooling costs	Increased heating/cooling costs
	Release or sequestration of greenhouse gases	Changes in long-term climate warming	Opportunity cost of respiratory impairment
	Dust generation	Increased respiratory impairment	Increased cost of infrastructure maintenance
	Changes in wind patterns	Increased fouling of infrastructure	
Low-diversity vegetation or animal communities	Reduced diversity and resiliency of regional ecosystems	Reduced natural pollination services	Opportunity cost of substitute inputs
		Crop damages and increased accidents due to wildlife population imbalances	Market value of crop and accidental losses
		Lost amenity and existence values	Insurance premiums for added exposure to losses
			Stated preference values or voluntary contributions for amenity and species existence
Accelerated genetic evolution	Disease generation	Animal and human morbidity and mortality	Opportunity cost of lost economic activity and mitigation efforts

Source: Adapted from Table 1 of Braden, J.B., Shortle, J.S., 2013. Agricultural sources of water pollution. In: Shogren, J. (Ed.), Encyclopedia of Energy, Natural Resource and Environmental Economics. Oxford: Elsevier Science, pp. 81–85.

environmental objectives, rather than bundled with other objectives. The reason is that producers can more easily make decisions on whether to supply environmental goods based on the costs of doing so when the reward is clearly linked to the desired outcome. Another reason is that the size of a payment that has other objectives (e.g., income support) may have little relationship to the potential environmental benefit that a recipient could generate. An old and well-established principle is that it is efficient to have at least as many instruments as objectives in economic policy (Tinbergen, 1956). This would dictate that there should be at least one instrument targeted to the income objective and another targeted to the environmental objective.

With the exception of mechanism 2 there has been a marked reluctance by policymakers in most countries to use taxes to address negative externalities in agriculture. Even if those who receive subsidies respond in the desired manner by adjusting their production practices or level of output, subsidies may be less efficient than taxes in reducing negative externalities because they can encourage polluters to enter the industry or existing high-polluting firms to continue to operate. In contrast, taxes would discourage entry and would not impede structural change that could lead to the exit of more polluting firms (Baumol and Oates, 1988).

Water Pollution and the Nonpoint Source Problem

Arguably, the most significant externality associated with agriculture in North America and Europe, and of great importance elsewhere, is water pollution. This section draws extensively on Shortle and Braden (2013). Negative water quality impacts from agriculture are a pervasive issue in regions with intensive crop and livestock production. Fertilizer, animal manures, and pesticides applied to agricultural land, sediment from eroded soils, and salts and heavy metals leached from soils are carried by irrigation return flows and storm runoff into surface waters causing a range of environmental damage. Pollutants seep into groundwaters damaging water supplies and move as base flow to pollute surface waters. Some pollutants move as gases from farm fields and manure storage facilities into the atmosphere but become water pollutants with atmospheric deposition. These complex and diffuse flows are referred to as nonpoint source pollution. Discharges from pipes or discharges into surface waters from barnyards and feedlots are classified as point source pollution. Pollution problems vary with types of agriculture and impacted water systems. Of widespread significance are damage from nutrient (nitrogen and phosphorous) pollution of fresh, estuarine, and coastal waters. Although nutrients are discharged into waters by industrial and municipal sources, and by atmospheric deposition of air pollutants, agriculture is often a major source. Nutrient pollution damages aquatic ecosystem and harms commercial and recreational activities (e.g., fisheries) dependent on them. Significant examples of nutrient pollution problems are found in the Chesapeake Bay, the Gulf of Mexico, and the Baltic Sea.

The dichotomy between point and nonpoint source pollution is extremely important for policy design. Emissions from point sources of pollution can generally be metered and regulated more or less directly. This allows the use of the emission-based policy instruments generally recommended by economists for the efficient control of polluting emissions from point sources: emission taxes and tradable discharge permits. Where possible, countries use effluent standards or technology standards for point sources, including agricultural point sources if these are regulated. The regulation of nonpoint pollution, which is by far the most important type of pollution in agriculture, poses problems because diffuse pathways make metering emissions difficult, and because nonpoint emissions are driven by uncontrollable natural processes, weather being the most important. In consequence, economists' preferred base for regulation, polluting emissions, is not available. The economic analysis of nonpoint pollution control is, therefore, concerned with the choice of observable pollution abatement activities or other outcomes to measure and manage nonpoint pollution (the compliance base), as well as choice of incentive mechanisms, and design details within those choices (Braden and Segerson, 1993; Shortle and Horan, 2001). As weather events can influence the timing and volume of emissions that reach a water body, violations of an ambient environmental goal may occur because of forces beyond human control. Nonpoint pollution management is, therefore, best framed as attempting to achieve a desired probability distribution of ambient conditions rather than a specific deterministic pollution target. For example, it might be desirable to hold concentrations of Nitrogen (N) in receiving waters below 10 mg l^{-1} for 90% of the time.

As a result of stochasticity and unobservability, efficiency in the control of nonpoint pollutants is not readily characterized by conventional rules about equalizing marginal costs of emission abatement. Instead, efficiency must be characterized in terms of cost minimization in the management 'levers' or 'observables' that are actually used. An obvious starting point is to look 'upstream' at observable factors that influence emissions. Examples in agriculture are fertilizer, manure, and pesticide applications; tillage practices; and installation of vegetative filters and buffers. An efficient nonpoint pollution control allocation would be described as the set of input choices by all nonpoint sources that minimizes the social costs of achieving a particular ambient pollution target. In principle, this allocation can be achieved in various ways. One would be through a set of input standards that command polluters to select the efficient allocation. Given the spatial variations in site characteristics, weather, and other factors that would determine optimal input structure for specific locations, the efficient input structure, and thus input standards, would vary from polluter to polluter. This heterogeneity would make such standards administratively complex and costly as inputs and input-specific rules and procedures would generally be required to govern many choices by many polluters. It would also incentivize local black markets in regulated inputs and legal challenges based on perceptions of unequal treatment or scientific uncertainty. Furthermore, the design would be informationally and computationally costly.

Another mechanism for achieving the efficient outcome is through taxes on inputs. If the ambient pollution level were simply equal to the sum of polluting emissions, and an emissions model predicted emissions without error, then an

efficient input tax structure would be one with rates that are proportional to the marginal impact of each input on emissions. These rates would be positive for inputs that increase pollution (e.g., fertilizer) but negative for inputs or activities that reduce pollution (e.g., conversion of streamside cropland to a riparian buffer). Tax rates would vary across inputs (nitrogen vs. phosphorus fertilizers) and polluter types (e.g., by type of crop and erodibility of soil) according to variations in marginal impact by input and pollutant. This is a potentially complex rate structure. With uncertainty about the impact of an input on emissions, the rate structure would become even more complex, affected by multiple moments of the probability distribution of impacts as well as possibly by geographic location, and therefore harder to quantify and defend. More plausible input-based instruments (taxes, standards, or a combination of the two) would involve a reduced set of regulated inputs; those that are easily observed and particularly influential. Limited and predetermined differential treatment of polluters through tax rates or input standards would reduce information costs and help minimize perceptions of inequity. However, these limitations would impose an efficiency loss through increased cost of pollution control, but with reductions in the transaction costs from design, implementation, and administration.

Input-based instruments are common in nonpoint pollution control (Shortle and Horan, 2013). In agriculture, examples include regulations on the use of pesticides and on waste handling at large confined animal enterprises, although the latter are essentially point sources of pollution. Input taxes are used to a limited extent. Several European countries levy environment-based taxes on pesticides and fertilizers. As noted earlier, the most common approach in agriculture is the provision of subsidies for voluntary adoption of pollution-reducing practices. Research has shown conventional subsidies to be ineffective in some cases and inefficient in general, because they encourage more farming, even if the pollution from each farm is reduced (Shortle *et al.*, 2012).

If a pollution model is available that specifies the relationship between inputs and output, it could be used to apply a policy instrument linked to an individual polluter's contribution to ambient pollution. The switch from inputs to indicators of environmental performance is appealing because it would shift the regulatory focus from the means to the ends. It might also offer possibilities for simplification. Despite this, there are a few examples of the use of such an approach. Belgium and the Czech Republic tax estimated ammonia emissions from large-scale animal operations. The Netherlands has experimented with taxing the use of nutrients in excess of the capacity of soils and crops to recycle these. Interest in performance-based instruments is prompted in part by research showing that efficiency and effectiveness in nonpoint pollution control is generally served better by targeting the outcomes of producers' choices than the choices themselves.

Owing to the inherent difficulties in regulating nonpoint sources of pollution, there has been heavy reliance on voluntary participation induced by education, subsidies, and other forms of positive incentives. Within this domain, market-based voluntary trading is an area of significant interest and innovation, particularly for nutrient pollution. Experiments with nutrient trading began in the United States in the early 1980s. They have primarily involved efforts to reduce nutrient emissions from nonpoint sources as an alternative to costly measures to reduce nutrient discharges from regulated sewage treatment plants. The results of early experiments were disappointing, with few trades taking place, but interest in trading has grown nonetheless. Trading programs to control nutrient pollution from point and nonpoint sources have been developed in Canada, the United States, and New Zealand and have attracted interest elsewhere (Shortle, 2013).

Markets for trading nonpoint pollutants developed to date in the United States and Canada are not the cap-and-trade permit markets of textbooks. Rather, these markets foster trade in emissions reduction credits earned by polluters when they reduce emissions below a baseline. The markets can be described as 'partially capped' because point source polluters face explicit discharge limits, whereas nonpoint polluters are not regulated but participate voluntarily as suppliers of credits. The one effort to date to create a true cap-and-trade market for nonpoint pollution is aimed at the reduction of nitrogen pollution of Lake Taupo in New Zealand.

The performance of pollution markets is powerfully affected by details of market design. An essential feature of markets for nonpoint pollutants developed to date is that they trade estimated or modeled reductions in nonpoint emissions in exchange for measured point source emissions. Economic research on the design of markets for estimated nonpoint emissions has focused largely on the appropriate trade ratio between monitored point emissions and those estimated for nonpoint sources. The point–nonpoint trade ratio is commonly defined as the number of nonpoint permits (or credits) that a point source must purchase to offset a unit of its own emissions. Trading programs developed to date almost always set this ratio in excess of one on the grounds that uncertainty in nonpoint emissions requires a margin of safety to assure that a nonpoint reduction will, in fact, offset point source emissions. Although this view is clearly appealing to real-world trading program designers, economic research has shown that this approach can increase rather than reduce environmental risk (Horan, 2001). Essentially, trade ratios in excess of one penalize substitution of nonpoint pollution reductions for point source pollution reductions. This penalty will bias pollution control toward a reliance on point sources, the result of which will be to leave the risky source, nonpoint pollution, relatively uncontrolled.

Another approach that focuses on environmental outcomes is to create economic incentives tied to actual water quality conditions. A number of variants of ambient-based incentive schemes have been proposed, including taxes, tournaments, and threat mechanisms intended to induce collective action amongst polluters (Segerson, 1988; Govindasamy *et al.*, 1994). However, this approach poses significant cognitive challenges for polluters. An efficient outcome would require polluters to be able to determine the relationship between their individual choices and ambient pollution levels and to understand the aggregate impacts of others on environmental outcomes. It requires sophisticated decision-making skills in uncertain situations. The behavioral economics literature indicates that the capacity of an individual to optimize in complex settings is limited. Ambient taxes also require strong assumptions

about polluters' strategic choices. Researchers have explored the issues using experimental economics laboratories and found that ambient taxes can perform well with respect to efficiency in laboratory settings, contingent on certain specific design features, when subjects are not allowed to communicate (Suter *et al.*, 2008). Communication between laboratory participants leads to group profit maximization and inefficient overabatement.

There is no example of the use of ambient taxes in their pure form. However, collective incentives have been addressed in other forms. In 1994, the US state of Florida enacted basinwide incentives as part of a suite of programs to reduce phosphorus pollution in the Everglades. The programs include an agricultural privilege tax imposed on cropland to fund pollution control initiatives. Reductions in phosphorus discharges below a 25% goal for the basin would result in collective credits (i.e., reductions in the tax rate) against the privilege tax. The program also provides credits to individual farmers based on farm-specific performance.

This discussion indicates that a variety of approaches can and have been used to address water pollution from agriculture. However, the problem remains pervasive and is a top priority of environmental policymakers in many countries. The lack of progress can be blamed, in part, on the challenges posed by the nonpoint problem and the transactions costs that governments would likely incur in implementing more effective approaches to reducing pollution. The political economy of agricultural regulation (the political challenge of trying to regulate agriculture) is also a factor because it often leads policymakers to rely on ineffective and inefficient voluntary compliance approaches.

Biodiversity

Agricultural development has historically been a major cause of reduced biodiversity. Agricultural land is created by converting wetlands, forests, prairies, and other landscapes into agricultural production. Typically, diverse plant and animal communities are replaced by much less diverse assemblages of commercially valuable species. Some of those species may have been engineered to combine traits unknown in nature. When a large fraction of the landscape is dominated by artificial communities, species that would otherwise have prospered can be edged out and replaced by ones better adapted to the new circumstances.

This historical relationship between agriculture and biodiversity suggests a need to protect biodiversity-rich landscapes from agricultural production, and this is in fact important where such landscapes are threatened by agricultural development. However, agricultural lands are essential to remaining species that find habitat in agroecosystems. Some species depend on 'natural' areas within agricultural landscapes, whereas others have adapted to croplands and pasturelands. In consequence, restoration and protection of habitat on agricultural lands is also important for biodiversity conservation. Taking current conditions as a baseline, changes in agricultural land use that restore or improve habitat generate positive externalities, whereas changes that diminish habitat generate negative externalities.

A loss of diversity can be economically significant in several respects (Declerck *et al.*, 2014). Some imperiled species may be economically important, for example, pollinators whose services are essential to some types of crops and predators that constrain deer populations and prevent crop losses and auto accidents. Species are also valued by some people for their mere existence or for viewing, as reflected in the financial contributions to or involvement in preservation causes and the establishment of conservation areas.

A variety of economic methods have been used to value the economic benefits of species diversity. The contributions of diversity to commercial values can be measured by the market value of losses associated with diminished diversity, the insurance premiums paid to hedge against losses or cost of substitutes for lost services, such as rented pollinator colonies. The contribution to amenity and existence values can be measured through stated preference or experimental methods (as discussed in the Section Nonmarket Valuation) or approximated by voluntary contributions to preservation causes including conservation areas.

Strategies for addressing losses of biodiversity are diverse and make selective use of economic instruments. In the United States (Walls and Riddle, 2013), the Endangered Species Act limits the rights of landowners who host species recognized as threatened or in danger of extirpation. These programs create powerful incentives to avoid involvement or to take preemptive actions, such as species elimination, thereby raising the ultimate cost of preservation. Other programs offer payments for ecosystem service provision (Parkhurst, 2013). For example, federal agricultural programs have included subsidies for converting cultivated land into vegetative cover and for the restoration of wetlands. Popular in the 1990s and early 2000s, the impact of these programs has been reduced by strong demand and high prices for agricultural products as well as reduced government funding. Subsidies are also known to create inefficiency by inducing more agricultural activity overall, even if some of its resources are diverted toward environmental improvements. Fueled by tax benefits available to contributors, in the United States, private organizations and government at many levels have worked together to purchase or place easements on land for conservation reserves (Parker and Thurman, 2013). In Australia, the states of Victoria and New South Wales have developed markets and banks for biodiversity conservation credits (Carroll *et al.*, 2009). However, many conservation investments are made opportunistically with little coordination to maximize their overall contributions to species diversity. As future conditions are uncertain and biodiversity depends on complex interactions between species, researchers have proposed the use of modern portfolio theory (Markowitz, 1954) to determine portfolios of species (Figge, 2004) and reserves (Ando and Mallory, 2012) that optimally balance risks and returns.

In the United States, some states restrict the conversion of land to other uses (e.g., urban development) to limit losses of unusually rich ecological resources, such as wetlands (National Research Council, 2001). The restrictions are coupled with markets where developers can trade 'credits' for ecological functions (Mills, 1980). Developers who create or enhance wetlands and are willing to accept permanent conservation easements receive credits that can be sold to others who seek

to eliminate or degrade wetlands elsewhere. The credits can be deposited in 'mitigation banks' and sold later. In many European countries, the conversion of land to other uses is controlled through planning laws.

Air Quality and Climate

Agricultural activities can result in a variety of air pollutants. Wind erosion and field operations can add particulate matter to the atmosphere. Winds can cause sprayed pesticides to drift. Livestock production releases hydrogen sulfide, ammonia, methane, volatile organic compounds, and odors. Particulates and nitrogen oxides are emitted from diesel- and gas-powered equipment, and from fields cleared of unwanted vegetative material by burning. These pollutants may affect human health and ecosystems, reduce visibility, and create nuisances. In general, however, agriculture is not considered to be a major source of ambient air pollution compared with major industrial, transportation, and power generation sources, and is little regulated at this time. Air emissions from agriculture often share the characteristics of water emissions (diffuse and stochastic), with the result that regulation would pose similar challenges. Ozone, nitrogen oxides, sulfur dioxides, and other pollutants generated by nonagricultural activity can adversely affect various types of crops and the returns from agricultural production.

Growing concern about human-induced climate change, which is driven largely by increased release of heat-trapping greenhouse gases (GHGs), has begun to focus more attention on agriculture's contribution to what can broadly be defined as air quality. Agriculture is not the largest source of GHG emissions – the combustion of fossil fuels for power generation, industry, and transportation are the major sources and are primary targets of regulatory initiatives. However, when measured relative to its share of gross domestic product (GDP), agriculture is an emissions-intensive sector. Although it accounts for only 6% of global GDP agriculture is estimated to account directly for 14% of total anthropomorphic GHG emissions, primarily in the form of carbon dioxide, methane, and nitrous oxide (IPCC, 2007). If emissions resulting from the conversion of land from forests to agriculture are included the percentage is higher. The food system as a whole is estimated to be responsible for 19–29% global GHG emissions with agricultural production, including indirect emissions associated with land-cover change, contributing 80–86% of the total (Vermeulen *et al.*, 2012). Agriculture is an unusual sector in that it also extracts carbon from the atmosphere in the production of biomass and can sequester this carbon for periods of time. Climate change resulting from increasing concentration of GHGs will also affect the sector. The concentration of carbon dioxide in the atmosphere could increase crop productivity. Production could be affected spatially, either positively or negatively, by climate change through increases in average temperatures, a higher incidence of temperature extremes, changes in the length of growing seasons, and changes in rainfall patterns.

Economic research on climate change policy is dominated by a debate between price-based and quantity-based instruments for reducing GHG emissions. Price-based policies would impose a tax on GHG emissions. By increasing the cost of those emissions, it would induce consumers and producers to substitute less GHG-intensive products and methods of production. For example, the meat of high methane-generating animals (such as cattle and sheep) and N_2O-producing nitrogen fertilizers would both become relatively more expensive. Consumers would be encouraged to substitute away from red meat and farmers would be encouraged to use less nitrogen. Quantity-based instruments, however, seek to impose limits on physical emissions. A common proposal is to allocate tradable emission allowances (permits) to emitters. Overall quotas would be set on GHG emissions and each emitter would be required to possess allowances sufficient to cover their emissions. The ability to trade allowances would provide flexibility, and the existence of the quota would generate a price. The initial allocation is a major issue. Theoretically, if initial allocations are sold to emitters, the equilibrium allocation and price that would emerge in the market should equal the allocation that would be produced by an emissions tax equal to the equilibrium price. This is a general finding for all pollution allowance markets – GHGs or otherwise. If permits are given away free of charge, however, they would act like a subsidy, encouraging more polluting activities than an equivalent tax, although the market would still produce an efficient short-run allocation of abatement effort. Free permit allocation also creates a windfall and competitive advantage for existing emitters relative to new firms who would like to enter the market. Of course, emitters argue strenuously for free allocations and governments are reluctant to create a competitive disadvantage for their emitters relative to those in other countries. Environmental groups argue that polluters should pay for the use of scarce climate resources.

A market for GHG emission allowances would allow the possibility of earning credits for efforts that remove carbon from the atmosphere. Planting trees, for example, would tie up carbon while releasing oxygen. Agricultural interests groups have argued that reducing tillage, growing perennial crops, and setting aside land for conservation are positive contributions of this type by retaining or returning carbon to the soil. Climate change is the result of GHG accumulation over decades, however, this turns out to be a temporary proposition. Over decadal time frames, trees die and degrade, cropland is likely to be tilled periodically, and conserved acreage may be returned to production. GHGs stored in the soil would be released. Only if ultimate releases were reflected in emission allowances would the initial award of credits be efficient. In effect, farmers would be paid a rent for temporarily storing carbon but would have to pay back if and when the stored carbon is released. A second complicating factor is the difficulty of distinguishing storage measures that would be undertaken as a matter of course from those induced by the availability of compensation. Rewarding efforts that would be undertaken anyway is an inefficient use of resources. Finally, both allowances and taxes are vulnerable to nonuniform application. If the United States, for example, taxes GHGs or imposes allowances while a major agricultural competitor, such as Brazil does not, or the two nations act in ways that produce different tax rates or allowance prices, some GHG-generating activity could simply move from one country to the other. This is known as carbon leakage. As global warming is truly a global problem, simply moving emissions around can

be counterproductive, unless it results in a shift of production to more emissions-efficient regions, that is, regions that can generate products with lower emissions per unit of output. However, apart from nations that generate few GHGs but are exposed to huge potential costs, like low-lying islands that will be affected by increases in sea level due to the melting of polar ice, most countries have every incentive to gain relative economic advantage through climate change policies and little incentive to adhere to binding international agreements. Accordingly, coordinated international action on climate change policies has been exceedingly difficult to achieve.

Agricultural Landscape Amenities

The agri-environmental externalities described in the Sections Water Pollution and the Nonpoint Source Problem, Biodiversity, and Air Quality and Climate pertain to the effects of agriculture on the quality of environmental resources. Another important type of ecosystem service associated with agriculture is rural amenities. The conversion of agricultural land into developed uses with urban expansion was long framed as a concern for the loss of agricultural production potential. However, the scope of benefits is now recognized to include the protection of various ecosystem services that are lost or degraded with conversion, and the loss of agricultural landscape amenities (Duke and Aull-Hyde, 2002; Gardner, 1977; Kline and Wichlens, 1996, 1998; Lynch, 2007). Being public goods, landowners can receive no compensation for the provision of amenities or local ecosystem services provided by farm land, possibly resulting in suboptimal supplies without public policy intervention. Concern for farmland preservation has led to state and local policy initiatives across the United States, but especially in the densely populated Northeast. The preservation of farmland and agricultural activities that are judged to be important for the maintenance of landscapes has also been a major policy focus in Europe. Indicative of the demand for such programs in the United States is that they are often the result of referenda in which voters directly choose to create and fund preservation programs. Also indicative of the demand are numerous studies demonstrating that people are willing to pay to protect farmland through various mechanisms (Bergstrom and Ready, 2009). Common tools for farm land protection in the United States include laws to protect agriculture from nuisance law suits (right to farm laws), tax incentives, conservation easements, and purchase of development rights. In Europe, restrictions on development through planning laws and the use of incentive payments through agri-environmental programs have been the principal mechanisms used to preserve landscape amenities.

Soil Quality

With few exceptions, soil is an essential input in agricultural production. To grow crops, soil is combined with water, seeds, fertilizers, and other capital and labor inputs. To some extent, these inputs are substitutable, for example, fertilizer can compensate to some degree for lower inherent productivity of soil. At the extreme, hydroponic production eliminates the need for soil altogether. However, for most agricultural purposes, soil is essential.

Soil is a renewable resource. New soil forms as rock wears down, plant matter degrades, and wind and water move soil particles from one place to another, but these processes take millennia to unfold. Meanwhile, by exposing soil to sun, wind, and rainfall, farming accelerates soil degradation. From the perspective of an individual economic decision maker, soil may, therefore, be viewed as an exhaustible resource, because of the length of time taken for renewal. An important long-run economic issue for agriculture (and for society as a whole) is whether net soil degradation imperils future economic prospects (in the form of reduced supplies of more expensive food and agricultural raw materials) – an intertemporal externality – and whether this problem stems from a market failure that warrants corrective action.

A common goal of soil conservation policy is to manage soils so that erosion rates do not exceed the rate of soil formation, referred to as the soil tolerance or T value. T values will vary across soils depending on the type and climate. In contrast, as noted in the Section Intertemporal Allocation, economically efficient soil conservation may entail some depletion of soil resources. An economically efficient allocation will maximize the present value of the flow of economic returns from the use of soil. If soil were a nonrenewable resource depleted by agricultural production, and if there were no external costs associated with soil erosion, an economically efficient intertemporal allocation would equalize the present value of the marginal products of soil from period to period. In other words, soil erosion would occur at a rate that causes the value of the marginal product to grow at the social rate of discount. A natural resource that 'grows,' as soil does, can accommodate a greater rate of depletion because some of it is offset by replacement. A resource that can be fully replaced by other inputs may be depleted more quickly because increases in its marginal value ultimately will induce full replacement by those substitutes.

In an economy where social and private incentives are fully aligned, ownership is secure and markets both temporal and intertemporal function smoothly, farmers would maximize the value of their operations by degrading soil at the socially optimal rate. However, real economic settings fall short of the ideal. Individuals face greater personal risk than society in general, which may lead to higher rates of personal discounting. Market values do not always accurately capture social values. Future prices and technologies are difficult to predict. In these ways, markets may fail to induce socially optimal decisions, including decisions about the conservation of soil. It is not clear that these failings are worse for agriculture and soil than for other sectors and resources. Unlike environmental externalities, the case for intervention in private soil conservation decisions is not transparent. Countries in which governments have taken a major role in directing food production do not inspire confidence that intervention will lead to more conservative practices.

Nevertheless, the cause of soil conservation has been taken up by governments in many nations. Approaches often include efforts to educate farmers and equip them with conserving technologies, such as reduced tillage practices (Baumhardt, 2014). In some cases, governments subsidize conservation practices. Punitive approaches to soil degradation are rarely, if

ever, used. The subsidization of conservation practices is problematic in several respects. As with other subsidies, it sustains a larger agricultural industry than may actually be efficient in the long run. It also tends to be unselective – providing uniform subsidies irrespective of the variation in benefits achievable in different settings.

Historically, soil conservation policies were motivated by concern about the impact of soil erosion on farm income, rural economic well-being, and sustainability of food supplies. However, eroded soil degrades water resources, and the offsite externality cost can significantly exceed the onsite productivity cost (Ribaudo, 1986). The case for soil conservation policies based on water quality protection has supplanted the historical motivation to some degree.

Water Supply

Water is essential for agricultural production. In humid regions, water is generally amply provided by nature, though periodic droughts can cause problems. In drier regions, water must be acquired. In some regions, water may be available from groundwater sources. Groundwater stocks are renewable resources that are depleted by pumping but can be recharged by infiltration of rain and snow. Like soil, an optimal allocation over time will maximize the present value of the flow of economic returns from water use. In optimal usage, the marginal benefit of extraction less the costs of pumping at any time should equal the social opportunity cost of extraction. The social opportunity cost is the present value of the future benefits forgone at the margin due to current use. Another source of water for agriculture in arid regions is from surface water taken from streams or lakes. Lakes may be natural or created to capture and store water. The economics of surface water management may entail dynamic elements when water can be stored and used over time. A key issue in the efficiency of both surface and groundwater management is allocation among competing uses. Competing uses include agriculture, energy production, industry, and domestic use. A competing use that is being recognized in some places is instream services. These include flows for recreational uses (e.g., white water rafting) and to maintain flow-dependent aquatic ecosystems.

As with all natural resources, a key consideration in determining the efficiency of water use is the nature of property rights (Anderson *et al.*, 2013; Griffin, 2006). Property rights structures vary greatly across countries, and sometimes within countries. For example, surface water in the United States is generally owned by someone. In water-rich Eastern United States, rights have historically been governed by the Riparian Doctrine. Under this doctrine, surface water rights attach to riparian land owners. These rights are typically not fixed quantitatively but require reasonable use. The riparian approach does not serve well when water becomes scarce relative to demand and water must be allocated among competing uses. In consequence, many Eastern States have developed water management plans that set priorities for water use, and require water users to obtain permits. In contrast, surface water is private property in some western states where the prior appropriation doctrine governs rights. The principles of this system are that water rights are transferable, involve quantification, and claims over water are determined by seniority. Some western states blend the riparian and prior appropriations doctrines. A third form found in many irrigation districts and some river basins is correlative shares. In this case, private property rights exist as a share in the available resource. In addition to defining and regulating private property rights, governments designate some water resources as state property and the federal government is held to have certain reserved rights to water. The FBR developed reservoirs in western states beginning in the early 1900s through midcentury, and conveyances to supply water to various users including irrigators. FBR reservoirs are managed for multiple uses (irrigation, flood control, power generation, public water supply, and environmental flows) with evolving priorities. Variants of surface water law are found in groundwater law.

A major concern in water use is generally inefficient allocation among competing uses, and in the case of groundwater stocks, over time. In some cases, this concern emerges because of open access to water. In many agricultural regions groundwater resources are open access resources. Economic theory predicts that individual users of open access resources do not have adequate incentives to conserve. The result is excessive depletion. Empirical tests sometimes find this result, but some also find that the economic cost of open access use is small. This result is known as the Gisser-Sanchez (1980) effect after a research publication that first found this relationship. The economics profession is generally favorable toward the use of markets for water allocation compared with administrative mechanisms, but variability in water supplies and externalities that result from water allocation across space (e.g., instream flows) and time (e.g., effects of groundwater depletion on salt water intrusion in coastal aquifers) can pose challenges to the design of efficient property rights and water institutions (Griffin, 2006).

Summary and Conclusion

As the leading use of land and water, agriculture has very significant impacts on the environment and natural resources. It is a leading source of pollution discharges to water, a profound disruptor of wildlife habitats, and is increasingly recognized as a contributor to GHG emissions. In contrast, agriculture can also contribute to landscapes, amenities, wildlife that depends on agroecosystems, and carbon sequestration. Many agriculturalimpacts on the environment are difficult to measure, monitor, and attribute to specific sources, and this creates fundamental difficulties for the application of policies to discourage or restrict practices that cause environmental problems.

In general, there has been a marked reluctance to address the negative effects of agricultural activity through taxes or regulation. Instead, policymakers have tended to rely on incentive payments and voluntary participation in schemes that attempt to improve environmental performance. Nevertheless, the design of policies to address the distinctive environmental challenges of agriculture is a field of active development and experimentation. Economic concepts and methods have considerable value in this process of innovation.

See also: Biodiversity and Ecosystem Services in Agroecosystems. Climate Change, Society, and Agriculture: An Economic and Policy Perspective. Land Use: Management for Biodiversity and Conservation

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Edaphic Soil Science, Introduction to

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Glossary

Alluvium A loose sediment deposited by moving water, such as during a flood event.
Available water capacity (AWC) The amount of water that is held in the root zone that can be extracted by plants.
Cation exchange capacity (CEC) The capacity of soil to hold nutrients, which is measured in terms of total amount of cations (positively charged ions) that a soil can retain exchangeably.
Colluvium A loose sediment transported under the influence of gravity, such as material washed down a hillslope.
Dispersion The complete disintegration of soil aggregates resulting in discrete soil particles.
Drainage The amount of water that is lost below the root zone.
Edaphic Of or relating to the soil, especially as it affects biota.
Evapotranspiration The sum of the direct evaporation from the soil surface and the water vapor transpired through plant leaves.
Exchangeable cations The cations that can be easily replaced or exchanged by other cations in soil, such as exchangeable Ca and Mg.
Field capacity (FC) The amount of water after excess water has drained away, in the laboratory commonly measured between −10 to −33 kPa.
Horizon A layer of soil, usually parallel to the ground surface, which has a unique set of morphological features making it distinguishable from other soil layers above it or below it.
Hydraulic conductivity The rate of water flow per unit gradient of hydraulic potential.
Permanent wilting point (PWP) A point where plants cannot exert the energy to remove water from the soil, in the laboratory measured at −1500 kPa.
pH A measure of acidity or alkalinity in soil, soils with pH < 7.0 are acidic and > 7.0 are alkaline.
Saturated hydraulic conductivity The saturated rate of flow of water per unit gradient of hydraulic potential.
Slaking Collapse of soil aggregates in water to form microaggregates.
Soil solution A liquid phase of the soil, mostly water with small amounts of dissolved ions.
Weathering The alteration of rocks and minerals through a variety of physical and chemical processes, resulting in the formation of soil minerals and horizons.

Introduction

The loose, mineral-rich skin of the Earth, soil, is the key component of the terrestrial ecosystem and serves numerous functions at the interface between the biosphere, hydrosphere, lithosphere, and atmosphere. Because of the multifunctionality of soils, there is not a unique definition for soil. For example, farmers use soil as a medium for growing plants for food and fiber; engineers use soils for the physical support of buildings, roads, and bridges; and soil is used as a filter for removing organic and inorganic contaminants from water or other media by various industries. From the agricultural production perspective, soil can be defined as 'the unconsolidated mineral or organic material on the immediate surface of the Earth that serves as a natural medium for the growth of land plants' (SSSA, 2013). In this context, soil serves many functions, including supplying water, nutrients, and oxygen to plants. The ability of a soil to supply essential plant nutrients, also referred to as 'soil fertility,' is dependent on the mineralogical and chemical properties of the soil, and nutrient cycling in the soil. In addition to soil fertility, soil physical properties and the interaction between soil and water are important for supplying water and air, and for providing physical support to plants.

This article will discuss the chemical and physical soil properties that are important for plant growth and yield in agriculture. However, before proceeding to such a discussion, a more inclusive definition of soil can be previewed as "the unconsolidated mineral or organic matter on the surface of the Earth that has been subjected to and shows effects of genetic and environmental factors of: climate (including water and temperature effects), and macro- and microorganisms, conditioned by relief, acting on parent material over a period of time. A product-soil differs from the material from which it is derived in many physical, chemical, biological, and morphological properties and characteristics (SSSA, 2013)." This definition highlights the importance of the factors and processes in soil formation, and recognizes their relevance in the observed properties of soil. From this definition, one can appreciate the likely influence of the soil-forming factors and processes on relevant soil properties for plant production. Throughout this article, reference will be made to four case study soil profiles from Australia, namely, (1) Pilliga, a reddish-yellow-colored sandy soil (Lixisol, IUSS Working Group WRB, 2007; Haplustalf, Soil Survey Staff, 2010); (2) Nowley, a bright red-colored soil with contrasting attributes in the upper and lower parts (Calcisol, IUSS Working Group WRB, 2007; Rhodudalf, Soil Survey Staff, 2010); (3) Toowoomba, a dark red-colored clayey soil (Nitisol, IUSS Working Group WRB, 2007; Rhodudalf, Soil Survey Staff, 2010); and (4) Callandoon, a gray-colored clayey soil (Vertisol, IUSS Working Group WRB, 2007; Haplustert, Soil Survey Staff, 2010; **Figure 1**).

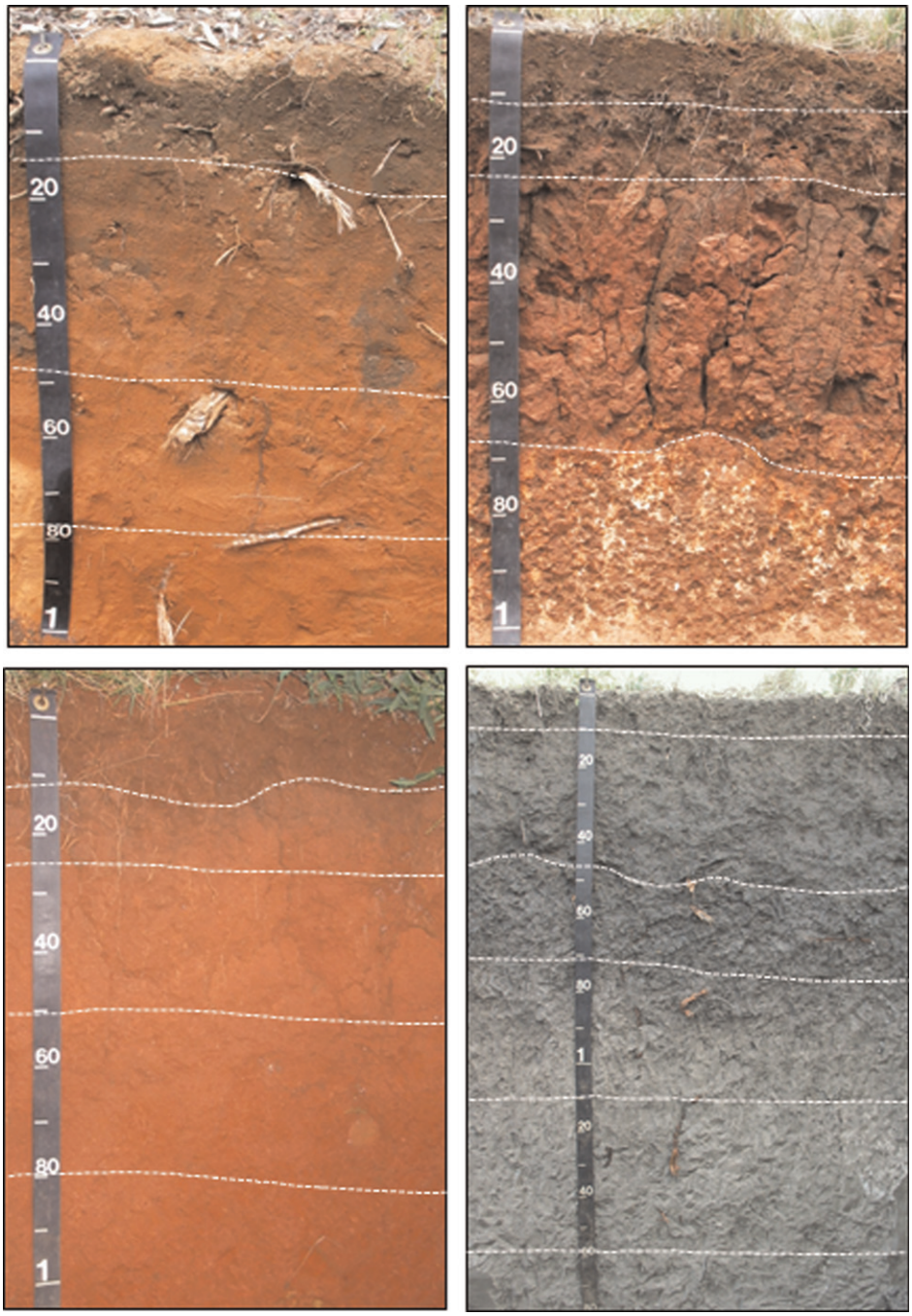


Figure 1 The four case study profiles, clockwise from top left; Pilliga, Nowley, Callandoon, and Toowoomba. The dashed lines indicate the horizon boundaries in the profiles.

Soil can be regarded as a three-phase system consisting of solid, liquid, and gas phases. To understand the chemical and physical properties and behavior of soil, it is necessary to know the proportions and types of solids present. The solid phase consists predominantly of inorganic materials with relatively smaller amounts of organic matter. The inorganic materials can be further subdivided into two parts – particles possessing a definite crystal structure (minerals) and inorganic materials that do not have any definite structure (amorphous or non-crystalline material). The amorphous fraction of soils, which may be significant in certain soils (e.g., soils derived from relatively fresh tephra deposits), is mainly composed of a mixture of variously hydrated oxides of aluminum, silicon, iron, and manganese. The crystalline fraction consists of a mixture of minerals inherited from the soil parent material and secondary minerals formed by the weathering processes within the soil.

The large variety in size and shape of solid particles and the manner in which they are arranged together produce a labyrinth of pores and channels in soils that is called pore space.

The pore space in soil is filled with either soil solution or air. The proportion of air and soil solution at any given time and place is highly variable, the quantity of one varying oppositely to that of the other. The soil solution is essentially water that contains dissolved gases and solutes of both inorganic and organic nature. In well-aerated soils the composition of soil air is quite similar to the atmosphere, except that microbial metabolism leads to higher carbon dioxide content (0.15–0.65%) in soil air compared to atmosphere (0.03%). The relative humidity of soil air is generally high.

Soil Variation in Space and Time

The exact composition and behavior of soil is highly variable due to the myriad of soil-forming processes that may operate at a given location and time. This variation manifests itself in profile thickness, the number of layers or horizons of soil in a profile, morphological attributes of the horizons (e.g., color), physical attributes of the horizons (e.g., size and arrangement of particles), chemical attributes of the horizons (e.g., pH and elemental concentrations), and the biotic fraction of the soil.

It is commonly held that the five most important soil-forming factors governing soil type and attributes are: the parent material of the soil, the climatic regime at the soil's location, the topographic position of the soil in the landscape, the influence of organisms, and the time over which the soil has been forming. The relative importance of these five soil-forming factors will vary from place to place, but there is almost always some effect of each factor on the soil's properties.

Parent Material

In many cases, the dominant soil-forming factor is the parent material of the soil. As the name suggests, soil parent materials are the hard or loose mineral materials from which soil horizons and profiles are derived. The common soil parent materials are rocks, river-borne sediment (alluvium), wind-borne sediment (eolian), hillslope sediment (colluvium), lakebed sediment (lacustrine), materials moved by glacial advance and retreat (glacial till), and volcanic ash. Obviously, for some of these parent materials to be present there must be certain topographic or climatic conditions met. But the nature of the parent material is very important to the properties and attributes of soil profiles, in particular to the suite of minerals present and the size of the soil particles. The top 20–25 km of the Earth's crust consists of approximately 95% igneous rocks or their metamorphic equivalents, 4% shale, 0.75% sandstone, and 0.25% limestone. The average chemical composition of common rocks is given in Table 1. It is evident that SiO_2 and Al_2O_3 account for >70% weight fraction of the lithosphere.

Igneous rocks are exposed mainly in mountainous areas or in lava flows and provide the bulk of the mineral substrate that is spread over the land surface by alluvial, eolian, colluvial, lacustrine, and glacial processes. Consequently, sedimentary rocks form a veneer over much of the crust covering approximately 80% of the land surface. In the case of crustal igneous rocks, silicon-based minerals, more commonly referred to as 'primary silicate minerals,' make up well over 95% of all minerals present. The average mineralogical composition of igneous rocks is 60% feldspars, 17% amphiboles and pyroxenes, 12% quartz, 4% micas, and 8% other minerals.

Table 1 Average chemical composition of major rocks of the Earth's crust

Analysis (%)	*Granite*	*Basalt*	*Sandstone*	*Shale*	*Limestone*
SiO_2	72.08	48.36	78.33	58.10	5.19
Al_2O_3	13.86	16.84	4.77	15.40	0.81
Fe_2O_3	0.86	2.55	1.07	4.02	0.54
FeO	1.67	7.92	0.30	2.45	–
MgO	0.52	8.06	1.16	2.44	7.89
CaO	1.33	11.07	5.50	3.11	42.57
Na_2O	3.08	2.26	0.45	1.30	0.05
K_2O	5.46	0.56	1.31	3.24	0.33
TiO_2	0.37	1.32	0.25	0.65	0.06
H_2O	0.53	0.64	1.63	5.00	0.77
P_2O_5	0.18	0.24	0.08	0.17	0.04
CO_2	–	–	5.03	2.63	41.54
SO_3	–	–	0.07	0.64	0.05

Note: Elemental concentrations are traditionally expressed as oxides because the analyses were done using XRF and elements were assumed in their oxide forms.
Source: Reproduced from Nockolds, S.R., 1954. Average chemical compoisition of some igneous rocks. Geological Society of America Bulletin 65, 1007–1032; Clarke, F.E., 1924. The data of geochemistry. U.S. Geological Survey Bulletin 770, fifth ed. Washington: U. S. Government Printing Office; and Klein, C., Hurlbut, C.S., 1999. Manual of Mineralogy, twenty-first ed. New York: John Wiley.

Primary minerals: Minerals formed at very high temperatures and inherited (unaltered) from igneous rocks and metamorphic rocks. These minerals usually occur in the sand (0.02 or 0.05–2.0 mm) and silt (0.002–0.02 or 0.05 mm) size fractions of the soil.

Common primary minerals in soils are as follows:

1. Feldspars – microcline, $KAlSi_3O_8$; orthoclase, $KAlSi_3O_8$; albite, $NaAlSi_3O_8$; and anorthite, $CaAl_2Si_2O_8$.
2. Quartz (SiO_2).
3. Micas – muscovite, $K(Al)_2[Si_3Al]\ O_{10}(OH)_2$, biotite, $K(Mg, Fe^{2+})_3[Si_3Al]\ O_{10}(OH)_2$).
4. Amphiboles – hornblende, $(Ca,Na,K)_{2,3}(Mg,Fe,Al)_5(OH)_2(Si, Al)_8O_{22}$).
5. Pyroxenes – augite, $(Ca,Na)(Mg,Fe,Al)(Si,Al)_2O_6$).
6. Olivines – forsterite, Mg_2SiO_4).
7. Rutile (TiO_2).
8. Zircon ($ZrSiO_4$).
9. Magnetite (Fe_3O_4).
10. Epidote $(Ca_2(Al,Fe)_3(OH)Si_3O_{12})$.
11. Tourmaline $(Na,Ca)(Li,Mg,Al)(Al,Fe,Mn)_6(BO_3)_3\ (Si_6O_{18})(OH)_4$.

The mineral composition of soils is highly variable depending on the parent material, extent, and duration of weathering, and pedoenvironmental conditions. Weathering is a complex process that occurs through physical, chemical, and biological processes. These weathering processes not only result in the transformation of primary minerals into secondary minerals, but also in the release of many essential plant nutrients, and the modification of edaphic soil properties. Goldich (1938) proposed a mineral stability series for sand

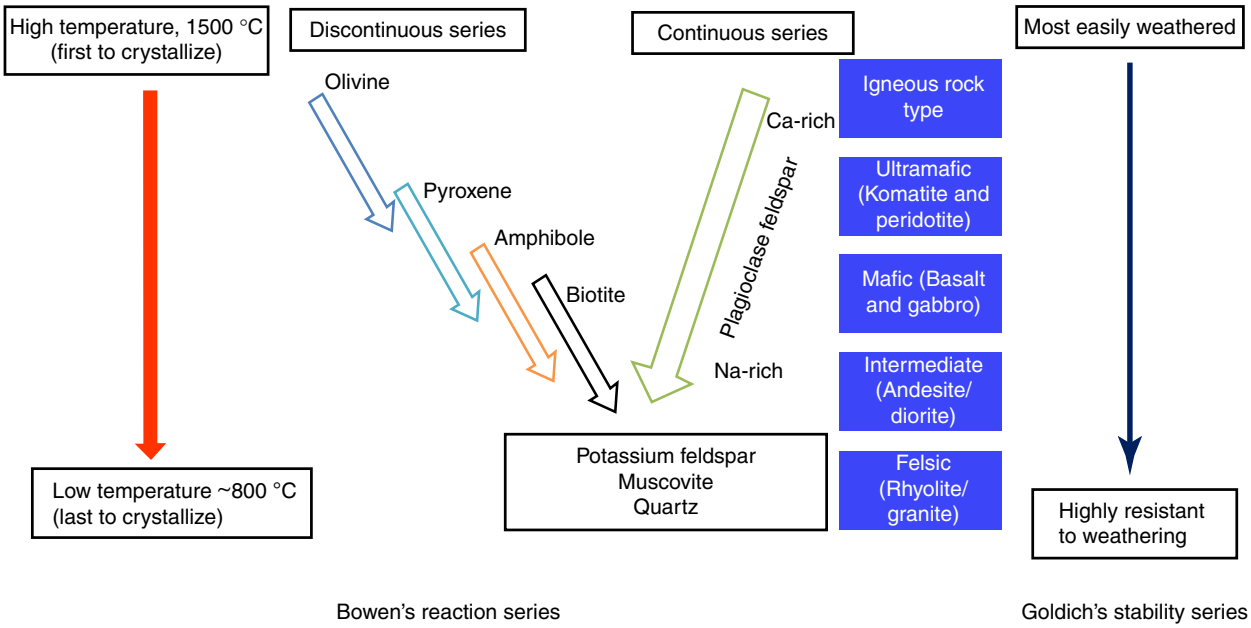


Figure 2 The stability order of primary soil minerals based on Bowen's Reaction Series and Goldich's Stability Series.

and silt particle size fractions, which is useful in predicting the stability of common primary minerals in soils. The Goldich Series is identical to the Bowen's Reaction Series that was formulated to explain the order of crystallization of the common silicate minerals from a magma. The minerals that are formed at higher temperatures (such as olivine, pyroxene, etc.) and then exposed to low temperature terrestrial conditions, will be farthest from their crystallization temperature (comfort zone), and will therefore chemically weather first. Quartz, at the other end of series, is closer to its preferred temperature and, therefore, is much more stable to weathering (Figure 2).

Parent rock in relation to soil fertility and other soil properties

In less weathered or relatively younger soils, a significant reserve of nutrient elements exist within the primary minerals. When present in the mineral structure, the nutrients are not available to plants; however, weathering processes release these nutrients very slowly to the soil solution. The mineralogical and elemental composition of igneous rocks is determined by the chemical composition of the magma from which it solidifies. Among the igneous rocks, granite and rhyolite contain relatively low concentrations of essential plant nutrients, with the exception of potassium (Table 1). In contrast, basalt and gabbro contain much higher concentrations of iron, magnesium, calcium, and many other trace elements. Thus, soils formed on basalt (or gabbro) are inherently more fertile than a soil formed on granite (or rhyolite), with the exception of K fertility.

The chemical and mineralogical composition of sedimentary and metamorphic rock is determined by the composition of the sediments and rocks from which they have originated. Sandstones and shales are generally composed of preweathered materials consisting of stable primary and secondary minerals; due to the lack of weatherable primary minerals these rocks have limited capacity to supply appreciable quantities of nutrient elements. Limestone is a rich source of Ca and Mg, and low levels of other essential plant nutrients. Ultrabasic rocks, such as peridote, olivinites, dunite, and serpentine, contain low concentration of Ca and very high concentrations of Mg, Cr, Ni, and Mn, which have a particularly strong influence on plant nutrition. Unique plant species survive on the soils formed on ultrabasic rocks and many of the plants growing on these soils have the capacity to hyperaccumulate trace metals such as Ni.

Secondary minerals: Secondary minerals in soils are formed from the weathering of primary minerals either through crystallization from soil solution or via alteration of primary minerals. These minerals often dominate in the clay fraction (<0.002 mm or 2 μm) of the soil and are often referred to as clay minerals.

Some common secondary minerals in soils are as follows:

1. Kaolinite – $Al_2Si_2O_5(OH)_4$.
2. Smectite – variable (layer charge between 0.2 and 0.6 per $O_{10}(OH)_2$, an ideal montmorillonite- $Na_{0.4}(Al_{1.6}Mg_{0.4})(Si_4)O_{10}(OH)_2$
3. Vermiculite – variable (layer charge between 0.6 and 0.9 per $O_{10}(OH)_2$, an ideal dioctahedral vermiculite – $Na_{0.7}(Al_2)(Si_{3.3}Al_{0.7})O_{10}(OH)_2$.
4. Goethite – α-FeOOH, the substitution of Al is very common in highly weathered soils and common composition is close to -α-$(Fe_{0.75}Al_{0.25})OOH$.
5. Hematite – α-Fe_2O_3, the substitution of Al is very common in highly weathered soils and common composition is close to -α-$(Fe_{1.9}Al_{0.1})_2O_3$.

Among the four profiles, only the Callandoon soil contains feldspars (microcline and albite) throughout the profile, all soils contain quartz with only trace amounts in the Toowoomba soil, and calcite is present at depth in the Nowley soil.

The four case study soils also provide good examples of the effects of different parent materials on soil attributes such as particle size distribution. The coarse-grained Pilliga profile is derived from the weathering of coarse-grained sandstone rock, whereas the texture-contrast Nowley profile is derived from a mixture of sandstone and basaltic colluvium. The fine-grained Toowoomba profile is derived from the weathering of fine-grained basalt rock, and the very fine-grained Narrabri profile is derived from basaltic alluvium.

Climate

Climate can have a substantial effect on soil profile development through the transformation, alteration, and movement of mineral solids and solutes inherited from the soil's parent material. From a soil formation standpoint, the two most important climatic factors are rainfall and temperature. As the amount of annual rainfall increases, so does the opportunity for topsoil organic carbon content to increase, for the washing of very small particles into the subsoil to occur, for the leaching of solutes to occur, and for the development of morphological features (e.g., color mottles or patches, nodules of Fe and Mn oxides) to occur due to fluctuating redox conditions in the soil. Such processes are very important for the development of multiple horizons in one soil profile. The effect of increasing temperature on the rate of chemical reactions in the soil shows that soil is important for soil development. In locations with higher air and soil temperatures, both the rate of organic matter decomposition and the rate of mineral transformation are faster. Soils of the equatorial tropics are commonly strongly weathered due to the high rainfall, high temperature climatic regime, with a preponderance of low charge clay minerals and iron oxides, both products of primary mineral breakdown. Under rainforest vegetation, such soils contain moderate organic matter contents at the soil surface. But with clearing and cultivation the supply of organic matter from the vegetation canopy to the topsoil decreases sharply, followed by a rapid decrease in soil organic matter (SOM). It follows, then, that soils with the greatest accumulation of organic matter in the topsoil are located in wet, cold locations. The high latitude, boreal regions of North America, Europe, and Asia, which are characterized by long cold winters and short cool summers, are home to extensive areas of organically dominated peat soils (Driessen and Dudal, 1991). In contrast, soils of dry, hot climatic regimes, such as those experienced in the deserts of northern Africa, the Middle East, and Asia are characterized by low organic matter contents and the accumulation of readily and sparingly soluble salts, including gypsum and lime (Driessen and Dudal, 1991).

Topography

The role of topography in soil formation is to mediate the development of horizons through effects on water and solute flow, and particle movement. In sloping landscapes with moderate to high rainfall, leaching of solutes and the washing of solids down the profile and across the soil surface leads to greater differentiation of topsoil and subsoil horizons in both chemical and physical attributes. Soluble salts and fine-grained particles tend to be transported to lower horizons and lower points in such landscapes, whereas insoluble materials and large-grained solids (including gravel) tend to be retained in upper horizons and landscape positions. In flat landscapes, deposition and organization of sediment is favored. Depending on the sediment grain size, imperfect drainage of water in flat areas can lead to the development of particular mineral suites. The Callandoon profile is a good example of this, with the fine-grained alluvial parent material favoring the formation and longevity of the shrink-swell mineral smectite.

Organisms

The soil formation factor of organisms is a requirement in all soils, as soil is differentiated from other loose regolith materials (e.g., fresh sediment) by the presence of vertical differentiation due to biotic activity. Although soil formation is rarely dominated by this factor, there are nevertheless many ways in which organisms may affect soil development. Plants, microorganisms (e.g., fungi and bacteria), mesofauna (e.g., earthworms and ants), macrofauna (e.g., burrowing animals and hoofed livestock), and humans are all responsible for altering physical and chemical properties of soil horizons under certain circumstances. In many agricultural landscapes, it is likely that of all the groups of biota humans have had the greatest impact: land clearing and cultivation leads to the mixing of soil horizons, changes to the hydrologic cycle, changes to the physical condition of the topsoil, and changes to nutrient cycling; the use of fertilizers alters the chemical status of the topsoil horizons; and irrigation alters the redox potential of the soil and nutrient cycling within the profile. Nevertheless, the other groups of biota also contribute to important effects in some situations. Plants improve the physical condition of topsoil through the binding effect of growing roots and the addition of organic matter through leaf litter. Microorganisms are responsible for organic matter breakdown and catalyze various chemical reactions in the soil. Mesofauna create continuous passages in soil, redistribute plant nutrients around the profile, and turns over topsoil. Macrofauna can exacerbate soil erosion by pulverizing the surface soil or burrowing into unstable subsoils (Hole, 1981).

Time

The final soil formation factor, time, is perhaps the most difficult to interpret without highly specific soil dating data. However, in concert with the other soil-forming factors, elapsed time is a crucial determinant of soil profile differentiation; the longer the soil parent materials have existed at a location, undergoing a range of soil-forming processes, the greater the likelihood that the soil will be well differentiated, with greater horizonation and usually more contrasting topsoil and subsoil horizons. Older soil profiles also tend to contain a greater proportion of resilient minerals, and secondary minerals that are breakdown products of less resilient minerals. Again, soils of stable landscapes in the tropics commonly express these attributes, with deep, brightly colored profiles containing much kaolinitic clay, and iron and aluminum oxides and hydroxides, all of which are resilient

secondary minerals (Driessen and Dudal, 1991). The bright red colors apparent in the Nowley and Toowoomba profiles are also a consequence of the formation of iron oxides through weathering of less resilient minerals over long periods of time.

Key Edaphic Soil Properties

One of the unique features of soil as a natural body is that profiles are assemblages of horizons (Churchman, 2010). The number of horizons in a soil profile can vary widely, but it is common for a profile to have four to six horizons in the top 1.5 m. Horizons are normally distinguished based on easy-to-assess morphological properties such as color, texture, and structure. In some soil types the horizons are largely unchanging with depth (e.g., Toowoomba and Callandoon profiles), whereas in others horizon attributes change markedly from the topsoil to the subsoil (e.g., Nowley profile in Figure 1). Although there are many different soil classification schemes used around the world, in virtually all of them an 'ABC' nomenclature is used, where the A horizons are surface or near-surface horizons showing evidence of organic matter enrichment, the B horizons are subsoil horizons showing greater color saturation or an accumulation of clay or better developed structure, and C horizons are largely unaltered parent material. In full soil profile descriptions, subdivisions of the A and B horizons are normally made based on changes in various morphological and chemical features, and in many soil classification schemes it is the presence of certain horizon types that dictates the allocation of a soil profile to a class. Two of the soil classification schemes most widely used around the world are the World Reference Base for Soil Resources (WRB) (IUSS Working Group WRB, 2007) and Keys to Soil Taxonomy (Soil Survey Staff, 2010), and both use topsoil and subsoil horizon types as the basis of soil-type allocation. Many of the most important edaphic soil properties are also used to describe certain horizon types. These key edaphic soil features are now discussed and how they are described in soil horizons and profiles is shown.

Texture

In soil science terms, texture is a particular combination of clay-, silt-, and sand-sized particles in a horizon. In common parlance it can be thought of as the feel of the soil, and it is a property usually assessed in the field. In most soil description systems there are between 10 and 20 different texture grades used. Using the Nowley soil profile as an example, the texture grade for the top horizon is clay loam and for the other three horizons it is clay. Although there are some slight differences in how silt- and sand-sized are defined around the world, a sand-sized particle is commonly defined as having a diameter between 2000 and 50 μm, a silt-sized particle has a diameter between 50 and 2 μm, and a clay-sized particle has a diameter less than 2 μm (Figure 3). Strictly speaking, the words 'clay', 'silt,' and 'sand' only refer to particle size, but it is common for soil scientists to associate various minerals with these different size fractions. For example, the difficult-to-weather mineral quartz is a very common component of the sand fraction in soils, whereas sheet silicate minerals such as kaolinite and smectite, which form in soil, usually exist in the clay fraction. The clay content is one of the most important attributes used to differentiate different horizons and subhorizons, and therefore to differentiate between different soil classes, or types. The Callandoon soil profile contains more than 40% clay in all horizons, leading to its classification as a Vertisol.

As an edaphic property, texture is critically important for a variety of reasons. From a physical standpoint, the texture profoundly influences water infiltration rate and conductivity, water storage, soil density, and soil strength. From a chemical standpoint, texture is very strongly linked to the availability of various plant nutrients. Generally speaking, the more clayey a horizon, the more likely it is to retain or hold both water and plant nutrients. These edaphic linkages will be explored in more detail in the following sections.

Structure

Texture refers to the size of soil particles, whereas structure refers to the spatial arrangement of those particles and the voids (pores and cracks) between them. Another unique feature of soil as a natural material is that individual particles aggregate together through a range of processes at various scales to yield 'peds' (Churchman, 2010) or 'aggregates.' The degree of pedality (strong, medium, weak, and apedal) is often assessed visually in the field, as is the dominant ped shape and size in each horizon. In most soil description systems, there are approximately 10 different ped shapes used. Clear examples of angular blocky peds (cube-like shape) can be seen in the red-colored third horizon of the Nowley profile, whereas the Pilliga profile lacks any discernible peds and is described as apedal. Together with an estimation of the pore volume and size of individual pores, these ped attributes give a qualitative account of the 'structural form' of a soil horizon. Like texture, structure is an important diagnostic property for the identification of certain horizon and profile types.

The stability of peds (aggregates) in a soil horizon depends on the way the sand-, silt-, and clay-sized particles are organized and the binding agents between these. It is commonly accepted that microaggregates (2–250 μm) are comprised of clay minerals that are bound together by either the presence of exchangeable cations on the clay surfaces or organic polymers bridged by polyvalent cations (e.g., Ca^{2+} and Al^{3+}) interacting with the clays (Figure 4). The presence of calcium carbonate ($CaCO_3$) and sesquioxides (Fe and Al oxides) also provide cohesion of microaggregates. Macroaggregates (250–2000 μm) are comprised of cohesive microaggregates and are primarily stabilized through enmeshment by plant roots and fungal hyphae. For soils with a pH range of 5.5–7, soil management that promotes a high level of biological activity (e.g., root growth, fungi, and microorganisms) will benefit aggregate stabilization and, in particular, macroaggregates. Also, avoiding management practices that result in the dominance of monovalent cations (e.g., Na^{+}) on the clays and the loss of soil carbon will promote cohesive microaggregates. At higher pH, $CaCO_3$ plays a crucial role and at lower pH, Fe and Al oxides will contribute to aggregation.

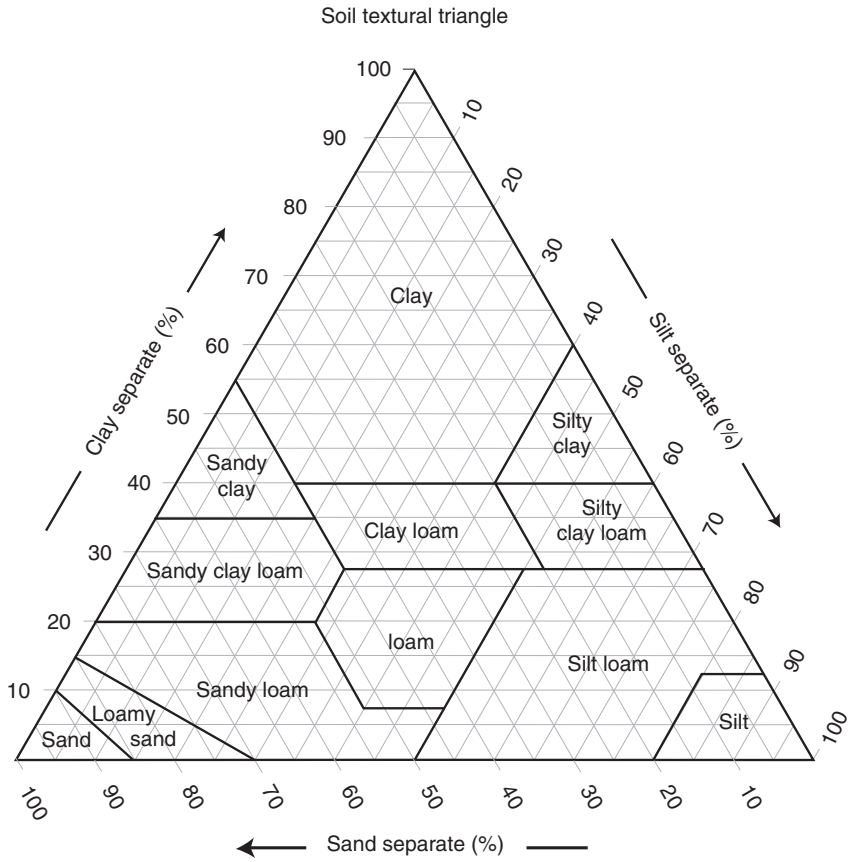


Figure 3 The soil textural triangle based on the USDA system, where sand comprises the 2.0–0.05 mm (50–2000 μm) fraction, silt 0.05–0.002 mm (2–50 μm) fraction, and clay the fraction which has a diameter less than 0.002 mm (<2 μm) (http://www.nrcs.usda.gov/wps/portal/nrcs/detail/soils/edu/kthru6/?cid=nrcs142p2_054311).

When aggregates are exposed to water, the stresses imposed may result in structural instability, leading to slaking or dispersion. Slaking is a physical phenomenon where aggregates essentially fall apart to form smaller macro- or micro-aggregates. In some situations slaking can be a desirable structural regeneration process, but if there is excessive slaking resulting in fragments <100 μm diameter, there is the potential for the soil to form surface seals, which will reduce water infiltration. Dispersion is a physicochemical process where individual particles within peds completely dissociate from each other on wetting, due to low electrolyte concentrations in the soil water and a surplus of exchangeable Na^+ on the surfaces of clay minerals. In these situations, the soil is said to have a high exchangeable sodium percentage (ESP), meaning that Na^+ comprises a larger proportion of the cation exchange capacity (CEC) than is normal (for sodic soils ESP > 15%). When such soil is wetted, the Na^+ present causes repulsive forces to overcome the strength of aggregation, leading to dispersion. Two other forms of structural instability are differential swelling and mechanical fragmentation. In the case of differential swelling, also referred to as mellowing, it is usually regarded as a desirable process as it increases the friability of the soil (Figure 4). The process of differential swelling depends on the rate of wetting and the presence of binding agents that hold the aggregates together. The main driving force is the presence of clay minerals that have a large swelling potential and this enables the aggregates to not be disrupted by the entrapped air within them (Figure 4). Finally, the exposure of wetted aggregates to the kinetic energy of raindrop impact will often result in their disruption and this is identified as mechanical fragmentation (Figure 4).

The structural form and stability of a soil are the key determinants of the soil's ability to support plant life. As is the case with texture, soil structure has a profound influence on water and gas movement in and through the soil, water storage, soil density, and soil strength. In turn, these properties dictate the ease with which seedlings germinate, the rooting patterns of growing vegetation, the ease with which plant roots extract available water, and the propensity of soil horizons to become waterlogged and anoxic.

Pore Space Relations

Together, the texture and structure of soil horizons govern the particular arrangement of the three phases of the soil, namely, the soil solids, soil solution, and soil air (Figure 5).

The arrangement of the soil particles provides the framework for the other phases and the assessment of this arrangement should provide useful information about the other phases. As can be seen in Figure 5 the total mass is comprised of the mass of the solid phase (M_s) and mass of any water

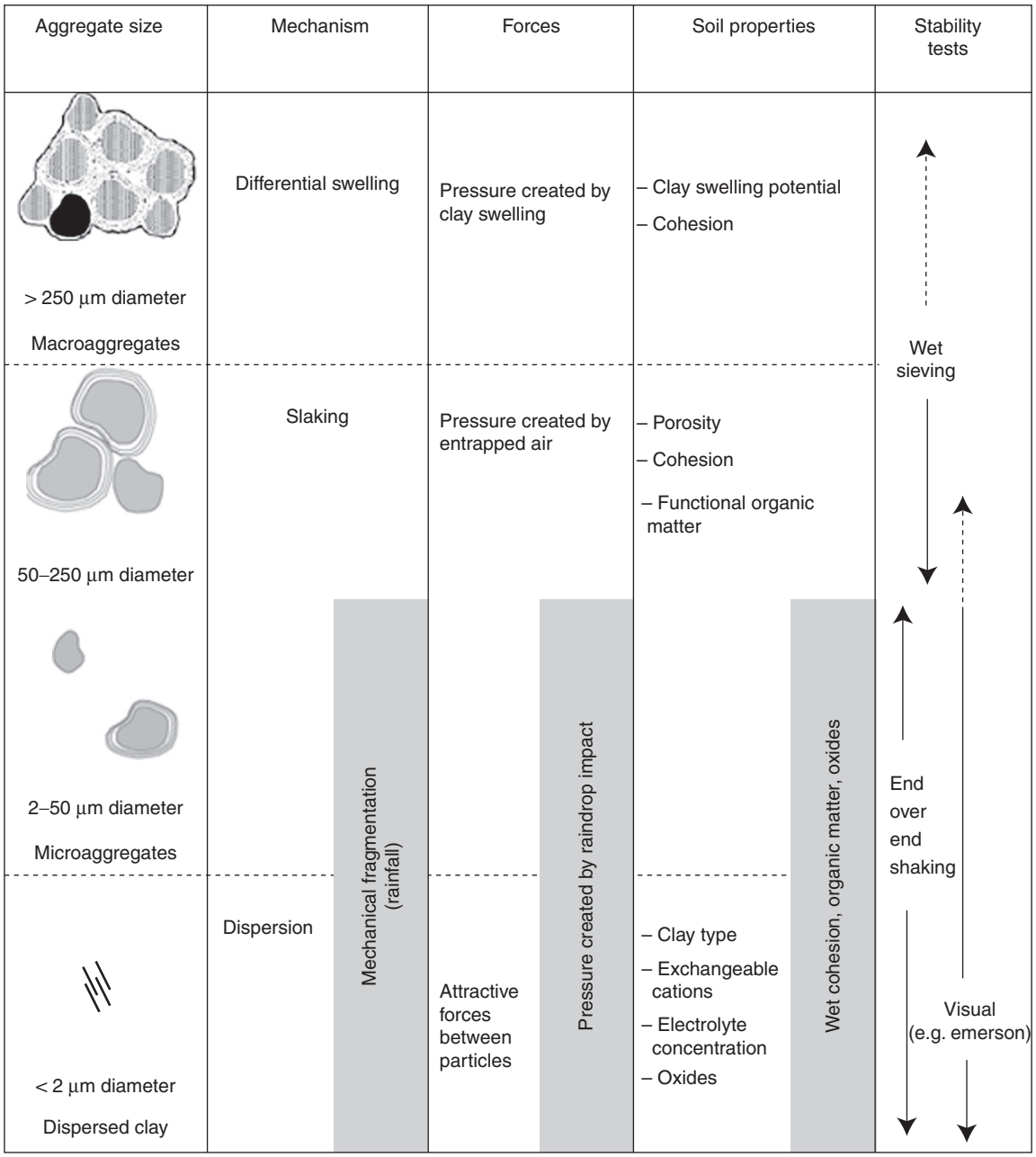


Figure 4 A summary of the major forces responsible for aggregate breakdown and dispersion, and the stability tests that may be employed to assess this. Reproduced from Field, D.J., 1999. Aspects of aggregate stability: Mechanisms, associated physico chemical properties, and assessment. In: Cattle, S.R., George, B.H. (Eds.), Describing, Analyzing and Managing Our Soil. Sydney, NSW: University of Sydney Publishing, pp. 135–148.

(M_w) present. The mass of air (M_a) by comparison is negligible and is not considered.

There are a range of minerals that make the soil solids and the measurement of these is known as the solid density (ρ_s), or mean particle density

$$\rho_s = \frac{\text{Mass of solid}}{\text{Volume of solid}} = \frac{M_s}{V_s} \quad [1]$$

The range of solid densities for some of the common minerals found in soil are given in Table 2, and a more comprehensive list of the solid densities of soil minerals can be found in Cresswell and Hamilton (2002). For most soils the coarse fraction is dominated by quartz and the fine fraction by the clay minerals (e.g., smectite, illite, and kaolinite) and all these minerals have similar ρ_s. The dominance of these minerals means that it is generally accepted that a ρ_s of 2.65 Mg m^{-3} is the value for density for the soil solids. In some soils the increased presence of iron oxides (e.g., hematite) will increase the ρ_s, whereas a dominance of organic matter may lower the ρ_s.

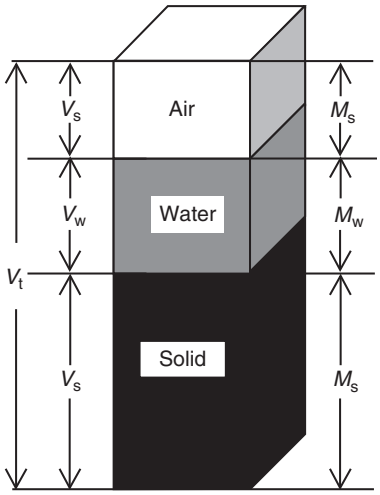


Figure 5 A schematic representation of the three phases in soil, where each phase can be measured as having a mass (M) and occupying a volume (V). Adapted from Hillel, D., 2004. Introduction to Environmental Soil Physics. Amsterdam: Elsevier Academic Press.

Table 2 Solid density for common soil minerals

Soil particle	*Solid density (Mg m^{-3})*
Quartz	2.65
Smectite	2.50
Kaolinite	2.60
Illite	2.50
Goethite	4.37
Hematite	5.26
Calcite	2.71
Gypsum	2.32
Halite	2.16

As described earlier, the soil structure is often evaluated using a description of size and shape of the soil peds, but the solid phase can also be measured in terms of its bulk density and is expressed as

$$\rho = \frac{\text{Mass of oven dry soil}}{\text{Total volume}} = \frac{M_s}{V_t}$$
$$\rho_s = \frac{\text{Mass of solid}}{\text{Volume of solid}} = \frac{M_s}{V_s} \quad [2]$$

The development of a pore phase when the soil solids are aggregated means that the bulk density (ρ) is always less than the solid density (ρ_s). The pore space can occupy from 30% to 60% of the total volume, resulting in a range of bulk densities. A broad relationship between bulk density and different texture grades has been developed and generally, an increase is the amount of silt or clay in a soil will result in a greater range of ρ and the distribution of pores that will develop when a soil is aggregated. The presence of clay that will swell and shrink in response to changes in moisture will also affect the ρ.

Soils with uniform textures throughout the profile usually show small changes in the bulk density with depth (Figure 6 (b), (c), and (d)). For uniformly clayey soils an increase in bulk density with depth may indicate the development of compaction, which can be the result of overburden pressures from the use of farm machinery in crop management (Figure 7 (c)). This problem has resulted in the adoption of controlled traffic practices, which ensure that the area of the field being affected by the excess weight of machinery is limited, avoiding increases in the ρ that will constrain root development. Profiles where there is naturally significant increase in clay content with depth may exhibit an increase in bulk density (Figure 6 (a)) and this is seen as quite normal.

The bulk density of the soil and the resulting porosity will affect how water and gas move through the soil and how easy it is for roots to penetrate the soil. The porosity of the soil is expressed using the relationship

$$\phi = \frac{\text{Volume of voids}}{\text{Total volume}} = \frac{(V_a + V_w)}{V_t} \text{or} \left(1 - \frac{\rho}{\rho_s}\right) \quad [3]$$

The pores and cracks that exist between soil aggregates are known as macropores and these are usually created by soil fauna, plant roots, or the shrinking and swelling of the soil (Table 3). The smaller pores that exist within aggregates are called micropores and these are responsible for storing the water in soil. The distinction between pores that freely drain as opposed to those that store water can be used to distinguish macropores from micropores, respectively (Table 3).

Having sufficient moisture in soil is a major limiting factor affecting plant growth in agricultural systems. It is estimated that up to 50% of the global surface is used for dryland agriculture and therefore having soil that can maximize its water storage capacity without the option of supplementary supply via irrigation is critical to most production systems.

Water in soil exists in the soil pores and the amount of water can be expressed as a mass or a volume. The mass of water in a soil is referred to as the soil's wetness (w) in g g^{-1}, whereas the volumetric water content reports water in terms of the volume (θ) it occupies in m^3 m^{-3}, both being expressed as follows

$$w = \frac{\text{Mass of water}}{\text{Mass of solids}} = \frac{M_w}{M_s} \text{ and } \theta = \frac{\text{Volume of water}}{\text{Total volume}} = \frac{V_w}{V_t} \quad [4]$$

As will be seen later, expressing water content on a mass basis will prove useful when correcting for water in the soil laboratory, but the use of volumetric water content is more useful biologically and agriculturally.

If the bulk density of the soil is indicative of the amount of pore phase, the volume of water in a soil can be calculated if we know the mass of water it contains, as follows;

$$\theta = \omega \times \rho \quad [5]$$

In addition to using eqn [3] to calculate ∅ when a soil is saturated, the amount of water is equal to the soil's porosity and this is identified for the four soil profiles in Figure 7.

The uniform texture of the Pilliga, Callandoon, and Toowoomba soil profiles has resulted in very little change in the overall porosity throughout the respective profiles (Figure 7(b), (c), and (d)). The decrease in the porosity with depth for Nowley (Figure 7(a)) is the result of the increased bulk density

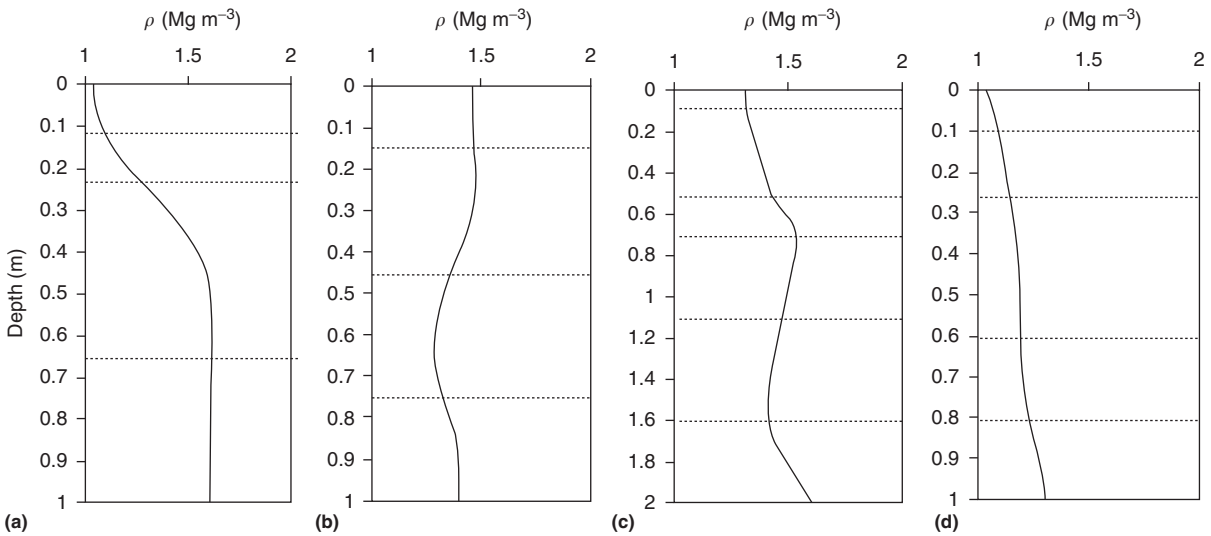


Figure 6 Change in bulk density with depth for the soil profiles. From (a) Nowley, (b) Pilliga, (c) Callandoon, and (d) Toowoomba.

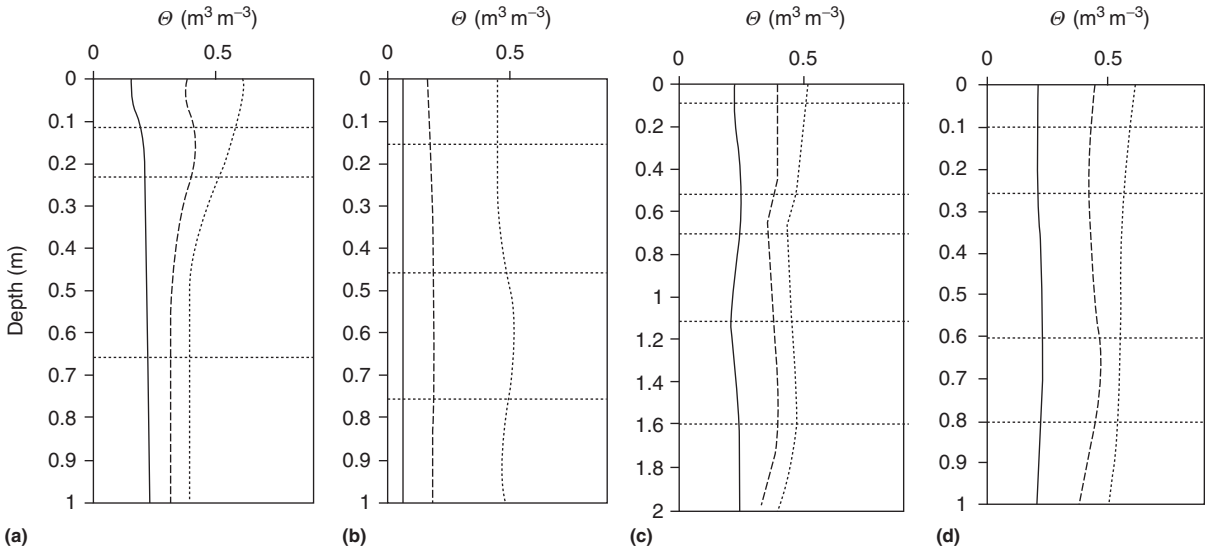


Figure 7 Change in the permanent wilting point (PWP) (solid line), field capacity (FC) (- - - -), and total porosity (————) with depth for the soil profiles. From (a) Nowley, (b) Pilliga, (c) Callandoon, and (d) Toowoomba.

Table 3 The relationship between pore size and functions in soil

Pore diameter (μm)	*Associated biotic agents functions*
5000–500	Earthworm channels and main plant roots; pores for rapid drainage and aeration
500–30	Grass roots and small mesofauna; normally draining pores
30–10	Fine lateral grass roots and fungal hyphae; very slow drainage pores
10–0.2	Root hairs, fungal hyphae, and bacteria; 'available water'
<0.2	Shrink-swell water in clays; residual water or 'nonavailable water'

Source: Reproduced from White, R.E., 2003. Soils for Fine Wines. New York, NY: Oxford University Press.

of this soil. In Figure 7, the term field capacity (FC) is used to describe the maximum amount of water the soil can store. It is clear that the difference between the amount of water at saturation (equivalent to the porosity) and the FC for the sandy Pilliga profile is very large compared to the soils with more clay. This is because packing of the sand grains results in larger pores that transmit water but are not able to store it. The pore size range of loam and clay soils is greater, resulting in more pores that can store water compared to sands. This can be seen in Figure 7 if the area between the FC and what is identified as the permanent wilting point (PWP), which is the point where plants cannot exert enough energy to remove water from soil surfaces and pores is compared. For the Pilliga profile, this area is less than that for the clayey Callandoon and Toowoomba soils, meaning that overall there is less available water in this profile

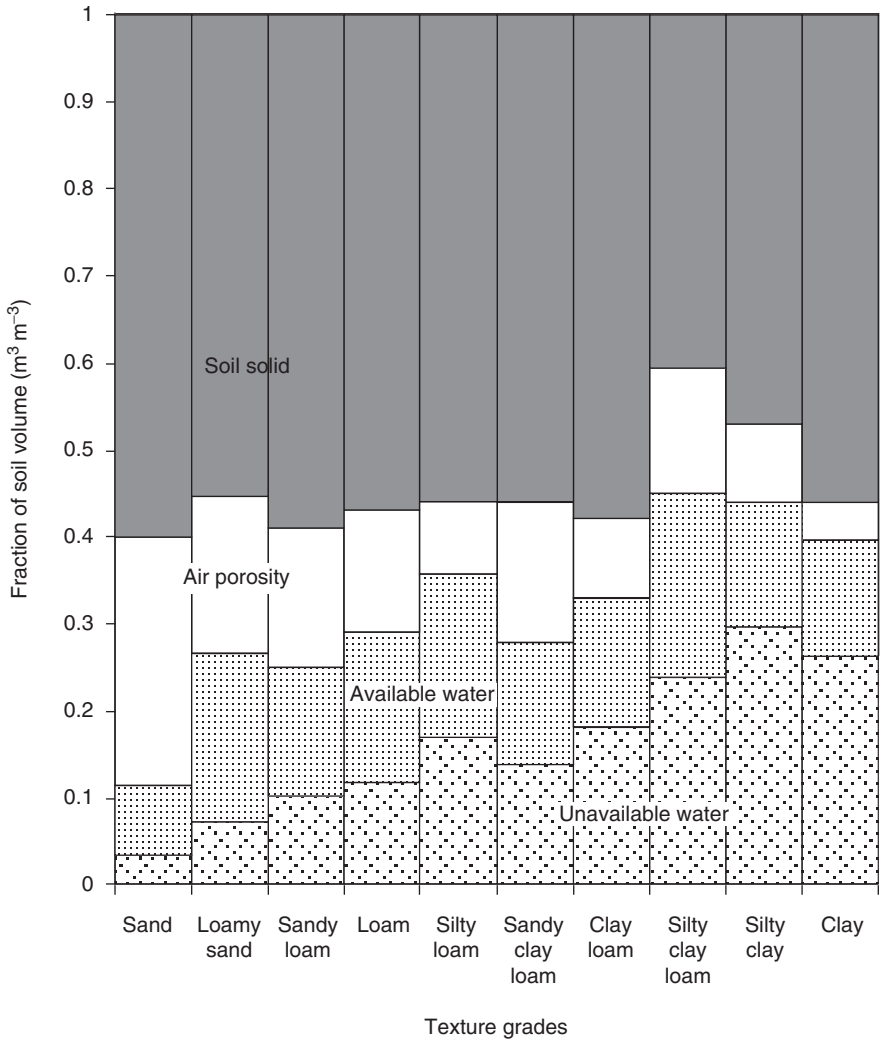


Figure 8 A representation of the volume occupied by the unavailable water, available water, air porosity, and soil solids for a range of soil textures.

(Figure 7(b), (c), (d)). To quantify this the potential volume of the soil that can hold water and what forces are acting on the soil to move water around, or the water potential are considered.

Soil Water Storage

A simplified illustration of the amount of water that can be stored in soil for a range of textures is presented in Figure 8. The difference in the amount of soil water stored (Figure 8) not only depends on the amount of pores present as discussed earlier but also the forces that are responsible for moving water into and through the soil.

Gravity is the dominant force that moves water into and through the soil when wet, exerting a force that is proportional to the height of water above the soil surface. This is known as the gravitational potential (ψ_g). Once water has entered the soil its storage is mainly affected by adsorption forces and the soil's capillarity. The adsorption of water when the soil is very dry is mainly due to the hydrogen bonding of water molecules to each other and the soil particle surfaces. This surface adsorption occurs because soil particles often carry negative charge, which attracts cations that are surrounded by a hydration shell of water molecules. Because soil particles have a specific surface area and are often charged means that plants have to exert energy to remove water from these surfaces. The larger specific surface area and potential surface charge usually present in clayey soils results in more water being unavailable compared to sandy soils, as the plants cannot overcome the adsorption energy of the soil surfaces.

The capillarity is a consequence of the particle geometry and attraction of solid surfaces for water. Pores can hold water if the air-water meniscus can hold up the column of water beneath it (Figure 9(a)). The combined effect of adsorption and capillarity on the free energy of water is described as the matric potential, ψ_m, and can be directly related to the pore radius. Usually, soil horizons with loamy texture grades have a pore size distribution that holds the most available water compared to clays and sands.

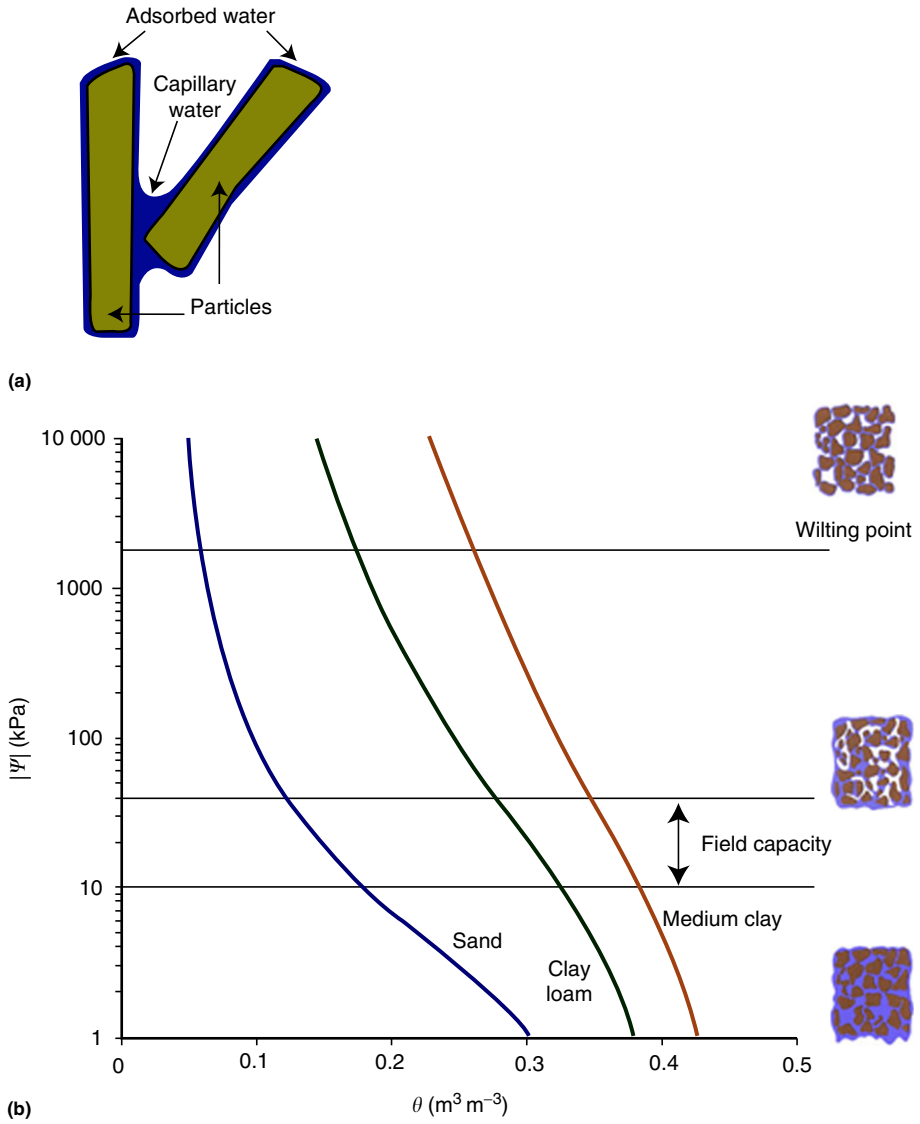


Figure 9 A representation of (a) adsorbed and capillary water and (b) the water retention curve for different soil textures, including water availability.

The total water potential of a soil is expressed as follows:

$$\psi = \psi_m + \psi_g + \psi_p + \psi_s \quad [6]$$

In eqn [6] the osmotic potential (ψ_s), is only measured in soils where there is enough dissolved salts to reduce the free energy of water, i.e., saline soil. In a saturated soil the $\psi_m = 0$. The pressure potential (ψ_g) in most circumstances is negligible and may be considered in relation to the presence of a soil water table, where above that water table ψ_m is negative and below the water table ψ_p is positive.

The relationship between the matric potential and volume of water held in the soil is represented as the water retention curve (Figure 9(b)). When all the pores are full of water the potential is equal to zero and the soil is said to be at saturation. As identified earlier, the FC is achieved when all the pores that freely drain in response to the gravimetric potential being greater than the matric potential have done so, leaving only medium and small pores filled. FC is commonly reported on the soil water curve between the potentials of -10 to -33 kPa, or the amount of water held in a soil after it has been allowed to drain for 2–3 days.

In most cases, once a soil has achieved FC there will be at least 10% air-filled porosity, which is required for healthy plant growth and root development. In Figure 7, the difference in area between the porosity and FC represents the air-filled porosity and for all depths in the four profiles it is greater than 10%. For sandy soils the rate of drainage from saturation to FC occurs faster than for clay soils, meaning that there is the potential for the clayey profiles, such as Callandoon (Figure 7(c)), to experience a number of days where the air-filled porosity is less than optimal. These conditions, often described as waterlogged, can lead to the loss of soil nutrients such as nitrogen. The air-filled porosity of a soil can also

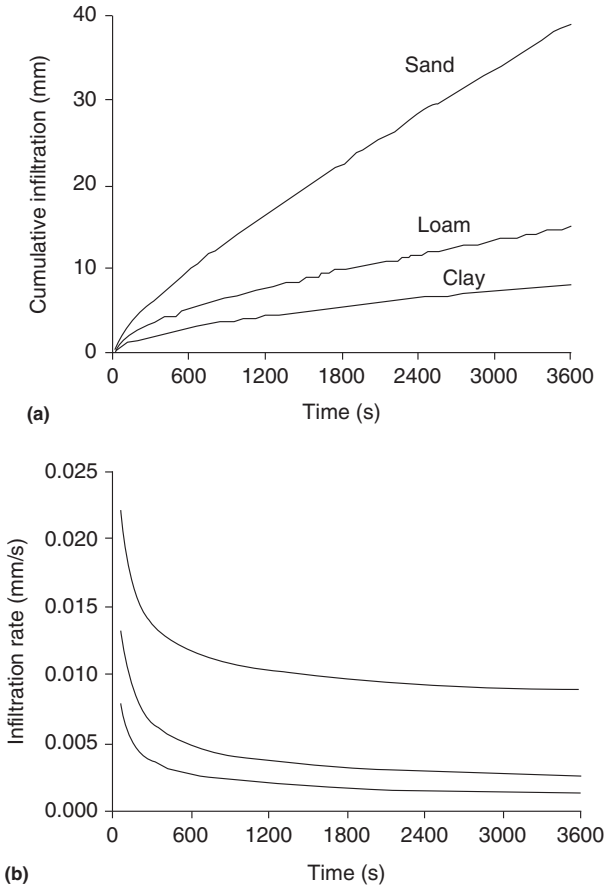


Figure 10 (a) Cumulative infiltration (b) and infiltration rate for sand, loam, and clay-textured soils. Reproduced from Minasny, B., George, B. H., 1999. The measurement of soil hydraulic properties in the field. In: Cattle, S.R., George, B.H. (Eds.), Describing, Analyzing and Managing Our Soil. Sydney, NSW: University of Sydney Publishing, pp. 185–204.

be calculated as follows:

$$\varphi_g = 1 - \left(\frac{\rho}{\rho_s}\right) - \theta \qquad [7]$$

As the soil dries it will become more and more difficult for plants to remove water and eventually there is a point reached where the plant will wilt and cannot recover its turgidity, known as the PWP (**Figures 7** and **10(b)**). The amount of water between the FC and PWP is known as the available water capacity (AWC) and can be expressed as

$$AWC = (\theta_{FC} - \theta_{PWP}) \qquad [8]$$

The unavailable water completes the moisture characteristic curve and this does influence soil that is prone to shrinking and swelling resulting in large cracks during dry periods, which close on wetting affecting the rate of water movement and distribution in the soil. For all practical purposes though the two fixed points that define the plant AWC are paid the most attention.

The estimates of FC and PWP are determined in the laboratory but the upper and lower limits of the AWC can also be determined in the field using the crops that will be grown. This is achieved by monitoring the change in the soil water content from when it is completely saturated until water is no longer available to plants, causing them to permanently wilt and die. Once the soil is saturated the moisture content is monitored until drainage has almost ceased and this is termed the drainage upper limit instead of the FC. Once the crop that is grown shows signs of significant stress the soil water content at this point is taken as the lower limit (LL) and is used instead of the laboratory determined PWP. A detailed description of this procedure can be found in Ratliff *et al.* (1983). The advantage of using this field technique is beyond being soil- and crop-specific; it also takes into account the rooting depth of the plants and the volume of soil that can be explored to extract water. In the case of irrigation, knowing when it is getting more difficult for a plant to extract water is used to schedule irrigation events. This critical limit is identified as the readily available water and this takes into account the amount of water that is adequate for plant physiological function and is termed the deficient available water.

Finally, when meteorologists refer to rainfall and farmers talk about water in the soil or water used for irrigation, they will usually express this as a height (e.g., mm of rainfall). Also, if the rooting depth of the plants that are grown is known this can be used to determine the lower limit to which the plant will explore the soil and where water can potentially be extracted from. Based on this it would be useful to be able to determine the volume of water held in each horizon of the soil as a length, d, and is calculated using the following relationship:

$$d = \theta \times 1000 \times z \qquad [9]$$

where d is the equivalent depth in mm and z is the thickness of the horizon in meters in a meter of soil.

Soil Water Infiltration

The entry of water through the soil surface is called infiltration. How much water enters and the rate of its entry into the soil is determined by the soil texture, its surface condition and the soil porosity (**Figure 10(a)**). The presence of stable soil aggregates on the surface will favor water entry, but if aggregates slake and disperse the liberated soil can block the soil pores reducing the infiltration. The presence of swelling clays in a soil can reduce the infiltration rate as the size of conducting soil pores is reduced. As soil becomes wetter with infiltration the gradient in the ψ_m becomes smaller and gravity becomes the only driving force the rate of infiltration will also reduce (**Figure 10(b)**).

The process of infiltration, once a soil surface is ponded, involves saturation at the soil surface layer of the soil profile, which is called the saturation zone (**Figure 11**). Below this is a zone that has a relatively constant water content that is less than saturation but greater then FC identified as the transmission zone. The initial nonlinearity in the infiltration curve is more pronounced the drier the soil as the ψ_m is the dominant force affecting water movement. At the wetting front the water content decreases rapidly to the initial water content of the soil profile. This decrease in the water content will reduce the overall water flow through the soil. Generally, an infiltration rate of >50 mm h^{-1} will allow water to enter the soil

and avoid excessive ponding, which may lead to runoff and erosion on sloping topographies. Under rainfall ponding may not be achieved and the infiltration is controlled by the rainfall rate and may result in unsaturated flow.

The longer that ponding conditions persists, the deeper the wetting front penetrates into the soil. Once the water supply ceases a process of redistribution of water in the profile takes place. After redistribution, the wetting front will move further into the profile and the redistribution of water stored in the profile moves from the area (A) to area (B) as demonstrated in Figure 11.

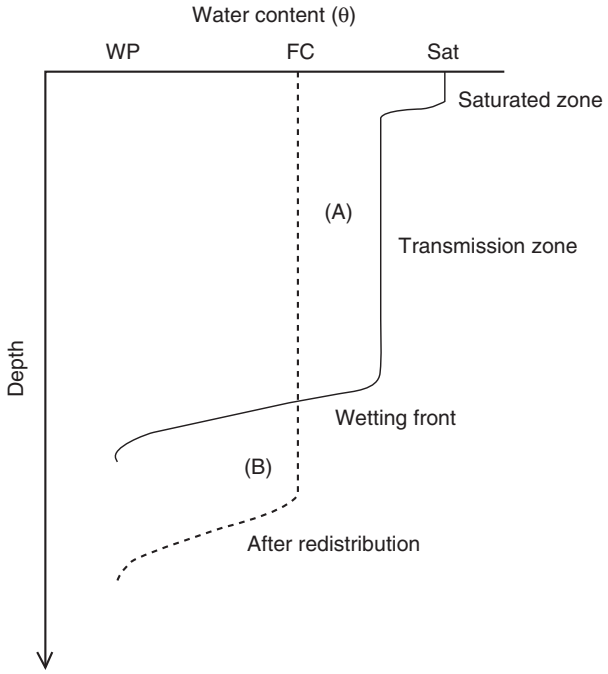


Figure 11 Vertical water infiltration in a soil profile, where Sat is the water content at saturation, FC is the field capacity of the soil, and WP is the wilting point. Reproduced from Minasny, B., George, B.H., 1999. The measurement of soil hydraulic properties in the field. In: Cattle, S. R., George, B.H. (Eds.), Describing, Analyzing and Managing Our Soil. Sydney, NSW: University of Sydney Publishing, pp. 185–204.

This movement of water through the soil is controlled by its hydraulic conductivity (K) and the assessment of the saturated hydraulic conductivity is given in McKenzie and Cresswell (2002).

The hydraulic conductivity of the soil follows Darcy's law, being

$$\frac{Q}{A} = -K\frac{\Delta h_t}{L} \quad [10]$$

where Q is the volumetric flow rate ($m^3\ s^{-1}$), A an area (m^2), K is soil hydraulic conductivity ($m\ s^{-1}$), h_t is the change in hydraulic head or total potential (m) of both matric and gravimetric and L is the flow path length (m). The saturated hydraulic conductivity determines the suitability of a soil for various uses as summarized in Table 4.

For all the soil profiles except Callandoon (Figure 10), the hydraulic conductivity is rapid or greater, and therefore is not limiting in water infiltration. Although the K_s for Callandoon is $<400\ mm\ d^{-1}$ at the surface, resulting in this soil being classed as slow to moderate (Table 4), when this soil dries it forms significant cracks which then allow the water to enter the profile and then infiltrate laterally into the soil. This process is desirable in heavy clay soils with small K_s, especially when irrigation is to be used, and is known as 'wetting from the bottom up.'

The decrease in the K_s for Nowley is due to the significant change in texture. The extremely high K_s for the Pilliga soil (Figure 12) throughout the profile means that is it prone to loss of water through deep drainage and this combined with the small water holding capacity this soil would not be suitable for crop production.

Maintaining a surface condition of the soil that does not impede infiltration is essential to avoid surface runoff (Table 4). The buildup of hydrophobic organic matter, such as waxes, at the soil surface can induce soil water repellency which can reduce water infiltration by an order of magnitude. Generally, severe water repellency is uncommon so it is not a widely spread issue. The subsurface flow of water from higher areas to the base of slopes will contribute to seepage. If the K_s is too large this will enable water to flow below the root zone before it is used by the plant and will contribute to deep drainage, which is a loss of valuable water from the system and

Table 4 Interpretation of saturated hydraulic conductivity in relation to drainage, runoff, and equivalent rainfall intensity

Drainage class	*Interpretation*	*Hydraulic conductivity (mm d^{-1})*	*Type of rainfall*
Extremely slow	Liable to waterlog; land restricted to shallow rooting plants	<8.5	Fine mist to drizzle
Very slow		8.5–30	
Slow	Poor infiltration may lead to overland flow and erosion on slopes	30–120	Slight to moderate rainfall
Moderate		120–480	
Moderate	No problems except on very steep slopes where erosion could occur	480–1500	Downpour to violent rainfall
Moderately rapid		1500–3000	
Rapid	No problems except on very steep slopes where erosion can occur	3000–6000	Violent rainfall
Very rapid		>6000	Extreme rainfall

Source: Modified from Hazelton, P., Murphy, B., 2007. Interpreting Soil Test Results. What Do All The Numbers Mean? Collingwood, VIC: CSIRO Publishing, with permission from CISRO.

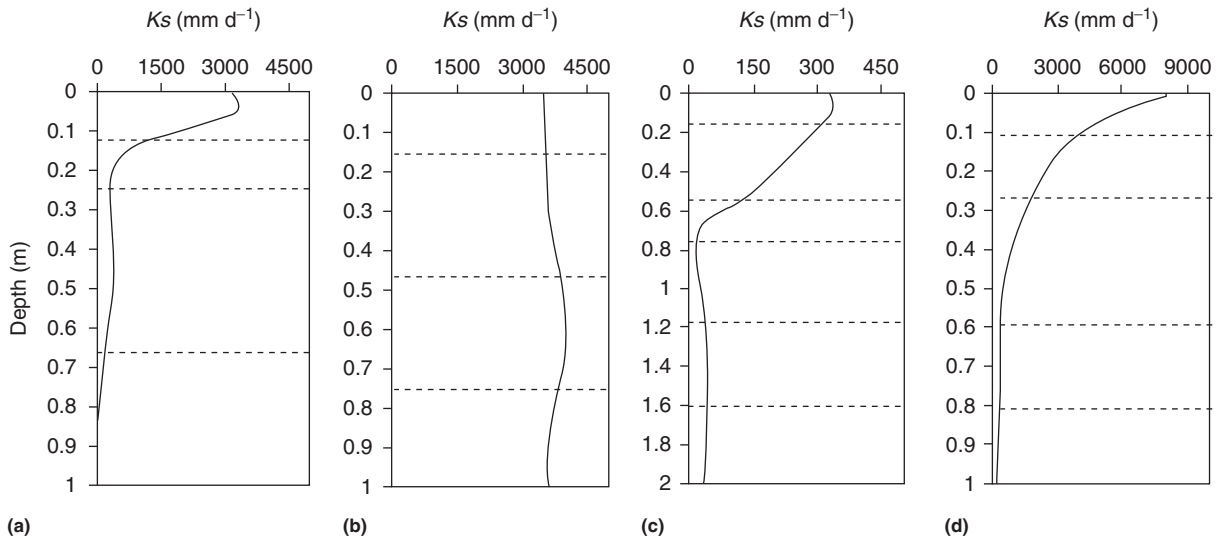


Figure 12 The saturated hydraulic conductivity for the soil profiles. From (a) Nowley, (b) Pilliga, (c) Callandoon, and (d) Toowoomba.

also has the potential to carry unwanted nutrients and other contaminants into the underlying ground waters.

A final account of water is when the area is considered as a discrete unit or catchment. In this case the hydraulic processes are accounted for using the water balance equation as follows:

$$P + I - R = ET + D + \Delta S \qquad [13]$$

The evapotranspiration from the soil–plant system is measured as ET and the responding change in the soil water storage is given as ΔS. The amount of water supplied through precipitation P and irrigation I, as well as, lost through runoff R and drainage D are also accounted for and all these parameters are measured in mm. When ET exceeds P for a period there is a loss of stored water ΔS and a soil water deficit develops. As described in Section Soil Water Storage, this comes from the plant available water and is dependent on the AWC and the rooting depth of the crop being grown.

Soil Strength and the Nonlimiting Water Range

The performance of plants is affected by other soil properties besides the amount of extractable water defined by the available water content (AWC). The ability of roots to enter and explore the soil is affected by the soil's strength. The soil strength is the resistance of the soil to deformation when exposed to shear forces. The shear strength of the soil is affected by the bulk density and its water content. This relationship is demonstrated in Figure 13 and it can be seen that an increase in clay content translates to an increase in the soil resistance, whereas an increase in water content decreases the soil resistance. In the field the soil strength is measured by determining the amount of resisting force when the soil is penetrated using a penetrometer. At FC the soil strength should be <2 MPa to enable root penetration and should not exceed 3 MPa at PWP. If the water content is not known a rule of thumb is that the soil strength should not exceed 2.4 MPa.

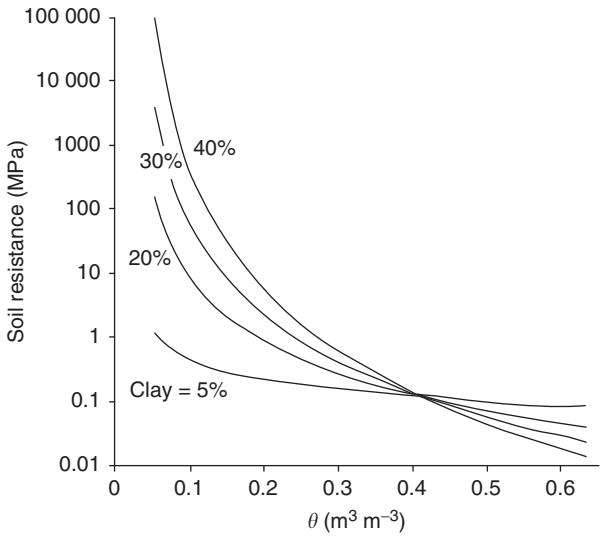


Figure 13 Changes in soil resistance with clay content and moisture content.

For most soil profiles it is expected that the penetration resistance will increase with depth and is affected by the changes in the soil texture, bulk density, and moisture content at the time of sampling. The penetration resistance for the soil profiles in Figure 14 was assessed using the dynamic penetrometer and it can be seen that both Nowley and the Toowoomba soil has a penetration resistance at depth which far exceeds the critical limit commended for plant root development. The dimensions of the cone tip of the penetrometer and its rigidity means that the penetrometer may be forcing its way through the peds in the soil, whereas roots are able to explore the tortuous cracks and pores. The natural planes of weakness resulting in cracks between the peds in the Nowley soil will provide for root development along the surfaces of the peds, and the fine peds developed in the Toowoomba profile will also enable root development (Figure 1). The penetration

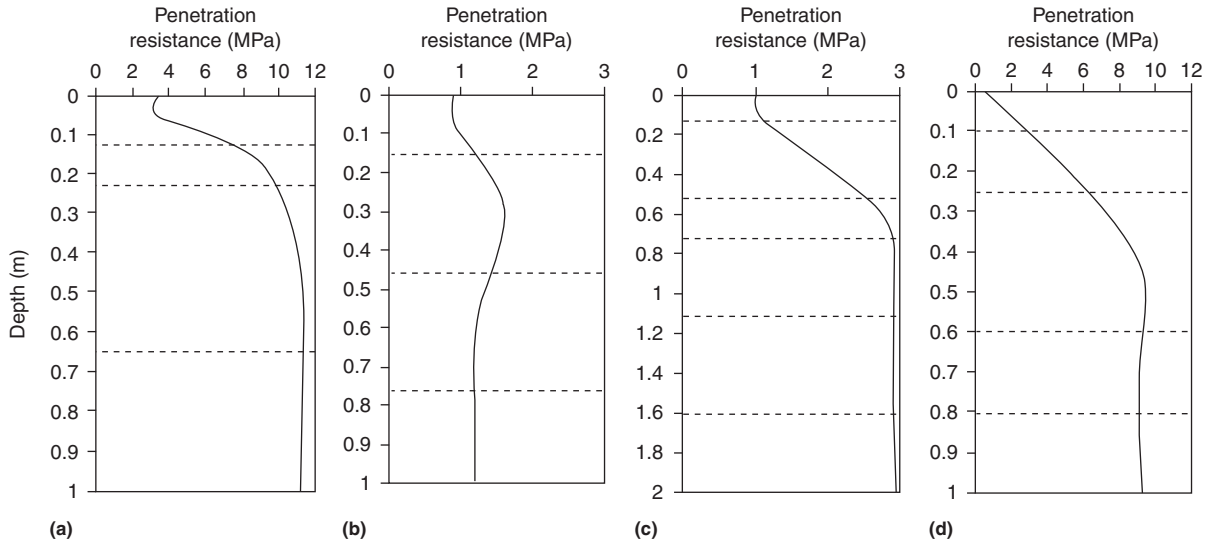


Figure 14 Changes in penetration resistance with depth measured using a dynamic penetrometer for the soil profiles at (a) Nowley, (b) Pilliga, (c) Callandoon, and (d) Toowoomba.

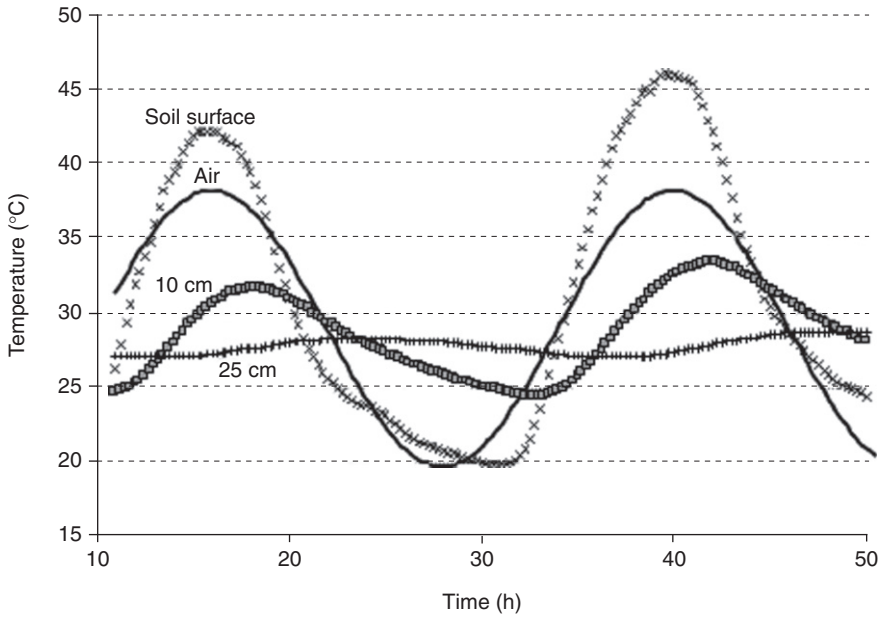


Figure 15 The change in soil temperature from the surface to a depth of 25 cm over a period of 40 h.

resistance for the Pilliga and Callandoon is not as limiting and the uniformly sandy texture in the Pilliga profile is probably responsible for little variation in strength with depth.

Soil Temperature

The main source of energy input to increase the soil temperature is solar radiation. The color of the soil surface, the amount of vegetation, and the slope of the land in relation to the sun all affect the soil temperature changes. The amount of heat a soil can absorb is defined as its thermal capacity and the transfer of the heat through the soil is controlled by its thermal conductance. These two properties moderate how the temperature of the soil varies with depth. This variation is greatest at the soil surface; with depth the variation in soil temperature decreases (Figure 15). It can also be seen that the change in soil temperature with depth over 24 h shows a lag with depth primarily due to the soil's thermal conductivity.

During the day dark colored soil reflects less radiation than light colored soil, but at night dark colored soil will radiate energy faster. The lack of vegetation on the soil surface will not protect the soil surface from solar radiation or insulate the soil from losing heat at night. An increase in moisture content will

also enable the soil to absorb more heat and this is because water has a higher heat capacity. This combination of water content and soil temperature will affect the germination of plants and the development and efficiency of soil roots.

Applying mulch to the soil surface is a process of spreading dead plant material which will reduce the temperature extremes and reduces evaporation at the soil surface. This is because mulch has a lower thermal conductivity, caused by the interlocking air spaces around the mulch material. The mulch will also protect the soil surface from the forces of water during rainfall minimizing the potential disruption of soil aggregates that could block soil pores. The mulch will also minimize the evaporation of water from the soil surface.

Soil Aeration

Soil aeration is critical for optimal functioning of the soil and it is generally governed by three factors: (1) soil porosity, (2) soil water content, and (3) the oxygen demand by soil organisms including microorganisms and plant roots. The lack of O_2 becomes a serious problem when its concentration falls below $0.1\,l\,l^{-1}$, which usually occurs at air-filled porosity $<10\%$. The availability of oxygen in the soil affects the soil redox potential, which in turn affects the forms of compounds of several important elements (e.g., N, S, and Fe) in the soil solution. Consequently, oxygen concentration has influence on the soil chemistry and its pedogenesis. Soils that develop a deep red color in the profile are said to have developed under well-drained conditions, whereas soils that are less well drained develop a yellow to brown color. In a normal toposequence soil at the top of the hill is usually red in color and as you move down the toposequence soil will change through brown into yellow in the lower slopes. At the bottom of the slopes where water accumulates the soil may experience long periods of waterlogging and are usually gray to black in color. These waterlogged soils may show bright yellow or orange stains along pores reflecting that the oxygen levels are fluctuating in the pore phase. In extreme cases, soils may become permanently waterlogged, which is typical in wetlands.

The availability of O_2 regulates the oxidation–reduction states of many plant nutrients. The oxidation–reduction reactions involve a transfer of electron between two species; the species undergoing reduction accepts an electron and the oxidizing species loses an electron. Redox potential (E_h), which is a measure of electrochemical potential or electron availability, is commonly used to predict chemical compounds or processes that regulate nutrient or metal availability in soils. Soil E_h values are generally between -1 and $+1$ V, with values decreasing with decreasing O_2 availability. The common oxidants in soils are O_2, NO_3^-, Mn^{4+} (Mn^{3+}), Fe^{3+}, SO_4^{2-}, and CO_2, whereas the reductants are various organic substrates and reduced forms of inorganic compounds (e.g. H_2O, N_2, Mn^{2+}, Fe^{2+}, H_2S, and CH_4).

In addition to the adverse effects on plant growth and microbial activity, prolonged anaerobic conditions affect the availability, transformation, and degradation of environmentally relevant organic and inorganic compounds.

Clay Minerals and Cation Exchange Capacity

The clay minerals can be broadly grouped into two categories: (1) phyllosilicates (layered aluminosilicates) and (2) nonphyllosilicates; both groups of minerals carry permanent negative or variable charge. Permanent charge in the phyllosilicates originates from the isomorphous substitution in their structure (mainly 2:1 layer minerals). For example, the substitution of Al^{3+} for Si^{4+} in the tetrahedral sheet or the isomorphous substitution of Mg^{2+} for Al^{3+} in the octahedral sheet will result in a net negative charge in the structure. Table 5 lists the phyllosilicates and associated permanent charge with each of the mineral groups. There is a wide range for the CEC values for each clay mineral or mineral group because of the inherent range in the isomorphous substitution, and other crystallographic and chemical properties of the minerals. The classification of the 2:1 phyllosilicates in Table 5 is based on the layer charge per formula unit (i.e., $O_{10}(OH)_2$); this layer charge determines the edaphic soil properties such as CEC, water retention, and transmission.

The variable or pH-dependent charge are primarily associated with hydroxyl groups of phyllosilicates, sesquioxides, allophone–imogolite, and humus; these charges are dependent on the pH and ionic strength of soil solution. Unlike the permanent charge in the clay minerals which is always negative, the variable charge can be negative, zero, or positive depending mainly on the soil pH (Figure 16). There is a characteristic pH for each mineral or humus compound at which the net charge is zero, i.e., positive and negative charges are equal, which is called as the point of zero charge (PZC) (Table 6). Variable charge minerals (and humus) will carry a net negative charge at pH values greater than its PZC value, and a net positive charge at pH values lower than its PZC value. For a soil containing a mixture of variable charge minerals, the PZC value of the soil

Table 5 The layer charge, cation exchange capacity, and specific surface area of phyllosilicates found in soils

Clay mineral/group	*Layer charge (mol per formula unit)*	*Cation exchange capacity ($mmol_c\,kg^{-1}$)*	*Specific surface area ($m^2\,g^{-1}$)*
Kaolinite	~0	30–100	6–54
Illite (clay mica)	0.75–0.90	100–400	30–120
Vermiculite	0.6–0.9	1200–2070	300–500
Smectite	0.2–0.6	800–1350	700–800
Chlorite	Variable	100–400	10–50
Palygorskite–sepiolite	Variable	50–450	800–900
Allophane–imogolite	Variable	100–400	400–1000
Zeolites	Variable	2200–4600	Variable > 1000

Note: In the case of illite, smectite, vermiculite, and chlorite, $O_{10}(OH)_2$ is considered as the formula unit.

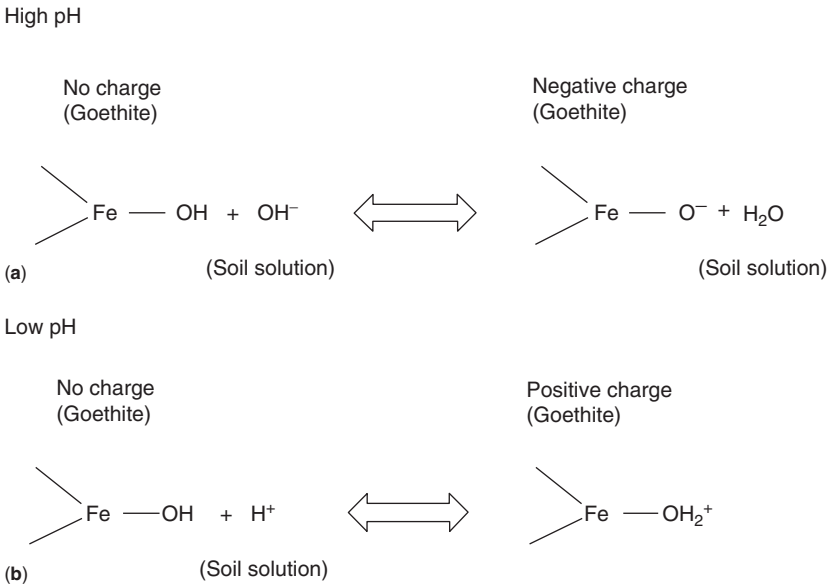


Figure 16 The development of negative and positive charges on the surface of a variable charge mineral, goethite, in response to varying solution pH.

Table 6 Point of zero charge (PZC) values for common soil minerals

Mineral	*PZC*
Kaolinite	4.0–5.0
Goethite, α-FeOOH	7.0–9.0
Hematite, α-Fe_2O_3	8.0–8.5
Gibbsite, α-$Al(OH)_3$	8.0–9.2
Boehmite, α-AlOOH	9.3–10.4
Quartz, SiO_2	2.0–3.0
Manganite, α-MnOOH	~1.8
Birnessite, α-MnO_2	1.5–2.5
Vernadite, δ-MnO_2	~1.5
Calcite, $CaCO_3$	8.0–9.5
Allophane	5.5–6.9

Table 7 Jackson's weathering sequence for minerals in the <5 μm fraction of soils

Weathering stage	*Clay fraction mineralogy*	*Extent of weathering*
1	Halite, gypsum	Less weathered or younger soils
2	Calcite, dolomite	
3	Olivine, pyroxene, amphibole	
4	Biotite, chlorite	
5	Feldspar (plagioclase, orthoclase)	
6	Quartz	
7	Muscovite, illite	Intermediate weathering
8	Vermiculite	
9	Smectite	
10	Kaolinite	Highly weathered soils
11	Aluminum hydroxide (gibbsite)	
12	Fe oxides – goethite, hematite	
13	Ti oxides – rutile, anatase	

Source: Reproduced from Jackson, M.L., 1964. Chemical composition of soils. In: Bear, F.E. (Ed.), Chemistry of the Soil, second ed. New York, NY: Reinhold, pp. 71–141.

will depend on the proportion of each of the variable charge component and the interactions among different components.

The negative charge of the clay minerals is an important soil characteristic for retaining essential nutrient cations (e.g., Ca^{2+}, Mg^{2+}, and K^{+}) and in providing buffering capacity to soils. Owing to their small sizes, soil clay minerals have very large specific surface area, which along with surface charge plays an important role in chemical reactions involving nutrient elements and other ions and molecules in soils. Soil clay minerals are also equally important for many physical properties of soil, such as soil moisture retention, solute and water transmission, and soil consistency.

Similar to Goldich's stability series for primary minerals, a weathering sequence has been proposed for the minerals in <5 μm fraction (Table 7). Highly soluble minerals, such as halite, gypsum, and calcite, are least stable and often exist in young soils or soils from arid environments where minimum leaching occurs. Among the phyllosilicates, 2:1 minerals are common in soils at early to intermediate stages of weathering. In highly weathered soils kaolinite, Fe and Al oxides are the most common clay minerals. Among the minerals not considered in Table 9, allophone and imogolite occur in volcanic ash derived soils and Spodsols (Soil Survey Staff, 2010); and palygorskite–sepiolite are common in dry regions in soils formed from sedimentary rocks or lacustrine deposits.

The clay mineral suites of the four soil profiles indicate intermediate to extreme weathering, according to the sequence presented in Table 7. Smectite dominates the clay fraction of Nowley and Callandoon profiles, with small amounts of kaolinite and illite being present in both soils. The clay fraction of Nowley soil also contains hematite, quartz, anatase, and traces of goethite throughout the profile. In contrast with the other two soils, kaolinite is the predominant phyllosilicate in the Pilliga and Toowoomba soils. Hematite is present in a significant amount in the clay fraction of the Toowoomba soil (also indicated by the red color of the soil, Figure 1), along with trace amounts of gibbsite and quartz in the clay fraction. The Pilliga soil also contains small amounts of quartz, anatase, goethite, and hematite in the clay fraction. The clay mineralogy data suggest the highly weathered characteristics of the Toowoomba soil; this is also evident to some extent in the Pilliga soil as well. The alluvially derived Nowley and Callandoon profiles have mixed mineralogy with a dominance of smectite.

Soil Organic Matter

In addition to the inorganic fraction, organic matter is an important constituent of the soil. Typically, surface soil contains between 0.5% and 5.0% organic matter depending on the land use and the climatic conditions. In addition to the climate, other soil-forming factors, i.e., parent material, relief, organism (vegetation), and time, also affect the SOM. Fine-textured soils generally have greater organic matter content than the coarse-textured soils due to: (1) better conditions for plant growth and (2) increased protection of SOM.

SOM consists of a range of C-containing substances that include living (i.e., roots, animals, and microorganisms) and nonliving fractions (freshly to partially decomposed residues of living fraction and well decomposed organic matter – humus). The nonliving fraction of SOM can be broadly classified into three categories: (1) nonhumic compounds ($\sim$20–30% of SOM), (2) humic compounds ($\sim$60–80% of SOM), and (3) black carbon or char (highly variable). The chemical structure and composition of nonhumic substances are well known, and these compounds are cellulose, hemicellulose, proteins, lignins, sugars, starches, polyphenols, waxes, and fats. Humic compounds, however, are dark colored polymeric molecules often with very complex and large structures. Char, or black carbon, in the soil is regarded as a chemically and biologically stable C pool, which can persist for a long period of time (millennia) (Schmidt and Noack, 2000). Limited data suggest that char constitutes a significant fraction of the soil organic C: for example, up to 45% and 60% of the soil organic C pool has been attributed to char C in German and Canadian Chernozems, up to 35% in Australian soils, and up to 18% in native prairie soils in the United States (Baldock and Smernick, 2002; and references there in).

The chemical composition of SOM comprises C (52–58%), O (34–39%), H (3.3–4.8%), and N (3.7–4.1%) (Sparks, 2003). Because C is the major constituent of SOM, traditionally SOM is estimated based on the soil C content, with the assumption that SOM contains 58% C.

There are several direct and indirect beneficial effects of SOM on plant growth. Certain N and P organic compounds can be directly absorbed by higher plants. Additionally, SOM has multiple indirect benefits in terms of chemical, physical, and biological soil properties. The decomposition and mineralization of SOM releases plant available forms of N, P, S, and micronutrients. The specific surface area of SOM is very high and there are a variety of functional groups on its surface. The presence of different types of functional groups (i.e., acidic, basic, and neutral) and the amphoteric nature of the functional groups, SOM provides both cation and anion exchange capacities to the soil. The negative charge in soils is predominantly provided by carboxylic and phenolic groups of SOM accounts for between 20% and 96% of the CEC of surface soils; with the contribution being particularly high ($>$65%) in sandy and highly weathered soils (Sparks, 2003). Thus, SOM serves as a major nutrient reservoir for both the organic and available forms of nutrients. Adsorption of many organic compounds and pesticides largely occur on the SOM and this process is important in preventing the leaching of chemicals into ground water.

Organic matter has a multitude of beneficial effects on soil physical properties including soil aggregation, increased aggregate stability, improved soil infiltration, increased water retention and improved plasticity. The dark color of humic compounds facilitates increased adsorption of solar radiation and increased soil temperature, which is vital for microbiological activity, seed germination and plant growth, particularly in the colder regions. Organic matter is the main carbon source for heterotrophic and larger organisms (e.g., earthworms) in soils.

The global soil C pool (2400 Pg or 10^{15} g) is the largest terrestrial C compared to the C present in vegetation (550 Pg or 10^{15} g) and atmosphere (760 Pg or 10^{15} g) (Batjes, 1996). In recent years, the role of SOM in the global carbon cycle has been highlighted and it has been suggested to be one of the main drivers of increasing CO_2 in the atmosphere and global warming. Human induced perturbations, such as deforestation, fires, artificial drainage, and tillage, have contributed to the increased oxidation of SOM. There is a substantial effort to reverse this process by increasing the soil C pool using a variety of approaches, including increased stabilization of soil carbon, increased addition of SOM, minimizing the mineralization of soil carbon and by adding stable form of carbon, such as biochar, to the soil.

The soil organic content in the surface horizon of all the four soil profiles is much greater than the subsoil horizons. There is an abrupt decline in the organic carbon content of the sandy soil (Pilliga profile), whereas the organic carbon content decreased gradually in the other three soil profiles. Additionally, the three profiles located in the native vegetation contain much higher organic carbon, particularly in the top horizon than the profile from a cultivated field (Callandoon profile).

Cation Exchange Capacity and Exchangeable Cations of the Four Case Study Profiles

The four soils differ considerably in their ability to retain cations, i.e., CEC (Table 8; Figure 17), which can be explained

Table 8 Some chemical properties of the four case study soil profiles

Pilliga profile										
Horizon	*pH (1:5 H_2O)*	*EC 1:5 (dS m^{-1})*	*Organic C (%)*	*Total N (%)*	*Cation exchange properties ($mmol_c\ kg^{-1}$)*					
					CEC	*Ca*	*Mg*	*Na*	*K*	*Al*
1	5.31	0.06	7.63	0.35	33.8	10.0	12.0	0.2	2.9	8.7
2	6.05	0.01	0.85	0.05	18.6	1.0	13.0	0.2	1.8	2.6
3	6.08	0.01	0.69	0.04	16.9	1.0	12.0	0.2	1.6	2.1
4	6.23	0.01	0.49	0.04	18.2	1.0	12.0	0.3	1.5	1.4
Nowley profile										
Horizon	*pH (1:5 H_2O)*	*EC 1:5 (dS m^{-1})*	*Organic C (%)*	*Total N (%)*	*Cation exchange properties ($mmol_c\ kg^{-1}$)*					
					CEC	*Ca*	*Mg*	*Na*	*K*	
1	6.10	0.18	3.88	0.15	190	110	66	0.6	16	
2	7.00	0.12	3.40	0.12	181	110	58	0.7	10	
3	8.70	0.16	0.82	0.04	322	190	130	3.8	4	
4	8.90	0.18	0.65	0.04	385	220	160	6.5	4	
Callandoon profile										
Horizon	*pH (1:5 H_2O)*	*EC 1:5 (dS m^{-1})*	*Organic C (%)*	*Total N (%)*	*Cation exchange properties ($mmol_c\ kg^{-1}$)*					
					CEC	*Ca*	*Mg*	*Na*	*K*	
1	8.26	0.07	1.54	0.12	265	160	91	8.3	11	
2	7.93	0.63	0.98	0.07	305	160	99	48	4.0	
3	8.08	0.96	0.93	0.05	330	160	110	61	3.9	
4	8.14	1.77	0.32	0.03	369	210	99	61	5.5	
5	8.01	0.88	0.11	0.02	269	110	91	65	7.5	
6	7.39	0.87	0.08	0.02	243	95	81	65	7.3	
Toowoomba profile										
Horizon	*pH (1:5 H_2O)*	*EC 1:5 (dS m^{-1})*	*Organic C (%)*	*Total N (%)*	*Cation exchange properties ($mmol_c\ kg^{-1}$)*					
					CEC	*Ca*	*Mg*	*Na*	*K*	
1	5.87	0.42	6.24	0.56	195	130	40	0.4	28	
2	6.26	0.21	5.24	0.40	170	120	32	0.5	21	
3	6.44	0.12	2.14	0.17	105	75	16	0.4	14	
4	6.78	0.44	0.50	0.05	75	55	20	1.1	2.0	
5	6.48	0.45	0.27	0.03	74	51	23	0.9	2.0	

Abbreviation: CEC, cation exchange capacity.

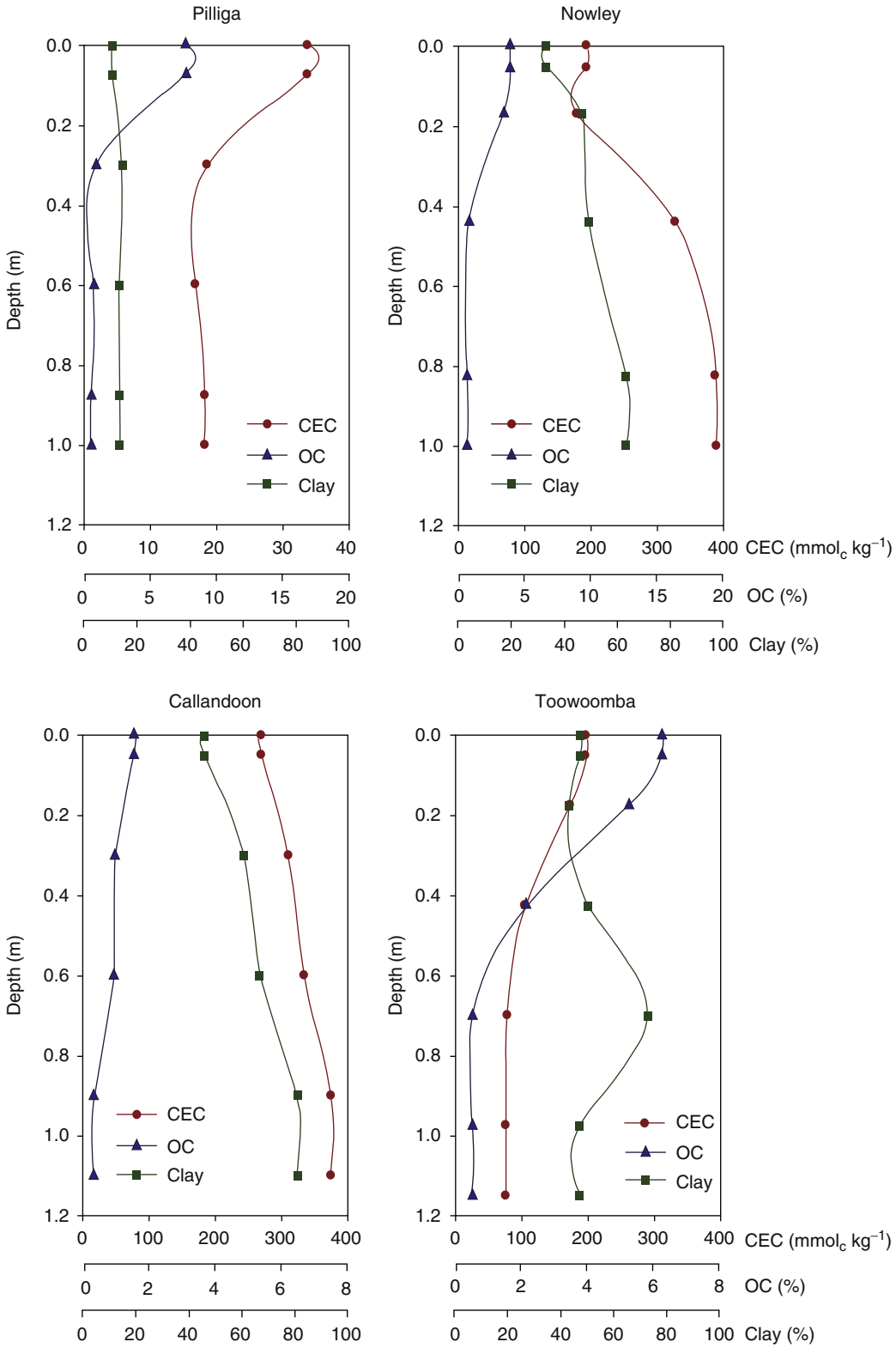


Figure 17 The cation exchange capacity (CEC), organic carbon (OC), and clay contents of the four case study profiles.

on the basis of their organic carbon and clay contents, and the clay mineral composition. The main differences are:

1. Consistently higher CEC for the Callandoon and Nowley soils that is in accordance with their high clay contents and smectite-dominated clay mineral composition.
2. Very low CEC values for the Pilliga profile, which has approximately 10% clay that is comprised predominantly of kaolinite; the contribution of organic carbon to the CEC of the surface soil is obvious with nearly twice the CEC as compared to the subsoil horizons (Table 8).
3. The Toowoomba profile has intermediate CEC values, with the values decreasing with soil depth, which is related to the decreased organic carbon content in the lower parts of the soil profile. Despite the presence of kaolinite and sesquioxides in the clay fraction, the CEC values are reasonable, with a significant contribution from the acidic functional groups of organic carbon in the soil.

Soil Biota

In addition to inorganic and organic soil components, soils are teeming with life that includes both fauna and flora. Based on their size, soil fauna has been classified into: (1) macrofauna (e.g., earthworms, beetles, termites, and ants), (2) mesofauna (e.g., springtales and mites) and (3) microfauna (e.g., nematodes and protozoa). Soil flora includes plant roots and microflora, such as bacteria, fungi, algae, actinomycetes, and very fine root hairs. Soil organisms perform a variety of functions in soils and the activities of flora and fauna in soils are ultimately related with plants being the primary producers of organic molecules and living tissues. (Brady and Weil, 2008). Soil fauna or primary consumers initiate the biochemical decay and mechanical breakdown of plant residues that is followed by complete decomposition by heterotrophic and saprophytic microorganisms. During the mineralization of SOM available forms of nutrients, most notably N, P, and S, are released. In addition to the inorganic transformations of N, S, and P, the availabilities of Fe and Mn in soils are largely controlled by the microbial-driven processes.

Many macro- and mesofauna (e.g., termites, ants, and beetles) redistribute soil solids or make major alterations to it and modulate soil structure in the bioturbation process. Earthworms are well known for their capacity to ingest large masses of soil, to create macropores and to enhance the aggregate stability of soils. The production of organic compounds by soil fauna and flora promotes soil aggregation, enhances aggregate stability, and increases water infiltration.

In agricultural soils, two symbiotic associations, those of legumes with rhizobia and plants with mycorrhizae, are extremely important in maintaining soil fertility. The fixation of atmospheric nitrogen, by the association of bacteria from *Rhizobium* and *Bradyrhizobium* genera with legume roots, represents the major source of N input in many agricultural soils. In the legume/rhizobia association, bacteria use C and nutrients in return for fixed N. The mycorrhizal association is a symbiosis process between the mycorrhizal fungus with a host plant, and in the process fungus derives carbon from the host plant and the plant receives increased inorganic nutrients (particularly P) from the fungus.

Because of their sensitivity to the changes in soil environmental conditions and their role in many key soil processes, microbial indicators (e.g., such as microbial biomass, diversity, and activity) are frequently used as soil quality indicators (Dilly *et al.*, 2006).

pH

Soil pH is a very important property from a plant growth standpoint. It is a measure of hydrogen ion activity in soil solution. Measured in the field or in the laboratory using an electrode or some form of indicator solution or test strip, soil pH is broadly linked to the pH of the parent material, but is often affected by pedological processes such as the leaching of solutes. In soil profiles of humid environments with parent materials containing appreciable concentrations of bases, it is common to observe increasing values of soil pH with depth in the profile due to the leaching of soluble bases. The Nowley profile is a good example of this scenario; the pH values of the four horizons shown, from top to bottom, are 6.1, 7.0, 8.7, and 8.9 (Table 8). The white patches evident in the bottom horizon of this soil are small areas of calcium carbonate or lime, which is a sparingly soluble salt that precipitates in soil, and which confers an alkaline pH to soil. In the Nowley profile, the local rainfall regime has resulted in lime being precipitated at a depth of 70 cm, in a zone of base accumulation.

The importance of soil pH to plant roots is twofold; firstly, there are direct effects, whereby at low soil pH values H^+ and Al^{3+} are common ions in the soil solution and are toxic to some plant roots, and secondly there are indirect effects, where at low or high soil pH values various plant micronutrients become unavailable and other elements (e.g., Al^{3+}) are converted into forms toxic to plant roots. Furthermore, the activity of microbial communities and a range of chemical reactions in soil are also affected by fluctuating pH.

Electrical Conductivity

Soil electrical conductivity (EC) is a critical edaphic property for plant growth. EC is measured in the field or laboratory using an electrode or electromagnetic sensing device, and is greater in soil that is moist, dominated by clay minerals and containing large amounts of soluble salts. Salinity of a soil profile is usually estimated through the measurement of EC of solution extracted from soil–water mixture or soil paste. The presence of soluble salts in a soil is partly linked to the soil's parent material, but is more strongly associated with the climatic regime of the area and in some cases the topographical location of the soil. The application of poor quality water or restricted drainage can also cause soil salinization, which is somewhat evident in the Callandoon profile with EC increasing in the subsoil (Table 8). The importance of salinity to plants is that large concentrations of salts raise the osmotic potential of the soil water, making it more difficult for plant roots to extract water, even if there is much water present in the soil. At very high concentrations, certain cationic (e.g., Na^+) and anionic (e.g., Cl^-) species may also directly interfere with cellular processes in plant roots. The activity of microbial communities and a range of chemical reactions in soil are also

affected by fluctuating EC. Generally, soils with EC of saturation extract > 4 dS m^{-1} are considered saline; however, sensitive crop plants (e.g., tomato) may be adversely affected at EC > 2 dS m^{-1}.

Plant Nutrients

The most important agricultural plant nutrients, nitrogen (N), phosphorus (P), and potassium (K), tend to be present in greatest concentrations in the topsoil horizons. This is due to the cycling of these elements through the rhizosphere, the incorporation of these elements into various organic compounds, and in agricultural soils, the application of fertilizers. Soil parent material is an important determinant of P and K status of the soil, but climate (rainfall) and organisms (N-fixing bacteria) are more important soil-forming factors governing the presence of topsoil N. Some exchangeable cations such as Ca^{2+} and Mg^{2+} are also important plant nutrients. The concentrations of these cations, which are exchanged onto negatively charged surfaces of clay minerals, depend partly on the soil parent material and partly on climatic and topographic processes. Exchangeable cation concentrations are not necessarily greatest in the topsoil horizons of soil profiles, and are sometimes used as diagnostic criteria for soil classification purposes.

Seventeen elements (also called nutrients) that are considered to be essential for crop plants along with their ionic forms utilized by plants are listed in Table 9. Plants take up nutrients in their available forms from soil solution through mass flow or diffusion processes. Plant nutrients in soils exist in various pools including soil solution, exchangeable, specifically adsorbed, mineral structures, chemical compounds and organic matter. At a given time only a small proportion of the total amount of the nutrient in soil is present in the plant available form and a dynamic equilibrium exists between various nutrient pools including the solution form.

Table 9 Essential plant nutrients and their plant available forms

Basic or structural nutrients *Name*	*Symbol*	*Plant available form*
Carbon	C	CO_2 and H_2CO_3
Hydrogen	H	H^+, OH^- and H_2O
Oxygen	O	CO_2
Primary or major nutrients		
Nitrogen	N	NO_3^- and NH_4^+
Phosphorus	P	HPO_4^{2-} and $H_2PO_4^-$
Potassium	K	K^+
Secondary nutrients		
Calcium	Ca	Ca^{2+}
Magnesium	Mg	Mg^{2+}
Sulfur	S	SO_4^{2-}
Micronutrients		
Boron	B	H_3BO_3 and $H_2BO_3^-$
Copper	Cu	Cu^{2+}
Chlorine	Cl	Cl^-
Iron	Fe	Fe^{2+} and Fe^{3+}
Manganese	Mn	Mn^{2+}
Molybdenum	Mo	MoO_4^{2-}
Nickel	Ni	Ni^{2+}
Zinc	Zn	Zn^{2+}

In soils, N mostly occurs in the organic form, which must be mineralized (conversion of organic nitrogen into inorganic form is called as mineralization) before plants can take it up. For all N-fertilizers, the applied and mineralized N ends up in the nitrate (NO_3^-) form, which is very mobile in most soils due to the predominance of the negative charge on soil colloids. Nitrate leaching is a common problem in many agricultural soils and particularly in light textured soils. Highly weathered soils are known to retain NO_3^-ions due to the presence of positive charge on Fe (and Al) oxides at acidic pH of these soils. Soils from the temperate regions, with the dominance of 2:1 phyllosilicates (e.g., smectite and vermiculite), can retain significant amount of ammonium (NH_4^+) ions in the interlayer space of these minerals. The losses of N in gaseous forms are also common under certain conditions, for example, nitric oxide (NO), nitrous oxide (N_2O), and dinitrogen (N_2) in anaerobic soils and ammonia (NH_3) in alkaline soils. Although a significant amount of fertilizer N is applied in most cropping systems, the fixation of atmospheric nitrogen by legume plants still remains the major source of N in many cropping systems throughout the world, particularly in low input agricultural systems.

The availability of P is a common problem in most acidic and alkaline soils due to the precipitation of insoluble compounds (Fe and Al-phosphates in acid soils and Ca phosphates in alkaline soils) or specific adsorption of phosphate ions onto crystalline and amorphous phases of Fe and Al oxides. Unlike nitrate, the available forms of P are immobile due to their chemical interactions with a variety of soil colloids.

Most of the K in soils is present in K-containing primary minerals, i.e., micas and feldspars. Depending on the extent of soil weathering, varying amounts of K minerals are present in different soil types. Temperate soils often contain abundant K-rich minerals and thus may require little or no application of K fertilizers, however, many sandy soils require the application K fertilizers for optimal plant growth. Soils at intermediate to advanced stages of weathering often contain illite (clay-size mica), which can potentially supply K. In many soils that contain clay minerals formed from the weathering of mica, such as vermiculite, the fixation of fertilizer applied K could become a problem in such soils that may be overcome by increasing the fertilizer application rates.

Secondary nutrients (Ca, Mg, and S) are usually present in adequate amounts in less weathered to intermediate weathered soils. Soil minerals, organic matter, and crop residues are all good source of secondary nutrients in soils. In highly weathered acidic soils, lime that is usually added to raise soil pH supplies Ca. Sulfur is also added as an impurity in low-grade fertilizers and through gypsum ($CaSO_4 \cdot 2H_2O$), which is used as an amendment in sodic soils.

Micronutrients, although required in very small amounts by crop plants, can be deficient in certain soil conditions, such as highly weathered acidic soils, sandy soils, highly alkaline soils, or in soils that are used for intensive farming. The cationic form of micronutrients (e.g., Fe, Zn, Cu, and Mn) usually are deficient in alkaline soil pH conditions and the deficiency of anionic form elements (Mo and B) are common in highly acidic to acidic soil conditions. In addition

to this, the availability of most cationic and anionic micronutrients is affected by their strong adsorption reactions to Fe and Al oxides.

Soil testing is done to evaluate the availability of nutrient elements in agricultural soils and to make fertilizer recommendations for the nutrients. Owing to the complex behavior of nutrients, variable chemical reactions of nutrient ions in different soil types, variable nutrient requirements of field crops, the use of different soil tests, and many other environmental and soil factors, it is not possible to suggest the critical deficiency or sufficiency levels for the nutrient elements that are universally applicable.

Conclusions

Soil is a finite resource that develops over a long time span. Despite the resilience and significant buffering capacity of soils, the increased exploitation of soils for food, fiber, and energy production can cause degradation with time and severely affect their productivity. Wind and water erosion, compaction and crusting, acidification, salinization, and loss of organic matter are the common features of degraded agricultural soils. Considering the complexity of soils, a multidisciplinary approach is required to understand the soil degradation processes. Additionally, spatial and temporal variability must be considered in sampling and modeling the processes and their impacts over geographical scales. There is a need for internationally coordinated efforts for a sustainable use of soils in order to protect them from degradation processes (Blaser, 2006). Future research programs should be based on improved understanding of the degradation processes and mechanisms, reliable and intelligent indicators for measuring and monitoring soil quality, and developing appropriate amelioration techniques and decision-making tools for sustainable use of soils.

See also: Biodiversity and Ecosystem Services in Agroecosystems. Land Use: Catchment Management. Land Use, Land Cover, and Food-Energy-Environment Trade-Off: Key Issues and Insights for Millennium Development Goals. Land Use: Restoration and Rehabilitation. Slum Livestock Agriculture. Soil: Carbon Sequestration in Agricultural Systems. Soil: Conservation Practices. Soil Fertility and Plant Nutrition. Soil Greenhouse Gas Emissions and Their Mitigation. Soil: Nutrient Cycling

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Emerging Plant Diseases

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Glossary

Aggressiveness A comparative measure of the degree of success of a virulent pathogen isolate on a particular host genotype. Aggressiveness is typically measured in terms of reproductive success.

Biotrophic pathogens The fungi, such as rusts and powdery mildews, that depend on healthy, living host tissue for growth and long-term survival. Biotrophs typically have a narrow host range. Biotrophic fungi stand in distinction to necrotrophic fungi that derive nutrition from host cells they have killed. Pathogens that derive their nutrition necrotrophically are often able to survive as saprophytes in the soil or on plant debris in the absence of a living host.

Gene-for-gene or qualitative resistance A resistance that is based on the expression of single genes typically inherited in a simple Mendelian fashion. Gene-for-gene interactions between hosts and pathogens are controlled by pairs of matching genes in hosts (the resistance gene) and pathogens (the avirulence gene) with the occurrence of a resistant reaction being dependent on the presence of both host resistance genes and the corresponding avirulence genes in the pathogen. Such resistance is pathotype specific being effective against some pathotypes and not others. This form of resistance contrasts with quantitative resistance that is typically controlled by several genes and is expressed equally against all pathotypes of a pathogen.

Host jump The range of host species susceptible to infection is broadened as a consequence of novel encounter between a pathogen and previously unexposed host species. Host jumps require no genetic change in either host or pathogen.

Infectivity The ability of the pathogen to cause a susceptible response on a particular host line.

Throughout ecological and evolutionary time, plant diseases have been important in shaping the structure and diversity of individual host species and communities (Burdon *et al.*, 2006). Although famous examples of devastating epidemics and their consequences have come down through time (e.g., the nineteenth century famine in Ireland, instigated by the potato blight fungus), new examples continue to accumulate. Changes in global climatic patterns, major expansion in the range of plant species associated with agricultural production, and greatly increased movement of people and goods between previously ecologically isolated areas, are all generating a complex mix in which different combinations of pathogens and hosts are brought together more frequently. This is leading to a marked increase in epidemics generated either by pre-existing pathogens or by novel pathogens (or pathotypes) that have developed through a variety of means of genetic recombination. This process has become so prevalent and the novel pathogens generated are often so aggressive, that emerging plant diseases now pose one of the greatest threats to the integrity, sustainability, and productivity of many natural and agricultural plant communities (Fisher *et al.*, 2012). However, it is important to recognize that this process is not entirely new. Indeed, the evolutionary history of many fungal groups is littered with evidence of jumps in the host range of individual pathogen species. This is particularly apparent in the rust fungi where many heteroecious rusts alternate between gymnosperm and angiosperm (e.g., *Melampsora pinitorqua* alternating between *Pinus sylvestris* and *Populus tremula*) or angiosperm and angiosperm hosts (e.g., *Puccinia urticae-caricis* alternating between *Urtica dioica* and *Carex* spp.).

What is an emerging disease? Emerging diseases have been defined as "any disease that is currently spreading within host populations." Although evolutionary change in the pathogen is not a necessary prerequisite for the appearance of an emerging disease, the tag 'emerging disease' carries with it the connotation of a change from the current status quo. However, the status quo is not in itself a situation in which disease is nonexistent. Rather in nonagricultural situations, many host–pathogen associations have coevolved over millennia. However, through the interactive effect of within-and-among season climatic variation, and host and pathogen variability, these interactions may display periodic ephemeral increases and decreases in disease occurrence and severity. Similarly, in many agricultural crops, epidemic cycles may occur on a near-annual basis depending on environmental circumstances. Such interactions are not considered here to be examples of emerging diseases – they are fluctuations representative of the 'normal' dynamics of many host–pathogen systems.

In contrast, emerging diseases may arise in a number of ways through:

1. existing well-recognized pathogens 'catching up' with anthropogenically generated changes in the distribution of existing host species, thus appearing in new geographic regions;
2. ecologically based jumps to new, previously unexposed hosts (no previous evolutionary contact);
3. environmental changes leading to increased aggressiveness in the pathogen or susceptibility in the host, or an expansion of the pathogen's range into parts of its host range from which it was previously excluded; or
4. genetic change leading to an alteration in the host range or infectivity of an existing pathogen species (novel pathogen genotype or species).

The nature of the first two of these mechanisms – potentially simple changes in the ecology of individual pathogens – reflect the way in which anthropogenic changes in many parts of the world have greatly increased the opportunity for long-distance dispersal with its attendant range of new opportunities. Before the advent of increasingly rapid and intense global transport, the flora of whole continent was essentially protected from encounters with exotic pathogens by isolation. Elements of the collapse of 'protection through isolation' can be seen in the spread of human diseases like plague in Europe in the fourteenth century and subsequently in the transmission of diseases from America to Europe and from Europe to the Pacific in subsequent centuries. This increased opportunity for pathogens and naive hosts to come into close contact is a common feature underlying the emergence of many animal, plant, and human diseases. Environmental changes leading to altered host–pathogen interactions are also heavily associated with anthropogenic activities ranging from the consequences of changed nutrient deposition from uncontrolled industrial emissions to changes occurring as a consequence of the local and regional effects of global climate change. Finally, changes in the ecology of individual pathogens and their distribution increase the possibility of juxtapositioning of previously separate entities and hence significantly increase opportunities for genetic recombination.

Ecological Changes in Distribution Causing Emerging Diseases

Pathogens 'Catching Up' with Anthropogenic-Generated Changes in the Distribution of Their Hosts

Classic examples of this class of emerging diseases come from agricultural situations where, over the centuries, crop species have been introduced and grown (often over large areas) in regions far from the original center of diversity of the crop and its coevolved pathogens. Over time, selection for traits other than disease resistance, combined with agronomic practices that favor pathogen increase (high nutrition and large, dense, and genetically uniform stands), make the crop particularly vulnerable to attack. Examples of these situations are found in agricultural (e.g., the Irish potato famine of the 1840s driven by the appearance of *Phytophthora infestans* and the first appearance of stripe rust of wheat caused by *Puccinia striiformis* in Australia in 1979), horticultural (e.g., the collapse of the coffee industry in Ceylon in the nineteenth century due to the impact of coffee rust *Hemileia vastatrix*), and forestry (the worldwide spread of *Dothistroma* needle blight on *Pinus radiata*) plantings. However, once host and pathogen have been reunited for some time and breeding efforts have begun to deploy genetic approaches to control, differentiating between subsequent periodic failings of resistance deployment strategies and whether it is appropriate to confer the status of a 'new emerging disease' is questionable. As identified earlier, when a pathogen has been present for some time and causes periodic epidemics, the status of emerging disease should perhaps be restricted to special circumstances where the threat is broad ranging. An appropriate example of the latter is seen in the threat facing global wheat production through the appearance and spread of a novel pathotype [Ug99] of *Puccinia graminis* f.sp. *tritici* from its area of origin (Uganda) through the Rift Valley to the Yemen and into central Asia (Singh *et al.*, 2011). This pathotype (and its descendants) are of particular concern because their unique combination of virulence genes renders more than 90% of the world's wheat cultivars and breeding materials susceptible to attack.

A further situation involving pathogens reconnecting with established host species is seen in invasive plant species and poses the question of whether pathogens native to an invasive host that later catch up with the invader in its new area, should be regarded as new or emerging diseases, and if so, after how long a time of separation? Two scenarios occur under this rubric: (1) the reuniting of pathogen and host occurs as a result of accidental introduction or natural spread of the pathogen or (2) as a consequence of deliberate attempts to control invasive host species that have typically spread as weeds associated with agricultural activities (biological control programs). An example of the accidental reunification of pathogen and host is seen in *Impatiens parviflora* from Central Asia and the Himalayas, which after its escape from botanical gardens in Europe in 1837, gradually became a dominant species of nutrient-rich forests in Europe. Approximately 80 years later, its native rust pathogen, *Puccinia komarovii*, appeared in these populations causing sufficient damage as to affect host demography albeit not host expansion.

Programs to control invasive plant species through the deliberate release of pathogens collected from their native range provide many examples of explosive epidemic increase with significant impacts on the targeted host species, for example, *Maravalia cryptostegiae*, *Uromycladium tepperianum*, *Puccinia chondrillina*, *Colletotrichum gloeosporioides*, and *Entyloma ageratinae* attacking *Cryptostegia grandiflora* (Australia), *Acacia saligna* (South Africa), *Chondrilla juncea* (Australia), *Miconia calvescens* (Tahiti), and *Ageratina riparia* (New Zealand), respectively (Vogler and Lindsay, 2002; Wood and Morris, 2007; Cullen, 2012; Meyer *et al.*, 2008; Barton *et al.*, 2007). However, the patchy track record of biological control programs emphasizes the inherent unpredictability of pathogen–host interactions and the very strong likelihood that far more dispersal events occur than are ultimately successful.

Jumps to New, Previously Unexposed Hosts

Some of the best known and longstanding examples of emerging plant diseases are the ones in which existing pathogens have been transported to an environment from which they were previously excluded (nearly always by distance from source populations) and in that new environment have come in contact with plant species that lack resistance. In this scenario, there is no evidence of evolutionary change in the aggressiveness or infectivity of the pathogen.

In some instances, the new hosts may be close taxonomic relatives of existing host(s) (e.g., *Cryphonectria parasitica* moving from Asian members of the genus *Castanea* to American chestnut *Castanea dentata*), whereas in others, relationships may be somewhat more variable and distant. A particularly good example of this latter situation is currently unfolding in Australia, where, following the initial identification of *Puccinia*

psidii on *Agonis flexuosa* in 2010, the pathogen's Australian host range has broadened to include more than 130 plant species in a diverse range of 33 genera including *Eucalyptus, Callistemon*, and *Melaleuca* of the Myrtaceae (**Table 1**; Carnegie and Lidbetter, 2012). Given that the pathogen's natural host range in South America involves various members of the same family, it would appear that the Australian host range is reflective of old Gondwanan connections between the flora of these two southern continents.

Typically, the establishment of new host–pathogen associations results from accidental or deliberate movement of the pathogen by humans. However, this is not the case always, and the unforeseen consequences of other activities may create bridges allowing the natural spread of pathogens from their endemic home to new areas. Thus, the relatively recent natural migration of *Melampsoridium hiratsukanum* from Far East to Europe and its appearance on gray alder in northern Europe has been attributed to the closing of a natural gap in the distribution of Siberian and European larches (the alternate host) in eastern Europe by foresters over the past few centuries.

Although examples of host jumps are frequently associated with movement of pathogens into new environments, this is not always the case. Indeed, there are many examples in the literature of exotic stands of important forestry species being attacked by pathogens that naturally occur on related native species. Thus, in Brazil, plantations of *Eucalyptus* species have been severely and repeatedly attacked by *Puccinia psidii*, a rust native to South America, where it has evolved with a number of Myrtaceous species including guava. In South Africa, the native species *Syzygium cordatum* is host to a number of canker and dieback pathogens in the Botryosphaeriaceae that are pathogenic on *Eucalyptus* species; while a range of *Mycosphaerella* species unknown on *Eucalyptus* in Australia cause damage to plantations in Vietnam. Similarly, in Europe, extensive plantations of North American pines have seen host jumps from native pathogens. In the nineteenth century, *Pinus strobus* stands were severely damaged by *Cronartium ribicola*, native to the Eurasian *Pinus cembra*, and more recently large-scale plantations of *P. contorta* in northern Sweden have been damaged by *Gremmeniella abietina*, a pathogen of native conifers.

The importance placed on newly emerging diseases is clearly influenced by their impact. Hence, although *Puccinia malvacearum*, native to Chile, has successfully spread throughout the globe, attacking a broad array of species in the Malvaceae, it is regarded as little more than an oddity as its hosts are neither economically nor ecologically important nor apparently much affected by the disease. A similar case is found in the Australian species *Puccinia lagenophorae* that is now extremely widespread and occurs at high frequency through much of the range of *Senecio vulgaris* in Europe, where although it can have an impact on seed production, it has no apparent lasting impact on host numbers or distribution. Unfortunately, for other introduced emerging pathogens, this is not the case – as is attested to by the dramatic attention-grabbing headlines that periodically occur in both the scientific literature and the popular press. Thus, epidemics of *Fusarium circinatum* (pitch canker) are having a major impact on a number of pine species in California with the potential for >80% of native *Pinus radiata* stands to be destroyed. Elsewhere, its appearance following spread from its putative origin in Mexico or by secondary spread from other infected areas poses a potential threat to economically important pine-based forestry industries in South Africa, Chile, and parts of Europe.

Similarly, *Phytophthora ramorum* (of probable Asian origin) is having a major ecological and economic impact in California, Europe, and the United Kingdom. In California, this invasive species first came to prominence as a consequence of its devastating effects on Californian oak woodlands, where it shows little sign of abating (Cobb *et al.*, 2012) as the tolerance of bay laurel has increased its impact on highly susceptible live oaks and tanoaks. In Europe, the spread of the same pathogen introduced independently from its home range, and although detected on a range of species, shows limited signs to establish in more natural vegetation. Instead, its persistence seems to depend on plantation of infected ornamental shrubs (*Rhododendron* and *Viburnum*). A recent extension of its host range in the UK to include plantations of Japanese larch (*Larix kaempferi*; Webber *et al.*, 2010) – the first time it has occurred on a commercially important conifer – has precipitated a major felling program in an attempt to reduce spread and impose a degree of control. These epidemics are at a relatively early phase and must be expected to continue at high amplitudes until constrained by the pathogen's environmental envelope or by significant reduction in the frequency and density of highly susceptible host individuals.

In the case of *F. circinatum* and *P. ramorum*, reaching a point on the evolutionary trajectory of these newly established host–pathogen associations at which a new ecological balance is established will be a very long-term process. However, more generally, the speed at which such a balance occurs will be host–pathogen combination, and possibly environment, specific. For short-lived species, an ecological, if not genetic, balance may be attained within decades. Successful biological control events that reduce host density and population sizes significantly provide examples here (e.g., the control of *Chondrilla juncea* with *Puccinia chondrillina* in Australia; Cullen, 2012). For long-lived host species, however, this process could take millennia (note, for example, the continuing major epidemic of white pine blister rust [*Pinus* spp. – *Cronartium ribicola*] in the western United States, even though major genes for resistance occurs in some host populations). However, for pathogens with broad host ranges, epidemics may not stop until the susceptible hosts have become extinct.

The different ecological trajectories hitherto shown by *Phytophthora ramorum* in southwestern United States and in Europe further highlight the difficulties involved in forecasting the future dynamics of new host–pathogen associations. In the United States, it is a devastating epidemic drastically altering species composition and dynamics of naive communities and in Europe, it is a destructive pathogen, although seemingly more dependent on trade with infected plant material from plant nurseries and garden centers and with limited effects on native communities. *Phytophthora cinnamomi*, also of probable Asian origin, provides another example. Since the middle of the twentieth century, it has transformed heathlands in southwestern Australia, although its frequent presence in

Table 1 Some examples of past, present, and potential future emerging plant diseases. Note that inclusion in any one category does not exclude the possibility that the disease is still a major problem or may yet migrate to currently disease-free areas

Species	*Hosts attacked*	*Origin*	*New environment*	*Impact*
Past emerging diseases				
Puccinia malvacearum	Wide host range on Malvaceae	Chile	Global	None
Erysiphe alphitoides	Wide host range including Fagaceae, Hippocastanaceae, and Anacardiaceae	First observed in Portugal	Nearly circum-global	Affects regeneration of deciduous *Quercus* spp. in Europe
Phytophthora cinnamomi	Wide host range including Proteaceae, Epacridaceae, and Myrtaceae	Possibly Asia	Western Australia	Major community changes due to loss of multiple species. Limited effects on other continents.
Ophiostoma ulmi	*Ulmus* spp.	East Asia	Europe and North America	Major impact, particularly on ornamental trees. Now replaced by *O. novo-ulmi* (see below under 'Newly emerging diseases').
Uncinula necator	*Vitis vinifera*	North America	Global	Earlier devastating epidemics (in Europe)
Sphaerotheca mors-uvae	*Ribes* spp. above all *R. grossularia* and *R. nigrum*	North America or/and Russia	Europe	Devastating damage on *R. grossularia* (past), now increasingly *R. nigrum*
Cryphonectria parasitica	*Castanea dentata*	East Asia	Eastern USA	Major community changes associated with loss of community dominant
Labyrinthula zosterae	*Zostera marina*	North Atlantic coasts	North Atlantic coasts	Extensive dieback of *Zostera* meadows, slow recover, and dramatic declines among waterfowl, particularly *Branta bernicola*
Newly emerging diseases				
Ophiostoma novo-ulmi	*Ulmus* spp.	Hybrid origin between one European and one North American strain, both originating from Asia, which met in Europe	Europe and western Asia (aggressive hybrid) North America	Major threat to elm forests and ornamental trees
Phytophthora ramorum	*Quercus* spp.	East Asia?	California, Oregon;	Devastating on dominant trees and strong effects on juvenile survival (North America)
	Larix kaempferi Various ornamentals		Western Europe	Extensive stand mortality planted larches (UK)
Discula destructiva	*Cornus florida*	?	North America	Devastation of dominant understorey shrub of many NE American temperate forests
Cronartium ribicola	5-needled pines	Asia and eastern Europe	North America	Major effect on dominant white pines and associated with impact on forestry
Puccinia lagenophorae	*Senecio vulgaris*	Australia	Western Europe	Widespread incidence on *S. vulgaris* in northwestern Europe; little apparent population impact

Puccinia komarovii	*Impatiens parviflora*	Central Asia	Europe	Widespread incidence on *I. parviflora* throughout Europe. No visible effect on host expansion
Gremmeniella abietina (European race)	*Pinus resinosa*	Europe	Eastern North America	Devastating epidemics on *Pinus resinosa*
Puccinia psidii	Wide host range in Myrtaceae including many Eucalyptus species	South America	Australia Hawaii	Potentially devastating to wide range of forest communities in Australia
Phytophthora alni	*Alnus* spp.	Europe ssp. alni of hybrid origin	Europe	Major effect resulting in tree dieback, particularly along slow-flowing watercourses
Fusarium torreyae	*Torreya taxifolia*	?	Florida, Georgia	Drastic population reduction of earlier common species, now critically endangered
Ceratocystis fagacearum	*Fagus* spp.	?	Eastern North America	Major community changes associated with loss of community dominant
Phytophthora austrocedrae	*Austrocedrus chilensis*	?	Patagonia	Major threat to *A. chilensis* and temperate naive forests at the Andean foothills as plantation of exotics are used to prevent disease spread
Future threatening diseases				
Erysiphe flexuosa	*Aesculus* spp.	North America	Europe	Potential threat to native *A. hippocastanum* on the Balkan peninsula
Dasyscypha willkommii	*Larix decidua*	Europe	Europe	Potential threat to high-altitude forests in the Alps
Hymenoscyphus pseudoalbidus (anamorph *Chalara fraxinea*)	*Fraxinus excelsior*	?	Northern Europe	First documented from Poland in 2000, now rapidly expanding, causing extensive host dieback and threatening the host
Heterobasidion irregulare	*Pinus pinea*	North America	Southern Europe	Established and now expanding within a small area in Italy, potential threat to Mediterranean pine and oak forests
Phytophthora lateralis	*Chamaecyparis lawsoniana*	East Asia	North America	Potential threat to native *C. lawsoniana* populations, also expanding on ornamentals on other continents

European and North American soils has not been linked to any epidemics. An alternative explanation is of course that past epidemics resulting in regime shifts and loss of susceptible species have faded out a long time ago.

Environmental Change Causing Emerging Diseases

Season-to-season variation in environmental parameters like rainfall and temperature are well known to drive differences in the incidence and severity of disease epidemics in host–pathogen associations. However, with patterns of precipitation and temperature widely predicted to change in current models of future climate, are there likely to be further increases in the incidence of novel disease problems? This question has been the focus of a growing number of studies in recent years, although a significant problem is to discriminate between epidemics due to more extreme although regularly occurring weather fluctuations (cf. the potato blight famine in Ireland) and long-term climatic trends.

Environmental change has the potential to affect the incidence of emerging diseases through (1) range expansion of existing currently exotic pathogenic fungi or (2) changes affecting the growth, development, or dispersal of native pathogens. There are a range of reasons to believe that range expansion of existing pathogenic fungi or their hosts into new areas will lead to significant and persistent disease epidemics. Ample evidence is provided by the long use of foreign provenances in Swedish and Finnish silviculture where planting of maladapted *Pinus sylvestris* provenances have repeatedly induced severe epidemics of major endemic pathogens (e.g., *Gremmeniella abietina, Phacidium infestans and Melampsora pinitorqua*). A case, where climate change may drive shifts in distribution boundaries to include previously unchallenged and susceptible host populations may become apparent in the European Alps, where high-altitude provenances of *Larix decidua* are unable to survive forestry cultivation at lower levels due to epidemics of *Lachnellula willkommii* (*Dasyscypha w.*) – a canker that under the harsh climate prevailing at high elevations only persists as a saprophyte on fallen twigs (Gaumann, 1950).

However, the effects of climate change are unpredictable and can lead to opposite effects in different areas. For example, warming conditions may result in reduced snow cover in some areas and increased snow pack in others. These differences – essentially different sides of the same coin – may then induce what essentially appear to be major disease outbreaks in some circumstances and significant declines in others. Thus, although reductions in snow cover (depth and persistence) will reduce the impact of endemic snow blight fungi like *Phacidium infestans* – in European boreal forest on *Pinus sylvestris* and in the European Alps on *Pinus cembra* – in other areas snow cover has increased, resulting in significant outbreaks of the parasitic fungus *Arwidssonia empetri* on the dwarf shrub *Empetrum hermaphroditum* – a dominant species of boreal, alpine, and arctic heaths (Olofsson *et al.*, 2011).

Another potential driver for new diseases is the radical change in the global nitrogen cycle which has resulted in accelerating eutrophication of large areas of Europe, eastern and southwestern North America, parts of South America, and East and South Asia, with consequent dramatic impacts on biota. Whether these changes are directly attributable to nutrient changes or are indirectly through changes in the activity of fungal pathogens has rarely been studied for natural communities. However, for nutrient-limited systems, that is the major part of the earth's terrestrial and aquatic biota, increased nutrient availability is more likely to promote both pathogen growth and reproduction. For a number of host–pathogen systems, increased concentrations of foliar nitrogen will favor disease, and rapid responses of increased disease severity among biotrophic and necrotrophic fungal pathogens have been demonstrated both in agricultural as well as natural settings.

Whether disease epidemics are due to a new invader or due to an earlier extant, although benign, endemic population may be difficult to assess due to lack of historical records. For example, during recent decades, forest diebacks have been frequently reported from Europe. First they were claimed to be the result of acidifying air pollution, later increasingly attributed to more extreme weather events or new diseases. Two cases that have attracted much recent attention are observed declines of beech and oak. Recent studies have shown that these declines were caused by several *Phytophthora* species – normally persisting as benign saprotrophic fine-root pathogens – that were favored by periods of high precipitation while the subsequent decline followed periods of protracted drought that hampered annual fine-root formation. Thus, unusual, although not extreme, variations in weather may have far-reaching effects for the reciprocal interaction between the involved partners and it is only in recent years that pieces of these often hidden interactions have been understood.

Disease outbreaks may attract public attention and it is often tempting to interpret observed epidemics as due to climate change or increased eutrophication. However, of key importance for understanding disease dynamics is to never forget the fundamental role of density dependence for disease dynamics. Changed land use, particularly the abandonment of centuries-long histories of livestock grazing, scything, and sampling of fire wood, has over large areas resulted in successional change, including shrubification and closed tree canopies. In such cases, disease outbreaks track pulses in host regeneration. Secondary succession of earlier farmland may also result in increased contacts between alternating hosts as is the case for the present outbreak of *Cronartium flaccidum* on *Pinus sylvestris* in northern Sweden and Finland, where the alternate host *Melampyrum sylvaticum* occurs in abundance on abandoned meadows.

More broadly, the environmental consequences of changing temperature and precipitation regimes, nitrogen loads, and altered land use as well as their interaction will, as mentioned above, have different, even opposing, impacts on different fungal pathogens. For some, little if any change in incidence or severity will be apparent; in other cases, however, such changes will alter the environmental envelope of individual species sufficiently to lead to an increase in activity (more frequent and severe epidemics even including regime shifts), whereas in other cases, the reverse is more likely to be the case.

Genetic Change in Pathogens Causing Emerging Diseases

Notwithstanding the importance of changes in host or pathogen distribution, or of environmental change, genetic changes in pathogens that result in alterations in host range, infectivity or aggressiveness play a very important part in the origin of many highly damaging emerging plant diseases. Such changes may occur through (1) simple single-gene mutations; (2) sexual recombination with closely related species; or (3) horizontal gene transfer (somatic hybridization) with or without subsequent parasexual reassortment.

The simplest of genetic changes that can lead to major epidemics are those typically seen in small grain cereal crops where monocultures of the one resistance genotype are often grown over very large areas, thereby imposing very strong selection pressures on the existing pathogen population in favor of novel genotypes with matching infectivity. Frequently, these changes occur through simple stepwise mutations involving one or two virulence genes as was the case when Australian triticales (wheat × rye crosses) protected from wheat stem rust attack by the resistance gene *Sr27* were rendered vulnerable following the appearance of a newly virulent pathotype of *Puccinia graminis* (McIntosh *et al.*, 1983). The emergence of the Ug99 strain of *P. graminis* and the threat it poses to wheat production over much of the globe is an excellent example of even relative simple genetic changes leading to the appearance of a major threatening disease.

The process of host-imposed selection is a natural part of all wild host–pathogen systems and is particularly apparent in associations in which gene-for-gene type interactions occur. However, although such selection leads to changes in the structure of wild pathogen populations, in those circumstances, the often complex resistance structure of wild host populations leads to epidemic outbreaks that are strictly limited in both time and space (Burdon and Thrall, 1999). There are no known cases where a simple single mutation increase in virulence in a fungal plant pathogen has been responsible for major disease epidemics in nonagricultural systems.

However, significant genetic change that gives rise to the emergence of new and devastating diseases does occur in wild pathogen associations. The primary mechanism for this is through hybridization. Hybridization between related organisms giving rise to a new taxon is increasingly recognized as a major evolutionary force in changing the adaptability of invasive plants and has been long identified as a major factor driving recurrent global human influenza epidemics. Fungi are no different in their capability to recombine, with hybridization occurring through two distinct routes – sexual recombination between closely related species or through horizontal gene transfer (somatic hybridization). In somatic hybridization events, genetic exchange occurring via anastomosis of vegetative hyphae is viewed as the most likely mechanism, although precisely how exchange occurs is still in question as direct observation of the process has rarely occurred. Exchange may result in transfer of whole nuclei, individual chromosomes, or of components of the cell's cytoplasm including plasmids and viruses. Where whole nuclei are exchanged, diploidization, recombination, and subsequent haploidization (parasexual recombination) may or may not subsequently occur (Burdon and Silk, 1997).

Regardless of the actual mechanism, the use of molecular technologies has shown that hybridization between different pathogen isolates, formae speciales, and species is much more common than previously thought and plays a significant role in the origin of several of the more important emerging diseases of agriculture, forestry, and natural systems. Somatic recombination between highly specialized taxon groups like the rusts has been detected between different formae speciales (*Puccinia graminis* f.sp. *tritici* and *P. graminis* f.sp. *secalis* causing stem rust of wheat and rye, respectively; Burdon *et al.*, 1981) or species (*Melampsora larici-populina* and *M. medusa* causing leaf rust of poplar; Spiers and Hopcroft, 1994). Of broader concern are instances of hybridization involving genera housing individual taxa with wide host ranges or pathogens of important dominant species. Probably the best example of the consequences of such events is found in the complex changes that have occurred as two pandemics of Dutch elm disease, the first caused by *Ophiostoma ulmi* and a subsequent epidemic caused by *O. novo-ulmi*, which swept across much of Asia, Europe, and North America during the twentieth century. These epidemics, and the continuing evolutionary changes occurring in *O. novo-ulmi sensu lato* as a consequence of horizontal gene flow, provide examples of an emerging disease that had its origin in the ecological consequences of geographic spread into naive populations but which has subsequently continued to rage as a result of evolutionary changes made possible by the resultant intimate juxtapositioning of taxa that were previously allopatric in distribution (Brasier and Kirk, 2010).

A well-documented example of the emergence of a new pathogen of a staple crop is seen in the emergence of *Pyrenophora tritici-repentis*, the causal agent of tan (or yellow) spot in wheat, which appears to have arisen as recently as 1941 as a consequence of interspecific virulence gene transfer from *Septoria nodorum* (Friesen *et al.*, 2006). Similarly, a novel variant of *Magnaporthe oryzae*, the causal agent of rice blast, has been reported attacking wheat in South America. The origin of this pathogen is unclear as yet but provides a further example of the constantly changing nature of pathogens and their propensity to generate new taxa with the potential to cause significant economic impact.

Sexual recombination events also play a role in the origin of a number of emerging and threatening diseases. Recently, this has been documented in the appearance of a number of *Phytophthora* hybrids. For example, in Europe, hybridization between *Phytophthora cambivora* (an introduced pathogen of hardwood trees) and *P. fragariae* (a pathogen of strawberries and raspberries) has given rise to a group of heteroploid hybrid taxa causing significant destruction to *Alnus* spp. – a host that neither fungal parent is capable of attacking (Brasier *et al.*, 2004). An alternative explanation for the origin of *Phytophthora* spp. *alni* is that it may have been generated on several occasions by hybridization between ssp. *multiformis* and ssp. *uniformis* or their respective ancestor (Ioos *et al.*, 2006).

The Identity of Future Emerging Diseases – Prediction?

As can be seen, there are many examples of diseases that through new ecological opportunities have jumped hosts or

through genetic changes such as recombination have evolved to give rise to major disease epidemics. Understanding the epidemiology and evolutionary biology underlying such processes is a crucial step in understanding the phenomenon of emerging infectious diseases. A major driving force in the epidemiology of any disease association is the interaction of host and pathogen life history features and the way these play out in terms of effective transmission, survival, and reproduction (McDonald and Linde, 2002; Santini *et al.*, 2013). Although each disease has unique features, there are also suites of attributes that permit grouping of different host and pathogen types. Thus, highly host-specific pathogens and those with a broad host range sit at opposite ends of one particular continuum that determines the amount of host material vulnerable to infection in any situation. Highly specific pathogens with clear boom-and-bust epidemiological patterns may be less of a threat than pathogens with broader host ranges. But how stable are these patterns under different environmental conditions? As host range broadens and pathogens become less specific, their impact on any individual host may rise as the total pathogen population size will be determined by the sum of its fecundity on all its hosts – not just on the host of particular focus. In particular polycyclic pathogens with sexual recombination that are able to respond rapidly to benign environmental conditions (climatic or nutritional) are likely to play an important role as increased pathogen populations will increase the likelihood for evolutionary change resulting in new host jumps. However, whether this will be the case or not is likely to vary broadly even among closely related taxa.

Over the past half century, particularly dramatic changes have been observed in Europe among the powdery mildews – including range expansions, new host jumps, and increased disease severity of earlier accidentally infected hosts. For example, four mildews have shown rapid range expansions from the east, one in the 1940s (*Erysiphe hypophylla* on *Quercus robur* and *Q. petraea*), two in the 1980s (*Microsphaera palcewskii* on *Caragana arborescens* and *Microsphaera vanbruntiana* var. *sambuci-racemosae* on *Sambucus racemosa*), and one in the 1990s (*Erysiphe syringae-japonicae* on *Syringia* spp.). At the same time, a further two mildews have moved in from the west, one in the 1950s (*Erysiphe azaleae* on *Rhododendron* spp.) and one in the 1990s (*Erysiphe flexuosa* on *Aesculus* spp.). Understanding the basis for such changes in the biology of individual interactions is vital to attempts to predict future emerging diseases. Furthermore, whether these and similar cases will have long-lasting effects on their respective hosts or whether such epidemics are transient remains to be seen. As demonstrated in the Park Grass Experiment at Rothamsted for the *Blumeria graminis-Anthoxanthum odoratum* system, environments favorable to the pathogen may favor selection for resistance within the host population, thus resulting in low disease levels. However, in situations involving invasive species, rapid evolutionary change like this is dependent on the preexistence of variation for resistance in the host population.

Countering Invasive Plant Diseases

One of the most frustrating aspects of any assessment of invasion ecology and its practical application to disease incursion and control strategies, is the lack of information as to the frequency with which nascent invasion events occur, the proportion of those that fail to gain a foothold, and even the number that do but remain unrecognized due to the low incidence of invading organisms and a general lack of observers on the ground. If this situation applies to visually obvious organisms like potentially weedy vascular plants, it is substantially worse in considerations of plant disease. Even for diseases of agricultural crops where the majority of pathology attention is focused and transfer of untreated material is more or less strictly controlled through quarantine approaches, major disease still spread both naturally and through accidental human-mediated transfer (e.g., *Puccinia striiformis* into Australia and *Tilletia indica* in the USA). Increasingly, a major focus of concern is with the booming global live plant export–import nursery trade where the probability of new emerging disease episodes involving soilborne pathogens is greatly enhanced by insufficiently rigorous controls (Brasier, 2008).

What approaches can be taken to minimize the arrival of diseases into new environments? The standard preinvasion response is one of maintaining effective quarantine barriers (usually at national boundaries). Such an approach provides a generalized response and has some benefits. However, given the mobility of the world's population and the effective dispersal mechanisms of many fungi, this approach, although valuable, is essentially only a temporary one that postpones rather than prevents incursion. Where concern is focused on the possible incursion of specific threatening pathogens, matching of the climatic envelope of pathogen distribution in its native range with that potentially available in the target area has been advocated. For example, this approach has been used to estimate geographic areas of highest risk following the arrival of *Puccinia psidii* in Australia. However, the overall predictive value of climatic matching approaches is often not overwhelmingly compelling and need to take into account a broader range of factors influencing the interaction (e.g., host range, variation in susceptibility and how this might be geographically structured, host community structure, etc.) and the possibility of uncertainty as to the actual taxon involved (Eolith *et al.*, 2013).

With postinvasion strategies, there is a gulf between the options available for the control of diseases of agriculture and those of native ecosystems. Thus, the appearance of a threatening crop disease would typically precipitate a three-phase response. The first stage, that of 'contain and destroy,' is applied when the pathogen is detected at a very early phase, where the area of ingress is limited and (preferably) isolated (e.g., *Phakopsora vinifera* in northern Australia) and/or the pathogen has limited dispersal capability. During this stage, the aim is to eradicate or, failing that, restrict distribution of the pathogen through effective area control. The second stage, 'manage and reduce,' relies on both short-term options provided by agronomic approaches (tillage, rotation cropping, rouging, pesticides) and long-term resistance breeding to ensure that the economic impact of the pathogen is limited in most, if not all, years. Finally, the third phase of 'abandonment' occurs where epidemics cannot be controlled and production is subeconomic, leading to crop replacement. Unfortunately, few of these postinvasion strategies have

application to plant diseases of native ecosystems. In these situations, if a pathogen successfully circumvents border quarantine barriers and initiates infection, the probability of disease detection early enough to affect eradication is extremely small. The management responses available to agricultural enterprises are not relevant and with the exception of the protection of amenity plantings and sites of especial significance, there is little that can be done (cf. the impact of *Cryphonectria parasitica* on American chestnut or the introduction of *Phytophthora cinnamomi* into complex *Banksia*-dominated shrublands in Western Australia).

Conclusions

For a long period, the main focus on new emerging diseases has been related to invasive pathogens that have passed oceanic borders. Nowadays the focus on emerging diseases is increasingly related to global change issues. Although ongoing and future environmental change is more likely to have an impact and may accelerate the emergence of new diseases, it is important to remember that hybridization events and host jumps have regularly occurred during evolutionary time, resulting in the fascinating diversification which now can be seen and understood. Thus, a major ongoing challenge as how to prevent the unwanted impacts of pathogens in agriculture, horticulture, and forestry is foreseen, but in general little, if anything, can be done to hinder them in natural situations.

See also: Climate Change and Plant Disease. Climate Change: Animal Systems. Plant Disease and Resistance

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Emerging Zoonoses in Domesticated Livestock of Southeast Asia

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Glossary

Emerging disease New infections resulting from the evolution or change of an existing pathogen or parasite resulting in a change of host range, vector, pathogenicity or strain; or the occurrence of a previously unrecognized infection or disease.
Endemic Prevalent in or peculiar to a particular locality, region, or people.
Evolution Evolution is the process by which genetic mutations that enhance reproduction become and remain more common in successive generations of a population.
Livestock Livestock are domesticated animals raised in an agricultural setting to produce commodities such as food, fiber, and labor.
Mutation A change in the DNA sequence.
Pandemic An epidemic occurring worldwide, or over a very wide area, crossing international boundaries and usually affecting a large number of people.
Reassortment Mixing of the genetic material of a species into new combinations in different individuals.
Recrudescent Breaking out again: renewing disease after abatement, suppression, or cessation.
Risk factor/determinant A variable associated with an increased risk of disease or infection.
Synergism Interaction of discrete agencies conditions such that the total effect is greater than the sum of the individual effects.
Zoonoses Diseases that is transmissible between vertebrates and humans.

Introduction

Southeast Asia (SEA) is known for its physical, political, cultural, and socioeconomical heterogeneity and is geographically divided into mainland and maritime (or Malay Archipelago) SEA comprising of Cambodia, Laos, Myanmar, Thailand, Vietnam, Peninsular Malaysia and East Malaysia, Brunei, Indonesia, the Philippines, Singapore, and East Timor, respectively. In the past two decades several zoonotic diseases, i.e., diseases that are transmissible between humans and animals (vertebrates), have surfaced in SEA, severely affecting the regional economy and devastating animal and human lives. The disease events reserved SEA as among the regions to be monitored for future emerging zoonotic diseases (Gilbert, 2012).

According to the World Organisation for Animals Health (OIE), emerging zoonoses are "new infections resulting from the evolution or change of an existing pathogen or parasite resulting in a change of host range, vector, pathogenicity or strain; or the occurrence of a previously unrecognised infection or disease" (WHO, 2011). While reemerging zoonoses are existing or endemic (possibly hypoendemic) communicable diseases resurging in terms of their frequency (incidence or outbreaks) or distribution over space and time, emerging zoonotic diseases may arise sporadically due to unique combinations or 'synergism' of several disease drivers, such as those that were seen in the explosive outbreaks of Nipah virus infection, SARS (severe acute respiratory syndrome), and the recent influenza H1N1 pandemic of 2009 (Morens and Fauci, 2013). These events usually attract more attention among the public and scientific community as they can be distinctive in terms of presentation and extraordinary in terms of magnitude, coverage, and socioeconomic implications.

Livestock farming is the principal source of livelihood for most countries in SEA except Singapore and Brunei. SEA is home to an estimated more than 2.65 billion chickens, 245 million ducks, 13.7 million head of buffalo, 46.1 million head of cattle, 71 million head of pigs, 13.8 million head of sheep, and 28.2 million head of goats (FAO, 2014). Animal agriculture and related activities in this region provides employment and side income, improves household dietary components and nutritional security, and provides food and economic well-being for their respective nations' (Randolph *et al.*, 2007). In the past decade, some of the livestock sectors in this region such as the poultry sector have significantly expanded. However, the rate of expansion is not even across the region whereby larger scale poultry farming is propagating, i.e., it is rapid in Thailand and Malaysia, but at a much lesser extent in Vietnam, Indonesia, and Cambodia. Nonetheless, livestock rearing in SEA has remained the practice of smallholders where the majority of livestock are reared in an extensive or backyard system (Ahuja, 2013; Del Rosario *et al.*, 2007). This type of animal husbandry has been linked to several emerging diseases and has been identified as a risk factor for future emerging infections (Biswas *et al.*, 2009; Grace *et al.*, 2012).

The poor 'bear a disproportionately high share of the burden of (zoonotic) disease' because of their close contact with livestock in unsanitary conditions and the low likelihood of needed healthcare (Grace *et al.*, 2012; WHO *et al.*, 2006). This is especially true for farmers in Asia and Africa where human and livestock habitat coalesced in small crowded spaces. Livestock agriculture employs more than 50% of households in SEA, among which more than 60% are maintained as backyard farms where biosecurity is almost impossible to implement. The unsophisticated nature of backyard system allows continuous interaction between various species or animals and humans and has been frequently reported as one of the most important emerging disease determinant in this region. In 2012, International Livestock Research Institute, Kenya produced a comprehensive report about transmission of disease in emerging

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livestock systems in the developing world, and in the report the institute mapped poverty to zoonoses occurrence worldwide (Grace *et al.*, 2012). SEA was highlighted as among the areas with high concentration of poor livestock keepers where intervention at the human–livestock interface could give positive impacts on zoonoses control. This article will highlight only the major emerging zoonosis and lingering or endemic zoonosis caused by infectious microorganisms originating from domesticated farm animals that have been reported in the SEA region for the last two decades. Non-zoonotic and transboundary emerging animal diseases of food security and economic importance will not be discussed.

Factors Influencing the Emergence of Zoonotic Infectious Diseases among Livestock in Southeast Asia

A combination of factors has been linked to the emergence and resurfacing of zoonotic and non-zoonotic trans-boundary diseases, which have been discussed extensively elsewhere. Briefly, the factors include microbial evolutionary adaptation such as genetic mutation and viral genetic recombination or reassortment, improvement of microbial switching capacities between host species, change in the size of susceptible or reservoir host populations, changes in human behaviors (particularly dietary choices, movement, and travel) and changes in livestock production and animal husbandry practices including animal trade policy, and ecological/environmental alterations such as for agriculture and urbanization (Brown, 2004; Coker *et al.*, 2011). These microbial, host, and environmental factors interact continuously, therefore actions or activities (intentional, natural, or accidental) that modify any of these key elements might generate opportunities for infectious agents to evolve into new ecological niches, access, and eventually adapt in new host systems.

The SEA region is an emerging market arena because of its changing physical and socioeconomic structures and rapidly expanding populations (Delgado *et al.*, 1999; Pingali, 2007). According to FAO (2012), the total population growth of SEA nations will increase from 523 831 in 2000 to 705 414 by 2030 (FAO, 2013; Jones, 2013). The changing population size and growth estimates have energized the livestock industry to meet the doubling protein demands by 2030 and lend impetus to the 'livestock revolution' in the region (Delgado *et al.*, 1999; Steinfeld, 2004). The growing demand for livestock has encouraged movement of animals and increased the exchange of products, services, and materials between countries. This, in turn, offers new opportunities for smallholder livestock producers in the region to market their products. Unfortunately, regional disharmony in disease control measures, surveillance, and implementation also conveniently allow veterinary pathogens to cross regional borders via legal and illegal animal movement and trade (Coker *et al.*, 2011; Liverani *et al.*, 2013).

SEA boasts a large proportion of the global rainforest and biomes. However, in the past century, an overall 1–2% annual decline of the existing rainforest has been recorded due to various reasons including urbanization, severe weather, logging, intensive agriculture, and industrialized animal production. Intensified farming of major commodity crops such as rubber and palm oil have resulted in clearance of large areas of jungle and forest in Indonesia, Thailand, and Malaysia (Miettinen *et al.*, 2011). The increasing consumer demand for animal product motivate local producers to diversify livestock production system innovatively within these plantations, therefore integrated farming system was widely introduced as it economizes on resources and improves farmer's yield and profits (Devendra, 2011; Devendra *et al.*, 1997). The combinations of crop and animal farming have largely and significantly benefitted the local, national, and regional economy. Nevertheless, the current practice of this farming system in SEA may increase risk of emerging infection via ecosystem–livestock–wildlife interface. According to recent literature reviews, more than 60% from approximately 1400 known pathogens to humans originate from animals, out of which more than 77% are promiscuous and readily infect multiple species including humans (Cleaveland *et al.*, 2001; Kuiken *et al.*, 2005; Woolhouse and Gowtage-Sequeria, 2005). The livestock–crop production within the vicinity of forest situates for livestock–wildlife pathogen exchange. These pathogens may become sustained among wild animals, complicating the control and eradication of livestock diseases. Domesticated animals at the ecosystem–wildlife interface provide a continuous supply of susceptible hosts for the amplification, evolution, and adaptation of novel pathogens from wildlife, serving as important passage for the pathogen to move from wildlife to humans (Chomel *et al.*, 2007; Liverani *et al.*, 2013). Human-origin or anthropogenic disturbances of wildlife ecosystem have in the past led to the emergence of previously unencountered disease agents or organisms blamed for catastrophic disease events such as those seen in the outbreaks of Nipah and SARS (Hughes *et al.*, 2007; Jones *et al.*, 2013).

Impact of Emerging Zoonoses on Southeast Asia

Impact on Food Security

Emerging zoonoses affect food security in two ways; gross reduction at the level of animal production and reduction in numbers of available food animals due to disease or compulsory culling to control the spread of infection to humans. For example, between 2003 and 2013, highly pathogenic avian influenza (HPAI) H5N1 in SEA resulted in the culling of a total of 175 million domestic birds (Van Kerkhove, 2009). In many countries, backyard and small poultry producers were the worst affected. Small- and medium-scale commercial poultry producers had to sell their properties and close their farms when chickens died or were culled whereas backyard producers lost their main source of protein and income (Rushton *et al.*, 2005). At the height of the outbreaks between 2003 and 2005, the production of broilers dropped significantly throughout the region. Thailand, for example, was the fourth largest poultry meat exporter in 2003 exporting nearly 485 000 tonnes of poultry meat. Immediately following the avian flu notification by the Thai authorities in 2004, poultry products were banned from major international trade flows which significantly drove the exportation of poultry down by 50% from 2003, destabilizing the local and regional markets broiler meat supply (Otte, 2008). In Malaysia, reported

clustered outbreaks of H5N1 among a flock of smuggled fighting cocks drove Singapore to restrict chickens and eggs imported from Malaysia as a precautionary measure to the perceived risk. As a result of the sudden reduction of supply of these produce, the price of chicken and eggs increased markedly in the local market (Agri-Food and Veterinary Authority of Singapore, 2004; Nicita, 2008), lowering consumer's purchasing power for basic necessities. Fortunately, the outbreak was rapidly controlled by the veterinary authorities and customer confidence and trade was therefore restored.

The worldwide outbreak of pandemic influenza A H1N1 2009 was initially linked to pigs because the genetic makeup of the virus partly includes swine-originated influenza genes (Malik Peiris *et al.*, 2009). It was apparent in the course of the outbreak that pigs played no active role in the pandemia and the epidemiology of the disease, but because of the partial genetic affiliation, the media-friendly 'swine flu' was used in reference to the disease (WHO, 2009). The term led to serious misunderstanding among consumers about the safety of consuming pork and pork products worldwide. As a consequence, many refrained from purchasing pork, leading to domestic and regional pork markets downturn. In fact, pork-importing countries within the region considered introducing trade restriction on live pigs as precautionary measures to safeguard the local pig industries and preserve human health (Johnson, 2009). At the same time, various groups in the region further insisted on stamping out all pigs to reduce risk of disease, even when neither viral evidence nor infection was observed. Outside of SEA, in Egypt, mass pig slaughtering was performed amidst fear of virus spread (Gusman, 2009). However, prompt risk communication emphasizing the lack of danger posed by pigs or pork restored consumer confidence and minimized the potentially disastrous consequences to the pig production industry in the region.

Impact on Human Health

The overall disease burden to human health is usually expressed as disability-adjusted life year (DALY), which measures the year lost due to ill health, disability, and early death (Lopez *et al.*, 2006). However, the true burden of emerging and reemerging zoonoses is difficult to estimate due to the lack of comprehensive information and systematically collected data worldwide. The OIE reported zoonosis to cause at least 2.4 billion cases of illness and 2.2 million deaths every year (Grace *et al.*, 2012). Reemerging zoonoses, which are often considered neglected, are the hardest to estimate because the prevailing cases occur in underdeveloped or developing nations including SEA, where data are not available or poorly recorded, stored, and managed. Systematic reports of cases – if present – are often not accessible and questionable data integrity makes estimation of disease impact challenging. However, it is universally accepted that zoonosis among livestock have in the past and will continue to cause extensive human sufferings and deaths. Classical zoonosis such as brucellosis, for example, resulted in major disability and debility of military personnel during World War II with more than 1300 cases reported in the US Army between 1942 and 1945 (Wyatt, 2013). Many soldiers contracted brucellosis through consumption of contaminated raw milk and cheese and later had to be discharged because of severe debility as a result of prolonged fever and complications caused by arthritis. The disease has continued to contribute to the global burden of human illnesses and sufferings (Dean *et al.*, 2012; Pappas *et al.*, 2006) especially in developing nations such as Syria and Mongolia. Recent emerging zoonoses such as HPAI H5N1 killed 383 of 647 infected people worldwide since 2003 while avian influenza H7N9 has resulted in 145 infections with 45 deaths (WHO, 2013) since early 2013. Novel Nipah virus infection in Malaysia and Bangladesh caused more than 270 deaths and chronic debilitating post-encephalitic conditions to many others.

Impact on Social and Economy

A recent study estimated the costs of major highly fatal zoonoses between 1997 and 2009 to be US$80 billion (World Bank, 2012). The socioeconomic impact of zoonoses includes the loss incurred from reduced livestock production, trade restrictions, declined consumers demand for products, and disease control/prevention activities including surveillance efforts. In addition, it includes the indirect cost of depressed economic activities of other businesses dependent on the livestock industry such as animal feed manufacturers, animal-related food producers, food retailers, and hospitality services (Otte *et al.*, 2004; Rushton, 2009). Non-affiliated activities such as tourism can also be negatively affected as reported during the outbreak of SARS and pandemic influenza H1N1 2009 (Coker *et al.*, 2011; Lau *et al.*, 2009).

The socioeconomic repercussion of emerging zoonoses was well documented for Nipah disease event in Malaysia (Ng *et al.*, 2009). The outbreak resulted not only in the culling of over one million pigs but also bankrupting town economy when residents moved away from affected areas. Nipah essentially destroyed the local pig industry at the time and the livelihood of many pig farming families. For example, an estimated 36 000 employment opportunities in the farms and other local business that were supported by the farming activities diminished and local town and real estate businesses had to close down when pig farm operations liquidated. The value of destroyed pigs was estimated at US$97 million with additional US$35 million losses for compensation paid by the government and US$120 million in trade to Singapore and Hong Kong (Nor and Ong, 2000). The effect of Nipah rippled or spread to other pig affiliated industry causing indirect losses to pig feed industry, oil and fats, utility, and real estate which amounts to RM 541 million (US$164 million) (Hosono *et al.*, 2006). Following the outbreak, the number of pig farms dropped from 1800 prior to January 1999 to only 796 after 21 July 1999 (Nordin, 2001) with most pig farmers leaving the pig industry for other livestock or unrelated animal farming opportunities.

On a larger scale, the HPAI H5N1 epidemic in the region had a similar impact as the Nipah outbreak in Malaysia. Direct losses to the poultry sector were as the result of massive culling of affected and at-risk flocks with estimated cumulative losses of up to US$10 billion between 2003 and 2005 in SEA alone (FAO, 2005). However, more costs from the disease ensued indirectly. For example, Malaysian exporters reported a combined loss of RM 2 million per day (US$526 000) as a

result of the trade restriction to Singapore, a 20% drop in local consumer demand for chicken, and a consequential reduction in the average chicken price. Additional costs were incurred from concurrent control measured implemented such as movement controls, active and passive surveillance, and public awareness campaigns. Malaysia spent an estimated US$50 000 per month in 2005 on movement control alone (FAO Regional Office for Asia and the Pacific, 2006). During the outbreak, Vietnam and Indonesia had to embark on mass vaccination of poultry as the number of human cases increased and had to invest in cold chain assurance of the vaccine, training of vaccinators, and mass communication campaigns. The total costs of delivering vaccinations alone during the first year of vaccine implementation in these countries were estimated to be US$22 million (Pongcharoensuk *et al.*, 2011).

Emerging Viral Zoonoses in Southeast Asia

Nipah Virus Infection

Between late 1997 and early 1998 a mysterious 'barking pig syndrome' appeared in a pig farm at a northern state of Peninsular Malaysia that rapidly spreads to the central states (Mohd Nor *et al.*, 2000). The disease in pigs was closely linked to clustered cases of febrile encephalitis among individuals occupationally exposed to pigs and led to the discovery of the novel Nipah virus (Chua *et al.*, 2000). In the initial phase of the outbreak, the clinical signs observed in pigs ranged from mild to severe respiratory symptoms with variable neurological signs, but with prevailing low mortality rates. A distinctive dry hacking cough from infected pigs resulted in the coined 'barking' syndrome which could be heard from a distance away. Within an incubation period of 7–14 days of exposure to infected pigs, farmers, and abattoir workers showed neurological clinical symptoms related to meningitis such as hypotonia, areflexia, segmental myoclonus, disorientation and confusion, and convulsion, which rapidly progressed to coma and death (Chua, 2003; Lam and Chua, 2002). The case–fatality rate from those infected was 40%, where 106 deaths occurred among the 265 infected by the end of the outbreak in 1999. Individuals who survived the infection had prolonged or permanent disabilities and approximately 8% of those who survived succumbed to recurrent neurological disease due to viral recrudescence (Chong and Tan, 2003; Tan *et al.*, 2002).

The Nipah virus, named after the location where the disease was first discovered at Sungai Nipah, Negeri Sembilan is antigenically and genomically similar to the Hendra virus isolated from bats in Australia and was later classified into a distinct taxonomic unit as the new genus *Henipavirus* of the family *Paramyxoviridae* (Chua *et al.*, 2000). A retrospective analysis of serum stored at the Veterinary Research Institute in Ipoh, Perak later indicated that the agent may have been circulating in the pig population in Malaysia as early as the mid-1990s. However, the impact among pigs may have been insignificant and humans were not affected allowing the disease to go unnoticed. Pigs were identified as the amplifier host for Nipah virus, resulting in the culling of approximately 1.1 million pigs as part of the outbreak response (Mohd Nor *et al.*, 2000; Nor and Ong, 2000). Most, if not all pig farming in Malaysia is done intensively, therefore culling was performed swiftly and efficiently via local intersectoral and interagency efforts. Backyard pig farming being uncommon in Malaysia combined with the fact that pig farms were located at a certain distance away from the residential areas may have helped curb the magnitude and spread of the outbreak. The culling of pigs was followed closely by diminishing cases of the disease among humans. Nipah outbreak has not been reported since.

Pteropus bats (flying foxes or fruit bats), which were found at the index farm, have since been proven in many studies to be the symptomless reservoir host of the virus (Halpin *et al.*, 2011; Rahman *et al.*, 2010; Yob *et al.*, 2001). The species that have been well studied for Nipah virus infection are *Pteropus vampyrus* (large flying fox) and *Pteropus hypomelanus* (island flying fox) (Chua *et al.*, 2002b; Epstein *et al.*, 2009; Rahman *et al.*, 2010, 2011, 2013; Yob *et al.*, 2001). Pteropid bats have coevolved with the virus over time and are more likely to shed the virus during reproductive seasons or following stressful events (Halpin *et al.*, 2011; Rahman *et al.*, 2011, 2013). Infected bats shed the virus in secretions and excretions such as saliva, urine, semen, and feces (Halpin *et al.*, 2011). Apart from bats in Malaysia, serological evidence of Nipah virus has been found in pteropids trapped throughout SEA such as Cambodia, Indonesia, and Thailand (Reynes *et al.*, 2005; Sendow *et al.*, 2006; Wacharapluesadee *et al.*, 2005), a finding that is not surprising given the distance traveled and migratory nature of these bats (Breed *et al.*, 2010; Epstein *et al.*, 2009). The spill-over event may have occurred when bats which were believed to have migrated from Borneo were attracted to fruit trees planted around pig farms and near pig pens, a practice that was abandoned following the Nipah. Pigs may have consumed partially eaten fruits contaminated with fluids or excreta from the bats. The virus was then amplified in pigs and consequently spilled to in-contact farm workers resulting in the outbreak (Chua *et al.*, 2000; Mohd Nor *et al.*, 2000). Outbreaks have not occurred in other countries that reported serological evidence of Nipah antibodies among sampled bats and no evidence of seroconversion have been reported in humans or domesticated animals in the respective countries.

The emergence of Nipah in Malaysia is unique and has since been linked to the extraordinary convergence of climatological and ecological drivers which created an ideal situation for the virus to surface (Chua *et al.*, 2002a; Epstein *et al.*, 2006; Field *et al.*, 2001). Complex interaction between urbanization, deforestation, and extreme climate changes were believed to have driven the bats from their natural ecosystem to another in search of food. At present, Malaysia has remained free from the Nipah disease and pigs screened in the yearly Nipah serosurveillance have not shown any evidence of Nipah virus antibodies. Nipah outbreaks have continued to occur in Bangladesh, where an obvious amplifier host has not been identified and the human-to-human transmission that was unobserved in the Nipah outbreak in Malaysia was evident (Homaira *et al.*, 2010; Hsu *et al.*, 2004).

Emerging Influenza A Viruses

Influenza viruses are members of the family *Orthomyxoviridae*, a group of single-stranded, negative-sense ribonucleic acid

(RNA) viruses and are classified on the basis of antigenic differences among their nucleopcapsid and matrix proteins as Influenza A, B, and C. Of these three, only influenza A viruses are established in different animal species including humans, horses, swine, and a wide variety of domesticated and wild birds. Influenza A viruses are further divided into subtypes based on the antigenic relationships of their hemagglutinin and neuraminidase surface glycoproteins (Lee and Saif, 2009). These viruses inhibit the gut of wild waterfowl, its natural reservoir, but are highly capable of evolving in aberrant hosts. Influenza A have been successful in developing various mechanisms to jump species – into domestic poultry, farm animals, and humans after undergoing 'genetic shift,' a periodic gene segment reassortment between host species that produce significant antigenic change improving virus capabilities to infect new host species (Chen *et al.*, 2004; Webster *et al.*, 1992).

Highly Pathogenic Avian Influenza A H5N1

The HPAI H5N1 causes severe morbidity and mortality among poultry and was the first avian flu to cause severe respiratory disease and high mortality among humans. In SEA, the reported case-fatality rate of H5N1 infection in humans vary between 50% and 80%, however the rate is acknowledged to be inflated due to an undetermined number of individuals who may have been silently or subclinically infected during the outbreaks (Le *et al.*, 2013; Wang *et al.*, 2012). The incubation period of H5N1 in chickens is tricky to measure but has been estimated to be between 2 and 3 days (Bouma *et al.*, 2009; Jeong *et al.*, 2009) in experimental settings after which highly variable clinical presentation developed that includes respiratory symptoms such as ocular and nasal discharges; coughing; snicking; dyspnea; swelling, of the sinuses and/or head; severe depression; reduced vocalization; marked reduction in feed and water intake; and cyanosis of unfeathered skin, wattles, and comb. Incoordination and nervous signs, diarrhea, drastic decline in egg production, and increased poor-quality eggs and sudden deaths (high mortality of up to 100%) were also reported. In domestic ducks, with an exception of rare sporadic outbreaks most HPAI viruses produce few clinical signs (Chen *et al.*, 2006; Ellis *et al.*, 2004). Viral transmission may occur when infected birds shed the virus via discharges from its body (saliva, respiratory discharges, and feces), or via contaminated fomites (feed, water, etc.) to susceptible hosts. Once exposed to infectious birds, the incubation period for susceptible humans have been reported to range between 3 and 9 days (Huai, 2008) leading to initial symptoms of headache, myalgia, diarrhea, sore throat, and rhinorrhea followed by fever, cough, and shortness of breath. At a later stage of infection, severe lower-respiratory-tract symptoms and deaths were frequently reported. The case-fatalities for H5N1 infection in humans varies between countries within the region depending on several factors such as accessibility to medical care, culture and belief of people, and the socioeconomic standing of the country's general population.

H5N1 virus has emerged as early as 1996 in farmed geese in Guangdong Province of southern China but was not notable until the H5N1 virus made a dead-end jump from poultry to humans in Hong Kong in 1997, where the outbreaks of H5N1 infection in poultry coincided with severe respiratory infection and fatalities in humans (Chan, 2002; Guo *et al.*, 1998). Avian influenza was formally reported in SEA in Vietnam at the end of 2003. The infection rapidly spread in the country's poultry population where severe respiratory infection and lethality occurred among poultry and humans. Within a few ensuing months the disease had spread to Thailand, Cambodia, Indonesia, Laos, and Malaysia (Sims *et al.*, 2005; WHO, 2012). Most outbreaks occurred among backyard poultry with instances of virus transmission to local commercial poultry farms usually via fomites (such as trucks, crates, and cages) and personnel. Even though the poultry industry is the major livestock industry undergoing rapid intensification in this region, 50–70% of poultry are raised in backyard farms where little biosecurity exists (Bethe, 2006; Boni *et al.*, 2013).

The risk factor for infection of H5N1 in human has been well reported. A paper published by Van Kerkhove provides a comprehensive review on the modes of virus transmission (Van Kerkhove, 2009). Consistent with the widely practiced backyard farming system, the most important and consistent risk factor for human infection across studies involves varying level of contact or exposure to live infected poultry. Direct contact when handling sick birds, consuming uncooked poultry products, and caring for sick poultry are some of the significant determinants found in most human avian influenza outbreaks. The environmental risk factor include local animal trade pattern (such as informal trading in the local community and trading live animal in markets), extent of surveillance and early detection, density of live animal markets, poultry husbandry system, density of free ranging chicken and ducks, and rice cropping intensity. Live poultry market is one of the most discussed determinant for avian flu (and a few other emerging zoonoses). This type of market supplies 'warm' meat preferred by most Southeast Asian countries and is widely found in this region. However, the activities and environment of the market apparently promote virus from infected birds to circulate and spread to other birds and humans via aerosolized virus particles, blood, or body fluids (Fournié *et al.*, 2012; Van Kerkhove, 2009). A few countries in SEA have since discouraged operations of live poultry markets to reduce the risk of emerging diseases. However, little success has been achieved in this effort because of cultural affiliations of this practice to the people in this region. Changes can only be seen with public education and awareness, and implementation of regulations by the local authorities.

Since its emergence in 2003 to January 2014, the World Health Organization has tallied 650 human confirmed cases of avian influenza and 386 deaths worldwide (WHO, 2014). SEA contributed to more than 50% of the cases and fatalities related to human H5N1 infection. Based on the formal notification to OIE between 2003 and 2013, Vietnam surpassed other nations in the world with 2682 outbreaks followed by Thailand with 1141 outbreaks. Indonesia, Myanmar, Cambodia, Laos, and Malaysia each reported 269, 114, 37, 19, and 16 outbreaks, respectively. Malaysia and Thailand have not reported any outbreaks since 2006 and 2009 respectively. HPAI H5N1 outbreaks were better controlled in a few SEA regions compared to others. The success in eradicating H5N1

Table 1 The human cases and deaths due to highly pathogenic avian influenza H5N1 from 2003 to 2013

Country	*2003–09*		*2010*		*2011*		*2012*		*2013*		*Total*	
	Cases	*Deaths*	*Cases*	*Deaths*	*Cases*	*Deaths*	*Cases*	*Deaths*	*Cases*	*Deaths*	*Cases*	*Deaths*
Cambodia	9	7	1	1	8	8	3	3	17	10	38	29
Indonesia	162	134	9	7	12	10	9	9	1	1	193	161
Laos	2	2	–	–	–	–	–	–	–	–	2	2
Myanmar	1	0	–	–	–	–	–	–	–	–	1	0
Thailand	25	17	–	–	–	–	–	–	–	–	27	17
Vietnam	112	57	7	2	0	0	4	2	2	1	125	62
Total	311	217	17	10	20	18	16	14	20	12	384	271

Source: Reproduced from WHO, 2013. Tuberculosis control in South-East Asia Region. Annual TB Report 2013.

virus depends primarily on early detection of virus introduction and prompt institution of control measures such as aggressive culling or stamping-out policy in the country (Coker *et al.*, 2011; Eagles *et al.*, 2009; OIE and FAO, 2007).

Indonesia and Vietnam were the worst countries affected by H5N1 in terms of human incidence and fatalities, which by the end of 2004 and 2005, respectively instigated the decision to perform mass vaccination of poultry (OIE and FAO, 2007). The vaccination was performed along with other control measures such as systematic annual testing and pre-movement testing of local poultry. Both countries have since been considered endemic for avian influenza H5N1. By 2006 Indonesia reported H5N1 outbreaks in 31 of its 33 provinces and 286 of 444 its districts (Sumiarto and Arifin, 2008). Even as this article was being written, Vietnam, Indonesia, Cambodia, Laos, Myanmar, and Indonesia continue to face intermittent outbreaks despite significant control efforts by the governing authorities. However, the incidence and the number of outbreaks in poultry along with those in humans has continuously declined over the past few years consistent with the declining global trend of avian influenza H5N1 worldwide (**Table 1**).

Pandemic Influenza A (H1N1) 2009 Virus

Between March and early April 2009, a novel influenza A (H1N1) virus emerged in the United States among individuals with travel history to Mexico (Novel Swine-Origin Influenza A (H1N1) Virus Investigation Team *et al.*, 2009; Malik Peiris *et al.*, 2009). Initial cases of influenza were later discovered to have occurred in Mexico before it was reported in the United States (Neumann *et al.*, 2009). The virus rapidly spread to the whole northern hemisphere and within the first few months had spread throughout the globe via human-to-human transmission leading to the first global influenza pandemic of the century. The virus was discovered to be the result of novel assortments of triple reassortant avian/human/swine (that include genes from classical swine influenza H1N1, North America avian H1N1, and human H3N2) and Eurasian avian-like swine viruses (Neumann *et al.*, 2009). Phylogenetic analyses suggest that both triple reassorted and Eurasian avian-like swine viruses have become established in the swine population in the late 1990s before the discovery of the novel H1N1. However throughout the outbreak period, no evidence of novel H1N1 infection occurred in pigs other than the possible human to pigs virus transmission on a pig farm in Canada (Howden *et al.*, 2009). It was concluded that even though components of the virus originated from pigs in the past, pigs did not play immediate nor active role in the transmission and epidemiology of the virus in the 2009 pandemia (Johnson, 2009).

The pandemic H1N1 struck almost every SEA countries, and post-pandemic surveillance among pigs in Thailand, Cambodia, and Vietnam suggest that reverse transmission of pandemic H1N1 2009 virus infection had occurred at rates of more than 20% among sampled pigs (Hiromoto *et al.*, 2012; Rith *et al.*, 2013; Sreta *et al.*, 2010; Trevennec *et al.*, 2012). Several phylogenetic analysis work indicated that human-to-swine pandemic H1N1 influenza virus transmission event is not uncommon, a finding that has also been observed for other human seasonal flu viruses (non-pandemic H1 and H3 influenza viruses) therefore implicating human as a significant contributor to the genetic diversity of influenza viruses in swine (Lycett *et al.*, 2012; Nelson *et al.*, 2011). Several episodes of reverse transmission of the virus from infected humans to pigs later proved that pigs will demonstrate very mild flu like symptoms on infection before recovery and can sustain the virus within the flock (Howden *et al.*, 2009; Pereda *et al.*, 2010; Rith *et al.*, 2013; Song *et al.*, 2010; Sreta *et al.*, 2010). At present, there was little evidence to suggest that the virus can be transmitted from infected pigs back to human. However, the finding indicated that countries must improve biosecurity measures at the human–swine interface as pigs are highly efficient in viral recombination and reassortment and thus may impact the human health somewhere in the future.

Low Pathogenic Avian Influenza H7N9

At the beginning of 2013, another avian influenza virus strain of low pathogenicity, H7N9 resulted in severe respiratory infection among humans. The infection first appeared in the southern part of China and later spread to a wider region within the country (CDC, 2013; Gao *et al.*, 2013). The infection in humans are severe and resulted in high case–fatality, however there was little clinical implications to poultry even though epidemiological evidence among human cases highly suggest some level of contact (direct or indirect) with this species (Chen *et al.*, 2013; Lee *et al.*, 2013). Fortunately, the low pathogenic avian influenza (LPAI) H7N9 have to date not been reported among the poultry populations of the SEA countries or any other countries. Many SEA countries imposed

temporary restriction of poultry importation from China to safeguard its substantial poultry farming industry and preserve human health (Lim, 2013; Tuổi Trẻ News, 2014).

Reemerging Endemic Bacterial Zoonoses

Bovine Tuberculosis

Bovine tuberculosis is a classical zoonotic debilitating disease mainly caused by Gram-positive acid-fast bacilli *Mycobacterium bovis* and to a lesser extent *Mycobacterium caprae*. These two species are members of the *Mycobacterium tuberculosis* complex group within the genus *Mycobacterium*. Other species included in this group are *M. tuberculosis*, *Mycobacterium africanum*, *Mycobacterium microti*, *Mycobacterium canettii*, *Mycobacterium pinnipedii*, and *Mycobacterium mungi* (Acha and Szyfres, 2001). Bovine tuberculosis may occur not only in cattle but a wide species of domesticated and wild animals. Bovine species (both domesticated and wild) other than cattle such as buffaloes and bison, and Cervidae such as deer and elk are especially susceptible; however, all warm-blooded species can be infected. Transmission of pathogen between animals occurs via aerosols, ingestion of the organism from contaminated materials, or inoculation via open wound. The incubation period for the disease is highly variable ranging from months to years. The animal may remain asymptomatic for a long period of time following infection, with some proportion of animals remaining latently infected lifelong. Granulomatous lesions or tubercle formations either generalized or localized is a major characteristic of tuberculosis. Infected animals will shed *M. bovis* in respiratory secretions, feces, and milk, and sometimes in the urine, vaginal secretions, or semen. The most usual form of tuberculosis is manifested via a low-grade fluctuating fever, weakness, inappetence, and chronic weight loss leading to progressive emaciation; however, acute and fulminating infection has also been reported (Cosivi *et al.*, 1998). Coughing is not pronounced in animals until lesions occur in the lungs. The chronic development of disease manifestations accompanied by lack of high or immediate mortality often masks the importance of tuberculosis; therefore it is widely believed that prevalence of bovine tuberculosis is under-reported worldwide.

Bovine tuberculosis also referred as 'zoonotic tuberculosis' is a disease of animal production and public health importance. It causes significant economic losses in countries with large cattle farming industry through loss of production, markets and trade, and additional expenditures from surveillance and control programs (Amanfu, 2006; Butler, 2010). SEA with estimated cattle and buffalo populations of more than 110 million (FAO, 2014) will be threatened if the disease is not well controlled. Even though data on bovine tuberculosis prevalence is not available in this region, it can be speculated that the production loss from the disease among cattle will be consistent to what has been observed in developed countries where data are systematically gathered. Accordingly, milk production of infected cattle was reported to decline up to 10% and infected cows had one fewer calves (Cosivi *et al.*, 1998). In countries where food safety regulations are implemented, meat inspection at the abattoir detect clinical signs of tuberculosis such as progressive emaciation and tubercle lesions in the organs, prompting immediate carcass condemnations (Biffa *et al.*, 2010). The impacts of bovine tuberculosis on public health increased where disease is highly endemic and especially affect populations with weakened immune system such those living with HIV/AIDS (human immunodeficiency virus infection/acquired immunodeficiency syndrome) (Cosivi *et al.*, 1998). Conservative estimates reported SEA having more than 3.5 million with HIV (SEARO, 2014), therefore at higher risk for infection compared to the general populations.

For centuries, zoonotic tuberculosis has contributed to the incidence of tuberculosis among humans worldwide. Similar to pathogen transmission between animals, zoonotic transmission of *M. bovis* from animals to human occurs primarily through consumption of contaminated animal products, most commonly unpasteurized milk but may also occur through other mentioned modes (Acha and Szyfres, 2001). However, incidence of zoonotic tuberculosis markedly declined following the introduction of pasteurization and structured veterinary disease control programs (Cousins, 2001). In general, zoonotic tuberculosis is reported to be responsible for approximately 3–15% of tuberculosis among humans worldwide (Michel *et al.*, 2010; Müller *et al.*, 2013). The rate varies with regions of the world depending on several factors such as veterinary disease control program and food safety regulation in the country. Cosivi *et al.* (1998) estimated zoonotic tuberculosis to be responsible for at least 15 000 DALYs per year (27 DALYs per 100 000 population) in SEA based on the conservative estimate of worldwide proportion of tuberculosis caused by *M. bovis* at 3.1% (Cosivi *et al.*, 1998). Estimation of *M. bovis* contribution to human tuberculosis in SEA is difficult because most laboratories in the region have insufficient capacity to isolate and culture the organism and differentiate *M. bovis* from *M. tuberculosis*, the predominant causal agent for human tuberculosis.

As with many other neglected or lingering infection in developed countries, information about bovine tuberculosis in countries within SEA is scarce or difficult to find. Many disease review efforts suggested little or no data from SEA countries can be accessed via mainstream scientific publications by which burden of the disease can be extrapolated. Evidence obtained from literatures for this article, although few, suggest that tuberculosis is increasingly observed among livestock (and reservoir) in this region, however the prevalence is highly variable. For example, evidence of bovine tuberculosis were found among buffaloes in Thailand at a high rate (Chanepaiboon *et al.*, 2000) and spatial analysis among dairy herds conducted in Thailand suggests herd-level prevalence of 10% and within herd prevalence of between 10% and 30% (Inchaisri *et al.*, 2003). However, limited study on bovine tuberculosis in the neighboring Laos suggested low prevalence at 1% (Vongxay *et al.*, 2012). No other data can be obtained from other parts of SEA even though efforts of controlling bovine tuberculosis are being actively conducted by many SEA countries veterinary services through test-and-slaughter policy combined with abattoir surveillance (FAO, 2012). Formal reports for diseases such as bovine tuberculosis are difficult to obtain due to multiple reasons including poor resource gathering and analytical supports, and lack of priority or emphasis

by respective countries' service institutions for publication of printed materials.

There are several important risks factors for the emergence of tuberculosis among cattle in SEA. The consistent determinants as reported for most underdeveloped or developing nations are lack of structured disease control programs at the farm level and inadequate disease surveillance by local veterinary authorities (Michel *et al.*, 2010; Müller *et al.*, 2013). Testing and culling system is highly resource intensive, therefore might not be performed adequately in many SEA resource-poor areas. Extensive livestock husbandry practices predominantly integrated or mixed farming practices provide additional challenges to disease control because animals may not be easily accessed for disease testing and monitoring. In addition, integrated farms in SEA are mostly located in the peri-urban areas where livestock dwellings coalescence or encroaches wildlife habitats, thereby improving disease spread at the livestock–wildlife and vice versa interface (Daszak *et al.*, 2012; Jones *et al.*, 2013). Wild animals are important reservoirs for *M. bovis* and many sophisticated disease-control strategies in developed nations failed to eradicate *M. bovis* because the organism perpetuates in sylvatic cycle (De Lisle *et al.*, 2001; Gortazar *et al.*, 2011; Nugent, 2011; Schmitt *et al.*, 2002). Wildlife reservoirs may continue to infect susceptible cattle despite avid testing and culling strategies of infected herds. SEA has abundant wildlife and endangered species that can be severely affected if bovine tuberculosis is not controlled. Evidence of tuberculosis infection in wild animals are been seen in a few SEA countries such as Malaysia and Thailand (Angkawanish *et al.*, 2010; Ong *et al.*, 2013). Moreover, wild boars and cervids that frequently roamed in integrated farm areas are well described as maintenance host of *M. bovis* for other domestic and wild animals in many parts of Europe and New Zealand (Jackson, 2002; Meng *et al.*, 2009; Vicente *et al.*, 2006). Tuberculosis among wildlife provides a unique challenge because sylvatic tuberculosis cannot be eradicated through animal testing and culling of precious or protected wildlife species. Any disease interventions will involve complex decisions from various sectors and authorities including the veterinary, wildlife and conservation authorities; biologists; wildlife and ecologists; environmentalists; and the general public (De Lisle *et al.*, 2001).

The WHO (World Health Organization) has recently declared a state of emergency for tuberculosis worldwide. Cambodia, Indonesia, Thailand, and Vietnam reported among the highest incidence of tuberculosis in the region between 2009 and 2013 (WHO, 2013). Tuberculosis in humans is predominantly caused by *M. tuberculosis* which can reversely be transmitted to cattle and a number of other animal species through close contact with infected farm workers or individuals (Ameni *et al.*, 2013; Krajewska *et al.*, 2012; Ocepek *et al.*, 2005). However, the significance of animals as reservoir for *M. tuberculosis* and perpetuator of the infection has not been well documented. Emerging markets in this region demand large human capital investment and services. Therefore, workers from countries ranked with high burden of tuberculosis must be screened before starting work in livestock farms as they can potentially transmit the infection to animals.

Brucellosis

Brucellosis, a disease with many names (Malta fever, undulant fever, Gibraltar fever, etc.) is another classical zoonoses that has lingered for decades and is showing signs of reemergence among animals and humans in this region. Brucellosis is listed as among the most widespread zoonosis worldwide but is often neglected in developing countries. The disease is caused by Gram-negative acid-fast stained bacilli of the genus *Brucella*. Several species of *Brucella* affect animals, however the most important disease-causing species for livestocks are *Brucella abortus*, *Brucella melitensis*, and *Brucella suis*, responsible for bovine, caprine or ovine, and pig brucellosis respectively. Species of *Brucella* are mainly host-restricted however *B. melitensis* has the capacity to infect across the mammalian species and is especially known for its virulence as compared to other species (Acha *et al.*, 2001; Pappas *et al.*, 2006; Seleem *et al.*, 2010).

Brucellosis causes major livestock production losses and is a significant threat to public health. In female animals, brucellosis typically causes abortion at the last stage of gestation. In farms where animal breeding is structured, for example, through synchronous breeding methods, multiple abortions or 'abortion storm' occur acutely in a herd or flock when the organism was first introduced. Infected animals shed *Brucella* via milk and may have subsequent normal parturitions where the organism will be shed through uterine discharges (Renukaradhya *et al.*, 2002). Shedding of the organisms may be lifelong with high proportion of infected animals becoming chronic *Brucella* carriers. In countries of SEA where majority of herd sizes are small and backyard or extensive system predominates, explosive abortions is not typical but seropositive farms will report higher rates of abortion and stillbirths. Lower milk yields of up to 25% have been recorded among infected herds (Acha *et al.*, 2001). In males, organisms are shed via semen and brucellosis may cause orchitis and infertility. The mortality rate is very low ($<2\%$) but extensive morbidity is common within a herd. Brucellosis among humans appear to be directly correlated with the prevalence of brucellosis among livestock as humans contract the infection mainly via consumption of unpasteurized milk or milk products, but may also be infected from eating infected meat, or direct contact with aborted materials from diseased animals. Human to human transmission is rare, therefore control of incidence in humans is best achieved via systematic control of brucellosis among animals. Once exposed to the organism, the incubation period for brucellosis in susceptible animals and humans is variable but ranged from 2 to 4 weeks. The initial sign for human brucellosis includes nonspecific flu-like symptoms of undifferentiated prolonged (undulant) fever, myalgia, and arthralgia with generalized inflammation of the reproductive organs. Clinical manifestations among males include orchitis and epididymitis.

Recent overview of global brucellosis burden indicated absence of data and studies on human brucellosis in SEA (Dean *et al.*, 2012). On the contrary, published data on brucellosis in animals are available but limitations include accessibility and language. Sufficient scientific and local publications exist to indicate that infection is endemic among livestock and is widely spread within respective countries.

Sporadic reports of cases and outbreaks in humans occurred in Thailand, Malaysia, and Indonesia due to various degrees of exposure to infected animals and animal products (Bamaiyi *et al.*, 2011; Danusantoso *et al.*, 1972; Jama'ayah *et al.*, 2011; Paitoonpong *et al.*, 2006; Wongphruksasoong *et al.*, 2012). The reemergence of brucellosis was reported in Thailand in 2003 where *B. melitensis*, a species that has not been reported in Thailand, was first isolated (Manosuthi *et al.*, 2004). Serological surveillance for *B. abortus* in Thailand estimated the prevalence rate of 3.3% in dairy cows (Jittapalapong *et al.*, 2008) with high herd level of 24.1%. In 2009, a large human brucellosis outbreak which caused three deaths was linked to goat herding in a local Thai village (Wongphruksasoong *et al.*, 2012). In certain provinces the seroprevalence among beef cattle reached up to 40% and among sheep and goats, the prevalence ranged from 10% to 20%. In Vietnam, reports of brucellosis in livestock are absent, nonetheless a study on the undifferentiated fever among patients in Vietnam reported 15.8% *Brucella* serologically positive patients (Nga *et al.*, 2006) suggesting that *Brucella* is indeed present among animal populations of Vietnam. In Indonesia, the seroprevalence of *B. abortus* differs widely, ranging between 0% and 46% with high prevalence rate in most provinces of Pulau Jawa and Nusa Tenggara (Putra, 2006). In South Sulawesi, the seroprevalence of brucellosis among Bali beef cattle is high at 19.3% (Mu¯ihanah *et al.*, 2013). In other parts of Indonesia, the cattle- and herd-level seroprevalence has been reported to be as high as 15–44.5% (Lake *et al.*, 2010), respectively, while the seroprevalence among pigs was 12.6% (van der Giessen and Priadi, 1988). In Malaysia, brucellosis among cattle and goats has lingered for many decades at a low prevalence rate but incidence progressively surged in the early 2000–10 following massive importation of live cattle and goats from *Brucella*-endemic countries late in 1990s. In 2010, several clustered outbreaks of *B. melitensis* among humans were linked to the increasingly popular practice of consuming raw goat's milk (The Star, 2010). Nationwide serosurveilance data suggest that serological evidence for bovine brucellosis of less than 3% is low at animal level but relatively high (21.7%) at herd or flock level (Anka *et al.*, 2013). The direct loss due to brucellosis to the farmers and government estimated from *B. abortus* infection from production losses, carcass condemnation, culling, compensation, and vaccination was approximately RM38 million (US$11 million) for 2010 (Anka, 2014). *Brucella melitensis* have a lower seroprevalence of 0.9% and 7% at caprine level and flock level in Malaysia (Bamaiyi *et al.*, 2010). In the Philippines, porcine brucellosis was a problem in the late 1950s; however, new information is not available to ascertain the current status (San Agustin and Castillo, 1950).

The risk factor of brucellosis in SEA among livestock has not been well studied. However limited studies published in Malaysia and Indonesia suggest that epidemiology of the disease in this region is similar to those in other developing countries (Al-Majali *et al.*, 2009; Muma *et al.*, 2007). Studies on herd-level risk factors for seroreaction to *Brucella* among cattle in Malaysia and Indonesia show extensive farming system to elevate the risk for bovine brucellosis (Anka *et al.*, 2013; Lake *et al.*, 2010). The frequency of wildlife encounter in this farm system is common and therefore was speculated to significantly contribute to the prevalence. As with bovine tuberculosis, wildlife are important reservoir and maintenance host of *Brucella* organism allowing for reintroduction of new infection into clean herds at the wildlife–livestock interface (Bengis *et al.*, 2004; Godfroid, 2002; Meng *et al.*, 2009).

Disease control and eradication program for brucellosis is carried out by most veterinary authorities in SEA countries at different capacities, implementation level, and range of available resources. In some countries such as Indonesia and Malaysia, eradication activities are accompanied by vaccination programs of infected herds to maintain low level of brucellosis at farm level. However, the implementation of vaccination program is mostly irregular, therefore benefits from the vaccination for brucellosis may be hard to assess. In countries where culling accompanied by compensation scheme is carried out, the amount of compensation disbursed generally need improvement as farmers often wavered from culling seroreactors when their losses are not adequately compensated.

Leptospirosis

SEA is endemic for leptospirosis as evident from the continuous reports of human leptospirosis cases and outbreaks. In the last decade, many countries within this region are seeing an increasing number of leptospirosis among humans and the disease has become one of the most important reemerging zoonosis (Pappas *et al.*, 2008; Victoriano *et al.*, 2009). Leptospirosis causes wide range of nonspecific symptoms that may be confused with flu, malaria, dengue hemorrhagic fever, hepatitis, scrub typhus, and many other febrile infections and may be accompanied by acute renal injury or acute lung injury, with case fatalities of 12–25% (Hartskeerl *et al.*, 2011; WHO, 2010). Thus, in countries where these diseases are endemic, leptospirosis is often underdiagnosed, and therefore underestimated. Thailand, Vietnam, Indonesia, and Malaysia have listed leptospirosis as one of the notifiable infectious disease in humans and a disease of priority to control at the respective country's national level.

Leptospirosis is caused the pathogenic spirochete from the genus *Leptospira* which consists of 17 species and more than 250 serovars that are categorized as pathogenic, intermediate, and nonpathogenic leptospirae. The taxonomy of leptopira is highly complex and can be confusing. The article by Bharti *et al.* (2003) provides excellent review on the classification of leptopira and will not be repeated here. Several species are reported more than others in causing clinical infection in both animals and humans which includes *Leptospira interrogans, Leptospira alexanderi, Leptospira fainei, Leptospira inadai, Leptospira kirscheri, Leptospira meyeri, Leptospira borgpetersenii, Leptospira weilii, Leptospira noguchii*, and *Leptospira santarosai*. *Leptospira* serovars may be clustered within geographical region and within a given region only 10–20 serovars are typically found. A number of serovars are found unique and clustered within limited region, however most serovars can be found across geographical boundaries (Nalam *et al.*, 2010). Most mammalian species including domesticated livestock and wildlife are reservoirs of pathogenic leptospires. Some serovars of leptospirae appear to prefer a single host species, however

little information exist about host preference of leptospirae to warrant claims of host specificity (Bharti *et al.*, 2003). Rodents, particularly, have probably coevolved with the spirochete, therefore are highly efficient as the reservoir. The high mobility of rodents further increased their effectiveness as reservoir host and perpetuator of the agent. Other mammals may also serve as important source of the leptospira. Infected mammal may excrete the leptospirae intermittently for months or lifetime thereby increasing the risk for those occupationally exposed to animals such as farmers, slaughterhouse workers, pet traders, veterinarians, rodent catchers, and sewer workers (McBride *et al.*, 2005; Vinetz, 2001).

In SEA, agricultural workers such as paddy or rice farmers are at higher risk of infection compared to individuals of other occupations (Padre *et al.*, 1988; Rafizah *et al.*, 2013; Seng *et al.*, 2007; Tangkanakul *et al.*, 2000, 2005); however, most clinical cases in humans are as a result of environmental contaminations following climatological events such as flooding (Amilasan *et al.*, 2012; Ivanova *et al.*, 2012; Kawaguchi *et al.*, 2008; Lau *et al.*, 2010) or recreational activities (Mortimer, 2005; Sapian *et al.*, 2012; Sejvar *et al.*, 2003). For agricultural workers, the risk is possibly associated with frequent contact with water bodies where livestock are used to assist in plowing the fields and pests such as rats comingle and secrete leptospires. The exact animal species secreting the pathogenic Leptospirae is often difficult to determine as pathogenic serovars often occur in multiple species. SEA has a favorable weather for the survival of leptospira as pathogenic leptospires prefer warm and humid climate (Levett, 2001; Victoriano *et al.*, 2009).

Most literatures from the region suggest that livestock is potentially an important reservoir for pathogenic leptospirae however prevailing evidence indicated that livestock may not be an important source of human infection in the SEA region (Chanepaiboon *et al.*, 2000; Kawaguchi *et al.*, 2008; Van *et al.*, 1998; Victoriano *et al.*, 2009). Clinical leptospirosis in cattle or pigs is rarely reported in any of the SEA countries therefore their clinical, production, public health, and economic implication are unclear. Much of the publications on livestock and leptospirosis in SEA focused on serological surveillance and serovar identification, not their actual role in clinical or human infection. According to literatures, within 10–14 days following exposure, clinical signs of cattle and swine leptospirosis include fever, abortion, still birth, infertility, and milk reduction (Arundel and Radostits, 2000). However, little information could be found on the clinical leptospirosis in livestock in this region, therefore the associated economic or production impact due to leptospirosis is unclear. A study in Vietnam suggest that infection with some leptospira serovars may reduce one live pig born per litter, equivalent to 8% loss of production (Boqvist *et al.*, 2002), no other studies can be found in Asia. In Laos, the serological surveillance using microscopic agglutination test (MAT) suggested that in cattle the leptospirosis prevalence is 53.6% and in pigs 22.7%, however the clinical impact of the prevalence was not evident. Moreover rice field farmers in Laos have significantly higher exposure to the organism whereby 88.7% were leptospira seropositive as compared to 9.3% in livestock farmer (Kawaguchi *et al.*, 2008; Vongxay *et al.*, 2012). In Malaysia, the work on livestock was performed in mid-1980s by Bahaman *et al.* who reported seroprevalence of leptospira species among domestic livestock in Malaysia to average of more than 20%, with highest seroprevalence observed among cattle (40.5%), buffaloes (31%), and pigs (16%) (Bahaman and Ibrahim, 1988, 1986; Bahaman *et al.*, 1987). However, cases of leptospirosis among livestock have never been reported leading many to suggest that leptospirosis is not an important disease of livestock in Malaysia. Furthermore, incidence of leptospirosis in humans in Malaysia is usually associated with recreational and urban exposures rather than agricultural farming activities. Similar observations were recorded in many countries within SEA. Study in Thailand noted little difference in the prevalence of leptopspira antibodies of various livestock between areas where leptospirosis was highly endemic and not endemic among humans. The prevalence of antibodies found using MAT in epidemic provinces was 77.2% in cattle, 86.1% in buffalo, and 60.4% in swine and similar prevalence was observed in nonepidemic province (69.8% in cattle, 82.2% in buffalo, and 62.5% in swine) (Suwancharoen *et al.*, 2000). In general, available evidence at present suggest that livestock is largely exposed to leptospirae organism but manifested little observable clinical signs. Therefore leptospirae may not be a significant agent for disease and production losses among livestock in this region. Livestock might be as important reservoir of leptospira, however their role in the epidemiology of leptospirosis in humans in this region is vague and need to be enlightened with additional studies.

Conclusion

SEA is an arena of emerging markets with human population that is expected to double by 2030. Livestock industries need to significantly expand to ensure adequate protein supply for the growing and more affluent human populations. To increase animal production, various measures were undertaken including expanding agricultural areas and increasing diversity of livestock production systems. Unfortunately these acts are often not supported by increasing environmental and public health regulations in this region. Increased animal movement across borders through legal and illegal trade will continue to occur as long as there is surplus demand for animal proteins. Without harmonization of regional disease controls and strengthening of veterinary disease control programs, emerging disease especially those that had been neglected will continue to threaten regional livestock industry. Deforestation and fragmentation of ecological niches in an effort to expand agriculture land have significantly benefited the local and regional economy and improved society's wealth. However, without doubt these activities are associated with emerging and reemerging infection of production animals in this region. Many infectious diseases in humans originated from animals and agricultural expansion and intensification/diversification promotes disease emergence through ecosystem–livestock–human interface. In addition, encroachments of livestock into wild animal habitat enhance disease transmission at livestock–wildlife interface. The spread of these infections would threaten regional food security and safety. Emerging zoonoses causes major losses through reduced economic activity directly from trade restriction that is often prompted by a nation's

precautionary behavior. The ripple effect from reduction in economic activity can spread to other livestock-related sectors at the national and international levels. Emerging and reemerging infection causes additional cost to the country through general precautionary and preventive measures such as establishment of quarantine station and procedures, restriction of animal importation, premovement testing, vaccination, surveillance, and monitoring. Tremendous downturn in livestock-affiliated economic activity and shock to livelihoods of those affected by the disease warrant collaborative interministrial and intersectoral efforts at national and international level to minimize emerging diseases in livestock and humans.

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Energy and Greenhouse Gases Footprint of Food Processing

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Introduction

The levels of energy consumption and emissions during food processing are difficult to generalize. Even when the food industry uses some common processes, for example, drying, centrifugation, refrigeration, freezing, etc., most food products have specific processes to transform the raw materials into processed foods. Energy consumption and emissions depend not only on the type of product, but also on the degree of processing, the processing technique, and the form of energy used. Low processed foods, for example, some fruits, vegetables, and tubers, require minimal energy at the processing stage, which normally consists of cleaning, sorting, and packaging. For other products that require cooking right before eating, energy consumption is generally transferred from the processing to the consumer step. At the highest end of the energy consumption spectrum during processing are the ready-to-eat products. This is not because of the energy consumed to process the food, but also because most ready-to-eat products are commercialized chilled or frozen.

Processing techniques that involve phase changes – drying, evaporation, distillation, and freezing – are energy intensive when compared to other processes. The type of energy used also plays an important role. The food industry uses two types of energy: thermal and electric. With the exception of some industrial parks with district heating, most of the thermal energy in food processing plants is generated by burning fossil fuels, which may also be used to generate electricity; however, some industries are able to burn byproducts of the processed food to reduce the consumption of fossil fuels. Depending on the technology and the age of the equipment, the efficiency of transforming chemical energy contained in the fuel into heat is generally 80% and above.

Electricity is mostly purchased from utility companies. Electricity is a high quality energy source because it is versatile and can be transformed easily into mechanical or thermal energy with high efficiencies. Unfortunately, the global efficiency of electricity from fuel to the processing plant gate is low because of the efficiency loss when transforming chemical energy into mechanical energy at the generation facilities. Efficiencies are normally 30% or less for regular coal or natural gas fired plants, or approximately 40% for combined cycles. Transmission of electricity also has losses that depend of the distance and the type of transmission lines. Owing to the conversion efficiencies and losses, electric and thermal energies cannot be added directly when calculating the total impact of energy consumption during processing. Therefore, there are two ways of reporting these energies. One is by reporting thermal and electric energy values individually, and the second is by expressing as the value as primary energy, which is a back calculation to the chemical energy contained in the fuels.

A consequence of energy use is the emission of carbon dioxide (CO_2), methane (CH_4), and nitrogen oxides (NOx). However, emissions also arise from intended or unintended escape of hydrofluorocarbons (HFCs) from refrigeration equipment, and CO_2 from processes, particularly the fermentation industry and wastewater treatment.

When analyzing energy consumption of food processing plants, two approaches can be followed: by process and by industry; and this article follows the 'by industry' approach. Owing to the involvedness that would require covering all food processing industries, a selected number of industries have been chosen for this article. The greenhouse gases (GHGs) section focuses on the generation of electricity and thermal energy, which are the main sources of emissions, and the emissions from refrigeration equipment.

Industries

Beer

Beer is a fermented beverage made from malted cereal, hops, yeast, and water; and carbonated in most cases. Malted cereals are the result of soaking the cereals in water, allowing them to germinate, and stopping the germination by drying right before they become a plant. The purpose of malting is to develop enzymes that in subsequent steps breakdown the starch into fermentable sugars. Barley is the grain of excellence for beer making because of the high concentration of enzymes generated during the malting process, but it is rarely used alone. Barley is generally combined with other malted and unmalted grains like rice, wheat, oats, rye, and, in some cases, corn and sorghum. Malted and unmalted grains are milled and mixed with enough water to form a paste, called the 'mash,' which is subjected to a progression of specific temperatures to allow enzymes to break down high molecular weight carbohydrates. Soluble compounds are then extracted from the mash by trickling water in a process called lautering that yields a dark sugary liquid, wort. The wort is filtered and subsequently concentrated by boiling, which also serves to reduce the microbial load. Also, hops are added during boiling. Once cooled the resulting liquid is fermented with either *Saccharomyces cerevisiae* to produce ale beers or *Saccharomyces uvarum* for lagers. *S. cerevisiae* is a fast-acting yeast that rises to the top during fermentation that is conducted at temperatures between 15 and 25 °C and can be completed in around a week. *S. uvarum*, however, is a slow fermenter that sinks to the bottom during fermentation and requires temperatures between 4 and 13 °C, which extends the fermentation process and requires a maturation step that can take a month or longer (Beer-FAQ, 2007). After fermentation, subsequent steps include conditioning, filtering, carbonation, and bottling.

Lagers are the most popular beers in the world. Large-scale breweries produce exclusively lagers, whereas ales are preferably crafted by smaller breweries and microbreweries. As a result of the popularity of lagers, there are more data on energy consumption available, because most life cycle assessments in

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Table 1 Total energy for the process of manufacturing 1 l of beer for different breweries

Source	*Thermal (MJ l^{-1})*	*Electricity (MJ l^{-1})*	*Total[a] (MJ l^{-1})*
Cordella *et al.* (2008)			3.5
Hospido *et al.* (2005)			0.61
ENDS Report (2005)	0.12	0.38	
Germany (2002)	0.85–1.20	0.27–0.41	
European Commission (2006)			1.00–1.60
Koroneos *et al.* (2005)			0.69[b]

[a]Source does not specify whether or not total energy is expressed as primary energy.
[b]Estimated from figure (kilogram product not including bottle).

Table 2 Energy consumption at different stages of beer making

Process	*Thermal (MJ l^{-1})*	*Electricity (MJ l^{-1})*	*Total (MJ l^{-1})*	*Source*
Cooling		0.144		Talve (2001)
Fermentation including clarification			0.121	Cordella *et al.* (2008)
Maturation		0.054[1]		Talve (2001)
Malting			0.857	Cordella *et al.* (2008)
Wort production			0.952	Cordella *et al.* (2008)
Mash infusion	0.37		0.029	European Commission (2006)

the literature have been conducted for lagers, especially in Europe. Therefore, data presented in this section will correspond exclusively to lager-type beers produced in different regions of Europe. Data on energy consumption for the production of beer are limited. Table 1 presents the total energy consumed to produce 1 l of lager at different breweries. Some sources express energy consumption as total energy in a broad range varying from 0.61 to 3.4 MJ l^{-1} without indicating if this is primary energy. Other sources separate energy into thermal and electric with relatively high variation in the reported values. When analyzing by processes (Table 2), malting and wort production are the most energy intensive operations. This is not unexpected because malting requires drying and wort production relies heavily on boiling, which are both highly tasking in terms of energy use.

Bread

Industrial bread production consists of three major processes: (1) mixing and fermentation; (2) proofing; and (3) baking (Figure 1) (Giannou *et al.*, 2003). There are three standard industrial mixing and fermentation techniques for typical breads – conventional straight dough, Chorleywood, and sponge and dough (Martin, 2004; European Commission, 2006). The straight dough process consists of step-wise mixing then fermentation. The sponge and dough is similar to the conventional process, but fermentation is conducted before the conventional mixing (during the sponge phase) using an optimized ingredient ratio (Martin, 2004; Mondal and Datta, 2008). The remaining flour is mixed in after the sponge phase during the conventional dough mixing phase. The Chorleywood is an alternative that utilizes rapid mechanical shear with chemical modifiers to facilitate dough development to reduce the processing length (Martin, 2004). The Chorleywood method is more common in European countries, whereas the sponge and dough method is typically used in the US (Martin, 2004), but smaller and artisanal bakeries may use the more traditional approach. Particularly with the emphasis that Europe has placed on energy efficiency and the larger per capita bread consumption – as much as three times greater than in the US (Clyma, 2007) – the faster Chorleywood process is likely preferred to save energy and produce more bread at a faster rate. Unlike typical breads, sourdough bread requires significantly longer proofing time (up to 24 h), because the process relies on the growth of lactic acid bacteria (as well as yeast) (European Commission, 2006).

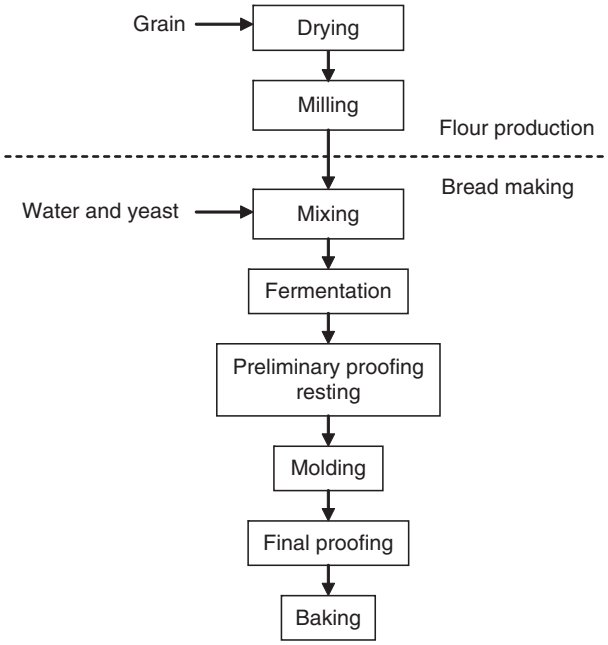


Figure 1 Flow diagram of the basic steps in flour production and bread making.

Table 3 Reported energy requirements for bread processing[a]

Subcategory (i.e., product, facility size, energy source)	*Thermal (MJ kg^{-1})*	*Fuel (MJ kg^{-1})*	*Electricity (MJ kg^{-1})*	*Total energy (MJ kg^{-1})*	*Source*
Large industrial bakery[b]	2.5		1.5		Andersson and Ohlsson (1999)
Small industrial bakery[b]	0.2		1.75		
Local bakery[b]	2.0		0.5		
Bakery A (994 kg bread per hour)[c]		1.73	0.28		Beech (1980)
Bakery B (1656 kg bread per hour)[c]		2.07	0.38		
Bakery C (2208 kg bread per hour)[c]		2.18	0.25		
Bread, cakes, and related products	0.38[d]	1.0	0.19		Brown *et al.* (1996)
Small Bakery	2.04		0.43		Dróżdż (2011)
Rolls	2.0		0.18		Nielsen *et al.* (2003)
Wheat	1.0		0.07		
Rye	1.0		0.07		
Frozen wheat	1.0		0.79		
Crispy rolls				2.4–6.9	Le-Bail *et al.* (2010)
Large bakery 1 (oil and electric for energy)[e]	3.0		1.01		Thompsson (1999)
Large bakery 2 (only electric)[e]			1.7		
Small bakery 1 (oil and electric for energy)[e]	3.8		1.03		
Small bakery 2 (only electric)[e]			2.23		
NS	3.0–6.16		0.24–0.87		Wojdalski *et al.* (2007)

[a]Some values include grain milling and drying, whereas others do not; thus, some differences may be attributed to the additional requirements associated with these processes.
[b]Estimated from Figure 5 in p. 33 of Andersson and Ohlsson (1999).
[c]Includes overhead energy consumption.
[d]Steam (megajoules per kilogram).
[e]Excludes milling and drying.
Note: NS, not specified.

Following the mixing and fermentation step, the dough is divided, permitted to rest (initial proofing), and molded to the desired shape (**Figure 1**) (Martin, 2004). The dough subsequently enters the proofing chamber (consisting of elevated temperature and humidity) to permit CO_2 production (leavening) within the dough (Mondal and Datta, 2008; Le-Bail *et al.*, 2010). Once the dough has reached the optimum volume, it proceeds to the oven for baking in either a batch or a continuous oven. Baking is a complex process consisting of physico-chemical changes such as dehydration, protein coagulation, starch gelatinization, gas exchanges, and Maillard browning (Vanin *et al.*, 2009). These changes occur in two major phases: (1) heating the dough and (2) the crust formation and browning (EU Freshbake, 2006; Le-Bail *et al.*, 2010).

Owing to the heating requirements for baking, bread production is a relatively energy-intensive process (**Table 3**). Larger industrial bakeries generally utilize fossil fuels and electricity for a variety of logistical reasons, whereas local, small, and medium bakeries rely more heavily on electricity (EU Freshbake, 2006). In facilities utilizing fuels as well as electricity, thermal energy is typically used for baking (EU Freshbake, 2006) and total consumption ranges from 2.4–6.9 MJ kg^{-1} (**Table 3**). In those same facilities, electricity is used for the other processes (including mixing and molding), and the electricity usage ranges from 0.2–1.5 MJ kg^{-1}. For more modern facilities that utilize primarily, or exclusively, electricity, the bread production process requires 1.75–2.2 MJ kg^{-1}. Overall, large-scale production can reduce specific energy consumption for processing; however, it is important to note that overall efficiency of production must take into consideration other factors, that is, greater transport distance from a large production facility to the consumer (Andersson and Ohlsson, 1999).

The actual bread-baking process utilizes less than 19% of the energy required by ovens during baking (Le-Bail *et al.*, 2010). Steam is added to the oven during baking to raise the humidity to enhance the quality of the final product, that is, volume, shape, and appearance. Steam generation requires approximately 16–25% of the energy for baking (Le-Bail *et al.*, 2010; EU Freshbake, 2006). The remaining energy is lost via oven walls or exhaust (29–60%), evaporation (15–35%), and heating of cooking devices/components (9–25%) (Le-Bail *et al.*, 2010). Preheating batch ovens can also be a considerable loss of energy with the specific energy consumption highly dependent on the number of batches that are processed. For example, preheating for one batch may require as much 6 MJ kg^{-1}, but processing 12 batches can reduce the specific energy to approximately 2 MJ kg^{-1}.

Canned Foods

Canned products must be pasteurized or sterilized to be regarded as safe during storage at room temperatures. Typically, before thermal processing, the raw materials are sorted, cleaned, modified (i.e., chopped, peeled, destemmed, homogenized), and combined with other ingredients, including sauces, brines, and additives. Once the cans are filled and sealed, they proceed to retorts or water baths for sterilization or pasteurization. The product is subjected to steam or submerged in water for precise time-temperature combinations to ensure safety and, depending on the product, may be subjected to agitation to facilitate the process.

Canned goods are shelf-stable products that can be divided into low and high acid foods. Low acid (pH > 4.6) canned products have to undergo commercial sterilization to insure a reduction of *Clostridium botulinum* spore counts for at least 12-logarithmic cycles. Because *C. botulinum* spores are not a concern when the product pH is less than 4.6, high acid foods are pasteurized at temperatures at or below 100 °C to eliminate organisms (i.e., molds) that cause microbial deterioration. Thus, low-acid foods require more intense thermal processing than high acid foods. Because heating the center of the product is the primary goal, other factors that impact heat penetration can also affect the extent of processing and energy required. Some of these factors include the size of the product pieces, rotation of the production during processing (i.e., still vs. rotary retort), thermal conductivity of the contents, homogeneity of the product, and size and shape of the can or jar.

Although canning is highly dependent on thermal processing and requires more processing energy than fresh products, it is generally less intensive than other processes – freezing and dehydration – that are also used to reduce microbial deterioration (Buffington and Zar, 1977). Singh (1986) reported that the fossil fuel requirements for thermal processing of fruits and vegetables averages approximately 2.6 MJ kg^{-1} product; the electricity requirement for all other aspects of the process was only 0.19 MJ kg^{-1} (**Table 4**). Other values reported for thermal processing fruits and vegetables range from 1.2 MJ kg^{-1} for tomatoes to 8.4 MJ kg^{-1} for canned peas. According to the European Commission (2006), tomatoes, generally processed as a high acid food following a pretreatment to guarantee proper pH values (Derossi *et al.*, 2011), required 0.75–0.85 kg steam per kilogram of final product.

Coffee

Postharvest processing of coffee berries is biphasic (**Figure 2**). In the first phase, the outer layers of the cherry are removed (milling) and the beans are dried. The second phase of coffee processing involves roasting the green beans to generate the desirable coloring and characteristic flavors associated with coffee drinks. Although the whole, roasted beans are fully processed, other products may also be generated from the roasted beans such as ground coffee and instant coffee products (Humbert *et al.*, 2009). Green beans may also be subjected to decaffeination processes.

Typically the first phase of processing is conducted near the site of harvest. Depending on the variety and the desired product, the coffee cherries undergo a dry or wet process (Gonzalez-Rios *et al.*, 2007; Mussatto *et al.*, 2011). Arabica (*Coffea arabica*) beans are processed via both the wet and dry method, depending on the harvesting region, whereas robusta (*Coffea canephora*) beans are primarily processed by the dry method (ICO, 2013). The dry milling method is the simplest and typically involves solar drying the whole cherry to the desired moisture content (11–12%), although mechanical dryers can also be used to facilitate the process (Viere and Schaltegger, 2007). For the wet method, the exterior layers – skin and pulp – of the cherry are mechanically removed with water and the remnant pulp, mucilage, is removed via fermentation (Mussatto *et al.*, 2011) or machine (Gonzalez-Rios *et al.*, 2007). The beans are subsequently dried to obtain the

Table 4 Processing energy requirements for the production of various canned food products

Product	*Steam (kg kg^{-1})*	*Thermal/Fuel (MJ kg^{-1})*	*Electricity (MJ kg^{-1})*	*Total energy (MJ kg^{-1})*	*Reference*
Canned fruit and vegetable products					
Fruits and vegetables		2.6	0.19		Singh (1986)[a]
Peas[b]		8.4			Barreiro *et al.* (1984)
	3.1				
Tomatoes	0.75–0.85		0.07–0.09		European Commission (2006)
Tomatoes		1.2	0.10		Singh *et al.* (1980)
Clingstone peaches				2.2	Carroad *et al.* (1980)
Fruits and vegetables				5.3	Pierotti *et al.* (1977)
Canned meat products					
Various meats (chicken, sausage, etc.)				10.3	Pierotti *et al.* (1977)
Meat	0.8–0.9		0.5–1.4		European Commission (2006)
Tuna		4.4	0.8		Hospido *et al.* (2006)
Seafood		1.0	0.5		Nielsen *et al.* (2003)
Seafood[1]				8.9	Pierotti *et al.* (1977)
Other canned products					
Specialty products[c]				7.0	Pierotti *et al.* (1977)
Meals; fruits and vegetables				2.4	Ritchie (2013)
Meal (pork and beans)				2.9	Calderon *et al.* (2010)

[a]As reported in Carlsson-Kanyama and Faist (2000).

[b]Only includes thermal processing data.

[c]Ingredients are varied and include fruit, vegetables, beans, sugar, meats, flour, juices, fats, and oils.

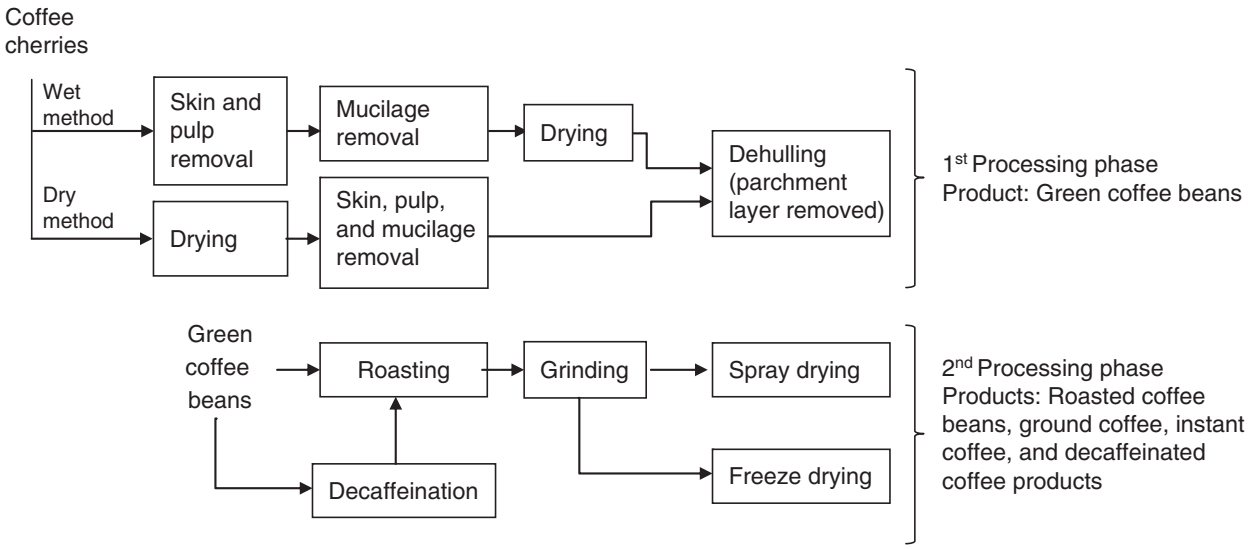


Figure 2 Flow diagram of the two phases of coffee processing.

proper moisture content. This process may involve sun-drying, the use of standard rotary drum dryers, or solar-powered dryers (Trubey, 2004). The final step of wet and dry milling is dehulling to remove the final layer – the parchment – and produce the green bean that is ready for roasting (ICO, 2013).

Owing to the immense variation in the milling and drying phase of coffee processing, the energy requirements differ extensively, particularly because the dry milling process requires significantly less energy than the wet milling process. The greater energy requirements of the wet process can be partially mitigated by the implementation of direct solar drying or solar-powered machinery during wet processing (Trubey, 2004). To complicate matters further, however, the potential to use direct solar drying (for either milling process) is geographically dictated, because climates with predominantly high humidity conditions would limit the radiant heat drying capacity. In addition, some facilities utilize fossil fuels (i.e., LPG), whereas others use firewood for the processing. One study cited a report by the European Commission (originally published in 2003) indicating that milling (unspecified type) required 0.16 MJ electricity per kilogram of green coffee beans and 1.8 MJ fuel per kilogram of green coffee beans (Ramirez *et al.*, 2006). Molina (2009) reported that wet milling electricity requirements ranged from 0.86–1.2 MJ kg^{-1} green coffee beans and firewood inputs ranged from 0.001–0.002 m^3 kg^{-1} of green coffee produced. Standard mechanical drying reportedly requires as much as 0.003 m^3 of firewood and 0.23 MJ of electricity per kilogram of green coffee (Trubey, 2004); thus, a significant portion of the energy requirements in the first phase is attributed to the drying process.

Whole green beans are roasted for 1–15 min between 180 and 240 °C to obtain the desired flavor, aroma, and color qualities (ICO, 2013). Roasted beans can be packaged and sold to consumers as whole beans or ground coffee or can be further processed to make instant coffee. Ramirez *et al.* (2006) reported that the production of roasted coffee required 2.2 MJ of fuel and 0.6 MJ of electricity per kilogram of coffee beans. However, an earlier report indicated that the total energy requirements may be as great as 12.4 MJ kg^{-1} of coffee bean (Pierotti *et al.*, 1977). In a recent LCA of green bean processing, the production of roasted, ground coffee required 2.6 MJ of fossil fuel per kilogram of product and 0.5 MJ of electricity per kilogram of product (Humbert *et al.*, 2009). However, the European Commission (2006) showed that the use of highly efficient roasters and water mist cooling of beans may reduce the processing requirements by 75% with the most efficient roasters using as little as 0.18 MJ kg^{-1} of roasted beans. In fact, according to Solomone (2003), improvements in the energy usage during the roasting phase should be emphasized over other aspects of coffee production.

For instant in coffee production, coffee is 'brewed' in the processing plant and the aqueous fraction is isolated from the spent grounds. Following concentration (by freeze concentration or evaporation), the liquid fraction is either spray-dried or freeze-dried to produce a granulated, soluble form of coffee (Sivetz and Desrosier, 1979). To manufacture spray-dried instant coffee from green beans, the specific energy requirements are very high – 30.2 MJ of fuel per kilogram of coffee and 8.3 MJ of electricity per kilogram of coffee (Humbert *et al.*, 2009). However, innovative methods to recover waste heat could potentially reduce energy demands during extraction (European Commission, 2006).

Corn Milling

Corn is processed according to two different methods: dry and wet. The dry process starts with dry kernels that are milled into a meal and used primarily for the fermentation industry, including ethanol and beverages. In the wet process (**Figure 3**), however, corn is fist soaked in water for 20–36 h at temperatures of 50 °C (Keller and Heckman, 2006) in what is called steeping, which generates a light steepwater byproduct rich in soluble compounds that is then concentrated by evaporation to produce heavy steepwater. Solids contained in the heavy steepwater are separated, mixed with fractions from other parts of the process, dried, and used as animal feed. The liquid

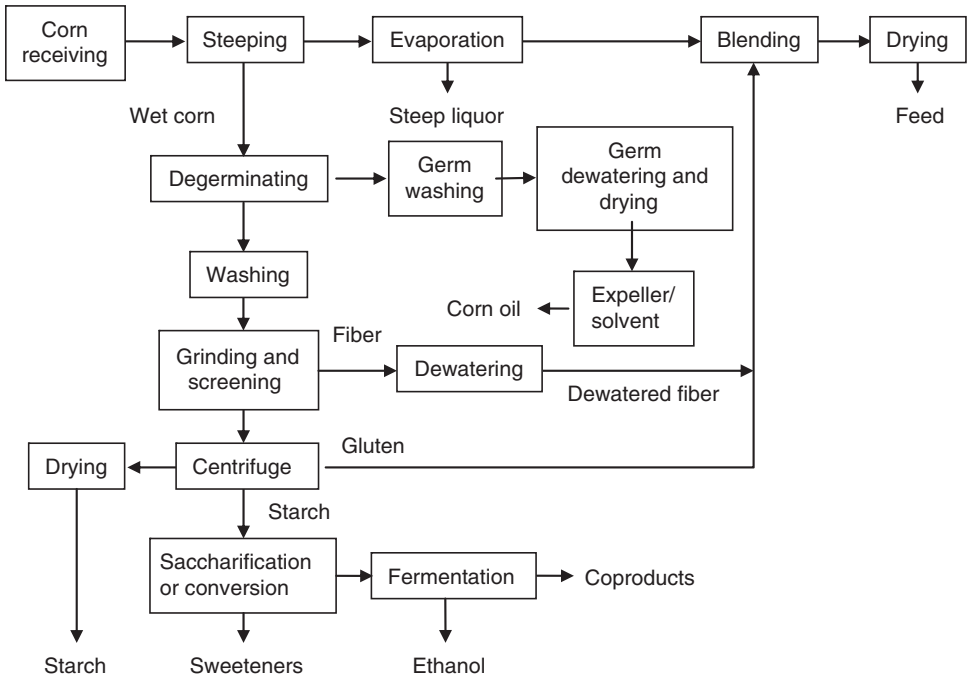


Figure 3 Simplified overview of a wet corn milling operation. Adapted from Keller and Heckman, 2006. Assessment Plan for Corn Steep Liquor (CAS #66071-94-1) in Accordance with the USEPA High Production Volume Chemical Challenge Program. 28 November 2006. Washington, DC: The Corn Refiners Association and EPA (Environmental Protection Agency) US, 1995b. Chapter 9: Food and agricultural industry, Section 9.9.7 corn wet milling. In Emission Factor Documentation for AP-42. Washington, DC: Environmental Protection Agency Office of Air Quality Planning and Standards Emission Inventory Branch.

stream is a concentrate of 40–60% solids called steep liquor, a basic nutrient in ruminant animals feed preparation, fermentation industry, and production of carboxylic acids (Keller and Heckman, 2006).

The corn kernels containing approximately one-third of the water added during steeping are processed in a germ separator, where the germ is removed and after drying used for the extraction of corn oil. The remaining material is washed and ground to produce a stream of hulls and a slurry containing starch, gluten, and other soluble organic compounds (EPA, 1995b). The hulls are combined with concentrated solids from the production of corn steep liquor and spent germs from the extraction of oil to produce, after drying, corn gluten feed. The slurry goes through a centrifuge that separates gluten, which after drying becomes gluten mill, and slurry that goes to a storage tank and from there used to produce modified and unmodified starch, dextrose, fructose, ethanol, etc.

Wet corn milling is an energy intensive operation because it involves dewatering, evaporating, and drying, all processes that requires significant amounts of energy. **Table 5** presents recent data for a wet corn milling operation of a scale of approximately 100 000 bushels a day (1 bushel of corn = 56 pounds = 25.4 kg) in the US. The table presents energy intensity in terms of incoming corn. Because of the assortment of products generated by the process and lack of mass flow data, it is not possible to allocate the specific energy expenses per unit of mass of different products.

In the dry process, dehulled corn kernels are first ground and then cooked, generally using a jet cooker. With the addition of enzymes, starch contained in the cooked slurry is transformed into glucose that then is used primarily to produce ethanol via fermentation. According to Tsiropoulos *et al.* (2013), using unspecified data sources from European facilities, it takes approximately 130 ton of corn to produce 88 ton of starch; and 1 ton of starch produces 1.1 ton of glucose. The energy requirements to convert corn into glucose are between 6.8 and 9.3 MJ kg^{-1} (Tsiropoulos *et al.*, 2013).

Dairy

Raw, unprocessed milk transported to a manufacturing plant can be processed into a plethora of dairy products, but one of the most common is pasteurized, homogenized liquid milk. To generate this commodity, fresh whole milk undergoes several processes – clarification, separation, homogenization, and pasteurization – before packaging (Korsstrom and Lampi, 2001). Clarification is the process of removing large particulates or contaminants from the milk; and separation is the process of separating the fat (or cream) from the skim milk (UNEP, 2000). Then the cream and skim milk are reunited in the proper proportions to generate the desired milk fat content (standardization) and homogenized. If necessary, the product may also be subjected to a flash heat treatment to remove undesirable aroma – deodorization. Finally, the milk is pasteurized to eliminate pathogenic microorganisms and to decrease spoilage microorganisms, thus extending the shelf approximately −4 °C for 10–28 days (Partridge, 2008). Although the requirements for pasteurized liquid milk are fairly low compared to other dairy products (**Table 6**), according to UNEP

Table 5 Estimated energy consumption for different processes in wet corn milling, based on a plant capacity of 100 000 bushel per day

Process	*MJ/(ton of corn)*			
	Electricity	*Steam*	*Fuel*	*Primary energy*
Corn receiving	18			54
Steeping	9	131		158
Steepwater evaporation	22	810		878
Germ recovery (1st grind)	28			87
Germ recovery (2nd grind)	14			45
Germ washing	1			3
Germ dewatering and drying	18	142	139	338
Fiber recovery	90			276
Fiber dewatering	16			48
Protein (gluten) recovery	41			128
Gluten thickening and drying	21		148	213
Starch washing	20			61
Starch dewatering and drying	111		1121	1463
Gluten feed dryer	40		931	1056
Total	450	1084	2340	4809

Source: Adapted from Galitsky, C., Worrell, E., Ruth, M., 2003. Energy Efficiency Improvement and Cost Saving Opportunities for the Corn Wet Milling Industry. An ENERGY STAR® Guide for Energy and Plant Managers. Berkeley, CA: University of California.

Table 6 Processing energy demand for various dairy products

	Description	*Thermal (MJ kg^{-1})*	*Fuel (MJ kg^{-1})*	*Electricity (MJ kg^{-1})*	*Total primary energy (MJ kg^{-1})*	*Source*
Milk	Milk		0.5	0.2		UNEP (2000)
	Milk				1.1	Ramirez *et al.* (2006a)
	Large-scale dairy 1[a]	1.7		0.5		Thompsson (1999)
	Large-scale dairy 2[a]	1.3		0.7		
	Small-scale dairy 1[a]	1.7		0.8		
	Small-scale dairy 2[a]	0.8		1.0		
	Small dairy			2.7		Eide (2002)[b]
	Medium dairy			0.7		
	Large dairy		0.3	0.2		
Cheese	Cheese		4.3	0.8		UNEP (2000)
	Cheese		5.4	1.3		Berlin (2002)
	Cheese				4.3	Ramirez *et al.* (2006a)
	Soft cheese				1.1	Molinari *et al.* (1995)[c]
Butter	Butter	0.8		0.6		Nielsen *et al.* (2003)
	Butter				2.2	Ramirez *et al.* (2006a)
Other dairy products	Dried milk				11.1	Ramirez *et al.* (2006a)
	Dried milk		20.6	1.4		UNEP (2000)
	Dried milk	7.9		1.4		Nielsen *et al.* (2003)
	Condensed milk				2.5	Ramirez *et al.* (2006a)

[a]Large-scale dairy 1 and small-scale dairy 1: Thermal energy source was oil; processes were not optimized. Large-scale dairy 2 and small-scale dairy 2: Energy was primarily derived from electricity; processes were more optimized.

[b]Estimated from figure.

[c]Calculated from data in figure without UF membrane.

(2000), the specific energy requirements for pasteurized milk in some dairy processing plants can still be reduced up to 75% on implementation of low-cost energy conservation techniques. However, in modern processing facilities, the heat recovered during pasteurization is up to 94% (Ramirez *et al.*, 2006a).

For shelf-stable milk, the product undergoes sterilization or ultra-high temperature (UHT) treatments rather than the milder pasteurization ones. The higher temperatures, although ensure the microbiological safety of the products at room temperature, typically require significantly more energy than pasteurized milk with the exception of indirect UHT (without direct contact with steam) that requires the same energy as pasteurization. The past two decades have seen a growing consumer demand for UHT and sterilized milk products in Europe (Ramirez *et al.*, 2006a). In France, for example, pasteurized milk comprises less than 14% of the market share of milk purchased; the remainder is UHT or sterilized milk (Ramirez *et al.*, 2006a).

For sweetened condensed milk, evaporated milk, and dried milk, pasteurized milk is concentrated by an evaporator (UNEP, 2000). To generate milk powder, the concentrate is spray-dried. The two processes – concentration and drying – are energy-intensive (Ramirez *et al.*, 2006a); thus, the production of dried milk requires 4–20 times more energy than pasteurized milk (**Table 6**). The variation in energy demand can be partly attributed to the heat-recovery capacity of the evaporators (UNEP, 2000). The type of evaporator can highly influence the evaporative efficiency – up to 7-fold – and the heat recovery and efficiency is dependent on several factors: (1) the number of evaporators in series that utilizes evaporated water from one unit as steam in the next (known as multiple effects or stages); (2) the use of vapor recompression – thermal or mechanical – to increase the pressure on the evaporated water from one unit to further elevate the heating capacity of the steam as it enters the next unit; and (3) the use of alternate technologies such as membrane filtration that require much less energy than traditional falling film evaporators (UNEP, 2000; Ramirez *et al.*, 2006a).

For canned evaporated milk, the concentrated milk is sealed in cans and sterilized by retort (UNEP, 2000). Unlike evaporated milk products, sweetened condensed milk does not undergo sterilization. Following concentration, sucrose and lactose are added to the concentrated milk which decreases the water activity and deters most microbiological growth without heat treatment (Farkye, 2009); thus, the energy demand for the production of sweetened condensed milk is less than evaporated milk (Ramirez *et al.*, 2006a).

Butter is produced from the unused cream isolated during the production of low-fat or skim milk. The cream is heated, cooled, and churned into butter (solids) and buttermilk (fluid) (Reddy, 2010). Following separation of the solids, the butter is formed, packaged, and cooled. Cultures and/or salt may also be added to the butter to generate a variety of end-products (Reddy, 2010). The most energy-demanding process during the butter production (not including milk pasteurization) is cooling (Ramirez *et al.*, 2006a).

For cheese, starter cultures are added to the cooled, pasteurized milk followed by rennet. The resulting curds and whey are cooked. Following removal of the whey, the blocks of curds are salted and molded. Depending on the processing methods, these steps comprise 7–14% of the total energy needed for cheese production and milk pasteurization accounts for 17–26% of the total energy (Xu *et al.*, 2009). If necessary, the cheese may also be maintained under controlled temperature and humidity for a specific duration – low temperatures and 90% humidity for soft cheeses and high temperatures and 75–85% humidity for hard cheeses – to develop characteristic flavors and aromas (known as ripening) (UNEP, 2000). According to Xu *et al.* (2009), ripening for more than 14 days can increase the specific energy demand by 9–65%. Generally, harder cheeses require longer ripening periods (UNEP, 2000). Thus, because of the variety of cheeses and processing methods used by cheese makers, the processing energy requirements can vary markedly (**Table 6**).

Yogurt and other fermented dairy products are produced by inoculating pasteurized milk or cream with various cultures (Vasiljevic and Shah, 2008). Numerous products are generated depending on the starting cultures utilized, the starting material (cream or milk), the extent of fermentation, and the flavor additives. Based on relative energy consumptions of dairy products, Feitz *et al.*, (2005) reported yogurt production required approximately six times more electricity and four times more fuel than pasteurized milk. In some cases, concentrated or dried milk is used along with fluid milk to produce yogurt (Gonzalez-Garcia *et al.*, 2012), which would potentially alter the total processing energy requirements because of the energy demand to produce the other concentrated milk products.

Yogurt or milk, can also be combined with other ingredients and subjected to rapid freezing to produce frozen yogurt or ice cream. Ice cream production involves many steps – preheating, mixing, pasteurization, homogenization, cooling, ageing (to stabilize the product), freezing, molding/extrusion (if necessary), and hardening – with many of the steps conducted at well below 0 °C (Korsstrom and Lampi, 2001). Although there is little data on ice cream processing, Korsstrom and Lampi (2001) reported that the energy consumption can range from 2.7 to 5.8 MJ kg^{-1} of ice cream, although they did not elaborate on how the energy values were calculated.

Flour

One of the most fundamental ingredients in baked goods (breads, cookies, cakes, etc.) is flour. Although this is typically wheat flour (Giannou *et al.*, 2003), there are a host of other flours – rice, rye, oat, and corn flour. However, for simplicity, the scope of this discussion will be wheat flour. The major step in the production of flour is milling (**Figure 1**) and consists of breaking up the grain with a series of corrugated rollers and sieves (EPA, 1995a). Before milling, the grains may be subject to drying, transport, storage, sorting/separating (to remove extraneous materials), cleaning, and tempering, which is the addition of moisture immediately before milling to facilitate the process (EPA, 1995a). The extent and necessity of grain drying is dependent on the harvest moisture content of the grain; thus, the energy demand for drying can vary by harvesting location and, even within a particular area, from year-to-year (Thompsson, 1999). Although the drying energy demands vary, Carlsson-Kanyama and Faist (2000) reported the energy requirements for grain drying to be 0.09 MJ electricity per kilogram and 0.01 kg oil per kilogram.

Using previously reported data, Thompsson (1999) generated a model of scenarios of energy efficiency within the baking industry and, in the model, the author reports milling utilizes 0.15–0.36 MJ electric energy per kilogram flour. Often milling energy demands incorporate all aspects of the production from receipt of the grain to flour production; thus, even transport mechanisms within the mill can affect the final energy demand (Thompsson, 1999). In addition, the primary energy demand for milling can vary depending on the size of the mill, according to Sundkvist *et al.* (2001). In their study of mills solely supplied by electricity, the average primary energy demands of small, medium, and industrial mills were 3.8, 0.6, and 0.9 MJ kg^{-1}. According to the Swedish LCA Food database (Nielsen *et al.*, 2003), mills that utilize both electricity and heat derived from fossil fuels, the average energy consumption is 0.3 MJ of electricity per kilogram of flour and 0.4 MJ of natural gas per kilogram of flour.

Table 7 Energy during the production of lemon, orange, and tomato juices

Product	*Process step*	*Units*	*Steam (kg kg^{-1})*	*Thermal (MJ kg^{-1})*	*Electric (MJ kg^{-1})*	*Source*
Lemon juice	Extraction	Per kilogram refined juice			0.03	Beccali *et al.* (2009)
	Refining	Per kilogram refined juice			0.01	
	Pasteurization	Per kilogram refined juice	0.05[b]		0.06[b]	
	Concentration	Per kilogram concentrated juice	2.28[b]		0.40[b]	
Orange juice	Extraction	Per kilogram refined juice			0.03	
	Refining	Per kilogram refined juice			0.01	
	Pasteurization	Per kilogram refined juice	0.05[b]		0.06[b]	
	Concentration	Per kilogram concentrated juice	2.58[b]		0.50[b]	
	Concentration	Per liter concentrated juice		1.20	0.02–0.03	Molinari *et al.* (1995)
Tomato juice	Hot break	Per kilogram concentrated juice		0.30		Molinari *et al.* (1995)
	Evaporation	Per kilogram product[a]	0.45–0.54		0.06–0.09	European Commission (2006)
	Evaporation	Per kilogram concentrated juice		12.9	0.11	Molinari *et al.* (1995)
	Pasteurization	Per kilogram product[a]	0.02–0.02		0.001	European Commission (2006)
	Pasteurization	Per kilogram concentrated juice		0.01	0.006	Molinari *et al.* (1995)
	Sterilization	Per kilogram product[a,c]		0.13	0.016	
	Sterilization	Per kilogram product[a,d]		0.26	0.016	

[a]Used 0.3 to adjust to proper Brix range (7–12 degrees).
[b]Includes cooling.
[c]Concentrated tomato juice (after traditional evaporation).
[d]Concentrated tomato juice (after RO+evaporation).

Juice

Commercial juices are the result of extracting liquids contained in fruits or vegetables and used primarily as beverages. The type of plant material used to produce juices varies by country and region of the world. The bulk of fruit juices production and commercialization are citrus – including oranges, lemons, tangerines, grapefruits, apples, and grapes; and, to a lesser extent, nectarine, peach, pears, pineapple, and berries. Of vegetables juices, tomato is produced in the greatest quantity.

The extraction process from different fruits and vegetables is generally process specific. The availability of data of energy consumptions during processing of fruit and vegetable juices is very limited; therefore this section will review only orange, lemon, and tomato juices.

Orange juice is commercialized as fresh unpasteurized, chilled (with pulp and without pulp), frozen concentrate, and canned. Lemon juice is generally commercialized as a frozen concentrate. Both oranges and lemons are citruses and the extraction processes are similar. Once transported to the processing plant, citrus fruits are first graded and washed before proceeding to juice extraction. To maintain quality, the juice is separated quickly from the peel, membrane, and seeds using extraction cups, or other methods, to prevent the extractives from contaminating the juice with bitter compounds. Then the extracted juice goes through screens to remove pulp and sacs. Further pulp removal is achieved by the finishing process. According to the literature found, extraction takes a modest amount of energy of approximately 0.03 MJ of electricity per kilogram of finished juice; and refining or finishing, about a third of that energy (Table 7). Pasteurization doubles the amount of electricity used during extraction, but also has a fairly small input of thermal energy. Concentration is by far the step that utilizes the most thermal energy. As stated by Beccali *et al.*, (2009), it takes 2.28 and 2.58 kg of steam to produce 1 kg of concentrate, which according to the same author is made with approximately 5 kg of refined juice. Assuming the service steam has a pressure of 1.37×10^5 Pa (20 psi), the enthalpy of steam at this pressure is 2.69 MJ kg^{-1}; and therefore, the thermal energy in the concentration process varies between 6 and 7 MJ kg^{-1} of concentrate. Assuming it takes approximately 3.3 MJ of fuel to deliver 1 MJ of electricity at the factory gate and an efficiency of the boiler/steam distribution system/evaporator to be approximately 80%, consumption of electricity at evaporation (compared on the basis of primary energy) is approximately 4.5 times less than thermal energy. Besides juice, citrus byproducts produce an assortment of valuable products, including energy recovery that will not be included in this discussion.

The process to produce tomato juice is different than the one for citrus. Production of tomato juice follows a similar process than other tomato products (Figure 4). There are two technologies to process tomatoes: cold break and hot break. The hot break consists of chopping the tomatoes at temperatures of 85–90 °C to deactivate pectinmethylesterases and polygalacturonases that cause degradation of pectins. In the cold break process, tomatoes are disintegrated at temperatures below 70 °C. The hot break process yields products with high viscosities which are less prone to syneresis. The cold break, however, generates a tomato paste that is thinner, but with a fresher aroma (Goodman *et al.*, 2002).

In the hot-break process, tomatoes are pumped through the hot-break system where tomatoes are heated and held to deactivate enzymes before proceeding to the juice extractor. In the cold-break system, tomatoes are crushed, heated in a heat exchanger, and then sent through the juice extractor that

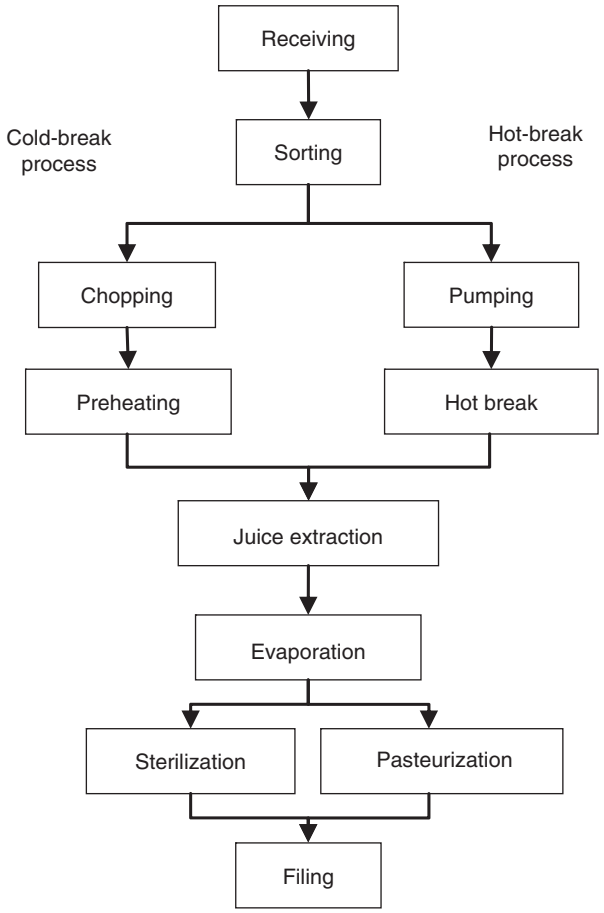


Figure 4 Tomato juice extraction process.

separates the juice from seeds, skin, and fibers. From there, the juice goes through a concentration process followed by pasteurization or sterilization and packaging. Typical values of energy consumption during tomato juice production are presented in **Table 7**.

In the data presented by Molinari *et al.* (1995), the use of reverse osmosis along with traditional evaporation techniques significantly reduces the amount of thermal energy required to concentrate tomato juice; however, the final product temperature is lower than the product of traditional evaporation, so slightly more energy is required to attain sterilization temperatures.

Meat

Meat can be obtained from virtually any animal, but the three most common sources are cattle, swine, and chicken. The basic universal processing steps in slaughterhouses consist of: (1) immobilizing and stunning the animal; (2) slaughtering and bleeding of the animal; (3) removing undesirable external parts (feathers, hide, hair, etc.); (4) decapitation; and (5) evisceration (or removal of internal organs) (IFC, 2007a; IFC, 2007b). The product of these processing steps is referred to as the dress carcass.

Although the major steps are the same in meat processing, there is some variation in the specific treatments of cattle, swine, and chicken that can affect the specific energy required for processing. Poultry carcasses, for example, are subjected to hot water treatment (50–60 °C) after bleeding to facilitate feather removal (Finnish Environment Institute, 2002) with lower temperatures ('soft-scalding') used for products to be chilled and higher temperatures ('hard-scalding') used for products to be frozen (Ramirez *et al.*, 2006b). Ramirez *et al.* (2006b) estimated that the difference in energy demand for the techniques is approximately 0.08 MJ kg^{-1}. Similar to poultry, pigs are also subjected to scalding (followed by mechanical or water abrasion) to facilitate the removal of hair; however, the process is not comprehensive and pigs require an additional hair removal treatment (Finnish Environment Institute, 2002). This involves the carcass being placed briefly in an oven (held at 900–1000 °C) to singe the persistent hairs as well as reduce the microbial load and alter the skin texture (IFC, 2007a; European Commission, 2005). In addition, if bacon is the desired end-product, the singeing is more extensive and the product requires additional treatments to generate a polished skin (or rind) (IFC, 2007a; European Commission, 2005). Owing to these heat treatments, the specific thermal energy requirements for pork processing tend to be greater than chicken and beef; however, the specific electricity (and total primary energy) requirements for chicken processing are greater than the beef and pork (**Table 8**).

The end-products of meat processing facilities are highly varied and, consequently, so are the energy requirements for processing (**Table 8**). The facilities may also debone, cut, grind, cook, dehydrate, sterilize/pasteurize, smoke, chill, or freeze the meat (European Commission, 2006; IFC, 2007a). Cutting and deboning can require an additional 0.76 MJ kg^{-1} of dressed carcass (primary energy) (Ramirez *et al.*, 2006b). For the production of hamburgers, Carlsson-Kanyama and Faist (2000) reported that grinding and frying the ground beef requires an additional 0.3 and 5.1 MJ of electricity per kilogram of product, respectively. Similarly, because of the extensive processing (compared to raw meats), sausages and salami require significantly greater processing energy than other meat products (**Table 8**).

The energy demand of these processes can also be affected by the types of meat. For example, the additional energy required to freeze meat after the initial processing is dependent on the type of carcass (in primary energy): beef, veal, or sheep requires 0.72 MJ per kilogram of product; pork requires 1.0 MJ kg^{-1} of product; and poultry requires 1.2–2.4 MJ kg^{-1} of product. The higher specific energy demands for poultry are attributed to the additional energy required for the hard scalding treatment, a prerequisite of frozen poultry (Ramirez *et al.*, 2006b).

According to the Finnish Environment Institute (2002), however, the heat recovery potential in slaughterhouses can be up to 0.21, 0.43, and 0.79 MJ kg^{-1} for cattle, pig, and poultry, respectively. In addition, the implementation of steam (or spray scalding) can potentially conserve energy in pork processing (European Commission, 2005) as well as reduce microbial cross-contamination in poultry processing (IFC, 2007b).

Table 8 Processing energy requirements for various meat products

Category	*Product units*	*Thermal (MJ kg^{-1})*	*Electricity (MJ kg^{-1})*	*Total primary energy (MJ kg^{-1})*	*Source*
Pork[a]	Cut meat	0.63	0.41		Nielsen *et al.* (2003)
Pork	Boneless meat	0.5[c]	3.5		Cederberg (2003)[b]
Pork	Slaughtered animal	1.3–2.2	0.75–1.3		Finnish Environmental Institute (2002)
Pork[a]	Dress carcass			2.1	Ramirez *et al.* (2006b)
Chicken[a]	Slaughtered animal	0.1–0.6	0.6–3.1		IFC (2007b)
Chicken[a]	Slaughtered animal	0.43	0.76		IFC (2007b)
Chicken[a]	Slaughtered animal	0.49	0.99		Nielsen *et al.* (2003)
Chicken[a]	Slaughtered animal	1.8	1.7–1.8		Finnish Environmental Institute (2002)
Poultry[a]	Dress carcass			3.1	Ramirez *et al.* (2006b)
Beef[a]	Cattle meat	0.18	0.16		Nielsen *et al.* (2003)
Beef	Beef (unspecified)			4.2	DEFRA (2006)
Beef	Slaughtered animal	0.58–0.79	0.64–0.79		Finnish Environmental Institute (2002)
Beef, veal, sheep[a]	Dress carcass			1.3	Ramirez *et al.* (2006b)
Various meats	Processed product	4.3[d]	0.83		Ramirez *et al.* (2006c)
Meat products[a]	Final product			5.5	Ramirez *et al.* (2006b)
Salami/Sausages	Finished product	3.6	2.7		Nordic Council (2001)
Salami	Finished product	3.2	3.6		Nordic Council (2001)
Various sausages[e]	Finished product	1.6	4.7		Nordic Council (2001)

[a]Chilled' or 'fresh.'
[b]Values estimated from figure.
[c]Reported as 'fossil fuel.'
[d]Reported as 'fuel+heat.'
[e]Vienna sausages.

Oils

Oils are lipid-rich extracts derived from diverse sources including seeds, nuts, fruits, and legumes. The oil is derived from milling – sorting and cleaning, removing husks, and crushing – and extraction from the source. Before extraction, the milled plant material may also be subject to conditioning (heating) to facilitate the extraction process (Brown *et al.*, 1996; Schmidt, 2007). Extraction can be solely mechanical (pressing), physical (boiling/heating), or chemical (by the addition and subsequent removal of hexane) or involve a combination of three processes (European Commission, 2006; IFC, 2007c; Schmidt, 2007). In addition, for many oils, a refining step is necessary. Refining is a multistep process which can vary depending on the oil and the use of physical or chemical techniques (IFC, 2007c). Degumming, neutralization, soap splitting, bleaching, deodorization, and hardening are the major steps involved in refining oils (IFC, 2007c; European Commission, 2006).

The processing for each type of oil can be widely varied, so energy consumption can vary considerably as well. In addition, reported energy consumption depends on how the values were obtained: by direct measurement or estimated with databases. Data presented in **Table 9** comes mainly from LCAs conducted by different authors using data from databases.

Soybean, rapeseed, and sunflower oils have similar extraction processes using hexane; and energy intensities to produce these oils are in the same order or magnitude. Traditional palm oil and kernel oil extraction have lower overall energy consumption than oils obtained with solvent extraction, because they use mechanical extraction and recovery of energy. The net energy consumption of palm oil extraction is fairly low, whereas the gross thermal energy consumption is high (**Table 9**). The reason for the difference is that many palm oil mills obtain most or all of the processing steam and electricity from the incineration of palm shells. In addition, palm kernels are a byproduct of milling during palm oil production (Schmidt, 2007). As a result, palm kernel oil production generally does not require as much energy as other oils.

Data for olive oil are limited and the lowest estimate is approximately 10 times less than the highest, which could be indicative of the difference in processes, estimation methods, and the inclusion or not of the refining step. Sources do not specify if the values correspond to net energy consumed or expressed as primary energy.

Rice

Once harvested, rice is either dried on site or transported to commercial dryers (**Figure 5**). At harvest, rice moisture content is too high to make it stable for long term storage; therefore, its moisture content needs to be lowered to approximately 13% to preserve its quality and safety (Howell and Cogburn, 2004). Drying is the most energy intensive operation during rice processing. It accounts for approximately 55% of the total energy used from farm production to finished product. Of the

Table 9 Energy required for the production of various vegetable oils on the basis of finished product. Energy values are specific for extraction and refining unless otherwise specified

Oil source	*Steam*	*Heat/Fuel (MJ kg^{-1})*	*Electricity (MJ kg^{-1})*	*Total energy (MJ kg^{-1})*	*Source*
Coconut[a]	0.52 MJ kg^{-1}	0.05	0.38		Schmidt (2004)
Olive[b]				0.32–0.42[c]	European Commission (2006)
Olive				2.9[c]	Ozilgen and Sorguven (2011)
Palm	0.21 kg kg^{-1}	1.07	0.17		Nilsson *et al.* (2010)
Palm[d]	8.80 MJ kg^{-1}	0.33	0.51		Schmidt (2007)
Palm kernel	0.21 kg kg^{-1}	1.08	0.17		Nilsson *et al.* (2010)
Palm kernel	0.33 MJ kg^{-1}		0.89		Schmidt (2007)
Palm kernel[a]	0.74 MJ kg^{-1}	0.07	0.54		Schmidt (2004)
Rapeseed	1.76 MJ kg^{-1}+0.27 kg kg^{-1}	1.05	0.52		Nilsson *et al.* (2010)
Rapeseed		1.60	0.43		Nielsen *et al.* (2003)
Rapeseed	1.8 MJ kg^{-1}		0.53		Schmidt (2007)
Soybean		2.24	0.23		Nielsen *et al.* (2003)
Soybean		0.71	0.15		Schmidt (2007)
Sunflower	1.76 MJ kg^{-1}+0.27 kg kg^{-1}	1.05	0.55		Nilsson *et al.* (2010)
Sunflower				2.0[c]	Ozilgen and Sorguven (2011)
Vegetables[e]	1.1–4.2 MJ kg^{-1}		0.09–0.23		European Commission (2006)

[a]Milling.
[b]Two-phase or three-phase extraction.
[c]Primary energy not specified.
[d]Gross energy.
[e]Various; refining.

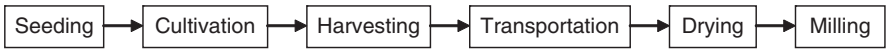


Figure 5 Production of milled rice. Adapted from Kasmapraphruet, S., Paengjuntuek, W., Saikhwan, P., Phungrassami, H., 2009. Life cycle assessment of milled rice production: Case study in Thailand. European Journal of Scientific Research 30 (2), 195–203.

remaining 45%, 15% goes to harvesting, 10% to cultivation, 10% to seeding, 6% to transportation, and 4% to milling (Kasmapraphruet *et al.*, 2009).

Energy use during drying varies significantly according to the type and variety of grain, type of dryer, drying temperature, relative humidity, initial moisture content, and final moisture content, among the most important factors. In the case of rice, initial moisture content also affects the head rice yield (HRY), which is the mass percentage of kernels that after milling have a length of 75% or more of the original length (Cooper and Siebenmorgen, 2007). Typical harvest moisture contents range from 20% to 30%, depending on the extent of rain (Bergqvist *et al.*, 2008); but in a study conducted in Arkansas, Bautista and Siebenmorgen (2009) found that the optimal harvest moisture content that maximizes HRY is 18.2–21.6% for long-grain varieties, 19.0–20.4% for medium grain cultivars, and 17.7–19.0% for the long-grain hybrid 'XL723.' According to Gunasekaran and Thompson (1986) energy to dry crops can vary between 3 and 8 MJ kg^{-1} of water removed. Specifically for rice, a recent study conducted on cross-flow dryers showed that the thermal energy required to dry rice ranged from 6.9 to 9.7 MJ kg^{-1} of water removed (Billiris, 2013).

As indicated by different authors, energy requirements for rice milling are at least one order of magnitude (10 times) less than the thermal requirements to dry (**Table 10**). Milling is the operation to transform rough unprocessed rice into white or brown rice. In **Table 10**, the average energy intensity of milling is approximately 55% more when expressed on the basis of paddy (rough rice, or unprocessed rice kernels) than of finished rice. The opposite would be expected because it takes approximately 1.5 kg of paddy (depending on the HRY) to produce 1 kg of rice. However, most sources do not report the HRY, which makes difficult to establish a fair comparison. In addition, energy use during milling depends on the degree of milling, which is the extent of removal or bran and germ from the kernel during milling (Cooper and Siebenmorgen, 2007). In a study conducted in Japan, DOM of 2, 5, and 10% required electricity intensities of 0.30, 0.38, and 0.96 MJ kg^{-1} of finished rice, respectively (Roy *et al.*, 2009).

Parboiling is a technique used around the world, but it is especially important in the developing countries of Asia. Parboiling consist of partially boiling the dry paddy while it is still in the husk, followed by drying, dehusking, and milling (Roy *et al.*, 2007). Data for rice parboiling in India and Bangladesh are presented in **Table 11**. Before milling, the parboiled paddy must be dried to 14–16% (Kapur *et al.*, 1997). This is particularly important because the moisture content of parboiled rice is typically in excess of 30% (Kapur *et al.*, 1997). Drying can be conducted via direct solar radiation to mitigate some of the energy requirements (Ahiduzzaman and Islam, 2009). Owing to hardening of the husk after parboiling, milling of parboiled rice requires more energy than rough rice (Borah and Prasad, 1994; Kapur *et al.*, 1997). Rice husk can be utilized as a source of energy – typically thermal energy although use as an electric energy source has been explored (Kapur *et al.*,

Table 10 Energy requirements to mill rice

	HRY	Fuel ($MJ\ kg^{-1}$)	Electricity ($MJ\ kg^{-1}$)	Average electricity ($MJ\ kg^{-1}$)	Country	Source
Per kilogram of rice			0.014	0.39	Europe	Carlsson-Kanyama (1998)
		0.12	0.23		Unknown	Singh (1986)
			0.08–0.14		India	Bureau of Energy Efficiency (BEE) India (2010)
		0.049	0.023		Thailand	Kasmapapruet *et al.* (2009)
Per kilogram of paddy (unprocessed rice kernels)			0.11	0.60	India	Borah and Prasad (1994)
	65%		0.093		India	Goyal *et al.* (2008)
			0.29		India	Kapur *et al.* (1996)
	68%		0.11		Bangladesh	Roy *et al.* (2007)

Table 11 Energy consumption to produce parboiled rice

Process	Units (kg^{-1})	HRY (%)	Thermal ($MJ\ kg^{-1}$)	Rice husk[a]	Electricity ($MJ\ kg^{-1}$)	Country	Source
Parboiling and milling	Paddy	70		0.20 kg kg^{-1}	0.14	Bangladesh	Roy *et al.* (2007)
		70		0.13 kg kg^{-1}	0.14	Bangladesh	
		68	3.1		0.20	India	Goyal *et al.* (2008)
	Rice			0.20–0.27 kg kg^{-1}	0.10–0.12	India	Bureau of Energy Efficiency (BEE) India (2010)
Parboiling	Paddy	66–69		1.6–2.8 MJ kg^{-1}		India	Roy *et al.* (2006)
				1.68 MJ kg^{-1}		Bangladesh	Ahiduzzaman and Islam (2009)
			0.87–1.5			India	Kapur *et al.* (1996)

[a]Typical rice husk energy density: 11.7–15.1 MJ kg^{-1} rice husk (Bureau of Energy Efficiency, India).

1997). Approximately 0.1 kg rice husk is generated by 1 kg rice (Kasmapapruet *et al.*, 2009) and the energy density of rice husk is 11.7–15.1 MJ kg^{-1} (Bureau of Energy Efficiency (BEE) India, 2010).

Sugar

Table sugar, or sucrose, is saccharose obtained commercially from beets and sugarcane. Sugarcane is grown in tropical and semitropical parts of the world, whereas beets belong to colder climates. In the US and Europe, beets are almost the exclusive sources of sucrose. In the UK, for example, 60% of the sugar is obtained from sugar beet, whereas the remaining sugar (from sugarcane) is imported (Vaccari *et al.*, 2005). In addition to beets, the US also produces sugarcane in the states of Florida, Louisiana, Texas, and Hawaii. In the US, there is also direct competition for sucrose from sweeteners obtained from corn. According to data from 2004, of the 45 kg consumption of sweeteners per capita in the US, approximately 60% were sweeteners from corn and the remainder was table sugar (Haley *et al.*, 2005).

One of the first steps in sugar production is the extraction of sugary juices from the plant material. Sugarcane is crushed and the juice separated from the bagasse, which is burned in boilers. According to Ramjeawon (2004), after sugar processing, there is a surplus of approximately 0.2 MJ of energy per kilogram of sugarcane from burning bagasse. The juice goes through a clarification process and then through evaporators to concentrate the clear juice into sugar liquor. Crystallizers then transform the sugar liquor into crystals that are separated with a centrifuge and dried to become raw sugar. Beets, however, are sliced and passed though a diffuser where sugar is extracted with water to produce a raw juice that then goes through similar steps as sugarcane.

Raw sugar can be used as is, but it is more commonly transported to sugar refineries to produce refined sugars. Many sugar mills produce straight refined sugar by cleaning up the concentrated liquor before the crystallization step.

Data on energy consumption of sugar production is limited and variable (**Table 12**), which makes generalizations challenging. In addition, the literature describes the use of thermal energy in many different ways – thermal, steam, hot water, and fuel – without specifying how the different forms of energy are transformed into each other. Because the process of raw sugar production requires phase changes (e.g., evaporation and crystallization), the need for thermal energy surpasses electricity by at least one order of magnitude. According to data for cane sugar, the refining process takes much less energy than production of raw sugar, but still requires more thermal energy than electricity.

Greenhouse Gas Footprint

There are natural greenhouses – carbon dioxide (CO_2), water vapor, methane (CH_4), and nitrous oxide (N_2O) – and man-made ones – HFCs, perfluorocarbons (PFCs), and sulfur hexafluoride (SF_6). All these gases are directly or indirectly emitted

Table 12 Energy or fuel needed to produce 1 kg^{-1} of sugar

		Thermal ($MJ\ kg^{-1}$)	*Steam ($MJ\ kg^{-1}$)*	*Fuel ($MJ\ kg^{-1}$)*	*Electricity ($MJ\ kg^{-1}$)*	*Total ($MJ\ kg^{-1}$)*	*Source*
Beets	Raw		11.49	5.84[k]	0.58		Brown *et al.* (1996)
	Unknown					5.5[a,l]	Vaccari *et al.* (2005)
	Refined					7.15[a]	European Commission (2006)
	Unknown	6.1			0.07		Nielsen *et al.* (2003)
	Raw			2.19[h]; 0.33[i]	0.74		Renouf *et al.* (2008)
Cane	Raw					0.27[b,c,d]	Ramjeawon (2004)
	Raw	21[e]			0.44[e]		Singh (1986)
	Raw			0.07[c,j,k]			Renouf *et al.* (2008)
	Refining process	1.16	1.73	0.58	0.21		Singh (1986)
	Refining process		4.21[f]	0.58[g]	0.15		Brown *et al.* (1996)

[a]Source does not indicate whether the data is primary energy or not.
[b]Primary energy.
[c]Net energy = gross energy − energy generated from bagasse.
[d]Assumption from text: 1 ton sugar is produced from 9.07 ton of sugarcane.
[e]Gross energy.
[f]Includes hot water (145–195F).
[g]Includes recharging of the charcoal filter.
[h]Natural gas.
[i]Coke.
[j]Coal.
[k]Nonspecified fuel.
[l]200 kWh ton^{-1} of beet × (3.6 MJ kWh^{-1})×(1 ton of beet/130 kg of sugar) = 5.5 MJ kg^{-1} of sugar.
Source: Adapted from Agribusiness Handbook: Sugar Beet. White Sugar, Rome, Italy: Food and Agriculture Organization of the United Nations, p. 7.

by food processing plants as a result of energy produced and acquired, use of fossil fuels, refrigeration equipment, materials used in the process, waste treatment, and other sources.

The levels of GHGs emitted by food processing plants depend on the degree of processing, the products, and the type of processing. As a generalization, the more extensive the processing, the more GHGs are produced at the processing stage, but it also reduces emissions at the consumption stage. For instance, with ready-to-eat products, the emissions of food preparation from households are transferred to the processing stage and vice versa for products that require less processing.

The type of processing dictates the type of greenhouse gas emissions. Freezing and refrigeration emissions are the result of energy consumption and fugitive emissions of refrigerants – HFCs. Processing by application of thermal energy – blanching, pasteurization, sterilization, evaporation, extrusion, drying, baking and roasting, and frying – emits mainly carbon dioxide from the combustion of fossil fuels. Emissions from mechanical processes (including electric motors) come from purchased or generated electricity. The type of packaging also influences emissions not only from the production of the package itself, but also from the production of the packaging materials. Embedded emissions of carbon dioxide and the perfluorocarbons CF_4 and C_2F_6 are common during aluminum packaging production; and embedded emissions of carbon dioxide are generated during paper, steel, and plastic packaging production.

Greenhouse Gases Emissions Inventory

A GHGs inventory is a computation of GHGs emitted to and removed from the atmosphere over a period of time. The inventory includes the six major GHGs – CO_2, CH_4, N_2O, HFCs, PFCs, and SF_6.

There are protocols to conduct GHGs inventories, but the one created by the Greenhouse Gas Protocol Initiative (GHG Protocol, 2004) is the most commonly followed. The GHG protocol divides emissions in two broad groups: direct and indirect. Direct emissions are GHGs generated by sources controlled by the reporting company; and indirect emissions are those resulting from activities developed by the reporting company, but they happen in facilities owned or controlled by another entity. To make a more accurate computation of GHGs emissions, the GHG protocol categorizes direct and indirect emissions in three broad scopes (GHG Protocol, 2004):

Scope I: Direct emissions from stationary and mobile sources owned or controlled by the entity, such as on-site generation of electricity, fuel burned by boilers, fugitive emissions from equipment (e.g., refrigeration equipment), on-site wastewater treatment, on-site solid waste treatment, vehicles, equipment, etc.
Scope II: Indirect emissions from purchased electricity, steam, and other energy sources.
Scope III: Other indirect emissions from sources that are not owned or controlled by the entity and are not included in Scope II, for instance employee commuting and traveling, services outsourced by the entity, such as off-site wastewater treatment and solid waste disposal.

The GHG Protocol (2004) prescribes the following sequence of steps to conduct the inventory: (1) defining the business goals of the inventory; (2) setting the organizational boundaries to identify the operations controlled by the company; (3) setting operational boundaries to identify the emissions related with each operation and their

Table 13 Emission factors for the combustion of selected fuels

	kg CO_2 per ton	*g CH_4 per ton*	*g N_2O per ton*
Anthracite coal	2857.6	303.6	44.2
Bituminous coal	2561.3	301.7	43.9
Subbituminous coal	1841.0	208.7	30.4
Lignite coal	1506.2	171.9	25.0
Coke	2783.7	300.1	43.6
Municipal solid waste	992.7	350.2	46.0
Agricultural byproducts	1072.4	290.4	38.1
	kg CO_2 std. cubic ft	*g CH_4 std. cubic ft*	*g N_2O std. cubic ft*
Natural gas (per scf)	0.055	53.02	0.10
	kg CO_2 per l	*g CH_4 per l*	*g N_2O per l*
Crude oil	2.72	0.11	0.02
Distillate fuel oil no. 1	2.69	0.11	0.02
Kerosene	2.68	0.11	0.02
Liquefied petroleum gas	1.53	0.07	0.01
Motor gasoline	2.32	0.10	0.02
Petroleum coke	3.87	0.11	0.02
Propane	1.48	0.07	0.01
Biodiesel (100%)	2.50	0.04	0.00
Ethanol (100%)	1.52	0.02	0.00
Vegetable oil	2.59	0.03	0.00

Note: Data calculated from Table 1 of EPA (2011) and, with exception of natural gas, converted to per metric ton or per liter basis.
Source: Adapted from EPA (Environmental Protection Agency) US, 2011. Emission Factors for Greenhouse Gas Inventories. Available at: http://www.epa.gov/climateleadership/documents/emission-factors.pdf (accessed 26.04.13).

characterization as direct or indirect emissions; (4) tracking emissions over time, which consist of choosing a base year and then recalculating base year emissions based on structural changes, such as mergers, acquisitions, outsourcing, insourcing, etc.; (5) identifying and calculating GHG emissions and converting the emissions into CO_2-equivalents; (6) reporting according to the accounting principles of relevance, completeness, consistency, transparency, and accuracy; and (7) verification, which is an optional step conducted by a third-party auditor.

Greenhouse Gases Emissions Inventory

Because carbon dioxide is not the only greenhouse gas and considering that all GHGs have different global warming potentials, a way to standardize emissions for the purpose of accounting is to use the concept of carbon dioxide equivalent, CO_2-eq. Using this approach, the global warming potential (GWP) of different gases are expressed relative to carbon dioxide, which is assigned the value of 1. So, for instance, the GWP of methane for a 100-year horizon is 21. This means its GWP is 21 times more powerful than carbon dioxide. Global warming potentials relative to CO_2 are calculated using different horizons, typically 20, 100, 500 years, with the 100-year horizon generally used for GHG emission inventories.

Based on the standardization just described, the GHG emissions expressed as CO_2-eq for a particular gas (i) is calculated as:

$$\text{GHG emissions in } CO_2\text{–eq}_{(i)} = \text{emission factor}_{(i)} \times \text{activity rate} \times \text{GWP}_{(i)}$$

Table 14 Emissions factors for electricity generation in selected countries 1999–2002

Country	*CO_2 (ton/MWh)*	*CH_4 (kg/MWh)*	*N_2O (kg/MWh)*
Iceland	0.001	0.000 03	0.000 01
Costa Rica	0.015	0.000 57	0.000 11
France	0.083	0.001 36	0.000 93
Colombia	0.157	0.002 80	0.001 85
Canada	0.223	0.003 90	0.003 51
Canada	0.223	0.003 90	0.003 51
Argentina	0.317	0.005 70	0.001 01
Ukraine	0.345	0.010 35	0.009 99
Russia	0.351	0.013 79	0.006 68
Nigeria	0.372	0.014 44	0.001 89
Nigeria	0.372	0.014 44	0.001 89
Mexico	0.593	0.016 76	0.002 30
US average	0.687	0.020 51	0.011 36
Poland	0.730	0.010 84	0.015 28
Morocco	0.809	0.018 74	0.014 67
Jamaica	0.819	0.037 16	0.007 43
Israel	0.839	0.017 69	0.013 18
Greece	0.887	0.014 53	0.011 41
India	0.999	0.016 64	0.019 59
Libya	1.146	0.036 99	0.007 05

Source: Adapted from EIA (Energy Information Administration) US 2007. Instructions for Form EIA-1605: Voluntary reporting of greenhouse gases. Appendix F. Electricity emission factors. Available at: http://www.eia.doe.gov/oiaf/1605/pdf/Appendix%20F_r071023.pdf (accessed 25.04.13).

where emission $\text{factor}_{(i)}$ = quantity of GHG produced per unit of activity rate, for instance kilogram of CH_4 per liter of diesel. A list of emission factors for different fuels is presented in Table 13. Emission factors for processes depend on the particular process, the technology, the capacity, and the age of the

Table 15 Global warming potential (GWP) for a 100-year horizon of selected gases

Gas	*Lifetime (years)*	*100-year GWP*	*Sources*
Carbon dioxide (CO_2)	Variable	1	Stationary and mobile emissions from fossil fuel combustion and processes
Methane (CH_4)	12	23	Combustion of fossil fuels, waste treatment, landfills, livestock
Nitrous oxide (N_2H)	114	296	Agriculture, stationary, and mobile emissions from fossil fuel combustion
Hydrofluorocarbons (HFCs)			Refrigeration and cooling systems, foams, propellants for aerosols
HFC-23	260	9 400	
HFC-32	5	550	
HFC 125	29	3 400	
HFC-134a	14	1 300	
HFC143a	52	4 300	
Perfluorocarbons (PFCs)			Semiconductor manufacturing, aluminum production
CF_4	50 000	5 700	
C_2F_6	10 000	11 900	
Sulfur hexafluoride (SF_6)	3 200	22 200	High voltage applications, semiconductor manufacturing, magnesium production

Source: Adapted from Intergovernmental Panel on Climate Change (IPCC), 2001. Climate change 2001: The scientific basis. In: Houghton, J.T., Ding, Y., Griggs, D.J., *et al.* (eds.) Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, MA: Cambridge University Press, p 881.

equipment among others. Their values can be found in specialized literature, reports, manufacturers, or direct measurement. The emission factors for electricity depend on the method of generation, such as coal fired plants, hydro, nuclear, natural gas, wind, etc. A list for selected countries is presented in Table 14.

Activity rate = level of the particular activity, for example, liter of diesel consumed.

$GWP_{(i)}$ = global warming potential for each gas, for instance the GWP for a 100-year horizon for CH_4 is 23 (from Table 15).

Then, the total GHG emissions for a process, or economic activity, that include '*N*' gases is calculated as:

$$\text{Total GHG emissions} = \sum_{i=0}^{N} \text{GHG emissions in } CO_2 - eq_{(i)}$$

See also: Dairy Animals. Fermented Beverages. Food Chain: Farm to Market. Food Security: Postharvest Losses. Global Food Supply Chains. Sugar Crops. Swine Diseases and Disorders. Virtual Water and Water Footprint of Food Production and Processing

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F

Farm Management

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Glossary

Cash flow budget A projection of the expected cash inflows and cash outflows for a business over a period of time.
Enterprise budget A projection of all the costs and returns for a single enterprise.
Liquidity The ability of a business to meet its financial obligations as they come due.
Operating cost Cost for the purchase of inputs and services used up relatively quickly, usually in one production cycle.
Opportunity cost Income that could be received by employing a resource in its most profitable alternative use.
Ownership cost Cost that results from owning an asset, regardless of how much it is used.
Partial budget An estimate of the changes in income and expenses that would result from carrying out a proposed change in the current farm plan.
Profitability The degree to which the value of a set of agricultural products exceeds the cost of the resources used to produce them.
Solvency The degree to which the liabilities of a business are backed up by its assets.
Whole farm budget A projection of the total income and expenses of a farm business over a certain time period.

Introduction

Farm management in the broad sense means making decisions on activities that ultimately produce plants and animals that can be used for food, fiber, and/or fuel. The end goal may be to use the products personally, or to sell them for cash. The farm manager must decide what to grow, how much to grow, how to grow it, how to sell it, and how to obtain resources to produce it.

Unique Decision-Making Environment

Farm managers and managers of other businesses make similar decisions. However, agriculture has some unique aspects that affect how farm management decisions are made.

Biological processes and weather

The laws of nature place some severe limitations on what a farm manager can accomplish. Crops require certain nutrients, including water, that may be in short supply. They require some minimum length of time to reach maturity and certain hours of daylight. Livestock can only consume a limited quantity of feed each day, and reproduce according to their biological schedules. Even attempts to control the effects of climate through irrigation of crops and confinement of livestock can be thwarted by sudden rainstorms, blizzards, and other natural events. The unpredictability of the production process is a significant concern in agriculture, far more than in most other industries. Weather, genetics, and disease all introduce elements of risk that most nonfarm businesses do not face.

Fixed supply of land

At least in the more developed countries of the world, nearly all the arable land is already under production. Other industries can buy more raw materials or replicate production facilities, but for many farm managers the supply of land is essentially fixed. How to gain access to land is a crucial management decision, and the price of farmland is often very sensitive to current economic conditions.

Small size of business

Approximately 58% of the farms in the United States have only one operator. A similar pattern holds true in much of the rest of the world. Even in countries where very large private or publicly owned farming operations have been tried, families engaged in farming still prefer to have their own enterprises. As a result, the roles of owner, worker, and manager are commonly filled by the same individuals.

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Perfect competition

In an industry with many small firms, no one business can significantly affect the prices at which products are sold or inputs are purchased. Moreover, agricultural products are often homogeneous, meaning that one producer's output may be essentially identical to the output of any other. In such cases, prices are determined by national, and even international, supply and demand conditions, which are often unpredictable. The farm manager must react quickly when conditions change. Achieving high rates of production efficiency and controlling costs are keys to managing a profitable business in this economic environment in a competitive industry.

Important Farm Management Issues in the Twenty-First Century

Advances in technology

Agricultural technology has been evolving for many centuries and will very likely continue to do so. Selective retention of the best species of animals and the best grain seeds has long allowed farmers to improve productivity. Scientific breeding based on genetic principles has served to accelerate this improvement in productivity. In recent years, biotechnology has been used to introduce useful genes into existing species. Crop varieties have been engineered to fit growing conditions at particular locations, to be resistant to certain herbicides and insects, and to have more desirable traits such as higher oil or protein content. New nonfood uses for crops, such as biofuels, will open new markets but also may change the desired composition of plants grown for specific uses.

One example of a recent technological change is the use of global positioning systems (GPS) to pinpoint exact locations in a field. Early uses of GPS allowed farmers to collect very precise data about crop yields, moisture, and incidence of pests. Applications of fertilizer, pesticides, and irrigation water can be modified to fit very small areas, improving the efficiency with which these resources are used. GPS can also be used to steer machinery, resulting in less overlapping application of crop inputs and less operator fatigue.

Information management

Farm managers have long kept accounts of production, expenses, and sales, historically in hand-written record books, but analyzing the resulting data was often a tedious chore. Several decades ago home computers were adapted for farm record keeping. The ability to collect information has increased tremendously in recent years, through the use of electronic sensors and wireless transmission of data. As a result, farm managers have more information available to them, and can process and summarize it more quickly. Sensors can be combined with automatic controls to continuously monitor temperature and humidity in livestock buildings, the cleanliness of grain being harvested, and the degree of moisture in the soil, and other conditions so that adjustments can be made quickly.

Financial transactions can now be made without the need to exchange cash or checks. The use of bar codes and debit or credit cards allows financial information to be sent to a central location instantly, so financial accounts can always be up to date, and transaction data can be easily stored for later access.

In previous eras, farm managers were frustrated by a lack of current and complete information with which to make timely decisions. Today, managers can be overwhelmed by the sheer volume of data available. A vital task of farm management today is to determine which information is critical to decision making, which information is merely interesting, and which information is not relevant.

Controlling assets

Not all farm assets have to be owned. Farm management relies on combining land, labor, and capital to produce crops and livestock efficiently. However, land may be rented, labor may be hired, and capital may be borrowed. Agriculture has long relied on both traditional and innovative land tenure systems in which joint ventures between landowners and farm operators have been mutually beneficial. Leases may call for a cash payment to the landowner, or some negotiated sharing of production.

Agricultural production often involves a considerable investment in seed, fuel, fertilizer, feed, and other inputs before any production is available to sell. Farm managers must depend on banks and other financial institutions to supply credit until revenues are realized. Using the proper mix of debt and equity capital can have a large impact on the long-term viability of the farm business.

Meeting consumer demands

Although agriculture has long been characterized by undifferentiated commodities and prices determined in national or global markets, increased concern with nutrition and food safety coupled with improved capability to measure the desired characteristics of agricultural products has made it possible to achieve higher selling prices by producing to meet consumers' tastes. Niche markets for organically produced food, lean meat, and specialty fruits and vegetables provide profit opportunities for the skilled producer. The trend toward more free trade among nations is expanding the number and variety of markets available to farmers and ranchers.

Environmental and climate concerns

Agricultural production has always involved the exploitation of resources such as soil, water, and energy. Increasing production to feed a growing world population while at the same time conserving resources for future generations has led to a search for 'sustainable' agricultural methods. Farm managers must take a long-term view when making decisions about which technologies to follow and what commodities to produce while still generating sufficient profits in the short run to earn a living. Farm managers must also be aware of possible trends in climatic conditions, and learn how to adapt their production methods accordingly.

Planning

Farm management can be divided into three sequential phases: planning, implementation, and evaluation. Most farm managers carry out all three functions at the same time, although the season of the year may affect which one gets the

most attention. And once the cycle has been completed, it typically starts all over again.

Planning involves looking ahead and anticipating what decisions have to be made and what information will be needed to make them. Planning can be strategic (deciding what the farm should do) or tactical (deciding how to do it).

Strategic Planning

Mission

Strategic planning starts with defining the mission of the business. A mission statement is a short summary of why the business exists. Because many farm businesses are operated by a single family, mission statements often reflect personal values and priorities as well as business considerations. An example of a mission statement for a farm could be: "Our mission is to produce safe and nutritious products and earn sufficient profit to continue operating, while maintaining and enhancing the quality of the land and water resources under our control to ensure long-term viability."

Goal setting

Goals serve as a reference point for making management decisions and measuring progress over time. The goals formulated by individual managers will depend on their values. Some managers value financial success and constant expansion of the business. Others desire a balance between work, leisure, and family time. Still others have a strong conservation ethic, and emphasize preserving resources for future generations.

To be effective, goals should be as specific as possible, with measurable levels of achievement, and a timetable for reaching those levels. An example would be a goal "to own 100 ha of class A farmland in Washington County within ten years" or "to pay off 10 percent of the operation's total debt within five years." Most farm managers have multiple goals, so they need to set priorities among them before they can become useful yardsticks for making decisions.

Internal scanning

Good farm managers also need to assess the strengths and weaknesses of the farm business. These strengths and weaknesses may be related to the physical resources, such as soil type, availability of water, drainage capability, uses for existing buildings, existence of perennial crops, and area of land controlled. The number of workers available and their individual skills will impact what enterprises are feasible. The financial resources of the business will determine if new enterprises can be considered and what risk management measures are necessary. A thorough and realistic assessment of the farm's physical, human, and financial resources will identify possible new enterprises and activities while eliminating those that have little chance for success.

External scanning

Critically surveying the social and economic environment in which the farm operates will increase the chances of reaching the goals set by the manager. Recognizing trends in consumer tastes, evaluating new technologies, and keeping updated about shifting supply and demand factors for products as well as for resources will allow the farm to remain competitive in the long run. Public policies will also affect a farm's competitive position. Macroeconomic policies lead to changes in interest rates, foreign exchange rates, availability of credit, and rates of inflation. Certain government programs may set a safety net under farm income or prices of specific commodities, impose regulations or subsidize farming practices that are friendly to the environment, give favorable treatment to underserved classes of producers or beginning farmers, or favor production of certain commodities such as biofuels.

Identifying strategies

After assessing both the internal resources and the external conditions, the manager must identify alternative strategies for achieving the previously specified goals. This stage is often called strategic management. Often more than one strategy is feasible, but some may be rejected as too risky or not timely. Several tools for evaluating alternative actions will be discussed later.

Implementation

Once a strategy is chosen, the manager must take the necessary steps to carry it out. In some cases a business plan will be formulated and presented to lenders, landlords, or partners in order to acquire the resources necessary to implement the strategy. The short-term decisions needed to carry a strategy through to completion are collectively called tactical management.

Evaluation

After a strategy is fully implemented, the manager must judge whether it has been successful based on the original goals that were formulated. Accurate assessment will require collection and interpretation of appropriate information. Useful tools for evaluation will be discussed later. Strategies should be monitored over time in case some internal or external conditions change and the strategy must be altered or abandoned. Many production processes in agriculture are repeated annually or more often, so evaluation should be completed before the next cycle begins.

Cost Concepts

Both planning and evaluation require a basic understanding of how to identify costs and returns related to each alternative strategy or action being considered or undertaken. Costs, in particular, have different management implications.

Ownership costs

Some costs arise simply from owning productive farm assets, regardless of how much they are used. Depreciation is the loss in value over time for assets such as machinery, equipment, and buildings due to age, wear and tear, and obsolescence. Depreciation can also be an accounting entry by which the initial investment outlay for an asset with a useful life of more than 1 year is allocated over the period for which it is owned. Note that land is one long-lived asset in agriculture that is not

depreciated because it is assumed to maintain its productivity indefinitely if managed wisely.

Interest represents the cost of having capital tied up in long-term assets, including land as well as depreciable assets. Interest can be the cost of borrowing funds from a lender, or the income foregone by investing the farmer's own capital in a farm asset rather than some other income-producing investment.

Other ownership costs can include insurance against theft or casualty, property taxes, and routine maintenance costs that are not related to degree of use.

Ownership costs are often referred to as fixed costs. Once an asset is purchased, the ownership costs are fixed in value, and do not vary according to how much the asset is used. Even if the asset is not used at all, the fixed costs still occur. It can be argued that assets such as machinery and buildings will depreciate more as their annual use increases. Nevertheless, the usual accounting convention is to base depreciation solely on age or years of ownership.

Operating costs

Operating costs occur only if an asset is actually used, and in direct proportion to its degree of use. Examples include fuel and repairs for machinery, electricity for buildings, and gas for drying grain. In addition, some inputs such as seed, feed, fertilizer, medicines, and pesticides are fully used in one production cycle and are thus also included in operating costs. Operating costs are sometimes referred to as variable costs, because in contrast to fixed costs they vary in direct proportion to the number of units of the enterprise produced.

Opportunity costs

Costs that involve a direct monetary outlay are called cash costs. They are the most visible type of cost, and typically represent a large proportion of total costs. However, some costs arise from using certain assets in the farm business rather than in some other capacity. These costs are called opportunity costs. The value of foregone interest from using the owner's own capital to purchase farm assets or supplies instead of placing it in some other investment has been mentioned. Most farm operators also have an opportunity cost for using their own labor on the farm instead of earning a wage elsewhere. Small farms under a sole proprietorship form of business typically do not provide a cash wage to their operators, but the operators' labor still has an imputed value. Other opportunity costs found in farming may include the value of raised crops that are fed to livestock rather than sold off the farm, or produce consumed by the farm family itself.

Budgeting

Expected costs as well as expected income from farming can be arranged in a particular format called a budget. Several types of budgets are commonly used in farm management, and each one has its own special purpose.

Enterprise budgets

A complete list of all expected costs and revenues associated with producing one unit of a particular type of crop or livestock is called an enterprise budget. The first step in developing a budget of this type is to define the enterprise. It can be the production of a common crop, such as rice, corn, wheat, or tomatoes, or it can be more specific, such as producing yellow corn, white corn, sweet corn, seed corn, or high-starch corn. Livestock enterprises can be the complete production of common types of livestock, such as beef cattle, dairy cattle, sheep, goats, poultry, or swine, from birth to market, or for only a specific life phase such as breeding, development, or finishing (Table 1).

The 'budgeting unit' is usually some measure of land area for crops, such as one hectare or one acre. For livestock the budgeting unit is often one head (i.e., one animal), but breeding budgets can also be developed for one litter of pigs, one batch of birds in a poultry house, or one cow unit, which includes not only the cow but also a certain percentage of a bull, a calf, and a replacement heifer, based on the relative proportion of each type of animal in a typical herd. Livestock enterprise budgets may also be based on a certain number of animals, such as 100 cows.

Enterprise budgets usually list the amount of product that is expected to be produced. For crops this is usually the yield per land unit, such as bushels per acre or tonnes per hectare. Some crops may produce more than one product. An example would be wheat, which produces both grain and straw. For each product an expected selling price is shown. Prices can be based on historical information or on current bid prices for future delivery, sometimes known as futures prices or forward contract prices. The expected volume of product multiplied by its selling price is known as the gross revenue (also called total revenue or gross income). The same units should be used for estimating the quantity to be sold and the price, such as kilograms and dollar per kilogram.

Variable or operating costs are generally listed next. They are usually estimated by specifying the quantity of a certain input that will be used for each unit of the enterprise carried out, such as seed or feed, and then multiplying that quantity by the expected purchase cost per unit. Again, it is critical that the quantity to be used and the purchase price are based on the same unit of measure. Some variable costs may be expressed simply as a cost per unit of enterprise, based on historical data, when the quantity to be used cannot easily be specified in other units. One example would be veterinary services for livestock, and another could be insurance per acre of a crop.

Fixed or ownership costs are usually listed at the end. Depreciation, interest, taxes, and insurance have already been mentioned. These can be applied to buildings and storage structures as well as to machinery and equipment. The cost for land can be expressed in several ways. If the land is rented, the value of the rent to be paid can be shown. Land that is owned by the farmer can be valued based on interest cost, either cash or opportunity or some combination, or the opportunity cost of not renting the land to another farmer. Other land costs such as real estate taxes and maintenance of fences, water lines, and irrigation systems should also be included.

Totals for both variable and fixed costs are usually shown within the budget, as well as the sum of all costs. The value of gross revenue minus variable costs is called gross margin, or income over variable costs. When gross margin is positive, that is, when expected revenue is greater than expected variable

Table 1 Enterprise budget example

Item	*Unit*	*Quantity*	*Price*	*Amount ($)*
Revenue				
Wheat grain	Tonne	3.0	$300.00	900.00
Total revenue				900.00
Operating expenses				
Seed	kg	100	$0.42	42.00
Fertilizer: Nitrogen	kg	65	1.00	65.00
Phosphorous	kg	35	1.32	46.20
Potash	kg	25	1.20	30.00
Herbicide	liter	0.9	15.00	13.50
Fuel, oil, lubrication	hectare	1	61.25	61.25
Machinery repairs	hectare	1	41.00	41.00
Labor	hour	3.75	14.00	52.50
Interest (operating expenses for 6 months)	$	$335.20	3%	10.54
Total operating expense				361.99
Gross margin (total revenue minus variable costs)				538.01
Ownership expenses				
Machinery depreciation	hectare	1	60.50	60.50
Machinery interest	hectare	1	51.50	51.50
Machinery taxes and insurance	hectare	1	6.25	6.25
Land charge	hectare	1	300.00	300.00
Miscellaneous overhead	hectare	1	16.00	16.00
Total ownership expenses				434.25
Total expense				796.24
Profit and return to management				103.76

costs, it will pay the farmer to go ahead and produce the enterprise in the short run. Even if the gross margin is not sufficient to cover all the fixed costs, the farm will be better off by producing. If no production took place, the fixed costs would still exist, so earning enough to pay for part of the fixed costs is better than the alternative.

Expected gross revenue minus total costs is called profit. Sometimes the term 'return to management' is used instead, because the value of the farmer's management time and ability is usually not included as an explicit cost. In some cases a total cost per unit of production sold is shown. This is computed by dividing the total costs by the number of units of the product that will be sold. When more than one product will be available to sell, the expected income from the less important products should be subtracted from total costs before they are divided by the units of the main product to be sold. This value is also called the breakeven price, and can be used as a benchmark by the farmer for making marketing decisions.

A similar process can be used to calculate a breakeven yield for the principal product. The budgeted total cost, minus expected income from secondary sources, is divided by the expected selling price of the primary product to find the minimum yield or quantity needed to pay the total costs of production.

An enterprise budget implicitly defines the package of technology the farmer has decided to employ to produce that particular product. The technology is embedded in the type and quantity of each input listed.

Enterprise budgets can be used to judge in advance whether it will be profitable to produce a certain enterprise. They can also be used to compare the profitability of several alternative enterprises. Finally, they can be used as building blocks for other types of farm budgets.

Whole farm budgets

Most farm businesses consist of more than one land unit of a crop or one head of a livestock specie. Indeed, many of them produce multiple enterprises on a large scale. Thus, it is useful to produce a budget showing all the enterprises on the farm combined, each aggregated to the actual number of units to be carried out. This aggregated budget is called a whole farm budget.

A whole farm budget must be first based on a whole farm plan. This plan includes a list of all proposed enterprises and the amount of each. It should be derived from a careful process of internal and external scanning, as described in the Sections Internal scanning and External scanning. It may be modified based on expected product and input prices for the upcoming production cycle.

Once the plan is chosen, the costs and returns from each enterprise budget can be multiplied by the number of projected units of that enterprise, and the results summed. The same structure of gross revenue, variable costs, fixed costs, and profit can be followed. Expected revenue from other sources besides the budgeted enterprises can be added to the enterprise revenue. Additional revenues could come from performing custom machinery services for other farmers or participating in certain government commodity programs.

Sometimes it is more logical to omit fixed costs from the enterprise budgets and simply add them into the whole farm budget. Many fixed costs do not vary directly with the number

of units of each enterprise that the farm plans to carry out, but are a set value. Examples are wages for a full-time hired employee, premium costs for liability and property insurance, payments for services such as bookkeeping and tax preparation, and depreciation on buildings.

Total revenue minus total costs is equal to expected profit at the farm level. Sometimes an intermediate value is calculated, called net farm income. It is equal to total revenue minus all costs except the opportunity costs of the farmer's own capital and labor. Net farm income is sometimes referred to as a return to equity capital, operator labor, and management.

Whole farm budgets can be created for both a short-term and a long-term planning horizon. A short-term budget usually reflects expected prices, yields, and costs for the next year or next production cycle. Values chosen will depend on near-term price forecasts and weather conditions. A long-run budget, however, will be based on average values observed over several years, perhaps modified for any trends that are expected to impact conditions during the farmer's planning horizon.

The best sources of data for both enterprise budgets and whole farm budgets are actual results from the same farm during recent years. Keeping accurate and complete records of crop yields, livestock production levels, rates of inputs used, and selling prices will provide reliable estimates for the next budgeting cycle. Of course, some budgets may include enterprises or technologies that have not been tried on the particular farm in question. In that case, records or observations of results obtained on nearby farms or experiment stations can be used.

Although a whole farm budget can summarize the expected revenue and costs for a particular mix of enterprises, it does not guarantee that this mix will maximize the profit potential of the farm. A series of comparative budgets can be prepared, each one based on different enterprises or a different number of units of the planned enterprises. Some plans may include added resources such as more land, additional labor, or new livestock facilities. The various budgets can be compared based on expected profit, riskiness, and environmental impact.

When many combinations and levels of enterprises are possible, a mathematical process called linear programming (LP) can be used to identify the farm plan that will maximize total profit or some other objective. The LP model must specify the objective to be maximized; the supplies of fixed resources such as land, labor, and capital that are available; the set of possible enterprises or activities; the quantity of each fixed resource that one unit of each enterprise requires; and the expected contribution of each enterprise unit toward the objective, for example, total profit. The LP solution will list the number of units of each enterprise that should be carried out in order to maximize the objective, as well as the value of adding one more unit of each fixed resource and the penalty for producing one unit of an enterprise not in the optimal solution. To be a useful tool, the LP model must be accurately specified; otherwise, results will not be reliable.

Partial budgets

Sometimes farm managers contemplate making changes that will affect one production practice, but will not alter other aspects of the farm. In such cases a partial budget can be prepared. A partial budget analyzes only the costs and revenues that would be changed as a result of some other change in the overall farm plan. Costs and revenues that would stay the same can be ignored, saving time and effort that would be needed to estimate them.

The first step in a partial budget is to define the change that is being considered. Only one change should be analyzed at a time, so that the effects of that particular change are clear. Second, all the potential changes in input use, costs of production, output levels, or selling prices should be listed. These can be categorized into four classes: added revenues, reduced costs, reduced revenues, and added costs. Once each projected change has been identified, a monetary value can be attached to it, using the best short-term or long-term price projections available. Finally, the added or reduced costs and revenues can be summed to find the expected net change in profit. The general equation is:

$$\text{Added revenues} + \text{reduced costs} - \text{reduced revenues} - \text{added costs} = \text{change in profit}.$$

A partial budget can be developed for one unit of an enterprise if the changes being contemplated would not affect the size of the enterprise or any other enterprises. More often, though, the changes will need to be budgeted at the level of the whole farm business (Table 2).

Sometimes it is useful to calculate the value of a certain key variable for which the net change in expected profit would be exactly zero. This is known as a breakeven value. Any variable can be chosen, but only one breakeven value can be calculated

Table 2 Partial budget example

Decision: Sell corn as standing silage instead of harvested grain (1 ha)			
Additional revenue		Additional costs	
Sell 25 tonne of silage @ $110	$2750	Phosphorus fertilizer: 36 kg @ $1.25	$45
		Potash fertilizer: 140 kg @ $1.10	$154
			$199
Reduced costs		Reduced revenue	
Harvesting grain	$85	Sell 10 tonne of corn grain @ $220	$2200
Hauling grain	$20		
Drying grain	$65		
	$170		
Net change in profit = $2750 + $170 − $199 − $2200 = + $521			

Table 3 Cash flow budget format

	Period 1	*Period 2*	*Period 3*	*Period 4*
a. Operating income				
b. Capital asset sales				
c. New loans to receive				
d. Total cash inflows (a+b+c)				
e. Operating expenses				
f. Capital asset purchases				
g. Loans to repay				
h. Total cash outflows (e+f+g)				
i. Net cash flow (d−h)				
j. Beginning cash balance				
k. Ending cash balance (i+j)				

at a time. The equation above can be used, substituting the best predicted values for all variables except the breakeven variable, which can be represented by some symbol, and setting the value for change in profit equal to zero. Then the equation can be solved algebraically for the value of the unknown variable. The farm manager can then form an opinion about whether the future value of the key variable is likely to be higher or lower than the breakeven value. An example of a key variable might involve the expected increase in average yield from adding irrigation to what is currently a nonirrigated operation.

Cash flow budgets

Sometimes the farm manager is concerned about having enough cash on hand to meet all expenses, investments, and loan payments when they come due. A special type of whole farm budget, called a cash flow budget, can be used for this sort of analysis. A cash flow budget is an estimate of all the expected cash inflows and cash outflows the farm will have during the next accounting period, often the calendar year. The cash flows are usually estimated separately for shorter time periods within the year, such as months or quarters, as well as summarized for the year as a whole.

A cash flow budget contains most of the same revenue and costs that are found in a whole farm budget, but it also includes some other sources and uses for cash. Four general categories of cash inflows are: cash income (generally from sales of farm products and other miscellaneous sources of revenue), sales of capital assets (revenue generated by selling long-term assets such as machinery, land, and buildings), new loans received (funds borrowed from outside lenders), and nonfarm revenue (infusions of cash generated from outside the business).

The categories for cash outflows are analogous to the inflow categories. Cash expenses are generally shown first. Note that cash expenses do not include depreciation nor opportunity costs, because they are not actually paid in cash. The next category is purchases of capital assets. These are assets that would normally last for more than one production cycle. The third category is repayment of loans. Both interest and principal payments are often combined in the loan payment category as both involve cash outlays. The last category is nonfarm expenditures, which can include cash withdrawals from the business, such as those used for family living expenses or other nonbusiness purposes (Table 3).

The difference between total cash inflows and total cash outflows is called net cash flow, which can be either positive or negative for each time period. Any cash funds left over from the previous accounting period are added to the expected cash inflow in the first time period to estimate the cash balance left at the end of the period. This balance is then added to the cash inflow for the next time period, and so forth, until all time periods have been budgeted.

The object of the budget is to project a positive cash balance at the end of each time period. If some periods do not project a positive cash balance, several actions can be taken. The most common one is to increase the amount of borrowing. This action may be shown in a separate section that projects loans and repayments from a line of credit that has been extended by a lender. The projection for the amount of cash to be borrowed should be large enough to show a positive cash balance at the end of the period. Many managers try to budget for a larger balance, to allow for any errors in projecting either the cash inflows or outflows.

Other revisions to the budget can include shifting sales to periods that have a cash deficit or moving cash expenditures to periods that have excess cash available. Of course, these changes must be realistic given the planned enterprises and production cycles for the budgeting period.

It is important to note that a cash flow budget does not measure expected profits for the farm. It merely tracks expected cash inflows and outflows, many of which are not considered income or expenses in the economic or accounting sense. Nevertheless, a cash flow budget is an important financial management tool, and should be shared with any lenders who will help finance the farm business.

Implementation

A successful farm manager must not only do a careful job of planning, but also must be able to acquire the proper type and scale of resources necessary to carry out the plan. Many good farm plans have failed because certain key resources were lacking. Farm businesses require a well-managed mix of financial, human, land, and physical resources to operate successfully.

Financial Resources

Most farmers start with some of their own assets, including a certain amount of cash with which to fund initial operating costs and investments. This is called equity capital. Farmers who have been in business for many years, or who are fortunate enough to inherit an ongoing farming operation, may operate entirely with equity capital. As long as a lack of capital does not limit the size or efficiency of the farm business, 100% of the return earned on capital goes back into the farmer's pocket.

Many farmers, probably a majority, depend on outside sources for loans, or debt capital. The wise use of debt capital in large measure determines whether farm businesses grow and prosper or eventually fail.

The most common source of debt capital for farmers is commercial banks. Banks are in business to lend money, for a variety of purposes. In particular, banks located in rural areas depend on farm loans for much of their business, and their loan officers become skilled at evaluating loan applications and monitoring agricultural credit lines. Banks particularly like to lend funds for purchasing crop inputs and feeder livestock because these funds are repaid quickly. Lenders expect the farmer to be able to repay the loans from the sale of the crops or livestock that were financed. Hence, these types of loans are called 'self-liquidating,' and carry a low level of risk for the lender.

Commercial banks also make loans for capital assets such as machinery, breeding livestock, buildings, and land. The assets purchased with the loan funds serve as collateral, although most lenders will ask for additional assets to be pledged, as well. Interest rates may be fixed for a few years, but often are adjusted later to match the interest rates that the bank must pay to obtain funds to lend.

Sometimes farm loans can be obtained from financing institutions created specially to assist agriculture. In the United States the Farm Credit System (FCS) functions as a cooperative or credit union for farmers. The FCS sells bonds on national money markets and passes the loan funds to the farmer members. The FCS is organized into several regional banks within the United States, each of which has local offices that accept loan applications and manage outstanding loans. Profits earned are passed back to the farmer members. The FCS and similar institutions lend exclusively to farmers and ranchers and thus have developed high degrees of expertise in analyzing agricultural credits. They generally provide loans for both short-term operating needs and longer-term asset purchases.

Not all farmers have the experience or equity necessary to qualify for credit from a private bank or credit institution. In some cases the federal government steps in as a temporary lender, to finance beginning or high-risk operators until they can obtain credit from commercial sources. Often the government lenders offer lower interest rates and longer terms, to improve the borrowers' repayment capacity. Some public sector lenders may make loans targeted at growers of specific commodities or certain groups that have been underserved in the past.

Another source of credit for farmers can be the businesses that supply them with seed, fertilizer, or machinery. These businesses extend credit as a way of encouraging farmers to purchase their products, which of course is a condition for receiving a loan.

Some farmers find that they can stretch their limited equity capital by leasing certain assets rather than owning them. Land is the most commonly leased asset, but lease agreements for machinery, buildings, and breeding livestock are also available. Leases may be offered by independent companies affiliated with equipment manufacturers or representing large investment firms.

Farmers who utilize credit must carefully manage how much they borrow and when they plan to repay it. Cash flow budgets, both short term and long term, are useful for testing the feasibility of credit use. Farm businesses that depend heavily on credit are said to be highly leveraged. Often they use credit to acquire additional resources, so that the business can operate at a more efficient level and fully support the operator and family members. In times of high prices and wide profit margins, being highly leveraged can help businesses increase net worth rapidly. By the same token, when prices are low or production is below average loan payments must still be made. Net worth may shrink as operating capital is diminished or some assets are liquidated. Eventually the farm may not be able to continue as a viable business. The prudent manager will employ one or more risk-control strategies to prevent such a situation from happening.

Human Resources

Historically, agriculture has been a very labor-intensive industry. Moreover, farming has often involved very hard physical labor under extreme climatic conditions. Fortunately, innovations in agricultural technology have reduced the physical effort needed to produce livestock and crops. At the same time, each farmer or farm worker is able to produce many more units, leading to higher net incomes. Ever more sophisticated machinery and equipment require more training and higher skill levels.

Unlike many industries, agriculture depends to a large extent on the labor supplied by the same individuals who own and manage farms. In the United States, only about a third of the total labor force in agriculture consists of paid employees. Even farms that do hire labor may have only one or two full-time employees. At the other extreme, there are farms that employ hundreds of workers annually. Labor management issues on these large farms are vastly different than those of smaller 'family' size farms.

Farm managers must deal with the seasonality of labor needs. Crop farms may need large amounts of labor during planting and harvesting seasons, but their needs are much lower during other months. Livestock operations may have high labor needs when offspring are being born, but not during other seasons. Farm managers must determine what mix of full-time and seasonal or part-time labor will assure that critical tasks are performed on time without committing to higher than necessary expenditures on wages and salaries.

Setting compensation levels for farm employees can be difficult, because each worker may have a unique job description and set of skills. Besides cash wages, farm employees often receive fringe benefit packages that include health

insurance, clothing, meals, and even housing. Some employers offer bonus schemes that reward workers with extra income or other benefits if performance levels meet or exceed certain standards. To serve as an effective incentive for higher job performance, the bonus must depend on factors that are at least partly under the employee's control.

Farm managers also need to be aware of laws and regulations that apply to farm workers. Such laws may address minimum wages, withholding for taxes or unemployment funds, safety considerations, immigration status, and work restrictions based on age.

Human resources also include consultants and hired experts. Some duties of a farmer can be outsourced more efficiently than they can be done in-house. Preparation of tax reports, farm accounting, crop scouting, and livestock health procedures are examples of services that are often contracted to outside consultants and practitioners.

Land Resources

Ever since humankind moved from hunting and gathering to growing crops and domesticating livestock, access to land has been critical. Many battles have been waged over rights to land necessary for feeding a growing population. The specific land tenure systems present in a country or region often determine the distribution of income and opportunities among its population.

Although some societies have operated with communal holding of agricultural land, most countries with highly developed agriculture allow land to be held as private property. This means that farmers must either own land themselves or enter into some type of rental agreement with the owner. Many farms involve a mix of owned and rented land.

Purchasing land usually requires a substantial capital outlay. Because land does not depreciate, assuming it is cultivated properly, it has a higher purchase price relative to its income-generating capacity than other agricultural assets. Purchases of farmland are often possible only with the use of borrowed funds. Lenders typically will not lend the entire purchase price for land, so the farmer must use equity capital for part of the purchase, called a down payment. Repayment terms for farm real estate loans are usually fairly long, as much as 20–30 years or more. For an established farmer, purchasing additional land is often made more difficult by the fact that land is immobile, that is, it cannot be moved to the farmer's current location. Therefore, farmers are often willing to pay a premium for a tract of land that adjoins or is very close to their present base of operations.

Agricultural land values have been the subject of much study and scrutiny. The value of a tract of farmland can be estimated using a standard formula for assets that provide an infinite stream of income, called a 'perpetuity.' First, the annual net income that can be earned from the land must be estimated by using the budgeting procedures discussed previously. This value is then divided by the discount rate, which is the expected real rate of return on similar assets. The discount rate can be estimated by subtracting the expected rate of inflation from the farm's cost of capital, including both debt capital and equity capital. The result is the amount that can be paid for the land that will allow the buyer to earn a rate of return equal to the discount rate. If the farmland is located near urban or recreational areas, its value may be higher than its expected returns in farming would indicate, due to its potential for other uses.

Farm managers who are not able to own a sufficient area of farmland often turn to rental arrangements. Renting or leasing land does not guarantee that the farmer will have use of it indefinitely, but it usually requires less of a capital commitment than ownership does. In many parts of the United States as much as 60–70% of the farmland is rented rather than owned by the operator.

The most straightforward type of rental agreement is called fixed cash rent. The farmer agrees to pay the landowner a set fee for the use of the land, and must supply all other resources such as labor, machinery, and crop inputs. The rent may be payable in advance, after the crop is harvested, or in several installments. The renter takes all the risk for uncertain prices, yields, and production costs. In some cases the tenant and the landowner may agree to a flexible cash rent arrangement, under which the actual rent to be paid varies according to the actual yields and/or prices attained. In these cases the landowner not only shares part of the risk, but also receives a higher return when results are better than expected.

Share lease arrangements are also common, and in some areas outnumber cash leases. Under a share lease the tenant and the landowner divide production in an agreed-upon proportion, and no cash payment is made. The size of the landowner's share generally reflects the productivity of the land, reaching as much as 50% in some regions. In addition, the owner and the tenant usually share the costs for inputs that are yield increasing in the same proportion as the crop is divided. This ensures that the optimal level of input use is maintained, that is, the level at which marginal cost and marginal revenue are equal is the same for both parties. Labor and machinery are typically contributed completely by the tenant, although many variations of share leases exist.

A key feature of a share lease is that the risks of low prices, low yields, or high input costs are shared between the tenant and the landowner in the same proportion as the crop and input costs are shared. Moreover, the tenant's capital requirement at the beginning of the crop cycle is reduced considerably, because no advance rent is paid and the landowner finances a portion of the crop inputs.

Share leases can also be used for livestock farming operations. Usually the tenant and the owner both own a share of the livestock, and pay for a like percentage of feed and other cash costs.

Other Capital Assets

Most farming operations also require machinery, storage buildings, livestock production buildings, processing and handling equipment for feed, water, and manure, and other types of capital assets. These assets can be acquired with either equity capital or debt capital, or some other combination. As noted earlier, these assets can also be leased from financial companies or farm landlords. In many cases they are designed for very specialized uses, so the farm manager must be committed to carrying out the enterprises for which they are

intended. They generally need to be used to their full capacity in order to keep ownership costs per unit of output at a minimum.

Managing Risk

No matter how carefully a farm manager develops budget projections of costs and returns, they will never be a perfect prediction. Random events such as weather, pests, accidents, disease, product prices, and input costs cannot be forecast with complete accuracy. This does not mean that the manager should not carry out any risky strategies; rather, certain measures should be taken to limit the damage should unfavorable outcomes occur. Several general types of risk-management tools are available.

Reducing the range of possible outcomes means that the chances of a very bad outcome are reduced, but the possibility of a very good outcome may also be reduced. Strategies that reduce the range of possible outcomes include using share leases, fixing selling prices in advance, spreading product sales over time, diversifying the mix of enterprises, and keeping financial leverage to a low level.

Insurance strategies allow the farm manager to pay a small fee on a regular basis in exchange for receiving a payment to offset damages suffered when a loss occurs. Insurance policies are available for property damage, liability suits, theft, injury, and death. Crop insurance policies that provide coverage for yield losses and unexpected declines in selling prices are becoming increasing popular. In the United States, commodity options are available which fix a minimum selling price for a product, for a fee.

A third general strategy is to maintain resources in reserve so that an adverse result is less likely to affect the survival of the farm business. Financial reserves and lines of credit are especially useful, but keeping a reserve feed supply for livestock or having someone who can provide backup labor and management in an emergency also falls within this category.

Control and Evaluation

The third phase of farm management is control and evaluation. In this phase the manager collects data, both physical and financial, and uses it to determine if progress is being made toward the goals that have been set for the farm business. Based on this information, needed changes in strategies can be identified and new budgets can be created for the next planning cycle.

Information Management Systems

Most businesses have accounting systems for tracking income and expenses. In many countries farmers are required to submit reports for income tax purposes, so those requirements may define the minimum amount of information needed. However, for effective management purposes additional information is needed. The total process for collecting, summarizing, and interpreting data about what takes place on the farm is called an information management system. The exact composition of a system will depend on the type of products that the farm produces, its legal and business organization, and the particular decisions that the manager faces.

The information management system should be no more complicated than necessary to meet the needs of the manager. Information is needed for two general purposes: internal reports that help the manager make more informed decisions about enterprise choice, technology to follow, marketing plans and financing strategies; and external reports, which may be required by lenders who are providing capital to the business, partners or landowners who share or rent resources, and the government to meet taxation and other obligations.

Several decisions must be made before an information management system can be put into practice. One such decision is the accounting period to use. The most common choice is 1 year, often the calendar year. However, other periods can be used if they better fit the particular needs of the business. Farms in the southern hemisphere may choose to start their accounting period late in the year, when annual crops are likely to be planted, and end it in the first half of the following year, after harvest is completed.

Cash accounting systems record income when it is received and expenses when they are paid. Accrual systems, however, recognize income when crops or livestock are produced, or at least when they are ready to be sold, even if they may be stored or held until a later time. Accrual accounting also records expenses when they are incurred, even if they are not paid at that time. This difference is particularly critical at the end of the accounting year, when mature crops and animals may still remain on the farm, and some expenses either have not been paid yet, or have been paid in advance. The fundamental purpose of accrual accounting is to recognize the value of farm products as income in the year they are produced, and to recognize all the costs of producing them in the same year.

Each time income is received or recognized, or an expense is paid or recognized, a transaction is entered into the accounting system. The details of each transaction usually include the monetary value, the date it occurred, the entity or person from whom the income was received or to whom the expense was paid, the purpose, the quantity sold or purchased, and the sale or purchase price. Transactions can be entered into a hand record book or a computerized system – the principles are the same.

Periodically transactions are posted to accounts. In a single-entry accounting system, transactions affect only income or expense accounts. In a double-entry system, adjustments are also made to asset and liability accounts. More details about these accounts are discussed later. The number and nomenclature for the various accounts depend on the type of commodities being produced, the specific inputs being used, and the degree of detail desired in the farm's financial statements. When an accounting system is implemented, a chart of accounts is defined, which shows the title for each income, expense, asset, or liability account that the farm wishes to use.

Financial Statements

Once an accounting year is completed and all the relevant transactions have been entered and posted, several summaries or financial statements can be created. Four such statements

have been recommended by the Farm Financial Standards Council, a group composed of accountants, lenders, and agricultural educators that has developed guidelines for financial accounting for farmers and ranchers. Their objective is to increase the degree of consistency in the terminology used, the formulas for calculating certain key ratios, and the procedure for handing certain accounting questions related to agriculture.

The net worth statement

The net worth statement, also called the balance sheet, is a summary of everything the farm business owns (assets) and owes (liabilities) as of a certain date. Traditionally, a net worth statement is developed at the end of the accounting year and is called the ending or closing statement. The same statement serves as the beginning statement for the next accounting year. A net worth statement can be created at any point in time, however. Because it is the primary document that lenders use to evaluate a farm's application for a loan, a current net worth statement may be requested for each new credit application. In a double-entry accounting system, the asset and liability accounts will always be up to date. However, if a single-entry system is being used, the farm manager will have to collect current information about each asset and liability on the date the statement is constructed.

Both the assets and the liabilities on the net worth statement are subdivided into several categories, according to how quickly they could be turned into cash (assets) or repaid (liabilities). Assets that normally are sold or used within the next 12 months are classified as current assets, as are other assets that can be easily converted to cash, such as stocks, bonds, or other financial assets. Assets that will normally be present on the farm beyond the next 12 months can be classified as intermediate (1–10 years) or long term (more than 10 years). In practice, intermediate assets usually consist of machinery, equipment, and breeding livestock, and long-term assets consist of land, improvements to the land, and buildings. In some accounting systems intermediate and long-term assets are combined under the heading of fixed or noncurrent assets. Liabilities are classified in a manner similar to assets, based on how quickly they are expected to be repaid.

Although the value of debts and other obligations are generally well known, assigning values to assets may require some judgment. In general, current assets are valued at the price for which they could be sold on the date of the statement, or their original cost. Depreciable assets, such as machinery, are generally valued at their original cost minus any depreciation expenses taken since that time. If the depreciation accurately reflects the loss in value of the item, the price that could be received for selling the asset should closely mirror the depreciated value. Owned land can be difficult to valuate. If it has been owned for several years, the purchase price may no longer reflect the market value, but market value for land in rural areas can be difficult to determine accurately.

The balance sheet can be constructed using a 'cost' approach, which generally values assets by using the original purchase price or the depreciated value, or using a 'market' approach under which assets are valued at their expected market price, if sold. The cost approach is generally the more conservative of the two methods, but market values are more useful for comparing the farm's financial condition with that of other farms.

The net income statement

The second-most common financial statement used in farm management is the profit and loss statement, also called the net income statement. It summarizes the income, expenses, and profit (or net income) generated by the farm during the past accounting cycle. Profit and loss statements can be generated using either cash or accrual accounting methods. Small farms often use a hybrid approach. Cash income and expenses are recorded throughout the year. Then, at the conclusion of the year, the value of all unsold production is added to the cash income and the value of all unsold production at the beginning of the year is subtracted. Thus, an increase in the value of current inventories results in a higher estimate of income, and vice versa. This ensures that the value of crops and livestock produced on the farm is counted in the year it is produced.

Expenses can also be adjusted at the end of the year, by adding to the total cash expenses any change over the accounting period in accounts payable and also by subtracting any change over the accounting period to expenses paid in advance. The result is an estimate of accrual net income, a more accurate estimate of the farm's net earnings than cash net income.

The farm manager must be careful not to count the receipt of loan funds or the repayment of loan principal as income or expense. These transactions simply represent borrowing and repaying capital provided by a lender and not earned income nor costs of production. Any interest paid on such loans is an expense, however.

The statement of cash flows

Loans received and repaid are included in the third statement, the statement of cash flows. Likewise, cash income and expenses as well as sales and purchases of capital assets are included in this statement. The statement of cash flows is very similar to a cash flow budget, except it summarizes past revenues and expenditures instead of projecting future ones. Nonfarm income transferred into the farm's finances, or funds withdrawn for nonfarm purposes are also reported in this statement. The sum of all cash inflows to the business, plus the cash that was in the farm bank account at the beginning of the year, should equal the sum of all the cash outflows, including the balance in the farm account at the end of the year. This is a good way of checking to see if all the cash received and used during the year has been accurately recorded.

The statement of owner equity

One more financial statement completes the recommended set. The statement of owner equity shows how the net worth of the farm changed from the beginning of the accounting year to the end. Net worth will change by the value of net farm income (accrual based) plus any outside funds invested in the farm (including gifts or inheritances) minus any funds withdrawn from the business. Net worth may also be changed by valuing some intermediate or long-term assets according to their market value, that is, the value they could reasonably be sold for, rather than their cost or book value, which is their

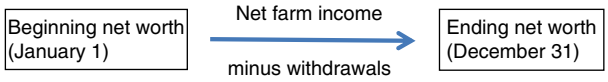


Figure 1 Relation between net worth and net farm income.

original cost minus any depreciation expense taken to date. Some farm accounting systems show net worth based on both cost and market values. Cost values more closely adhere to traditional accounting rules, but market values give a better picture of the value of the farm's assets for the purpose of collateralizing loans (Figure 1).

Farm Business Analysis

An accurate set of financial statements can provide valuable information for calculating certain ratios and indicators of the financial health of the farm. Three general areas of financial management are important: solvency, profitability, and liquidity.

Liquidity

Liquidity is the ability of a farm to meet its cash flow obligations on time. One common measure of liquidity is working capital, calculated by subtracting the current liabilities shown on the net worth statement from the current assets shown on the same statement. This is an estimate of how much cash would be left over if all the assets that will be sold or used up in the next year were used to pay all the liabilities that are due within the next year. A similar measure is the ratio of current assets to current liabilities, usually called the current ratio. Of course, a cash flow budget, as described in the Section Cash flow budgets, does a much more detailed job of analyzing the liquidity of a farm.

Solvency

Solvency refers to the relative values of a farm's assets and liabilities. Solvency is usually measured using current market values for capital assets. This allows lenders and managers to compare farms against each other, and to industry standards. The most common measure of solvency is simply the farm's current net worth. It represents the value of the farm's assets that would be left if all liabilities were paid to zero. Because net worth is closely tied the size of the farm business, the ratio of total liabilities to total assets is also used to evaluate solvency, allowing farms of different sizes to be directly compared.

Profitability

Profitability is the degree to which the value of a farm's production exceeds the cost of the resources used to produce it. An absolute measure of profitability is net farm income. If the opportunity costs for the farmer's own labor and capital are subtracted, the remainder is profit and return to management. A positive profit means that the farm has produced crops and livestock that have a greater value than the seed, fertilizer, fuel, labor, feed, and other inputs that were used up in their production. Profits are also highly correlated with farm size. To compare the profitability of farms of different sizes, several ratios are used. The asset turnover ratio is equal to the gross revenue for the entire farm divided by the value of its total assets. It reflects the efficiency with which land, machinery, breeding livestock, and other resources are turned into food, fuel, and fiber. Another common ratio is the rate of return on assets (ROA), which is a measure of how much the total assets earned, on a percentage basis. It can be compared to what the farmer could have earned if the total value of the assets had been invested elsewhere.

To be useful, all farm business analysis measures must be compared to benchmark values. Past records from the same farm calculated in the same way can show if the farm is progressing or going downhill in each area. Comparing to projected values from enterprise or whole farm budgets developed at the beginning of the year will show if reality exceeded expectations or otherwise. Perhaps, the most useful benchmarks are comparable ratios for the same year from similar types of farms located in the same area. Farm managers can quickly determine in which areas their business exceeded other farms, and which areas need improvement.

Enterprise Accounting

Just because a farming operation is profitable overall does not mean that each part of the farm is earning a profit. Only by matching income and expenses to individual enterprises can the weak and strong areas of the farm be identified. Enterprises can be defined in the same manner as for enterprise budgets. Generally, each major crop or livestock species is evaluated separately, although livestock enterprises can be further divided by phase of development. In managerial accounting, businesses are divided into profit centers, and each one is analyzed to see how well it contributes to the overall profits of the company. Farm enterprises are analogous to profit centers.

Some enterprises generate products that may be used as inputs by other enterprises. The most common example is grain or forage that is grown on the farm and fed to livestock on the same farm. To fairly assign income and expenses to each enterprise, the market value of the fed crops should be attributed to the crop enterprises as income and assigned as costs to the livestock enterprises that consume them. This adjustment is called an internal transaction. The income to one enterprise is exactly offset by the cost to the other enterprise, so there is no effect on total farm net income or profit. Other examples of internal transactions include assigning the nutrient value of animal manure used as fertilizer as income to the livestock and an expense to the crops, and assigning the value of weaned calves as income to the beef cow herd and an expense to the feedlot enterprise.

The time period used for enterprise analysis often differs from the whole farm accounting year. Enterprises are more logically summarized from the beginning to the end of each production cycle. A winter wheat crop may be sown in one accounting year, harvested in the next year, and sold in the third year. An accurate evaluation of that crop would include transactions occurring in three different accounting years. However, certain vegetable crops or a livestock enterprise such as swine farrowing may have multiple production periods within the same year.

To assign revenue and costs to the proper enterprise the farmer should enter them in separate sections or columns of the record book when transactions are posted. In a

computerized accounting system different numerical codes are assigned to each transaction, with each code representing a different enterprise.

Summary

Farm management is both a science and an art. It requires vision about the future of agriculture, but it also requires skill at collecting and interpreting data, searching for new resources, and dealing with uncertain outcomes. It requires much patience, but can also yield great rewards.

See also: Production Economics

Relevant Websites

http://www.extension.iastate.edu/agdm/
Ag Decision Maker, Iowa State University.
http://www.agmanager.info/
Ag Manager.info, Kansas State University.
http://www.farmdoc.illinois.edu/
Farmdoc, University of Illinois.

Fermentation: Food Products

DY Kwon, Korea Food Research Institute, Songnam, Republic of Korea
E Nyakudya, Research Center for Industrial Development of Biofood Materials, Jeonju, Republic of Korea
YS Jeong, Jeonbuk National University, Jeonju, Republic of Korea

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Glossary

Backslopping Practice of retaining small quantities of fermented product from the successful manufacture of a fermented product in the previous batch and using it as the inoculum or starter in the next batch.
Condiment An edible substance such as sauce that can be added to food to impart a particular flavor, or to improve its flavor, or to complement the dish.
Heterofermentative Producing a fermentation resulting in a number of end products.
Homofermentative Producing a fermentation resulting wholly in a single end product.
Probiotics The World Health Organization defines probiotics as "live microorganisms, which when administered in adequate amounts, confer a health benefit on the host."
Spontaneous fermentation Also called natural fermentation is a method of fermentation that does not require addition of a starter culture such as yeast to start and control the fermentation of the substrate.

Introduction

Fermented foods are of great importance because they provide and preserve great amounts of nutritious and healthy foods in a wide diversity of flavors, aromas, and textures, which enrich the human diet. They are the source of alcoholic beverages, vinegar, pickled vegetables, sausages, cheeses, yoghurts, vegetable protein amino acid/peptide sauces and pastes with meat-like flavors, and leavened and sour-dough breads. Fermented foods are food substrates that are invaded or overgrown by edible microorganisms whose enzymes, particularly amylases, proteases, and lipases hydrolyze the polysaccharides, proteins, and lipids to nontoxic products with flavors, aromas, and textures pleasant and attractive to the human consumer (Steinkraus, 1997). Fermentation also ensures microbiological safety of food and may also make some foods more digestible, and in the case of cassava, fermentation reduces toxicity of the substrate. Milk, meat, cucumber, and cabbage are the main substrates used in the commercial production of fermented food. These substrates yield over 400 varieties of cheese of 20 distinct types and a very extensive range of yoghurt and fermented milk drinks, fermented sausages and salamis, pickles, and sauerkraut (Caplice and Fitzgerald, 1999).

Fermented Vegetables

Sauerkraut

Sauerkraut is a fermented product made from cabbage and has its roots in central Europe. Germans and the Alsatians prepare sauerkraut as their national dish (Sauerkraut, 2009). Sauerkraut has also been used in Germany for medicinal purposes; traditionally in many parts of southern Germany, some families would feed their children raw sauerkraut two times every week – this was believed to support and strengthen the intestines of the sick children. Sauerkraut is also traditionally produced in the Balkans using whole heads of cabbage instead of shredded cabbage. It is usually produced by spontaneous fermentation. In spontaneous sauerkraut fermentation, *Leuconostoc mesenteroides* initiate the fermentation process, followed by the growth of other lactic acid bacteria (LAB), mainly *Lactobacillus brevis*, *Pediococcus pentosaceus*, and *Lactobacillus plantarum* species, among which *L. plantarum* is responsible for the second phase of fermentation and high acidity of the produced sauerkraut. The dominant species, present in the fermentation, shift within 1 week from less acid-tolerant heterolactic to more acid-tolerant homolactic fermenting LAB species. Shredded cabbage fermentations start with 10^6 colony-forming unit (cfu) g^{-1} aerobic microorganisms, 10^6 cfu g^{-1} enterobacteriaceae, and less than 10^2 cfu g^{-1} yeasts and molds (Tamang and Kailasapathy, 2010). According to Tamang and Kailasapathy (2010), during the first 2 or 3 days of sauerkraut fermentation, less acid-tolerant LAB dominate, but after that more acid-tolerant LAB predominate. Each of these populations reaches concentrations of 10^8–10^9 cfu g^{-1}. The fermentation is complete in 2 weeks and at that time the most acid-resistant *L. plantarum* predominates. Salt concentration and fermentation temperature can also affect the growth of the naturally present microorganisms and the sensory properties of the sauerkraut (Wiander and Ryhanen, 2005). Two percentage of salt is usually added to the traditional fermentation, and to reduce salt waste.

In a study of two commercial sauerkrauts, Plengvidhya *et al.* (2007) reported that glucose and fructose were the primary fermentable sugars in the cabbage, with concentrations of 1.5% and 2.2%, respectively, and sucrose concentration was less than 0.2%. Lactic acid, acetic acid, and mannitol were produced, and on the 14th day the pH value of all the tanks increased from 3.4 to 3.7.

Kimchi

Kimchi is a group of fermented cabbage, radish, and garlic foods and is consumed on a daily basis in Korea. The flavor of kimchi is dependent on the ingredients, fermentation conditions, and LAB involved in the fermentation process (Lee *et al.*, 2005). Kimchi is stored for several months, when

lactic acid fermentation occurs (Lee and Lee, 2006). More than 100 types of vegetables can be used to prepare kimchi (Kim and Chun, 2005). Chinese cabbage, radish, and cucumber, with a seasoning mixture made of red pepper powder, garlic, ginger, and green onion, are among them (Nam *et al.*, 2009).

Kimchi is made through lactic acid fermentation of cabbage at low temperatures to ensure proper ripening and preservation. Because kimchi is representative of a typical open ecosystem, each batch of fermented food has a different composition of bacteria and this is dependent on ingredients and fermentation conditions, which can be variable.

LAB are the most important microorganisms in kimchi fermentation. Using conventional methods of isolation and phenotypic identification, the following species are found to be responsible for kimchi fermentation: *L. mesenteroides*, *Leuconostoc pseudomesenteroides*, *Leuconostoc lactis*, *L. brevis*, and *L. plantarum* (Kim and Chun, 2005). *Leuconostoc mesenteroides* was reported to predominate during the first hours of fermentation (Kim and Chun, 2005). The pH value gradually falls to 4 and then *L. plantarum* becomes predominant (Kim and Chun, 2005). To obtain a product of constant quality, a starter culture consisting of *L. mesenteroides* and *L. plantarum* strains was used, and the product was not different from conventional kimchi. *Leuconostoc citreum* HJ-P4, a strain isolated for kimchi fermentation, with high dextransucrase activity and adapted to grow at low temperature, has been proposed to be used as a starter culture to produce kimchi commercially (Yim *et al.*, 2008).

Fermented Beans and Cereals

Tempe

Tempe is a solid fermented soybean product prepared using nonsalted soybeans. Tempe has an overwhelming advantage in terms of odor over other nonsalted fermented soybeans (Tamang and Kailasapathy, 2010). It is widely consumed in Indonesia and there has been considerable interest in the West, especially in the USA, in developing tempe as an alternative source of protein. In Indonesia, 750 000 tons of soybeans per year are consumed as tempe (Ito, 2002). In the USA, Europe, and Japan, some food companies produce tempe on a large scale (2–6 tons week^{-1}).

Rhizopus oligosporus (*Rhizopus. microsporus* variety *oligosporus*), a fungus, is the major microorganism for the fermentation of tempe, though some bacteria have been isolated from natural tempe (Tamang and Kailasapathy, 2010). In addition, *Klebsiella pneumoniae*, *K. pneumoniae* subsp. *ozaenae*, *Enterobacter cloacae*, and gram-positive bacteria were isolated as vitamin B12-producing bacteria in tempe (Okada *et al.*, 1985). LAB is the second most important microorganism in traditionally made tempe in Indonesia. The key role of bacteria is to lower the pH of soybeans, to prevent pathogenic bacteria from growing dominantly, and to provide *R. oligosporus* with a suitable environment to multiply. Tempe preparation is rapid and takes only two days at most to complete. It is perishable and is consumed as a meat substitute. Among the nonsalted fermented soybeans, only tempe has been accepted worldwide (Tamang and Kailasapathy, 2010).

Tempe contains not only dietary fiber, saponins, and isoflavones of soybean origin but also superoxide dismutase, an enzyme that eliminates active oxygen. Strong thrombolytic activity (average 450 IU g^{-1} dry weight) was observed in tempe extract (Sumi and Okamoto, 2003). In laboratory-made tempe, the content of γ-aminobutyric acid, which improved blood flow to the brain and inhibited the elevation of blood pressure, increased when tempe was placed in an anaerobic environment after normal aerobic fermentation (Aoki *et al.*, 2003). It was also reported that a phytoestrogen, equol, derived from soybean isoflavone had a suppressive effect on prostate cancer (Horii, 2008).

Fermented Soybean Paste

Fermented soybean paste is indigenous to the cuisines of east and southeast Asia. Miso is a traditional Japanese food, and its consumption dates back to AD 700. Miso is a brown and salty fermented thick soybean paste. It contains vitamins, microorganisms, salts, minerals, plant proteins, carbohydrates, and fat. Miso also contains saponin-inhibiting lipids peroxide, trypsin inhibitor, isoflavon, lecithin, colin, prostaglandin E, and others. It is used on a daily basis as a flavor in soups and solid foods in Japan and some parts of Asia. In addition, miso adds a unique burst of flavor to salad dressings, vegetable dishes, baked tofu, sauces, and marinades. According to Hesseltine (1965); Shibasaki and Hesseltine (1962) there are three basic types of miso. There is kome miso, made from beans and rice; mugi miso, made from beans and barley; and mame miso (sold as hatcho miso in the UK) made from soybeans alone. For the production of kome and mugi misos, the koji is produced by soaking polished rice overnight in water, steaming it for approximately an hour, then inoculating with mould spores. Incubation is for 50 h at 35° with thorough stirring at least twice. The *Aspergillus oryzae* strains used for these fermentations should be higher in amylolytic activity. *Saccharomyces rouxii* and *Torulopsis* are the yeasts and *Pediococcus halophilus* and *Streptococcus faecalis* are the bacteria, principally involved in miso's spontaneous fermentation.

Miso is considered as a food with health-promoting benefits, such as effectiveness in relieving fatigue, regulation of the intestinal function, digestive supplement, protection against gastric ulcer, decrease of cholesterol, decrease of blood pressure, whitening ability, prevention of diseases associated with adult lifestyle habits, apoplexia cerebri, accumulation of brain metabolism, protection of aging, healing radiation damage, and prevention of cancers for biological effects (Watanabe).

Bibliographically, Korea developed and used its own traditional fermented foods 2000 years ago (Kwon *et al.*, 2011). Korean soy foods are increasingly present on the worldwide market, and because kochujang (fermented red pepper paste with soybean flour) and fermented soybean pastes (doenjang and chungkukjang; both chungkukjang and chungkookjang are used in the reports) were registered in CODEX in July, 2009, they are now internationally accepted foods (Kwon *et al.*, 2010). Most fermented soybean pastes are salty and savory and some are spicy. They are often used as condiments to flavor foods such as stir-fries, stews, and soups. Fermentation changes the physicochemical and organoleptic

properties of soy products such as color, flavor, and active components. Differences in their color, flavor, and active components are due to different production methods such as the conditions of fermentation; the addition of wheat flour, pulverized meju, rice; and the presence of different microflora such as bacteria or yeasts used in their production, as well as whether the soybeans are roasted (as in chunjang) or aged (as in tauchu) before being ground. In addition to physicochemical properties, the fermentation of these soybean products changes the bioactive components, such as isoflavonoids and peptides, in ways that may alter their physiological properties in terms of healthy health functions and efficacies.

Fermented Cereal

Cereal-fermented foods involve a lactic acid fermentation step in most cases, which can be associated with an alcoholic fermentation step depending on the process used (e.g., brewing). It is now commonly known that lactic acid fermentation contributes to human welfare through the preservation of foods, the development of organoleptic characteristics and nutritional improvement of foods, and the health-promoting effects of lactic acid bacteria (probiotics) (Nout and Motarjemi, 1997; Charalampopoulos *et al.*, 2002; Kohajdova and Karovicova, 2007).

Lactic acid cereal-fermented foods and beverages are made from a great variety of cereals involving different processing methods. Maize, millet, and sorghum grains in Africa are used to produce such lactic acid-fermented foods like *ogi* (Benin, Nigeria), *togwa* (Tanzania), *bushera* (Uganda), *ben-saalga/koko* (Burkina Faso, Ghana), *gowe* (Benin), *mawe* (Benin), *kenkey* (Ghana), *hussuwa* (Sudan), *mahewu* (Zimbabwe), *poto poto* (People's Republic of Congo). In many African countries, the same cereals can be germinated to produce malt for their use in brewing of cereal slurries to make traditional beers of thick consistency, called under different vernacular names such as *dolo* in Burkina Faso; *bili bili* in Tchad; *burukutu* in Nigeria; *pito* in Ghana; and *kaffir*, a Bantu beer, in South Africa. In Mexico and Guatemala, maize is used to produce *pozol* whereas rice is used to produce *selroti*, *bhaati jaanr*, *idli*, *dosa* in India, and *burong isda* in the Philippines. In the Himalayas, various cereals like finger millet, wheat, maize, and barley are used to produce different kinds of fermented beverages like *kodo ko jaanr* and *gahun to jaanr*, and if we consider the particular case of the Balkan Peninsula, rye, wheat, millet, maize, rice, barley, and oat are used alone or in mixtures to produce *boza*.

Fermented Milk

Yogurt

Yogurt is the most popular and successful fermented milk product all over the world and is manufactured by scientifically sound technologies in modern dairy factories. It is similar to some traditionally made yogurt manufactured thousands of years ago. Yogurt is a widely consumed highly nutritious fermented milk, defined by the Codex Alimentarius (FAO/WHO, 2003) as a coagulated milk product resulting from the fermentation of milk by *Streptococcus. thermophilus* and *Lactobacillus delbrueckii* subsp. *bulgaricus* (formerly *Lactobacillus bulgaricus*). Among the factors contributing to the great success of this fermented milk product, the image of a natural product, attractive organoleptic characteristics (fresh, acidulated taste, and pleasant flavor), nutritional value, prophylactic and therapeutic properties, and moderate cost (due to the high productivity of the production lines) can all be mentioned (Tamime and Robinson, 2007). Varieties of yogurt available include plain (set), fruit-flavored, whipped, drinking type (stirred), smoked, dried, strained, and frozen (Tamime and Robinson, 2007).

The desirable typical flavor of yogurt comes from a mixture of lactic acid, carbonyl compounds (acetaldehyde, acetone, diacetyl, acetoin), nonvolatile acids (pyruvic, oxalic, succinic), volatile acids (formic, acetic, propionic), and a large series of degradation products from the catabolism of proteins, fats, and lactose. In general, yogurt has less lactose and more lactic acid, galactose, peptides, free amino acids, and free fatty acid than milk (Tamime and Robinson, 2007). Apart from its high nutritional value, yogurt has a lot of health benefits. Beneficial health effects are presumed to depend on the ability of *S. thermophilus* and *L. delbrueckii* to reach the gastrointestinal tract alive, where they persist and/or multiply. However, there have been conflicting studies concerning the culture recovery of *L. delbrueckii* subsp. *bulgaricus* and *S. thermophilus* from fecal samples after yogurt ingest; whereas some authors reported recovery of both bacterial types (Mater *et al.*, 2005; Elli *et al.*, 2006), some others have failed to do so (del Campo *et al.*, 2005).

Cheese

Cheese in Europe has traditionally been considered the preferred outlet for milk after local fresh milk requirements have been met. The EU cheese market is the largest in the world. Cheese has therefore provided much better export opportunities than any other dairy product as the willingness to pay for high quality European cheese has always been high.

Most cheeses in Europe are produced on a commercial scale using the appropriate LAB starter culture. Thermophilic strains are generally used in cheeses with a high cooking temperature such as Swiss and Italian types (Caplice and Fitzgerald, 1999). Secondary microflora are added in some processes to improve texture (e.g., the production of CO_2 by Propionibacterium in Swiss cheese) and flavor (e.g., by the production of diacetyl). Moulds, yeasts and bacteria other than lactic acid bacteria are used as secondary microflora in some varieties of cheese.

Fermented Fish

There are many varieties of fermented fish products available at present. Fermented fish products include liquid products such as fish sauce also known as *nampla* in Thailand, *kecap ikan* or *bakasang* in Indonesia, *patis* in the Philippines, *nouc-mam* in Vietnam, oyster sauce, *hoi-sin* sauce, and paste products such as fish and shrimp pastes also known as *belacan* or *terasi* in Indonesia and Malaysia, and dry and semidry fermented fish.

Lightly salted fermented fish are mostly produced in southeast Asia (Adams *et al.*, 1985; Ishige, 1993; Phithakpol *et al.*, 1995) and their traditional culinary use is widespread throughout the region. Plaa-som is a popular Thai fermented fish produced according to family or local geographical preferences, especially in the central, northeastern, and northern parts of Thailand (Saithong *et al.*, 2010). According to Saithong *et al.* (2010), differences exist in production methods of plaa-som and the use and proportions of raw materials, which typically consist of freshwater fish, salt, a carbohydrate source (cooked or raw rice), and garlic. All ingredients are mixed and left to ferment at ambient temperature (25–30 °C) for 3–5 days in either a covered-lid cooking pot, a wrapped package using a thin plastic sheet, or a plastic bag. The traditional production of plaa-som is based on spontaneous fermentation due to the development of the microflora naturally present in the raw materials. The quality of the end-product is dependent on the microbial load and on the spectrum of the raw materials. At present, the production of plaa-som on a large scale has become an important branch of the fermented food industry in Thailand and efforts are being made to develop effective starter cultures for use in plaa-som production to help improve the fermentation process.

Fermented fish products are also found in other parts of the world including the Scandinavian region in Europe, Africa, and the Middle East. In Scandinavia, whole herring or trout eviscerated but retaining the roe, are immersed in low concentration brine for 30–40 h, during which vigorous fermentation takes place (Tamang and Kailasapathy, 2010). These products are known as surstromming for herring and rakorret for trout (Beddows, 1985). Surstromming is regarded as a great delicacy in Sweden. In France and Spain, fermented anchovy products are common. Anchovy is used in the preparation of *nouc-mam*, *nampla*, and *jeotkuk*. The fish is beheaded and gutted (or ungutted in Spain), then layered with salt in barrels, weighed down to extract the pickle as it forms, and fermented for 6–7 months. The fermented fish retains its form. Lactic acid bacteria are found as the dominant microorganisms in many fermented fish products (Orillo and Pedersson, 1968; Saisithi *et al.*, 1986; Olympia *et al.*, 1992; Østergaard *et al.*, 1998). A combination of low pH and organic acids (especially lactic acid) is the main preservation factor in fermented fish products. Generally, pH should be below 5–4.5 in order to inhibit pathogenic and spoilage bacteria (Owens and Mendoza, 1985). The enzymes for the fermentation process come partly from the digestive system of the fish and partly from the bacteria that are naturally present in the fish and salt. The accumulation of lactic acid prevents the decomposition of protein into its basic components such as CO_2 and H_2O (Olympia, 1992).

Fermented Meat

Fermented meats originated independently in a number of regions around the world, although European-style products now predominate in terms of their scale of production and the degree to which they have been subjected to scientific scrutiny (Tamang and Kailasapathy, 2010). These sausages are produced by fermenting with LAB a mixture of minced meat mixed with fat, salt, curing agents (nitrate/nitrite), sugar, and spices. Fermentation temperatures are usually less than 22 °C for dry and mould-ripened sausages and 22–26 °C for semidry varieties (Lucke, 1998). Traditional sausages are usually manufactured in small-scale plants following spontaneous fermentation. Sausages produced with and without added starter culture have final pH of 4.6–5.0 and 4.0–4.5, respectively. European fermented sausages formulated with nitrite are produced with added starter culture, generally consisting of lactic acid bacteria (*lactobacilli* and *pediococci*) and catalase-positive cocci (*S. carnosus*, *Micrococcus varians*). The use of starter cultures ensures a good quality, standardized, and safe product.

The production and consumption of fermented meats expanded throughout Europe in the middle ages and were adapted to climatic conditions (e.g., smoked in northern Europe and dried in Mediterranean countries). A wide variety of fermented sausages is being produced in Europe and the variations depend on raw materials, microbial populations, and processing conditions. For example, northern-type sausages, which contain beef and pork as raw meats, are ripened for short periods (up to 3 weeks), and are usually subjected to smoking. In these sausages, shelf life is mainly due to acid pH and smoking rather than drying. However, Mediterranean sausages mostly use only pork. These sausages are ripened for longer periods (several weeks or even months), and are not typically smoked. Undry and semidry sausages are fermented to reach low pH values, and are usually smoked and cooked before consumption. Shelf life and sausage safety are mostly determined by pH drop and reduced water activity, as a consequence of fermentation and drying, respectively. The product may be considered stable at room temperature when $pH < 5.0$, and the moisture:protein ratio is below 3.1:1 (Sebranek, 2004). Moisture:protein ratios are defined for the different dry and semidry fermented sausages in the USA, whereas water activity values are preferred in Europe.

Typical fermented products were initially based on the development and growth of desirable indigenous flora, sometimes reinforced with backslopping, which is the addition of a previously ripened fermented sausage with adequate sensory properties. However, this practice usually yielded a high heterogeneity in product quality. The use of microbial starters, as a way to standardize processing as well as quality and safety, is relatively new. At present, most fermented sausages are produced with a combination of lactic acid bacteria to achieve adequate acidulation, and two or more cultures to develop flavor and facilitate other reactions such as nitrate reduction. The most important microorganisms used as starters belong to one of the following groups: lactic acid bacteria, *Micrococacceae*, yeasts, and molds (Leistner, 1992).

One of the few studies reporting the effects of the consumption of probiotic meat products on human health was carried out by Jahreis *et al.* (2002). These authors evaluated the effect of daily consumption of 50 g of probiotic salami containing *Lactobacillus paracasei* LTH 2579 on the immunity system and blood triglycerides and cholesterol levels of healthy volunteers for a few-weeks period, and obtained moderately satisfactory results.

Fermented Alcohols

Rice Wine

Rice wine is a generic name referring to alcoholic beverages made from cereals, mainly rice, in east Asia. The beverage is known as 'rice wine' in the West because its alcohol content is approximates that of a wine. Rice wine is called sake in Japan, cheongju in Korea, and shaosingjiu in China. Sake is the national and traditional drink of Japan and is one of the most popular traditional nondistilled alcoholic drinks in the world. Most Japanese elderly people, 61% of aged men and 18% women, prefer *sake* and beer according to a questionnaire survey (Jin *et al.*, 2005). It is prepared from rice using *koji* and is a clear, pale yellow liquid containing 15–20% alcohol (Tamang and Kailasapathy, 2010). Unique strains of *Saccharomyces cerevisiae* have evolved to conduct these fermentations, generating products with high ethanol content (12–20%), attractive flavor, aroma, and odor (Kodama, 1993). The first organisms that develop in the mash under traditional fermentation conditions are nitrate-reducing bacteria such as *Pseudomonas*, *Achromobacter*, *Flavobacterium*, or *Micrococcus* spp. (Murakami, 1972). These are followed by *L. mesenteroides* var *sake* and *Lactobacillus sake*, and yeasts (Kodama and Yoshizawa, 1977). The presence of lactic acid bacteria in controlled amounts is essential for satisfactory sake fermentation because the pH of the basic mash is too high for good yeast growth or a satisfactory flavor in the finished product (Wood, 1977). The highly refined *sake* brewed by the most skillful brewers using very highly polished rice at low temperatures of 9–11 °C for 25–30 days is known as *gonjoshu* (Kodama and Yoshizawa, 1977). Most LAB that spoil *sake* are homofermentative rods and are more tolerant to ethanol and acid than nonspoilers (Inoue *et al.*, 1992). *Saccharomyces cerevisiae* strains with disrupted ubiquitin-related genes produced more ethanol than the parental strain during *sake* brewing (Wu *et al.*, 2009). Several researchers have reported on improved strains for *sake* production on an industrial scale (Hirooka *et al.*, 2005; Kotaka *et al.*, 2008; Hirasawa *et al.*, 2009).

Wine

Wine is defined as the alcoholic fermentation of grape juice or other fruits without distillation. Red wine is produced from red grapes and other dark-colored grapes. White wine is made by fermenting mashed white grapes or from dark-colored grapes with the skin, pulp, and seeds removed. Red wines and white wines have markedly different flavors, and individual wines within the white or red classification may have noticeably different tastes as well (Robinson, 1994). Consumption of red wine is common in the traditional Mediterranean diet (Trichopoulou *et al.*, 2003). Traditional winemaking has been illustrated by Walker (1998). Grapes are collected from the vineyard, destemmed, crushed, pressed, and macerated, and fermented by naturally present yeasts or by adding starters. After the desired fermentation, the mass is filtered to remove sediments and is stored in wooden casks for maturation for several months, and then bottled, matured, stabilized, and filtered into clear red or white wines (depending on the color of grapes).

Until 75–100 years ago, most wines were produced by spontaneous or natural alcoholic fermentation of grape juice by indigenous yeast flora (Pretorius, 2000). Muller-Thurgau in 1890 introduced the concept of inoculating wine fermentations with pure yeast cultures. As a result, the quality and quantity of wine production have improved (Pretorius, 2000). The source of yeasts is from the surface of the grape berry; the surface of winery equipment that come in contact with the juice during crushing, pressing, pumping, and fermentation; and air (Raspor *et al.*, 2006). Various strains of *S. cerevisiae* and *Saccharomyces bayanus* act as the principal yeasts in the fermentation of wine. At present, many wine makers purchase commercial dried preparation of these yeasts for inoculation into grape juice and for initiation of the alcoholic fermentation (Fleet, 1998). Wine fermentation is initiated the by growth of various species of non-*Saccharomyces* yeasts (e.g., *Hanseniaspora uvarum*, *Kloeckera apiculata*, *Candida stellata*, *Candida colliculosa*, *Metschnikowia pulcherrima*, *Kluyveromyces thermotolerans*) as well as *Saccharomyces* yeasts, which are generally limited to the first 2–4 days of fermentation, after which they die (Fleet, 1993; Moreira *et al.*, 2005). They achieve maximum populations of 10^6–10^7 cfu ml^{-1} before death, thereby influencing the metabolic behavior of the fermentation and the products released into the wine, and their death is attributed to an inability to tolerate the increasing concentrations of ethanol, which is largely produced by the *Saccharomyces* species (Tamang and Kailasapathy, 2010). After 4 days or so, the fermentation is continued and completed by *Saccharomyces* species, especially strains of *S. cerevisiae*, *S. bayanus*, and in some cases *Saccharomyces paradoxus* (Moreira *et al.*, 2005).

Others

Vinegar

Vinegar is a highly acceptable condiment used in pickling and preservation of cucumber and other vegetables. Vinegar has long been used as a seasoning and preserving agent and is produced by a fermentation process from wine, apple juice, honey, rice, malted barley, etc. (Giordano *et al.*, 2003). In northeastern regions of Asia, such as China and Japan, vinegar is traditionally produced from cereals, primarily rice (Haruta *et al.*, 2006). Vinegar is not just a solution of acetic acid, but a complex matrix composed of alcohols, acids, aldehydes, and ketones (Wang and Jin, 2000; Suomalainen and Kangasperko 1963). The production of vinegar depends on mixed fermentation, which involves both yeasts and bacteria. Acetic acid bacteria, particularly those belonging to the genera *Acetobacter* and *Gluconacetobacter* (De Ley *et al.*, 1984; Yamada *et al.*, 1997) are used for industrial vinegar production because of their remarkable ability to oxidize ethanol to acetic acid and high resistance to acetic acid. The fermentation is initiated by yeasts, which break down glucose into ethyl alcohol with the liberation of carbon dioxide gas. Following on from the yeasts, acetobacter oxidize the alcohol to acetic acid and water. The yeasts and bacteria exist together in a form known as commensalism. The acetobacter are dependent on the yeasts to produce an easily oxidizable substance (ethyl alcohol). It is not possible to produce vinegar by the action of one type of microorganism alone.

For a good fermentation, it is essential to have an alcohol concentration of 10–13%. If the alcohol content is much higher, the alcohol is incompletely oxidized to acetic acid. If it is lower than 13%, there is a loss of vinegar because the esters and acetic acid are oxidized. In addition to acetic acid, other organic acids are formed during the fermentation, which become esterified and contribute to the characteristic odor, flavor, and color of the vinegar. Acetaldehyde is an intermediate product in the transformation of the reducing sugar in fruit juice to acetic acid or vinegar. Oxygen is required for the conversion of acetaldehyde to acetic acid. In general, the yield of acetic acid from glucose is approximately 60%. A combination of microorganisms such as moulds, yeasts, lactobacilli, and acetic acid bacteria is employed in traditional Chinese solid state fermentation, resulting in vinegars with better flavor (Jiang *et al.*, 2010). The principal bacteria are *Acetobacter acetic*, *Acetobacter xylinum*, and *Acetobacter ascendens*. The main yeasts are *Saccharomyces ellipsoideus* and *S. cerevisiae*. It is important to maintain an acidic environment to suppress the growth of undesirable organisms and to encourage the presence of desirable acetic acid-producing bacteria. It is common practice to add 10–25% by volume of strong vinegar to the alcoholic substrate to attain a desirable fermentation.

Microorganisms in Fermented Foods

Fermented foods are those foods that have been subjected to the action of microorganisms or enzymes so that desirable biochemical changes cause significant modification to the food (Chacko *et al.*, 2010). Filamentous moulds, yeasts, and bacteria constitute the microbiota in indigenous fermented foods and beverages, which are present in or on the ingredients, utensils, or environment, and are selected through adaptation to the substrate (Tamang, 1998). At present, all human cultures rely on fermented food products and the microbes that produce them (Scott and Sullivan, 2008). Different types of microorganisms are used in the production of different types of foods. **Table 1** shows selected species that may be used to produce various fermented food products.

Worldwide, lactic acid bacteria by tradition are the most commonly used microorganisms in the preservation of foods. Their importance is mainly associated with their safe metabolic activity while growing in foods utilizing available sugar for the production of organic acids and other metabolites (Balasubramanyam and Varadaraj, 1995). Their common occurrence in foods and feeds coupled with their long-lived use contributes to their natural acceptance as GRAS (generally recognised as safe) for human consumption (Aguuire and Collins, 1993). In Asia, mainly moulds of the genera *Aspergillus*, *Rhizopus*, *Mucor*, *Actinomucoe*, *Amylomyces*, *Neurospora*, and *Monascus* are used in the manufacture of fermented foods (Chacko *et al.*, 2010). In Europe, mould-ripened foods are primarily cheeses and meats.

Healthy Functions of Fermented Foods

Fermented foods have immense functional and therapeutic values possessing antioxidant, antimicrobial, probiotic, low-cholesterol, essential amino acid, bionutrient, and some important bioactive or health-benefit compounds; some of these are considered as potential sources of medical therapy for humans (Tamang, 2007).

Fermented Vegetables (Kimchi)

Kimchi was selected as one of the world's healthiest foods in 2006 by *Health* magazine due to its many beneficial properties (Nam *et al.*, 2009). Among the best functional components are β-carotene, chlorophyll, vitamin C, and dietary fiber (Park, 1995). Treatment of lactic acid from kimchi was found by Park *et al.* (2008) to play a role in the prevention of fat accumulation and to improve obesity-induced cardiovascular disease, particularly atherosclerosis, by attenuating the TNF α-induced changes of adipokines. Glycoprotein antimutagenic substances were isolated from a culture supernatant of *L. plantarum* isolated from kimchi (Rhee and Park, 2001), and antioxidants were isolated from kimchi (Sim and Han, 2008; Sun *et al.*, 2009). It has been reported that the consumption of kimchi causes weight loss; prevents constipation and colon cancer; reduces serum cholesterol (Park *et al.*, 2006); exerts antistress principles (Lee and Lee, 2009); is beneficial because kimchi contains *S*-adenosyl-L-methionine, a bioactive material used in the treatment of depression, osteoarthritis, and liver disease; has antiobesity effects (Kong *et al.*, 2008); and inhibits atherosclerosis (Kim *et al.*, 2008). A potential probiotic strain of *L. plantarum* isolated from kimchi inhibited the growth and adherence of *Helicobacter pylori* in an MKN-45 cell line, with small peptides as the possible inhibitors (Lee and Lee, 2006).

Fermented Soybean Products

Soybeans are well-known for their health-promoting benefits, which include antioxidation, antiobesity, antidiabetes properties, and prevention of osteoporosis and cancers such as breast and prostate cancer (Anderson *et al.*, 1998; Anderson and Pasupuleti, 2008; Messina, 1999). Many studies, which are insufficient and inconclusive, suggest that these kinds of health functions are primarily due to esterogenic properties of isoflavones but the results are still controversial (Kwon *et al.*, 2010). There are hundreds of *in vitro* studies showing that genistein has antioxidant properties, inhibits the growth of a wide range of both hormone-dependent and hormone-independent cancer cells, including breast (Pagliacci *et al.*, 1994; Peterson and Barnes, 1996; Zava and Duwe, 1997), prostate (Kyle *et al.*, 1997), colon, and skin cells (Adlercreutz and Mazur, 1997; Akiyama and Ogawara, 1991; Constantinou and Huberman, 1995) and that genistein also inhibits the metastatic activity of both breast (Peterson and Barnes, 1996; Scholar and Toewa, 1994) and prostate (Santibáñez *et al.*, 1997) cancer cells independent of the effects on cell growth. Daidzein, one of the two primary isoflavones in soybeans, exhibits anticancer effects (Jing *et al.*, 1993). Recently, genistein was also demonstrated to have antiinflammatory properties (Hernandez-Montes *et al.*, 2006; Verdrengh *et al.*, 2003), and it was found that genistein decreased cisplatin-induced apoptosis by regulation of p53 production in kidney, and reactive oxygen species production in cisplatin-treated normal kidney

Table 1 Selected species for various fermented foods

Food	*Microorganisms of fermented products in the world*	*References*
Fermented vegetables		
• Sauerkraut	• *Leuconostoc mesenteroides*, *Lactobacillus brevis*, *Lactobacillus plantarum*, and *Pedicoccus pentosaceus*, *Coliform* spp.	Wiander and Ryhanen (2005)
• Kimchi	• *L. mesenteroides*, *Leuconostoc pseudomesenteroides*, *Leuconostoc lactis*, *L. brevis*, *L. plantarum*, *Streptococcus faecalis*, and *Pfediococcus pentosaceus*	Kim and Chun (2005)
Fermented soybean and cereals		
• Tempe	• *Rhizopus oligosporus*, *Klebsiella pneumoniae*, *K. pneumoniae* subsp. *ozaenae*, and *Enterobacter cloacae*	Hesseltine (1965)
• Miso	• *Aspergillus oryzae*, *Saccharomyce rouxii*, *Torulopsis etchellsii*, and *Lactobacillus* sp.	Shibasaki and Hesseltine (1962), Hesseltine (1965)
• Doenjang	• *Bacillus subtilis*, *Staphylococcus sciuri*, *Enterococcus faecalis*, and *Citrobacter* or *Enterobacter*	Chang *et al.* (1977)
• Cereals	• LAB	Kohajdova and Karovicova (2007)
Fermented milk		
• Yogurt	• *Streptococcus thermophilus* and *Lactobacillus delbrueckii* subsp. *bulgaricus* (formerly *Lactobacillus bulgaricus*)	Tamime and Robinson (2007)
• Cheese	• *Lactococcus* spp., *Pediococcus* spp., *Streptococcus* spp., *Leuconostoc* spp., *Propionibacter* spp., Cheese moulds, and yeasts	Caplice and Fitzgerald (1999)
Fermented fish		
• Surstromming	• LAB	Beddows (1985)
• Fish sauce (Indonesian)	• *Pseudomonas*, *Enterobacter*, *Moraxella*, *Micrococcus*, *Streptococcus*, *Lactobacillus*, *Staphylococcus*, and *Pediococcus*	Adams *et al.* (1985)
• Korean fish products from anchovy	• *Bacillus cereus*, *Clostridium setiens*, *Pseudomonas halophillus*, and *Serratia marcescens*	Adams *et al.* (1985)
Fermented meat	• *Lactobacilli* spp., *Pediococci* spp., *S. carnosus*, and *Micrococcus* varians	Leistner (1992), Sebranek (2004)
	• *Lactobacillus sake*, *Lactobacillus curvatus*, and *L. plantarum*	Leistner (1992), Sebranek (2004)
Fermented alcohols		
• Rice wine	• *Pseudomonas, Achromobacter*, *Flavobacterium*, or Micrococcus spp., *L. mesenteroides* var *sake* and *L. sake*, and *A. oryzae*	Kodama and Yoshizawa (1977), Wood (1977)
• Wine	• *Saccharomyces cerevisiae*, *S. bayanus*, and *S. paradoxus*	Fleet (1993), Moreira *et al.* (2005)
Others		
• Vinegar	• *Saccharomyces ellipsoideus*, *S. cerevisiae*, *Acetobacter* spp., *Gluconobacter* spp., *Xylinum*, and *A. ascendens*	De Ley *et al.* (1984), Haruta *et al.* (2006), Yamada *et al.* (1997)

Abbreviation: LAB, lactic acid bacteria.

HK-2 cells (Sung *et al.*, 2008). The previous review of the authors (Kwon *et al.*, 2010) described in detail the antiobesity effects of soybean for type 2 diabetes. Some studies of the effects of soybeans, including isoflavonoids and soy proteins, on glucose metabolism are inconsistent, and the mechanisms have not been extensively studied. However, other studies showed positive effects on hypocholesterolemia, for example, 46 postmenopausal women taking isolated isoflavone extracts had significantly increased high-density lipoprotein cholesterol and a decrease in apolipoprotein B, the primary apolipoprotein in low-density lipoprotein particles (Clifton-Bligh *et al.*, 2001; Goodman-Gruen and Kritz-Silverstein, 2001).

In soy protein nutrition, the sulfur amino acids, methionine and cysteine, are the limiting amino acids. However, the relatively low sulfur amino acid content of soybeans may actually provide an advantage in terms of calcium retention, ironically. The reported hypercalciuric effect of protein is likely to be at least partially due to the metabolism of sulfur amino acids. The skeletal system serves as one of the main buffering systems in the body; as a result, the hydrogen ions produced from the metabolism of sulfur amino acids cause demineralization of bone and excretion of calcium in the urine. Thus, bean protein may improve calcium retention relative to animal and grain proteins. Soy protein also has a cholesterol-lowering effect in monkeys (Terpstra *et al.*, 1984) and in men (Wong *et al.*, 1998), and protein hydrolyzate or hydrolyzed peptides of soybeans decrease blood cholesterol and glucose levels (Yoshikawa *et al.*, 1999). Lunasin, a 43 amino acid peptide from soy, has been shown to have numerous biological properties including anticancer and antiinflammatory activities (Mejia and Dia, 2009; Park *et al.*, 2001). In fact, the authors identified hypocholesterolemic, a peptide from fermented soy products, including doenjang and soy protein isolates, are known to activate peroxisome proliferator–activated receptors (PPARs) and liver X receptor

signaling and to inhibit sterol regulatory element-binding protein-1c signaling, contributing to insulin sensitization (Jhala *et al.*, 2003; Ronis *et al.*, 2009). In addition, soy-fed CD-1 mice exhibited enhanced insulin sensitivity, especially in white adipose tissue, due to the potentiation of phosphorylation of AMP-activated protein kinase and acetyl-CoA carboxylase and upregulation of the expression of genes involved in peroxisomal fatty acid oxidation and mitochondrial biogenesis and in skeletal muscles by increasing glucose uptake (Cederroth *et al.*, 2008).

It is also well-known that substituting vegetable oils, such as soybean oil, for animal fat reduces the risk of high blood pressure, thrombosis, platelet generation, and cholesterol accumulation (Meydani *et al.*, 1991). Soybean oils contain health-promoting linoleic, linolenic acids, and phytochemicals. Both short- and long-term fermented soybeans contain more beneficial components to ameliorate metabolic disorders than unfermented soybeans. The changes in nutritive and nonnutritive biofactors during fermentation and their capacity for ameliorating metabolic disorders were reported in Asian countries, especially Korea. Fermentation of soybeans increased isoflavonoid aglycones, modified isoflavonoids such as equol and small peptides, and these changes enhanced the prevention of metabolic disorders.

Fermented Dairy Products (Yogurt)

Probiotic foods are a group of health-promoting products called functional foods, with large commercial interest and growing market shares (Arvanitoyannis and van Houwelingen-Koukaliaroglou, 2005). Their health benefits are based on the presence of selected strains of lactic acid bacteria, and when taken up in adequate amounts, confer a health benefit on the host. They are administered mostly through the consumption of fermented milks or yoghurts (Mercenier *et al.*, 2003).

Among the health benefits, improvement of lactose intolerance symptoms among lactose maldigestors has been clearly demonstrated (Rizkalla *et al.*, 2000; Labayen *et al.*, 2001; Pelletier *et al.*, 2001). This physiological effect is thought to be not only due to the lowering of the lactose content in yogurt by 20–30% as compared to milk, but also due to the contribution of bacterial β-galactosidases to increase enzymatic activity in human intestines. Yogurt has also been used in the management of acute diarrhea disorders as recommended by the FAO/WHO (2003). Yogurt feeding in children with acute watery diarrhea decreased stool frequency and shortened the duration of diarrheal episodes (Boudraa *et al.*, 2001). A further benefit may accrue from its recognized immunomodulation capacity (Meydani and Ha, 2000). Yogurt consumption seems to enhance the immune response, particularly in immunocompromised populations such as the elderly (Tamang and Kailasapathy, 2010). Yogurt consumption has also been associated with decreased risk of progression and promotion of colon cancer by modulating cell proliferation and increasing cellular apoptosis (Rachid *et al.*, 2002).

Fermented Alcohols

It has been estimated that the medicinal use of wine dates back to 2200 BC, making it the oldest known medicine (Robinson, 2006). Historically, wine has been used as an antiseptic, a painkiller, and to treat dermatological conditions and digestive disorders (Feher *et al.*, 2005; Robinson, 2006). Epidemiological studies from diverse populations have revealed that individuals who habitually consume moderate amounts of wine experience a 20–30% reduction in all-cause mortality, particularly cardiovascular mortality, when compared with individuals who abstain or who drink alcohol to excess (German and Walzem, 2000; Ruf, 2003). It has been well documented that a moderate intake of alcoholic beverages produces positive effects on antioxidants, lipids, and platelets (reviewed in Lindberg and Amsterdamk, 2008). There is ample evidence supporting the health benefits associated with regular and moderate consumption of wine, particularly polyphenol-rich red wine (Guilford and Pezzuto, 2011). Phenolic compounds in red wine may prevent the oxidation of LDL and is linked with the reduction of certain cancers (Mannistö *et al.*, 1997). Clinical studies and work performed with animal models indicate that wine may protect against cardiovascular disease, atherosclerosis, hypertension, certain types of cancer, type 2 diabetes, neurological disorders, and metabolic syndrome (Guilford and Pezzuto, 2011).

Vinegar

Vinegar's antiseptic properties make it a powerful defense against bacteria, virus, and fungus. Because of its antifungal abilities, vinegar is commonly used to treat a number of scalp problems including itching and dandruff. Vinegar is also used as a pain reliever and is believed to help lower bad cholesterol, reduce high blood pressure, heal respiratory infections, relieve constipation, and prevent diarrhea. Vinegar is also believed to help the body balance its blood glucose levels. This can help people suffering from diabetes, as well as individuals who want to keep their glucose and energy levels stable throughout the day. Consuming vinegar is believed to flush toxins from the body, improve immune system function, eliminate yeast in the digestive tract, and cleanse the urinary tract.

Conclusion

Modern consumers worldwide are increasingly becoming interested in their personal health and expect the food they consume to be not only safe but also healthy or even capable of preventing illnesses. Fermented products have a very important role to play in human diet not only in terms of nutrition but also in the promotion of good health. One possible reason for the lower incidence of diseases such as obesity, diabetes, or even breast cancer among Asians is that they consume a lot of fermented foods including soybean products, which are unique to the Asian traditional diet. Fermentation makes it possible to provide and preserve large quantities of nutritious food in a wide variety of flavors, aromas, and textures to feed the increasing population of the world. However, careful selection of specific strains combined with proper production and handling procedures are necessary to ensure that desired benefits are provided to consumers.

See also: Fermented Beverages

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Fermented Beverages

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Glossary

Gelatinization A disorganization and loosening of the internal structure of starch granules by heating, rendering the starch more amenable to enzymic hydrolysis.
Isomerization The transformation of relatively insoluble resinous materials in hops to more soluble and bitter compounds that impact the taste and appearance of beer.
Maillard reaction A nonenzymatic reaction between amino acids and sugars induced by heat that leads to color and flavor formation.
Malolactic fermentation A conversion of the more sour malic acid into the less sour lactic acid.
Procyanidin Molecules found widely in plant tissues that are formed by the polymerization of monomeric polyphenols and which have antioxidant properties and may contribute beneficially to bodily health.
Scion Part of a plant attached to another plant.

Introduction

It is increasingly asserted that static civilization developed some 6–8000 years ago in the Fertile Crescent on account of the 'discovery' of beer and bread, or some would say wine (McGovern, 2010). Surely, though, humankind has been sensing the pleasures of alcohol for rather longer than that, for unquestionably wherever there was a source of fermentable sugar (be it grapes or honey and more besides) and adventitious yeast, then there would have been circumstances for the production of alcohol and for humans to taste it and discover the mood-changing impact that could be had.

Through ages, the benefits of alcoholic beverages – now being produced routinely through emerging practices – will have been recognized as being one of the more pleasurable means by which foodstuffs could be preserved and modified.

To this day, most of the approaches to producing the diverse alcoholic beverages are deeply traditional in nature. Reference to the Sumerian poem The Hymn to Ninkasi emphasizes the broad similarity between beer production 8000 years ago and that which occurs today (Bamforth, 2008). Certainly the advances in fundamental scientific understanding, especially within the past 150 years, have allowed the refinement of beer making and that of other beverages. Yet the standard approaches have not hitherto become radicalized.

Through history the production of a beverage such as beer has progressed from being the purview of the women of households and broader communities, through refinement in monastic environs and onward to the advent of large-scale production brewers (once called common brewers) when the industrial revolution shifted workforces from domestic employment to factories with less opportunity for home brewing (Hornsey, 2003). Progressively, these large brewers became ever bigger, through consolidation as well as organic growth, events facilitated by technological developments such as design of ever larger fermenters; establishment of artificial refrigeration and pasteurization; development of railroad systems; and the evolution of more refined, flexible, and individual packages, such as kegs, glass bottles, and cans (Bamforth, 2009).

Some of these developments have also been applied to beverages other than beer, including wine and cider; however, many alcoholic beverages retain a more artisanal perspective. For drinks, such as beer and wine, too, there has been the same yearning for 'local' values, articulated in the beer industry with the word 'craft.' The reality is that beer production at any scale (just as for other alcoholic beverages) is a craft, pursued by technical people who rejoice in communities of like-minded individuals, in the case of brewing through organizations, such as the Institute of Brewing and Distilling (an organization that welcomes producers of other alcohol beverages, too, including cider), the Master Brewers Association of the Americas, and the American Society of Brewing Chemists. In the world of wine there is the American Society for Viticulture and Enology.

Taking brewing as an example, there are now more than 2500 breweries in the United States with many more at the planning stage. Government in the United States has had much to do with shaping the brewing and other alcoholic beverage industries. The era of prohibition between 1920 and 1933 saw a decline in the number of breweries from 1179 at the time of the signing into law of the Volstead Act to 703, 2 years after Roosevelt repealed the ban. Postprohibition rationalization led to a situation where only 89 breweries were functioning in the United States in 1978. President Carter's signing of an act in 1978 led to the legalization of home brewing the following year, from which came the seemingly endless spawning of smaller (and some not so small) brewing companies.

Governmental decisions can have profound impacts on businesses such as brewing. In the United Kingdom, Prime Minister Thatcher's government introduced the Beer Orders in 1988, which basically encouraged larger brewers to shift from becoming brewers per se to retailers as they were now forbidden to own an excessive number of pubs as had been the case in prior days of vertical integration (Bamforth, 2010). The realization that largest profits are to be made either from retailing beer or from brewing vast amounts of beer for wholesale distribution led to the major UK brewers selling their brewing activities to the larger global brewers, such as (the then) Interbrew, Heineken, and Carlsberg and diverting their

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investment into pubs and hotels. Meanwhile the same phenomenal growth of smaller brewers has occurred as in, United States, leading to some 1000 breweries in a landmass that fits approximately twice into California.

The world of brewing is characterized, then, by (at one extreme) phenomenally large companies such as Anheuser-Busch Inbev, which produces approximately one quarter of the world's beer, and South African Breweries-Miller and the other tiny breweries so small that they slot into categories such as 'nanobreweries.'

There have been similar trends in other alcoholic beverage industries. And so there has been the advent of major alcoholic beverage companies, which focus on a diversity of products including wines and spirit, for example, Diageo and Constellation, although there is a plethora of almost boutique wineries in regions like the Napa Valley of California, as well as the advent of an incipient craft distilling sector.

Governments have a history of profoundly shaping the alcoholic beverages industry through their taxation demands. In Europe, there is tremendous discontinuity within the supposed 'borderlessness' of the European Economic Community when it comes to taxation (**Table 1**). This leads understandably to substantial crossborder shipping of purchased alcohol from countries with less demanding tax rates to those that levy substantially larger amounts (e.g., France–UK and Sweden–Denmark).

Tax, though, can have other substantive impacts on the shape of the beverage business, which again can be illustrated with reference primarily to beer. In Nigeria, in 1988 the banning of imports of barley and malted barley (to preserve scarce currency) led to a focus on alternative raw materials and approaches to the brewing of beer, featuring primarily materials readily available within the country. Similarly in Japan, tax laws have dictated that products containing $<25\%$ malt attract a significantly lower tax rate. These products, known as Happoshu, are produced using materials, such as sugar, rice, and corn. They cannot be called beer, but in every respect they are presented through package and image as beer, yet at a substantial discount. Even cheaper are the so-called Third Category products, taxed at a lower rate still because they contain zero malt but are rather fermented from the likes of pea starch and soybeans. As a consequence of these developments, there has been a precipitate fall in 'conventional' beers in Japan, with a continuing growth in these new genre products.

In the United States, a differential between tax rates for beer and spirits has spawned the so-called Malternatives. Because beer is taxed at a significantly lower rate than distilled beverages, the quest for flavored alcoholic beverages has led to the development of processes wherein a bland beer produced in a brewery is decolorized and then flavored as required, with flavors such as fruit or cola. Generally these products have either names that are recognized as being associated with spirits such as vodka or are accorded whimsical names. Either way they appeal to the young, who find them easier to drink than bitter beer (or tannic wine, for that matter).

As one shall see, the production of beer involves much use of water and energy, with alternate addition and removal of liquid, something that baffles many at a time of considerable ecological and environmental attention and desire to conserve resources. It would certainly be feasible to produce palatable products in radically different ways that are based on making additions to a bland alcohol source (Heymann *et al.*, 2010). However, such products in the United States would be prohibitively expensive on a tax basis.

The flavored alcoholic beverages certainly makes the government focus on the issue of alcohol and health. The UK government in 1987 issued guidelines for responsible drinking, amounting to a weekly consumption of 21 units for a man and 14 for a woman, where 1 unit is 8 g of alcohol. However, in the UK as in other countries, there are concerns about minorities who abuse alcohol, for example, through binge drinking in social contexts lending themselves to irresponsible behavior. As such, it is too easy for officialdom to lose sight of the fact that for the greater length of time, alcohol in some

Table 1 Rates of excise duty and value added tax in the European community

Country	*Beer (cents per pint at 5% ABV)*	*Wine (cents per 75 cl bottle at 11% ABV)*	*Spirits ($ per 70 cl bottle at 40% ABV)*	*VAT%*
Austria	18.0	0	3.7	20.0
Belgium	15.5	46.7	6.5	21.0
Denmark	32.2	141.7	7.5	25.0
Finland	112.4	307.7	16.1	23.0
France	10.3	3.5	6.2	19.6
Germany	7.1	0	4.8	19.0
Greece	23.5	0	9.1 +	23.0
Ireland	59.1	260.2	11.5	23.0
Italy	21.2	0	3.0	21.0
Luxembourg	7.1	0	3.9	15.0
Netherlands	24.5	70.0	5.6	19.0
Portugal	13.8	0	4.1	23.0
Spain	7.6	0	3.1	18.0
Sweden	70.4	241.7	21.0	25.0
UK	89.2	305.9	12.1	20.0

Abbreviation: ABV, alcohol by volume.

Note: VAT rate for wine is 12%; + 50% less for ouzo.

Source: Reproduced with permission from British Beer and Pub Association, 2012. Statistical Handbook. London: British Beer and Pub Association. (Original data was quoted in Pounds Sterling as at April 2011. An exchange rate of £1 = $1.61 has been employed and values rounded to one decimal point).

form or the other has been a staple feature of society and frequently a normal and not unusual component of the diet and the dinner table.

There is indeed increasing evidence that there are real merits in the consumption of alcohol in moderation (Ford, 2003). Although red wine more than any other beverage has captured the attention, notably in response to the countering of atherosclerosis, claims that this is due to its uniquely high levels of resveratrol have been challenged. It is now generally accepted that there is nothing unique about red wine in this context and that the key component is likely alcohol per se (Rimm *et al.*, 1996). As such, any beverage referred to in this article in the same equivalent terms in terms of alcohol content would be expected to have a comparable effect. That a product such as wine may be perceived as being superior has rather more to do with the other behavior of wine drinkers with regard to diet and exercise. In reality, beer possesses rather more nutritive value than wine in respect of factors such as high levels of silicate, which may counter osteoporosis, antioxidants which may be at least as effective as those from wine, significant levels of vitamin B such as folate, and the presence of significant amounts of soluble fiber and putative prebiotics (Bamforth, 2004; Preedy, 2008).

Despite this apparent superiority of beer over wine from a health perspective, there has been a very real shift in the drinking habits of people in traditional beer drinking countries, from beer to wine. This can be inspected in the context of overall trends in a breadth of countries (Table 2).

Table 2 Drinks consumption (per capita, 2010)

Country	*Beer*	*Wine*	*Spirits*
Australia	84.0 (−6.7)	23.7 (+17.3)	0.9 (−30.8)
Belgium	78.0 (−21.0)	25.7 (+18.4)	1.2 (0)
Brazil	65.8 (+32.7)	1.7 (−10.5)	–
Canada	71.0 (+5.3)	12.3 (+26.8)	1.7 (−15)
China	33.3 (+88.1)	1.9 (+137.5)	2.7 (+68.8)
Czech Republic	144.0 (−9.4)	19.0 (+18.8)	3.0 (−13.3)
Denmark	64.6 (−36.8)	33.3 (+7.8)	1.3 (+18.2)
Finland	87.9 (+12.1)	10.7 (+21.6)	1.9 (+5.6)
France	30.5 (−15.7)	47.4 (−15.4)	2.7 (+12.5)
Germany	107.4 (−14.4)	20.3 (−12.1)	2.2 (+15.8)
Republic of Ireland	90.0 (−29.7)	16.4 (+47.7)	1.7 (−22.7)
Italy	28.6 (+1.8)	43.3 (−15.1)	0.2 (−60)
Japan	45.6 (−18.4)	1.8 (−18.2)	2.3 (+9.5)
Netherlands	72.0 (−13.0)	23.0 (+22.3)	1.3 (−23.5)
New Zealand	70.8 (−9.7)	20.9 (+16.8)	1.7 (+13)
Norway	56.0 (+7.7)	15.0 (+42.9)	1.0 (+25)
Portugal	59.0 (−8.5)	43.3 (−22.7)	1.1 (−26.7)
Russia	72.7 (+91.8)	9.1 (+51.7)	5.1 (−21.5)
Slovakia	78.5 (−9.9)	14.2 (+21.4)	3.9 (+5.4)
South Africa	62.0 (+15.2)	7.0 (−13.6)	0.7 (–12.5)
Spain	76.6 (+6.1)	25.9 (−23.1)	1.8 (0)
Sweden	52.8 (−6.4)	21.7 (+34)	1.2 (+9)
UK	73.7 (−23.9)	21.4 (+24.4)	1.8 (+12.5)
USA	81.9 (−6.1)	9.1 (+24.7)	2.3 (+15)

Note: Values in parentheses indicate growth or decline since 2000. Values are given as liters or, for spirits as liters of pure alcohol.

Source: Reproduced with permission from British Beer and Pub Association, 2012. Statistical Handbook. London: British Beer and Pub Association.

Beer

Barley starch supplies most of the sugars from which the alcohol is derived in the majority of the world's beers. Barley needs first to be malted, which comprises the controlled germination of grain followed by drying. The raw barley kernel is hard and not readily milled. During germination enzymes are developed that degrade the cell walls and protein during sprouting and go on to degrade starch in the brew house. Barley was originally selected for the brewing of beer because it retains a husk on threshing and this formed the filter bed in most breweries in which the extract of malt (wort) is separated from residual material after brewing (Bamforth, 2006).

Barley grain as harvested is dry (<12% moisture) or needs to be dried in order to preserve it and help prevent its infestation. The water content needs to be increased, usually to between 42% and 46%, in order to promote germination.

Not all barley varieties can be malted successfully. The so-called malting grades (as opposed to feed grades) are degraded readily, either because they have a structure amenable to hydrolysis or because they can produce higher levels of enzymes.

Barley used for malting should also have low protein content as, *pro rata*, for a grain of given size the less protein is present, the more starch there is. Therefore, fertilizer use for malting barley should be limited.

Barley also needs to be alive and also it should not be dormant. Dormancy is a natural condition designed to prevent grain from germinating when on the ear. It is prevalent when barley is grown in colder, wetter regions. Storage relieves the condition.

Kilning is essential to stop germination: by driving off the moisture, the metabolism of the grain is halted and the malt is stabilized for storage. Kilning must be carried out carefully because many of the malt enzymes that are needed to carry on polymer degradation in the brewery are heat sensitive. Therefore, heating is started at a relatively low temperature to start to drive off moisture. When the water level has perhaps been halved, the enzymes are more stable in this drier environment, and the temperature can be increased.

The other function of kilning is to introduce color and modify flavor. The more intense the heating, the darker is the color of the malt. Color is due to the melding of amino acids and sugars in the Maillard reaction. Therefore, the better-modified malts, with higher levels of polysaccharide and protein breakdown, will give darker malts during heating. The flavor changes involve removal of unpleasant characters, such as bean sprout and grassy notes, and development of pleasing malty aromas. A selection of malts is listed in Table 3.

Malting and mashing are really successive stages in a common enzymic conversion of barley into wort. The former is a low-temperature process, the latter a high temperature one. Before mashing, malt is stored for a minimum of 2–4 weeks to facilitate subsequent processing.

Malt must be milled before mashing. The smaller the particles the better the solute/solvent transfer from milled grist to the liquid. The conversion of the polymers that was begun in the malt house continues in the mash. This is often started at a relatively low temperature (e.g., 50 °C) to allow action of the more heat-sensitive enzymes, before raising the temperature to approximately 65 °C to induce gelatinization (melting) of the

Table 3 Malts used for brewing

Product	*Purpose/comments*
Pilsner malt	Mainstream malt for pale lager beers
Vienna malt	Mainstream malt for darker lagers
Munich malts	For darker lager beers
Pale malt	Mainstream malt for pale ales
Chit malt	Permissible as adjuncts in countries such as Germany with restrictions such as Reinheitsgebot
Green and lightly kilned malts	Alternate to exogenous enzymes
Diastatic malts	High enzyme potential for use in mashing with high levels of adjuncts
Smoked malts	For beers with smoky character, for example, rauchbier
Wheat malts	For wheat beers
Rye malts	For specialty beers
Oat malts	For specialty beers, including stouts
Sorghum malts	For *Sorghum* beers; malted millet may also be used as a richer source of enzymes
Cara Pils	To afford color and malty and sweet characters to lighter beers
Amber malt	To afford bread crust and nutty characters to beer and color
Crystal malt	To afford toffee and caramel characters to beer and color
Chocolate malt	To afford chocolate, roast, coffee, burnt, and bitter characters to beer, plus color
Black malt	To afford harsh, astringent, roast, and burnt notes to beer plus color
Roasted barley	To afford sharp, dry, burnt, and acidic notes to darker beers (n.b. drier than roasted malts)

Abbreviation: n.b., nota bene.

starch and attendant action of starch-degrading enzymes. For starches from some other cereals (e.g., corn and rice) the temperature is higher and this is why they are cooked separately before adding to the mash. During mashing, proteolytic enzymes continue the degradation of proteins and peptides into amino acids that the yeast will depend on for growth. However, some polypeptide needs to go through to the finished beer in order to support foam.

A trio of enzymes leads to the conversion of typically 80% of the starch in a mash to fermentable sugars in conventional mashing operations. Light and low carbohydrate beers are those in which the nonfermentable degradation products (dextrins) are fully or largely converted into fermentable forms. This can be achieved by the use of either glucoamylase or pullulanase of microbial origin or by adjustments to mashing that allow the endogenous enzymes to work more fully.

After perhaps an hour of mashing, the liquid portion of the mash, known as sweet wort, is recovered by separation over a time period either by filtering through residual husk or through membranes to the kettle. Here it is boiled, usually for approximately 1 h, and this serves various functions, including sterilization of wort, precipitation of potentially problematic proteins, and the driving away of unpleasant grainy characters originating in the barley. As there is a driving off of water the wort becomes concentrated. This is especially important for those brewers practicing high gravity brewing in which the wort is run to the fermenter at high strength; then after fermentation (in which higher than target alcohol levels are produced) the beer is diluted to the desired strength. This technique allows maximization of fermenter capacity. To facilitate these higher gravities, many brewers also add adjunct sugars at this stage, and most of them introduce at least a proportion of their hops.

The hops have two principal components: resins and essential oils. The resins are changed (in a process called isomerization) during boiling to yield the materials that provide the bitterness to beer. This process is rather inefficient. Nowadays, hops are often extracted with liquefied carbon dioxide and the extract is either added to the kettle or extensively isomerized outside the brewery for addition to the finished beer (thereby avoiding losses due to the bitter substances' tendency to stick on to yeast).

The oils are responsible for the 'hoppy nose' on beer. They are very volatile and if the hops are all added at the start of the boil then all of the aroma will be eliminated. In traditional lager brewing, a proportion of the hops is held back and only added toward the end of boiling, which allows the oils to remain in the wort. For obvious reasons, this process is called late hopping. In traditional ale production, hops are added to the finished beer, enabling a complex mixture of oils to give a distinctive character to such products. This is called dry hopping.

After the precipitate produced during boiling has been removed by straining through whole hops in a hop back or separation according to centripetal forces in a whirlpool, the hopped wort is cooled and pitched with yeast. There are many strains of brewing yeast (ale yeast *Saccharomyces cerevisiae* or lager yeast *Saccharomyces pastorianus*), and brewers look after their own strains because of their importance in determining brand identity. Ale strains collect at the surface of the wort if it is fermented in an open vessel, whereas lager yeasts settle to the bottom of the fermenter. This differentiation is blurred with modern cylindroconical fermenters, in which both types of yeast settle at the base of the fermenter when the beer is chilled after fermentation and primary maturation. Both types of yeast need a little oxygen to support membrane synthesis and growth, but otherwise alcoholic fermentation is anaerobic. Ale fermentations are usually complete within a few days at temperatures as high as 20 °C, whereas lager fermentations at as low as 6 °C can take several weeks. Fermentation is complete when the desired alcohol content has been reached and when unpleasant butterscotch and honey-like aromas due to the vicinal diketones diacetyl

Table 4 Major beer styles

Style	*Origin*	*Notes*
Ales and stouts		
Bitter (pale) ale	England	Dry hop, bitter, estery, malty, low carbonation (on draught), and copper color
India pale ale	England	Similar, but substantially more bitter
Alt (n.b. alt means 'old')	Germany	Estery, bitter, and copper color
Mild (brown) ale	England	Darker than pale ale, malty, slightly sweeter, and lower in alcohol
Porter	England	Dark brown/black, less 'roast' character than stout, and malty
Stout	Ireland	Black, roast, coffee-like, and bitter
Sweet stout	England	Caramel-like, brown, and full-bodied
Imperial stout	England	Brown/black, malty, and alcoholic
Barley wine	England	Tawny/brown, malty, alcoholic, and warming
Kölsch	Germany	Straw/golden color, caramel-like, medium bitterness, and low hop aroma
Weizenbier (wheat beer)	Germany	Hefeweissens retain yeast (i.e., turbid). Kristalweissens are filtered. Very fruity, clove-like, high carbonation
Lambic	Belgium	Estery, sour, and 'wet horse-blanket,' turbid. Lambic may be mixed with cherry (kriek), peach (peche), and raspberry (framboise), etc. Old lambic blended with freshly fermenting lambic = gueuze
Saison	Belgium	Golden, fruity, phenolic, and mildly hoppy
Lagers		
Pilsner	Czech	Golden/amber, malty, and late hop aroma
Bock	Germany	Golden/brown, malty, and moderately bitter
Helles	Germany	Straw/golden, low bitterness, malty, and sulfury
Märzen (meaning 'March' for when traditionally brewed)	Germany	Diverse colors, sweet malt flavor, and crisp bitterness
Vienna	Austro-Hungaria	Red-brown, malty, toasty, and crisply bitter
Dunkel	Germany	Brown, malty, and roast-chocolate
Schwarzbier	Germany	Brown/black, roast malt, and bitter
Rauchbier	Germany	Smokey
Malt liquor	US	Pale color, alcoholic, slightly sweet, and low bitterness

Abbreviation: n.b., nota bene.

Source: Reproduced with permission from Bamforth, C.W., 2006. Scientific Principles of Malting and Brewing. St. Paul, MN: American Society of Brewing Chemists.

and pentanedione, which develop during all fermentations, have been mopped up by yeast. The yeast is harvested for use in the next fermentation.

The 'green beer' is matured by a period of clarification through cold storage (typically $-1\,^{\circ}C$), before filtering. Filtration is generally aided by diatomaceous earth or perlite and various stabilizers may be used to remove materials that may cause haze, such as polyphenols or proteins. The filtered beer is adjusted to the required carbonation before packaging into cans, kegs, glass, or plastic bottles.

The array of beer styles is vast and major types are listed in Table 4.

Wine

Although wines have long been produced from all manner of plant materials, discussion in the present section is restricted to the products based on the grape (Boulton *et al.*, 1996).

Sound viticulture is a critical precursor to making wines of excellence. Many wineries tend to grow their own grapes or buy them from nearby vineyards. For growing wine grapes there should be minimal summer rain, hot or at least warm days, cool nights but little risk of frost. Other key factors are the depth, nutrient, and moisture content of soil and how readily it drains. Unless a soil is extremely acidic or alkaline, it is unlikely to be a major issue. Some regions are especially susceptible to diseases, such as Pierce's disease and phylloxera. Excess water uptake by grapes can also cause berries to swell and burst, which in turn enables rot and mold growth, for example, *Botyritis cinerea*. Winemakers refer to it as 'gray mold' when unwanted but 'noble rot' when deemed desirable! The character of certain wines depends on this infection, for example, the Sauternes from France.

Within the primary wine grape genus *Vitis* the main species are *Vitis vinifera*, *Vitis lubruscana*, and *Vitis rotundifolia*. Commercial vines tend to be 'scions' of *V. vinifera* grafted onto the rootstocks of the other *Vitis* species best suited to local soil and climate.

The time of harvesting has a significant role to play in determining the sweetness/acid balance of grapes. Grapes grown in warm climates tend to lose their acidity more rapidly than those from cooler environs.

Ripe fruit should be picked immediately before crushing. White grapes should be chilled before crushing, or they may be picked by night.

Nowadays the vessels used for extracting grapes and fermenting wine are fabricated from stainless steel and are jacketed to allow temperature regulation. Grapes are moved by screw conveyors from the receiving 'bin' to the stemmer-crusher. They pass from there either to a drainer, a holding tank, or (in the case or red grapes) directly to the fermenter.

Stems are not usually left in contact with crushed grapes so as to avoid off-flavors. This is not uniformly the case. For example, Pinot noir is sometimes fermented in the presence of stems in order to garner its distinct peppery character.

It is not necessary to separate the juice from skins immediately for red wine, but is so for white or blush wines. The color is located in the skin as polyphenolic molecules called anthocyanins. Blush wines are lighter than rose wines. For the latter, overnight contact between juice and skin with a modest fermentation allows the appropriate extraction of anthocyanins. After rose or blush juice has been separated from the skins it should be protected from oxidation by the addition of sulfur dioxide (SO_2). The rapid separation of skin and juice for white wines also minimizes the pick up of astringent tannins. The process may also impact other flavor compounds, for example, the flavors that impact Muscat. For certain grapes/wines, therefore, there is a balance to be struck in terms of oxygen availability, SO_2 use, contact time, and temperature.

The pH during fermentation should be maintained below 3.8. Wines then tend to ferment more evenly, there is a reduced likelihood of malolactic fermentation, and the wine develops better sensory properties. Furthermore at higher pH SO_2 is less inhibitory to wild yeast. Maintaining this low pH is especially important for white wines.

To accelerate juice settling so as to obtain a clearer product, pectinase enzymes are frequently added at the crushing stage to minimize the level of pectin, which originates in the wall material of the grape. The enzyme also allows easier pressing and affords higher yields.

Once the juice has separated from skins it is held overnight in a closed container. Thereafter, it is racked off (or centrifuged) before the addition of yeast. In locations where the grapes do not ripen well owing to a short growing season it may be necessary to add sugar (sucrose). Such a practice is illegal in some locales, for example, California.

The organic acids that are present are predominately tartaric acid in grapes grown in warmer climates but malic acid in grapes from colder climates.

The relevant species of yeast are *S. cerevisiae* and *Saccharomyces bayanus*. Contrary to commercial-scale brewing, dried yeast is extensively employed in wine-making, where adherence to a specific yeasts strain is frequently deemed of low significance. The chief limiting factor in wine fermentations is nitrogen, i.e., the amino acids are a must. The level of assimilable nitrogen is regularly increased by the addition of diammonium phosphate.

White wines are fermented at 10–15 °C, whereas reds are produced at 20–30 °C. Fermentation is inherently more rapid at the higher temperature, with the attendant increase in production of flavor-active volatiles such as esters. Rose and blush wines are fermented akin to white wines.

Fermentation tends to be progressively inhibited as the ethanol concentration rises, especially at higher temperatures.

The varietal character of certain wines is better preserved at lower fermentation temperatures. As in the case of beer, high levels of undesirables such as hydrogen sulfide can arise if fermentations are sluggish. In all cases, fermentation should be complete within 20–30 days. The progress of fermentation is monitored by measuring the decline in Brix value.

Wine is usually racked off the yeast once fermentation is complete. However, some winemakers leave the wine in contact with the yeast for several months, perhaps with intermittent rousing.

Color and flavor extraction from red grapes is maximized by mixing – either by pumping or stirring. Extraction is also greater at higher temperatures and increased ethanol concentrations.

White wines are either centrifuged or treated with the clay bentonite, which will also adsorb protein. Red wines are primarily fined in order to reduce their astringency. Fining agents include gelatin, egg white, and isinglass.

One of the biggest threats to wine is oxidative browning. The ingress of oxygen after fermentation should be minimized. Sometimes 'pinking' of white wines in bottle is prevented by adding ascorbic acid. But the chief antioxidant is SO_2, by reacting with the active peroxides in wine. Any hydrogen sulfide present in wine may be eliminated by the addition of low levels of copper.

Red wines usually undergo malolactic fermentation, performed by the lactic acid bacteria *Pediococcus*, *Leuconostoc*, *Oenococcus*, and *Lactobacillus*. In this process, malic acid is degraded to lactic acid with an attendant decrease in total acidity and a net increase in pH. The bacteria concerned prefer a relatively high pH and tend to be inhibited by SO_2. They also do not perform well at too low a temperature. Grapes from warm climates tend to contain less malic acid and therefore benefit less from such fermentation than do grapes from relatively cold areas.

The best Champagnes and sparkling wines are produced from the juice of Pinot noir or Chardonnay grapes. There must be rigorous avoidance of color development, hence the extensive use of SO_2. Fermentation in bottle is affected by a culture of *S. bayanus* that is flocculent and able to perform at high alcohol concentrations. The parent wine, invert sugar, and yeast are delivered into pressure-resistant bottles sporting a lip for the application of a crown cork. A headspace will be left in the bottle before it is laid on its side and held at 12 °C. The wine will ferment to dryness over a period of several weeks to more than a year. Then follows the process of 'riddling' in which the yeast is worked into the neck of the bottle. The yeast is loosened by hitting the bottom of the bottle with a rubber mallet or by using a shaking device. Then the bottle is put neck down into a rack at an angle of 45°. The bottle is rotated a quarter turn daily until the yeast sediment has all arrived at the cap. Then the inverted bottle is chilled to 0 °C and carried through a brine bath cold enough to yield a frozen plug of wine approximately 3.5 cm long. The cap is removed and as the ice plug is forced out it scrapes the yeast with it. The bottle is immediately turned upright again, refilled with wine containing sugar and some SO_2, corked, and labeled. Certain wines are carbonated simply by bubbling with carbon dioxide before packaging.

Contrary to most beers, wines tend to benefit from aging, which is performed either in tank, barrel, or bottle. The extent of aging is likely to be less for white wines than for reds. Some wines, for example, chardonnays, are aged in oak barrels, from which some characteristics are derived. Burgundy and Loire whites are led on the lees for up to 2 years ('sur lies').

Cork taints on wine can come from several sources. Trichloroanisole affords a musty or moldy character, geosmin an earthy note, and 2-methylisoborneol a chlorophenolic aroma.

Fortified wines are products in which fermented, partially fermented, or unfermented grape must be enriched with wine-derived spirit. The chief fortified wines are sherry (originating in Spain), port (from Portugal), and madeira (from the Portuguese archipelago of Madeira).

Sherry is only made from white grapes, but port and madeira may be produced from either red or white grapes. Wines on which sherry is based tend to be dry and the fortification occurs postfermentation. If the sweetness needs to be increased, this is done through the addition of grape-derived products downstream. Such additions usually comprise wines that have been fortified at the start of fermentation: by adding alcohol at the start of fermentation, yeast action is arrested, resulting in retention of sugar. Port is usually fortified approximately half way through the primary fermentation, and so tends to be sweeter than sherry through the preservation of unfermented sugars. Madeira may be fortified through either route depending on the sweetness desired.

The wines used to make sherry derive much of their character from aging in oat 'butts.' Sometimes, however, there is the development of *flor*, a film of yeast on the surface. In contrast, characteristics derived from the grape are substantially more important for wines going into port, especially red port. Much of the character of madeira develops in the estufagem process, which is a heating of the product at, say, 50 °C for 3 months.

Cider

Cider is an alcoholic drink produced by fermenting extracts of apples, though in the United States the term generally describes a nonalcoholic product, with the alcoholic product being termed 'hard cider.' Perry is the equivalent product made from pears.

The UK is the biggest producer of cider. The biggest selling style of cider is as a clear carbonated, light flavored beverage in bottle or can with an alcohol content of between 1.2% and 8.5% alcohol by volume (ABV). Increasingly, there is a trend toward chaptalization – i.e., the addition of sugars or syrups before fermentation to supplement the carbohydrate derived from apple. For the most part modern ciders may comprise only 30–50% apple juice. There has been extensive new product development in recent years, leading, for example, to higher alcohol products, 'white' ciders stripped of their color, the so-called 'ice' versions, and ciders flavored with diverse other components (Lea, 2011).

In France, ciders tend to be of lower alcohol content and to be distinctly sharp in flavor. Those from the Asturias region of Spain are relatively vinegary and foamy, whereas those from Germany tend to have relatively high alcohol content.

The best cider apples tend to have high sugar contents, of up to 15%, and a range of acidities from 0.1% to 1%. Their fibrous structure makes it easier to effect pressing, delivering higher yields of juice. It is possible to store them over a period of several weeks without losing texture, during which period their starch converts into sugar. Finally, they have a high tannin content (perhaps tenfold higher than in dessert apples), this being important for body and mouthfeel. Cider is usually produced from more than a single cultivar in order to achieve the preferred balance of acidity, sweetness, and astringency/bitterness.

Sometimes the substrate derived directly from the apple is supplemented with apple juice concentrate (AJC). Alternatively, the apple juice may be supplemented with cane or beet sugar or hydrolyzed corn syrup.

In modern cider-making facilities a high speed grater mill will feed a hydraulic piston press to crush the apples. The juice is afforded a coarse screening before it is run to tanks fabricated from fiberglass, stainless steel, polyethylene, or wood.

Some blending of juices may occur before fermentation and additions made. In particular, there may be a blending with sugars or AJC. The free amino nitrogen level may be raised to 100 mg l^{-1} by the addition of ammonium salts. Thiamine may be added but this must be separate from the addition of sulfite as the latter will destroy it. Other vitamin Bs that are required are pantothenate (2.5 ppm), pyridoxine (1 ppm), and biotin (7.5 ppb). Such materials are especially likely to be limiting if the cider maker is using significant quantities of AJC or sugars. If the apple juice and its additions are too 'bright' then it will be necessary to add some solids (e.g., bentonite) to act as nucleation sites, the escaping CO_2 relieving inhibition of the yeast and also serving to maintain agitation in the fermenter. Pectolytic enzymes are sometimes added to initial fruit pulp or to the juice immediately before fermentation.

SO_2 is traditionally added to prevent the growth of contaminating microorganisms. It is less critical from that aspect with the advent of dried wine yeast, but it is still important from a flavor perspective. The effectiveness of SO_2 increases as the pH decreases because it is the undissociated form of bisulfite that has antimicrobial properties. The pH is lowered to <3.8 by the addition of malic acid before the addition of sulfite.

Nowadays, the vast majority of cider fermentations are pitched with yeast rather than taking advantage of endogenous microflora. Many of the cultures now added were originally isolated from the cider factories themselves, but some cider makers use wine yeasts with well-defined characteristics. Since the 1980s, there has been widespread use of active dried wine yeast. Where temperature control is affected, this is likely to be within the range 15–25 °C.

Ciders may be subjected to malolactic fermentation. This is favored if there is no sulfiting in fermentation and storage and also by autolysis of yeast when the cider is allowed to stand unracked on its lees. As sulfiting is so widespread these days the malolactic fermentation is probably less significant than it once was.

The color of cider arises through the oxidation of polyphenols in the juice. It can be regulated by the addition of sulfite. If the latter is added immediately after pressing then nearly all color development is suppressed. If SO_2 is added later there is less reduction of color.

The color of finished cider is standardized by the addition of caramel or other permitted colorants. The color is removed from specialty products like white ciders by the action of adsorbents such as activated carbon.

The traditional high bitterness and astringency of ciders originates with the procyanidins. Procyanidins with a degree of polymerization (DP) 2–4 are bitter and are referred to as 'hard tannins.' Those with a DP of 5–7 are astringent ('soft tannins'). The relative delivery of bitterness and astringency depends both on the apple cultivar and on how the apples are processed. Oxidized polyphenols adsorb (become tanned) onto the apple pulp and this suppresses both astringency and bitterness. If oxidation occurs in the absence of the pulp, then there is a relative transition from bitterness to astringency as the units polymerize. Alcohol tends to enhance bitterness but suppress astringency.

As in the case of beer and wine, the yeast produces a range of volatile components (e.g., esters), and the key variables are yeast strain, fermentation temperature, and the clarity and nutrient composition of the fermentation feedstock.

Racking consists of removing the newly fermented cider from its lees. In modern cider making this may occur relatively quickly and in the absence of maturation, before blending and packaging. More traditional processing has the cider left on the lees for several weeks, with racking into tanks for months of storage with minimum contact with air.

Initial clarification of cider is by natural settling, by fining (bentonite, gelatin, chitosan, and isinglass), or by centrifugation. The ciders will be filtered before packaging and may be blended, aided by expert tasting. Most ciders are pasteurized and carbonated *en route* to final pack.

Mead

Mead (fermented honey/water mixtures) developed in many countries around the world and the product may be flavored with spices (e.g., cinnamon, cloves, and nutmeg) herbs (e.g., chamomile, lavender, and oregano), even hops, in which case it is known as metheglin. Mead incorporating fruit is referred to as melomel, and the fruits include blackberry, raspberry, and strawberry. If grape juice is included then a pyment results and products including malted barley are called braggot. Mead may be distilled or concentrated by freezing to yield honey jack (Gupta and Sharma, 2009).

Modern production of mead comprises adding honey to 3–4 volumes of water with whatever addition of fruit, hops, herbs, or spices is required. After boiling, the surface froth is skimmed off and brewer's yeast added. Fermentation is at 15–25 °C for 3–6 weeks before aging in oak casks at 10–15 °C for up to 10 years.

Sake

Sake is essentially a rice wine, yet production is more akin to that of beer with the conversion of rice starch into a fermentable form before the action of yeast to produce alcohol. Products typically have an alcohol content of 18–20% ABV, although this is often reduced to some 15% ABV before packaging (Akiyama, 2010).

There is much ritual and tradition in the production of sake. The water must be colorless, tasteless, and odorless. The rice is the short grain japonica variety that becomes sticky when cooked. It is polished more extensively than the rice employed for general food use so as to lower the levels of undesirable protein, lipid, and minerals.

Sake production involves parallel fermentations: saccharification of the rice starch and fermentation of the resultant sugar occur simultaneously. Koji (*Aspergillus oryzae*) produces starch-degrading enzymes that generate the fermentable sugar. Sake yeast (*S. cerevisiae* var. *sake*) converts the sugars into alcohol. These side-by-side events mean that the sugars are progressively released and made available for the yeast to ferment, without the latter being exposed to inhibitory high sugar levels.

White rice is reduced in weight by 25–50% to remove the outer layers that compromise clarity and flavor. Rice for the premium sakes receive the most milling. The milled grain is steeped until its moisture level attains approximately 30% before transfer to a wooden tub with holes in the base to admit steam. The tub is placed over a metal vessel containing boiling water for approximately 1 h and this leads to the gelatinization of the starch.

A proportion of this rice is used to make Koji, a culture of *A. oryzae*. One-fifth of the rice from the steaming stage is cooled to approximately 30 °C and transferred to a double walled solar-like room that retains heat. Dried spores of *A. oryzae* are scattered over the surface and kneaded in. Several hours later, the mix is transferred to shallow cedar trays that are put on shelves and covered with a cloth for up to 2 days. The mix is stirred twice every 4 h to equilibrate the temperature.

The making of moto starter is basically similar to making koji, but the process is prolonged so that still higher levels of enzymes are developed. Moto is the seed mash and represents $<10\%$ of the total rice. Steamed rice infected with yeast from the air is sealed in a cloth bag and buried within uncooked polished rice immersed in water. After 4–5 days the water is removed by filtration and the polished rice steamed. A second mash is then produced by adding this yeasty water to the remainder of the steamed rice and a proportion of koji rice. The moto is ready for use after 5 days. An alternative procedure that lessens the risk of contamination with lactic acid bacteria is to mix steamed rice, koji rice, and water, and divide it into shallow wooden tubs. The mixture is stirred every 3–4 h through the night before grinding the next day using wooden paddles attached to bamboo poles. The rice is rubbed against the bottom of the tubs until the grains are reduced to approximately a third of their size and the mash comprises a thick paste. The paste is then transferred to a single large wooden vat and left for 2–3 days at 8 °C. Hot water is now added to the mash, thereby raising the temperature and stimulating airborne yeasts. The mix is maintained at 25 °C for 20–25 days before using as a starter for the main mash.

To produce moromi, the koji and moto are mixed in large wooden vats over a period of 4 days with a regime of progressively increasing rates of addition of rice and koji rice to the moto. Temperatures are at first allowed to rise to 15 °C, but on the third day the temperature is lowered to 9–10 °C. After a period of up to 18 days, the mixture is filtered through weighted cotton sacks over a wooden 'sake boat.'

New sake is held for 10 days at a low temperature before pasteurizing at 60 °C and transferring to sealed vats that are

traditionally fabricated from Japanese cedar. Up to a year's storage leads to a mellowing of the flavor and a pick up of notes from the wood. Subsequent blending is followed by adjustment to final strength before bottling.

Modern vessels are likely to be fabricated from stainless steel and rectified alcohol is often used as a supplement. Activated charcoal may be employed in place of sake boats.

There are diverse types of sake, from the standard Futsu-shu, which is the major sake produced and is the equivalent of table wine, through premium products (from more highly polished rice).

Sakes are customarily served at 20 °C when compared for taste. The precise manner by which sake is served depends very much on the season, any food that it is accompanying and on the type of sake. Heating is the norm in the winter months, though not for better grades of the drink. Many experts would be of the opinion that warming sake distorts the taste and should be avoided. However, another opinion is that dry sake is better warm (not hot).

Chicha

This product is primarily made from maize, but can also be made from yucca and cassava. Other materials might also be incorporated as a source of carbohydrate or flavoring (Steinkraus, 1996).

Chicha de jora is traditionally produced from a yellow maize called jora and has a pale straw-like color, a milky appearance and is somewhat sour with a cider-like aftertaste. It typically contains only 1–3% ABV. Maize (corn) is sprouted and extracted, the liquid then being boiled before fermentation, traditionally in enormous earthenware vessels. Traditional production has famously incorporated mastication, with the formation of balls that are flattened and laid out to dry.

A Selection of Other Fermented Beverages

Palm wine (or toddy) is produced from the sap of the palm tree. It is common in various locations in Asia and Africa, and is referred to by diverse names. Fermentation is through the action of endogenous yeasts for a few hours, leading to sweet products of up to 4% ABV (Steinkraus, 1996). Distillation of palm wine yields products including arrack.

Pulque is a viscous and milky drink made in Mexico by fermentation of the sap of agave plants. Fermentation, by *Zymomonas mobilis*, is carried in vessels of oak, fiberglass, or plastic and is seeded by the addition of mature pulque.

Tepache is produced in Mexico from the flesh and rind of the pineapple together with coconut, sweetened with Pilloncillo (or brown sugar) and honey and flavored with cinnamon or clove. It is only mildly alcoholic (through the action of endogenous organisms) and it may be served mixed with beer, perhaps spiced with chili.

Kumiss is traditionally produced by fermenting mare's milk and is a staple in the steppes of Central Asia. As the sugar content of the milk is not especially high, these drinks are of modest alcohol content (0.7–2.5% ABV). Commercial production of the drink may likely be from cow's milk, perhaps fortified with sucrose. Unpasteurized milk is fermented for hours or days while physically agitating. The primary organisms are yeasts and lactic acid bacteria, leading to a relatively sour product.

Whisk(e)y

Whisky (Scotch) and whiskey (Irish and other forms of the product) is a beverage made by fermenting extracts of cereals, distilling, and maturing, normally in oak. The major cereals used are barley, wheat, rye, and corn (maize). Malted barley is employed as a source of flavor and enzymes, which are responsible for converting not only the barley starch but also that of adjuncts into fermentable sugars. The malts may be 'peated,' i.e., flavored with the smoke from peat burnt on the kiln (Russell, 2003).

Rye is quite widely used in eastern Europe and is sometimes malted. In the United States, corn is especially widely used. Wheat has largely replaced corn in Scotch grain whiskies as the cost of importing grain from the United States became prohibitive and it is also used in some American whiskies.

Malt is essentially mashed as in the case for beers. Wort from unmalted grain, however, is not separated from the spent grains because modern continuous distillation processes do not demand it. Fermentation and distillation are affected with all of the grain materials still present. Unlike for the brewing of beer, there is no boiling of worts.

The initial processing in the production of grain whiskies is significantly different from that for malt whiskies. The first stage in production is the hammer milling of the cereal. The cereal is mashed with 2.5 parts water typically at 40–45 °C with some malted barley included as a source of enzymes. The slurry is now pumped to a cooker wherein the mash is mixed and injected with steam to achieve gelatinization of the cereal. The temperature will be raised to 130–150 °C and held there for a relatively short period of time. The contents of the cooker are now discharged to a flash cooling vessel. The impact of this is to release any residual bound starch from the grain matrix. The temperature falls rapidly to approximately 70 °C. The slurry is mixed with a separate slurry of malt (10–15% of the total grist bill) that may be at 40 °C but alternatively may be at the conversion temperature for starch (65–70 °C). The malt enzymes then catalyze the hydrolysis of the malt starch and also that from the cooked grain. Food grade enzymes may also be added – and to some extent there may still be the use of unkilned malt as a source of enzymes. Mashing will typically be for up to 30 min. The whole mash contents are transferred to the fermenter. There is no boiling, so enzymes can continue to work.

Specific yeast strains particularly suited to whisky production have been developed. Hybrids emerged from *S. cerevisiae* and *Saccharomyces diastaticus* that produce a spectrum of enzymes fully capable of hydrolyzing starch to fermentable sugar. Thus the distilling strains enable high alcohol yield.

Fermentation on a small scale may be in closed wooden barrels, but on a larger scale it will be in stainless steel vessels known as washbacks. There is little temperature control during fermentation, other than to target the initial temperature,

which may typically be in the range 19–22 °C. Typically, the fermentation is complete within 40–48 h.

The stills used in the production of whisky are of two types: batch and continuous. Batch (or pot) stills employ double or triple distillation and generate a highly flavored spirit. Continuous stills provide lighter flavored spirits that are mostly employed in blending.

Whiskies are matured in oak casks. Although American bourbon and rye whiskies are put into new oak casks, Scotch, Irish, and Canadian whiskies are filled into casks that have previously been employed for Bourbon or sherry. The bourbon casks used for Scotch whiskies must be filled at least once with bourbon and the latter must have been in the cask for at least 4 years. Aging of whisky in most countries must be for at least 3 years. There is a significant loss of alcohol by evaporation in this time, referred to as the 'angel's share.' In the maturation there is the development of mellowness and a decrease of harshness.

In Scotland, the final products may be a blend of whiskies from more than 10 grain distilleries and up to a 100 malt distilleries. There is an astonishing interaction and cooperation between separate companies to enable this. The blending is deliberately complex so that the unavailability of 1 or 2 whiskies in any single blending will not be noticeable.

Bourbon is made principally from corn plus added rye and barley and is aged in charred barrels. A close relative is Tennessee whiskey (USA), which is produced using a sour mash process. Canadian whisky (Canada) is a light product from rye and malted rye, with some corn and malted barley. Corn whiskey (USA) is from maize and is aged in barrels that have not been charred. Rye whiskey (USA) is from rye mixed with corn and barley and is aged in newly charred oak barrels.

Cognac

The grape vines employed for the base wine for cognac production are nearly all from Charente and the adjacent regions of Deux-Sèvres and Dordogne. The grape varieties must be at least 90% of either Ugni blanc, Colmbard, or Folle Blanc. Ugni blanc is by far the major variety, affording wine high in acidity and relatively low in alcohol, which renders it most suitable for distillation. The microflora employed for fermentation is endogenous. Sulfur dioxide is not employed. Fermentation is relatively fast, the wines being maintained on the lees and subjected to malolactic fermentation. The sooner the distillation is performed after fermentation, the better the quality of the product (Lea and Piggott, 2003).

The still must have a capacity of <30 hl and must be heated by an open fire.

The wood employed for aging of cognac has great significance. The fineness of the grain impacts the extent to which phenolics and other tannins are extracted, as does the shape and size of the barrel made from that wood and the extent to which the wood is charred in the shaping process. The wood is generally dried in the open air for more than 3 years. New spirit is introduced to this new wood for a period of 8–12 months before transferring to older barrels, thereby avoiding excessive astringent and bitter characteristics. Oxygen enters through the stave and is used by enzymes contributed by molds in reactions that have a role in the aging process. There is also volatile loss through the stave. Several batches will be blended during aging.

Armagnac and Wine Spirits

Armagnac is in South West France. The main vinestocks used for armagnac are the same as for cognac. The wines must be distilled in the Appellation area, with the maximum content of distilled alcohol allowed being 72% ABV. Again the use of sulfur dioxide is forbidden (Lea and Piggott, 2003).

Two types of still are used: the continuous Armagnac still and two-stage pot stills. Heating is always by open fire, although nowadays it is likely to be fueled by propane gas rather than by wood.

Wine spirits are usually aged in oak casks. Coarse-grained wood is preferred because more oxygen can then enter into polymerize tannins. Oxygen ingress is also important for the oxidation of some of the alcohol to acetic acid, which in turn reacts with alcohol to generate flavorsome esters during aging.

Expert blending is performed and the alcohol concentration lowered to a minimum of 40% by the addition of distilled water. Caramel may to be added to enhance color.

Brandy

This is obtained from wine spirits blended or not with wine distillates distilled to less than 94.8% ABV, such distillates not exceeding 50 Proof maximum in the final product. The product is aged in oak for more than 1 year, unless the casks hold <1000 l in which case aging must be for a minimum of 6 months. The making of brandy is an opportunity to salvage defective wines or deal with production surpluses, although top quality brandies may be made from wine specifically produced for the purpose. Brandies must be $>37.5\%$ ABV (Lea and Piggott, 2003).

Rum

The chief producing countries for rum are Barbados and Santo Domingo. Nowadays the coastal planes of Guyana (Demerara) are rich in estates producing sugarcane (Lea and Piggott, 2003).

At harvest time the fields of sugarcane are set alight in order to sanitize the soil, the stems are scorched in this process and the canes subsequently wither and are harvested by machete, a strategy thought to yield a superior product when compared to rum made from cane harvested by machine. The canes are topped to remove the leafy parts and the cane are then ferried to mills.

In the processing, the canes are cut and crushed and the juice limed, clarified, and evaporated. Various fractions are generated, but the key product for rum is molasses. The nature of the molasses depends on cane variety, soil type, climate, cultivation, and harvesting conditions. They are delivered hot to the distillery either by pipe or by tanker and are stored at 45 °C. The molasses are mixed with water in line. Lighter flavor rums may incorporate cane juice (12–16% w/v sucrose).

Formerly, adventitious yeasts were used to effect fermentation, but nowadays pure cultures of *S. cerevisiae*, *S. bayanus*, and *Schizosaccharomyces pombe* are used. Before fermentation, the molasses are diluted to 45 Brix and their temperature elevated to 70 °C in order to destroy contaminating organisms. The pH is lowered by the addition of sulfuric acid and the whole clarified by putting into a conical-bottomed settling tank, from which the sludge can be decanted from the cone. Ammonium sulfate is added as a source of nitrogen. Fermentation is conducted at 30–33 °C to a final sugar content of 16–20 Brix and this is reached in 24 h with an alcohol yield of 5–7% ABV.

Distillation is conducted in pot stills that were traditionally of copper or wood but now more likely to be fabricated from stainless steel. As for whisky there are also column stills of stainless steel or copper (Coffey stills). Pot stills afford heavier rums that need prolonged maturation, whereas the column stills are employed for lighter rums, or to generate the neutral spirits that can be used for the production of gin and vodka.

Rum is aged in bourbon oak casks. It is racked at 83–85% ABV. As the main production locale is tropical, aging is quite rapid and may be complete within 6 months. There may first have been a blending of light rums produced in column stills with heavier rums out of pots. Furthermore, there may be transfers between casks for successive maturation periods.

Vodka and Flavored Spirits

Vodka is essentially pure alcohol in water, though flavored variants are available. Gin comprises distilled alcohol flavored with a range of botanicals. Similar to this are Aquavit (caraway or dill), Anis (aniseed, star anise, and fennel), and Ouzo (aniseed and mastic) (Lea and Piggott, 2003; Blue, 2004).

Vodka comprises pure unaged spirit distilled from alcoholic matrices of various origins and usually filtered through charcoal. Materials added in the production of vodka include sugar at up to 2 g l^{-1} and citric acid at up to 150 mg l^{-1}. Some vodkas have glycerol or propylene glycol added to enhance the mouthfeel. Among the flavored vodkas are those infused with pepper, buffalo grass and apple and pear leaves, brandy, and port.

A neutral alcohol base is frequently produced quite separately from the vodka per se, perhaps by a different company. It is chiefly produced from cereals (e.g., corn and wheat) but other sources of fermentable carbohydrate include beet and molasses in western countries, sugarcane in South America and Africa, and potatoes in Poland and Russia. The fermentation is effected by *S. cerevisiae*, notably distillers' strains. The alcohol is purified and concentrated by continuous stills before carbon treatment.

The word gin is a corruption of genievre, the French word for juniper. Distilled gin is produced by distilling neutral alcohol and water in the presence of botanicals. The product is diluted further with alcohol and finally brought to its final strength with water.

The alcohol for gin may come from grain-, molasses-, potato-, grape-, or whey-based fermentations. The prime traditional flavorings are the juniper berry, coriander seed, and Angelica, together with the peel of orange and lemon. Other materials may also be used in the formulation of gins and these include cassia bark, cubeb beris, liquorice, orris, almonds, and grains of paradise.

Water quality is critical for the production of gin and, as for beer, this explains the traditional locales where the drink was first made and became popular.

Gin is produced in copper pot stills similar to those used in the production of whisky. The botanics are added either loose or suspended in a bag.

Sloe gin is produced by steeping sloe berries in gin. The mix is sweetened with sugar, filtered, and bottled. Nowadays, flavorants may be employed in place of the berries per se.

Pimms is based on a secret recipe and is compounded from gin and liqueurs.

Liqueurs are produced by dissolving or blending several components. For the most part they are 35–45% ABV, although some are less strong. The alcohol must be from a fermentation process. The other key ingredients in these products are sugar (to deliver both sweetness and mouthfeel), flavors (that may be either the plant material per se or distilled essential oils or extracts from those botanics), and color (which again may be of 'natural' origin or via an approved colorant).

Cream liqueurs incorporate milk fat, sodium caseinate, and an emulsifier. Through homogenization procedures, the size of the fat globules is reduced to one that allows a stable emulsion to be obtained.

A representative list of liqueurs and some other beverages is given in Table 5.

Other Distilled Beverages

Schnapps is a clear colorless beverage, typically of 40% ABV produced by the distillation of fermented fruit, which accords some flavor to the beverage. Chief among the fruits used are apple, apricot, cherry, pear, and plum. The French equivalent is *Eau de Vie* ('water of life') (Lea and Piggott, 2003).

Tequila is a traditional Mexican distilled product derived from fermentations of blue agave plant. Margarita is a cocktail comprising tequila, Cointreau, and lime juice.

Absinthe is a distilled product of 45–74% ABV with an anise-flavor derived, *inter alia*, from wormwood, green anise, and sweet fennel. It is customarily green but colorless versions are available. It is customary to dilute absinthe with water before drinking. In most countries it is made in a manner analogous to gin, employing distillation in the presence of botanicals.

A traditional way of drinking absinthe involves putting a sugar cube on a perforated spoon that is held over the glass containing the beverage and approximately three times the volume of ice-cold water is poured through the spoon. The mixture becomes cloudy.

Cachaça is a spirit produced by the distillation of fermented sugarcane juice (as opposed to the molasses used in the production of rum) and it originates in Brazil. It is typically between 38% and 48% ABV.

Pisco is a colorless, sometimes yellow, grape brandy from Peru and Chile. Pisco in Peru is made using copper pot stills. By law the aging must be for at least 3 months in a container

Table 5 Some liqueurs and specialty alcoholic products

Product	*Notes*	*Country of origin*
Absinthe	Brandy flavored with sweet almonds and apricots	France
Advocaat	Brandy-base. Egg yolks, sugar, and vanilla	Holland
Akvavit	Anise, caraway seeds, coriander dill, fennel, and grains of paradise	Scandinavia
Amaretto	Apricot kernel and bitter almond flavor	Italy
Anis	Anise/Star Anise/fennel flavor	Diverse
Arrack	Distillation of alcohol from grapes, sugarcane, rice, or dates. Word means 'sweat'	Arabic
Bailey's	Irish whiskey and chocolate	Ireland
Benedictine	Brandy flavored with 27 plants (including cardamom, cinnamon, cloves, juniper, nutmeg, tea, and myrrh) and sugar. Colored using saffron and caramel	France
Bitters	Diverse, including *Angelica* root, artichoke leaf, cascarilla, *Cassia*, *Gentiana*, bitter orange peel, quinine, thistle leaves, wormwood leaves, and yarrow flowers	Various
Campari	Red product made by blending 68 herbs with quinine, Chinese rhubarb, cinchona bark, and orange peels	Italy
Cassis	Macerated blackcurrants in neutral spirits and brandy	France
Chartreuse	Blend of 130 herbs and honey in brandy	France
Cherry brandy	Distilled juice of cherries, fermented in presence of crushed cherry stones, perhaps blended with Armagnac	Mainland Europe
Cointreau	Blend of distillates from bitter and sweet orange peel, plus sugar	France
Drambuie	Scotch whisky suffused with herbs, spices, and heather honey	Scotland
Grande Marnier	Cognac blended with distillates of bitter orange and sugar	France
Malibu	Light rum/coconut	Barbados
Ouzo	Aniseed and fennel and mastic distilled in copper stills <1000 l	Greece
Pastis	Aniseed and liquorice	France
Raki	Aniseed	Turkey
Pernod	Spirit base suffused with star anise, fennel, chamomile, coriander, veronica, and other herbs	France
Sambuca	Anis, star anise, Elderflower, invert sugar	Italy
Southern Comfort	Grain-based spirit containing peach and orange and sugar	US
Tia Maria	Cane spirit/rum base with coffee and spices and sugar	Jamaica

that does not change the physical or chemical characteristics of the beverage and neither can any additions be used that influence the properties of the drink.

See also: Analyses of Total Phenolics, Total Flavonoids, and Total Antioxidant Activities in Foods and Dietary Supplements. Breeding: Plants, Modern. Domestication of Plants. Food Microbiology. From Foraging to Agriculture. Genomics: Plant Genetic Improvement. Spices and Aromatics. Sugar Crops. *Terroir*: The Application of an Old Concept in Modern Viticulture. Tree Fruits and Nuts. Virtual Water and Water Footprint of Food Production and Processing

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Food Chain: Farm to Market

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Glossary

Corporate social responsibility The approach a company takes in its contribution as a member of the community, especially in the areas of the environment and labor rights.
Food accessibility The ability to procure the food that is available in an area.
Food availability The presence of food in an area.
Food security The availability and accessibility of wholesome, culturally appropriate foods that are free from contamination.
Foreign direct investment A private industry's investment into a nation's infrastructure for purposes of engaging in the production and retail process of a commodity.
Horizontal integration Where many suppliers sell product to a limited number of other firms or intermediaries in the production chain.
Intergovernmental organization An organization with representatives and funding from member nations that agree to function under the mandate of the organization, examples include the World Trade Organization and the United Nations.
Oligopoly A situation where the market is shared by a small number of producers or sellers.
Transnational corporation A corporation whose production chain occurs in many different countries.
Vertical integration Where one firm owns the systems or processes in multiple steps of the production chain that were traditionally separate companies.

Introduction

Food chains are a set of complex interactions that bring food sources from the producer to the consumer. They are impacted by government policies, ecological potential, availability of technology, the skill of producers, and the ability of producers to invest in the production process (Food and Nutrition Division, 1997). There are two common ways in which the food chain can be described, as food supply chains or as food value chains. There is an important distinction between these two terms. Value chains are a marketing perspective. They look at what will add value to the product from the consumer's point of view, so in terms of production they are a retrograde examination. This evaluation of where in the production process value is added to the product has led to the development of concepts such as 'corporate social responsibility (CSR),' and the marketing of products that are labeled as 'Fair Trade,' 'Organic,' 'Dolphin Safe,' and 'Ecofriendly' to name a few (Smith, 2008). However, supply chains refer to the flow of goods from the producer to the consumer and the evaluation process aims to increase the efficiencies of this movement of goods. The supply chain point of view will be the primary focus of this article. Food sources, food processing, food transport, infrastructure requirements, as well as societal requirements and restraints will be the primary discussion of this article, but the impact of the value chain will not be ignored and its impact on the evolution of food supply chains will be discussed (**Figure 1**).

Food supply chains can range from simple, such as those seen with subsistence farmers who produce a large portion of their own food, to complex, where the global food chain and all of its international regulations that allow trading between countries and multinational corporations occur. The distance food must travel for consumption is based on its market worth and desires and many exotic foods are part of a global food supply (and value) chain purely out of consumer-driven wants. Yet, the food supply chain began as a need. Every living organism must consume food for energy and life – none are exempt.

Human history describes our earliest food supply as essentially hand-to-mouth. Hunter-gatherer societies caught or collected the food they would eat or their family would eat. During this time, conserved food processing was developed. This includes preservation techniques such as smoking, drying, and salting. Although at the time this was to allow food to last longer and to prevent food waste and perhaps starvation, it was these techniques that would eventually allow for trade of food products as well (Smith, 2008). The basis behind this original food chain was subsistence; one must eat to live.

As time passed and the crop domestication, as well as animal domestication developed, greater amounts of food were produced. At this point, a farmer was able to produce more than he needed, and could produce enough food to support more than his immediate social structure of responsibility (Diao *et al.*, 2007). When this occurred, all people did not need to take part in the food production process. Instead, the economy that grew from domesticated farming originated as a method to provide food for all persons despite not all persons being involved in farming. If people did not grow their own food or did not grow enough of their own food, they bartered for food by trading with their skill set. This persists today in areas of the world where money is not readily available and where the goal and struggle is still to meet the person's basic caloric needs. This is a food chain driven by need and not preference, caloric intake was the primary goal and the type and quality of food were of lesser concern.

When defining food security there are three main components: availability, access, and safety (Havas and Salman,

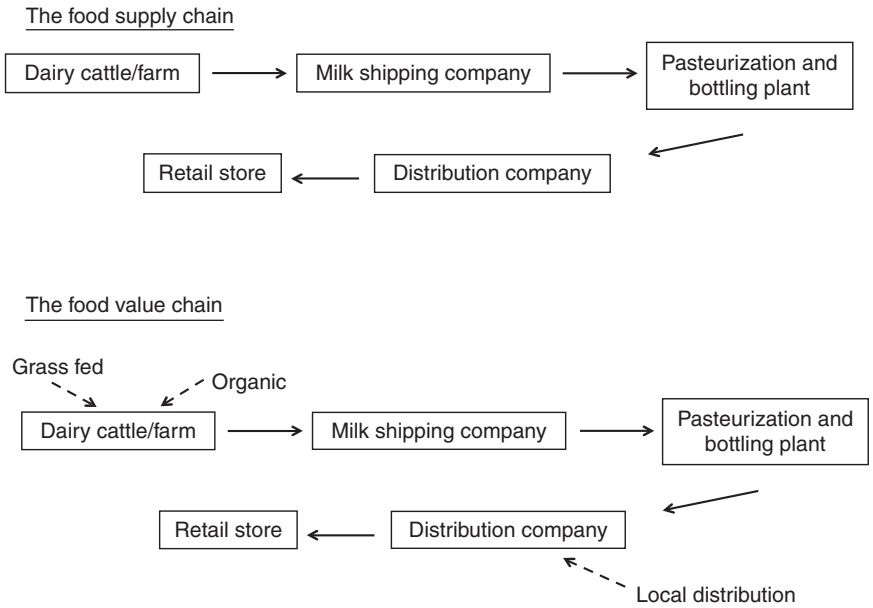


Figure 1 An example of dairy food supply vs. food value chains.

2011). Availability is the presence of the food within one's market reach. One's food market may be local, on the internet, through retail, or other resources, but one must be able to resource that item. Access is not just the availability but also the ability of one to buy the item. Food safety is the ability to buy food free from contaminants and reasonably free from pathogens. The food supply chain is focused on food availability, whereas the food value chain also ensures safety and considers access, as well the cost of foodstuffs at a price point with the greatest profit for the marketer but still within the reach of the target population.

Typically, in any food chain there are four primary roles to consider: the producer, the supplier, the processor, and the retailer. These roles can be condensed and one group may take care of each role, or there may be many steps and many individuals involved. The producer is the farmer, the one who grows the plant or raises the animal to harvest the raw material. The supplier is an intermediary. They buy the raw supplies and sell them to the processors. Processors prepare the food for consumption and sell the final product to a retailer for sale to the consumer. Processors are often defined as adding value to the agricultural product via postharvest processes before marketing (Wilkinson, 2004). Yet, based on the production practices, producers can also add market value to a product. The local supermarket exhibits this when one sees the phrases organic, cage-free, without hormones, or other product descriptions that come from the producer level.

A food chain can be a complex process. There are often many suppliers to one processor and many retailers who receive the final goods. National and international laws regulate the international trade and production of these goods and the international market's food chain is working to integrate small-scale farmers as well as corporations so that everyone can benefit. The 'Buy Local' movement and the ability of small farmers to integrate further complicate this.

The Food Chain

The University of Wisconsin published a tiered system to define a food chain. There are four tiers described in their system. The first tier is the locally procured food where the producer and the consumer interact. The second tier is the use of intermediaries to move locally and regionally grown food from the producer to the consumer. The third tier is for national grocery and distribution companies that have strong relationships with their consumers through product confidence and low prices. The contact with the farm is lost at this level. The final tier, the fourth tier, is the distribution of food globally where products are sold to retailers for sale but are not sold directly from the company itself to the consumer. There is a requirement of certificates defining the origin of location and there is no relationship with the consumer (Center for Integrated Agricultural Systems, 2010). This is a useful framework to discuss the framework of supply chains in countries of differing levels of development.

The type of market that predominates in an area may be related to the development of a country. There is not a singular purpose behind food consumption. Although it can be argued that the primary purpose is to meet caloric needs, there are many places where food is consumed socially, for cultural celebrations, for indulgence, and for traditions. All of these reasons for consumption drive the food supply chain, and have fed the food value chain. To simplify the discussion, the reasons behind food consumption and their associated food supply chains will be described as buyer-driven and producer-driven foodstuffs. Buyer-driven markets predominate in the developed world as they reflect social values that go beyond caloric intake of food. This could be argued to be a luxury of societies with enough food to eat. Once availability and access are achieved, then food has the ability to take on social values as well. Yet, producer-driven foodstuffs are universal. These are the staple crops and livestock meats needed by every

person in the world as well as the processed, mass-produced food markets.

Buyer-Driven Markets

Buyer-driven commodity chains are those that are controlled by retailers. They coordinate with many trading partners to meet consumer demands (Gereffi and Christian, 2008; Busch and Bain, 2004). This has become an oligopolic market, or a market where a small number of retailers, sellers, or suppliers meet the needs of the many consumers. The niche markets that develop in this type of market are in response to a backlash against mass food production. Often they are characterized by incorporating values into the food product and demand CSR, food safety, environmental sustainability, and using products to exemplify the social platforms. Organic, genetically modified organisms-free, and fair trade foods are examples of this (Busch and Bain, 2004). Foods that are exotic to the geography of the buyer but are thought to enhance health are often a part of the buyer-driven market. In the United States, this can include coconut water, quinoa, exotic fruits and vegetables, acai berries, and more. For these items, quality is the driving factor behind cost.

In buyer-driven food chains access is not an obstacle for the target population, but availability may be. In fact the lesser the availability of a product translates into rarity, as with most uncommon market items, they are also more expensive. Therefore, as the prices of market items rise, due to limited availability, the smaller the proportion of the population that has the income to access the item and the more targeted the supply chain is to those consumers. The retail market recognizes a consumer desire and makes that item available, but at a cost. This originated with spices and teas in the 1600s and it led to the creation of the East India Tea Company of Norway and Great Britain (Christensen, 2012). These were luxury items that were not necessities – nutritionally or culturally. Overall buyer-driven food chains are items that are not cultural or traditional food items, but are foods incorporated for some additional perceived social value or standing (Busch and Bain, 2004).

Interestingly, as the food value chain adjusted to this consumer demand, private industries raised standards beyond those of national concern or trade standards. Countries themselves cannot demand this exceedingly high quality of foodstuffs within their trade regulations purely for the purpose of quality. This raised the private standards of these foods beyond those set forth by the World Trade Organization (WTO) solely for the purpose of the value chains. Such quality demands create a challenge for farmers competing to supply these goods on an international scale. Private regulations applied to farmers can include food safety and quality issues, branding of the food product, and certifications such as fair trade and organic (Busch and Bain, 2004). It becomes difficult for most farmers to meet these high standards and pass the corporations' audits while still making a profit. The ones that most struggle to benefit from this trade is the small-scale farmer (Vorley and Fox, 2004).

However, these private standards have also sought to protect the farmer and the environment in a movement calling for CSR. These international trade standards under the auspices of the WTO result in global competition where countries leverage their comparative advantage to find their niche in the global market. For some, the comparative advantage is human labor, and this is a resource they compete with internationally. The result can be low wages or environmental depletion that is associated with processing and production (Friedmann, 2005; Roberts and Parks, 2009). The private standards, in many ways, have stepped in and created value around social platforms to protect these unskilled labor groups and their local environments. Fair trade has developed to ensure fair prices to small-scale producers; organic foods have given rise to demand reduce pesticide and chemical use; and ecofriendly farming certifications aim to highlight environmentally sustainable items (Friedmann, 2005; Raynolds and Wilkinson, 2007). Coffee, chocolate, and bananas are just a few of the products that have flourished under fair trade; and organic food items are almost commonplace in the supermarkets of the United States. Examples of environmentally friendly certifications are the Rainforest Alliance's Better Banana program (Rainforest Alliance, 2009) and the Marine Stewardship Council's sustainable fishing certification (Marine Stewardship Council, 2011).

An additional challenge that fair trade certification attempts to address with buyer-driven markets is that the suppliers and the retailers, not the producers, often drive the price points. This is in direct relation to the oligopoly that has developed surrounding the buyer-driven markets and the retailers' control. Producers are often small-scale farmers with little limited distribution markets who sell at the best price available. If global prices fall they are often the ones who have to produce for cheaper rates at the expense of labor costs or other benefits (Vorley and Fox, 2004). Typically, the price to the farmer or producer is less than 20% of the final profit on the item (Busch and Bain, 2004). This is associated with the ability of intermediaries to buy from many different sources and the competition that results is at the producer level. It is exacerbated by the lack of cost data at the producer level. The majority of pricing data collected is at the retail level, leaving a knowledge gap about the price points at lower levels of the supply chain (Busch and Bain, 2004).

Producer-Driven Chain

The complementary supply chain is the producer-driven chains, also known as bulk commodities, where mass production and not necessarily quality production is the focus. In food supply jargon these are considered food staples. They are the products that are either calorically dense or high in protein such as meat and poultry, rice, potatoes, wheat, and corn. The crop staples are more universally consumed, but as developing nations become richer, a demand for meat and poultry follows. As for the grains, small-scale producers grow many of these grains locally, but there is also a large international market. In fact, in 2011, US$1.3 trillion worth of food staples were imported across the globe (Trade and Markets Division, 2011). This high volume food supply chain grew out of the post-World War II practice of exporting food surpluses for sale in other countries as international aid. Food processing corporations are often typically behind these efforts. Perturbations in the market that causes fluctuation in the costs of these staple foods also lead to hunger (Friedmann, 2005), a major concern associated with the rise in the cost of food seen

during the global recession that started in 2008 (Trade and Markets Division, 2011). Global hunger concerns arise and large proportions of the global population go without enough to eat. This is because it is not available, nor can they afford the small amount that is available. These are foods that meet caloric needs and not culinary fancies.

As a result of the severe price fluctuations seen in food staples in the years of the Great Recession (2008–13), the International Group of 20 (G20) created an agricultural information system known as the Agricultural Market Information System (AMIS). The insecurity with the economy, the reduced supply associated with droughts, and the rising cost of fuel needed to transport these foodstuffs led to extreme volatility in food prices. The concerns of rising hunger were significant and the AMIS is meant to be a better predictor of these crises (Trade and Markets Division, 2011). The typical rules of supply and demand are muddied by extreme global phenomenon and reliance on food made half a world away, and now the international market can contribute to severe food insecurity in many places in the world. Food self-sufficiency is growing enough food within your own country and food security is having availability of enough food, which is now done through national crops and import crops. When the latter part of the supply is impacted as severely as it was during the global recession, food insecurity develops. (World Health Organization and World Trade Organization, 2002; Commodities and Trade Division, 2003).

The reason for the price instability is the relatively small number of large-scale producers that feed this supply chain. The international coarse grain trade includes corn, sorghum, barley, oats, and rye (Capehart and Allen, 2013). The United States is the world's major producer of corn, soybean, and wheat crops. The primary wheat exporters in 2012 were the United States, Argentina, Canada, the European Union, Russia, and Australia. Corn is a crop primarily exported by the United States and then Argentina (Foreign Agricultural Service, 2012). Rice as a staple crop was growing in popularity. The major exporting countries in 2012 included Thailand, Vietnam, India, and Pakistan; clearly Southeast Asia is a significant contributor to rice production (Foreign Agricultural Service, 2013). These are the foci of crop productions that feed the world. Therefore, weather, increased demand via population growth, increased demand associated with an increasing animal protein demand, and the increased use of crops as biofuels threaten food security and increase the cost of these commodity crops. As the national food security is based on imports as well as local growth and as greater profit can be made by selling goods at home, importing countries are often the ones who feel the dearth of the harvest the most. In addition, the importing country's consumers also absorb costs that accumulate in the supply chain, such as international trade requirements for testing, processing, and shipping. As oil prices rise, the costs of moving staples around the world also rise. Finally, new scientific processes that utilize plants, such as corn, for fuel also reduce the crop available for consumption and thus create a higher demand and higher cost.

Corn clearly plays a significant role in the global food supply chain. It feeds the animal supply chain and thus availability of animal protein, processed foods, and then the coarse grain market as well. International markets are at the mercy of the US crop and market prices as the US supplies approximately 75% of the world market with only 15–20% of its own crop. So domestic US demands impact the global supply (Capehart and Allen, 2013). A drought year in the United States and these increasing demands from animal production, biofuel, and processed food industries have an impact on the overall supply and play a role in determining price points. A legislative requirement to develop biofuels exacerbated food supply issues in years of poor harvest as well. So, corn is a crop that related best to supply and demand principles of economics. As supply drops and demand increases, so does the cost of the crop. With corn this is a trickle-down effect to the cost of meat, processed foods as well as adding additional demands on the supply chains of wheat and soy, thus increasing their prices as well (Action Aid International USA, 2012; Tenebaum, 2008). Availability in the food supply chain of these commodity or staple crops is volatile year-to-year and likely will remain so.

The relationship with the supply chain for producer-driven versus buyer-driven foods is based on the complexity of the product. Consumer-driven foodstuffs are often niche products. They are produced with a high level of quality, in smaller amounts, and sold to a specific market. These include items such as truffles, exotic fruits, coconut water, acai berries, quinoa, and others. In fact, bulk food staples, as will be discussed in the Section Transnational Corporations and Food Processing, can become niche product if they gain in popularity in areas outside the typical growing area. This has happened with quinoa and coffee. Their markets are highly regulated by the private sector and demand traceability. There are often 'voluntary' standards that inhibit entry to the market by farmers not already incorporated into an elaborate food chain. Owing to the small number of buyers and smaller target audience, the food chain is highly integrated between producers, suppliers, processors, and retailors (Vorley and Fox, 2004).

Finally, free trade agreements have benefited producer-driven industries. These agreements are authorized under the WTO, which ensures fairer trade, but not free trade (World Trade Organization, 2011a,b). The WTO provides a platform for nations to negotiate fair trade agreement based on their mutual risks and benefits without allowing politics and protectionism to play a role (World Trade Organization, 2009). The bilateral or regional agreements can further limit trade restriction so as to open markets to free trade agreement trading partners. Quotas and tariffs are often eliminated in these agreements allowing a free flow of goods through partner nations. The United States has numerous free trade agreements. The most well known is likely the North American Free Trade Agreement with Mexico and Canada. The result of this streamlined trading platform is also a global movement of goods creating a supply chain from one end of the globe to the other.

The Role of Food Security

Food security is the availability, access, and safety of foodstuffs (Havas and Salman, 2011). National food security means that a nation state has access and availability of safe, wholesome foodstuffs. National food self-sufficiency is the ability of a

national government to supply all of its nation's food needs through domestic production (Thomson and Metz, 1998). This is almost unheard of today. Today, food security is achieved through local production and import; countries rely on both. Yet, this is a macrolevel of security; having enough food being available in the country does not mean all localities have the same access. Food deserts crop up in impoverished, environmentally depleted, and infrastructure poor areas of a country. Food supplies in these areas may originate from local production, or, due to the lack of infrastructure, they may rely on processed foodstuffs. The results of poorly executed food supply chains are poor nutrition that results in starvation or obesity due to a lack of nutritionally balanced foodstuffs. Food deserts are defined not only by the lack of availability of foodstuffs, but also access associated with monetary costs and the time associated with accessing the food, preparing it, and cooking it while considering the time available in the household (Economic Research Service, 2009a,b). Therefore, national food security is a complicated concept and difficult to ensure at all levels between the individual and the nation.

Import is a significant means for many nation states to achieve food security. This international food supply has become highly regulated via intergovernmental organizations (IGOs), primarily by the WTO. When greater globalized trade took hold in the early 1980s, the post-World War II Global Agreements on Trades and Tariffs (GATT) was determined to be inadequate for the purposes of agricultural trade and intellectual property concerns. It also lacked an ability to enforce trade rules. The need to restructure in order to regulate a free market was central to these talks and the goal was to remove nontrade-related tariffs among member states. As a result of the round of Uruguay roundtable, the GATT negotiations of the 1980s led to the establishment of the WTO. The WTO was established in 1995 and it now regulates international trade and, thus, the international food supply chain, with the legal rights to enforce its regulations (World Trade Organization, 2009).

The WTO mandated other IGOs to create sanitary and phytosanitary standards for international trade: the World Organization for Animal Health created the standards for trade of animals and animal products, the International Plant Protection Convention for plant products, and a joint mandate for the Food and Agricultural Organization (FAO) and World Health Organization (WHO) for food products (World Health Organization and World Trade Organization, 2002; World Trade Organization, 2011a,b). The mandates to these organizations and the resulting standards created by each have resulted in a baseline requirement regarding plant, animal, and food health in order for trading to occur. If the nation importing the goods has more stringent requirements for testing or validation those requirements must be in place for domestic products as well. Under a concept called the 'most favored nation status,' nations cannot restrict trade for reasons other than those that are scientifically and medically based. All nations are favored nations should they meet the requirements for the product they are trying to trade. They cannot have any additional restrictions based on political or economic agendas should they meet the guidelines. In addition, the technical barriers to trade that are addressed by the WTO include standardizing label requirements and ensuring that domestic and imported products have the same requirements. This harmonization has made international trade and nontariff-related trade barriers predictable and limited (World Trade Organization, 2009, 2011a,b). This increases the efficiency of trade as well. The result has been a global growth in the movement of food and food-related products in the international trading system (Busch and Bain, 2004).

International Trade

International trade of food goods has been present for hundreds of years. The spice routes have been around since the Golden Age of Greece, where the first spice routes were created. The Romans took over with a bustling trade between Egypt and India. Up to 120 large ships moved spices from India to Egypt each year during this period. At the decline of the Roman Empire, Arabs gained control and kept it until Italians become involved in Constantinople. During the Crusades, the Palestinians kept the trade alive, and eventually the rest of Europe joined in as well. Marco Polo was the one who first described the supply chain. Essentially, India and numerous outlying islands farther to the east sold to traders in India, but India was not the sole supplier. By 1412, major ports of trade had grown in Morocco to facilitate trade from the east to Europe. The spices and goods from the east were so foreign and so sought after that many Christians of the day were convinced that they came from the Garden of Eden. Italy and Portugal were the primary initial players but interest in the markets expanded (Cliff, 2011). The trade between Europe and the East gave rise to multinational corporations of the day such as the Dutch and the British East India Companies (Cliff, 2011). In the late 1500s, this trade had extended to the new territories controlled by Spain in what is now Mexico, with Acapulco Bay being a major trading port as well. Typical galleons that anchored in the bay were from Manila and took 6 months to make the journey. Yet, these voyages were repeated every year from 1565 to 1815 (1616). Clearly, international trade was worth the investment and risk, even in the early years.

Since the beginning of global trade in the 1500s and 1600s many things have not changed. In the post-World War II era, there was a concerted effort to help countries recover through the development of economic reforms and trade standards, but the overall mass production for local consumption was the primary industry. This is most likely due to a lack of highly efficient transport and refrigeration at the time. In addition, communication and technology made shipment tracking and sales more difficult. As a result, the processed food industry arose. Many of these foods were shelf-stable, ready-to-eat, and based on convenience, whereas the domestic farms continued to provide the majority of fresh fruits and vegetables and meats. Much of the export was surplus foodstuffs and what was exported was called the Green Revolution, or agricultural development as a way to influence the political chess match of communism versus democracy in developing countries around the world (McMichael, 2009). The Green Revolution developed higher-yield crop varieties and brought inorganic fertilizers and pesticides into the norm. They assisted many countries avoid starvation, and the industrialized nations were

able to become food self-sufficient and to grow surplus crops (International Food Policy Research Institute, 2002). This drove the trade during this period of time, it was no longer trade from colonies to the colonial power, but instead exports flowed from the industrialized countries to the developed countries. So, the flow of goods reversed itself when considering the political power of the trade partners (McMichael, 2009).

As technology improved, the most current version of globalization took hold. International transport of goods was becoming time efficient and economically beneficial; refrigeration became possible; the internet made communication and shipment tracking a reality; and computers allowed for the management of a global business. So in the past 30 years, global trade of food has expanded significantly. It no longer includes solely shelf-stable and agribusiness products and agricultural surpluses. It includes almost any product one can think of: meat, eggs, poultry, fresh fruits and vegetables, beverages, processed snacks, and so on. It can all be integrated and coordinated to get products to the supermarket on time and to reduce loss in the supply of perishable items. An example of this was the invention of cold storage facilities. These facilities provide the opportunity to extend the shelf life of perishable goods so that the product has a longer period of time to make it to the market. Further, it allows for middlemen to be able to purchase these cold-stored goods with enough of a shelf life remaining to get them to another consumer market. An example of cold-storage facilities comes from India. Potatoes are more often kept in cold storage before making it to the consumer. In addition, to the added benefit of extend shelf-time, the cold-storage facilities have extended the availability of potatoes beyond their local growing season (Reardon *et al.*, 2012). As a result of technology, to include cold storage, the Supermarket Revolution was spawned.

Transnational Corporations and Food Processing

Foods involved in trade fall into two categories, processed and raw. Food processing is a system that adds value to food postharvest and before marketing. (Wilkinson, 2004). It processes agricultural and livestock products into intermediate or final food sources for the consumer. This is done through the input of materials, labor, and technology. The level of processing is not part of the definition (United States Department of Commerce, 2008). Value added by the processing increases the ease of preparation or consumption for the consumer and there are numerous food processing sectors. The leading sectors in the US industry are meat products, other food manufacturing, dairy products, grain preserving, fruit and vegetable preserving, and specialty products (United States Department of Commerce, 2010). Other food manufacturing includes syrups, snack foods, coffee, tea, condiments, and spices (United States Census Bureau, 2012).

The Codex Alimentarius was developed in 1963 to facilitate international trade through mandatory food standards. When the WTO was commissioned in 1995, it mandated the Codex Alimentarius Commission to continue their work and to define these standards underneath the new trade organizations umbrella. It is these standards by which trade of processed foods is often conducted, although other standards for semiprocessed meats and crops may apply as well. The Codex Commission is made up of delegations from all member countries. Historically, industries have been overrepresented. The 1989–91 Codex Commission had representation from 105 countries and 140 food and agrochemical companies. Further, there were 660 industry representatives and 26 public interest representatives (Sklair, 2002). So, the regulation of supply chains is largely impacted on an international scale by the transnational food processing corporations such as Nestle, ConAgra, Heinz, and Dole.

Transnational food processing corporations not only benefit from assisting in the establishment of intergovernmental trade standards, but also from their sheer size in terms of production. These large corporations take advantage of the economy of scale when buying ingredients from suppliers (Vorley and Fox, 2004), with transport, and with regard to the terms of trade. Not only can they buy in large amounts to produce large amounts, they also have the infrastructure to create competition among suppliers so as to find the lowest cost possible to create their product. Further, they are able to invest in technology that increases efficiency around the flow of the supply chain. This assists with production rates and benefits the profit margin as well. The complex nature of a supply chain is growing, the journal *Food Engineering* reported that 40% of companies that responded to a survey stated they were using radiofrequency ID trackers. These allow for tracking of the supply items through the use of computers and handheld scanning equipment (United States Department of Commerce, 2010). As a result of automation and improved technology, food production is much more rapid and efficient. In fact, some retail companies, such as Walmart, are requiring this technology from their suppliers (United States Department of Commerce, 2010), further limiting the pool of qualified suppliers in that food chain.

In the United States, transnational food-related corporations include commodity traders and food processors. Commodity traders are often horizontally integrated. They consolidate the product supply within the supply chain itself, so as to control the majority of the supply chain or at least a large portion of it. Commodity traders deal with minimally processed foods, such as grains, feeds, and slaughtered meat and poultry. In the United States 60% of the terminal grain handling facilities that ship product oversees are owned by only four companies: Cargill, Cenex Harvest States, Archer Daniels Midland (ADM), and General Mills. For corn exports, three companies manage 82% of the exports: Cargill, ADM, and Zen Noh. As for meats, Tyson, ConAgra, Cargill, and Farmland Nation manage 81% of beef packing as well (Commodities and Trade Division, 2003). This concentrated food supply chain reduces competition and this competitive pricing. This has a global impact, because many of these companies are leading US exporters and also the leading global exporter.

The vertically integrated corporations are those corporations that own or control large portions if not all of the processing procedure. These can be companies that provide processed or semiprocessed goods. Examples of such companies are Dole, Chiquita, and Tyson. For Tyson, they own the entire process from the chick to the packaged meat and money

only changes hands when the final product is sold to the retailer. The impact of such integration is the lack of data on price points at intermediate steps. For example, the cost of labor at a pineapple farm or the current cost of a chick is largely unrecorded and unknown in the global marketplace. This makes it difficult to know how much to charge when outside producers are trying to integrate into the supply chain, especially when there are larger producers who create the majority of the supply chain. Since they have no data to contribute to the cost point, it is at the whim of the buyer and not based on market rates. Further, when prices decrease within the production chain it does not necessarily trickle down to the consumer. There is no competition within the supply chain to drive prices or oversight of the process through market data. Finally, when a corporation owns the majority of the market, it has no competition forcing its prices downward (Commodities and Trade Division, 2003).

As a result of the transnational corporations (TNC's) ability to integrate horizontally and vertically, as well as to play a role in the international standard setting, the international food trade only has a limited set of players. The impact of the international trade on the marginalized farmer without the capital or infrastructure to compete is either of no effect, as they make a living off of the local market, or a negative effect when these corporations become national trading competitors with smaller scale farmers and retailers. Although the more readily available producer-driven food supply chain (rice, wheat, soy, and other grains) is a boon for urban consumers, it creates a problem for many of the world's small-scale producers. The imported foodstuffs are often cheaper than the locally grown items. It was predicted that small-scale producers would be able to compete in the fresh fruit and vegetable market trade as developed countries demand these products year round, even when out of local and national growing season. However, the role of small farmers has been less than was predicted due to the high industry standards for trade that they do not have the capital to allow them to achieve. The standards are no longer those of just the WTO, but are also the private industry standards, including supermarket standards. Monitoring a large number of small-scale farmers compared with a few large-scale facilities is easier for private industry, and this is what is occurring (Commodities and Trade Division, 2003).

Many TNCs, such as Nestle, Kraft, General Mills, and Pepsico, produce highly processed products. These complex food products are prepared from a variety of ingredients from multiple sources. Food products can also be produced in stages at various locations. Most commonly, these food supply chains are the food products that expand beyond 'staple' food products. The demand is growing with urbanization. There has been an increasing need to have foodstuffs that are easy to move, easy to prepare, and that are resistant to decay. Further, of the foodstuffs available, processed foods are also the cheapest and the least nutritious. These are popular items in food deserts, urban areas, and often in areas of poverty – limiting the nutrition in those areas (Economic Research Service, 2009a,b).

Not only are processed foods the major imports and exports for most countries, but the processed food sector is also a significant proportion of the overall manufacturing sector. According to FoodDrink Europe, the food and drink industry is the leading industry in the European Union in terms of monetary turnover (€956 billion) and contribution to employment (>4 million). It is the leading global exporter of foodstuffs and contributes 17.8% to the global food and drink trade (FoodDrink Europe, 2012). The focus of processed food companies is to create a 'consumer-ready' and 'value-added' product from the raw ingredients. They compete against one another in the industry based on the total sales. In 2012, Pepsico was the leading food processing company with US$38 396 000 in sales. The other top five companies were Tyson Foods, Nestle (Canada and the United States), Kraft, and Anheuser Busch. Nestle had the largest net profit of US $10 500 000 (Food Processing, 2012). This industry is not solely about food security and supply for countries; it is also about economy, employment, industry, and business.

Supermarket Revolution

This processed food industry would not be as profitable without a platform to sell food goods to consumers. The distribution of these food goods is through the retail market. This includes local, national, and international grocery chains. The traditional grocery store still sells approximately 58% of the processed food goods in the United States (United States Department of Commerce, 2010). The increased trade around the world has had a profound effect on retailers though and it is referred to as the Supermarket Revolution.

The Supermarket Revolution began in the 1990s. Retail supermarkets and their chains began moving beyond the developed nations of the world and into the developing nations. This revolution began as urbanization and an increase in income in the developing world, but its success was based on the foreign direct investment (FDI) that occurred with the entry of supermarkets. This FDI was made possible through the liberalization of the market associated with the development of the WTO, and through improvements in technology that allowed for improved supply chain management. This last point allowed the international supermarkets to have competitive prices in the local markets. For example, in Latin America and Southern Africa Walmart has been a leader in the FDI (Commodities and Trade Division, 2003; Wilson, 2012); Carrefour and Ahold are also major investors in Central and South American supermarket chains (Commodities and Trade Division, 2003). The supermarkets initially outcompete local retailers in the processed food sector and, within 10–20 years, the supermarkets in Central and South America, Southeast Asia, and Southern Africa have began to outcompete the local retailers in the fruit and vegetable market as well. In the end, supermarkets outcompete by offering lower prices for goods and higher diversity. This competition drives down the overall food prices and can lead to increased food security, especially for the urban poor (Reardon and Gulati, 2008). Yet, the accessibility of nutritious foodstuffs to the urban poor is limited, and the poor tend to rely on processed foods and ready-to-eat foods that have a lower nutritional value but are readily available (Kennedy *et al.*, 2004). The increased availability and access to food associated with the supermarket revolution does not necessarily translate to nutritional equality as well.

This revolution developed in three waves. The first wave began in South America, Central Europe, and South Africa in the early 1990s. At that time supermarkets accounted for only 5–10% of the market share, and by the 2000s they were greater than 50% of the market. The second wave was in Central America, Southeast Asia, and Mexico. By the 2000s, supermarkets in these regions accounted for 30–50% of the market share. In some regions of South and Central America the market share rose as high as 70% (Commodities and Trade Division, 2003). Finally, the third wave was made up of China, Vietnam, India, and Russia. As of 2011, supermarkets were emerging in Southern and Eastern Africa as well. There were patterns to the emergence of these supermarkets: they started in urban areas and spread to the rural areas; they were first accessible to the rich, then the middle class and finally the poor; initially they featured processed foods; then semi-processed foods and finally fresh foods (Reardon *et al.*, 2012; Milligan and Brown, 2011).

Yet this boom of supermarkets, which has likely improved global access to food, is not without its shortcomings to the small-scale producers and the traditional retailers. They have struggled against the competition in some locations. Urban retailers are most affected, and they only can gain a foothold in the market if they modernize. Outside support may be needed by these local retailers to modernize in an effective way (Reardon and Gulati, 2008). Yet, the impact of the Supermarket Revolution extends down the supply chain all the way to the farmers. Approximately 80% of supermarket goods are processed, shelf-stable products purchased from food processing corporations such as Kraft, General Mills, Nestle, Proctor and Gamble, ConAgra, and others. Most farmers that contract with food processing corporations are medium- to large-scale producers as they can support the larger contracts and can afford to meet the privately enacted standards driven by the CSR movement. As a result, small-scale farmers are poorly represented in this supply chain. Only, small-scale farmers with the largest land ownings, equipment, and access to infrastructure such as roads and irrigation are the ones that are able to break into the international supply chain (Reardon and Gulati, 2008; Commodities and Trade Division, 2003). There is great opportunity associated with the Supermarket Revolution for all farmers, but it is dependent on its ability to exclude or include the small-farmer sector of the country (Commodities and Trade Division, 2003). Overall, farmers involved in a supermarket supply chain can earn anywhere from 20% to 50% more in terms of net income than farmers selling goods via traditional routes (Reardon and Gulati, 2008). Thus, extending the opportunity down the supply chain could potentially benefit all farmers.

A Description of Global Export

According to the WTO, the top ten exporters of agricultural products and food in 2011 were (in decreasing order of percentage of world trade): the European Union (39%, 2011), the United States (9.7%, 2011), Brazil (5.7%, 2011), China (4%, 2011), Argentina (3.3%, 2011), Canada (3.2%, 2011), Indonesia (2.4%, 2011), Malaysia (2.3%, 2011), and Thailand (2.3%, 2011). The top three leaders' food trade earnings were US$520.4 billion, US$131.3 billion, and US$77.4 billion, respectively. The countries with the lowest overall trade in agricultural products in the top ten, still earned US$31.6 billion, US$44.2 billion, and US$31.7 billion in food trade, respectively (International Trade Statistics Section, 2012). Many of these countries trade the majority of their food products regionally. Europe, in 2005 and 2011 sold 81.2% and 78.1% of its food products elsewhere in Europe. North America, composed of Canada and the United States, sold 47.1% and 41% of its food goods within North America in 2005 and 2011. Asian countries revealed a similar trend, selling most of their goods to other Asian countries during the same years (55.7% and 56.4%, respectively). Interestingly, many of the leading agricultural exporters are also significant food importers from other leading exporters. The European Union's 2011 food imports accounts for 38.2% of the world's foods imports, followed by the United States (7.9%, 2011). Japan and China have the next highest share in imports with each importing 5.5% and 5.2% of the world food in 2011 (International Trade Statistics Section, 2012).

Although many countries were not leaders in world food importation, the food that they did import accounted for a large share of all their economies merchandise imports in comparison to these import and export leaders. For example, the European Union imported 38.2% of the world's food with a total value of US$549 billion, but it only accounted for 8.8% of their European Union's merchandise imports in 2011. Yemen's food imports accounted for 42.6% of all imports at a value of US$3.6 billion. Côte d'Ivoire's food imports have a total value of US$1.7 billion and account for 25.1% of their total imports. Syria, Senegal, and Sudan's food imports account for 21.1%, 22.9%, and 23.1% of total imports at a value of US$3.5, $1.4, and US$2.1 billion, respectively. Of course, there are other countries whose food imports account for greater than 20% of their total merchandise imports, but the value exceeds US$10 billion. Egypt's food imports in 2011 accounted for 23% of all imports at a value of US$13.6 billion, and Algeria's imports accounted for 22.6% of all imports at a value of US$10.7 billion. Clearly, the percentage of the total imports has very little correlation to the overall value in comparison to other countries (International Trade Statistics Section, 2012).

The Food Chain in the United States

Overview

The majority of the US food supply comes from domestic sources, but as the food supply system matured and Americans demanded more variety and convenience from their food products, imports also grew. The demand for a variety of fruits affected by the seasonality of the growing seasons and an increasing demand for nutritious foodstuffs also define the US's import markets. Every year, American farmers produce approximately US$143 billion in crops and US$153 billion in livestock (Massey, 2013). Less than 2% of the labor force consists of farmers. Farmers contribute approximately 1% to the gross domestic product (GDP) directly. This 1% translates into US$200 billion and is primarily concentrated in the

Midwest, California, and the East coast. Yet, greater than 16% of the labor force is involved in the food sector overall, and the industry as a whole makes up 11% of the national GDP. Despite the limited number of farmers in the United States, the average US citizen only spends approximately 11% of their income on foodstuffs. The global average is double that number at 20–30%. This is due to the highly advanced and productive nature of the US food supply (Monke, 2004).

Delineating the Protein Food Supply Chain

The animal protein sector of the US market will be used to describe the complexity of the food supply chain. Groups such as Cargill, Cenex, and multinational organizations have been discussed above. Animal protein production business in the United States has become highly integrated and this is especially true in the livestock sector. Livestock farmers are of a larger scale than ever before; they also generally raise a single species in enclosed housing. Further, beef cattle, hog, and poultry farmers often only raise certain age groups of animals. One farmer raises young animals, and adults are 'finished' by another farmer. Much of this highly industrialized system developed to allow greater value to the end product and to increase efficiency by the farmer.

The value of these animals and the payment received by farmers today is no longer driven by a daily, weekly, or monthly market system, but is instead based on services provided and contractual agreements. Livestock systems have geographic niches throughout the United States. Beef cattle feedlots are primarily found in Northern Texas, Kansas, Nebraska, Eastern Colorado, and Iowa. The leading dairy states are California, Wisconsin, Idaho, New York, and Pennsylvania. Hogs are found in Iowa, Minnesota, and North Carolina (Hoskin, 2012). Broilers are most predominant in Georgia, Arkansan, and the Delmarva Peninsula (Delaware, Maryland, and Virginia) (MacDonald, 2008). According to the 2007 US Census of Agriculture, there were approximately 96 million cattle and calves, 68 million hogs, 350 million layer birds, and 9 billion broiler birds in the United States in 2007 (National Agricultural Statistics Service, 2009). To highlight the complexity of the agricultural industry, the beef supply system and value chain will be discussed in detail and brief overviews of the pork, dairy, and poultry industries will be given.

Most of the livestock industry in the United States is segregated by production groups, often based on age and maturity of the animal. Beef cattle originate from cow–calf operations, often on ranges and pasturelands. When the animals are weaned, they are sold to finishing operations at feedlots (National Animal Health Monitoring System, 2011). The assurance in the supply of the calves has to be worthwhile to the feeder, finisher, or processor who is buying the calves in order to lock in an agreed-upon price. Small-scale farmers likely have a lesser ability in meeting the demands of these contracts. The result is that larger-scale farms are more vertically integrated, that is the producers sell to the same buyers in the production chain year after year. This is likely due to the use of contracts and on sales based on market value chain characteristics (National Animal Health Monitoring System, 2011). In the United States, the 10 largest feedlot operations account for 30% of the beef feeding capacity as well. Further, 10.5% of the industry are owned by the JBS Five Rivers and Cargill corporations. The move toward corporation and multiple owners versus single owner feedlot systems represents the benefits gained out of the economy of scale (Galyean, 2010). Feedlots can range in size from a few hundred head of cattle to thousands of head of cattle (Harvey, 2012; **Figure 2**).

Dairy production has increased dramatically since 1970. Milk production per cow has doubled whereas farm numbers have decreased a little over seven-fold from 650 000 farms in 1970 to 90 000 farms in the 2000s. Despite the number of farms being much smaller the average herd size has also grown five-fold, from 20 head of cattle to 100 head of cattle. Of all the milk produced, one-third is used for fluid milk sales. The rest is processed into other dairy products such as cheese, butter, yoghurt, ice cream, and so on. Almost half of the milk produced is made into cheese, with mozzarella being the most popular cheese type in the United States. In fact, the largest demand, and the major economic force behind the US milk industry is the demand for cheese. Its demand has doubled in the past 25 years, whereas fluid milk demand has declined slightly (Hoskin, 2012; **Figure 3**).

The pork industry in the United States has changed dramatically in the past 20 years, but the United States continues to be a leader in pork production with total pork sales numbering US$18.1 billion in 2007. Between 1992 and 2004, the number of farms involved in pork production dropped by 70%. Nonetheless, similar to beef, the number of swine in the United States remained stable at 60 million head of swine. Farms went from owning 945 swine on average in 1992 to 4646 swine in 2004, with more than 50% of the farms owning >5000 head of swine in 2004 (Key and McBride, 2007; Environmental Protection Agency, 2012; **Figure 4**).

The US swine industry is broken into two parts, but there are many phases to the actual pork production cycle. Breeding occurs shortly after a sow's piglets are weaned. Sows give birth almost precisely at 3 months, 3 weeks, and 3 days after breeding (113–116 days) (Environmental Protection Agency, 2012; Key and McBride, 2007). Many sows farrow or give birth to 3–5 litters in their lifetime and each litter is approximately made up of 8–12 piglets. When piglets are between 6 and 10 weeks the pigs move into a grower/finisher phase. The grower/finisher phase of production is the stage where the pigs are fed free choice until they reach market weight, which is approximately 250–275 lb (Environmental Protection Agency, 2012). Most phases are split into two- or three-tiers of production. Breeding and gestation often occurs at one location whereas farrowing, nursery, and growing/finishing are done at another location (Environmental Protection Agency, 2012). These production phases are either done through one business or through separate businesses focused on phase of production (Key and McBride, 2007), farrowing, and nursery age pigs are often raised in one location and then transported to a grower/finisher farm. The leading hog producing states in the United States are Iowa, North Carolina, Minnesota, Illinois, and Indiana (Pork Checkoff, 2012).

Poultry production has changed dramatically since the early twentieth century when a large number of households owned at least a few chickens. Today, the industry comprises farms that focus on one area of production for one species.

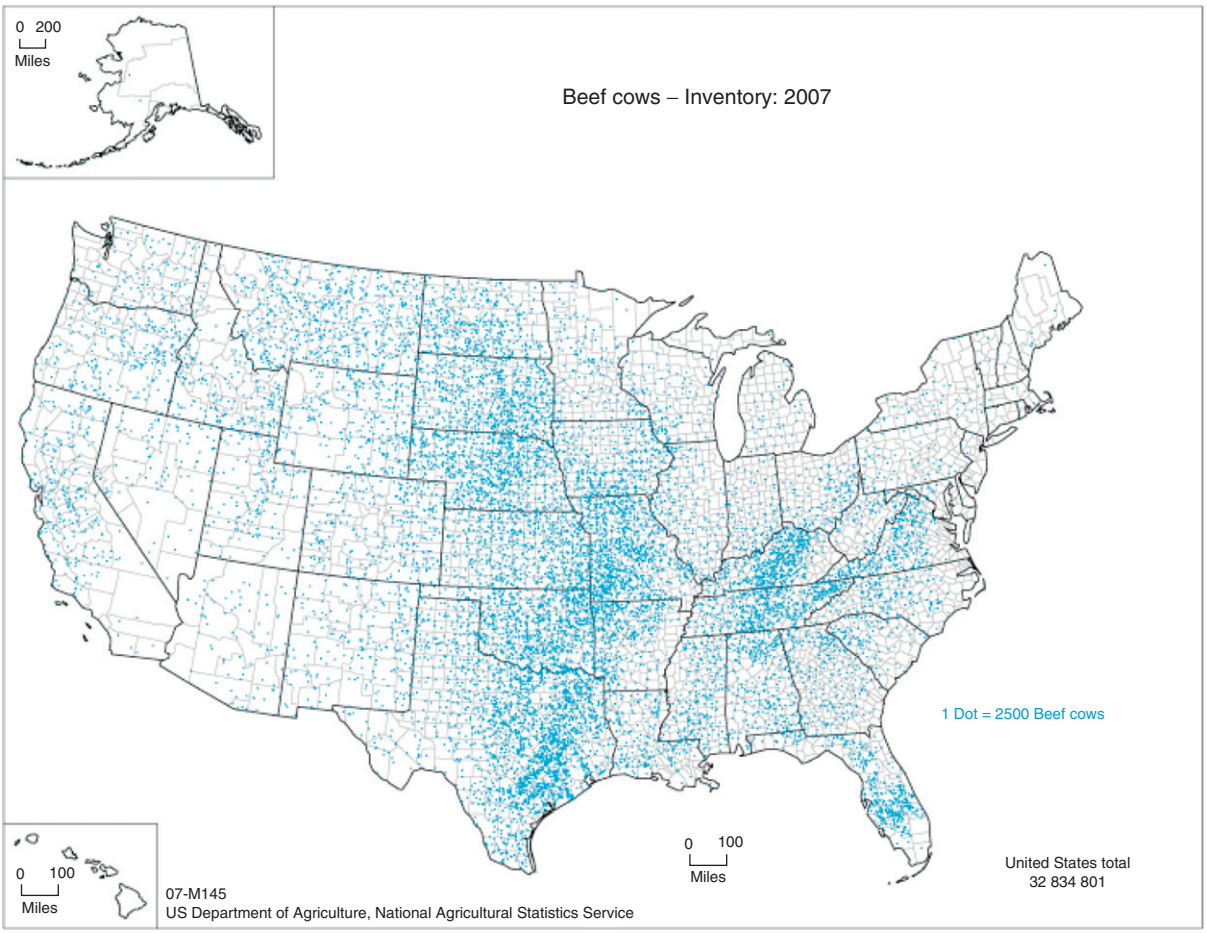


Figure 2 Beef cattle distribution in the United States, 2007. Reproduced from United States Department of Agriculture.

Birds are raised as layers (eggs) or broilers. Farmers may also be pullet producers (young chickens) that are supplied to broiler and layer production farms. (MacDonald, 2008; Harvey, 2012). In total, approximately 18% of poultry products are exported from the United States and it is the leading global poultry producer, as well as the second leading egg producer and poultry product exported (Harvey, 2012).

The majority of the poultry production is found in the broiler production industry. Broilers are young birds raised for meat (Economic Research Service, 2009a,b). The majority of farms are found in the area spanning Delaware to Georgia on the Eastern Seaboard and extending as far West as Oklahoma and Texas. The leading poultry producing states are Georgia, Arkansas, Mississippi, and North Carolina, in order of decreasing production. Production is coordinated differently than other animal production systems. The growers supply all the needs and labor for growing the birds from pullets to market weight birds, which takes approximately 6–8 weeks. A group known as 'integrators' manages the pullets, feed, and processing industries and contracts with the growers to prepare the birds for slaughter and therefore market (MacDonald, 2008). They, therefore, supply the pullets (young birds), veterinary care, and feed for the birds. The processors essentially contract out the cost of growing the birds (**Figure 5**).

The egg industry is markedly different from the broiler industry in that it is vertically integrated, meaning that one company owns the birds, manages the eggs, and sells the eggs. Yet, typically, the layer stock is still purchased from another company, with chicks arriving at the laying farm from the hatchery within 1 or 2 days after hatching. At the laying farm they are either placed in a laying cage or raised in a pullet house where they are fed until they reach approximately 3 pounds (1.4 kg) in weight, which takes approximately 15 more weeks. Between 15 and 18 weeks of age the hens are moved to the laying barn where daylight length is increased and feed becomes *ad libitum* or always available as layer hens regulate the food intake. The daylight exposure assists in initiating the onset of egg laying. At 60–70 week approximately 50% of the birds are laying, which is typically seen as the economic breakeven point for the producer. At this point, farmers will induce a molt in the birds, to increase the egg-laying life of the majority of the birds in the flock to approximately 100–110 weeks of age. At this point, between 100 and 130 weeks of age, most hens are sent to a spent hen facility where they are processed for meat production into items such as pet food, canned chicken, chicken soup, etc. or for disposal. The molting process is critical to farming efficiency and deserves more explanation. Molting is the process where hens lose their old feathers and grow back new ones. It is a

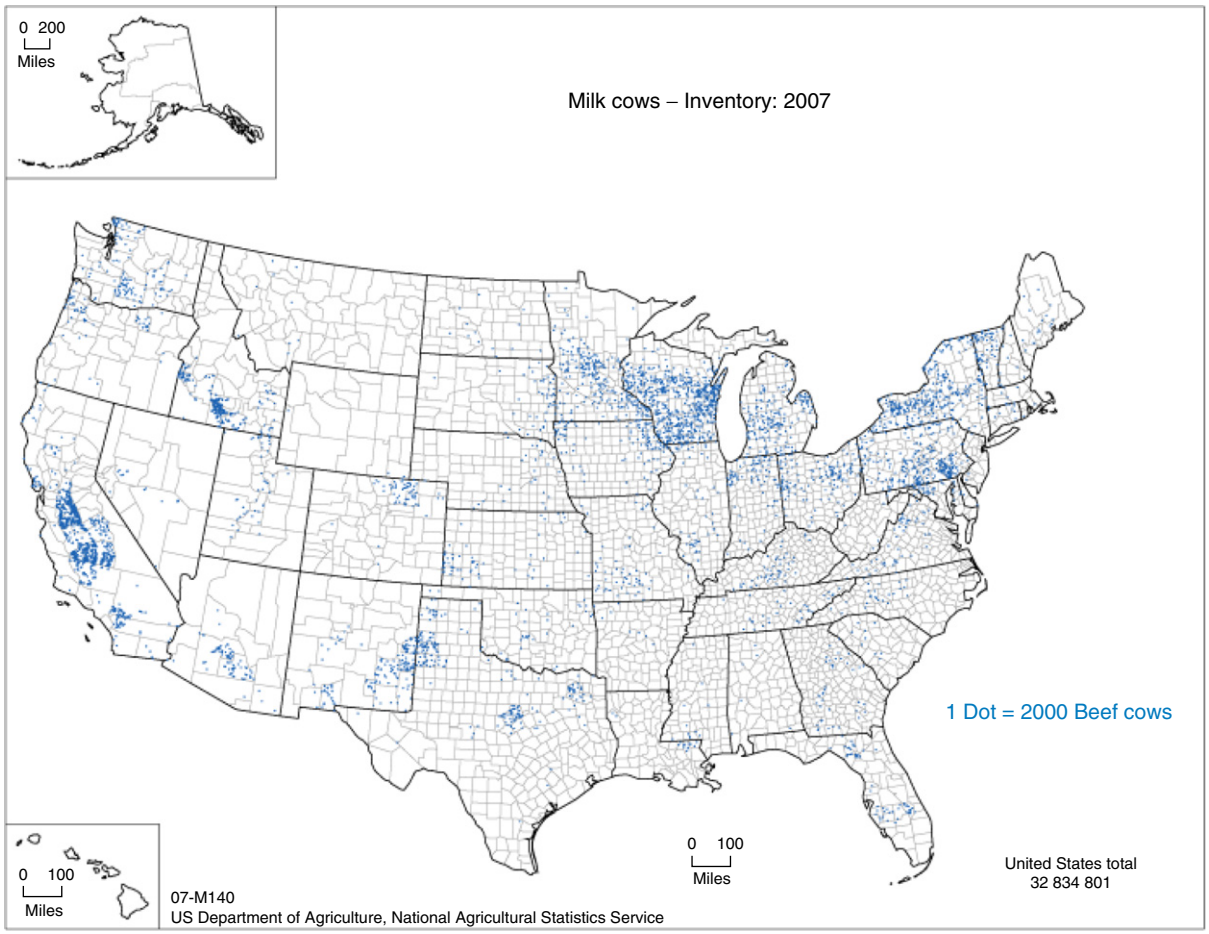


Figure 3 Dairy cow distribution in the United States, 2007. Reproduced from United States Department of Agriculture.

hormonal process coupled with light manipulation (Carey and Brake, 2007).

Social Values and Food in the United States

Developed countries have experienced a sharp decline in the number of farmers whereas the size of the farms has increased dramatically (Martinez, 2010). Although 70% of the poorest people in the world rely on animal agriculture for their survival (Zoonoses and Veterinary Public Health Department, 2006), developed nation populations are essentially disconnected from their food sources. They contact the end products but never interact with the crops or animals that provide the nutrition. Their food products are already slaughtered, pasteurized, gathered, processed, and packaged before the consumer even considers them as a food product. The system is industrialized for economy of scale and the product flow occurs at regional, national, and global levels. This is true of the United States as well. Since the 1990s, the realization within the American public that national animal production standards were not in line with consumer values has resulted in the popularity of a number of movements. These include the 'Buy Local' movement, in support of smaller scale local farmers and a lesser reliance of fossil fuels to gain food availability (Martinez, 2010; ERS); organic foods, related to concerns about pesticides, the use of hormones, and other additives; and the cage-free and grass-fed poultry and beef management movements, which address animal welfare. For example, the number of local farmers markets almost doubled between 1998 (2756) and 2009 (5274) (Martinez, 2010).

The Food Chain in India

With a population now exceeding 1.21 billion people, the Republic of India faces a unique set of challenges in the production, supply, and distribution of food. Since gaining independence from the British in 1947, India has radically transformed farmers' agricultural practices in order to achieve greater food security, yet the flow of goods remains traditional in many respects. The rise of the middle class, increasing urbanization, and changes in food preferences are predicted to have significant impacts on the country's food chain in the years to come.

Background

India has a long and rich farming tradition, dating back to 9000 BC. The amount of arable land in India is second only to

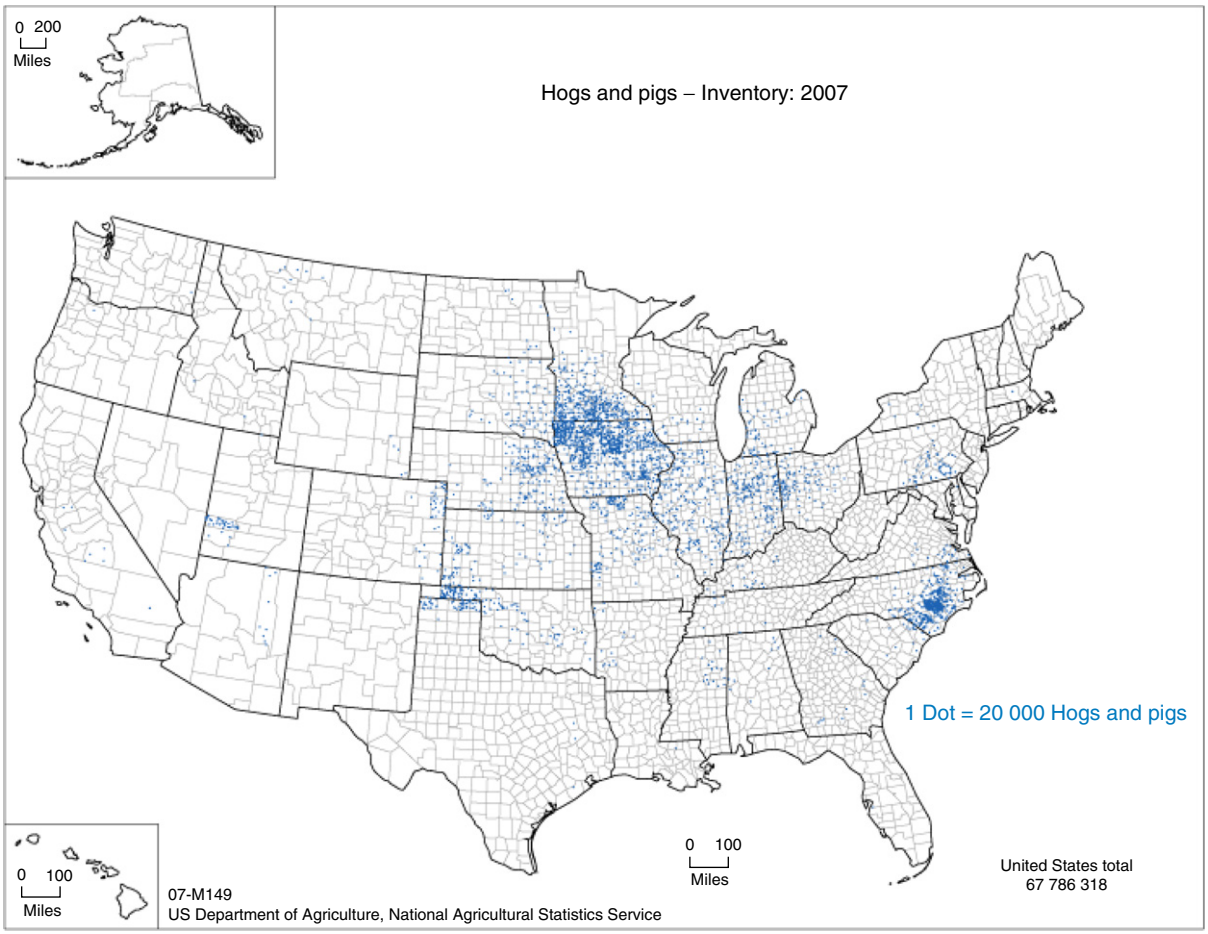


Figure 4 Swine distribution in the United States, 2007. Reproduced from United States Department of Agriculture.

the United States (Economic Research Service, 2012). Over time, the variance of soil and climatic conditions across the country has led to the geographic concentration of certain crops. For example, approximately 90% of the wheat currently grown in India is concentrated in the northern part of the country.

At the time of Independence, approximately 9 in 10 Indians were involved in some form of agriculture (Parvathi and Arulselvam, 2013). Yet food shortages plagued the country, as they had under colonial rule. The nascent Indian government pledged to support the most malnourished of its populace by guaranteeing a minimum supply of affordable grain. To meet this demand, India was forced to import as much as 10 million tons of food per year (Saha, 2013). In the 1950s, flooding and drought in the northern regions of the country exacerbated the existing food insecurity, and the people of India were threatened with widespead famine.

In 1967, the Indian government responded by instituting the technologies of the Green Revolution. As championed by the plant geneticist M.S. Swaminathan, the use of high-yielding seed varieties, accompanied by improvements in irrigation and the adoption of chemical fertilizers and pesticides, produced stellar advances in the country's food production. By the late 1970s, India boasted a record grain output of 131 million tons, and a food surplus was soon established. In the four decades after 1968, India's production of cereals more than doubled. The government targeted hunger reduction among its poor through heavy subsidies for wheat, rice, and sugar crops.

In the decades following the Green Revolution, the Indian government has demonstrated comparatively low levels of investment in agricultural research. According to the Center for Policy Alternatives in New Delhi, public investment in farming actually fell by one-third from 1980 to 2002. This trend has been accompanied by limited access to loans for farmers. As a result, there has not been any official (or unofficial) expansion of technologies to improve crop yield, and only approximately 40% of Indian farms are irrigated today. Since the mid-1990s, there have been 150 000 suicides among small farmers in India, with most of these attributed to financial strain. As a result of production challenges, the two primary sources of protein and calories in the Indian diet – lentils/peas (pulses) and vegetable oils – are increasingly being imported because farmers cannot meet the country's demand.

Structure of the Food Chain

Agricultural Produce Marketing Acts and Agricultural Produce Marketing Committees

In India, state governments are broadly responsible for the legislation and regulation of the agricultural sector, including

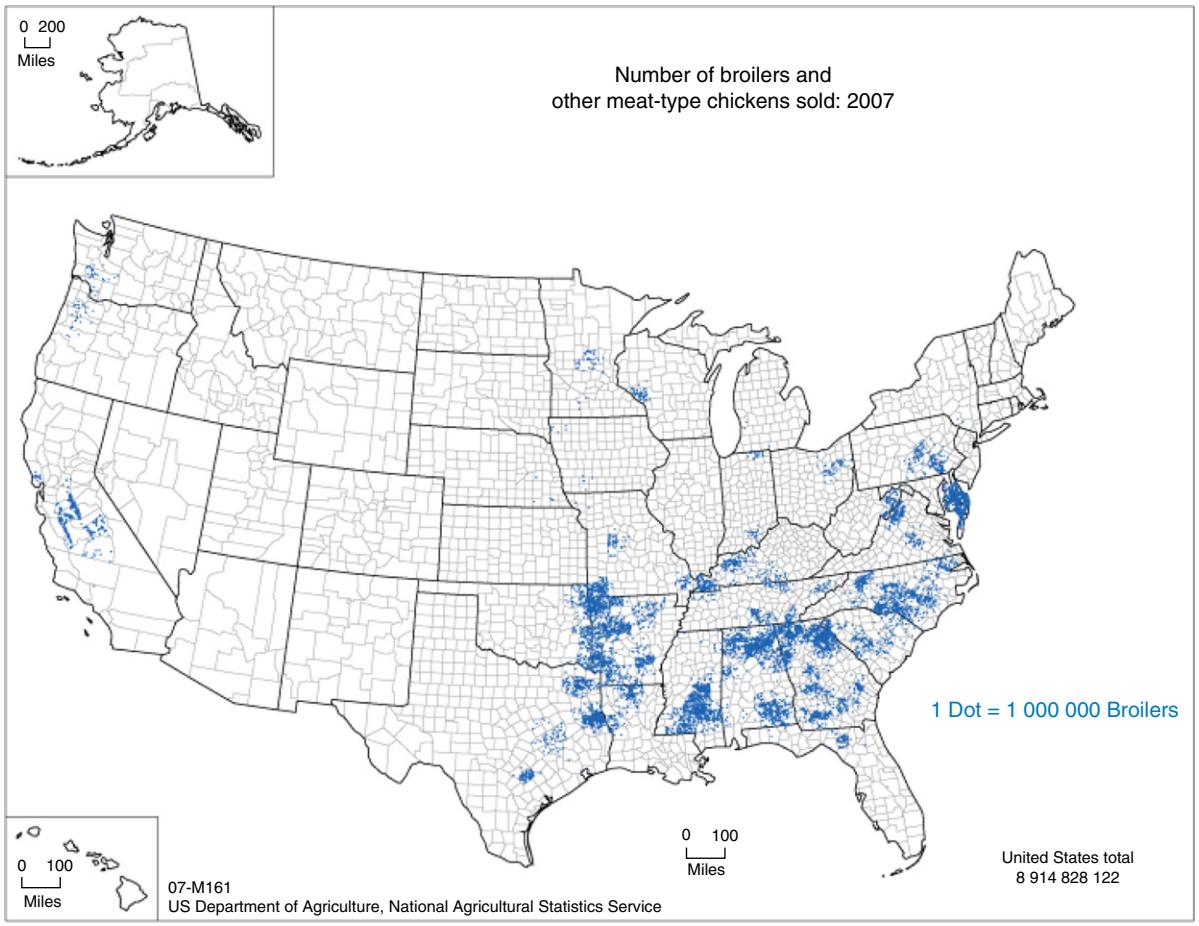


Figure 5 Poultry distribution in the United States, 2007. Reproduced from United States Department of Agriculture.

Farmer (unregulated) → Preharvest Contractor (unregulated) → Commission Agent/Broker (APMC regulated) → Wholesaler (APMC regulated) → Retailer (unregulated) → Consumer

Figure 6 The food supply chain in India. Reproduced from Gujral, J., Joshi, P., Anuradha, R.V., 2011. Facilitating Legislative and Administrative Reforms in Agricultural Marketing by Leveraging the Competition Commission of India. Canberra, Australia: Australian Centre for International Agricultural Research.

produce, livestock, and products of livestock. The Agricultural Produce Marketing Acts (APMAs) establish agricultural produce and marketing committees (APMCs) in each state to control the sale, storage, and marketing of produce. APMCs have approximately 12 members, who are either nominated by the state government or elected by the market areas.

Local market yards, called mandi, are established by the APMCs for the purposes of trade. Farmers typically sell their produce in these wholesale markets or through a broker (who charges a commission) and prices are set in an open auction. Retailers purchase produce through the APMC-regulated wholesalers and market them to the final consumers (Figure 6).

Critics of the existing trade system cite innate problems with efficiency, the accompanying lack of innovation in food storage and transport, and restrictive policies that limit farmers' ability to sell outside of the mandi (such as directly to private food retailers). The supply chain also includes overcrowded roads and a largely underdeveloped, unrefrigerated rail system. By some estimates, the average farmer receives less than a fifth of the price the consumer pays (Singh *et al.*, 2002).

Food Corporation of India and Targeted Public Distribution System

Although the legal responsibility for agricultural trade rests in the states, the federal government plays a powerful role in its heavy procurement of agricultural products for public distribution. In 1964, the Food Corporation of India (FCI) was established under the Food Corporation Act. The FCI is a parastatal agency with the following goals (Food Corporation of India, 2014):

- effective price support operations for safeguarding the interests of the farmers;

- distribution of food grains throughout the country for public distribution system; and
- maintaining satisfactory level of operational and buffer stocks of food grains to ensure National Food Security.

The FCI is organized on a regional basis and is closely associated with the local food supply chains described above; in fact, the FCI is mandated to buy exclusively through the mandi. Approximately half of India's grain market is funneled through the agency, which typically procures supplies from surplus areas and delivers them to deficit areas. This amounts to 22 million tons of grain over 1500 km, or 12 million bags of grain transported every month.

Before each crop season, the FCI establishes a minimum support price (MSP) for 24 major crops, including seven cereals (rice, wheat, barley, sorghum, pearl millet, finger millet, and corn), five pulses (chickpea, pigeon pea, mung bean, black lentil, and red lentil), eight oilseeds (peanut, canola, toria, soybean, sunflower seed, sesame, safflower seed, and niger seed), coconut, raw cotton, raw jute, and virginia flue-cured tobacco. These prices are calculated on the basis of recommendations from the Commission of Agricultural Costs and Prices and are intended to reflect the costs of various agricultural inputs. The MSP is also susceptible to the influence of economic and political factors, and could potentially be used to incentivize farmers to plant certain crops over others.

In 1997, the FCI began using the Targeted Public Distribution System (TPDS) (replacing the Universal Public Distribution System) to deliver food to its citizens in need of assistance. TPDS establishes two categories of need (families below and above poverty line), and distributes a limited amount of grain to these families at subsidized rates. Critics of this system claim that not enough families have been identified and that the allotment of grain is insufficient to meet their dietary needs. There has also been a perceived 'leakage' of the national grain supply – a mismatch between procurement and distribution due to poor transport, inadequate storage, and failures in marketing.

Future Trends

Personal wealth and urbanization

According to the United Nations, India is predicted to have a population of 1.42 billion by 2026. In recent years, the country has been characterized by rapid economic development – rises in both GDP and average individual income. Furthermore, as in many developing countries, India's urban population has increased at the same time as its middle class has swollen. Over the past four decades, the urban population within the country has expanded from 17% to 30% (Sup Lee, 2012). City dwellers also generally have more disposable income for food purchases. As a result, urban food markets face much higher consumer demands than those in rural areas.

The food chain in India is being significantly altered by social changes as well. Women are increasingly present in the workplace, which means they have less time at home for food preparation. Lifestyles are becoming more fast paced, particularly in urban areas. Thus, the wealthiest consumers are spending more of their food budget (58%) on highly processed foods because of the convenience factor (Minten *et al.*, 2009). There is also more widespread access among the general population to modern, food-related technology such as microwaves and refrigerators.

Shifts in food preferences

Changes in India's demography have been accompanied by significant shifts in food preferences. Many consumers are substituting higher-value fruits, vegetables, and protein such as fish, meat, and dairy for the traditional grains and pulses. For example, cereals accounted for a much smaller percentage of total food expenditures in 2007 – only 24% in the urban population and 32% in the rural population (as compared with 34% and 56%, respectively, in 1972) (Minten *et al.*, 2009). In 2009 alone, spending on fruits and vegetables increased by nearly 9% as compared with the previous year. Meat, eggs, and fish were purchased at an increase of approximately 30%, whereas spending on cereals was unaltered (Winterbottom and Jadhav, 2011).

In addition to nutrition and health, many consumers in India are becoming more concerned with food safety and quality. The Food Safety and Standards Authority of India (FSSAI) enforces national laws and regulations pertaining to the production and retail of food supplies, although many producers have also instituted internal food safety management systems.

In general, there is a growing demand for variety in food products, with modern consumers preferring several choices over a single brand. In India, and throughout Asia, the retail food market is rapidly being filled with packed and branded products. Even in poor areas, producers recognize that they can charge higher prices after establishing loyalty and a 'brand value' of quality and safety (Minten *et al.*, 2013). Illegal brands, which are designed to mimic those that are well known, are often associated with lower quality and safety. This phenomenon is symptomatic of the relatively minor enforcement of intellectual property rights throughout the country and elsewhere in the developing world.

Modernization of distribution networks

As discussed earlier in the Section Supermarket Revolution, India is part of the third wave of the 'Supermarket Revolution.' With only 4% of food markets surpassing 500 sq ft, the vast majority of retailers are still small and are family owned. However, a recent surge of larger food retail chains (such as Reliance Fresh and Namdhari Fresh) is predicted to bring improvements in supply chain management, including the use of more modern, temperature-controlled warehouses and transportation (Goyal, 2010). Reliance Fresh, which was created by Reliance Industries in 2006, grew from just 330 stores in 2007 to 1400 as of 2013. At approximately 4000 sq ft each, these stores are filled with fresh fruits and vegetables, dairy products, and assorted other groceries and household staples. Attracted by the rapidly growing economy, large foreign corporations such as Tesvo (UK), Carrefour (France), and Walmart (United States) will likely be entering the Indian market in the near future.

Many supermarkets contract their goods from local suppliers in addition to big distributors. Increasingly in India, fresh food retail chains are purchasing fruits and vegetables

directly from farmers rather than through the government-run mandi (wholesale markets). This arrangement has the potential to improve the livelihoods of small producers, as well as lower operational and storage costs for the private enterprises (Goyal, 2010). To promote these changes, the Indian government has made some significant reforms to agricultural marketing policy. In 2003, an amended Model APMC Act was circulated, which relaxes the regulations on farmer direct marketing and allows for the establishment of private markets and contract farming. It has since been implemented by 16 states.

Conclusion

The food chain has moved from subsistence to local production to a complicated, highly integrated global system that has created numerous challenges and benefits. The food chain has also become an industry, generating a food value chain along with the food supply chain. This global market and its value chain have yielded increased standards for trade reasons as well as social values. As a result the supply import/export supply chain has become dictated by economy of scale, capability to create certain levels of quality, and that is accessible to distribution chains. The result is that not all food producers are able to become integrated into the food chain. In addition, although in many places, food security has improved overall, food's availability is not evenly distributed, and accessibility is limited by income, creating nutrition, and hunger problems persist. The United States has developed a complicated food industry, and the protein industry was highlighted to show the compartmentalized nature of the industry. India is a country with an interface between traditional agriculture and modern industry. The challenges facing India are its geographic span, population size, and a centralized model of food distribution. The food chain is not a simple topic, and is different between each country in the world, and within each country of the world. Yet, the principles and challenges discussed here highlight some of the characteristics and the infrastructure of the food supply today.

See also: Agricultural Labor: Demand for Labor. Agricultural Labor: Supply of Labor. Food Law. Food Marketing. Food Security: Development Strategies. Food Security: Postharvest Losses. Food Security: Yield Gap. Global Food Supply Chains. Human Nutrition: Malnutrition and Diet. International Trade. Regulatory Conventions and Institutions that Govern Global Agricultural Trade

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Food Engineering

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Definition

Even though the word engineering has come to us through many languages (Latin, French, and now English), it ultimately stems from classical Greek. It is a combination of *εν*(*ι*) – eni: in or into, and the verb *γείνομαι* (geinomae): to create, to engender, to bring into being. Engineering sciences are by definition synthesizing sciences: they aim at conceptually creating a product or process, and within this activity, being a science, they strive to obtain insight into nature. This synthesizing nature is in contrast to the more analytically oriented disciplines, such as chemistry, physics, or biology, which just aim to understand specific aspects of nature. The engineering sciences employ and combine parts of these disciplines into the creation of products and processes. The food engineering sciences are thus the sciences that are related to the creation of food. Traditionally, this has been mostly interpreted as the scientific field of designing processes for producing or stabilizing foods. More recently, the food products themselves have become more central in the approach of food engineers.

In a technical sense, foods are different from most chemical products by their complex composition and by their very complex morphology. Most chemical products consist of just one molecule (ethylene, styrene, or caprolactam), or a relatively simple molecular mixture of homologs (gasoline and diesel). A chemical product usually does not have a specific structure on larger scales than the molecular scale. Food products typically have hundreds or even thousands of constituents, which are arranged in a very particular structure. The structure is a major determinant of the overall properties of the food product. In contrast to the production of chemicals, the preservation, modification, or creation of the structure of a food is, therefore, a major goal of any production process.

The production of sufficient, safe, and palatable food is a critical issue for society. Therefore, food engineers are employed not only by food processing companies (both the production of ingredients from raw agricultural materials and the production of end products), or by their suppliers (equipment manufacturers and suppliers of packaging concepts), but also by governmental and consulting agencies.

Food Engineering in a Changing Human Society

The spread of humanity over the globe, from the original tropical areas where food is available throughout the year toward areas where food is not available year-round, has been made possible by the preservation of foods. By the storage of foods, one can subsist on foods that were harvested at one specific time in the year.

Food preservation went hand-in-hand with the development of human civilization; one might even argue that food preservation has precipitated civilization as we know it. Foods that are harvested need to be stored in central locations, to ensure the right conditions and to protect them against others that might not have stored sufficient foods. Preserving foods also mean specialization: next to the harvesters, protectors, builders, potters, administrators (to check who would be entitled to the foods), and many others were necessary. The abundance of one particular food in one area, and the abundance of other foods in other areas, then gave rise to trade and development of a commercial system.

Until 1950 – Availability of Safe Foods

Therefore, the activities that food engineering nowadays comprises, are not new, but are as old as humanity. Many techniques have been developed over the millennia. The production of beer and wine has been developed in the near East (earliest findings in Iran and Georgia from 7000 BC); the baking of bread goes back to at least 30 000 years. All those processes were meant to make stable foods that are safe for consumption. They have been developed through experience and trial and error; acquisition and application of systematic insight was not yet a main driver in the development.

One usually only speaks about food engineering as a recognizable field, with the invention of processes as the appertization process by Nicolas Appert at the beginning of the nineteenth century, for the sterilization and stabilization of foods in jars and cans over prolonged periods of time by heating of a packaged product. Although Appert used glass jars, sterilization in tin cans was invented by Peter Durand in 1810. Food engineering was then taken to a next level by the creation of margarine by Hippolyte Mège-Mouriés in 1869 and by the development of pasteurization by Louis Pasteur in 1862.

The basis of food engineering is, therefore, in the preservation of foods: to prevent spoilage by microorganisms and enzymes, and to preserve the nutrients such that the product would stay palatable after opening the package. This remained the primary focus of the field until the middle of the twentieth century. The global development of agriculture and food production ensured the supply of sufficient foods for many, more developed, parts of the world. The increased affluence of the population in the 1960s and later led to more and more attention to the quality of the foods: not only just the availability of safe food safety but also its nutritional and sensorial quality became important.

1950–2000 – Toward Diversity of Foods

Even though food safety remained and remains a *sine qua non* for food engineering, new developments set additional challenges. In the 1950s and 1960s, the population in many countries became more affluent. At the same time, the mechanization and use of auxiliary chemicals (pesticides and

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fertilizers) made agriculture much more productive, which precipitated a change from a shortage into an abundance of foods. Thus, food products had to be optimized for consumers who now could choose what to buy.

Therefore, the last three decades of the twentieth century gave rise to the development of an ever-greater diversity of food products. The popularity of refrigerators and freezers enabled the development of chilled and frozen supply chains. Also instant products that either needed reconstitution with water or would only need heating up became popular. Cartoons from that time sometimes depicted the future of foods as 'space food,' provided in tubes and pills. This reflected the developments in food engineering, which enabled the production of instant products and pure ingredients.

In reality, the diversity of foods exploded. Although instant foods (soups, potato mash, and whole meals) became available, consumers also got access to fresh (chilled), frozen, stabilized foods, including products that originate from almost any place in the world. One is now comfortable and familiar with Chinese, Thai, Japanese, Mexican, Italian, African, and many more foods and also has access to the ingredients necessary to prepare them.

2000 and Beyond – Food Engineering for Health

Although our affluence increased, our lives changed. People started to consume other and more energy-rich foods. The average family could afford a car, and thus individuals exercised less. At around the turn of the millennium, concerns of public health emerged due to the rising incidence of overweight and obesity in many regions in the world, which is accompanied with a striking increase in diabetes type II, cardiovascular diseases, and some types of cancer. In the twenty-first century, being overweight is just as large a health problem in the world as malnutrition is in areas still plagued by poverty and famine.

The increased concern for nutrition-related health led to a new development, which was toward the inclusion of specific ingredients that were claimed to have a specific, beneficial effect on the consumer's health: the functional foods. These foods do not aim solely at general nutrition, but aim to establish a specific effect on one's health or well-being. Functional foods include foods that are fortified with vitamins or calcium, or with probiotic ingredients (living microorganisms that are claimed to positively complement the natural ecology in the gut), prebiotics ingredients (indigestible fiber that is claimed to positively affect the ecological balance in the human gut), unsaturated fats and oils (e.g., those containing ω-3 and ω-6 fatty acids), ingredients helping in reducing weight (e.g., fiber, but also encapsulated emulsions) or reducing cholesterols levels (phytosterols, e.g., in margarine).

Food engineering was important in several ways. First, the ingredients that deliver the health benefits need to be produced. In many cases, this requires separation and isolation methods to purify the components from their raw materials. Examples are the isolation of lactoferrin, lactoperoxidase, and several fatty acids from milk, the isolation of fiber from milk and other streams and the isolation of, for example, fish oil. In addition, fermentation provided new strains of probiotic microorganisms (mostly lactic acid bacteria and bifidobacteria), whereas enzymatic conversion of lactose yielded prebiotic oligosaccharides.

Second, the ingredients need to be integrated into foods that have good taste and quality. This requires techniques for stabilization of the ingredients (e.g., by freeze drying), encapsulation (e.g., for fish oil), and structuring (e.g., incorporation of phytosterols in margarine). A third, recent contribution of food engineering has been to the understanding of the breakdown of food matrices and the release and bioavailability of ingredients using food engineering concepts in the modeling and simulation of the processes taking place in the gastrointestinal tract.

2000 and Beyond – Food Engineering for Taste

Although the increased affluence has given one more concern about health, it also had the positive effect that consumers worldwide have more time and resources to spend on high-quality food. Dining in a restaurant is now common everywhere, whereas media pays much attention to sophisticated food, through television shows, often with famous chefs, who have become celebrities. The increase in popular interest for the systematic understanding of the changes in foods during preparation, led to the emergence of molecular gastronomy and gastronomic engineering (e.g., This, 2002; Aguilera, 2011). These are new branches of food engineering that explicitly aim at the creation of new sensorial experiences in a restaurant setting (i.e., not foods that are stored over time, but products that are created and immediately served to the consumer). Here, good understanding of the underlying molecular and mesoscopic processes taking place in the food, while being prepared, gives an enormous scope to create innovative textures with various ingredients.

Food engineering has been involved through the development of new processes for the isolation and purification of components meant for these products. Examples of these new processes are the isolation of gelling agents for the spherification of juices (Gibbs, 2011), or the availability of protein isolates from various sources that can be used to form new textures.

Second, food engineering has provided better understanding of the processes taking place within a food matrix during preparation: for example, the better understanding of the denaturation of proteins has led to the employment of cryogenic denaturation instead of heat denaturation to 'fry' an egg. The realization that crispiness is related to the glassy state, created the possibility to have crispy slices made from vegetables, or even liquids.

The field of gastronomic engineering is under full development. Aimed not at very large-scale production but at the creation of individual products, it widens the field of food engineering, and brings it closer to the homes of individual consumers.

2000 and Beyond – Food Engineering for Sustainability

Although the increased affluence created much more comfort and room for enjoyment for people in most of the regions in

the world, this also created an enormous expansion in the use of resources. The use of fossil resources exploded due to the ubiquitous use of cars and transportation, the use of energy-intensive materials (e.g., concrete, steel, and plastics), and the use of fertilizer. The production of food exploded as well; whereas the global population increased by a factor of 6 in the twentieth century, the production of food increased by a factor of 7. At the same time, consumers buy more luxury foods, such as meat. Nowadays, 33% of all cropland is used for feeding cattle, 70% of the land that was previously forested in the Amazon is now used as grazing pasture, and the cattle is responsible for an estimated 18% of all greenhouse gas emissions – more than all traffic in the world.

It is, therefore, not surprising that a third trend (next to health and gastronomy) has been toward more sustainable production. Given the burden that the production of meat is on our resources, there is a trend among young consumers (especially in Europe) to want to reduce the consumption of meat. Although a few become vegetarians, many become 'flexitarians,' willing to forego meat for a few days in the week, but not always. There is thus a growing market for meat analogs and plant-based protein products. Food engineering contributes significantly to the improvement of the palatability of these products.

Food manufacturers and food engineers have in recent years strived for more efficient processes. Process integration (reusing heat and water on several spots in a production process), process intensification (more than one process step simultaneously carried out in the same or smaller equipment), and development of processes that intrinsically use less water and energy for drying are examples.

In addition, many processors or raw materials (cereals, beets, and potatoes) now aim not only to produce their main ingredient(s) but also to use all side streams for high-quality products; this development is known as food biorefining or side stream valorization, and includes, for example, the complete refining of whey into individual proteins, isolates, and other components, but also the use of leftover material for production of bioenergy, the isolation of proteins from leaves, sugar beet, or potato.

Current Fields of Food Engineering

The processing of raw materials into an ingredient or a food that can be preserved and is palatable, generally requires many steps. A sequence of these steps is a process. Typical, large-scale processing plants, as can be found for the production of beer, dairy products, sugar and sucrose or fructose syrups, flour, beverages, canned products, and instant meals, consist of a rather long chain of many steps.

The raw material when received from the fields is usually first cleaned, and soil and stones removed. This is often done by a combination of mechanical action and rinsing with water. The raw material matrix is then opened. This is often done by some degree of disintegration: milling (wheat), flattening (soy), cutting (sugar beet or cane), or mashing (potato). Cells may open up by heating.

In the production of ingredients, the primary extraction of components takes place by extraction (with water, as with sugar beet and cane) or mechanical expression (with oil containing seeds, such as soy, olives, sunflower seeds, and peanuts) often followed by a secondary extraction with solvents (hexane for oils). The extract then needs to be purified, as many other components will have joined the component(s) that were desired. This is often done through centrifugation, sedimentation, filtration, and sometimes through precipitation. Finally, the product needs to be stabilized, which can be done by packaging and heating or by dehydration (e.g., crystallization of sugar or spray drying of a protein isolate). The raffinate (the remains of the matrix after extraction) may be further processed to isolate other components, for it is used as lower value stream, for example, cattle feed, or is discarded.

Nowadays, many end products (pasta sauces, peanut butter, margarines, ice cream, etc.) are composed from individual ingredients; they may, therefore, be called fabricated foods. The product, is created through simple mixing (for liquid products) and heating, baking (for cookies, crackers, and other bakery products), or structured using extrusion (soy-based meat analogs, starch-based expanded snacks, and ice cream) or molding (confectionery and liquorice). When the end product has a high water activity, it needs to be heated for stabilization.

Both in the production of ingredients and in the assembly of end products from ingredients, processes are sequences of a number of steps, which can be categorized into:

- Thermal stabilization (preservation) processes
- Nonthermal stabilization processes
- Cooling and freezing
- Dehydration processes
- Separation and isolation processes
- Chemical and biochemical conversions
- Mixing and structuring processes

Thermal Stabilization Processes

Heating a product inactivates microorganisms and enzymes, which both will change and degrade the food over time, when still active. At the same time, heating also changes the texture of products: vegetable products tend to soften, due to the partial hydrolysis of the pectin in the cell walls, whereas meats will become stiffer due to the denaturation of their protein-based matrix.

Different forms of stabilization by heating can be defined. Blanching is short heating of a product with the aim of inactivating enzymes and microorganisms, but not their spores, which would require longer and more intense heating.

Blanching is a short heating process often for just a few minutes. It is not sufficient for preservation in isolation, but is generally applied before freezing or nonthermal preservation of a product. Even though most processes slow down tremendously in frozen products, chemical conversions, such as enzymatically catalyzed reactions do proceed, albeit at a very slow pace. A frozen product that has not been blanched will slowly degrade under the influence of oxidation (e.g., by lipoxygenases or polyphenol oxidases) and hydrolysis (e.g., by lipases). Blanching also induces some changes in texture that may be beneficial. For example, French fries are blanched before they are (pre-)fried, which rinses some of the reducing sugars from their surfaces, which would cause excessive

browning due to Maillard reactions during frying. Before mushrooms can be canned and sterilized, they first need to be blanched. This shrinks the mushrooms and removes part of the water from the mushrooms, which would otherwise give excessive shrinkage during canning and sterilization. Blanching is generally done by immersion in hot water or by blanketing with steam.

Thermal pasteurization is done by more intensive but still relatively short heating, which inactivates not only the enzymes, but also most of the microorganisms in vegetative state. This is not sufficient to inactivate bacterial spores, and will give a lengthening of the shelf life, but not an indefinite shelf life. Pasteurized products generally have to be stored refrigerated. Many fluids that are heat sensitive, are pasteurized, such as milk, fruit juices, and beer. One form of pasteurization is called high-temperature, short-time processing: this implies heating the product for a short time to a high temperature. The short time ensures that the product quality is not overly affected, whereas the high temperature ensures sufficient inactivation of pathogenic microorganisms.

Sterilization is done by much longer and more intense heating. If the heating is sufficiently long and intense, not only the bacteria in their vegetative state will be inactivated but also bacterial spores. Products that are sterilized can be preserved almost indefinitely. Sterilization in a can or glass jar done for long times is often called appertization. Sterilization usually affects the quality of the product significantly. Proteins are denatured, and may even start to decompose, leading to the formation of sulfur containing off-flavors. Nonenzymatic (Maillard) browning between proteins and sugars, and also caramelization, will lead to a darkening of the color, and may lead to a bitter, 'cooked' flavor. Of course, these effects are not in every product equally detrimental to the taste, so some products can be sterilized more easily than others.

Sterilization is typically done with liquids (milk), but with solid products, such as vegetables, mushrooms, meat products such as sausages, and soups and sauces). Typical packaging used for the solid products are metal cans, glass jars, and more modern, plastic pouches, which allow faster heating and cooling.

Methods of heating

There are various ways of heating products. A fluid is usually heated either indirectly in a heat exchanger, and then cooled in the same way, or directly by injection of steam, followed by rapid expansion and flashing off of the steam. The direct heating and cooling is much faster, and can, therefore, lead to a much better product quality; however, it does require mixing of the product with (condensing) steam, and flashing of steam, which may entrain flavors from the product.

Ohmic heating does not rely on convective or conductive heating through the walls, but relies on the imposition of an electric (AC) current, which heats the product through the energy dissipation due to its electric impedance. As the heat is generated in the product itself, heating can be much faster. It does require the heating to be done with electricity, which is more expensive than using steam.

Other ways of heating products are, for example, using radio-frequency heating (which relies on the application of an alternating electrostatic field with frequencies in the GHz range) and microwave heating, which uses a magnetron type antennae to generate an intensive radio-frequency field. Both types heat the product from the inside and can thus be very fast. Both methods, however, use electricity to heat the product and require expensive equipment.

Nonthermal Stabilization Processes

It is also possible to pasteurize or sterilize a product without heating the product. The potential advantage is that the product will not experience thermal damage and will remain fresher in taste. One of the earliest examples of this is the use of filtration and centrifugation. In the processing of juices and liquid dairy products, the product is filtered using (often ceramic) microfiltration membranes, with pore size of approximately 1 μm. Bacteria are retained by the membrane, whereas the liquid product passes the membrane. The retentate can then be thermally pasteurized and added to the permeate or be used for a different purpose. In the case of a product containing proteins and reducing sugars (such as milk), the separation of the sugars (which pass the membrane) and the proteins (which, due to their aggregation in micelles, end up in the retentate) leads to much less browning and bitterness, and a much better taste. An alternative is the use of centrifuges instead of the membrane (**Figure 1**).

The use of high hydrostatic pressures has gained much attention in the past decades, as it was found that application of several thousands of bars (hundreds of MPa) inactivates bacteria in their vegetative state, but affects the texture and quality of the product much less (San Martin *et al.*, 2002). Although it can be applied to both liquids and solids, the process is most promising for solid products: pressure equalizes with the speed of sound, whereas conductive transport of heat takes many orders of magnitude more time. A few products have already been launched (guacamole, some marmelades, hams, and some fish products). Products are typically packed into

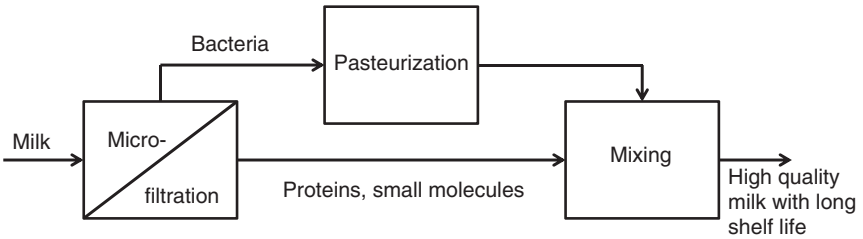


Figure 1 Using a combination of size exclusion and thermal preservation.

flexible plastic pouches, which are put in a pressure chamber, which is then filled with water, and put under pressure. Even though the process is effective for the inactivation of vegetative cells, inactivation of bacterial spores is not possible as of now. Only pasteurization is, therefore, possible at this moment.

Another development is the application of a pulsed electric field over the product (Castro *et al.*, 1993), which has to be electrically conducting for this technique. Typical fields can be up to 5–25 kV m^{-1}; short pulses are needed to minimize the power consumption (and to minimize the generation of heat in the product). The electric field causes polarization of ions against the cell membrane of bacteria, and if sufficiently intense, may induce the cell membrane to form pores, which lead to leakage of the cell cytoplasm, and ultimately cell death. Because bacterial spores are protected by a thick, nonconductive cell wall, they are not susceptible for this type of inactivation, and therefore products can only be pasteurized. A relatively new application of this technique is not for pasteurization, but for mildly opening plant cells, for example, for the isolation of components (sugar from beet or cane, oils, and antioxidants). Owing to the larger size of plant cells, they are opened more easily and thus lower electric fields are required.

Other nonthermal methods that have received attention are, for example, the use of intense pulses of light (especially UV light inactivates microorganisms effectively, Gomez-Lopez, 2007), which mostly works on the surface of products. It is, of course, important that the light pulses do not discolor the product, so this is not applicable on any product. Some people have claimed microbial inactivation with the application of intense magnetic fields. Although the mechanism that would be responsible for this is not completely clear, research in this field continues.

Finally, some endeavors were made in product stabilization using bacteriophages: viruses that attack spoilage or pathogenic bacteria. This type of biological pasteurization is interesting because exceedingly small amounts of phases are needed, and they multiply themselves; and resistance against the phages is unlikely, because the phages evolve with the evolving bacteria. However, most food producers are uneasy with adding viruses to their products, even though they are inactivated (usually thermally) in the final product. It remains to be seen whether this technology will, therefore, be allowed and applied on larger scales.

Cooling and Freezing

Cooling a product to 0–4 °C will slow enzymatic and nonenzymatic processes, and growth of bacteria. It has, therefore, become the standard for preserving perishable products at home, and many supply chains are now refrigerated: for example, meat, vegetables, many juices, and dairy products. An emerging problem with the ubiquitous use of chilling (refrigeration) is that psychrophilic bacteria, which can grow well at low temperatures, are becoming more prevalent.

Although most quality changes in a product are slowed down at lower temperatures, they do not stop completely; therefore, only storage times of days to weeks can be achieved. For longer preservation, the product may be frozen. By cooling to approximately −20 °C, most of the water in the product is captured in ice crystals. As the ice crystals only contain water, the surrounding matrix increases in concentration, and will obtain a lower water activity, which contributes to the longer shelf life. Even in the frozen state many enzymatic processes do not stop completely, and therefore the product's enzymes need to be inactivated by blanching. In this way, a product can be stored over longer time.

Freezing does compromise the quality of the product. The formation of the crystals means that there is displacement of other material from around the crystal. Thus, the matrix of the product is damaged. It is well known that freezing vegetables that are high in moisture leads to loss of the turgor (stiffness) of the tissue: the once firm and stiff vegetable now becomes limp and after defrosting will leak much juice. Meat will also show loss of juice after defrosting: also here the cells are damaged, leading to leakage of the cell cytoplasm, even though the firmness of meats is not affected to the same degree.

The extent and type of damage depends on the rate of freezing. Slow freezing will result in large crystals and thus extensive damage to the product's structure. Fast freezing of vegetables will lead to substantially less damage because most crystals will remain small enough to fit inside the cells, and therefore the cell walls are not compromised. Therefore, many new developments deploy methods to allow faster freezing. Although freezing is usually done in a blast freezer (blowing frigid air around the product) or, for packaged products, in a bath containing brine or another nonfreezing liquid, one can also immerse the product in liquid nitrogen or bring it in contact with solid CO_2.

Dehydration

Any spoilage process needs moisture. Bacteria do not grow at a water activity lower than approximately 0.85; and molds do not grow below a water activity of 0.8. Although in many traditional products a low water activity is attained by adding salt (a saturated NaCl solution, containing ~36 wt% salt, has a water activity of ~0.76) or sugar (a 60 wt% solution of sugar has a water activity of ~0.9), the most straightforward way to achieve a low water activity is to remove part of all of the water in the product.

Owing to the small molecular weight of the water molecule, one has to remove most of the water to obtain a significant reduction of the water activity. Traditional drying is usually done by exposure to air, preferably with the assistance of solar heating; examples are the drying of tomatoes, fruits, fish (e.g., the Norwegian lye fish), meat strips, and spices beans. Unfortunately this process is not well controlled, depends on the weather conditions, and is not easily scalable to larger product capacities.

Therefore, solid products are industrially dried using tray driers, in which products are exposed to hot or dry air for a considerable time. This is done in the preparation of, for example, not only raisins, dates, prunes (dried plums), figs, apricots, peaches, apples and pears, cranberries, blueberries, cherries, strawberries, but also with pasta and pastries. Typical drying times may range from minutes to several hours, for larger products that contain much water.

Liquid products are usually first concentrated in an evaporator. Here, the product is heated indirectly possibly at under pressure using steam. About the same amount of moisture will evaporate from the product as the amount of steam that condenses in the heat exchanger. Evaporators can be easily cascaded, in which the vapors from one stage, are condensed in the next stage and thus to evaporate another amount of moisture from the product. Five- or six-stage evaporators are usual in large operations (e.g., in processing juice from sugarcane or beet or in dairy processing). The resulting concentrated slurry may already have lost most of its moisture and have up to 80 wt% solids; however, this is not yet sufficient, and the slurry is then dried. As evaporators cost a lot of energy to evaporate the water, in newer plants part of the concentration is done with reverse osmosis: Here, the water molecules are forced, under high pressure of 60–100 bar, to permeate through a thin membrane, whereas all other molecules, being larger and not soluble in the membrane, are retained by the membrane. This process is limited by the difference in osmotic pressure between the feed (a concentrated solution) and the permeate (essentially water), and therefore the last part of the concentration process is often still done through evaporation.

A spray drier is used for fluid products that are heat sensitive. Here, the slurry is atomized using great pressure into tiny droplets, which are injected into a large space that is filled with hot air. The air heats the droplets, which remain relatively cool to the (fast) evaporation of the moisture; the product, therefore, remains substantially cooler than the surrounding air. The typical residence times of the droplets can be very small: down to a few seconds. After this, the droplets will have lost most of their moisture, and have become solid. They often need to undergo a final drying step to remove the last remnants of the moisture, and cool it down, to ensure that the powder will not be sticky (i.e., be in the glassy state). A fluidized bed drier is often used for these last steps; a bed of particles, which are kept in motion by an upward air flow, ensuring a very intensive air–solid contact and intensive mixing of the powder. This fluidized bed also leads to agglomeration of the primary particles from the spray drying chamber, which are 'glued' together into much larger agglomerates. This is important as the small primary particles (which can be as small as a few micrometers) are detrimental to the health of the workers handling and using the powders.

For products that are not that heat sensitive, a more efficient process is drum (or belt) drying. Here, the slurry is applied in the form of a thin film onto the metal surface of a drum, that is heated with steam on the inside. A typical temperature of the drum is 120–140 °C. The drum rotates slowly, and because the product film will start to boil its moisture away, the film will become dry after some time, and can be scraped off the drum when it has rotated by some degree. Although this process requires less energy, it exposes the product to more intensive heating, which may reduce the quality of some products. The product coming off a drum dryer may have a flay morphology, and may be grinded to smaller particle sizes when required.

For products that are extremely heat sensitive – for example, products that rely on flavors, such as coffee, tea, or that contain proteins that should not be denatured – one can apply freeze drying. Here, the slurry is first frozen and then milled into small grains while being frozen. The product is then spread out over trays, which are inserted in a vessel, which is evacuated. The low pressure causes the ice to be sublimated. Owing to the sublimation process that requires a lot of heat, the trays are usually heated. The end product is highly porous (ice crystals were present which leave open pores), and has not been exposed to any high temperature. The quality of the product can, therefore, be very high, albeit at a much large use of energy.

Separation and Isolation Processes

The food industry can be roughly divided into (1) processors that stabilize and finish products that come off the land and can be eaten in that form (vegetables, meats, and fruits), (2) processors that produce ingredients from raw materials, and (3) processors that assemble ingredients (and raw materials) in end products. The second category is a very important one and comprises the sugar industry, much of the potato, soy, corn, and wheat industry, and a large part of the dairy industry. Many of the foods that one consumes are prepared from ingredients, and almost all products contain separately isolated ingredients. Separation and isolation of components from the raw produce is, therefore, an extensive part of the food industry. A few classes of separation processes will be discussed without any claim on completeness.

Phase separation and mechanical isolation

An ingredient may be released by mechanical means. Pressing soy beans (that are flattened and heated to denature the cell membranes) or olives, will result in the oil being pressed out. Although this oil is not pure, and still contains particles from the original matrix, and will contain water droplets and aqueous components inside those, the oil can be of high quality because its thermal history is limited. In olive oil, this is called the virginal pressing.

Milk fat is conventionally removed by centrifugation: the fat, being lighter, creams up, and can be removed easily. In renneted milk, the whey can be removed from the precipitate by pressing. In the processing of potatoes, the potatoes are first mashed, which leaves a suspension of starch granules in an aqueous phase that contains most of the other components. The starch may be removed by hydrocyclones, in which centrifugal force is used to mechanically separate the starch from the aqueous solution.

In case the phase to be removed consists of small particles ($<10\,\mu m$), which do not have a large difference in density with the surrounding medium, filters can be applied. Beer and wine are usually clarified by filtration after fermentation, to remove the last yeast cells from the liquid and obtain a clear product. First, the product is mixed with a filter aid, typically highly porous particles made of silica or similar. The suspension is then filtered; the particles are retained, and incorporate in their pores the fine particles (cells or debris from disintegrated cells) that were present in the product. The filter aid plus retained material is waste. Microfiltration is a newer process. Here, a membrane (thin filter) is applied that typically has pores in the range of 0.1–10 μm, allowing the removal of particulates without the use of filter aid. A crossflow over the

membrane is used to keep the retained material from accumulating on the membrane.

Macromolecular separation: Ultrafiltration, solubilization and precipitation, and extraction

The clear liquids that are obtained from the phase separation operations described above can be further refined. One way, used extensively in the dairy industry, is ultrafiltration. This is the use of a membrane with very small pores, typical 1–10 nm. Small molecules can pass relatively unhindered through these pores, and are pushed through by a typical pressure difference over the membrane of 2–15 bar, whereas macromolecules such as proteins and large carbohydrates are retained. The accumulation of these components on top of the membrane is kept in check with a strong crossflow. Although this process does allow for separation of proteins that are in solution, it does not allow the separation of macromolecules that are still in the solid phase, and it hardly allows the separation of macromolecules from each other.

In many cases, solubilization and precipitation is used. In the production of caseins from milk, the liquid is acidified, which induces precipitation of the casein, but not of the whey proteins. The precipitate is then isolated, washed, and neutralized, giving relatively pure casein. In the case of a protein concentrate from, for example, soy, the soy that has been heated and flaked to open up the cell structure and defatted by pressing and extraction with hexane, is contacted with a mixture of ethanol and water (or in some cases a low pH aqueous solution), which solubilizes much of the carbohydrates in the soy flakes (and some of the proteins). The remaining flake is much richer in proteins, and can be isolated and dried to form a soy protein concentrate. Although this product is still rich in (insoluble carbohydrate) fiber and only consists approximately 70% of protein, a soy protein isolate is much purer (90% protein). It is made by first solubilizing the proteins themselves from the soy flakes in water, isolating the solution, and then lowering the pH such that the proteins precipitate. They can then be isolated, and dried to form a much purer protein fraction. Other protein isolates (from pea, lupine, or other crops) are made in the same way.

The extraction process is quite similar: a solvent is used to remove one (group of) component selectively from a solid matrix. Soy oil is isolated in this way: after flaking and heating to open up the cell matrix, and after mechanically pressing most of the soy oil from the flakes, they are contacted with hexane, which dissolves the oil. The flakes are separated, heated to evaporate the hexane that is left behind in the flakes, and the hexane is evaporated (distilled), to yield the oil as bottom product. Although extraction processes are common household processes (preparation of tea and coffee), they are also quite common in the decaffeination of coffee beans (usually with dichloromethane or supercritical carbon dioxide as solvent), and in the isolation of specific, highly valuable components, such as essential oils and flavors and fragrances.

Isolation of small components: Nanofiltration, ion exchange, and chromatography

In many cases, streams contain small components that may be valuable or may have to be removed before the stream can be discarded: small carbohydrates, peptides, and minerals. Small carbohydrates, such as lactose, may be removed by nanofiltration: filters having pores that allow the passage of molecules of 100–1000 g mol^{-1} molecular weight, but not the passage of any larger molecules. Thus, by choosing the appropriate membrane, one can retain lactose, whereas having water and minerals permeate the membrane. By choosing a membrane with particularly small pore size, one may even separate divalent from monovalent ions (divalent ions have a larger hydration mantle and are thus larger in an aqueous environment).

Ionic components may be removed with ion exchange resins. These are swollen polymeric materials that contain many charged groups, which are paired with counter-ions in solution. Beads of these resins are packed into columns. The fluid flows through the bed and comes into contact with these beads. Ionic components pair up with the immobilized ionic groups in the resin, effectively immobilizing these components from the feed. By later displacing them with another salt, they can be isolated. This way not only divalent cations (e.g., calcium and magnesium) are often removed, but also how individual proteins can be separated based on their ionization.

For very specific, high-value components, size exclusion chromatography may be used. This method, which was originally developed in the pharmaceutical field, is not only used for purification of high-value proteins but also for the isolation of fructose in the preparation of high-fructose syrup. Here, a column of stacked, swollen beads, which have very small pores is used. These pores are accessible for smaller molecules, but much less for larger molecules; their molecules are too large to easily fit inside the pores. Many of the small molecules diffuse into the pores, and are retained for some time in the beads, whereas larger molecules are excluded and simply flow with the fluid. Thus, a separation in time is achieved. A new development is the use of affinity chromatography, in which ligands are immobilized onto carrying beads (themselves stacked into a column), which may complexate with specific components, removing them from the fluid. Affinity chromatography also originates in the pharmaceutical industry, but now finds a few applications in the food industry, especially in the isolation of specific proteins.

Crystallization

Some products, such as sucrose, lactose, salt, and fats and oils are separated by crystallization. A crystal is usually made up of only one molecule (possibly with some water in the lattice), and having a component crystallize and then removing the crystals is an effective way of separating such a component. Crystallization can be done by cooling a saturated solution (which then becomes supercooled) or by evaporating moisture from a saturated solution (which created a supersaturated solution). In both cases, crystals will be formed. As inclusions may be formed, crystallization often has to be followed by resolubilization and recrystallization to form even purer materials.

Chemical Changes to Produce Ingredients and Products

Although many ingredients can be directly isolated from agricultural raw materials, in a few cases much more highly

valuable materials can be obtained by chemical or biochemical modification.

One example is the hydrolysis of (wheat or corn) starch into glucose syrup, which is an ingredient for the beverage industry. The starch is isolated (see Section Phase separation and mechanical isolation), and heated to above 60 °C, which gelatinizes (solubilizes) the starch from the starch granules. The enzyme α-amylase is added, which hydrolyzes the glycosidic bonds between the glucose units in starch, and reduces the starch into small oligosaccharides (maltodextrins). The subsequent addition of gluco-amylase, capable of hydrolyzing the last glycosidic bonds, leads to the conversion of the starch into glucose.

High-fructose syrup is produced by converting the glucose, using the enzyme glucose (or xylose) isomerase, partly into fructose, which is sweeter. One may then use size exclusion chromatography to purify the fructose, and recycle most of the glucose back to the conversion.

Sports drinks are often prepared by partially hydrolyzing proteins with the help of hydrolytic enzymes (proteases); the hydrolysate is already partly digested and can be taken up much more quickly by the body to help a sportsperson restore his or her performance. Almost fully hydrolyzed proteins are used for hypoallergenic infant formula for children with bovine protein allergies: The hydrolysates do not have the protein structure anymore, and therefore do not trigger the immune response.

A more modern example is the production of galacto-oligosaccharides, which are not only a prebiotic, required in infant formula, but are also associated with boosting the immune system and mitigating the development of allergies; they are thus also added to a variety of prebiotic drinks and products for both children and adults. They can be produced from lactose with the help of galactosidases, enzymes that may hydrolyze or synthesize lactose into oligosaccharides, depending on the reaction conditions. Fructo-oligosaccharides, having similar properties, can be prepared enzymatically from saccharose, or by enzymatic hydrolysis from inulin (Figure 2).

Structuring Processes

The properties of an end product not only depend on the molecular composition, but also to an even greater degree on the way that these ingredients are positioned in the product. The structure is a major determinant of the properties of the product.

There is a range of processes that is developed for structuring products: baking processes, extrusion processes for making snacks, pasta, par-boiled products, and even ice cream, whereas some intermediate products (powders, granulates, and tablets) are structured to improve their ease of handling and ease of incorporation into an end product.

Structuring end products

In baking, a dough or batter is first prepared by combining ingredients (flour, fat or butter, possibly a protein source such as eggs, sometimes sugar, and flavorings) into a material that allows mixing and the development of some kind of deformable structure. In wheat dough, this is initially the network formed by the gluten. This dough is then stored to allow leaving by fermentation or a chemical reaction (in case of the use of baking powder), and the structure is fixated by heating in an oven. In many cases, the original structuring role of gluten or fat is transferred to another ingredient: in baking

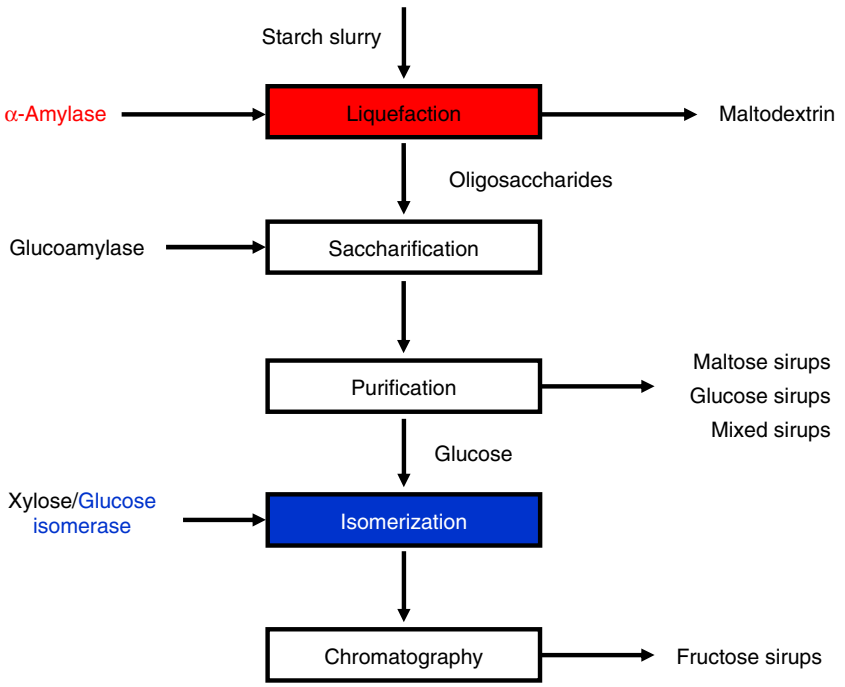


Figure 2 The process for making high-fructose syrups involves the enzymatic hydrolysis of starch into oligosaccharides and glucose, the enzymatic isomerization of glucose into fructose, and chromatographic enrichment of the fructose syrup.

bread the starch that retrogrades to form a gel; in the case of many cookies, the sugar.

Extrusion is basically the mixing, dissolution, and deformation of a mixture under high stress, heating, and the subsequent squeezing of the slurry through a small die. The conditions inside an extruder can be well controlled. This is important, for example, in the production of pasta, where the starch needs to gelatinize but not melt (i.e., starch granules need to swell but not disintegrate) and the gluten needs to form a good network. Inside an extruder, the pressure can be set to as high as 30–40 bar, allowing the temperature to rise far above 100 °C, without having any evaporation. This high temperature melts or dissolves most components, and as soon as the product is squeezed through the die, the excess moisture will flash off. This leads to a sudden expansion of the product, which is solidified almost instantly by the loss of moisture and reduction in temperature. Thus, a porous, crispy product results. This is the basis of the production of many snacks.

A relatively simple structuring process for multiphase liquid products (emulsions or foams) is a homogenizer: an emulsion is squeezed through a small hole. Especially at the compressional (downstream) side, larger droplets break up into smaller ones, allowing the product to become more stable against creaming or other forms of instability. Colloid mills and ball mills impose a very strong deformation field, to much the same effect. A relatively new structuring process for emulsions is membrane emulsification. Here, a to-be-dispersed phase is pressed through the small pores of a microporous membrane, that is strongly wetted by the continuous phase that flow over the downstream side of the membrane. The dispersed phase emerges at the mouths of the pore on the surface of the membrane, in the form of small droplets, which are ultimately detached and taken up by the continuous phase flowing over the membrane. By using microengineering methods, it is possible to have spontaneous detachment of the droplets, which can lead to monodisperse emulsions (Van Dijke, 2010). This very new development is not yet used on larger scale but holds much promise for future emulsion products.

Structuring ingredients

Spray drying processes are often also structuring processes: the small primary droplets partially coalesce and form agglomerates that may have significant porosity. Subsequent further processing in a fluidized bed may reduce or increase this porosity to improve the processability of the powder, whereas the addition of other components to the fluidized bed may lead to an outer layer of another component. Spray- or freeze-dried products are often coated with some lecithin, to reduce their hydrophilicity, which improves their dispersability in water and ultimately improves their reconstitution properties. Crystallization is by definition a structuring process because the crystal lattice type shapes and sizes of the crystals largely determine their properties in terms of processability and dissolution properties.

Crystallization for structuring is important not only for the classical crystalline products (sucrose, lactose, and salt), but also in most solid, fat-based products, such as butter, margarine, chocolate, and ice cream. The 'soft solid' character of these products is created by cooling the mixture, whereas deforming, to the right degree of supercooling, which induces the formation of small crystals. When the product is put to rest, the crystals form a network that gives the product its consistency. Hence, these products are usually made in a scraped surface heat exchanger or similar, or sometimes even in an extruder, and then put to rest to have the crystals age and the network form.

Education in Food Engineering

Food engineering education has always relied onto two pillars: unit operation design and practical courses. The theory is usually on methods to design unit operations, based on relations that correlate the behavior of materials and products under different conditions, such as fluid behavior, vapor pressures, and water activities. Second, exposure to practice during practical courses (i.e., in pilot plants) gives the students a feeling of the scales and phenomena on larger scales. In many curricula, internships done within an industry augments this experience and prepares them for the situation in a real factory.

In recent years, the present-day technology is changing one's perspectives. The ubiquitous presence of information, via computers, tablets, and cell phones means that the task of education shifts from the supply of information toward guidance of how to use and sift data and information. At the same time, geographical distances become less important: email and Skype are available to anyone, and distance learning and massively open education are becoming commonplace, allowing students to share classes while being in different parts of the world.

In addition to this, the nature of the scientific discipline has changed with the availability of massive computational power. A large part of food engineering used to be on how to interpret complex phenomena and relate it to the large-scale behavior of a system: for example, predicting mass or heat transfer rates in systems exhibiting turbulent flow, or non-Newtonian properties. The development of computational fluid dynamics (CFD), particle- and agent-based modeling techniques and process system simulators (e.g., Aspen Plus, SuperPro Designer, and many others) have made it possible to accurately model the behavior on small scale and quantitatively predict the behavior on larger scales.

Massively Open Online Courseware

Traditionally, the courseware developed by universities and polytechnics used to be proprietary; only available to students who are enrolled in a program within that institute. The omnipresence of internet has made it difficult to retain the materials within the institute, however; therefore, a number of institutes have made much of their courseware freely available. At the same time, they offer 'massively open' courses and lectures through the internet. Attendants can then be assessed online, and ultimately obtain a certificate. Although this is not a replacement of the traditional academic and technical curricula, it does make some of the material available for anyone – the moment he or she finds the need for it. This is in line with the Connectivism theory (Siemens, 2005), which states,

following Vygotsky's zone of proximal development (Vygotsky, 1978), that knowledge is generated through laying connections.

This development has the potential to revolutionize and democratize teaching. Food engineering, with its heavy reliance on computation and design challenges, may be very suitable for this approach. The approach is opposite to the model of teacher–tutor system, which allows the student to have direct contact with the teacher during the execution of relevant tasks. This model is the basis of most academic education, especially during practicals, working classes, and thesis preparation phase. This model may be more prevalent in continental European universities, which lay more emphasis on the concept of 'Bildung'; personal development instead of acquisition of skills (e.g., Watson, 2010). The massively open online courseware approach complements this, and will find its own niche in a world that is saturated with information but not with insight.

Simulations in education

Many of the engineering sciences are involved in predicting behavior of products or processes on larger scales from properties on small scale. Examples are the prediction of heat or mass transfer rates based on viscosities, flow rates, densities, and similar; or the prediction of the stability of an emulsion based on droplet sizes and rheological behavior of the continuous phase. This is usually done through correlations, which correlate the behavior under different conditions and in different system. CFD is the technique to directly calculate the behavior of a system on small scale, over a fine grid or large collection of elements, and from this, numerically integrate toward the behavior on large scale. Modern CFD methods can even directly simulate part of the turbulence at high Reynolds numbers (large-eddy simulations) and from this predict the influence of turbulence. Development of methods as dissipative particle dynamics (e.g., Moeendarbary *et al.*, 2009) and lattice Boltzmann methods (e.g., Kulrattanarak *et al.*, 2008) has made it possible to even simulate the behavior of the full complex, multiphase systems, which foods generally are.

Education has to respond to this by introducing and using these methods in the curricula, and by adapting the core of the field, from correlations and general guidelines, toward how to use these computational tools, and extract the right (generalizable) insight from it. This will make it possible to have more emphasis on the complexity of foods, and from there be able to make the connection to the sensorial and digestive properties of the produced products – these were traditionally out of scope due to the complexity involved.

Thus, in the next decade one will experience major changes, not only in the methods of education but also in the number, spread, and background of the recipients, and in the type of the scientific subjects.

Future Challenges for Food Engineering

Although food engineering is a mature discipline, offering suitable operations for the production of a very wide range of products and ingredients, there are large societal challenges that need to be addressed by the field.

Although part of humanity is still suffering from undernutrition, they are now outnumbered by the number of people suffering from overnutrition. Obesity is the largest pandemic in history and its incidence is increasing rapidly everywhere in the world. Overweight and obesity are closely correlated with cardiovascular diseases, with the occurrence of diabetes type II, with different forms of cancer, and with a variety of symptoms called the metabolic syndrome. Understanding how the production of new foods by new processes may help to mitigate this problem is becoming more and more urgent.

The global population is rising, from approximately 7 billion in 2013, to approximately 9–10 billion in 2050. On top of that, the number of affluent people in many regions rises, which means that consumers are able to and want to buy more luxury foods, such as meat and processed foods, which require more agricultural and fossil resources to produce. It is estimated that in 2050, one will need approximately 70% more primary production to cope with both effects. At the same time, our fossil resources are becoming more difficult to find and exploit, which makes them less available and will lead to more environmental stress in their production. Many agricultural lands are overexploited to show serious signs of degradation by erosion or depletion, which leads to the suggestion that 70% increase in production cannot be achieved without a serious reconsideration of the postharvest chain. At this moment one loses approximately 30–50% of all produced foods somewhere in the chain. This shows that there is potential to improve our food production system and find an answer to the rising demands and stagnating sources.

A third challenge is the emergence of the so-called bio-based economy (Langeveld, 2012). As the development of fossil resources is a major force in our global economy, one has known that these fossil resources are finite. The unbounded rate at which these resources were made available has led to an explosion of the global population and has changed the face of the Earth. Now, one faces a transition back, from a fossil resources-based economy, toward a bio-based economy, in which one has to use bio-based materials and energy, also for nonfood purposes. But because our population has grown by at least an order of magnitude over this period, one needs to become much better in the use of these biological resources. Already one has seen tension over the 'food or fuel' issue; this may become more serious if one does not develop an economy in which one can produce both foods and materials and fuels from the same resources.

There are a number of scientific and technological developments that may help us in approaching these challenges with some vigor.

Food Digestion Engineering and Human Health

The nutritional sciences have identified many of the mechanisms that underpin the metabolism of nutrients. Food engineering has developed sophisticated processes to produce products with the right sensory properties. It is amazing that not much is known about the part between the product as it is eaten and one's metabolism.

The process of disintegration and dissolution of food products in mouth, stomach, and intestines, though very

complex, shares many characteristics with the processes food engineers have applied for the assembly of ingredients and products, and in recent years, they have started to apply their methods to the understanding of the digestion process. Experimental rigs as simplified simulators of the gastrointestinal tract may contain a semipermeable membrane (mimicking the small intestine wall; Tharakan *et al.*, 2010). Peristaltic flow is generated by a pump, whereas pneumatic squeezing cuffs generate local segmentation. This has been used to study the effect of viscosity and segmentation on the uptake of riboflavin, which could then be described relatively as simple food engineering principles. Others have used simple tanks-in-series models to describe the fate of microorganisms during passage through the intestinal tract in animals and humans.

Singh and coworkers have studied the behavior of food in the stomach and developed various *in vitro* stomach models, for example, a relatively simple model stomach system and a more complex human gastric simulator (Kong and Singh, 2008, 2010). Products undergo a number of changes during primary digestion in the stomach. Gastric juices penetrate into the product. Acid and protease dissolve some components, which induces porosity, facilitating the penetration of gastric juice. With increasing porosity, the outer layer becomes fragile, and the mechanical action of the stomach then erodes the outer layer away, exposing the less digested parts. This may give rise to a steady erosion of the product when the penetration is not too deep, or a mechanism in which the product first swells, due to the absorption of the gastric juice, and only later disintegrates (Kong and Singh, 2008, 2009). Generally, cooling of foods favors a transition from an erosion mechanism to a disintegration mechanism.

Other studies have modeled the flow and muscular action in the gastrointestinal tract, using CFD, which showed, for example, that ingested fluids may bypass the solids foods that are digested and are already present in the stomach (the so-called Magenstraße), and that the antrum contraction, creating a jet back into the gastric body, is important in the disintegration of solid foods.

Following *in vivo* digestion is much more complicated, and simplifications are required. In many cases, animals are used for this – invasive studies are possible, even though there are differences in the gastrointestinal tract characteristics. For example, Bornhorst *et al.* (2013) showed in pigs that although the starch digestion from brown and white rice is similar, that of proteins was much slower in brown rice. They showed that the pH in the stomach is nonhomogeneous and the amount of gastric juice depends on the type of rice, whereas at the same time bran was shown to accumulate in the stomach.

Several noninvasive methods have become available for study of the digestion process. In some cases, probes have been used to measure contractions or other conditions (Vassallo *et al.*, 1992), whereas magnetic resonance imaging studies could show the typical motions of the stomach while digestion takes place (Pal *et al.*, 2007).

One may expect that better insight in the mechanisms of digestion will lead to a better design of food products (and processes to prepare them), targeted to achieve the right effects in humans: better controlled satiety to mitigate overconsumption, reduction of the glycemic index without compromising the taste, less inactivation of pro- and prebiotics during passage through the upper gastrointestinal tract, and better support of the microbial ecology in the lower gastrointestinal tract. One might even expect that if one knows how one's body processes foods, one may adopt some of these principles into production processes in the food industry.

Food Production in a Bio-Based Economy

Since the nineteenth century, one has developed an economy that was based on using fossil resources, such as coal, oil, and gas, which, although finite, can be supplied with almost limitless amounts as long as they have not been depleted. The current volatility in prices of fossil resources shows that this depletion is not far off. A short-term solution is at hand using shale oil and gas, but these are only extracted at great environmental costs. In the long term, one has come to realize that one has to find renewable resources. Biomass and agricultural materials are in that category.

At the same time, one knows that one's limitless emission of components such as CO_2, CH_4, and many others, has led to global warming, which in its turn gives rise to instabilities in the local climates around the globe. One of the routes to mitigate these effects is to use resources that sequestrate some of these components during their creation. This is exactly what happens during the growth of agricultural products.

The biorefinery

Traditionally, food ingredient industries concentrated on the production of one ingredient: sugar from sugar beet or cane, starch from potato or wheat, or cheese from milk. There is an increasing awareness that the total production system can be adapted to the complete conversion of the raw material into valuable products. The Dutch potato processor Avebe, for example, a traditional producer of potato starch, now also produces a number of potato protein fractions and isolates with excellent technical and nutritional functionality, from the stream that used to be a waste stream from the production of starch. Many industries consider isolating valuable components from waste streams, or changing their production method such that the waste streams can become valuable products.

Parallel to food processing, a new industry has arisen, that processes raw agricultural products not in foods, but in nonfood products; mainly biofuels. The first generation of these factories converts the starch in corn, sugarcane, or other products into bioethanol. This is done through a rather traditional fermentation process: the corn is milled, mashed, and diluted with water, and fermented with yeasts, leading to a beer that has 3–5% ethanol. This beer is distilled into almost pure bioethanol. The rest is dried into spent grains and generally used as cattle feed. The large-scale implementation of this technology has led to a rise in corn prices, leading to social unrest in many countries. Further, the widespread cultivation of corn has replaced part of the soy production in the United States, which was taken over by other countries, such as Brazil, which had to clear parts of the Amazon rainforests.

The second-generation processes takes into account that nonfood production should not compete with food production. It uses indigestible fractions, usually cellulosic or lignocellulosic in nature. These are conventionally waste, or

are burned for heat or energy; however, in many cases dehydration of these streams requires too much energy to make this a viable option. By using enzymatic treatment, it is possible to digest and convert these materials into fermentable fluids. Although the current options are not yet up to par with the efficiency of the first-generation feedstock, they are improving rapidly, and will soon be applied on large scale.

A lot of research goes into the development of new crops for nonfood products that do not compete with food production. An example of this is the growth of (micro-)algae. These organisms are efficient and fast growers, and grow in fresh water or sea. Cultivation of a sea area the size of Portugal would suffice for the transport fuel consumption of Europe (Wijffels and Barbosa, 2010). They can accumulate large amounts of lipids, which may be used as biofuels, whereas the proteins may be used for the production of plastics, or, potentially, might be interesting for feed or food production as well. The main bottleneck is that the concentration of microalgae in the water is small (maximum a few per cent), which implies that harvesting is inefficient. Finding ways to harvest and process these algae efficiently is an area of major development. One may envisage that – when this type of biorefinery takes off in large scales – the availability of large amounts of raw protein may transform the fields of feed and food science.

Food Micro- and Nanoengineering

The beginning of the twenty-first century was accompanied with the rise of micro- and nanotechnology – the technology of systems that have a dimension between 0.1 and 100 μm (microtechnology) and between 1 and 100 nm (nanotechnology).

Microfluidics already have an impact in the field of sensor technology, which will allow the measurement of other and more parameters. The metal–oxide–semiconductor field-effect transistor-based pH sensor is now not only common, but is also applied as ion selective field effect transistor to analyze for specific ions. The so-called micrototal analysis systems form small labs-on-a-chip, allowing for complex analyses, up to complete chromatographic, and even NMR analyses. Taste receptors have been placed on chips, allowing for direct measurement of affinities between flavors and these receptors.

Microfluidics will also have an impact on the production of foods. Microsieves are membranes made photolithographically from silicon wafers, and can have an active layer as thin as 0.1 μm, have a porosity up to 80%, and have completely monodisperse pore size down to approximately 20 nm. Metallic microsieves, made through electrodeposition, are now available, which will have an impact on membrane separations.

Although membrane emulsification was developed in the 1990s (Nakashima *et al.*, 1992), it has obtained a new impulse through the development of the microchannel systems (Kawakatsu *et al.*, 1997), basically microfluidic devices with transverse channels of specific shape, that spontaneously form droplet when a to-be-dispersed phase is pressurized through them. Systems such as the edge-based droplet generation type, show that up-scaling to practically relevant yields is possible (Van Dijke *et al.*, 2010). Thus, microfluidics may not only lead to better products, such as completely monodisperse emulsions, but also to new products, such as stable multiplex emulsions, in which ingredients may be encapsulated, or which could be used in low-calorie products.

The trend toward the use of ingredients that have a specific effect on one's health (pro- and prebiotics, antioxidants, micronutrients) also motivates the quest for product forms that allow for 'smart release' of components, protecting these bioactive ingredients in some parts of the gastrointestinal tract (e.g., the stomach), but releasing them in others, activated by some form of trigger (e.g., in the duodenum or colon). Nanotechnology may well bring us these types of encapsulates.

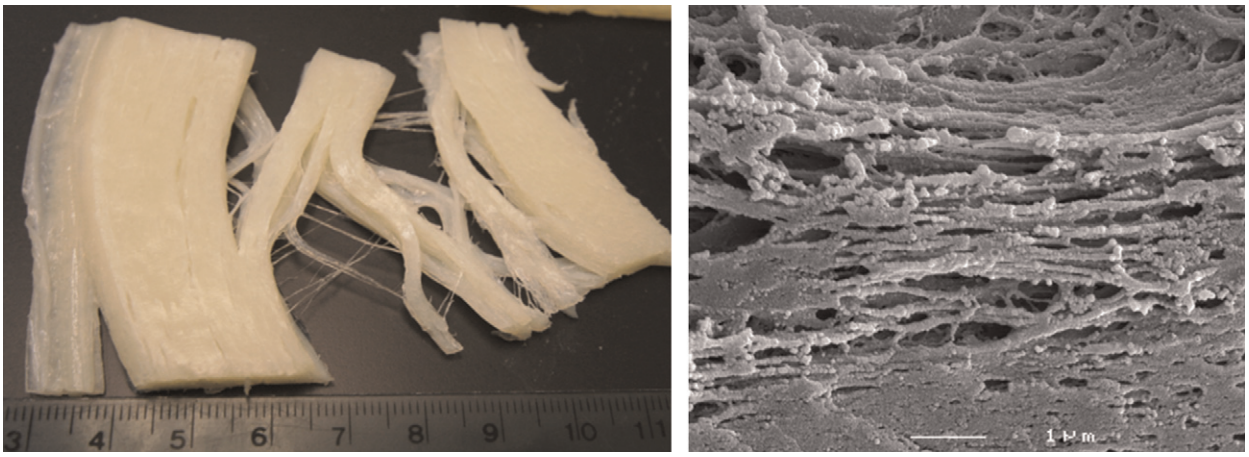


Figure 3 An example of directed self-assembly: Hierarchically fibrillar protein structures made by shearing a 30 wt% dispersion of calcium caseinate that is slowly solidified by crosslinking with transglutaminase. The structure was shown to consist of fibrils of ~100 nm diameter, packed into bundles of ~100 μm thick, which themselves are arranged into larger scale bundles evident in the left-hand side pictures. Reproduced from Manski, J.M., van der Goot, A.J., Boom, R.M., 2007b. Formation of fibrous materials from dense calcium caseinate dispersions. Biomacromolecules 8 (4), 1271–1279, with permission from American Chemical Society and Manski, J.M., van der Zalm, E.E.J., van der Goot, A. J., Boom, R.M., 2008. Influence of process parameters on formation of fibrous materials from dense calcium caseinate dispersions and fat. Food Hydrocolloids 22 (4), 587–600.

The farthest, yet perhaps most rewarding step would perhaps be the 'positional assembly' of food ingredients into a specific structured matrix. Several groups work on food printers, which, however, do not yet allow for the creation of structure below the level of 10 μm (Lipton *et al.*, 2010). However, just like any microtechnology, this printing technology obeys a scaling relation similar to Moore's law: every year, the details that can be made are smaller.

The use of directed self-assembly, in which the natural tendency of molecules to cluster together is steered with the help of a larger-scale field, may allow for the creation of structure even below 100 nm (Manski *et al.*, 2007a,b). That may ultimately lead to meat-like structures created with plant proteins, which would help in creating products that are more sustainable (e.g., plant-based protein products replacing meat products; **Figure 3**).

Conclusion

Although food engineering is a mature field, there are major societal challenges that will transform the field in the next decades: global concerns about health, sustainability, and the coproduction of food and nonfood products. The field can respond by absorbing the new possibilities that arise from new scientific and technological possibilities: new simulation instruments based on the unprecedented computational power available, new possibilities from the fields of micro- and nanotechnology.

Food engineering education will follow suit by employing more digital facilities, shifting the emphasis from understanding the detailed mechanisms, toward synthesizing process systems, and predicting the taste and health impact of products even before the products have been made.

See also: Consumer-Oriented New Product Development. Determining Functional Properties and Sources of Recently Identified Bioactive Food Components: Oligosaccharides, Glycolipids, Glycoproteins, and Peptides. Energy and Greenhouse Gases Footprint of Food Processing. Human Nutrition: Malnutrition and Diet. Virtual Water and Water Footprint of Food Production and Processing

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Relevant Website

www.fpe.wur.nl/uk
Wageningen UR.

Food Labeling

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Glossary

Health claims Statements that are made in reference to the positive nutritional value of a food. Regulations dictate specific rules and wording for health claims.

Insoluble fiber The type of fiber found in foods that add bulk to the stools and helps food pass more quickly through the stomach and intestines. It is found in wheat bran, vegetables, and whole grains.

Negligible source There are rules in food labeling that allow for rounding down to zero, or to other low values that reflect the food contains an insignificant amount of a nutrient.

Nutrient content claim Statements that describe the relative amount of nutrients in a product, i.e., 'low in,' 'reduced,' 'free,' 'good source,' 'excellent source.' There are regulatory requirements surrounding use of such terms.

Principal display panel The part of the food label that is used to declare the contents of the product for retail sale.

Qualified health claims Are allowed for specific nutrients and health conditions. They are granted based on petition to FDA and are permitted for use accompanied by significant and specific disclaimers.

Significant Scientific Agreement claims The most robust category for health claims that is held for statements that reflect agreement among credible experts that a nutrient has a positive health effect on the body. There is an evidence-based review and assessment by Food and Drug Administration (FDA) that health claim statements meet such a standard.

Soluble fiber The type of fiber in foods that attracts water and turns to gel during digestion. This slows digestion. Soluble fiber is found in oat bran, barley, nuts, seeds, beans, lentils, peas, and some fruits and vegetables. It is also found in psyllium, a common fiber supplement.

Structure/function claims Claims may be made that reflect how a nutrient affects the structure or function of the body. Regulations dictate specific rules and wording for health claims.

Introduction

Food label is the primary means for communicating with a consumer about a product. The label is highly regulated in the United States and in most parts of the World. Most countries have been updating their food labeling regulations in the past years to better reflect the global regulatory environment. It is regulated to ensure that the label contains all critical information and that it is accurate. The label not only is a means of communicating the contents of a container to a consumer but can also provide critical information to a food allergic individual. The nutrition information contained in the label conveys data on calories and key macro- and micronutrients that can help consumers to prevent obesity and ensure adequate intake of nutrients commonly underconsumed. The food label is where food policy meets the road and becomes personal to a consumer.

Food labels are used to attract customers as much as to inform them the contents of the product. Food labels are effective tools for marketing, but the manufacturer has the responsibility to ensure that the food label is accurate and in compliance to all applicable regulations and that it is truthful and not misleading. The label must present an accurate description of the contents, so that consumers are not deceived about the product. The criteria for labeling in the United States are well described; the measures by which to evaluate truthfulness are not subjective and, in fact, food labeling is quite simple – as long as one knows the rules.

The following information presents the requirements for labeling food in the United States. General food labeling requirements are presented for specific countries representing other regions of the World, including Australia, Brazil, China, Chile, Costa Rica, European Union (EU), India, and Japan. However, this article is not a complete guide to food labeling around the world and specific information should be obtained for food labeling in any given country outside the United States. This article provides specific information about labeling for food products intended for distribution in the United States.

General Food Labeling Requirements

Regulations determine when a product must be labeled and what information must be included. For most food products, there is a requirement for a principal display panel (PDP) and an information panel. The name of the food must be stated that is compliant with any applicable standard of identity. The manufacturer name and address must be given so that a consumer can contact the manufacturer with questions, complaints, and even compliments. The net weight for the product must be listed on the front panel. Nutrition labeling, ingredients, and allergens must be listed on the information panel. Where applicable, cooking instructions and other safe food handling instructions must be presented, which should be sufficient to ensure consumer food safety. Optional information includes a variety of possibilities for health claims and for promoting what is not in the product, for example, preservatives, genetically modified ingredients, *trans* fat, or artificial colors. Although this information is

optional for a manufacturer, there are robust rules that must be followed.

More complex than the label itself is determining when a product must be labeled with a full declaration of ingredients or nutrition information. Packages sold in multipacks or single-serve items and small packages are provided with special rules.

The Federal Agencies That Regulate Food Labels and Their Statutory Authority

In the United States, meat, poultry, and egg products are regulated by the Food Safety and Inspection Service (FSIS); all other food products are regulated by the Food and Drug Administration (FDA). The Federal agencies that have jurisdiction over these products have been granted authority through several principal statutes; these include the Federal Meat Inspection Act, the Poultry Products Inspection Act, the Egg Products Inspection Act, the Agricultural Marketing Act, the Federal Food, Drug, and Cosmetic Act (FFD&CA), and the Fair Packaging and Labeling Act. Additionally, the Federal Trade Commission (FTC) operates under the FTC Act (FTCA) to regulate advertising, an extension of labeling, and prohibits false and misleading advertising.

There are key similarities and differences in the approaches that the FSIS and the FDA take for regulating food labels. It is critical to understand which Federal agency has authority for the product; the determination of jurisdiction is referred to as 'amenability.' Amenability is based on the formulation of the product, as opposed to the final product. The food product is not amenable to FSIS regulations if it contains (1) 3% of less raw meat or less than 2% cooked meat, or (2) less than 2% cooked poultry meat; less than 10% cooked poultry skins, giblet, or fat, separately; and less than 10% of cooked poultry skins, giblet, fat, or meat in combination provided that the poultry ingredients were prepared under domestic or foreign inspection and the product is not represented as a poultry product (USDA, 2005b). Although the FSIS has installed this definition formally only for poultry products, they have extended it historically to determine amenability for meat products as well. The FSIS has also exempted specific foods, for example, bagel dogs, pork and beans, and gravy mixes. Other exemptions include product included in institutional pack and used as soup bases and flavorings that contain less than 15% of cooked poultry meat. Thus, bouillon cubes, poultry broths, gravies, sauces, and flavorings are also exempt from the FSIS (9 CFR Section 381.15(c)) and are regulated by the FDA. The FSIS has authority to exempt items with appropriate rulemaking procedures, so the list of foods exempted is subject to change.

The FSIS was granted authority to include catfish as an amenable species under the Food, Conservation, and Energy Act of 2008. The FSIS published a proposed rule mandating continuous inspection of catfish in 2011. However, in May 2012, the Government Accountability Office published their report on Seafood Safety, stating that the United States Department of Agriculture (USDA) should not be granted responsibility for catfish and that authority should remain with the FDA GAO, 2011. Reasons included inefficient use resources and duplication of efforts and that the new authority for the FDA granted under the Food Safety Modernization Act (FSMA) of 2010 provides the FDA with ample capacity to continue their regulation of catfish and therefore labeling of catfish products.

The authority of the FTC is also understood, although the food label is not defined as 'advertising.' The FTCA states that the FTC shall prohibit the false advertisement of 'foods, drugs, and cosmetics' (15 USC Section 52) and prevent 'unfair or deceptive acts of practices in or affecting commerce' (15 USC Section 45(a)(1)). This is broad authority that the FTC utilizes to take action on false and misleading labeling of food products ('Fresh Grown Preserve Corp v. FTC' 125 F.2d917 (2d Cir. 1942). An advertising claim, including claims on labels, may be deemed false or misleading if it is not adequately sustained in accordance with FTC guidelines. The courts have upheld FTC's authority to proceed with action against false labeling of food products. One of the most interesting of food label claim cases involves FTC's pursuit of POM Wonderful™. The FTC has battled POM Wonderful LLC, makers of a popular pomegranate juice, for more than 3 years to date, stating that the brand makes misleading claims about the health benefits of the beverage. They have held the company to a standard for substantiation of claims of two randomized, well-controlled, human clinical trials, which the FTC proclaims that they lack. The makers of the product believe that this is an excessive standard that applies only to pharmaceutical products and have continued to battle the FTC in legal disputes. The case continues at this date but has clearly galvanized the existence of FTC's legal authority over food labeling and advertising (FTC, 2013).

When Packages Must Be Labeled

The requirement is clear that all foods must be labeled. However, the complexity of food packaging and marketing practices require further clarification of how foods are labeled. First, it is important to note that 'labeling' extends beyond the food package and includes point-of-purchase materials, promotional brochures, and shelf information. Next, the label required depends on the format the product leaves the facility or inspected establishment for FSIS-regulated products. For example, meat products may be wrapped in a protective covering that is exempt from marking and labeling requirements if placed within a package for shipping that meets all mandatory labeling requirements. Additionally, meat products may be shipped from one inspected establishment to another for further processing without each package being labeled, provided that the immediate containers with protective coverings are packaged in shipping container that is labeled 'Packed for Institutional Use Only.' The unlabeled products may not be removed for further distribution or sold at retail (9 CFR Sections 301.2 and 381.1). Unprocessed meats may be removed from the shipping container for resale and distribution to retailers, including restaurant, provided that the product bears a legible official mark of USDA inspection and the establishment number.

Whole bird or cut poultry may be distributed in protective coverings and further sold to retailers without marking on the packages, provided that the shipping container bears all

required labeling features (i.e., product name, handling statement, mark of inspection, establishment number, net weight, ingredients, signature line, nutrition facts, and safe handling instructions, if needed).

Given the wide variations in mandatory labeling for meat and poultry products according to USDA regulation, it is prudent to refer to the regulation in 21 CFR for specific requirements for labeling the type and package of meat or poultry product intended.

Prior Approval Required for Meat and Poultry Products

Food labels on FDA-regulated products and FSIS-regulated products must comply with all requirements, but meat and poultry product labels require that the FSIS approve their content and context before marketing. This 'prior approval' requirement for the FSIS has evolved over the year, reflecting the size of the industry, the number of products in the marketplace with frequent changes to their labels, and finite resources of the Agency. Previously, each label on a meat or poultry product was submitted to the Agency for approval. Modifications to labels required resubmission and approval. Only minor modifications were able to be approved by local inspectors in the establishment. This need gave rise to a new industry of 'label expeditors' who act as intermediaries between companies needing rapid label approvals to get products into the marketplace and resource-constrained federal label reviewers. Regulations were changed to allow the current practice of sketch approval based on submission of a label application to the FSIS (Sketch labeling). A sketch-approved label may be modified by the company as long as they follow the requirements contained in the regulation. There is also provision for generic labeling that does not require submission for approval by the agency. These provisions have streamlined the label review process for the FSIS and provided needed speed-to-market capability for the industry.

Mandatory Requirements of the Food Label

There are six required elements of the label for FDA-regulated product and eight for FSIS-regulated products. For FDA products, the PDP must include the name of the product or identity and statement of net quantity. Other information is required to be on the Information Panel which is placed to the right of the PDP. The Information Panel states the name and address of the manufacturer, packer, or distributor; the ingredient statement, the nutrition fact panel; and allergen statement. FSIS-regulated products require the product name, inspection legend and establishment number, handling statement, net weight statement, ingredient statement, address line, nutrition facts, and safe handling instructions. The rationale for the difference between the two regulatory agencies is explained by the nature of the foods they regulate. Meat and poultry products are generally highly perishable and handling instructions may be needed to ensure food safety; whereas, FDA-regulated products may be shelf stable and less prone to bacterial growth but may present an array of allergen risks that need to be communicated to consumers. This statement is a generalization of the foods the respective agencies regulate, but it helps to put the agencies in context of the products they oversee in order to explain the myriad of differences between their regulations.

Placement and prominence of the required elements are specified in regulations. The type size must be prominent and conspicuous and easy to read. The information must be in such terms as "to render it likely to be read and understood by the ordinary individual under customary conditions of purchase and use" (9 CFR Section 317.2(b)).

Principal Display Panel

For the FSIS and the FDA, the PDP is the part of the label most likely to be displayed, presented, shown, or examined under customary conditions to the consumer (9 CFR Section 317.2 (d); 21 CFR 101.1). For FSIS-regulated products, the PDP must contain the name of the product (compliant with standards of identity, if applicable), net quantity of contents, the official inspection legend, number of the official establishment, and if necessary, handling information (e.g., Keep Refrigerated). For FDA-regulated products, it must contain the name of the product (compliant with standards of identity, if applicable) and net quantity of contents. Similar handling information is also typically found on the PDP, if applicable (e.g., Keep Frozen).

Size of the PDP is also regulated and the regulations are similar for the two agencies. For rectangular packaging, the PDP is one entire side. For a cylindrical container, the PDP is an area 40% of the product at the height of the container times the circumference of the container, the width of which is one-third of the circumference, and the height of which is as high as the container. For any other configuration of container, the PDP is 40% of the total surface area.

Type size is also regulated. All information appearing on the PDP shall appear prominently and conspicuously, but in no case may the letters or numbers be less than one-sixteenth inch in height (9 CFR Section 317.2 (m) meat; 9 CFR Section 381.116 (c) poultry; 21 CFR Section 101.1 (FDA)).

Information Panel

The Information Panel is found to the right of and immediately contiguous with the PDP. It must contain the ingredient statement, name and address of the manufacturer or distributor, and nutrition labeling, if required. Safe handling instructions, including cooking/preparation instructions, may be placed anywhere on the label.

Type size is also regulated. All information appearing on the information panel shall appear prominently and conspicuously, but in no case may the letters or numbers be less than one-sixteenth inch in height. Type size is regulated (9 CCFR Section 317.2 (m) (meat); 9 CFR Section 381.116 (c) (poultry); 21 CFR Section 101.2 (FDA)).

Product Name, Placement, and Prominence

The name of the product included on the PDP must comply with naming requirements in order to accurately convey to

consumers the contents of the container. The name must be consistent with a standard of identity or be a common or usual name, or a truthful description of the product.

Standards of identity are listed in regulation. They are found as follows: for meat, see 9 CFR Section 319; for poultry, see 9 CFR Section 381.155–381.174; and for FDA products, see 21 CFR Sections 130–169. Standards have also been created by other authoritative bodies, including the Codex Alimentarius Commission. If they exist and the product complies with the standard, they must be used. Standards of identity are found for ice cream, cheese, bacon, hot dogs, and much more.

For products with no standard of identity or common name, descriptive names may be used. A descriptive name describes the food: its character, manner of preparation, and ingredients; for example, chopped, sliced, smoked, grilled, with pimento, and rosemary infused.

The standards control components and ingredients in the product and were created to prevent imitation products from being presented as real. For example, the standards control fat that may have at one time been a driver of economic validity for the product but today may be undesired from a consumer preference perspective. Both the FDA and the FSIS have adopted provisions to allow companies deviating from standards of identity to avoid labeling products as 'imitation.' Products must be labeled as 'imitation' if they are nutritionally inferior to standardized products. This means, technically, that a food which is reduced from standard in fat, salt, saturated fat, or cholesterol must be labeled as 'imitation.' However, these modifications may be made to comply with consumer preferences and companies long ago sought the agencies' considerations that foods be labeled appropriately but without the stigma that 'imitation' confers. Both agencies enable qualifying products to be labeled with the standardized name, provided that other information is included that describes the components of the product for the consumer. These labels are descriptive names, which list the food, bacon or cheese, for example, along with other ingredients, for example, water, tenderizing solution, 2% milk – whatever distinguishes the food product from the standardized product. Reduced fat versions of standardized products may be labeled 'Reduced Fat' or 'Low Sodium,' provided that regulatory requirements for use of the term are satisfied. In this way, the regulatory agencies opened the way for food companies and marketers to satisfy consumers' desires for a wide variety of foods that meet their nutrition needs and lifestyle preferences while still complying with the key regulatory requirement to provide truthful and not misleading information about products to consumers.

Naming configurations may also note geographic significance to consumers. Different regions of the world have specific character, for example, Tuscan, Southwest, the Middle East. When these terms are used that do not refer to the region where the product was made, they may be used in conjunction with the term 'style' or 'type,' for example, Tuscan-style Marinara Sauce or Southwestern-style Grilled Chicken. Poultry products long had strict standards regarding geographic origin, but the FSIS has installed policies that allow more flexibility today. However, if a duck product is labeled 'Long Island Duck' and not 'Long Island-style Duck,' it should be understood that the duck was raised on Long Island.

Some geographic terms have been deemed by the FSIS to no longer have geographic significance and are now in general use as trade names. These terms do not require use of 'type' or 'style.' For example, Vienna Sausages are small hot dogs that generally come in cans and Italian Sausage is a spicy sausage and may be mild or hot, but it is now commonly known as 'Italian Sausage' and is permitted without additional qualifiers.

Country of Origin Labeling

USDA's Agriculture Marketing Service installed regulations for country of origin labeling (COOL) in March 2009 and is responsible for the implementation, administration, and enforcement of COOL regulations. Under COOL, retailers must provide their customers with information about the origin of various food products, including meats, poultry, raw fruits and vegetables, and fish and shellfish. Mandatory COOL requirements help consumers to make informed purchasing decisions about the food they buy.

Imported meats, poultry, raw fruits and vegetables, and fish and shellfish must bear the name of the country of origin, preceded by the words 'Product of' (9 CFR Section 327.14). The country of origin statement must appear on the immediate container for the product and must be immediately under the name of the product. It must also be located next to the name of the product on any outside, consumer-facing packaging. In March 2013, the USDA proposed to add to the COOL requirements for muscle cuts of meat, further requiring that there be separate designations for geographic locations where the animal was born, raised, and slaughtered in order to provide full information to consumers. The proposal also will eliminate the allowance for commingled muscle cuts, making the US COOL requirements more parallel with those of Europe.

The FDA does not require COOL for imported foods; however, it is a requirement of the US Customs and Border Protection (CBP) as authorized by the Tariff Act of 1930 and CPB regulations (19 CFR Part 134). Repackers are required by CBP to mark containers of repackaged imports with the English name of the country of origin. In the event that further reprocessing or material added to the article in another country results in a 'substantial transformation' of the product, the other country becomes the country of origin within the meaning of CBP's labeling requirements, 19 CFR 134.1(b) and 134.11. As a result, there have been seizure actions and other regulatory follow-up involving imported shrimp that was peeled, deveined, and repacked in the United States and labeled as a product of the US FDA-received congressional, industry, and field inquiries regarding FDA's jurisdiction and policy on COOL for this product. However, CBP and the FDA have sustained that peeling, deveining, and repacking is not a 'substantial transformation' of the product, sufficient to permit the shrimp to be declared as a product of the United States. The threshold for 'substantial transformation' includes that the product loses its primary character. For example, an imported product, such as shrimp, is peeled and deveined or otherwise preserved after importation but is still identified and sold as 'shrimp.' If labeled as a 'product of the USA,' it would be misbranded because the labeling would be false and

misleading within the meaning of section 403(a)(1) of the FFD&CA. However, if an imported product, such as shrimp, is peeled, deveined, and incorporated into a shrimp dish, such as 'Shrimp Quiche,' the product is no longer identifiable as shrimp but as 'Quiche.' The quiche is a product of the USA. Therefore, labeling it as 'Product of the USA' would not be a violation of the FFD&CA. It is not sufficient to declare a product to be 'imported by' or 'distributed by' without also declaring its country of origin. An imported product, such as shrimp, which is peeled and deveined, is labeled as 'Imported by' or 'Distributed by' a firm in the USA. Such labeling would not violate the FFD&CA, but it would not meet the CBP requirement for COOL. The product would also have to be clearly identified as to country of origin.

The FDA's policy regarding false or misleading COOL is to defer to CBP. Such labeling is also a violation of the Tariff Act of 1930, which is enforced by CBP, and CBP can generally deal with this problem more efficiently than FDA.

Net Quantity Declaration

Net quantity declarations enable consumers to make value comparisons for similar products at point of purchase. All labels sold at retail must state the accurate quantity of the package contents by avoirdupois weight, liquid measure, or numerical count (9 CFR Section 317.2(h)). Generally, if the food is solid, semisolid, or viscous, it should be expressed in fluid measure (e.g., fl oz) (21 CFR Section 101.105(a)). The net quantity statement is placed on the PDP as a distinct item in the bottom 30% of the panel, in lines generally parallel with the base of the container (21 CFR 101.105(e) and (f); 9 CFR Section 317.2(h)).

FSIS-regulated products do not require metric measures be listed, but FDA regulations require that net contents be labeled in both metric (grams, kilograms, milliliters, and liters) and US Customary System (ounces, pounds, and fluid ounces) terms. The metric statement may be placed either before or after the US Customary statement, or above or below it. Each of the following examples is correct (21 CFR Section 101.105):

Net weight 1 lb 8 oz (680 g)
Net wt 1 lb 8 oz 680 g
500 ml (1 pt 0.9 fl oz)
Net contents 1 gal (3.79 L).

The size of the net quantity declaration is also regulated and is dependent on the area of the PDP. The declaration must be conspicuous and easily legible boldface print or type and lettering may be no more than three times high as it is wide (9 CFR Section 317.2(h)). The FSIS and the FDA share minimum type size requirements. The area of the panel is calculated as follows: for a rectangle or square, the area is the height multiplied by the width (both in inches or both in centimeters); for a cylinder, use 40% of the product of the height by the circumference (21 CFR Section 101.1).

For the net quantity statements, the minimum type size is the smallest type size that is permitted based on the space available for labeling on the PDP. Determine the height of the type by measuring the height of the lower case letter 'o' or its equivalent when mixed upper and lower case letters are used, or the height of the upper case letters when only upper case letters are used (21 CFR Section 101.105(h) and (i)).

For the net quantity statements, the minimum type size is the smallest type size that is permitted based on the space available for labeling on the PDP. Determine the height of the type by measuring the height of the lower case letter 'o' or its equivalent when mixed upper and lower case letters are used, or the height of the upper case letters when only upper case letters are used (21 CFR Section 101.105(h) and (i); 21 USC Section 671(meat)).

Minimum Type Size	*Area of PDP*
1/16 in. (1.6 mm)	5 sq. in. (32 sq. cm.) or less
1/8 in. (3.2 mm)	More than 5 sq. in. (32 sq. cm.) but not more than 25 sq. in. (161 sq. cm.)
3/16 in. (4.8 mm)	More than 25 sq. in. (161 sq. cm.) but not more than 100 sq. in. (645 sq. cm.)
1/4 in. (6.4 mm)	More than 100 sq. in. (645 sq. cm.) but not more than 400 sq. in. (2580 sq. cm.)
1/2 in. (12.7 mm)	More than 400 sq. in. (2580 sq. cm.)

The FSIS exempts net weight labeling for small packages of less than 0.5 ounces that are individually wrapped and labeled. However, their shipping container must declare the accurate net quantity of the container and must not be otherwise false or misleading (9 CFR Section 317.2(h)(9)(ii)). The FDA provides exemptions for small packages provided that they display the following or an equivalent representation: 'Not labeled for individual sale.'

There are provisions for reasonable variance from declared weight caused by loss or gain of moisture during the course of distribution or storage, provided that the deviation is unavoidable given good distribution and good manufacturing practices and that the product is not rendered misbranded (9 CFR Section 317.2(h)).

Ingredients

Ingredient labeling carries with it specific requirements that dictate knowledge of the product formulation and functionality of ingredients. All ingredients must be declared by their common or usual names on the label in descending order of prominence by weight (USDA, 2005a; 21 CFR Section 101.4). The descending order of predominance requirements do not apply to ingredients present in amounts of 2% or less by weight when a listing of these ingredients is placed at the end of the ingredient statement following an appropriate quantifying statement, for example, "Contains _ percent or less of ___" or "Less than _ percent of ___." The blank percentage within the quantifying statement shall be filled in with a threshold level of 2%, or, if desired, 1.5%, 1.0%, or 0.5%, as appropriate. No ingredient to which the quantifying phrase applies may be present in an amount greater than the stated threshold.

Ingredients that are combinations of subingredients may be listed by an established common or usual name of the ingredient followed by a parenthetical listing of all ingredients contained therein in descending order of predominance except that, if the ingredient is a food subject to a definition and

standard of identity that has specific labeling provisions for optional ingredients, listings of subingredients must not list the ingredient itself.

Ingredients are identified by functionality, for example, leaving agents (baking powder, monocalcium phosphate, and calcium carbonate), firming agents (calcium salts), yeast nutrients (calcium sulfate and ammonium phosphate), and dough conditioners (L-cysteine and ammonium sulfate).

Sugar is an interesting ingredient for labeling. Some manufacturers would like to present multiple sources of sweetness as 'sugar,' whereas others want to conceal high levels of sugar in their products but presenting sweeteners by their multiple names. For the purposes of FDA's labeling, sugar is derived from sugarcane or sugar beets, and all other sources of sweetness must be accurately labeled (21 CFR Section 101.4(20)).

The term 'flavorings' is used to designate natural spices and natural spice extracts. Nonnatural flavors must be represented as 'artificial flavors.' Only spices, spice extracts, essential oils, and oleoresins may be presented as 'natural flavor,' 'natural flavoring,' 'flavor,' or 'flavoring' (21 CFR Sections 182.10 and 184). Hydrolyzed ingredients, such as hydrolyzed proteins or autolyzed yeast, may not be presented as a 'flavor' and must be separately labeled. The FDA declares that an artificial flavoring means any substance, the function of which is to impart flavor, which is not derived from a spice, fruit or fruit juice, vegetable or vegetable juice, edible yeast, herb, bark, bud, root, leaf or similar plant material, meat, fish, poultry, eggs, dairy products, or fermentation products thereof (21 CFR Section 101.22(a)(1)).

The use of artificial smoke for flavor and artificial colors must not only be identified in the ingredient statement but must also be on the product label next to the product name.

Chemical preservatives must also be declared on the label. The ingredient must be labeled by its chemical name and the purpose of its use (9 CFR Section 381.120). The FDA declares chemical preservative means any chemical that, when added to food, tends to prevent or retard deterioration thereof but does not include common salt, sugars, vinegars, spices, or oils extracted from spices, substances added to food by direct exposure thereof to wood smoke, or chemicals applied for their insecticidal or herbicidal properties (21 CFR Section 101.22(a)(5)).

Allergens

Significant legislation was passed in the United States in 2004 supporting allergen labeling. The Food Allergen Labeling and Consumer Protection Act (FALCPA) amended the FFD&CA to reinforce the criticality of consistently and clearly labeling food allergens. The FALCPA requires that any ingredient containing protein derived from one of the 'Big Eight' allergen food and food groups must be labeled: milk, wheat, soy, peanut, tree nut, fish, crustacean shellfish, and egg. The allergen must be clearly identified in plain English on the information panel of food labels. These eight foods and food groups account for 90% of all food allergies. The FALCPA also requires the type of tree nut (e.g., almonds, pecans, and walnuts), the type of fish (e.g., bass, flounder, and cod), and the type of Crustacean shellfish (e.g., crab, lobster, and shrimp) to be declared.

The FSIS is not included in the authority granted by the FALCPA, but the FSIS supports voluntary statements on labels to inform consumers who are allergic of sensitive food ingredients. They encourage clear listing of the eight major allergens and other specific ingredients, including monosodium glutamate, sulfites, lactose, and Yellow #5 (tartrazine). They support similar language as required by the FALCPA, i.e., use of the words 'Contains:' before listing allergens and in providing the specific source of the specific ingredient in a parenthetical statement (e.g., 'casein (from milk)').

Use of terms that refer to the manufacturing environment, for example, 'Made in a plant that also produces soy, peanuts, and tree nuts,' is permitted, but it is not without controversy. Manufacturers may also use the term 'May Contain' in reference to allergens that they fail to control in the manufacturing, storage, or distribution process. The application of good manufacturing practices and effective sanitation programs should preclude the use of such phrases and they are regarded by some consumer groups inadequate and ineffective ways to protect food allergic and sensitive individuals. Food manufacturers should take all necessary steps to control allergens, prevent cross-contamination in the food manufacturing environment, and provide consumers with reliable information that they can use. Use of 'catch all' phrases is not useful to consumers, because the intent is to leave the consumer with the responsibility to decide whether to take a risk and consume the food or avoid it altogether. These terms should not be used to mislead consumers.

Other allergenic foods (e.g., sesame) are not required to be declared in accordance with the FALCPA. Canada includes sesame, mustard, and sulfites in their list of major allergens declared on labels and classifies fish and shellfish together as 'seafood.' The EU lists cereals containing gluten, crustaceans, mollusks, eggs, fish, peanuts, nuts, soybeans, milk, celery, mustard, sesame, lupin, and sulfur dioxide at levels above 10 mg/kg, or 10 mg/l, expressed as sulfur dioxide. The EU also updated their 2003 and 2006 food allergen labeling requirements in 2011, with the Food Information for Consumers Regulation 1169/2011. The new regulation is built on current allergen labeling provisions for prepacked foods and introduces a new requirement for allergen information to be provided for foods sold nonpacked or prepacked for direct sale. It also requires that a label state any use of milk, rather than the more nebulous terms of casein, sodium caseinate, lactoglobulin, or lactalbumin that could be used alone previously. The new regulation will be in effect from December 2014.

A food product may be subject to recall if it contains a major food allergen as an ingredient not declared on the food label in accordance with FALCPA requirements. Penalties for noncompliance under the FALCPA include civil sanctions, criminal penalties, and the potential for the seizure of products or for a request for a recall by the manufacturer or distributor. Nearly half of all recalls (40%) in the United States are due to undeclared food allergens (Expert Recall 2012). The FDA will have increased ability to ensure that food allergen management programs are in place with implementation of the FSMA, which requires hazard analysis and installation of preventative controls, including allergen programs.

Address

The information panel must also include the name or trade name and place of business for the manufacturer, packer, or distributor for the food product. If the name of the distributor is listed, it may be preceded by the term 'Prepared For' or 'Distributed By.' If the business is listed publically and is available in a telephone or city directory, then the listing of place of business may contain only the city, state, and postal zip code. If not publically available, a street address must be given. The purpose is to enable a customer to contact someone with regard to the food and information must be made accessible to consumers.

Handling Statements

Products that must be maintained frozen or refrigerated in order to protect their perishable state must be labeled prominently on the PDP with special handling information, including 'Keep Frozen,' 'Keep Refrigerated,' or 'Perishable – Keep Refrigerated or Frozen' (9 CFR Section 317.2(k) (meat); 9 CFR Section 381.125(a) (poultry)). Other special handling and warning statements that must be included comprise protein foods used for weight loss diets, foods containing psyllium husks, unpasteurized juices, and shell eggs (21 CFR Section 101.17 (FDA)).

Safe handling instructions are also required for meat and poultry products that are raw or partially cooked (i.e., not ready to eat) and sold to the retail market. (9 CFR Section 317.2(l) (meat); 9 CFR Section 381.125(b) (poultry)) They should not be used for ready-to-eat food products and products intended for further processing are exempt. Safe handling instruction tells the consumer how to safely prepare the food to eat. Instructions include 'Cook Thoroughly' and must appear in lettering no less that 1/16 in. in height and must be placed prominently on the label such that "it is likely to be read and understood under customary conditions of purchase and use."

Failure to utilize the safe handling instructions effectively is a liability to a manufacturer. In the 2007 case involving ConAgra's Banquet line of pot pies, chicken pot pies were identified to contain *Salmonella* and eventually 401 illnesses were reported in 41 states. The company acknowledged that chicken pies were involved and initially refused to recall turkey pot pies, asking consumers to cook the products thoroughly before eating. Eventually, they recalled all pot pies and stated that their cooking instructions were 'unclear,' leaving too much discretion to consumers to understand the performance of their particular microwave oven. However, the case had long lasting effects on the ConAgra brand with six civil lawsuits being settled.

Nutrition Labeling

The Nutrition Labeling and Education Act (NLEA) of 1990 brought sweeping changes to the way food products are labeled in the United States and successfully impacted the development of similar nutrition labeling rules in other countries. Both the FDA and the USDA adopted regulations implementing the law that went into effect in 1994. The law authorized the FDA to require nutrition information labeling on packaged foods and to regulate nutrient content and health claims for all foods.

The objectives of the NLEA were to clear up consumer confusion about food label information, help consumers to make more healthful food choices, and encourage food manufacturers to make to sell more healthy products. Nutrients were required to be listed on a Nutrition Fact Panel, including calories, calories from fat, saturated fat, and sugars; other nutrients could be made available, and the nutrient information per serving had to be placed in the context of a daily diet. In 2003, regulation for labeling of *trans* fat was added.

A question that has been raised for two decades is whether nutrition labeling impacts food choices. It is agreed that in order to impact health, consumers must use the labels and understand what they mean. According to the 2008 Health and Diet Survey conducted by the FDA (FDA, 2008), 54% of consumers reported often using the food label when purchasing a food item for the first time. There are indications of increased use of food label information in the years immediately after the implementation of NLEA. In the 1990 Health and Diet Survey, 30% of consumers said that they changed their minds about buying a food product because they read the nutrition label. By the end of 1995, approximately 1 year after the food labeling legislation went into effect, 48% reported using the label to drive purchase decision (Levy and Derby, 1996). Over the years, although this number has not increased, it has remained stable, with 49% of respondents in the 2008 survey reporting changing their minds about purchasing a product based on reading the nutrition label.

The matter of changing food behavior is a greater question than one of providing information. Knowledge of nutrient content may or may not alter behavior, because dietary practices and food consumption patterns are influenced by a myriad of factors. However, behavioral change may not be easily effected without awareness, and making consumers aware of nutrient content of foods with clear and honest representation of claims was the intent of the 1994 NLEA.

Products to be Nutrition Labeled

Nutrition labeling is required for all FSIS-regulated products, including major cuts of raw meat and poultry, and ground products. The original regulations were amended in 2012 to include single-ingredient, major cuts of raw meat and poultry. Exemptions exist for small businesses, small packages (less than 0.5 ounce or less than 12 sq. inches), and for custom-ground products at retail. Nutrition labeling is required for all FDA-regulated prepackaged food products.

Nutrition Fact Panel – Required Elements

The following information must be contained on the Nutrition Fact Panel ('the Panel'). The format, order, and type size is specified (9 CFR Section 317.309(d) (meat); 21 CFR Section 101.9).

Serving size

The term serving or serving size means the amount of food customarily consumed per eating occasion by persons 4 years of age or older. It is expressed in a common household measure that is appropriate to the food. The serving size declared on a product label is determined from the 'Reference Amounts Customarily Consumed Per Eating Occasion' (reference amounts) that appear in regulation (21 CFR 101.12(b)).

For products sold in discrete units (e.g., muffins, sliced products, such as sliced bread, or individually packaged products within a multiserving package) and for products which consist of two or more foods packaged and presented to be consumed together where the ingredient represented as the main ingredient is in discrete units (e.g., pancakes and syrup), the serving size is declared as follows:

1. If a unit weighs 50% or less of the reference amount, the serving size is the number of whole units that most closely approximates the reference amount for the product category;
2. If a unit weighs more than 50%, but less than 67% of the reference amount, the manufacturer may declare one unit or two units as the serving size;
3. If a unit weighs 67% or more, but less than 200% of the reference amount, the serving size is one unit;
4. If a unit weighs 200% or more of the reference amount, the manufacturer may declare one unit as the serving size if the whole unit can reasonably be consumed at a single eating occasion.
5. For products that have reference amounts of 100 g or ml or larger and are individual units within a multiserving package, if a unit contains more than 150% but less than 200% of the reference amount, the manufacturer may decide whether to declare the individual unit as 1 or 2 servings.

Calories: 'calories, total,' 'total calories,' or 'calories'

A statement of the caloric content per serving, expressed to the nearest 5-calorie increment up to and including 50 cal, and 10-calorie increment above 50 cal, except that amounts to less than 5 cal may be expressed as zero. Energy content per serving may also be expressed in kilojoule units, added in parentheses immediately following the statement of the caloric content.

Calories from fat

A statement of the caloric content derived from total fat in a serving, expressed to the nearest 5-calorie increment, up to and including 50 cal, and the nearest 10-calorie increment above 50 cal, except that label declaration of 'calories from fat' is not required on products that contain less than 0.5 g of fat in a serving and amounts to less than 5 cal may be expressed as zero. This statement shall be declared as provided in paragraph (d)(5) of this section. If 'Calories from fat' is not required and, as a result, not declared, the statement "Not a significant source of calories from fat" shall be placed at the bottom of the table of nutrient values in the same type size.

Calories from saturated fat (voluntary)

A statement of the caloric content derived from saturated fat in a serving may be declared voluntarily, expressed to the nearest 5-calorie increment, up to and including 50 cal, and the nearest 10-calorie increment above 50 cal, except that amounts to less than 5 cal may be expressed as zero. If present, this statement is indented under the statement of calories from fat.

Fat: 'fat, total' or 'total fat'

A statement of the number of grams of total fat in a serving defined as total lipid fatty acids and expressed as triglycerides. Amounts shall be expressed to the nearest 0.5 (1/2) g increment below 5 g and to the nearest gram increment above 5 g. If the serving contains less than 0.5 g, the content shall be expressed as zero. Daily Reference Value (DRV) used for calculating %DV is 65 g.

Saturated fat: 'saturated fat' or 'saturated'

A statement of the number of grams of saturated fat in a serving defined as the sum of all fatty acids containing no double bonds, except that label declaration of saturated fat content information is not required for products that contain less than 0.5 g of total fat in a serving if no claims are made about fat, fatty acid, or cholesterol content, and if 'calories from saturated fat' is not declared. If a statement of the saturated fat content is not required and, as a result, not declared, the statement "Not a significant source of saturated fat" shall be placed at the bottom of the table of nutrient values. Saturated fat content is indented and expressed as grams per serving to the nearest 0.5 g (1/2) gram increment below 5 g and to the nearest gram increment above 5 g. If the serving contains less than 0.5 g, the content shall be expressed as zero. DRV used for calculating %DV is 20 g.

Trans *fat: 'trans fat' or 'trans'*

A statement of the number of grams of *trans* fat in a serving, defined as the sum of all unsaturated fatty acids that contain one or more isolated (i.e., nonconjugated) double bonds in a *trans* configuration, except that label declaration of *trans* fat content information is not required for products that contain less than 0.5 g of total fat in a serving if no claims are made about fat, fatty acid, or cholesterol content. The word '*trans*' may be italicized to indicate its Latin origin. *Trans* fat content is indented and expressed as grams per serving to the nearest 0.5 (1/2)-gram increment below 5 g and to the nearest gram increment above 5 g. If the serving contains less than 0.5 g, the content, when declared, shall be expressed as zero. If a statement of the *trans* fat content is not required and, as a result, not declared, the statement "Not a significant source of *trans* fat" shall be placed at the bottom of the table of nutrient values.

Polyunsaturated fat: 'polyunsaturated fat' or 'polyunsaturated' (voluntary)

A statement of the number of grams of polyunsaturated fat in a serving defined as *cis,cis*-methylene-interrupted polyunsaturated fatty acids may be declared voluntarily, except that when monounsaturated fat is declared, or when a claim about fatty acids or cholesterol is made on the label or when a claim for 'fat free' is labeled then declaration of polyunsaturated fat is required. Polyunsaturated fat content is indented and expressed as grams per serving to the nearest 0.5 (1/2) gram increment below 5 g and to the nearest gram increment above

5 g. If the serving contains less than 0.5 g, the content shall be expressed as zero.

Monounsaturated fat: 'monounsaturated fat' or 'monounsaturated' (voluntary)

A statement of the number of grams of monounsaturated fat in a serving defined as *cis*-monounsaturated fatty acids may be declared voluntarily except that when polyunsaturated fat is declared, when a claim about fatty acids or cholesterol is made on the label, or when a claim for 'fat free' is made on the label, then declaration of monounsaturated fat is required. Monounsaturated fat content is indented and expressed as grams per serving to the nearest 0.5 (1/2) g increment below 5 g and to the nearest gram increment above 5 g. If the serving contains less than 0.5 g, the content shall be expressed as zero.

Cholesterol

A statement of the cholesterol content in a serving expressed in milligrams to the nearest 5-milligram increment, except that label declaration of cholesterol information is not required for products that contain less than 2 mg cholesterol in a serving and make no claim about fat, fatty acids, or cholesterol content, or such products may state the cholesterol content as zero. If cholesterol content is not required and, as a result, not declared, the statement "Not a significant source of cholesterol" shall be placed at the bottom of the table of nutrient values in the same type size. If the food contains 2–5 mg of cholesterol per serving, the content may be stated as 'less than 5 mg.' DRV used for calculating %DV is 300 mg.

Sodium

A statement of the number of milligrams of sodium in a specified serving of food expressed as zero when the serving contains less than 5 mg of sodium, to the nearest 5 mg increment when the serving contains 5–140 mg of sodium, and to the nearest 10 mg increment when the serving contains greater than 140 mg. DRV used for calculating %DV is 2400 mg.

Potassium (voluntary)

A statement of the number of milligrams of potassium in a specified serving of food may be declared voluntarily, except that when a claim is made about potassium content, label declaration is required. Potassium content is expressed as zero when the serving contains less than 5 mg of potassium, to the nearest 5 mg increment when the serving contains less than or equal to 140 mg of potassium, and to the nearest 10 mg increment when the serving contains more than 140 mg. DRV used for calculating %DV is 3500 mg.

Carbohydrates: 'carbohydrate, total' or 'total carbohydrate'

A statement of the number of grams of total carbohydrate in a serving expressed to the nearest gram, except that if a serving contains less than 1 g, the statement "Contains less than 1 g" or "less than 1 g" may be used as an alternative, or if the serving contains less than 0.5 g, the content may be expressed as zero. Total carbohydrate content is calculated by subtraction of the sum of the crude protein, total fat, moisture, and ash from the total weight of the food. DRV used for calculating % DV is 300 g.

Dietary fiber

A statement of the number of grams of total dietary fiber in a serving, indented and expressed to the nearest gram, except that if a serving contains less than 1 g, declaration of dietary fiber is not required or, alternatively, the statement "Contains less than 1 g" or "less than 1 g" may be used, and if the serving contains less than 0.5 g, the content may be expressed as zero. If dietary fiber content is not required and as a result, not declared, the statement "Not a significant source of dietary fiber" shall be placed at the bottom of the table of nutrient values in the same type size. DRV used for calculating %DV is 25 g.

Soluble fiber (voluntary)

A statement of the number of grams of soluble dietary fiber in a serving may be declared voluntarily except when a claim is made on the label or in labeling about soluble fiber, label declaration is required. Soluble fiber content shall be indented under dietary fiber and expressed to the nearest gram, except that if a serving contains less than 1 g, the statement "Contains less than 1 g" or "less than 1 g" may be used as an alternative, and if the serving contains less than 0.5 g, the content may be expressed as zero.

Insoluble fiber (voluntary)

A statement of the number of grams of insoluble dietary fiber in a serving may be declared voluntarily except that when a claim is made on the label or in labeling about insoluble fiber, label declaration shall be required. Insoluble fiber content shall be indented under dietary fiber and expressed to the nearest gram except that if a serving contains less than 1 g, the statement "Contains less than 1 g" or "less than 1 g" may be used as an alternative, and if the serving contains less than 0.5 g, the content may be expressed as zero.

Sugars

A statement of the number of grams of sugars in a serving, except that label declaration of sugars content is not required for products that contain less than 1 g of sugars in a serving if no claims are made about sweeteners, sugars, or sugar alcohol content. If a statement of the sugars content is not required and, as a result, not declared, the statement "Not a significant source of sugars" shall be placed at the bottom of the table of nutrient values in the same type size. Sugars shall be defined as the sum of all free mono- and disaccharides (such as glucose, fructose, lactose, and sucrose). Sugars content is indented and expressed to the nearest gram, except that if a serving contains less than 1 g, the statement "Contains less than 1 g" or "less than 1 g" may be used as an alternative, and if the serving contains less than 0.5 g, the content may be expressed as zero.

Sugar alcohol (voluntary)

A statement of the number of grams of sugar alcohols in a serving may be declared voluntarily on the label, except that when a claim is made on the label or in labeling about sugar alcohol or sugars when sugar alcohols are present in the food, sugar alcohol content is declared. For nutrition labeling purposes, sugar alcohols are defined as the sum of saccharide derivatives in which a hydroxyl group replaces a ketone or aldehyde group and whose use in the food is listed by the FDA

(e.g., mannitol or xylitol) or is generally recognized as safe (e.g., sorbitol). In lieu of the term 'sugar alcohol,' the name of the specific sugar alcohol (e.g., 'xylitol') present in the food may be used in the nutrition label, provided that only one sugar alcohol is present in the food. Sugar alcohol content is indented and expressed to the nearest gram, except that if a serving contains less than 1 g, the statement "Contains less than 1 g" or "less than 1 g" may be used as an alternative, and if the serving contains less than 0.5 g, the content may be expressed as zero.

Other carbohydrate (voluntary)

A statement of the number of grams of other carbohydrates may be declared voluntarily. Other carbohydrate is defined as the difference between total carbohydrate and the sum of dietary fiber, sugars, and sugar alcohol, except that if sugar alcohol is not declared (even if present), it shall be defined as the difference between total carbohydrate and the sum of dietary fiber and sugars. Other carbohydrate content is indented and expressed to the nearest gram, except that if a serving contains less than 1 g, the statement "Contains less than 1 g" or "less than 1 g" may be used as an alternative, and if the serving contains less than 0.5 g, the content may be expressed as zero.

Protein

A statement of the number of grams of protein in a serving, expressed to the nearest gram, except that if a serving contains less than 1 g, the statement "Contains less than 1 g" or "less than 1 g" may be used as an alternative, and if the serving contains less than 0.5 g, the content may be expressed as zero.

There are additional qualifiers for labeling protein: When the protein in foods represented or purported to be for adults and children of 4 or more years of age has a protein quality value that is a protein digestibility-corrected amino acid score of less than 20 expressed as a percent, or when the protein in a food represented or purported to be for children greater than 1 but less than 4 years of age has a protein quality value that is a protein digestibility-corrected amino acid score of less than 40 expressed as a percent, either of the following shall be placed adjacent to the declaration of protein content by weight: The statement "not a significant source of protein" or a listing aligned under the column headed 'Percent Daily Value (%DV)' of the corrected amount of protein per serving, calculated as a percentage of the DRV or Reference Daily Intake (RDI), as appropriate, for protein and expressed as percent of DV. When the protein quality in a food as measured by the Protein Efficiency Ratio is less than 40% of the reference standard (casein) for a food represented or purported to be for infants, the statement "not a significant source of protein" shall be placed adjacent to the declaration of protein content. Protein content may be calculated on the basis of the factor of 6.25 times the nitrogen content of the food.

A statement of the corrected amount of protein per serving, calculated as a percentage of the RDI or DRV for protein, as appropriate, and expressed as percent of DV, may be placed on the label, but is required if a protein claim is made for the product or if the product is represented or purported to be for use by infants or children under 4 years of age. (Only allowed for protein of good quality, with protein digestibility-corrected amino acid score of greater than 40%.) The 'corrected amount of protein (gram) per serving' for foods represented or purported for adults and children 1 or more years of age is equal to the actual amount of protein (gram) per serving multiplied by the amino acid score corrected for protein digestibility. If the corrected score is above 1.00, then it shall be set at 1.00.

For the purpose of labeling with a percent of the DRV or RDI, a value of 50 g of protein shall be the DRV for adults and children 4 or more years of age, and the RDI for protein for children less than 4 years of age, infants, pregnant women, and lactating women shall be 16 g, 14 g, 60 g, and 65 g, respectively.

Vitamins and minerals

A statement of the amount per serving of the vitamins and mineral calculated as a percent of the RDI and expressed as percent of DV.

For purposes of declaration of percent of DV, foods represented or purported to be for use by infants, children less than 4 years of age, pregnant women, or lactating women shall use the RDIs that are specified for the intended group. Similarly, the percent of DV based on both the RDI values for pregnant women and for lactating women shall be declared separately on foods represented or purported to be for use by both pregnant and lactating women. When such dual declaration is used on any label, it shall be included in all labeling, and equal prominence shall be given to both values in all such labeling. All other foods shall use the RDI for adults and children 4 or more years of age.

The declaration of vitamins and minerals as a percent of the RDI includes vitamin A, vitamin C, calcium, and iron, in that order, and includes any of the other vitamins and minerals listed below when they are added as a nutrient supplement, or when a claim is made about them. Other vitamins and minerals need not be declared if neither the nutrient nor the component is otherwise referred to on the label or in labeling or advertising.

The percentages for vitamins and minerals are expressed to the nearest 2% increment up to and including the 10% level, the nearest 5% increment above 10% and up to and including the 50% level, and the nearest 10% increment above the 50% level. Amounts of vitamins and minerals present at less than 2% of the RDI are not required to be declared in nutrition labeling but may be declared by a zero or by the use of an asterisk (or other symbol) that refers to another asterisk (or symbol) that is placed at the bottom of the table and that is followed by the statement "Contains less than 2 percent of the Daily Value of this (these) nutrient (nutrients)." If vitamin A, vitamin C, calcium, or iron is present in amounts less than 2% of the RDI and the statement "Not a significant source of _ (listing the vitamins or minerals omitted)" is placed at the bottom of the table of nutrient values, label declaration of the nutrient(s) is not required. Either statement shall be in the same type size as nutrients that are indented.

The following are RDIs used for calculating DV for vitamins and minerals that may be labeled:

Vitamin A, 5000 International Units
Vitamin C, 60 mg
Calcium, 1000 mg
Iron, 18 mg

Vitamin K, 80 μg
Thiamin, 1.5 mg
Riboflavin, 1.7 mg
Niacin, 20 mg
Vitamin B6, 2.0 mg
Folate, 400 μg
Vitamin B12, 6 μg
Biotin, 300 μg
Pantothenic acid, 10 mg
Phosphorus, 1000 mg
Iodine, 150 μg
Magnesium, 400 mg
Zinc, 15 mg
Selenium, 70 μg
Copper, 2.0 mg
Manganese, 2.0 mg
Chromium, 120 μg
Molybdenum, 75 μg
Chloride, 3400 mg

Graphics

Nutrition labels may appear in a variety of formats, depending on the size of the package, the nutritional content of the products, nutrient content claims made, and whether the product is customarily consumed as it is or with additional ingredients, for example, cereal with milk. Formats include full, simplified, and tabular.

Health Claims

A variety of health claims may be made for food products. Generally, these include nutrient content claims, structure/function claims, qualified health claims, and claims with significant scientific agreement (SSA). Nutrient content claims state facts about the presence of positive ingredients (e.g., protein and iron) in a food and are presented in a relative manner, demonstrating that the food is a 'good' or 'excellent' source of the nutrient. Foods may also carry claims that they are reduced in negative nutrients, for example, sodium and saturated fat and may be 'reduced,' 'light,' 'lite,' or 'free.' Structure/function, qualified, and SSA claims may refer to the role of nutrients in supporting health.

Nutrient Content Claims

To label foods with nutrient content statements, the specific language declared in regulations must be used and declared criteria must be met. No other statements regarding nutrient content are allowed in labeling. An express nutrient content claim is any direct statement about the level (or range) of a nutrient in the food (e.g., low sodium) (9 CFR Section 317.313 (b) (meat); 21 CFR Section 101.54). Nutrient content claims are made in relationship to Daily Reference Intake values.

They include:

'High' claims: The terms 'high,' 'rich in,' or 'excellent source of' may be used on the label, provided that the food contains 20% or more of the RDI or the DRV per reference amount customarily consumed. The label must clearly identify the food that is the subject of the claim (e.g., the serving of broccoli in this product is high in vitamin C).

'Good Source' claims. The terms 'good source,' 'contains,' or 'provides' may be used on the label, provided that the food contains 10–19% of the RDI or the DRV per reference amount customarily consumed. The label must clearly identify the food that is the subject of the claim (e.g., the serving of sweet potatoes in this product is a 'good source' of fiber).

'Fiber' claims. If a nutrient content claim is made with respect to the level of dietary fiber, that is, that the product is high in fiber, a good source of fiber, or that the food contains 'more' fiber, and the food is not 'low' in total fat as defined in regulations, then the label must also disclose the level of total fat per labeled serving.

The disclosure must appear in immediate proximity to claim and should be in a type size no less than one-half the size of the claim.

'More' claims. A relative claim using the terms 'more,' 'fortified,' 'enriched,' 'added,' 'extra,' and 'plus' may be used on the label to describe the level of protein, vitamins, minerals, dietary fiber, or potassium, provided that the food contains at least 10% more of the RDI for vitamins or minerals or of the DRV for protein, dietary fiber, or potassium (expressed as a percent of the DV) per reference amount customarily consumed than an appropriate reference food and where the claim is based on a nutrient that has been added to the food.

'High potency' claims. The term 'high potency' may be used on the label to describe individual vitamins or minerals that are present at 100% or more of the RDI per reference amount customarily consumed.

'Light' and 'Lite' Claims

'Light' claims. The terms 'light' or 'lite' may be used on the label provided that:

1. If the food derives 50% or more of its calories from fat, its fat content is reduced by 50% or more per reference amount customarily consumed compared with the reference food; or
2. If the food derives less than 50% of its calories from fat, the number of calories is reduced by at least one-third (33.3%) per reference amount customarily consumed compared with an appropriate reference food.
3. The declaration must appear in immediate proximity to the most prominent such claim (e.g., '1/3 fewer calories and 50% less fat than the regular cheese').
4. A 'light' claim may not be made on a food for which the reference food meets the definition of 'low fat' and 'low calorie.' A product for which the reference food contains 40 cal or less and 3 g fat or less per reference amount customarily consumed may use the term 'light' or 'lite' without further qualification if it is reduced by 50% or more in sodium content compared with the reference food (21 CFR Section 101.56).

Calorie and Sugar Labeling and Claims

Calorie content claims include the terms 'calorie free,' 'free of calories,' 'no calories,' 'zero calories,' 'without calories,' 'trivial

source of calories,' 'negligible source of calories,' or 'dietarily insignificant source of calories' and may be used on the label or in the labeling of foods, provided that the food contains less than 5 cal per reference amount customarily consumed and per labeled serving.

The terms 'low calorie,' 'few calories,' 'contains a small amount of calories,' 'low source of calories,' or 'low in calories' may be used on the label, provided that the food has a reference amount customarily consumed greater than 30 g or greater than 2 tablespoons and does not provide more than 40 cal per reference amount customarily consumed, or the food has a reference amount customarily consumed of 30 g or less or 2 tablespoons or less and does not provide more than 40 cal per reference amount customarily consumed. These terms may be used for meal products and main dish products, provided the product contains 120 cal or less per 100 g.

The terms 'reduced calorie,' 'reduced in calories,' 'calorie reduced,' 'fewer calories,' 'lower calorie,' or 'lower in calories' may be used on the label provided that the food contains at least 25% fewer calories per reference amount customarily consumed than an appropriate reference food.

Sugar content claims include terms such as 'sugar free,' 'free of sugar,' 'no sugar,' 'zero sugar,' 'without sugar,' 'sugarless,' 'trivial source of sugar,' 'negligible source of sugar,' or 'dietarily insignificant source of sugar' and may be used for foods that contain less than 0.5 g of sugars per reference amount customarily consumed and per labeled serving or, in the case of a meal product or main dish product, less than 0.5 g of sugars per labeled serving. Sugar content claims must be immediately accompanied, each time it is used, by either the statement "not a reduced calorie food," "not a low calorie food," or "not for weight control."

The terms 'no added sugar,' 'without added sugar,' or 'no sugar added' may be used only if no amount of sugars or no ingredients that contain sugars, such as jam, jelly, and concentrated fruit juice, have been added. The product must bear a statement that the food is not 'low calorie' or 'calorie reduced' (unless the food meets the requirements for a 'low' or 'reduced calorie' food) and that directs consumers' attention to the nutrition panel for further information on sugar and calorie content.

The terms 'reduced sugar,' 'reduced in sugar,' 'sugar reduced,' 'less sugar,' 'lower sugar,' or 'lower in sugar' may be used on the label, provided that the food contains at least 25% less sugar per reference amount customarily consumed than an appropriate reference food (21 CFR Section 101.60).

'Sodium' and 'Salt' Claims

Sodium content claims include the terms 'sodium free,' 'free of sodium,' 'no sodium,' 'zero sodium,' 'without sodium,' 'trivial source of sodium,' 'negligible source of sodium,' or 'dietary insignificant source of sodium' that may be used on the label, provided that the food contains less than 5 mg (mg) of sodium per reference amount customarily consumed and per labeled serving or, in the case of a meal product or a main dish product, less than 5 mg of sodium per labeled serving. The food must contain no ingredient that is sodium chloride or is generally understood by consumers to contain sodium, unless the listing of the ingredient in the ingredient statement is followed by an asterisk that refers to the statement below the list of ingredients, which states: "Adds a trivial amount of sodium," "adds a negligible amount of sodium," or "adds a dietarily insignificant amount of sodium."

The terms 'very low sodium,' or 'very low in sodium,' may be used on the label, provided that the food has a reference amount customarily consumed greater than 30 g or greater than 2 tablespoons and contains 35 mg or less sodium per reference amount customarily consumed, or the food has a reference amount customarily consumed of 30 g or less or 2 tablespoons or less and contains 35 mg or less sodium per reference amount customarily consumed and per 50 g (for dehydrated foods that must be reconstituted before typical consumption. These terms may be used on the label of meal products and main dish products, provided that the product contains 35 mg or less of sodium per 100 g of product.

The terms 'low sodium,' 'low in sodium,' 'little sodium,' 'contains a small amount of sodium,' or 'low source of sodium' may be used on the label, provided that the food has a reference amount customarily consumed greater than 30 g or greater than 2 tablespoons and contains 140 mg or less sodium per reference amount customarily consumed, or the food has a reference amount customarily consumed of 30 g or less or 2 tablespoons or less and contains 140 mg or less sodium per reference amount customarily consumed and per 50 g (for dehydrated foods that must be reconstituted before typical consumption). These terms may be used on the label or in labeling of meal products and main dish products provided that the product contains 140 mg or less sodium per 100 g.

The terms 'reduced sodium,' 'reduced in sodium,' 'sodium reduced,' 'less sodium,' 'lower sodium,' or 'lower in sodium' may be used on the label or in labeling of foods, provided that the food contains at least 25% less sodium per reference amount customarily consumed than an appropriate reference food.

The term 'salt free' may be used on the label only if the food is 'sodium free.' The terms 'unsalted,' 'without added salt,' and 'no salt added' may be used on the label only if there is no salt added during processing and the food that it resembles and for which it substitutes is normally processed with salt. If the food labeled 'salt free' is not sodium free, the statement, "not a sodium free food" or "not for control of sodium in the diet" must appear adjacent to the nutrition label of the food bearing the claim.

Fat Content Claims

Fat content claims include the terms 'fat free,' 'free of fat,' 'no fat,' 'zero fat,' 'without fat,' 'negligible source of fat,' or 'dietarily insignificant source of fat' or, in the case of milk products, 'skim' may be used on the label provided that the food contains less than 0.5 g (g) of fat per reference amount customarily consumed and per labeled serving or, in the case of a meal product or main dish product, less than 0.5 g of fat per labeled serving.

The terms 'low fat,' 'low in fat,' 'contains a small amount of fat,' 'low source of fat,' or 'little fat' may be used, provided that the food has a reference amount customarily consumed greater

than 30 g or greater than 2 tablespoons and contains 3 g or less of fat per reference amount customarily consumed, or the food has a reference amount customarily consumed of 30 g or less or 2 tablespoons or less and contains 3 g or less of fat per reference amount customarily consumed and per 50 g of food (for dehydrated foods that must be reconstituted before typical consumption). These terms may be used on the label meal products or main dish products provided that the product contains 3 g or less of total fat per 100 g and not more than 30% of calories from fat.

The terms 'reduced fat,' 'reduced in fat,' 'fat reduced,' 'less fat,' 'lower fat,' or 'lower in fat' may be used on the label, provided that the food contains at least 25% less fat per reference amount customarily consumed than an appropriate reference food. The identity of the reference food and the percent (or fraction) that the fat differs between the two foods and are declared in immediate proximity to the most prominent such claim (e.g., 'reduced fat – 50% less fat than the regular brownies')and quantitative information comparing the level of fat in the product per labeled serving with that of the reference food that it replaces (e.g., 'Fat content has been reduced from 8 g to 4 g per serving.') is declared adjacent to the most prominent claim or to the nutrition label.

Reduced fat claims may not be made on the label or in the labeling of a food if the nutrient content of the reference food meets the definition for 'low fat.' Reduced fat may be used on the label of meal products and main dish products, provided that the food contains at least 25% less fat per 100 g of food than an appropriate reference food and the identity of the reference food and the percent (or fraction) that the fat differs between the two foods are declared in immediate proximity to the most prominent such claim (e.g., reduced fat spinach souffle, '33% less fat per 3 oz than the regular spinach souffle').

The term '_ percent fat free' may be used on the label of foods, provided that the food meets the criteria for 'low fat.' A '100% fat free' claim may be made only on foods that meet the criteria for 'fat free,' meaning they contain less than 0.5 g of fat per 100 g and that they contain no added fat.

Fatty Acid Content Claims

The label or labeling of foods that bear claims with respect to the level of saturated fat shall disclose the level of total fat and cholesterol in the food in immediate proximity to such claim each time the claim is made and in type that shall be no less than one-half the size of the type used for the claim with respect to the level of saturated fat.

The terms 'saturated fat free,' 'free of saturated fat,' 'no saturated fat,' 'zero saturated fat,' 'without saturated fat,' 'trivial source of saturated fat,' 'negligible source of saturated fat,' or 'dietarily insignificant source of saturated fat' may be used on the label provided that the food contains less than 0.5 g of saturated fat and less than 0.5 g *trans* fatty acid per reference amount customarily consumed and per labeled serving, or in the case of a meal product or main dish product, less than 0.5 g of saturated fat and less than 0.5 g *trans* fatty acid per labeled serving.

The terms 'low in saturated fat,' 'low saturated fat,' 'contains a small amount of saturated fat,' 'low source of saturated fat,' or 'a little saturated fat' may be used on the label of foods, provided that the food contains 1 g or less of saturated fatty acids per reference amount customarily consumed and not more than 15% of calories from saturated fatty acids. These terms may be used in labeling meal products and main dish products, provided that the product contains 1 g or less of saturated fatty acids per 100 g and less than 10% calories from saturated fat.

The terms 'reduced saturated fat,' 'reduced in saturated fat,' 'saturated fat reduced,' 'less saturated fat,' 'lower saturated fat,' or 'lower in saturated fat' may be used on the label, provided that the food contains at least 25% less saturated fat per reference amount customarily consumed than an appropriate reference food. The identity of the reference food and the percent (or fraction) that the saturated fat differs between the two foods are declared in immediate proximity to the most prominent such claim (e.g., 'reduced saturated fat. Contains 50% less saturated fat than the national average for nondairy creamers'). These claims may not be made on the label of a food if the nutrient content of the reference food meets the definition for 'low saturated fat.'

Cholesterol Content Claims

The terms 'cholesterol free,' 'free of cholesterol,' 'zero cholesterol,' 'without cholesterol,' 'no cholesterol,' 'trivial source of cholesterol,' 'negligible source of cholesterol,' or 'dietarily insignificant source of cholesterol' may be used on the label, provided that the food contains less than 2 mg of cholesterol per reference amount customarily consumed and per labeling serving or, in the case of a meal product or main dish product, less than 2 mg of cholesterol per labeled serving. Additionally, foods must contain 13 g or less of total fat per reference amount customarily consumed, per labeled serving, and per 50 g if the reference amount customarily consumed is 30 g or less or 2 tablespoons or less (for dehydrated foods that must be reconstituted before typical consumption) or, in the case of meal products, 26.0 g or less total fat per labeled serving, or, in the case of main dish products, 19.5 g or less total fat per labeled serving.

For food that contains more than 13 g of total fat per reference amount customarily consumed, per labeling serving, or per 50 g if the reference amount customarily consumed is 30 g or less or 2 tablespoons or less (for dehydrated foods that must be reconstituted before typical consumption) with water or a diluent containing an insignificant amount, as defined in 21 CFR 101.9(f)(1), of all nutrients per reference amount customarily consumed, the per 50 g criterion refers to the 'as prepared' form), or in the case of a meal product, more than 26 g of total fat per labeled serving, or, in the case of a main dish product more than 19.5 g of total fat per labeled serving, they must contain less than 2 mg of cholesterol per reference amount customarily consumed and per labeling serving, or, in the case of a meal product or main dish product, less than 2 mg of cholesterol per labeled serving, and 2 g or less of saturated fatty acids per reference amount customarily consumed or, in the case of a meal product or main dish product, less than 2 g of saturated fatty acids per labeled serving.

The identity of the reference food and the percent (or fraction) that the cholesterol was reduced are declared in

immediate proximity to the most prominent such claim (e.g., 'cholesterol-free margarine, contains 100% less cholesterol than butter').

The terms 'low in cholesterol,' 'low cholesterol,' 'contains a small amount of cholesterol,' 'low source of cholesterol,' or 'little cholesterol' may be used on the label provided that the food contains 20 mg or less of cholesterol per reference amount customarily consumed and 2 g or less of saturated fatty acids per reference amount customarily consumed. Foods must also have a reference amount customarily consumed greater than 30 g or greater than 2 tablespoons and contain 13 g or less of total fat per reference amount customarily consumed and per labeled serving. For foods that have a reference amount customarily consumed of 30 g or less or 2 tablespoons or less and contain 13 g or less of total fat per reference amount customarily consumed, per labeled serving, and per 50 g (for dehydrated foods that must be reconstituted before typical consumption), the food must contain 20 mg or less of cholesterol per reference amount customarily consumed and per 50 g (for dehydrated foods that must be reconstituted before typical consumption) and 2 g or less of saturated fatty acids per reference amount customarily consumed.

Health Claims

The FDA publishes regulations officially recognizing certain associations between food ingredients and health. Depending on the robustness of the scientific data, these may be Qualified Health Claims of Claims of SSA. The greatest threshold for a health claim in FDA's classification is an SSA claim.

In evaluating a petition for an authorized health claim, the FDA considers whether the evidence supporting the relationship that is the subject of the claim meets the SSA standard. This standard derives from 21 U.S.C. 343 (r)(3)(B)(i), which provides that the FDA shall authorize a health claim to be used on conventional foods if the agency "determines based on the totality of the publicly available evidence (including evidence from well-designed studies conducted in a manner that is consistent with generally recognized scientific procedures and principles), that there is SSA among experts qualified by scientific training and experience to evaluate such claims, and that the claim is supported by such evidence." This scientific standard was prescribed by statute for conventional food health claims and by regulation (21 CFR Section 101.14(c)).

Qualified health claims fall short of the threshold for SSA claims. The genesis of qualified health claims was the court of appeals decision in Pearson versus Shalala. In that case, the plaintiffs challenged FDA's decision not to authorize health claims for four specific substance–disease relationships in the labeling of dietary supplements. Although the district court ruled for the FDA, the US Court of Appeals for the DC Circuit reversed the lower court's decision. The appeals court held that the First Amendment does not permit the FDA to reject health claims that the agency determines to be potentially misleading unless the agency also reasonably determines that a disclaimer would not eliminate the potential deception. The appeals court also held that the Administrative Procedure Act required the FDA to clarify the SSA standard for authorizing health claims. In 1999, the FDA published guidance for the submission of health claims, entitled Guidance for Industry: SSA in the Review of Health Claims for Conventional Foods and Dietary Supplements (US Department of Labor, 1999).

Significant Scientific Agreement Claims

The list of currently approved SSA claims includes the following:

- Calcium, Vitamin D, and Osteoporosis (21 CFR 101.72)
- Dietary Lipids (Fat) and Cancer (21 CFR 101.73)
- Dietary Saturated Fat and Cholesterol and Risk of Coronary Heart Disease (21 CFR 101.75)
- Dietary Noncariogenic Carbohydrate Sweeteners and Dental Caries (21 CFR 101.80)
- Fiber-containing Grain Products, Fruits and Vegetables, and Cancer (21 CFR 101.76)
- Folic Acid and Neural Tube Defects (21 CFR 101.79)
- Fruits and Vegetables and Cancer (21 CFR 101.78)
- Fruits, Vegetables, and Grain Products that contain Fiber, particularly Soluble fiber, and Risk of Coronary Heart Disease (21 CFR 101.77)
- Sodium and Hypertension (21 CFR 101.74)
- Soluble Fiber from Certain Foods and Risk of Coronary Heart Disease (21 CFR 101.81)
- Soy Protein and Risk of Coronary Heart Disease (21 CFR 101.82)
- Stanols/Sterols and Risk of Coronary Heart Disease (21 CFR 101.83)

Qualified Health Claims

The list of currently available Qualified Health Claims includes the following:

Qualified Claims about Atopic Dermatitis
- 100% Whey-Protein Partially Hydrolyzed Infant Formula and Reduced Risk of Atopic Dermatitis

Qualified Claims about Cancer Risk
- Tomatoes and/or Tomato Sauce and Prostate, Ovarian, Gastric, and Pancreatic Cancers
- Calcium and Colon/Rectal Cancer and Calcium and Recurrent Colon/Rectal Polyps
- Green Tea and Cancer
- Selenium and Cancer
- Antioxidant Vitamins and Cancer

Qualified Claims about Cardiovascular Disease Risk
- Nuts and Heart Disease
- Walnuts and Heart Disease
- Omega-3 Fatty Acids and Coronary Heart Disease
- B Vitamins and Vascular Disease
- Monounsaturated Fatty Acids From Olive Oil and Coronary Heart Disease
- Unsaturated Fatty Acids from Canola Oil and Coronary Heart Disease
- Corn Oil and Heart Disease

Qualified Claims about Cognitive Function
- Phosphatidylserine and Cognitive Dysfunction and Dementia

Qualified Claims about Diabetes
- Chromium Picolinate and Diabetes

Qualified Claims about Hypertension
- Calcium and Hypertension, Pregnancy-Induced Hypertension, and Preeclampsia

Qualified Claims about Neural Tube Birth Defects
- 0.8 mg Folic Acid and Neural Tube Birth Defects

Qualified health claims are allowed only as described in regulation, which include disclaimers about the quantity or quality of the scientific evidence supporting the health association.

Structure/Function Health Claims

Structure/function claims are the most frequently used of the health claims recognized by the FDA. These claims describe the role of a nutrient or dietary ingredient intended to affect normal structure or function in humans, for example, 'calcium builds strong bones.' In addition, they may characterize the means by which a nutrient or dietary ingredient acts to maintain such structure or function, for example, 'fiber maintains bowel regularity,' 'antioxidants maintain cell integrity,' or they may describe general well-being from consumption of a nutrient or dietary ingredient. Structure/function claims may also describe a benefit related to a nutrient deficiency disease (e.g., Vitamin C and scurvy), as long as the statement also tells how widespread such a disease is in the United States.

The manufacturer may create the claim – there is no prescribed list of claims – but is responsible for the accuracy and truthfulness of these claims. Structure/function claims are not preapproved by the FDA and are held to the standard that they are truthful and are not misleading. Structure/function claims must support a health state and not attempt to ascribe conditions that prevent, cure, or treat a disease. Such statements are understood to be claims made possible only for drugs, and a food so labeled would be subject to seizure as an unapproved drug.

Front-of-Pack Labeling Initiatives

There is an ongoing effort to improve the relevance and utility of nutrition label information to consumers. A variety of nutrition rating systems and symbols appeared on the front of food packages starting in the mid-2000s – meant to make it easier for consumers to make healthful choices. It is possible that the plethora of nutrition rating systems seen in grocery stores today lead to confusion in the grocery aisle and not clarity.

In an effort to address the situation, the US Congress directed the Centers for Disease Control and Prevention to undertake a study with the Institutes of Medicine with additional support provided by the FDA and the USDA. The task was split into two phases. A first report analyzed the nutrition rating systems and the scientific research that underlies them and was released in 2010 (IOM, 2010). The second report delved into consumer use and understanding of front of package systems and was released in 2011 (IOM, 2011).

The report concludes that it is time for a move away from front-of-package systems that mostly provide nutrition information on foods or beverages but do not give clear guidance about their healthfulness and toward one that encourages healthier choices through simplicity, visual clarity, and the ability to convey meaning without written information. The report recommends that the FDA develop, test, and implement a single, standard front-of-pack symbol system to appear on all food and beverage products, in place of other systems already in use. The symbol system should show calories in household servings on all products. Foods and beverages should be evaluated using a point system for saturated and *trans* fats and sodium and added sugars. The more points a food or beverage has, the healthier it is. This system would encourage food and beverage producers to develop healthier fare and consumers to quickly and easily find healthier products when they shop.

The food industry, both manufacturers and retailers, have been active in creating a variety of nutrition rating and symbol schemes, including Facts Up Front, NuVal, and Guiding Stars. The FDA is working to revise and update nutrition labeling in a uniform manner that presents relevant information most clearly to consumers – information that hopefully improves food choices and public health in the long term.

Global Approaches to Food Labeling

The following tables summarize approaches to food labeling in Europe, Asia Pacific, and Latin American regions of the World. For each country identified, the regulatory authority and legal standards, general labeling requirements, nutritional labeling requirements, and general approach to health claims are identified.

Australia

Authority: Food Standards Australia New Zealand (FSANZ)
General Labeling Standard: Part 1.2 of the Australia New Zealand Food Standards Code (ANZFSC)
Mandatory Nutrition Labeling: Yes
Nutrition Labeling Standard: Standard 1.2.8

General labeling requirements	*Nutritional labeling requirements*	*Health claims approach*
Prescribed name or description of the food	Panel must be set out in specific format	All health claims are required to be supported by scientific evidence
Lot identification	Energy	Can be preapproved by FSANZ or self-substantiated by food businesses
Name and business address in Australia or New Zealand of the supplier	Protein	

Mandatory warning and advisory statements	Fat
Ingredient listing	Saturated fat
Date marking	Carbohydrate
Nutrition information panel	Sugars
Percentage labeling	Sodium
Directions for use or storage	Number of servings per package
Country of origin	Serving size

Brazil

Authority: Ministry of Agriculture, Livestock, and Food Supply, National Agency of Sanitary Surveillance (ANVISA)

General Labeling Standard: Resolução RDC n° 123, de 13 de maio de 2004, Lei n° 10.674, de 16 de maio de 2003, Resolução RDC n° 259, de 20 de Setembro de 2002

Mandatory Nutrition Labeling: Yes

Nutrition Labeling Standard: Resolução – RDC n° 360, de 23 de Dezembro de 2003, Resolução RDC n° 359, de 23 de Dezembro de 2003, Resolução – RDC n° 163, de 17 de Agosto de 2006

General labeling requirements	*Nutritional labeling requirements*	*Health claims approach*
Name of food	Serving size with household measurement	All health claims must be approved by ANVISA on a case-by-case basis
Brand	Energy (kcal and kJ)	Foods using health claims on packaging or advertisement must be registered under category of
Quantity indication	Protein	Food with functional properties and health claims'
Net weight	Carbohydrate	
List of ingredients	Total Fat	
Country of origin of manufacturing company	Saturated fat	
Country of origin of importer	*Trans* fat	
Expiration date	Dietary Fiber	
Lot number	Sodium	
Handling information	Vitamins/Minerals	
'Contains Gluten' or 'Does not Contain Gluten' statement	% Daily requirements with reference to the basis in a 2000 kcal, or 8400 kJ diet	
Nutritional information		
Labeling of certain biotechnology ingredients where the genetically modified content of the labeled ingredient exceeds 1%		

China

Authority: Ministry of Health

General Labeling Standard: General Rules for the Labeling of Prepackaged Foods GB 7718

Mandatory Nutrition Labeling: No

Nutrition Labeling Standard: GB 28050. Mandatory for special diet food and principal and supplementary foods for infant and babies and foods making a nutrition claim on package

Nutrition Labeling of Prepackaged Foods

General labeling requirements	*Nutritional labeling requirements*	*Health claims approach*
Product name and description name of food	Energy value (kJ)	Scientific evidence-based approach for approval of health claims
List of ingredients	Protein	Functional foods must be registered with government
Quantitative labeling	Fat	Reduction of disease risk claims and special functional claims must follow GB16740
Net weight and configuration	Carbohydrate	27 Categories of claims are allowed
Address and contact information of manufacturers and distributors	Sodium	
Date of manufacture	Per 100 g or 100 ml and per serving	
Shelf life		
Conditions for the storage		
Food production license number		
Code of the product standard		

Costa Rica

Authority: Ministry of Health, Ministry of Economy and Commerce

General Labeling Standard: RTCA 67.04.54:10 (Central American Technical Regulation)

Mandatory Nutrition Labeling: No. Mandatory when nutritional claims are made RTCA 67.01.60:10

Nutrition Labeling Standard: Not existent

General labeling requirements	*Nutritional labeling requirements*	*Health claims approach*
Product name	Energy value (kJ)	Health claims approved by the FDA, EU, or other recognized governmental agencies can be used. All other claims must be approved by the Ministry of Health

Net content	Protein	A list of preapproved claims is found under Annex G of the regulation
Artificial color and flavors (if any)	Carbohydrates	
Ministry of Health registration number	Fat	
Ingredients listing	Saturated fat only if product contains more than 0.5 g total fat	
Quantity labeling of ingredients	Sodium	
Manufacturer's name and address	Value of nutrients used in claims	
Importer's name and address if applicable	Per serving, 100 g or 100 ml	
Lot number and expiration date		
Country of origin		
Storage and use instructions		

Chile

Authority: Ministry of Health

General Labeling Standard: Decree 977, Title 2

Mandatory Nutrition Labeling: Yes

Nutrition Labeling Standard: Decree 977, Title 2. Nutritional composition and advertisement for foods

General labeling requirements	*Nutritional labeling requirements*	*Health claims approach*
Name of the food product	Energy value in calories	All health claims shall be truthful, proven through scientific methods, and recognized by international organizations
Net content in metric units	Protein Available carbohydrates	There is a list of preapproved health claims
Name or company name and address of the manufacturer, packer, distributor, or importer	Fats	
Country of Origin	Sodium	
Number and date of resolution authorizing import	Quantity of any other nutrient, dietary fiber, and cholesterol, concerning which a representation of properties is made	
Date of manufacture or packing date	Per 100 g or 100 ml, and per serving	
Lot code	Number of servings in the container	
Expiration date or shelf life	Size of each serving	
List of all ingredients		
Instructions for storage		
Instructions for use		

European Union

Authority: European Commission, The Council of the EU, The European Parliament

General Labeling Standard: Current: EC Labeling Directive (2000/13/EC). After December 2014: Regulation 1169/2011 on the provision of food information to consumers

Mandatory Nutrition Labeling: Currently no. Mandatory required if a claim is made. Yes after December 2014

Nutrition Labeling Standard: Council Directive 90/496/EEC

General labeling requirements	*Nutritional labeling requirements*	*Health claims approach*
Name of the food	Energy value	European Parliament and Council Regulation 1924/2006 sets conditions for use for health claims
List of ingredients	Protein	Foods must fit a specific nutrient profile to make health claims Regulation 432/2012 establishes the EU-positive list of 222 approved health claims
References to allergens	Carbohydrate	
QUID information	Fat	
Net quantity	Sugars, saturates, fiber, and sodium shall be declared if a nutrient content claim is made of these nutrients	
Durability indication		
Storage conditions/ conditions of use		
Name and address of food business operator		
Country of origin		
Instructions for use (where required)		
Nutrition declaration		

Abbreviation: QUID, quantitative ingredients declaration.

India

Authority: Ministry of Health and Family Welfare

General Labeling Standard: Food Safety and Standards (Packaging and Labeling) Regulation

Mandatory Nutrition Labeling: Yes

Nutrition Labeling Standard: Food Safety and Standards (Packaging and Labeling) Regulation

General labeling requirements	*Nutritional labeling requirements*	*Health claims approach*
Name of food	Energy kcal	Health claims are classified as: Nutrient function claims, other function claims, disease risk reduction claims
List of ingredients	Protein	Claims related to disease risk reduction shall be made from the list of approved claims (Annexure IV)
Nutritional information	Carbohydrates	Any new claim on disease risk reduction must be authorized
Declaration regarding veg or nonveg: brown color symbol for nonvegetarian; green color symbol for vegetarian food	Sugars	
Statement regarding presence of added colors and flavors	Fat	
Name and address of manufacturer	Other nutrients for which nutrient claims have been made	
Name and address of importer in India if applicable	Amount of vitamins and minerals	
Net quantity		
Lot/code/batch identification		
Date of manufacture		
Best before and Use by date		
Country of origin for imported foods		
Instructions for use		

Japan

Authority: The Ministry of Health, Labor and Welfare (MHLW), The Consumer Affairs Agency

General Labeling Standard: Japan Agriculture Standard Law, Food Sanitation Law

Mandatory Nutrition Labeling: No, except for nutrition claims

Nutrition Labeling Standard: Except for foods with nutrition claims

General labeling requirements	*Nutritional labeling requirements*	*Health claims approach*
Name of the product	Energy	There is a list of health claims preapproved by the MHLW
Country of origin	Protein	All other food for specified health uses claims must be submitted for approval under: regular, qualified, standardized, reduction of disease
Name of the importer	Fat	
Ingredients, other than additives, in descending order of weight percentage	Carbohydrates	
Food additives in descending order of weight on a separate line from other ingredients	Dietary fiber	
The net weight in metric units only	Sodium	
Best-before date	Per 100 g, 100 ml, package or serving	
Storage instructions		
Labeling of certain biotechnology ingredients where the genetically modified content of the labeled ingredient exceeds 5%		

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15 USC Section 52
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21 CFR 101.105(e) and (f)
21 CFR Section 101.1
21 CFR Section 101.1 (FDA)
21 CFR Section 101.105
21 CFR Section 101.105(a) and (b) and (c)
21 CFR Section 101.105(h) and (i)
21 CFR Section 101.14(c)
21 CFR Section 101.17 (FDA)
21 CFR Section 101.2 (FDA)
21 CFR Section 101.22(a)(1)
21 CFR Section 101.22(a)(5)
21 CFR Section 101.4
21 CFR Section 101.4(20)
21 CFR Section 101.54
21 CFR Section 101.56
21 CFR Section 101.60
21 CFR Section 101.9
21 CFR Sections 182.10 and 184
21 USC Section 671(meat); 21 USC Section 467 (poultry)
9 CCFR Section 317.2 (m) (meat)
9 CFR Section 317.2 (m) meat
9 CFR Section 317.2(b); 9 CFR 381.115(b)
9 CFR Section 317.2(d) (meat); 9 CFR Section 381.116 (poultry)

9 CFR Section 317.2(h)(2) (meat); 9 CFR Section 381.121(c)(6) (poultry)
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9 CFR Section 381.120
9 CFR Section 381.125(a) (poultry)
9 CFR Section 381.125(b) (poultry)
9 CFR Section 381.15(c)
9 CFR Sections 301.2 and 381.1(b) (definition of 'immediate container'); 9 CFR Section 317.2 (definition of 'protective covering')
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Food Law

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Food Law

Food law is a part of the law that encompasses all rules, regulations, case law, and soft law regarding food. This makes food law a 'functional area of law,' placing attention on societal application rather than on doctrinal distinctions. It includes national and international, private and public, criminal and administrative provisions with regard to food.

Most countries of the former British Empire belong to the common law family of law. In food, they have been influenced by the approach in the Adulteration of Food and Drink Act of 1860 and the Food and Drug Act of 1872. This shows that in the central position the concept of 'adulteration' still holds today. From this part of the world, we will discuss food law in the United States.

The civil law family of law – continental European countries and their former colonies – and its related approach to food is represented by the EU. The development of US federal food law dates back to the beginning of the twentieth century. It is mainly based on criminal law approaches. EU food law is halve a century younger. The EU does not have its own system of criminal law. For both reasons, EU food law is mainly based on administrative law approaches. Given this distinction, it may be expected that US food law is drafted in terms of 'don'ts' and EU food law in terms of 'dos.'

Food trade is globalizing. Since the 1960s international standards are developing. International food law has taken up momentum after the entry into force of the WTO agreement in 1995.

Since 1990s the private sector has taken the initiative in regulating (international) trade in food (Figure 1).

This section addresses the international dimension of food law (Section 2), American food law (Section 3), European food law (Section 4), and private food law (Section 5). The last section introduces some organizations active in food law.

International Food Law

In the global arena different players address food. The United Nations (UN) lay emphasis on human rights. The Food and Agriculture Organization (FAO) and the World Health Organization (WHO) have the lead in the core elements of standard setting: risk assessment and risk management. The World Trade Organization (WTO) plays a major role in application of food standards in trade and dispute resolution. WHO operates risk communication structures, seminal in incident management. International food law is a meta-framework (van der Meulen 2011). It does not apply to actions by stakeholders, but makes requirements on national food law that in its turn does address actions by individual stakeholders.

Human Right

The human right to adequate food is recognized in the Universal Declaration on Human Rights (Article 25) and international treaties such as the International Covenant on Economic, Social and Cultural Rights (Article 11). Organizations such as FAO and the UN Committee on Economic, Social and Cultural Rights have further elaborated this right. See, for example, the voluntary guidelines to support the progressive realization of the right to adequate food in the

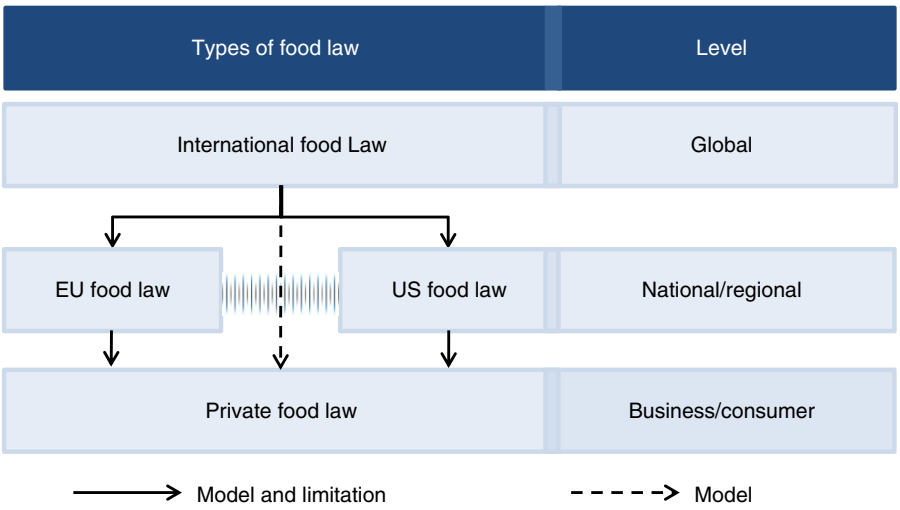


Figure 1 Levels of food law discussed in this contribution.

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context of national food security at http://www.fao.org/docrep/meeting/009/y9825e/y9825e00.htm. The right to adequate food is realized if people have access to food that

1. provides sufficient nutritional value and micronutrients to lead a healthy and active life;
2. is free of hazardous substances;
3. is acceptable within a given culture.

Complementary to human rights are the state obligations:

1. To respect – generally people can care for themselves and their families. This ability may not be curbed without justification.
2. To protect – if self-sufficiency of citizens is threatened by others the government must do its best to protect them.
3. To fulfill – this obligation encompasses a policy obligation and a relief obligation. A prudent government adopts policies supporting and promoting the ability of the population to provide for itself; it must do its best to provide assistance if people cannot provide for themselves through no fault of their own.

Below we see that mainly the second aspect of adequate food (safety) and the second state obligation (to protect) are taken up in food regulatory systems (Figure 2).

Standard Setting

Risk assessment

Risk assessment for international standard setting is undertaken in three joint FAO and WHO committees: the joint FAO/WHO Committee on Food Additives (JECFA); the Joint FAO/WHO Meetings on Pesticide Residues (JMPR); and the Joint FAO/WHO Meetings on Microbiological Risk Assessment (JEMRA). They advise on maximum limits for food additives, pesticide residues, microbes, and on other food safety issues.

Codex Alimentarius

In 1963, FAO and WHO established the Codex Alimentarius Commission (CAC). CAC established specialized committees, hosted by member states all over the world. 186 CAC members, 185 countries, and the EU are part of the Commission.

Food standards are established through an elaborate procedure of international negotiations (FAO/WHO 2006). All standards together are called 'Codex Alimentarius' (Latin for 'food code'). It also includes advisory provisions called codes of practice or guidelines, mainly addressing food businesses.

At present, Codex comprises more than 200 standards, close to 50 food hygiene and technological codes of practice, approximately 65 guidelines, more than 1000 food additives and contaminants evaluations, and more than 3200 maximum residue limits for pesticides and veterinary drugs (FAO/WHO 2002, FAO/WHO 2006, Masson-Matthee 2007).

Codex procedural manual

The 'constitution' of the Codex Alimentarius is the Procedural Manual. It gives the procedures and formats for setting Codex Standards and Guidelines, and also some general principles and definitions (Table 1). The principles relate among other things to scientific analysis (Table 2).

Codex standards

CAC's work has resulted in a collection of internationally agreed food standards that are presented in a uniform format.

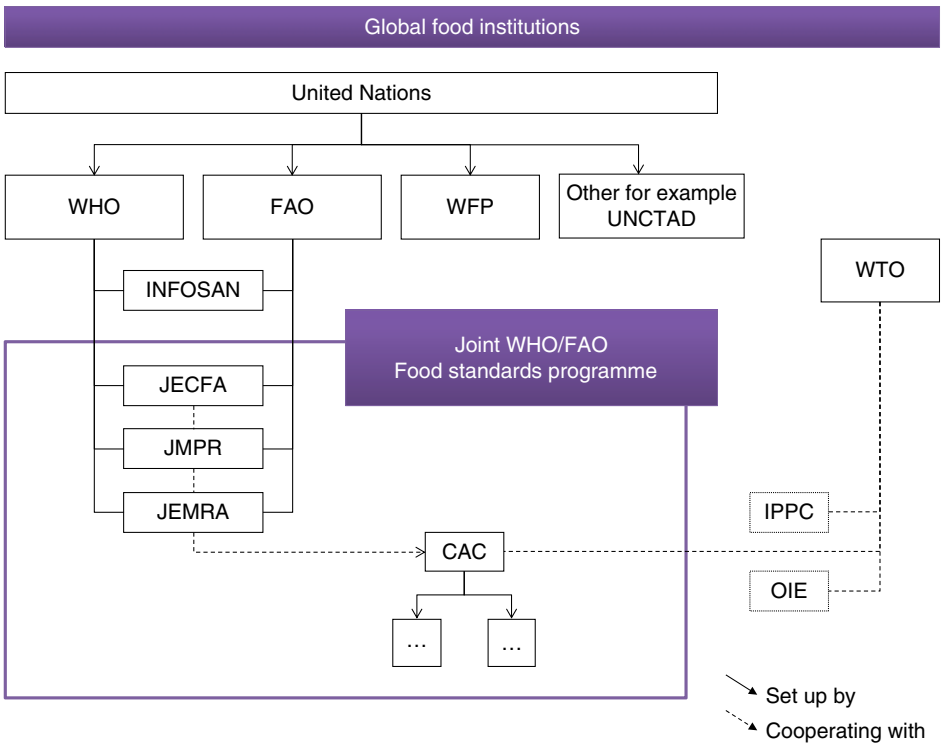


Figure 2 Global food institutions.

Table 1 Some definitions in the Codex Alimentarius Procedural Manual

'Food' means any substance, whether processed, semiprocessed, or raw, which is intended for human consumption, and includes drink, chewing gum, and any substance which has been used in the manufacture, preparation, or treatment of 'food' but does not include cosmetics or tobacco or substances used only as drugs.
'Food hygiene' comprises conditions and measures necessary for the production, processing, storage, and distribution of food designed to ensure a safe, sound, wholesome product fit for human consumption.

Table 2 Example of principles in the Codex Alimentarius Procedural Manual

The food standards, guidelines, and other recommendations of Codex Alimentarius shall be based on the principle of sound scientific analysis and evidence, involving a thorough review of all relevant information, in order that the standards assure the quality and safety of the food supply.

Table 3 Definition of food additive in the Codex General Standard for Food Additives

'Food additive' means any substance not normally consumed as a food by itself and not normally used as a typical ingredient of the food, whether or not it has nutritive value, the intentional addition of which to food for a technological (including organoleptic) purpose in the manufacture, processing, preparation, treatment, packing, packaging, transport or holding of such food results, or may be reasonably expected to result (directly or indirectly), in it or its byproducts becoming a component of or otherwise affecting the characteristics of such foods. The term does not include contaminants or substances added to food for maintaining or improving nutritional qualities.

Table 4 The principles of HACCP according to Codex Alimentarius

Principle 1	Conduct a hazard analysis.
Principle 2	Determine the Critical Control Points (CCPs).
Principle 3	Establish critical limit(s).
Principle 4	Establish a system to monitor control of the CCP.
Principle 5	Establish the corrective action to be taken when monitoring indicates that a particular CCP is not under control.
Principle 6	Establish procedures for verification to confirm that the HACCP system is working effectively.
Principle 7	Establish documentation concerning all procedures and records appropriate to these principles and their application.

Most of these are of a product-specific nature (what in the US are called standards of identity and in the EU vertical legislation). Standards of a horizontal nature are often called 'general standards,' such as the General Standard for the Labeling of Prepackaged Foods (CODEX STAN 1-1985 (Rev. 1-1991)).

According to this general standard, the following information shall appear on the labeling of prepackaged foods: the name of the food; this name shall indicate the true nature of the food; list of ingredients (in particular, if one of a list of eight allergens is present); net contents; name and address of the business; country of origin where omission could mislead the consumer; lot identification; date marking and storage instructions; and instructions for use.

The Codex General Standard for Food Additives (CODEX STAN 192-1995) sets forth the conditions under which permitted food additives may be used in all foods (Table 3).

Codex codes

In addition to the formally accepted standards the Codex includes recommended provisions called codes of practice or guidelines. There is, for example, a set of hygiene codes including the 'Hazard Analysis and Critical Control Point (HACCP) System and Guidelines for its Application' (Table 4).

Legal force

Codex standards do not legally bind. They present models for national legislation. Member states undertake to transform Codex standards into national legislation. However, no sanctions apply if they do not honor this undertaking.

Trade and Dispute Settlement

The WTO was established on 1 January 1995 by the agreement establishing the World Trade Organization as the result of the so-called Uruguay round of trade negotiations and signed in Marrakesh on 15 April 1994 (WTO Agreement). It is the institutional continuation of the General Agreement on Tariffs and Trade 1947 (GATT). It endeavors to liberalize international trade. The basic treaty addressing trade in goods is GATT. GATT recognizes that exceptions to free trade can be necessary to protect higher values such as health and (food) safety.

The agreement on the Application of Sanitary and Phytosanitary Measures (SPS) ensures that countries only apply measures to protect human and animal health (sanitary measures) and plant health (phytosanitary measures) based on the assessment of risk, or in other words, based on science. If the measures are in conformity with international standards, no scientific substantiation of necessity is required. These measures are by definition considered necessary. For food, these international standards are the Codex Alimentarius. This inclusion of Codex in the SPS Agreement greatly enhances its significance. WTO members who follow Codex need not

substantiate the necessity of their sanitary and phytosanitary measures.

WTO agreements bind WTO members. The Dispute Settlement Understanding provides procedures to resolve conflicts. If a party so requires, the Dispute Settlement Body (DSB) forms a panel to adjudicate. Panel decisions can be appealed to the Appellate Body (AB). WTO cannot enforce decisions taken in this procedure; but it can allow the winning party to implement economic sanctions in case of non-compliance. These sanctions are usually additional import levies on goods from the state found at fault.

Incident Management

In case of global food safety incidents such as the Melamine crisis, WHO holds a key position. The International Health Regulations 2005 grant powers to its member states. WHO has set up a worldwide information exchange network INFOSAN (International Food Safety Authorities Network) to enable rapid action.

US Food Law

Constitutional Basis

In the United States of America, food largely is a matter within the powers of the states. The involvement of federal authorities (to which this contribution is limited) is mainly based on Congress' power to regulate interstate commerce (**Table 5**).

Development

Early development of US food law was sparked by economic adulteration, that is, replacing quality ingredients by inferior substances such as addition of chalk to bread and sand to coffee. In 1820, Frederick Accum documented adulteration in the UK. As it was widespread it was difficult to find a single type of food that was not adulterated; he scarcely found some genuine foods (Accum 1820, Hutt and Hutt 1984, Wilson 2008, Fortin 2009).

From the very first, food was regulated in connection with medicinal drugs, and later, medical devices and cosmetics were also regulated. Developments in these areas mutually influenced each other.

Before the independence of the United States, British common law applied the earliest food safety law. The essence was plain and direct: (1) Do not poison food and (2) do not cheat (Hutt 1960, Fortin 2009). 'Adulterated food' in the common law consisted of food that was unfit for human consumption or contained some deleterious substances, whereby rendering it dangerous to health. Packaged food with labels was rare, so there was no common-law offense of mislabeling. However, there existed the offense of falsely representing merchandise for sale (Hutt 1960, Fortin 2009).

Table 5 Article I, section 8, clause 3 of the USA Constitution

Powers of Congress
The Congress shall have Power (...)
To regulate Commerce with foreign Nations, and among the several States, and with the Indian Tribes.

Through the late 1800s, nearly all food laws were state and local. Federal activity was largely limited to regulate imports and exports.

Public support for passage of a federal food and drug law grew as journalists exposed frauds and dangers, such as the use of poisonous preservatives and dyes in food (Fortin 2009). A final catalyst was the 1905 publication of Upton Sinclair's *The Jungle*. Sinclair's portrayal of nauseating practices and unsanitary conditions in the meatpacking industry captured the public's attention. In 1906, President Theodore Roosevelt enacted the Pure Food and Drug Act (21 USC §1 *et seq.*) and the Meat Inspection Act 21 (USC §601 *et seq.*) into law.

Major amendments to these Acts were stalled until the Elixir Sulfanilamide disaster of 1937. The agonizing deaths of more than 100 children spurred the passage of the Federal Food, Drug, and Cosmetic Act of 1938.

In the 1950s, concerns over synthetic food additives, pesticides, and cancer were high. In 1958, the Food Additives Amendment was enacted, requiring the evaluation of food additives to establish safety. The Delaney Clause forbade the use of any substance in food that was found to cause cancer in laboratory animals (Fortin 2009).

In the second half of the first decade of the twenty-first century, a series of high-profile food safety incidents struck the USA. In response, president Barack Obama enacted the FDA Food Safety Modernization Act (FSMA) into law in January 2011. The FSMA places emphasis on preventive food safety systems (Fortin 2011).

Authorities

Regulatory authorities

When the United States Department of Agriculture (USDA) was created in 1862, the Congress authorized it to employ chemists. Eventually, this chemical division became the U.S. Food and Drug Administration (FDA) in 1930 (Hutt 1990, Fortin 2009). FDA was transferred from USDA in 1940 and into the Health Department (now the Department of Health and Human Services) in 1953. FDA received its statutory basis in 1988. Currently, the authority to regulate food is divided among USDA (meat and poultry), FDA (most other foods), and a series of other agencies (with relatively small tasks).

The functions of risk assessment and risk management are combined.

Inspection

The authority to inspect compliance with food law is divided among FDA, state and local governments, two agencies under USDA (FSIS (Food Safety Inspection Service) for meat in interstate commerce and APHIS (Animal and Plant Health Inspection Service) for imports and exports), and several other agencies.

Legislation

Structure of Federal Food Drug and Cosmetic Act

The basic Act in American food law is the Federal Food Drug and Cosmetic Act (FFDCA) (**Table 6**).

Table 6 Definition of food

FFDCA SEC. 201 [21 U.S.C. 321] (f)
The term 'food' means (1) articles used for food or drink for man or other animals, (2) chewing gum, and (3) articles used for components of any such article.

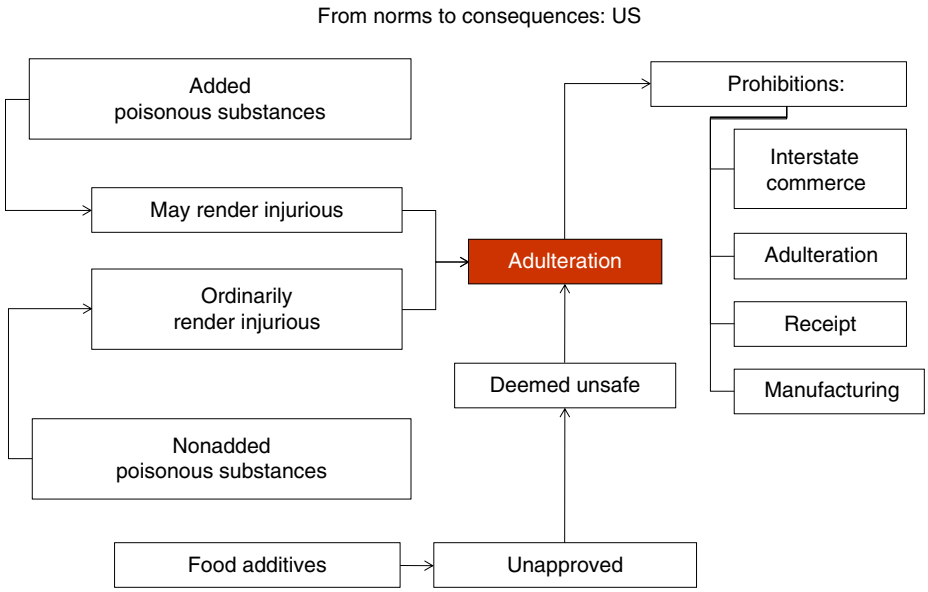


Figure 3 Structure of US food law illustrated as an example of adulteration.

Table 7 Section 402(a)(1) FFDCA

A food shall be deemed to be adulterated if it bears or contains any poisonous or deleterious substance which may render it injurious to health; but in case the substance is not an added substance such food shall not be considered adulterated under this clause if the quantity of such substance in such food does not ordinarily render it injurious to health.

This Act applies a funnel structure. At the heart of the funnel are the concepts 'adulteration' and 'misbranding' (FFDCA Sec. 301 [21 USC §331] Prohibited acts) (All US acts are codified in the US Code. *See* the References section.) All situations regarding food that the FFDCA and regulations based on it try to avoid are defined as fulfilling one of these concepts (Adulteration: FFDCA Sec. 402 [21 USC 342]; Misbranding: FFDCA Sec. 403 [21 USC 343]). To situations of 'adulteration' or 'misbranding', the FFDCA applies prohibitions, penalties, and instruments of law enforcement (FFDCA Sec. 303 [21 USC §333] Penalties).

Consequences

According to Sec. 301 of the FFDCA, the following are prohibited: adulteration or misbranding of food, introduction of adulterated or misbranded food into interstate commerce, receipt in interstate commerce of adulterated or misbranded food, and manufacture of adulterated or misbranded food.

In case of a violation, the perpetrator risks prison of up to 1 year the first time and up to 3 years after a first conviction, or a fine of up to $1000 for first offenders and $10 000 for recidivists.

Further, the FFDCA provides powers of establishment inspection, seizure of products; mass seizure; detention of products, import detention and injunction.

To these powers the FSMA added the power to impose a mandatory recall (Figure 3).

Adulteration

Poisonous or deleterious substance

The concept of adulteration is mainly about the safety of the food, but quality aspects ('economic adulteration') are also taken into account. A difference is made between substances that are added to the food or that are naturally present. To the former a more strict regime applies (Table 7).

Prior authorization

In the 1950s, the USA introduced a requirement of prior authorization for food additives (Table 8). Products within the definition need to be authorized or enjoy Generally Recognized As Safe (GRAS) status. Failing this, foods containing them are considered adulterated (Table 9).

Table 8 Section 201(s) FFDCA [21 USC 321]

The term 'food additive' means any substance the intended use of which results or may reasonably be expected to result, directly or indirectly, in its becoming a component or otherwise affecting the characteristics of any food (including any substance intended for use in producing, manufacturing, packing, processing, preparing, treating, packaging, transporting, or holding food; and including any source of radiation intended for any such use), if such substance is not generally recognized, among experts qualified by scientific training and experience to evaluate its safety, as having been adequately shown through scientific procedures (or, in the case of a substance used in food prior to January 1, 1958, through either scientific procedures or experience based on common use in food) to be safe under the conditions of its intended use (...)

Table 9

FFDCA section 402(2)(C): A food shall be deemed to be adulterated if it is or if it bears or contains any food additive that is unsafe within the meaning of section 409.

FFDCA section 409 (1)(a): A food additive shall, with respect to any particular use or intended use of such additives, be deemed to be unsafe for the purposes of the application of clause (2)(C) of section 402(a), unless (1) ...; (2) there is in effect, and it and its use or intended use are in conformity with, a regulation issued under this section prescribing the conditions under which such additive may be safely used.

Table 10 FDCA SEC. 402. [21 USC 342] (a) (4)

A food shall be deemed to be adulterated if it has been prepared, packed, or held under insanitary conditions whereby it may have become contaminated with filth, or whereby it may have been rendered injurious to health.

This concept of food additive is wider than the concept of food additive in the Codex Alimentarius (and in EU food law) in that it is not limited to substances with a technological function. A food additive that has not been on the US market before 1958 has to undergo safety assessment, except when it is GRAS. In other words, if within the scientific community consensus has been reached on the safety of a certain product (category), it no longer needs to be risk assessed by authorities. On a voluntary basis, FDA's opinion can be sought as to the GRAS status of a product.

Hygiene

Hygiene requirements are also brought within the ambit of the concept of adulteration (Table 10).

The FSMA introduced that food facilities have to implement a written hazard analysis and risk-based preventive control plan (HAPCP). HAPCP is a modernized version of HACCP as elaborated in the Codex Alimentarius and applied in the EU. The main difference is in the focus on hazards generally not limited to critical control points (section 418 FDCA) (Fortin, 2011).

Misbranding

General

The most important requirements regarding labeling have been added to the FFDCA by the Fair Packaging and Labeling Act (1966) and the Nutrition Labeling and Education Act (NLEA) (1990).

From section 403 FFDCA [21 USC 343] follows that a food is misbranded if its labeling is false or misleading in any particular or if the label fails to provide mandatory information.

The most important mandatory requirements are set in regulations by FDA (21 CFR 100–169). The label must indicate: the name of food; the net quantity; the address of producer; and a statement of ingredients and nutrition information. Additionally, imported foods must state their country of origin.

Claims

The topic of claims is addressed in section 403 (r) FFDCA (included by NLEA). Two types can be distinguished: nutrient-level claims and health claims. For nutrient-level claims, 12 terms have been defined in the law. To be labeled 'light,' for example, the product must contain one-third fewer calories or half the fat of the reference food.

A health claim is defined as any claim made on the label or labeling that expressly or by implication characterizes the relationship of any substance to a disease or health-related condition. It is allowed to make a health claim if one of the three conditions is fulfilled: (1) it is authorized by FDA, (2) it is based on an authoritative statement from a scientific body, or (3) if the quality and strength of scientific evidence is not sufficient for authorization by FDA, a qualification to this effect – for example, referring to minority positions in science – can be made.

US (food) law: All US legislation can be approached via the Federal register at http://www.gpoaccess.gov/fr/; all Acts of parliament are codified in the United States Code (USC): http://www.gpoaccess.gov/uscode/index.html; and all regulations are codified in the Code of Federal Regulations: http://www.gpoaccess.gov/cfr/index.html

European Food Law

Treaty Basis

European legislation regarding food is based on the treaty provision on harmonization for the internal market (Article 114 Treaty on the Functioning of the European Union – TFEU) along with the provision on agriculture (Article 38 TFEU) and the instructions to ensure a high level of health protection

(Article 168 TFEU) and a high level of consumer protection (Article 169 TFEU).

Development

Through a reform following the BSE crisis of the 1990s, the food sector has become one of the most regulated sectors in the EU. The dichotomy of adulteration and misbranding does not work very well for analyzing EU food law. Instead, provisions can be categorized as follows (Van der Meulen 2013). There are public powers of law enforcement (Regulation 882/2004) and incident management along with the legislation addressing food businesses.

Most of the legislation addressing food businesses can be further subdivided into one of the three categories: legislation on the product, legislation on the process, and legislation on presentation. The whole structure is embedded in general principles (Figure 4).

Authorities

Risk assessment

In the EU the risk assessment function is separated from the other functions of public authorities. It is the responsibility of the European Food Safety Authority (EFSA) in Parma, Italy.

Risk management

Risk management at the EU level in the form of legislation is the shared responsibility of the European Parliament, the Council, and the European Commission or can be delegated to the European Commission. The Commission can take emergency measures.

Inspection

Official controls are the responsibility of the member states. The European Commission's Food and Veterinary Office (FVO) in Ireland audits the performance of the national competent authorities.

Legislation

Concepts of EU food law

Regulation 178/2002, the General Food Law (GFL), provides some general concepts, obligations, requirements, and principles of food law (Table 11).

Principles of EU food law

Food law should aim at the protection of human life and health and (other) consumers' interests (Article 5 GFL). In protecting life and health it should be science based, that is, to say, based on risk analysis (Article 6 GFL). When scientific

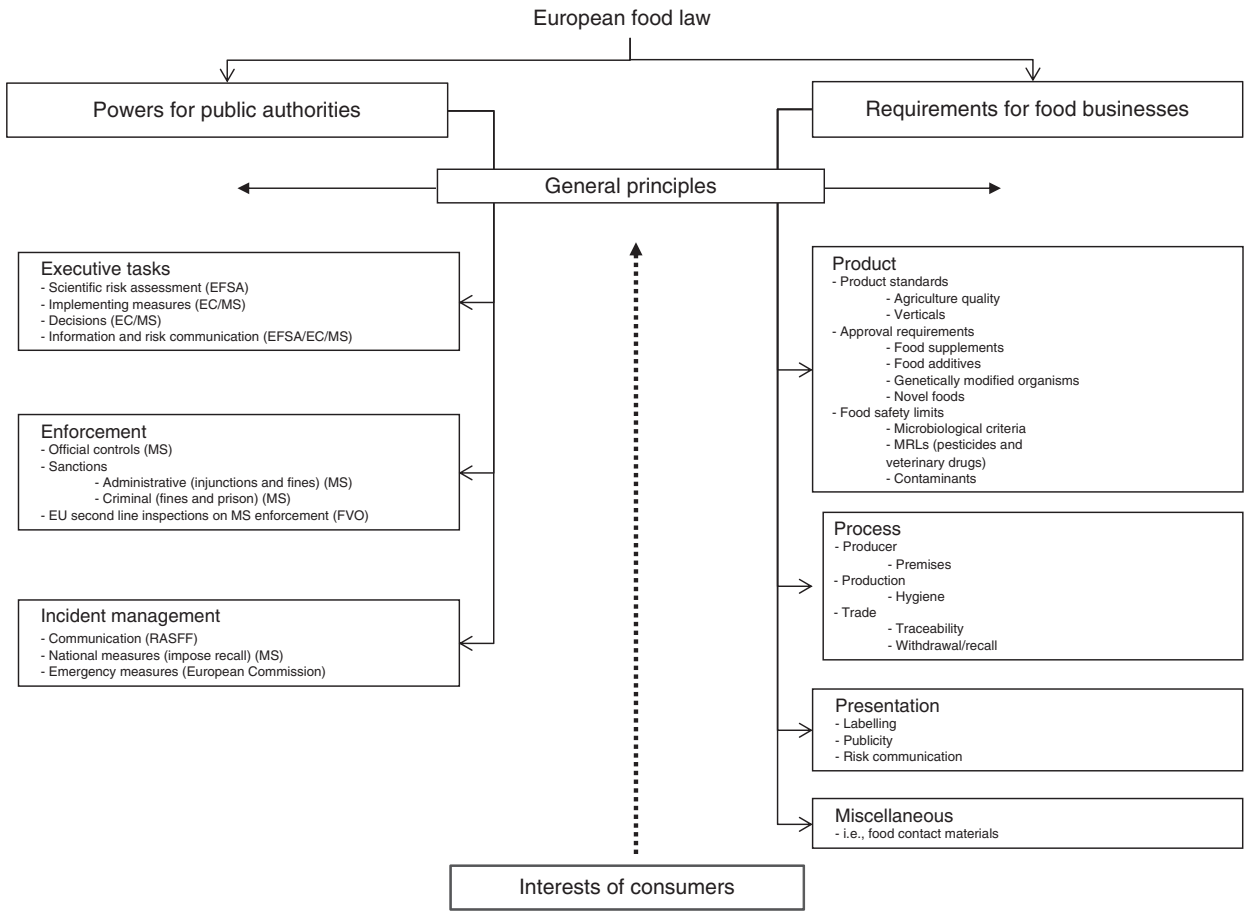


Figure 4 Structure of EU food law.

Table 11 Article 2 Regulation 178/2002 Definition of 'food'

For the purposes of this Regulation, 'food' (or 'foodstuff') means any substance or product, whether processed, partially processed or unprocessed, intended to be, or reasonably expected to be ingested by humans.

'Food' includes drink, chewing gum and any substance, including water, intentionally incorporated into the food during its manufacture, preparation or treatment. It includes water (...).

'Food' shall not include:

(a) feed;
(b) live animals unless they are prepared for placing on the market for human consumption;
(c) plants prior to harvesting;
(d) medicinal products (...);
(e) cosmetics (...);
(f) tobacco and tobacco products (...);
(g) narcotic or psychotropic substances within the meaning of the United Nations Single Convention on Narcotic Drugs, 1961, and the United Nations Convention on Psychotropic Substances, 1971;
(h) residues and contaminants.

risk assessment is inconclusive, the precautionary principle justifies temporary measures to be taken to protect from possible risks (Article 7 GFL).

Where international standards – such as the Codex Alimentarius – exist or their completion is imminent, they shall, in general, be taken into consideration in the development or adaptation of food law (Article 5(3) GFL). The definition of food, for example, is tailored on the Codex and also the principles of HACCP as elaborated in the Codex are incorporated in EU food law.

Food businesses are responsible to ensure compliance. Member states are responsible for enforcement (Article 17 GFL).

Product

Legislation addressing the product falls under three categories: (1) compositional standards, (2) prior authorization requirements, and (3) limits on contamination.

Composition

Vertical legislation, legislation about the composition (recipe) or quality of products, loses in relevance.

Prior authorization

The general rule is that producers are free in their choice of ingredients. Increasingly, exceptions to this rule are made in the sense that approval is required for certain products. Approved products are included in the so-called positive lists (lists of products that may be used).

The most important categories for which approval is required are food additives (Regulation 1333/2008), genetically modified foods (Regulations 1829/2003 and 1830/2003), and novel foods (Regulation 258/97). Food additives are (synthetic) substances that are not foods by themselves but are added to foods for technological purposes such as conservatives, gelling agents, and colors. Genetically modified foods are foods consisting of, or made from, organisms to which gene technology has been applied. Novel foods are all (other) foods that have not been consumed to a significant degree in the EU before 1997.

The most important criterion for authorization is scientific risk assessment. No GRAS exemption exists.

Contaminants

Finally, there is a legislation setting limits to the presence of undesirable substances (contaminants) or organisms in food. (*See* Framework regulation 315/93; Regulation 1881/2006 on mycotoxins and chemicals; Regulation 2073/2005 on microbiological criteria; Regulation 396/2005 on pesticide residues; Regulation 470/2009 and Regulation 37/2010 on veterinary drugs; Directive 96/22 on hormones; and Regulation (EURATOM) 3954/87, Regulation (EURATOM) 944/89 and Regulation 297/2011 on radioactive contamination.) The limits are set on the basis of scientific risk assessment. To residues of products (like veterinary drugs) that have not been approved or for which no lowest safety level can be established, a zero tolerance may apply.

Process

To ensure food safety, processes must be under control in production as well as in trade. Practices aimed at preventing food safety risks are known as 'hygiene.' At the heart of EU legislation on food hygiene is the HACCP system (Regulation 853/2004). It requires food businesses to analyze their processes to establish where hazards may occur, how to recognize them, and how to deal with them to maintain food safety. Application of the system must be documented.

In trade, a requirement of traceability applies (Article 18 GFL). Food businesses must record where their inputs come from and where their products go. If an incident occurs this information must enable authorities to swiftly identify the origin of the problem and its dispersal to eliminate the cause and take care of the consequences.

Finally, businesses that have reason to believe that a food they have brought to the market may not comply with food safety requirements are under obligation to withdraw it from the food chain and recall it from consumers (Article 19 GFL).

Presentation

General

A large part of food legislation addresses the information food businesses provide to consumers regarding their product through advertising and – mainly – labeling (Regulation 1169/2011). Labeling may not be misleading (Table 12).

All prepackaged food products must be labeled in a language easily understood, i.e., in the national language of the member state.

There are approximately 12 required (mandatory) pieces of information, the most important of them are: name under which the product is sold; list of ingredients; quantity of certain ingredients or categories of ingredients; presence of allergens (list of 14); net quantity; date of minimum durability or, in the case of foodstuffs which, from the microbiological

Table 12 Article 2(2)(j) Regulation 1169/2011

'labeling' means any words, particulars, trade marks, brand name, pictorial matter or symbol relating to a food and placed on any packaging, document, notice, label, ring or collar accompanying or referring to such food.

point of view, are highly perishable, the 'use by' date; name or business name and address of the manufacturer or packager, or of a seller established within the Union; and a nutrition declaration.

Specific labeling requirements demand the presence of additives, novel ingredients, and genetically modified organisms to be mentioned on the label.

Claims

Regulation 1924/2006 addresses nutrition and health claims (OJ L 404, 30.12.2006). Nutrition claims must conform to the annex of this regulation, which states among other things that the expression 'light' may only be used in case of a reduction of at least 30% of certain nutrients or energy. Health claims, for example, claims about the effects of a certain food on health must be approved and science based. Foods bearing health claims are sometimes called 'functional foods.' All EU legislation is available at: http://eur-lex.europa.eu/

Private Food Law

Legal Basis

On the basis, mainly, of contract law and, to a lesser extent, some other private law instruments such as intellectual property, a quasi-regulatory framework emerges from the private sector.

Private Standards

For different reasons such as compliance (due diligence) with their own obligations to provide safe food, exporting public law requirements beyond their own territory, chain orchestration and the like, businesses – retail, in particular – have started to require producers to adhere to certain practices formulated in the so-called private standards (also known as private voluntary standards, or private schemes). To prove compliance with the private standard, producers are required to show certification provided by an independent third party (auditor). The owner of the standard licenses the auditor to use the certification mark (a trade mark) and to authorize businesses that pass the audit to use this mark in their communications.

Well known are the food safety standards of the British Retail Consortium (BRC), the International Featured Standards (IFS), the Safe Quality Food (SQF) standards, and ISO 22.000. Outside the domain of food safety, Fair Trade is a well-known private standard.

Content

The content of private standards is defined by a standard-setting organization. This organization can be set up by the businesses requiring the standard to be applied (BRC), by producers and retailers collectively (GlobalGAP), by auditors (Dutch HACCP), by NGOs (Fair Trade) or other, for example, round tables representing different stakeholders, may be including the public sector.

Food safety standards often have the HACCP system as defined in the Codex Alimentarius as their core elaborating on its implementation.

Harmonization

The proliferation of private standards has prompted the largest retailers in the world to set up the Global Food Safety Initiative (GFSI). They have agreed to accept on their shelves products certified for any standard that have passed the GFSI benchmark. In this way it is sufficient for producers to be certified against one single standard instead of many.

Organic

One of the earliest examples of a private standard is the organic standard. It relates to sustainable agricultural practices, in particular, the use of pesticides and fertilizers. In the USA, the EU, and many other countries the organic standard is no longer private but has been incorporated in legislation.

The World of Food Law

The following organizations are relevant in food law.

European Institute for Food Law

The European Institute for Food Law www.food-law.nl is an independent network of food law experts, providing research, consultancy, and training. In cooperation with Wageningen Academic Publishers it publishes a series of books on food law (http://www.wageningenacademic.com/eifl).

European Food Law Association

The European Food Law Association (EFLA) is an association of practitioners (regulatory affairs, legal profession, and government) and academics in food law. The membership is from a wider area than just the EU (www.efla-aeda.org).

European Food Law Association/UK

The UK has a national branch of EFLA (http://www.rdg.ac.uk/foodlaw/efla.htm).

NVLR

NVLR is the national food law association in the Netherlands (http://www.NVLR.nl).

Food Law Academy

The Food Law Academy (www.foodlawacademy.nl/ or http://www.wageningenur.nl/nl/show/Food-Law-2.htm) is a joint venture of the European Institute for Food Law and Wageningen Academy that provides training in food law, such as the annual summer school in food regulatory affairs.

FoodFirst Information and Action Network

The FoodFirst Information and Action Network (FIAN) (http://www.FIAN.org) is an NGO focussing on the right to food comparable to Amnesty International.

Global Harmonization Initiative

The Global Harmonization Initiative (http://www.globalharmonization.net) is an organization of food scientists aiming to support meaningful standard setting through international scientific consensus. A core issue of concern is zero tolerances.

Journals

The most important international journals on food law are the Food and Drug Law Journal (US) (http://www.fdli.org/pubs/Journal%20Online/) and the European Food and Feed Law Review (http://www.lexxion.eu/effl). See also the Journal of Food Law & Policy (http://law.uark.edu/current/journals/journal-of-food-law-policy.html) and World Food Regulation Review (http://www.researchinformation.co.uk/wfrr.php).

See also: Food Labeling

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Food Marketing

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Glossary

Community-supported agriculture (CSA) A direct farm-to-consumer marketing arrangement in which consumers purchase shares of a farm's produce, usually in advance, and receive deliveries of fresh produce throughout the growing season. CSA arrangements are sometimes called 'subscription agriculture.'

Concentration ratio The ratio of sales attributed to the *N* largest firms to total industry sales. Concentration ratios reported by the U.S. Census Bureau and used in this article include 4-firm, 8-firm, and 20-firm ratios.

Downstream firms Firms in the food marketing chain that are closer to the final consumer. For example, a supermarket is downstream from a food-processing company.

Everyday low price strategy An approach to supermarket pricing that involves offering relatively stable prices across the store's assortment of products.

Farm stand A direct farm-to-consumer marketing arrangement. A farm stand may be operated from a year-round permanent structure or from a vehicle, trailer, or temporary structure during harvest periods. Stands may be on the farmer's premises but are often at the side of a major highway or thoroughfare.

Farmers' market A facility or area where multiple farmers/growers gather on a regular recurring basis to sell a variety of fresh fruits, vegetables, and other farm products directly to customers. The number of farmers' markets has increased markedly over the past decade making them one of the most prominent direct farm-to-consumer formats.

Pick-your-own operation A direct farm-to-consumer marketing approach that involves the final consumers coming on to the farmer's premises and harvesting produce directly from the field or orchard. The consumer pays the farmer, usually by weight or volume harvested, on leaving the operation.

Promotional pricing strategy An approach to supermarket pricing that involves higher general prices across the product assortment in conjunction with frequent and heavily featured temporary price reductions for selected items. This strategy is alternatively called a high–low (or Hi–Lo) strategy in the academic and trade literature.

Thrifty Food Plan A low-cost but nutritionally balanced basket of food items compiled by the United States Department of Agriculture's (USDA) Center for Nutrition and Policy Promotion. The cost of the Thrifty Food Plan is the basis for Supplemental Nutrition Assistance Program allotments to low-income households.

Upstream firms Firms in the food marketing chain that are more distant from the final consumer. For example, a flour miller is upstream from a bakery.

Introduction

The food marketing system provides the link between farms and consumers. As raw farm commodities move through the food marketing system, a myriad of value-adding activities take place to transform these commodities into something more accessible, more useful, more palatable, or otherwise more attractive to the final customer. In fact, the vast majority of what consumers pay for food represents value that is added by the food marketing system. Statistics compiled by the United States Department of Agriculture (USDA) indicate that farm-gate value accounts for only 15.5 cents of the typical dollar an American consumer spends on food. The remaining 84.5 cents pay for value created by activities in the food marketing system (Canning, 2011).

The marketing system adds value in four ways (Kohls and Uhl, 2002). First, food manufacturers take agricultural commodities and change their form into something more desirable to the customer. This is what happens when a commodity like wheat is transformed into bread. Second, value is added to assembling products that are geographically distant from population centers and making them easily accessible to consumers. The year-round abundance of fresh foods throughout the industrialized world is a testament to the logistical capacity and global reach of today's food distribution system. Third, a steady supply of foodstuffs is facilitated by numerous storage facilities, warehouses, and distribution centers that allow processors and retailers to respond to consumer demands in a timely fashion throughout the year. The fourth, and final, way the marketing system adds value is through activities that facilitate ownership transfer as products move from the farm to the consumer. Brokers, agents, financiers, insurance providers, and many others participate in this system by providing the necessary support services that facilitate food marketing activities.

The activities performed by participants in the food marketing system are in response to important social and demographic changes. Since World War II, the US population has more than doubled in size and has grown in diversity (**Figure 1**). Other sociodemographic shifts included a steady increase in household incomes, a decrease in household sizes, and increased participation of women in the workforce. These trends have fundamentally changed and shaped the demand for food, with emphasis on convenience, ethnic belongingness, and food quality.

The link between diet and health has also become much more important to the calculus of food producers and

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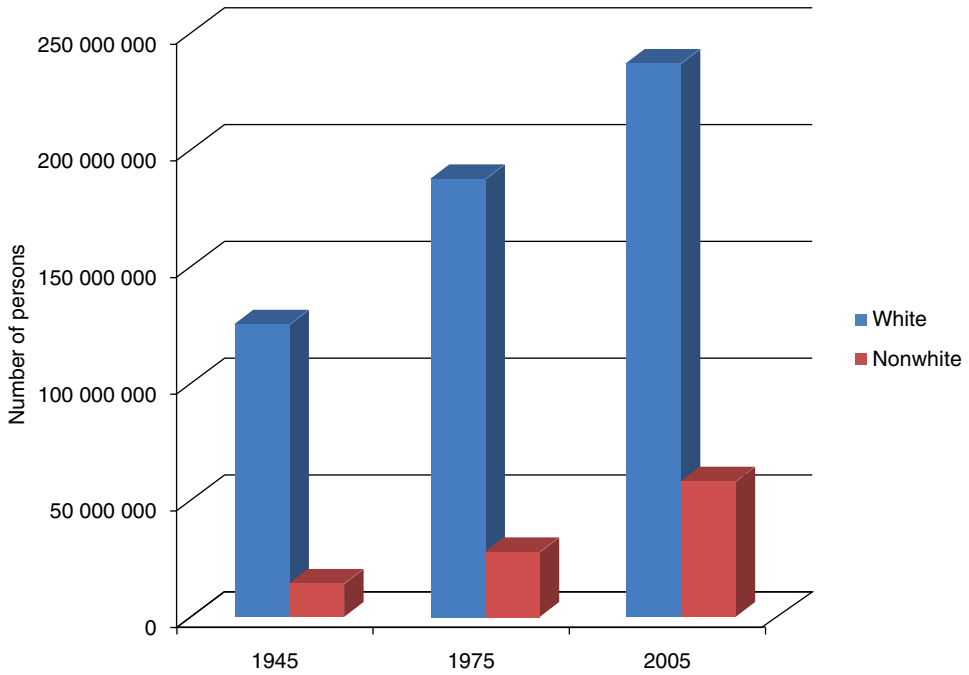


Figure 1 Post-World War II growth in size and diversity of the United States population. Reproduced from Population Estimates, U.S. Census Bureau.

marketers. This is due in part to an aging population. In 1945, only 5.6% of the population was 65 or older compared to 12.4% in 2005 (US Census Bureau, 2013). The population as a whole has also grown more aware of the role of food and lifestyle on health outcomes. Foods are no longer perceived as a means to basic subsistence. Instead, they are also directly linked to health and wellbeing (Siro *et al.*, 2008).

The food marketing system has responded to these trends by building convenience into the food supply, supplying a more diverse array of foods, and innovating into new product offerings (New Products, ERS, USDA, 2013). **Figure 2** shows that over the past 20 years, the number of new product introductions per year has nearly doubled. The decline in the new food and beverage product introductions in the past 2 years is the result of a pullback in discretionary spending from both the producers and consumers during tight economic conditions of the recent recession (New Products, ERS, USDA, 2013).

In the remainder of this article the authors provide a survey of key participants in the food marketing system. The authors first characterize food manufacturers and food wholesalers and then move on to downstream retailers serving the food-at-home (FAH) and food-away-from-home (FAFH) markets. Relatively more emphasis is placed on these downstream participants because upstream segments of the food system are addressed at length elsewhere in this volume. In the latter part of the article, the authors highlight some key issues that are influencing food marketing activities today and that are likely to remain important in the decades ahead.

Food Manufacturers

The food manufacturing industry – NAICS codes 311 and 3121: Food and Beverage Manufacturing (North American Industry Classification System (NAICS), United States Census Bureau, 2002) – transforms raw livestock and agricultural materials into processed food products (including companion/pet food). The food and beverage industry is the largest employer in the entire manufacturing sector and has the largest number of establishments, second only to fabricated metal product manufacturing. Approximately one out of every 10 manufacturing companies is a food or beverage manufacturer, accounting for over 14% of the employment in the whole manufacturing sector in 2011. The bakeries and tortilla manufacturing (NAICS, 3118) accounts for more than a third of the establishments in the food and beverage manufacturing and almost 18% of the employment. Although the meat processing industry accounts for only 12% of the total establishments, it is by far the largest employer in the food and beverage industries.

The contributions of separate food and beverage industries to the total number of establishments and employment are presented in **Table 1**. Although the number of food manufacturers declined from 1998 to 2011 by 8%, the size distribution did not change noticeably (**Figure 3**). Over the reference period, about a third of all food manufacturers are small with less than five employees and more than half of the manufacturing population has less than 10 employees. While all size categories experienced a decline, most of the 8% reduction was absorbed by small manufacturers of less than 10 employees.

Food Wholesalers

Food wholesalers store and distribute food products. They include merchant wholesalers, manufacturers' sales branches, and brokers. The U.S. Census Bureau keeps detailed information on merchant wholesalers in industries like general line

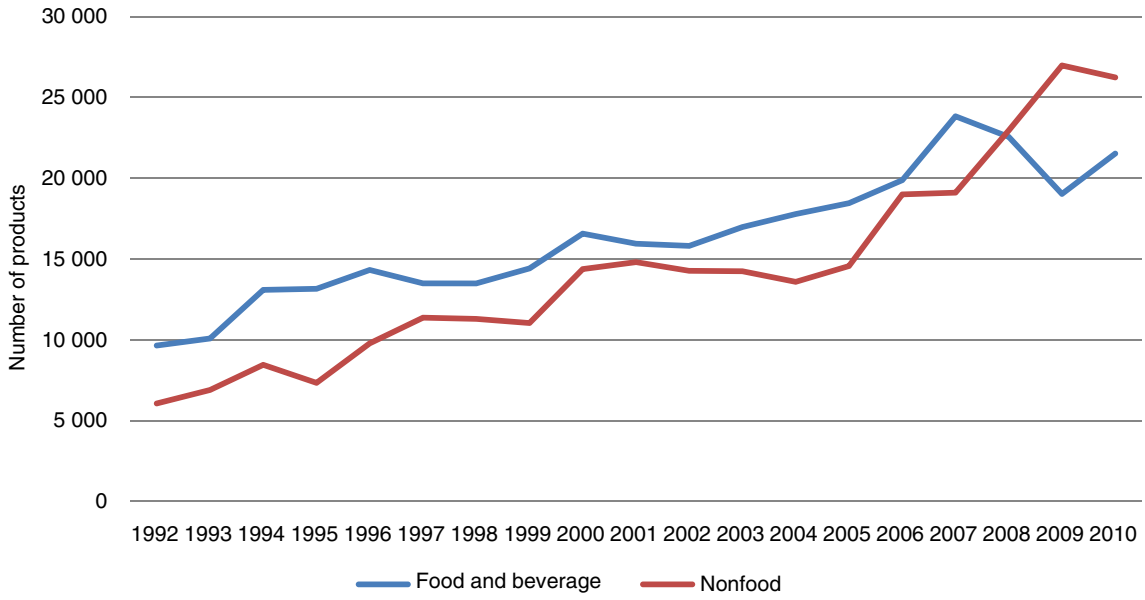


Figure 2 New product introductions of consumer packaged goods, 1992–2010. Data from Datamonitor provided through USDA, Economic Research Service (ERS).

Table 1 Food and beverage manufacturing industries – proportions, 2011

NAICS code	*NAICS code description*	*Total establishments*	*Paid employees*
31	Manufacturing	295 643	10 984 361
311	Food and beverage manufacturing	30 384	1 558 721
Percent of total food and beverage manufacturing			
3111	Animal food manufacturing	5.72%	3.22%
3112	Grain and oilseed milling	2.59%	3.41%
3113	Sugar and confectionery product manufacturing	5.48%	4.36%
3114	Fruit and vegetable preserving and specialty food manufacturing	5.50%	9.95%
3115	Dairy product manufacturing	5.22%	8.77%
3116	Animal slaughtering and processing	11.99%	31.36%
3117	Seafood product preparation and packaging	2.04%	2.01%
3118	Bakeries and tortilla manufacturing	34.62%	17.98%
3119	Other food manufacturing	10.90%	10.50%
312111	Soft drink manufacturing	1.51%	3.26%
312112	Bottled water manufacturing	0.96%	0.52%
31212	Breweries	2.40%	1.64%
31213	Wineries	8.87%	2.32%
31214	Distilleries	0.70%	0.39%

Abbreviation: NAICS, North American Industry Classification System.
Source: Reproduced from County Business Patterns, U.S. Census Bureau.

groceries, packaged frozen foods, dairy products, poultry and poultry products, confectionery, meat and meat products, fresh fruits and vegetables, etc.

As a means of cutting costs, retailers have consolidated through mergers. This practice has likely triggered a similar strategy upstream with wholesalers becoming involved in horizontal and vertical mergers to meet larger-scale needs of the retail mergers (Martinez, 2007). Consistent with this trend, data from the County Business Patterns, U.S. Census Bureau, indicate a drop in the number of establishments in all but confectionery merchant wholesalers throughout the period of 2003–11. However, there is no evidence that the number of large wholesalers grew.

The Food-at-Home Market

Firms that sell food items primarily for consumption off premises comprise what is commonly referred to as the FAH market. Statistics compiled by the USDA Economic Research Service indicate that the FAH market in the United States accounted for nearly 676.6 billion dollars in 2011 (United

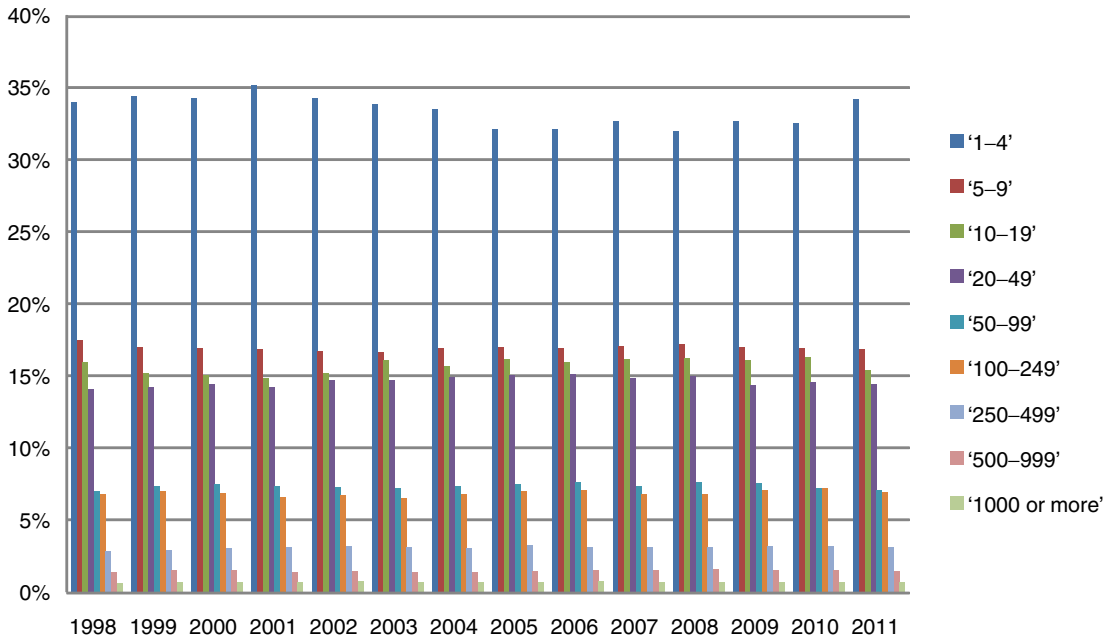


Figure 3 Size distribution of US food manufacturers, percent by number of employees. Reproduced from County Business Patterns, U.S. Census Bureau.

Table 2 Share of food-at-home expenditures by retail format and year

Retail format	*1991*	*1996*	*2001*	*2006*	*2011*
Supermarkets	63.5	75.0	70.1	65.5	63.8
Supercenters and warehouse clubs	2.1	3.3	8.9	14.7	16.0
Smaller grocery stores	12.4	1.3	1.2	0.8	1.4
Other stores	8.4	5.3	4.8	4.9	4.9
Convenience stores	2.7	2.7	2.6	2.6	2.4
Specialty food stores	2.4	2.2	2.0	2.3	2.3
Mass merchandisers	1.0	1.6	1.7	0.9	0.6
Home deliveries, mail orders	1.3	2.1	3.1	2.8	2.7
Farmers, processors, wholesalers, and others	6.1	6.4	5.5	5.5	5.9

Source: Reproduced from United States Department of Agriculture, Economic Research Service (USDA-ERS), 2013. Food Expenditures. Available at: http://www.ers.usda.gov/data-products/food-expenditures.aspx (accessed 10.12.13).

States Department of Agriculture, Economic Research Service (USDA-ERS), 2013). The distinguishing feature of firms in this sector is that they stock a broad array of food items for final sale. Food preparation for on-site consumption may occur at these establishments, and commonly does. However, such food service activities, if they exist at all, are secondary to the sale of grocery and/or perishable foodstuffs.

Retail Formats Serving the Food-at-Home Market

Table 2 lists the retail formats that comprise the FAH market. Supermarkets and supercenters are the dominant retail formats in this sector and accounted for an overwhelming majority of all purchases in 2011. Supermarkets provide a broad array of perishable and nonperishable food items and a full line of nonfood grocery items. Many, if not most, provide service departments such as a delicatessen, an in-store bakery, and/or a pharmacy. The Food Marketing Institute (FMI) defines supermarkets as stores with at least 2 million in annual sales and with a product assortment ranging from 15 000 to 60 000 stock-keeping units (Food Marketing Institute, 2013). Supercenters have grown increasingly important over the past 20 years. The supercenter format combines a discount department store with the perishable and nonperishable food product offerings found in a large supermarket. Examples of this format include Walmart Supercenters and SuperTarget. In comparison to supermarkets, supercenters will commonly have less breadth than supermarkets in some grocery food categories, especially shelf-stable categories such as salad dressings and cake mixes. However, they have a much larger footprint and carry a much broader assortment of nonfood items such as clothing, housewares, electronics, and sporting goods.

Warehouse clubs share the same North American Industry Classification Code as supercenters and so are listed with supercenters in Table 2. Like supercenters, warehouse clubs carry perishable and nonperishable food items along with a

broad array of other merchandise. The breadth of product and brand offerings in food categories, however, is much smaller than would be found in a supermarket or supercenter. Patrons of warehouse clubs include both household and small-business customers who pay an annual membership fee. Items are sold and purchased in much larger wholesale sizes. Sam's Club (Walmart Stores, Inc.) and Costco Wholesale are examples of warehouse clubs.

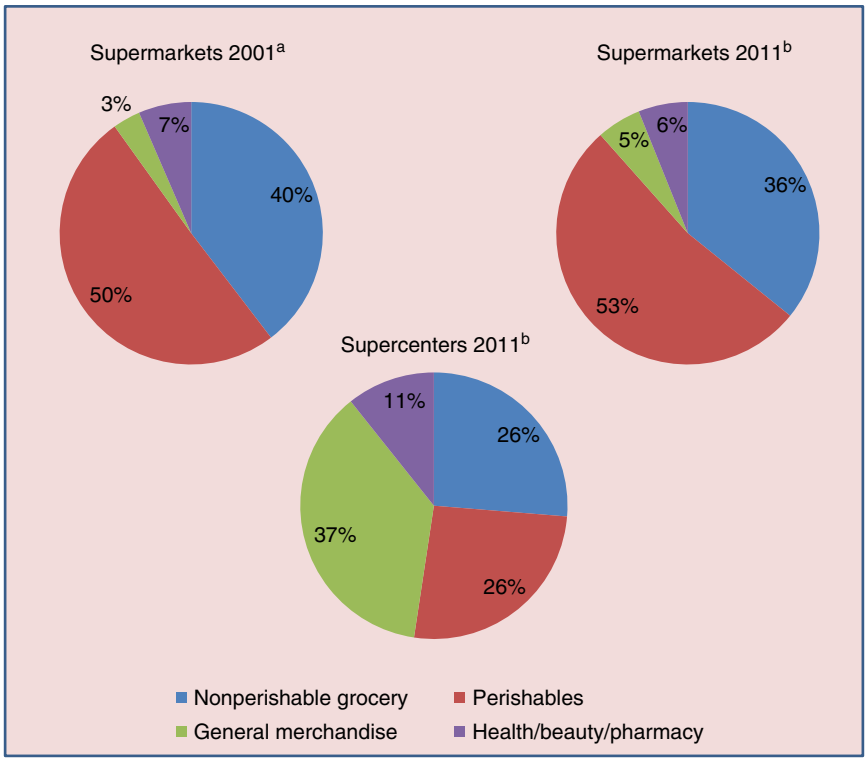
Retail formats accounting for much-smaller shares of the FAH market include smaller grocery stores and convenience stores, both of which carry a narrower range of grocery items and perishable foods; and specialty food stores such as bakeries, meat markets, and seafood markets. Establishments classified as 'other stores' in Table 2 account for about 5% of the market and include establishments such as drug stores (e.g., Walgreens) and variety stores (e.g., Dollar General) that carry grocery items but derive the majority of sales from items other than food. Mass merchandisers often carry limited selection of food items and accounted for less than 1% of the FAH market in 2011.

Key Features of Supermarkets and Supercenters

As the dominant players in the FAH market, it is worth highlighting the key features of supermarkets and supercenters. Figure 4 presents a rough breakdown in sales for the two retail formats. Perishable food items account for half or more of food and grocery sales in each format. The key difference is the much larger role of general merchandise and health, beauty, and pharmacy products within the supercenter format. This reflects the fact that the leading supercenter chains evolved from discount department stores that were and remain very strong in these items. For supermarkets, Figure 4 shows that the rough breakdown between perishables and groceries has remained remarkably stable over the past 10 years. The slight increase in share of sales from perishables and the 4% reduction in share of sales from groceries can likely be explained by competition between supermarkets and supercenters, with each format playing to its respective strengths.

Figure 5 provides a breakdown of supermarket and supercenter shares by major departments within the store. With exception of floral sales, supermarkets and supercenters account for between 75% and 90% of sales of perishable items. The meat department, fresh produce department, and dairy case are the largest contributors to sales of perishables. Supermarkets and supercenters also account for 74% of grocery food items. They also play important, albeit less dominant, roles in pharmaceuticals, health and beauty products, and nonfood grocery items.

Figure 6 shows that the concentration ratios among supermarkets increased between 1997 and 2002. Consolidation among supermarket businesses via mergers during this



a. Based on data presented in Heller (2002)
b. Based on data presented in Chanil and Major (2013)

Figure 4 Sales composition for supermarkets 2001 and 2011 and supercenters 2011. (a) Reproduced from data presented in Heller, W., 2002. 55th annual consumer expenditures study. Progressive Grocer (Sept.). Available at: http://www.progressivegrocer.com/ (accessed 10.12.13). (b) Reproduced from data presented in Chanil, D., Major, M., 2012. Deconstructing the market basket Progressive Grocer. Available at: http://www.progressivegrocer.com/ (accessed 10.12.13).

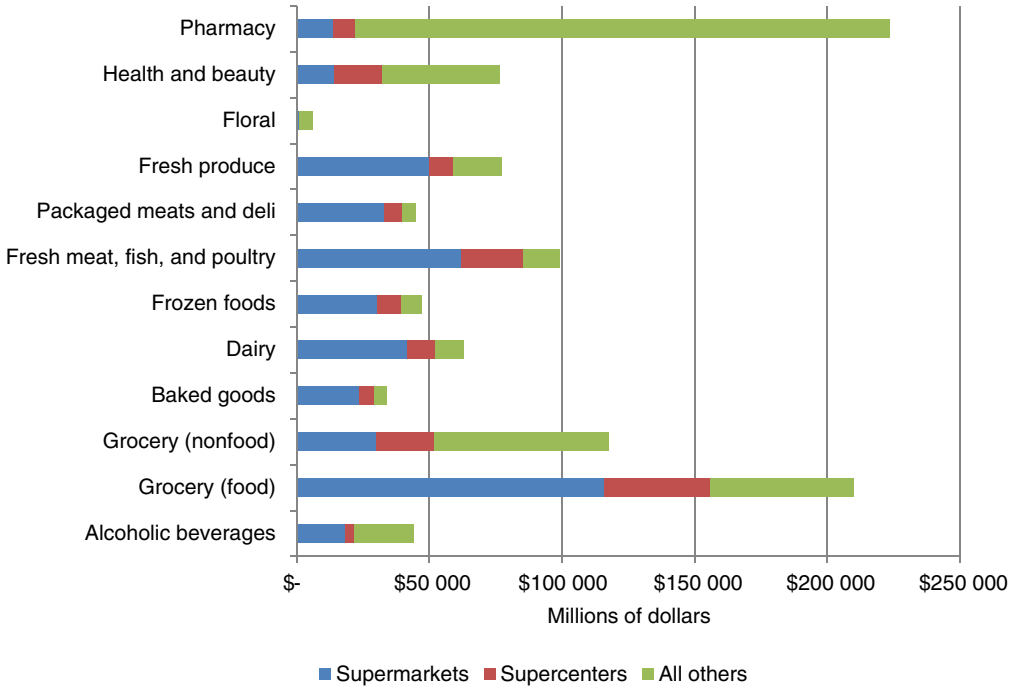


Figure 5 Supermarket and supercenter share of major departments, 2011. Reproduced from data presented by Chanil, D., Major, M., 2012. Deconstructing the market basket Progressive Grocer. Available at: http://www.progressivegrocer.com/ (accessed 10.12.13).

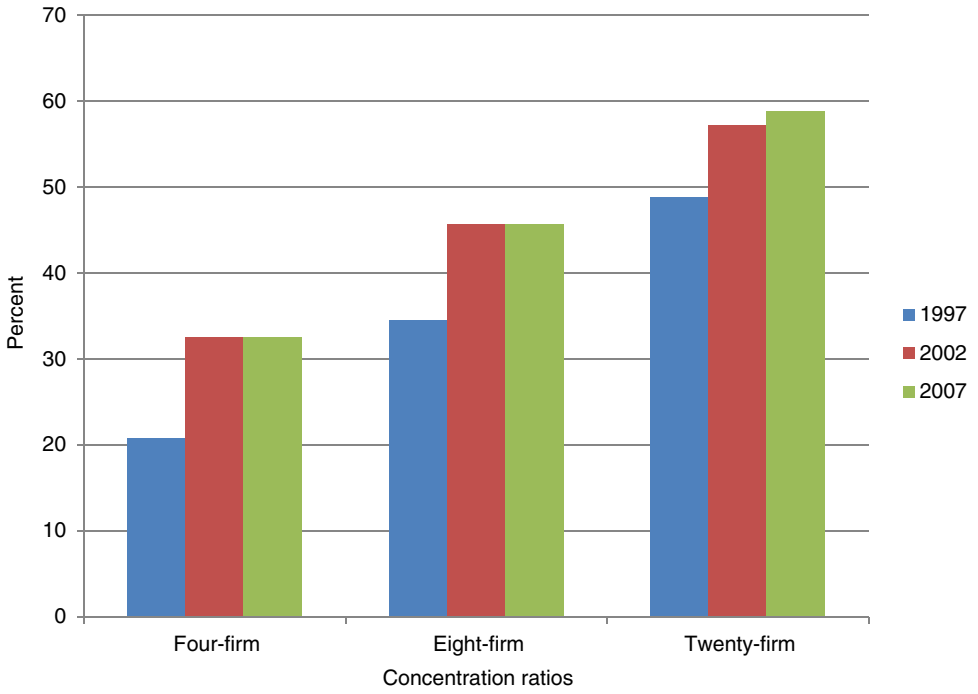


Figure 6 Supermarket concentration ratios: sales of the 4, 8, and 20 largest companies divided by total supermarket sales. Reproduced from 1997, 2002, and 2007 Economic Census, U.S. Census Bureau.

period can explain most of this increase (Martinez, 2007). Between 2002 and 2007, 4-firm and 8-firm concentration ratios have remained remarkably stable and there was only a slight increase in concentration among the 20 largest firms. Although industry concentration measures have been stable, Table 3 reveals that there were important changes to the internal industry structure over the past 10 years. One striking change is the new importance of the supercenter format.

Table 3 Leading supermarket and supercenter chains by sales

Company	*2012 Ranking*	*2002 Ranking*	*2012 Establishments*	*2002 Establishments*
Walmart Stores Inc.	1	4	3217	1103
Kroger Co.	2	1	2430	2429
Safeway Inc.	3	2	1450	1568
Supervalu Inc.	4	10	1496	550
Ahold USA Inc.	5	5	756	1245
Publix Super Markets Inc.	6	7	1054	687
Delhaize America Inc.	7	6	1546	1464
H-E-B Grocery Co.	8	11	299	278
Lone Star Funds	9	na	690	na
Meijer Inc.	10	13	197	153
Whole Foods Market	11	27	306	130
Trader Joe's Co.	12	na	362	na
Great Atlantic & Pacific	13	na	315	na
Target Corp.	14	na	252	na
Giant Eagle Inc.	15	19	183	120

Source: Reproduced from Progressive Grocer, 2012b. The super 50. Available at: http://www.progressivegrocer.com/ (accessed 10.12.13) and Urbanski, A., 2002. The slow shakeout. Progressive Grocer 81, 17–24.

Walmart increased from fourth place in 2002 to first place in 2012 on the list of largest food retailers. Most of the 3217 establishments reported for Walmart in 2012 were supercenters, but this number also includes 170 Walmart Neighborhood Market Stores, which are much closer in size and assortment to a traditional supermarket, and 10 Walmart Express stores. These smaller stores show the company's willingness to explore and branch into additional retail formats, beyond the supercenter. In a recent Progressive Grocer survey, the majority of respondents listed Walmart as a very serious competitive threat. In the South and Midwest, regions where the company has the strongest presence, an even larger percentage (more than 70% of respondents) classified Walmart a very serious competitive threat (Progressive Grocer, 2012a). It is also worth pointing out that Target Stores appears among the top retailers in 2012 providing further evidence of the new importance of the supercenter concept in food retailing. A second noteworthy trend is the growing importance of the 'fresh market' variant of supermarket. This can be seen by the rise in Whole Foods from 27th place in 2002 to 11th place in 2012. Moreover, Trader Joes, not even a top 50 supermarket chain in 2002, was at 12th place in 2012. Both chains emphasize organic food items and sustainable supply chains. They also offer center-of-store brands and assortments that differ markedly from supermarket and supercenter retailers.

Competition and Trade Practices

The full price of a product to consumers includes both (1) the out-of-pocket or monetary cost paid at the cash register and (2) a variety of monetary and nonmonetary costs that are associated with identifying product attributes, prices, and travel to and from the sellers' location. Economists call this latter group of costs as search costs. The primary economic function of food retailers is to reduce search costs by providing consumers access to a broad array of goods and services at one location. According to Richards and Hamilton (2013), supermarkets play an intermediary role and face demands from both food manufacturers and consumers. Manufacturers demand shelf space, which provides access to consumers, whereas consumers demand a broad assortment of products. Competition and trade practices influence the distribution of value among these three groups. Topics of primary interest include choice and management of product assortments, supermarket pricing strategies, and trade arrangements between supermarkets and food manufacturers. Each of these topics is addressed below.

Store assortment

Search costs depend on the number of products carried by the store. The size of supermarkets and the assortment of products contained therein have increased over time. **Figure 7** shows that median square footage increased markedly from 1994 through 1999 and then again from 2003 to 2006. As shown earlier in **Figure 2**, there was also a sizable increase in the number of new products. Sullivan (1997) argues that consumer search costs decline as the number of products increase for the simple reason that it is more likely that the consumer will find the items in his/her desired basket of goods on one shopping occasion and will thereby avoid the need to visit multiple retailers or settle for an actual basket that is incongruent with his/her desired basket. However, Sullivan (1997) also argues that as the assortment of products increases, the addition of more products will have less impact on search costs. This is for two reasons. First, the likelihood that one additional product will match the desired basket declines as the number of products becomes large. Second, a large number of products will increase the difficulty of identifying locating the desired products.

Supermarkets understand the importance of managing product assortment and this is one reason for the emphasis on category management initiatives among food retailers (Van Herpen and Pieters, 2002). Within the supermarket, a category represents a similar group of products and brands. For example, salad dressings, sliced luncheon meats, and prepared breakfast cereals would each be considered a category. Category management involves treating each category as a profit

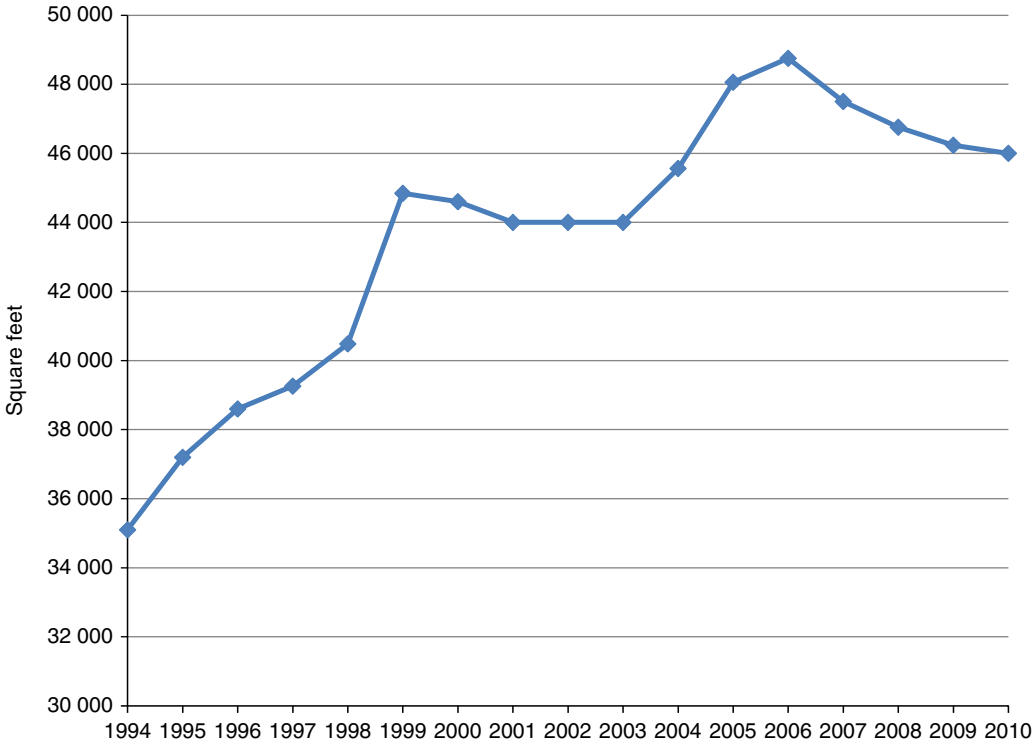


Figure 7 Median supermarket size. One square foot is 0.0929 m^2. Reproduced from Food Marketing Institute (FMI), 2013. Supermarket Facts. Available at: http://www.fmi.org/research-resources/supermarket-facts (accessed 10.12.13).

center. Category managers determine assortments and then price and promote brands within the category in order to maximize category profits (Nijs *et al.*, 2007). Hamilton and Richards (2009) show that optimal assortment depends on the degree of product differentiation within the category. Unsurprisingly, their model suggests that supermarkets will stock fewer product variations within a category when differentiation is low. However, they find that the same is true if differentiation within a category is high. This is because adding new products to the category reduces sales of existing products. The logic from their model is that profit margins are high for highly differentiated products and so the cannibalization effect of deepening the category becomes especially important in these categories. Hamilton and Richards (2009) also show that optimal assortment depends on the degree of differentiation among competing retailers. As consumer loyalty to the retailer increases, they predict that retailers will lower the number of product variants within categories.

Pricing

Approaches to pricing by supermarkets are commonly characterized as (1) everyday low pricing (EDLP) which involves offering relatively stable prices over time across the store's assortment of products or (2) a promotional strategy that involves higher general prices across the product assortment but frequent promotions and temporary (and often steep) price reductions for selected items. Choice between these pricing strategies depends to some extent on clientele being served. Bell and Lattin (1998) find that shoppers making less frequent visits and larger purchases per visit, which they call 'large-basket' consumers, prefer stores that follow an EDLP strategy. However, frequent shoppers with small purchases per shopping occasion tend to prefer stores with a promotional strategy. Bell and Lattin (1998) reason that this is because large-basket consumers will generally need to purchase items from a broad range of categories and are thereby less capable of selectively purchasing from only those categories with a temporary price reduction. Thus, large-basket consumers are primarily interested in the expected price of the overall basket and find EDLP establishments to be the more attractive option. Ellickson and Misra (2008) provide further support for these arguments. They find that the EDLP strategy is preferred by stores in geographic markets with households that are larger, lower-income, and with less access to private transportation.

The degree of industry concentration facing any given geographic market is much higher than the ratios presented earlier in **Figure 3** and so competitive interactions among supermarkets competing for the same geographic customer base are of considerable interest. Ellickson and Misra (2008) examined a national dataset containing store-level information on pricing strategies. Interestingly, their data show that many supermarket chains do not follow a consistent EDLP or promotional strategy chain-wide. In fact, pricing strategies often vary depending on geographic market. Moreover, their results show that competitors in the same geography tend to coordinate on the choice of an EDLP or promotional strategy and that this coordination on pricing strategy cannot be explained solely by similarities in customer and store characteristics. When competitors adopt similar pricing tactics, it is generally thought to facilitate tacit price

cooperation (Besanko *et al.*, 2010), which could then lead to higher consumer prices. Store loyalty programs represent another common strategy that reduces price competition by increasing the costs of switching from one store to another (Kim *et al.*, 2001). Indeed, Hamilton and Richards (2009), mentioned above, show that an increase in-store loyalty causes an increase in price levels along with a decrease in product assortment.

Slotting fees

Slotting fees, payments by food manufacturers to food retailers in return for retail shelf space, have probably been the most controversial topic in relationships between food retailers and manufacturers over the past two decades. These fees were introduced as an industry practice during the mid-1980s (Sullivan, 1997) and are now commonplace in supermarket supply chains. Slotting fees have been the subject of Congressional inquiry and an investigation by the Federal Trade Commission (FTC). Of particular concern is whether slotting allowances hinder competition by providing a mechanism whereby retailers can commit to higher prices and/or whether the practices of paying slotting fees restrict access to retail channels and thereby constitute an entry barrier to would-be food manufacturers (Federal Trade Commission, 2003). Achrol (2012) studied the impact of slotting fees on new product innovation, consumer prices, retailer profitability, and retailer efficiency measures. He concluded that slotting fees have lessened competition among food retailers and have likely contributed to higher consumer prices and higher retail profit margins but less innovation in new product introductions.

More benign explanations for slotting fees have also been put forward, some of which are consistent with economic efficiency. For example, an argument can be made that slotting allowances correct informational problems through the supply chain by allowing manufacturers to make credible signals to retailers about the quality of new product introductions (Federal Trade Commission, 2003). For obvious reasons, retailers would wish to avoid new products that have a low likelihood of success in the marketplace. To the extent that manufacturers are better informed about the prospects of new products, retailers may be reluctant to believe manufacturers' stated claims of product quality when offered new products to add to their assortments. An upfront payment, in the form of a slotting fee, provides the retailer with some assurance that the manufacturer truly believes that the new product is viable. Otherwise, the manufacturer would not possibly be able to recoup the slotting fee through the proceeds of future sales. A slotting fee meets the conditions for what Kirmani and Rao (2000) classify as a default independent signal because the manufacturer bears the cost of the signal regardless of whether the new product turns out to be viable in the marketplace. This means that slotting fees may play another role as well, that of requiring manufacturers to better internalize the risk inherent in new product introductions. When a new product fails, the retailer loses the revenue that could have otherwise have been generated with the space taken by the new product. A slotting fee provides a mechanism whereby the retailer can pass this risk back to the manufacturer (Sullivan, 1997; Federal Trade Commission, 2003).

The FAFH Market

Food services and drinking places (NAICS codes 7221, 7222, 7223, and 7224) engage in preparing and selling meals, snacks, and beverages to customers for immediate on-premise and off-premise consumption. Commonly referred to as food away from home (FAFH), these services include full- and quick-service restaurants, hotels and motels, direct selling at retail stores, bars and vending machines, schools, and colleges, etc.

The food marketing system provided approximately $1.24 trillion worth of food in 2010, almost half of which was provided through food services (Food Service Industry, ERS, USDA, 2012). Due partly to changing sociodemographic profile of the US population, the demand for FAFH has been growing. Households now spend almost half of their food budget on FAFH (**Figure 8**). Several features of the FAFH, convenience, affordability, quality, etc., make FAFH appealing to the population

Figure 9 depicts the FAFH that has become more affluent with smaller household size and more women in the

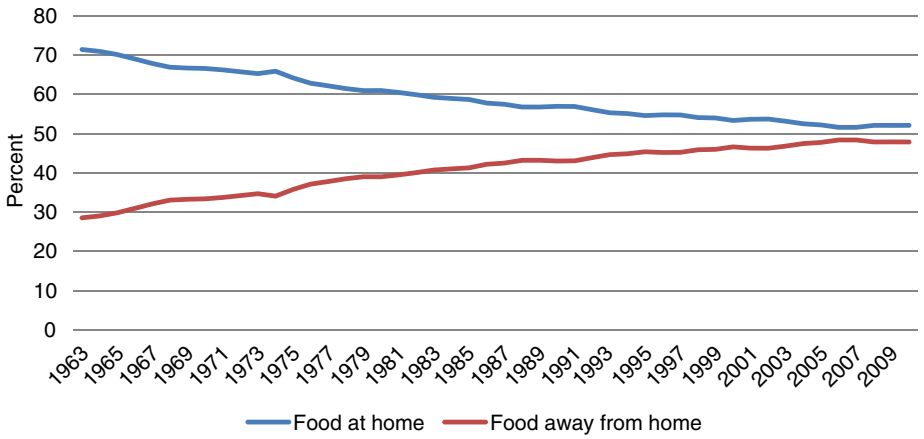


Figure 8 Shares of total food expenditures, 1963–2010. Reproduced from USDA, ERS Food Expenditure Data Series.

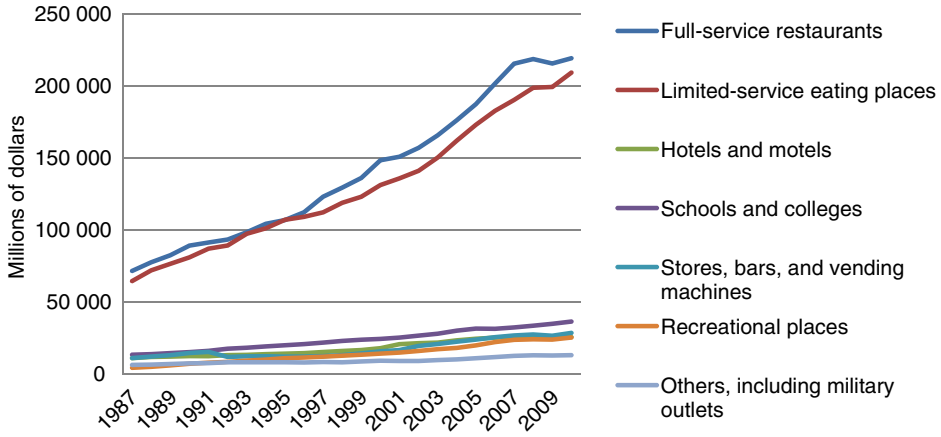


Figure 9 FAFH sales by subcategory, 1987–2010. Reproduced from Food Expenditure Data Series, ERS, USDA.

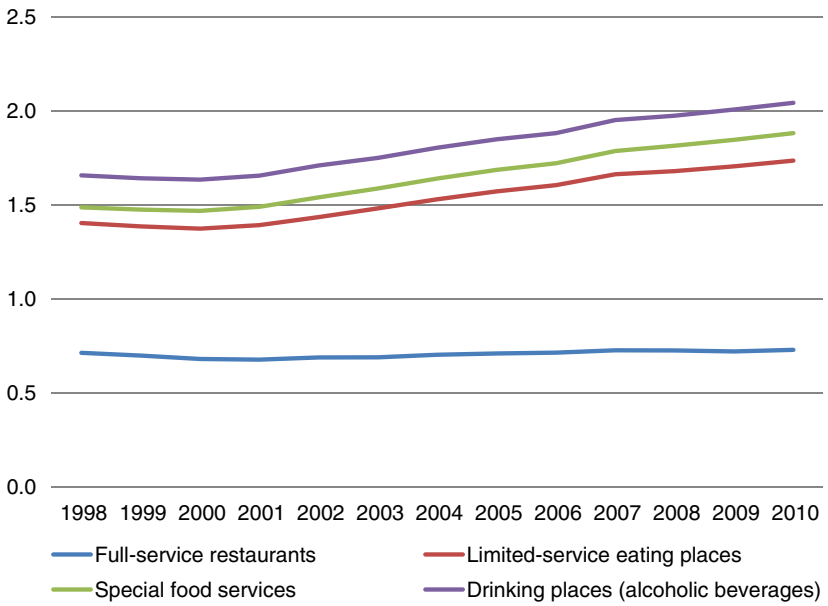


Figure 10 FAFH establishments by subcategory per 1000 population, 1998–2010. Reproduced from County Business Patterns, U.S. Census Bureau.

workforce. The proportion of working women increased from 37.70% of all employees in 1970 to 47.25% in 2010 (U.S. Department of Labor, Bureau of Labor Statistics, 2011).

Expenditure levels by subcategory: The largest two subcategories – full- and quick-service restaurants – account for over three quarters of all FAFH expenditures. These two subcategories mainly differ in services they provide. The quick-service establishments do not generally have waiters/waitresses, and patrons generally order or select items and pay before eating. Full-service restaurants provide waiters/waitresses services and patrons pay after eating.

Over the past decade, the full- and quick-service restaurants held similar market shares. But a closer look at the establishments in the food service category reveals that the market for quick-service restaurant services has grown more rapidly than for full-service restaurants mainly due to convenience of access (Stewart *et al.*, 2004). This trend manifests itself in the growth path of the number of outlets (per 1000 population) in limited- versus full-service subcategories. Although the number of full-service restaurants per 1000 population stayed relatively unchanged in the period of 1998–2010, the corresponding number for quick-service restaurants grew by almost 46% for the same period (**Figure 10**). Nevertheless, the per capita sales in full-service category outpaced that of quick-service category in 1987–2010, except in 1995.

Developments in the demand for FAFH reflect consumers' attitudes toward diet and health as well. Although there seem to be convincing evidence in the literature that meals consumed away from home are more calorie-dense (Lin *et al.*, 1999), the magnitude and direction of the effects of FAFH consumption on weight and health are a matter of ongoing research. Considering the convenience, quality, and practicality of FAFH, it has even been suggested that, despite high calorie density, it should be included in dietary

recommendations such as the Thrifty Food Plan (TFP). You *et al.* (2009) suggest that considering moderate FAFH in the TFP yields similar nutrient and food group composition as the original TFP, whereas greatly increasing the practicality and adaptability of the recommended dietary pattern.

Direct Farm-to-Consumer Markets

There has been growing consumer interest in local foods in recent years. Although 'local' is assumed to relate to geographic proximity, there is no universally accepted definition of local. The Food, Conservation, and Energy Act of 2008 (2008 Farm Bill) defines local foods as locally or regionally produced food products, in which the total distance the product is transported is less than 400 miles from the origin of the product or within the State in which it was produced (Sec. 6015).

Food products with a local origin appeal to consumers for many reasons – environmental, as it helps to avoid long-distance transportation and not contribute to greenhouse emissions; enhancing own-community by providing business to local farmers; security in knowing their food was produced by whom and how; better understanding the origin of their food; perceived better nutritional quality and freshness, etc. Interest in supporting local food systems is also rising among policymakers (Martinez *et al.*, 2010; King *et al.*, 2010).

Local foods are typically marketed directly to consumers (direct-to-consumers) or directly sold to restaurants, retail stores, schools, etc. The latter is referred to as direct-to-grocer/restaurant or intermediated (Low and Vogel, 2011). Direct-to-consumer marketing is done through farmers' markets, community-supported agriculture (CSAs), farm stands, 'pick your own,' etc.

Beginning with the 1997 Census of Agriculture, USDA's National Agricultural Statistics Service (NASS) has collected information on direct-to-consumer marketing outlets that sell food for human consumption. This is the only measureable indicator of direct-to-consumer marketing channel for local foods (Martinez *et al.*, 2010). According to this source, 136 817 farmers sold $1.21 billion worth of farm products directly to consumers in 2007. This is an increase from 93 140 farmers with sales level of $0.55 billion a decade ago (**Figures 11** and **12**). Although the majority of operations engaged in direct-to-consumer marketing are small, for example, less than $25 000 (**Figure 11**), the bulk of sales is easily attributable to large operations (**Figure 12**). Vegetable and fruit farms dominated the direct-to-consumer sales by generating $679 million or 56% of the total sales, whereas only 26% of the operations are produce farms. Although almost a quarter of all direct-to-consumer operations are in beef cattle ranching and farming, their contribution to the total sales is marginal, in the range of 6–12%. Operations in direct-to-consumer marketing in North Central, West, and Northeast regions generated the highest levels of sales and have the highest growth rates from 1997 to 2007 (Diamond and Soto, 2009).

Low and Vogel (2011) estimate that foods marketed exclusively through intermediated channel (direct-to-grocer) generated $2.7 billion in local food sales. This is three times higher than the value of foods marketed exclusively through direct-to-consumer and two times higher than the value of local foods marketed by using a combination of direct-to-consumer and direct-to-grocer channels. They also report that small farms with annual sales less than $50 000 are more likely to rely exclusively on the direct-to-consumer channel. Medium-sized firms (annual sales between $50 000 and $250 000) are likely to rely either on direct-to-consumer marketing or a mix of direct-to-consumer and intermediated channels. Large farms (annual sales $250 000 or more) are equally likely to use either exclusively or both.

Selected Issues in Food Marketing

The U.S. food market has undergone major changes in the past couple of decades. New products as well as new ways of producing, processing, packaging, and handling food products

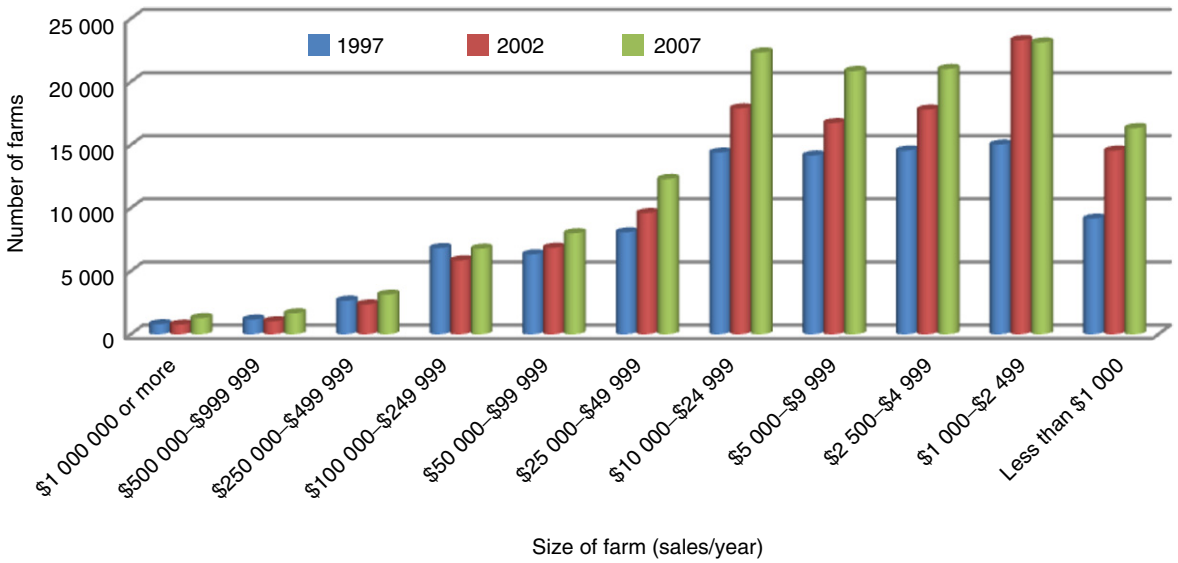


Figure 11 Number of farms marketing directly to consumers by farm size. Reproduced from Census of Agriculture, NASS, USDA.

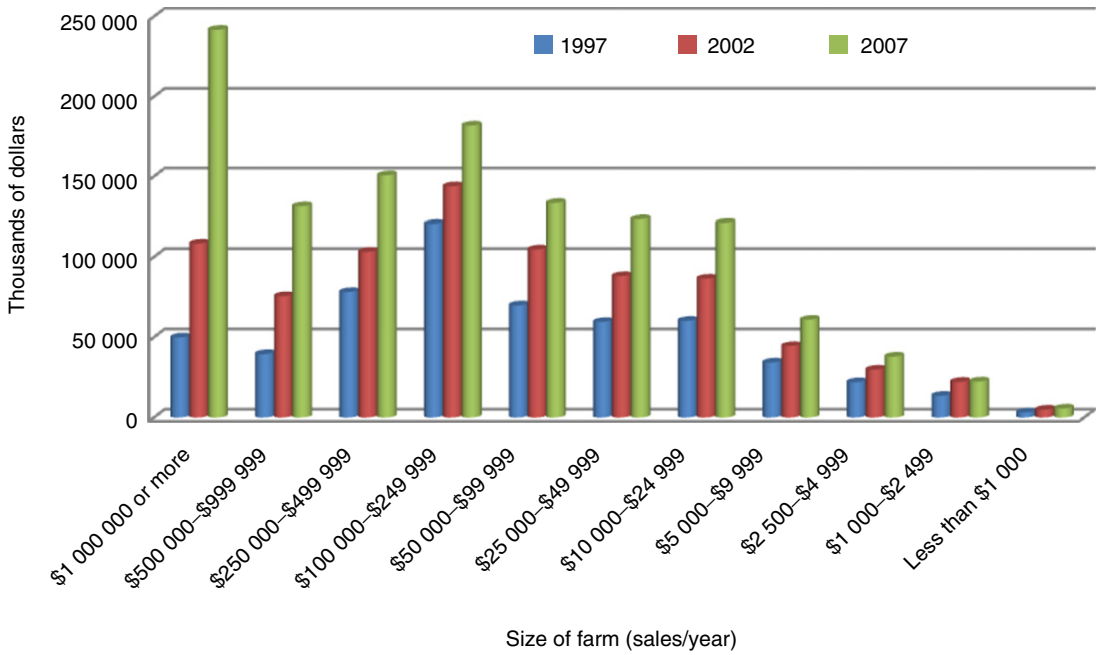


Figure 12 Sales for direct-to-consumer farms by farm size. Reproduced from Census of Agriculture, NASS, USDA.

have emerged. There are several factors that have brought about these changes on food markets. Some of these important factors that will be discussed in Sections are Health Concerns, Nutritional labeling, Food safety, and Functional foods as well as environmental and sustainability issues.

Health Concerns

There is no question that nutrition and health issues are in the forefront of many individual, government, and societal concerns (Nayga, 2008). For example, poor diets and rising obesity rates now dominate the current food, nutrition, and health policy debate in many countries including the United States. Globally, the increasing obesity rates are going to be a major issue and challenge not only for individual choices but also for public policies and programs. Increasing understanding of the correlation between diet and health issues such as obesity, chronic disease, stroke, etc., has also led to significant changes in food markets. According to a report by National Alliance for Nutrition & Activity (NANA), obesity rates have doubled in adults and tripled in children and adolescents over the past two decades. This is a major concern given that obesity increases the risk of cancer, heart disease, diabetes, high blood pressure, and arthritis-related disability (National Alliance for Nutrition & Activity, 2010). All these diet-related health problems have fueled consumers to demand more information about the nutritional content and safety of the food products they buy. As a result, the US government has introduced a number of regulations to help consumers make informed decisions when purchasing and consuming food products.

Nutritional labeling

Food labeling became a concern as the food-processing industries were rapidly increasing. The first regulation on food labeling was passed in 1906, and it mainly addressed the issue of food adulteration or misbranding. It was not until 1973 when nutritional content was first included on the food label. Over the years, food labeling has undergone many changes in an attempt to provide consumers with the necessary information about food products. The most significant development on food labeling came about after many scientific research and important reports from the Surgeon General, the National Academy of Sciences, and the Institute of Medicine increasingly revealed the close relationship between diet and health (Gillet, 2011). Concerns about the obesity issue and the effect of diet on health have partly resulted in the legislation of the Nutrition Labeling and Education Act (NLEA) in 1990. The NLEA regulations require the display of a 'Nutritional Facts' panel on processed foods. The panel also provides information about the standard serving size and a breakdown of nutritional content including calories. Elements such as total and saturated fats, cholesterol, and sodium must always be shown, whereas other nutrients can be suppressed if they are zero. The regulations also update the list of nutrients that appear on the nutritional facts panel and define nutrient content claims and health claims.

Although the NLEA mandates the mandatory nutritional labeling of food products, it only covers the FAH market (i.e., food products sold in grocery stores). It does not cover the food away from home market which includes fast-food restaurants and cafeterias. Food consumption trends in the United States, however, have changed significantly over the past 20 years as previously discussed. A quick look back four to five decades shows an extremely different household structure compared to today, namely, a two-parent, single-income household where the wife was a stay-at-home mother. Given the norms in that era, the wife tended to prepare each meal at-home, eliminating much of the need to

eat-away-from home. In 1960–61, approximately 21% of the food allocated budget was spent away-from-home. This share has increased significantly since the 1960s with close to half of the food budget now being spent away-from-home (Department of Labor, 2006). Numerous factors have contributed to increased consumption of food away from home, most notably: more women in the workforce, more two-income households, and advertising and promotion by food chains.

Many studies have reported a correlation between food away from home consumption and obesity (Kruger *et al.*, 2008; Boutelle *et al.*, 2007; Chung *et al.*, 2007; Duffey *et al.*, 2007; Schröder *et al.*, 2007; Niemeier *et al.*, 2006; Taveras *et al.*, 2005; Bowman *et al.*, 2004; Kant and Graubard, 2004; Mancino *et al.*, 2004; Thompson *et al.*, 2004; Binkley *et al.*, 2000). Eating more fast-food meals has also been linked to eating more calories, fat, saturated fat, and sugary soft drinks and less fruits, vegetables, and milk (e.g., Boutelle *et al.*, 2007; Schröder *et al.*, 2007; Taveras *et al.*, 2005). Consequently, as obesity is becoming a more serious issue, health-consciousness has powered the trend toward full nutrition disclosure in restaurants as well. In fact, in March 2010, the US Congress passed a national law requiring chain restaurants with 20 or more outlets to list calories and other nutrition information on menus and menu boards (Center for Science in the Public Interest, 2013). Although some restaurants have been supportive of this idea and have tried to help FDA write some of the regulations regarding menu labeling in restaurants, many other 'ready-to-eat' food enterprises have opposed these new regulations. Part of the opposition is due to menu-related obstacles, including too many menu variations, limited space on the menu for labeling, and loss of flexibility in changing the menu. There are also personnel-related obstacles that include difficulty in training employees to implement nutrition labeling, and not enough time for food service personnel to implement nutrition labeling. However, despite the obstacles of menu labeling, this regulation seems to have a lot of support from American consumers. An estimated 78% of Americans support menu labeling in restaurants (Department of Public Health, CO, 2010).

Food safety

Despite the fact that food has never been as safe as it is today, food safety remains a major issue. The Centers for Disease Control and Prevention (CDC) estimated that in the United States, roughly 1 in 6 Americans (or 48 million people) gets sick, 128 000 are hospitalized, and 3000 die of foodborne diseases every year (see Centers for Disease Control and Prevention, 2013). Although developments related to the adoption of Hazard Analysis Critical Control Point (HACCP) and other safety standards may have helped reduce the incidence of foodborne illness in the United States, infections with *Salmonella*, *Escherichia coli* O157:H7, *Campylobacter*, and *Listeria* remain and are alarmingly an ever-present phenomenon.

There has been some progress though. For example, data released through FoodNet comparing 2011 with 2006–08, rates of infection were significantly lower for *Shigella* (43% decrease) and *E. coli* O157 (25% decrease), and higher for *Campylobacter* (14% increase) (**Figure 13**). The incidence did not change significantly for *Cryptosporidium*, *Listeria*, *Salmonella*, *Vibrio*, and *Yersinia* infections. In addition, the overall incidence of infection with six key pathogens transmitted commonly through food was significantly lower in 2011 compared with 1996–98 (**Figure 14**). For individual pathogens, the incidence of infection was significantly lower in 2011 compared with 1996–98 for *Shigella* (65% decrease), *Yersinia* (52% decrease), *E. coli* O157 (42% decrease), *Listeria* (35% decrease), and *Campylobacter* (22% decrease), but was higher for *Vibrio* (76% increase). It did not change significantly for *Salmonella* or *Cryptosporidium*.

Who are at greater risk of foodborne illness? They are the children and the elderly. The incidences of laboratory-confirmed infection with *Campylobacter*, *Cryptosporidium*, *Salmonella*, Shiga toxin-producing *E. coli* (STEC) O157 and

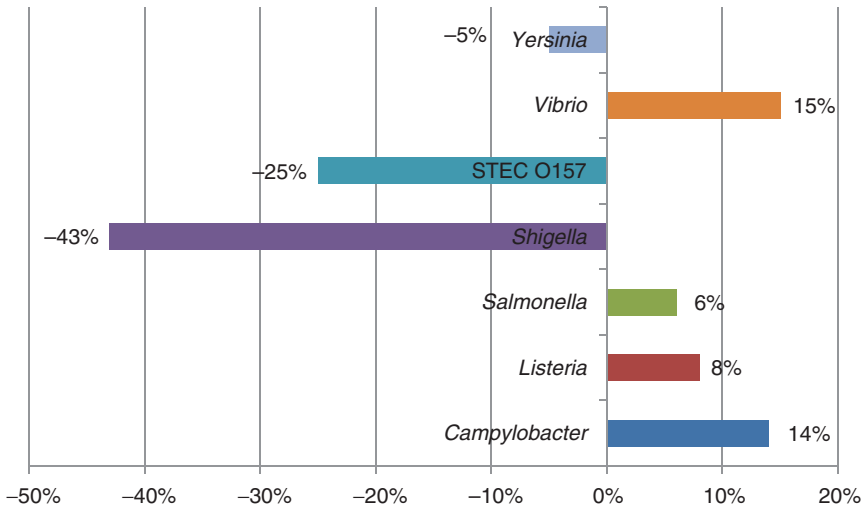


Figure 13 Incidence of laboratory-confirmed bacterial infections: percentage change in 2011 compared with 2006–08. Reproduced from Foodborne Diseases Active Surveillance Network (FoodNet), CDC. Available at: http://www.cdc.gov/foodnet/data/trends/trends-2011.html/ (accessed 10.12.13).

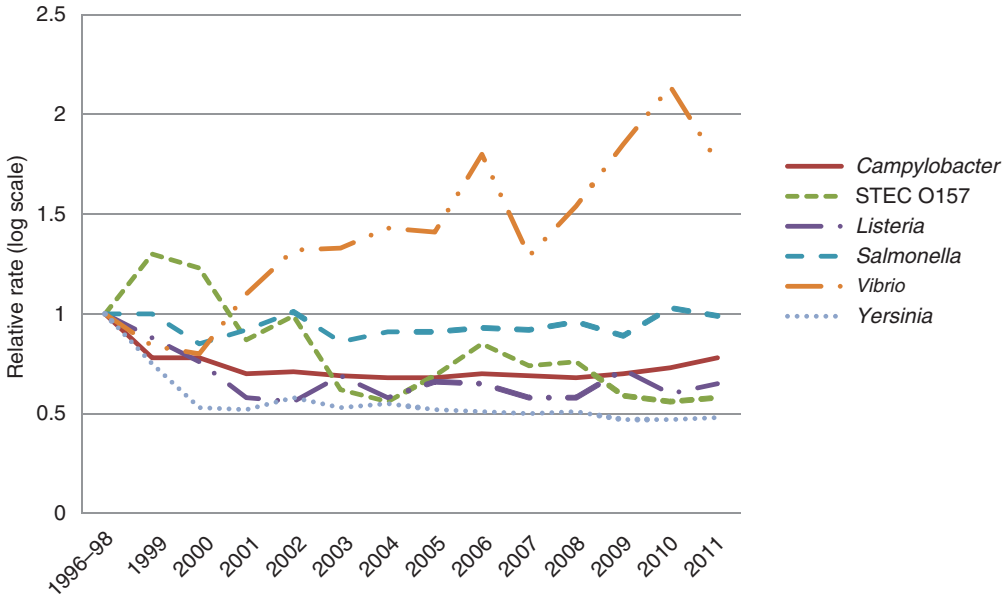


Figure 14 Relative rates of laboratory-confirmed infections with *Campylobacter*, *E. coli O157*, *Listeria*, *Salmonella*, and *Vibrio*, compared with 1996–98 rates, by year – Foodborne Diseases Active Surveillance Network, United States, 1996–2011. Reproduced from Foodborne Diseases Active Surveillance Network (FoodNet), CDC. Available at: http://www.cdc.gov/foodnet/data/trends/data-for-figures-2011.html#data-fig3 (accessed 10.12.13).

non-O157, *Shigella*, and *Yersinia* have been highest among children aged <5 years, whereas the incidences of *Cyclospora*, *Listeria*, and *Vibrio* infection have been highest among adults aged ≥65 years. Young children and older adults were also more likely to have severe complications or die from these illnesses. Thirteen percent of infections, 24% of hospitalizations, and 57% of deaths occurred among adults aged ≥65 years.

Budget declines have led to a governmental decision to cut funds on different programs including food safety programs. This is expected to also affect food markets. As food safety programs are trying to hunt down foodborne illnesses, a slowdown in this progress is expected to occur as a result of the US government budget cuts or 'sequester.' For instance, USDA has already projected that food safety will be particularly hard hit by furloughs, as approximately 87% of the budget will now go to food inspectors and 'support' for inspectors (Parnass, 2013).

One recent development related to food safety was the start of a new livestock identification program to help agriculture officials track livestock in cases of disease. This program helps ensure that sick animals' movements can be reviewed as part of an effort to control the spread of the disease. It also means that healthy animals can continue to move freely to processing facilities and also help investigators determine the source of a disease and whether it happened naturally or if someone tampered with the food system. Although this new program, which took into effect in March 2013, is mandatory, it applies only to animals being shipped across state lines. It also gives states flexibility in deciding how animals will be identified.

Functional foods

Health-related concerns have an influence on decisions made by consumers to reduce the consumption of harmful ingredients (e.g. fats and salt) and to increase the consumption of beneficial food components into their diets (Brown and Schrader, 1990; Capps and Schmitz, 1991; Chang and Kinnucan, 1991). According to Willett (2002), 60% of the risk of chronic diseases potentially is preventable with lifestyle modifications, including changes in diet. Consequently, functional foods have increased in popularity in recent years. Functional foods generally are defined as foods or food components that may provide a health benefit beyond basic nutrition. Functional foods are believed to offer consumers an increased ability to reduce the risk of certain diseases or health problems (Schmidt, 2000). Research conducted by the International Food Information Council (2005) showed that consumer demand for functional foods has increased steadily since 1996, which makes the development of these types of products potentially profitable (Singletary and Morganosky, 2004). It is no surprise then that many food companies now are developing food products with functional or health-related attributes.

In addition to functional foods, there is also an increasing demand for food products that reflect the growing trend of food allergenicity. For example, the NPD Group, a provider of market information and advisory services, is continually tracking top dieting and nutrition-related issues facing consumers and reported that 1 in every 3 adults claimed to cut down or avoid gluten completely in January 2013. Interest in gluten-free menu items at restaurants also is growing. In NPD's CREST® food service market research, which tracks daily how consumers use restaurants, consumers are asked if they ordered something off the menu that was listed as high protein, whole grain, sugar-free, or described in another way. The incidence of consumers ordering food described on the menu as gluten-free or wheat-free has grown over time and is now more than double what it was 4 years ago.

Environmental and Sustainability Issues

In addition to an increasing demand for functional foods, there is an increasing demand for sustainable food products. Examples of this trend are demand for local and organic food, as well as demand for carbon footprint information in food production.

Organic products

Organic foods now occupy prominent shelf space in the produce and dairy aisles of most mainstream US food retailers. The marketing boom has pushed retail sales of organic foods up to $21.1 billion in 2008 from $3.6 billion in 1997. The US organic industry grew as an increasing number of retailers sell a wider variety of organic foods through the development of private-label product lines by many supermarkets, and the widespread introduction of new products.

A broader range of consumers has also been buying more varieties of organic food. Organic handlers, who purchase products from farmers and often supply them to retailers, sell more organic products to conventional retailers and club stores than ever before. Ironically, however, organic farms have struggled at times to produce sufficient supply to keep up with the rapid growth in demand, leading to periodic shortages of organic products.

Food miles and local foods

In recent years, expansion of international food trade has significantly increased the transportation of food products around the world with negative impacts on the environment. Food transportation, especially by air and road, consumes large quantities of fuel and energy, releasing greenhouse gases (GHG) which contribute to global climate change. Food that is sourced by the major retailers from global supply chains can be imported from many thousands of miles (Smith *et al.*, 2005; Kloppenburg *et al.*, 1996). The globalization of food-supply chains exacerbated the problem and led to the situation where information on where the food comes from and information about the social and environmental impacts associated with production and transportation of food are less visible to consumers. The majority of food consumed today passes through a complex network of a few large, centralized producers, processors, transporters, and distributors before reaching the final marketplace.

This trend has prompted many consumers to question the environmental and social sustainability of their food choice. As previously discussed in the Section Health Concerns, food safety and environmental issues as well as ethical motivations related to food production and processing are some of the reasons that concern consumers. Consequently, demand for alternative foods, such as local food, is increasing dramatically. This fact is confirmed by the growing number of alternative food markets and local producer/consumer networks recorded in the United States. According to the Agricultural Marketing Service, there are now over 5274 farmers' markets operating in the country, up from 1755 in 1994.

Recent media and grassroots interest is using food miles, which is the distance food travels from the time it was produced until it reaches the consumers (Paxton, 1994), as a metaphor to explain several benefits associated with local food systems. However, the concepts of local food and food miles have become powerful polemical tools in policy discourses built around sustainable alternative food systems (Coley *et al.*, 2009; Lang and Heasman, 2004). Another debate on the food miles concept concerns the appropriateness of using food miles as a transport emission indicator. Distance traveled is not necessarily a good indicator for transport emissions, and fails to consider other environmental impacts (including other GHG emissions) associated with food production. For instance, Saunders *et al.* (2006) showed that the energy used in producing lamb in the UK is four times higher than the energy used by New Zealand lamb producers, even after including the energy used in transporting New Zealand lamb to the UK. Thus, lower food miles do not necessarily mean lower environmental degradation. Therefore, the issue about the environmental effects of food miles is still under debate in the scientific literature because a number of studies have provided inconsistent empirical evidence on whether domestic or imported food products generate a greater environmental impact (Carlsson-Kanyama, 1997; Blanke and Burdick, 2005).

However, despite some questions remaining on whether imported or local food is more sustainable, food miles information is increasingly being used as a quality cue of food products, in both the global and local markets. In the local market scenario, the implementation of a labeling scheme on food miles might also reflect consumers and local producers' growing interest on environmental characteristics of food products.

Carbon footprint

Food's carbon footprint is the GHG emissions produced by growing, rearing, farming, processing, transporting, storing, cooking, and disposing of the food. Owing to increasing interest in environmental and sustainability issues, there is an increasing demand from consumers and private industries to reduce carbon or GHG emissions associated with food production. Hence, the market for sustainable products is expected to expand significantly in the future.

It is also no longer just environmentalists and policymakers who are concerned about GHG emissions but also food producers and retailers. For example, Walmart has announced plans to label each of its products with a sustainability rating and has subsequently requested that every Walmart supplier provide information about its GHG footprint, a direct measure of climate impact. Walmart has also developed their own 'sustainability index,' which they said will create a more transparent supply chain and drive product innovation.

Summary

The food industry is often characterized as mature and stable in the popular press. The overview provided here shows that consumer food markets are, in fact, quite dynamic and are responsive to consumer demands. Food markets have evolved, along with changing consumer demographics, into sophisticated and efficient systems that supply a broad array of fresh and processed food items sourced from all over the world.

Competition in consumer food markets is especially interesting. Over the past decade, new formats such as warehouse clubs and, especially, supercenters have become a key factor influencing competition in the retail food market. Innovative fresh market retailers that emphasize organic foodstuffs and sustainable supply chains are also emerging as important players. Finally, traditional food retailers face competition from food service firms as time-strapped consumers devote more and more of their food spending to the away-from-home market. As food retailers have consolidated, the sector has caught the interest of academicians interested in market organization and regulatory agencies concerned about fair trade practices.

The article also addressed the consumer and regulatory trends that are shaping the food marketing system in the United States and around the world. These include concerns about food and health. Specific issues in this arena include food safety, the role of the food marketing system in rising rates of obesity and associated health problems, and the development and promotion of functional foods. These concerns are behind recent changes in food safety policy and nutrition labeling. Consumers are also more interested about the source of their foods and the effect of their foods on the environment. This is one factor behind the growth in direct farm-to-consumer market venues and to sustainability initiatives by processors and retailers. These trends provide challenges as well as opportunities for the food system in the coming decades.

See also: Agribusiness Organization and Management. Changing Structure and Organization of US Agriculture. Climate Change, Society, and Agriculture: An Economic and Policy Perspective. Consumer-Oriented New Product Development. Food Chain: Farm to Market. Food Labeling. Government Agricultural Policy, United States. Market-Based Incentives for the Conservation of Ecosystem Services in Agricultural Landscapes: Examples from Coffee Cultivation in Latin America. Markets and Prices

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Direct Farm-to-Consumer Markets

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Safety, Health, Labeling, and Sustainability

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USDA Food Safety and Inspection Service.
http://www.fda.gov/Food/
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Introduction

Importance of Microorganisms in Foods

Every food harbors its own microbiota that may be specific and characteristic of a given point in the production process and of storage conditions. In processed foods, the microbiota consists of microorganisms from the raw materials that survived the processing, preservation, and storage conditions as well as microorganisms that contaminated the food during handling and processing. In raw foods, their characteristics, handling, and environmental conditions as well as farming practices will dictate the predominating microbiota.

Some microorganisms can be considered useful, if the changes due to their growth in foods are deemed beneficial, for example, in terms of flavor, texture, and appearance. But microorganisms can also be able to spoil foods. From the point of view of sensory rejection (deterioration), the spoilage microbiota consists of microorganisms that can grow on a food, causing undesirable changes. The potential of microorganisms to spoil food rests on their ability to produce metabolites that are associated with spoilage and that will lead to rejection of foods by consumers. In general, many microorganisms in a food are capable of producing undesirable metabolites when they grow above a certain level (Gram *et al.*, 2002). The growth of spoilage microorganisms in foods may result in changes in sensory properties, such as color, odor, texture, and appearance. Additionally, some microorganisms pose a health risk, and they are considered pathogenic. The characteristic of the disease will depend on a number of factors inherent to the food, pathogenic microorganism, and affected individual.

There are many microorganisms that are naturally present in foods, sometimes as contaminants. Bacteria stand out the most, both as pathogens and as spoilage microorganisms. For example, *Pseudomonas* spp. and other Gram-negative psychrotrophic microorganisms can be responsible for reduction of shelf life of high-protein, chilled foods stored under aerobic conditions, such as meat and dairy products. *Pseudomonas* is associated with postprocessing contamination of pasteurized milk Eneroth *et al.* (2000). *Shewanella putrefaciens* is an example of psychrotrophic microorganism responsible for the deterioration of chilled seafood (Chai *et al.*, 1968). Although vegetative forms of microorganisms play an important role in food spoilage, spore-forming bacteria are of great relevance for processed food, such as canned foods, vacuum-packaged meat, and thermally processed foods, because their spores survive lethal treatments (Ternstrom *et al.*, 1993).

In addition to bacteria, fungi are a very important group to be concerned with. Fungi are involved not only in food production but also in their spoilage and mycotoxin production, which may have several adverse effects to human and animal health. Fungi may gain access to foods through different routes, such as in the field (pre- and postharvest and during processing and storage). Fungi are the most diverse microorganisms of importance for food industry as they can grow on many different substrates with varied water activity (a_w), pH, and temperature (Dao and Dantigny, 2011). These microorganisms have developed mechanisms that allow them to adapt to high acidic conditions (Prusky and Yakoby, 2003), very low a_w, such as 0.75, and to survive thermal processing (Dao and Dantigny, 2011).

Viruses, protozoan, and parasites play a major role as causes of foodborne diseases in several countries. These microorganisms have variable resistance to lethal treatments used in food processing. Although they all share a common characteristic of not being able to grow in foods, they may be able to survive in these substrates.

Factors Affecting Microbial Behavior in Foods

The fate of microorganisms in foods depends not only on the physical and nutritional characteristics of the food but also on a set of extrinsic and intrinsic factors of the food and their interactions. Factors, such as temperature, pH, water activity, and redox potential, can be considered the most important factors driving microbial fate in foods. Food industry takes advantage of the fact that these factors can be conveniently manipulated to prevent microbial contamination and growth in foods.

Temperature

Among factors affecting microbial behavior in foods, temperature is for sure the most important one. According to Jay (2000), microorganisms can be classified into three groups according to their growth temperature domains: Psychrotrophs grow well at 7 °C or below and have an optimal growth temperature range of 20–30 °C; mesophiles grow well between 20 and 45 °C and have an optimal growth temperature range of 30–40 °C; and thermophiles grow well at 45 °C or higher and have an optimal growth temperature range of 55–65 °C. Most foodborne pathogens are mesophilic microorganisms, with exception of *Listeria monocytogenes*, *Yersinia enterocolitica*, and *Clostridium botulinum* type E, which have markedly psychrophilic behavior. *Alicyclobacillys*, *Geobacillus stearothermophilus*, and *Bacillus sporothermodurans* are examples of thermophilic microorganisms of importance in foods and beverage industries.

Storage at low temperatures is one of the most important ways of slowing microbial metabolic activity in foods. However, cellular sensitivity to cold stress depends on many factors, including temperature, cooling/freezing rate, culture medium, strain, and storage time (Beales, 2004). It has been well

documented that microorganisms adjust the lipid composition of their membranes in response to temperature changes to insure membrane functionality (Russell, 1984; Mastronicolis *et al.*, 1998). Microorganisms growing at low temperatures change the fatty acid composition of their phospholipids and glycolipids to optimize membrane fluidity. This is necessary for nutrients to continue passing through the membrane and for cellular respiration (Berry and Foegeding, 1997).

Reduction of temperature leads to increase of lag time in foodborne microorganisms, culminating with the extension of shelf life. Therefore, it is one of the most used methods to preserve shelf life of minimally processed, pasteurized, and raw foods. Low temperatures will inhibit the development of mesophiles and thermophiles, but not of psychrotrophs. The growth of psychrotrophic microorganisms can be inhibited by adjusting other extrinsic and intrinsic parameters.

pH

It is well established that most microorganisms grow better in pH values close to 7.0, although a few can grow in pH values below 4.0. Bacteria tend to be more sensitive to pH than filamentous fungi and yeasts, and pathogenic bacteria are even more sensitive. Spoilage microorganisms of the lactic acid bacteria (LAB) group, for example, may grow in pH values as low as 2.0. Pathogenic microorganisms, such as *Cl. botulinum*, will not grow in pH values below 4.6. Because of its pathogenic potential, pH 4.6 is used as a limit for a food to be classified as of low acidity (>4.6) or high acidity (<4.6). The pH has a marked importance in the definition of intensity of thermal processing, with low and high acid foods being processed above and below 100 °C, respectively.

The minimum and maximum pH values tolerated by each microbial species depend also on other factors. For example, the minimum pH required for the growth of certain lactobacilli depends on the type of acid used: Citric, hydrochloric, phosphoric, and tartaric acids enable growth at lower pH values than acetic and lactic acids (Jay, 2000). Minimum concentrations of these acids or preservatives are used for inactivating or inhibiting microorganisms. In principle, growth could be inhibited by inactivation or disruption of the cell membrane, cell wall, metabolic enzymes, protein synthesis, or genetic material (Eklund, 1989).

Although the pH 4.6 marks the point below which pathogenic microorganisms cannot grow, the occurrence of several outbreaks associated with acidic products, such as fruits and fruit juices, have shown that inability to grow in foods with $pH<4.6$ should not be confounded with ability to survive.

All microorganisms have an optimal pH range for their growth and survival, and they are more sensitive to internal than external pH changes. When these changes are significant, they may lead to loss of viability. Acids usually inhibit essential reactions by increasing the concentration of hydrogen ions, which reduces the internal pH of the cell. The cell's ability to grow depends on its ability to change the environmental pH enough to reach its optimal range (Jay, 2000). Filamentous fungi have developed a mechanism to circumvent the effect of weak acids and keep homeostasis and internal pH. This mechanism requires adenosine triphosphatase (ATPase), which helps to remove excess protons from the cell (Beales, 2004). Hence, filamentous fungi and yeasts are capable of tolerating lower pH values than bacteria and are associated with the spoilage of acidified foods and products made with acidic fruits. Many microorganisms in more acidic environments than the ideal may require a higher minimum temperature for growth and even a higher minimum water activity (Booth and Stratford, 2003).

Water activity

Water activity is related to the amount of water available for the metabolic reactions within the cell. In fresh foods, a_w exceeds 0.99 (Jay, 2000). In general, bacteria need higher water activity than fungi, and Gram-negative bacteria need higher water activity than Gram-positive bacteria. Most bacteria associated with food spoilage grow at a_w above 0.91, whereas most filamentous fungi can grow at a_w as low as 0.80. *Staphylococcus aureus* can grow at a_w of 0.86, whereas *Cl. botulinum* needs a_w of at least 0.94. Like filamentous fungi, yeasts can withstand lower pH than bacteria, and the same goes for water activity. The lowest water activity required by a bacterium is 0.75 (halophilic bacteria), whereas xerophilic molds and osmophilic yeasts can grow at a_w of 0.65 and 0.61, respectively (Jay, 2000). The general effect of reducing water activity to a value below the optimum value is to increase the lag phase and reduce growth rate. Lowering the water activity causes what is known as osmotic stress.

Most microorganisms have evolved to function only within certain water activity ranges. Water activity outside the optimal range may reduce the essential metabolic functions of the cell and inhibit a large part of the physiological processes, such as nutrient absorption (Roth *et al.*, 1985) and deoxyribonucleic acid replication (Meury, 1988). In response to osmotic stress, microorganisms produce biocompatible solutes, such as trehalose, glycerol, sucrose, and mannitol. These biocompatible solutes help to balance the osmotic pressure of the cell and preserve protein function (Beales, 2004).

Other factors

It is evident that water activity and pH interact with temperature, because individual microorganisms or groups grow in a wide range of storage conditions. In addition to temperature, pH, and water activity, other factors are also important, such as the redox potential (Eh), packaging system, food structure, relative moisture, and atmospheric composition. Some anaerobic bacteria such as those from the genus *Clostridium* need an environment with reduced Eh to grow ($Eh=-200$ mV), whereas those from the genus *Bacillus* require positive Eh to grow. The bacteria that grow better in slightly reduced Eh conditions are called microaerophiles, which includes some LAB, such as *Lactobacillus* (Jay, 2000).

Studies have also discussed how the presence and concentration of some gases in the environment prevents or promotes microbial growth. Oxygen prevents the growth of anaerobic microorganisms in modified packaged foods, but high concentrations can increase the speed of oxidation reactions or even allow the faster growth of aerobic microorganisms. Carbon dioxide is the gas used in modified atmosphere packages that possess antimicrobial properties. Nitrogen is not absorbed by foods and is used as filler gas. The

atmosphere within the packages will be different depending on foods packaged, storage conditions, and package material. Several studies have been performed regarding the fate of foodborne microorganisms in modified packaged foods. However, the major concern in these products is related to the potential growth of psychrotrophic pathogens, such as *L. monocytogenes*. Some examples include the growth of *Listeria innocua* in fresh cut mixed leafy salads packaged in modified atmosphere (Scifò *et al.*, 2009) and survival of *L. monocytogenes* and *Salmonella* Enteritidis in sea bream packaged in modified atmosphere enriched with carbon dioxide (Provincial; Guillen *et al.*, 2013).

The combination or interaction of extrinsic and intrinsic parameters is very important for controlling microbial growth. Considering this, the concept of hurdle technology has been developed and applied for production of several foods, such as salami. The hurdle technology considers the combination of extrinsic and intrinsic factors aimed at increasing the stability and safety of foods, but at the same time insuring freshness and nutrition of foods.

Even with the application of multiple barriers to guarantee shelf-stable and safe products, microorganisms will use mechanisms to adapt to function optimally in physiologically normal environments. Any extreme change in environmental conditions causes stress on the microorganism, which may result in loss of viability or sublethal injuries leading to inactivation or inability to grow in foods.

To survive in foods, microorganisms have developed physiological and genetic mechanisms that enable them to withstand stressful conditions, such as cold shock, preservatives, heat shock, etc. For example, when exposed to cold shock, some microorganisms can produce specific protein groups, called cold shock proteins, which enable them to adapt and survive cold. The addition of preservatives, such as sorbates and benzoates, also activates specific repressor genes, which are probably necessary for optimal adaptation of microorganisms to preservatives, weak acids, and low pH (Beales, 2004). A low–medium pH lowers the inner pH of microbial cells to a point that the cell can no longer tolerate, inhibiting their development. However, some microorganisms can survive this stress by making use of passive and active mechanisms to regulate the inner pH of the cells.

The principles and mechanisms associated with the interaction of extrinsic and intrinsic factors should always be taken into account, whether it is for the formulation of a new product or the establishment of a new process.

Microbiological Spoilage of Foods

Bacterial spoilage of foods

Although many bacteria can grow in foods, only some specific groups are responsible for their spoilage (**Table 1**). The survival, growth, and occurrence of these microorganisms in foods are affected by many different factors, including storage temperature, oxygen availability, food composition, pH, thermal treatment, and competing microbiota, among others.

Bacterial spoilage occurs faster and more evidently in high-protein foods, such as meat, milk, fish, and dairy products. Most of these foods are rich in nutrients and have high water activity as well as pH values close to 7.0 Huis in't Veld, 1996. However, the occurrence of certain microorganisms in these foods is mainly promoted by temperature and atmosphere. Temperature is a limiting factor as it can favor the growth of some spoilage microbial groups and impair the growth of others. For example, low temperature favors the growth of psychrotrophic bacteria over the growth of mesophiles and thermophiles. In this context, *Pseudomonas* spp., a strictly aerobic psychrotrophic bacterium, prevails as the main spoilage microorganism in chilled fresh meat and may cause color, odor, and flavor changes as it degrades amino acids and fats (Gill and Newton, 1978; Labadie, 1999). They create a slimy layer on the surface of the food as they grow. This species, together with *S. putrefaciens*, *Photobacterium phosphoreum*, and some *Vibrio* spp., is the main microorganism involved in the spoilage of seafood (Broekaert *et al.*, 2011; Chai *et al.*, 1968; Gram and Huss, 1996; Gram and Dalgaard, 2002). Moreover, *Pseudomonas* spp., together with other psychrotrophic species, is responsible for proteolysis and hydrolytic rancidity of raw milk and dairy products and also for changes on the surface (slime), pigmentation, and odor of cheeses (Champagne *et al.*, 1994). Despite the high fat content of butter and cream, these can also be spoiled by this group of bacteria (Wang and Frank, 1981). In addition to changes promoted by psychrotrophic and LAB, cheese may also be spoiled by coliforms (early blowing) or gas-producing, anaerobic, spore-forming bacteria, such as *Clostridium tyrobutyricum* (late blowing) (Ledenbach and Marshall, 2010). Eggs are a very popular food and are also used as ingredients in many foods. They have many barriers that prevent the access and growth of microorganisms within them. The prevailing microbiota in the spoilage of this product is composed of Gram-negative bacteria, including *Pseudomonas* spp., which rot the product and change its color (Shebuski and Freier, 2010).

A small change in the way a food is packaged, such as the use of vacuum or modified atmosphere, can change the profile of the spoilage microorganisms from aerobic to facultative or strictly anaerobic. In meats and meat products stored under these conditions, spoilage is caused by LAB, Enterobacteriaceae, and sometimes *Brochothrix thermosphacta* (Dainty and Mackey, 1992). *Brochothrix thermosphacta* is an important species associated with the spoilage of meats and meat products and grows in both aerobic and anaerobic conditions (Pin *et al.*, 2002; Russo *et al.*, 2006).

Other changes in the spoilage microbiota of high-protein foods may be induced by changing water activity and adding a competing microbiota. For example, curing, salting, and fermenting meat products inhibits the growth of the natural spoilage microbiota and promotes the growth of bacteria better adapted to these conditions, such as species of the genera *Micrococcus* and *Staphylococcus* and some LAB (Cerveny *et al.*, 2010; Huis in't Veld, 1996; Samelis *et al.*, 2000).

The presence of complex nutrients in fruits and vegetables, such as cellulose, polysaccharides, hemicellulose, and pectin and in some cases the acidic pH, limits the bacterial spoilage of these foods. However, some bacteria are capable of producing extracellular lytic enzymes that degrade these polymers, releasing nutrients for their growth. This softens the flesh and produces acids, alcohols, and metabolites with unpleasant odors and flavors. The main bacterium species responsible for

Table 1 Main bacteria involved in the spoilage of specific food groups

Types of food	*Main groups responsible for spoilage*	*References*
Refrigerated, fresh meats (aerobic atmosphere)	*Pseudomonas* spp. and other psychrotrophs	Ellis and Goodacre (2001); Gill and Newton (1978)
Refrigerated, fresh meats (vacuum or modified atmosphere)	*Brochothrix thermosphacta*, *Clostridium* spp., *Shewanella putrefaciens*, *Enterobacteriaceae*, and lactic acid bacteria (LAB)	Garcia-Lopez *et al.* (1998); Gill and Newton (1978); Labadie (1999); Russo *et al.* (2006)
Meat products (cured, salted, or fermented)	*Micrococcus*, *Staphylococcus*, *Enterococcus*, and LAB	Cerveny *et al.* (2010); Huis in't Veld (1996); Samelis *et al.* (2000)
Seafood (fresh)	*S. putrefaciens*, *Aeromonas* spp., *Photobacterium phosphoreum*, and *Pseudomonas* spp.	Chai *et al.* (1968); Gram and Huss (1996); Gram *et al.* (2002)
Seafood (processed and salted)	*Brochothrix thermosphacta*, LAB, *Enterobacteriaceae*, and *Vibrio* spp.	Jørgensen *et al.* (2000); Leroi *et al.* (2001)
Refrigerated, raw milk	*Pseudomonas* spp., *Bacillus*, *Micrococcus*, *Aerococcus*, *Lactococcus*, and *Enterobacteriaceae*	Champagne *et al.* (1994); Ledenbach and Marshall (2010)
Ultra-high-temperature milk	*Bacillus* spp.	Stone and Rowlands (1952); Ternstrom *et al.* (1993)
Cheeses	Psychrotrophs, Coliforms, *Clostridium tyrobutyricum*, *Clostridium sporogenes*, *Lactobacillus*, and *Leuconostoc*	Hutkins (2001); Ledenbach and Marshall (2010)
Butter and cream	*Pseudomonas* spp. and Coliforms	Wang and Frank (1981)
Eggs and related products	*Serratia*, *Pseudomonas*, *Proteus*, and *Aerobacter*	Shebuski and Freier (2010)
Vegetables	*Erwinia carotovora*, *Pseudomonas* spp., *Corynebacterium*, *Xanthomonas campestris*, and LAB	Lund (1992); Tournas (2005)
Fruits	*Pseudomonas* spp., *Erwinia*, *Lactobacillus* spp., *Xanthomonas*, and *Acidovorax*	Kalia and Gupta (2007)
Fruit juices	*Alicyclobacillus* spp. and *Propionibacterium* sp.	Smit *et al.* (2011); Walker and Phillips (2007)
Bakery products	*Bacillus* spp.	Voysey and Hammond (1993)
Canned foods	*Thermoanaerobacterium thermosaccharolyticum*, *Moorella thermoacetica*, *Desulfotomaculum nigrificans*, *Clostridium butyricum*, and the facultative anaerobe *Geobacillus stearothermophilus*	Evancho *et al.* (2010)

this deterioration is *Erwinia carotovora*, present in nearly all vegetables (Tournas, 2005) and some fruits (Kalia and Gupta, 2007). However, the intrinsic factors of bakery products limit bacterial growth and favor the prevalence of filamentous fungi as the main spoilage microorganisms (Saranraj and Geetha, 2012). However, bacteria from the genus *Bacillus* spp. may cause a type of spoilage in bread known as ropiness, which is characterized by brown and black stains, release of a rotten fruit odor, and a sticky and moist breadcrumb (Rosenkvist and Hansen, 1995). *Bacillus subtilis* is the main species responsible for this spoilage, but other members of the genus, such as *Bacillus licheniformis* and *Bacillus megaterium*, have also been identified causing this spoilage (Voysey and Hammond, 1993).

Thermal treatment preserves and insures the safety of some types of food, but it also allows specific spoilage microorganisms to prevail in the treated food. In ultra-high-temperature milk, spoilage is caused mainly by spore-forming bacteria of the genus *Bacillus*, which resist thermal treatment and produce enzymes that promote sweet coagulation, gelification, and odor changes (Kalogridou-Vassiliadou, 1992; Ternstrom *et al.*, 1993). *Alicyclobacillus* spp. and *Propionibacterium cyclohexanicum* are the main microorganisms associated with the spoilage of fruit juices that survive thermal treatment and may cause off-flavors, off-odors, discoloration, and turbidity (Smit *et al.*, 2011; Walker and Phillips, 2007). Canned foods submitted to industrial sterilization methods are spoiled exclusively by facultative or strictly anaerobic spore-forming bacteria, such as *G. stearopthermophilus*, *Clostridium sporogenes*, and *Desulfotomaculuns nigrificans*, among others (Evancho *et al.*, 2010).

Yeast spoilage of foods

Yeasts are very important unicellular eukaryotic microorganisms involved in both food and beverage production and spoilage (Querol and Fleet, 2006). These microorganisms spoil foods with high sugar or salt contents, low pH, or other characteristics that give them a competitive advantage over bacteria (Kurtzman, 2006; Smits and Brul, 2005). Most yeasts produce extracellular enzymes, such as proteases, lipases, amylases, and pectinases, and also volatile and nonvolatile

Table 2 Main yeasts involved in the spoilage of specific food groups

Types of food	*Main groups responsible for spoilage*	*References*
Fresh meats	*Candida* spp., *Rhodotorula* spp., *Debaryomyces* spp., *Trichosporon* spp., and *Torulopsis* spp.	Fleet (1992); Osei Abunyewa *et al.* (2000)
Dry and salted meat products	*Debaryomyces hansenii*, *Yarrowia lipolytica*, *Candida*, *Trichosporon*, *Cryptococcus*, and *Rhodotorula*	Dalton *et al.* (1984); Encinas *et al.* (2000); Fleet (1992); Osei Abunyewa *et al.* (2000); Saldanha-da-Gama *et al.* (1997)
Yogurts	*Saccharomyces cerevisiae* and *Hansenula anomala*	Fleet (1990); Hansen and Jakobsen (2003); Rohm *et al.* (1992)
Cheeses	*Candida* spp., *Kluyveromyces marxianus*, *Debaryomyces hansenii*, and *Pichia* spp.	Johnson (2001)
Butter	*Candida parapsilosis*, *Candida zeylanoides*, and *Yarrowia lipolytica*	Lopandic *et al.* (2006)
Fruits and vegetables	*Saccharomyces*, *Candida*, *Zygosaccharomyces*, *Torulopsis*, *Rhodotorula*, *Hansenula*, *Debaryomyces*, and *Pichia* spp.	Jacxsens *et al.* (2001); O'Connor-Shaw *et al.* (1994)
Bakery products	*Saccharomyces*, *Debaryomyces*, *Kluyveromyces*, *Pichia*, *Candida*, and *Zygosaccharomyces*	Van der Zee and Huis in't Veld (1997)
Chocolate, honey, and candy	*Zygosaccharomyces* spp., *S. cerevisiae*, *Torulopsis apicola*, *Hansenula anomala*, and *Kloeckera apiculata*	Thompson (2010)
Carbonated soft drinks	*Saccharomyces* spp., *Zygosaccharomyces* spp., *Torulaspora delbrueckii*, *Pichia anomola*, *Dekkera* spp., and *Candida* spp.	Lawlor *et al.* (2010)

metabolites that affect the sensory characteristics of food, especially flavor and texture. The main genera associated with food spoilage are *Saccharomyces*, *Candida*, *Zygosaccharomyces*, *Debaryomyces*, *Rhodotorula*, and *Pichia* (**Table 2**).

Yeasts play a small part in the spoilage of meats. Despite the competition with bacteria, some yeasts manage to grow on the surface of fresh meats (Nielsen *et al.*, 2008), whereas others may have their growth promoted by changes in intrinsic and extrinsic factors that inhibit bacterial growth (Fleet, 1992; Osei Abunyewa *et al.*, 2000).

Yeasts are also known for their important role in the dairy industry, especially for the production of some fermented products, maturation of some cheeses, and whey fermentation for bioactive compound production (Marth, 1987). However, yeasts are the main cause of yogurt and fermented milk spoilage because the low pH provides a selective environment for their growth. Their presence is associated with off-flavors and gas production (Fleet, 1990; Rohm *et al.*, 1992). These microorganisms also spoil cheeses, and most contamination stems from the brine used in the production process (Kaminarides and Laskos, 1992). Yeasts are normally not involved in butter spoilage, but they have already been detected on spoiled butter (Lopandic *et al.*, 2006).

Yeasts play an important role in the spoilage of fruits and vegetables, especially because of the exposure of these foods to the environment and their minimal processing (Barth *et al.*, 2010). Some of their intrinsic factors, such as pH, also limit bacterial growth. Yeasts are also involved in the deterioration of bakery products, causing white and pink stains or fermenting the carbohydrates, with subsequent production of volatile compounds and alcoholic odor (Legan and Voysey, 1991). In carbonated beverages, the growth of spoilage yeasts is usually characterized by a great production of gas, packaging distension and rupture, abnormal effervescence, excessive turbidity, sedimentation, off-flavors, and off-odors (Lawlor *et al.*, 2010). Osmophilic yeasts, together with xerophilic fungi, are the only microorganisms involved in the spoilage of high-sugar foods with low water activity, such as chocolates, confectionary products, and honey (Thompson, 2010). *Zygossacharomyces bailli* is involved in spoilage of low-pH beverages containing preservatives and high-sugar foods because it has developed mechanisms to adapt these stress factors. These yeasts play a major role in spoilage of beverages, such as fruit juices, soft drinks, chocolate fillings, confectionary creams, etc.

Filamentous fungi spoilage of foods

Filamentous fungi are capable of growing on many different foods, such as grains, meats, milk, fruits, vegetables, seeds, and high-fat products. They are an important group of food spoilage organisms and cause significant economic losses in agriculture and the food industry (Gerez *et al.*, 2013). Spoilage caused by filamentous fungi may manifest as discoloration, off-flavors, loss of structure, loss of texture, formation of visible mycelium, and production of volatile compounds, all of which affect the quality of foods and beverages (Alvo and Raghavan, 1993). These obligate aerobic microorganisms are capable of growing in wide ranges of pH, temperature, and water activity and of using a great variety of substrates as food (Dao and Dantigny, 2011; Sperber, 2010). Filamentous fungi grow more commonly in products with low pH and water activity. They are located mainly on the surface of the food because of their dependence on oxygen. The main food spoilage fungi are *Penicillium*, *Aspergillus*, *Rhizopus*, *Mucor*, *Geotrichum*, *Fusarium*, *Alternaria*, *Cladosporium*, *Eurotium*, and *Byssochlamys* (**Table 3**). Some of these species are also known for their ability to synthesize secondary toxic metabolites called mycotoxins, constituting a problem for agribusiness and the food industry.

Controlling Microbiological Spoilage of Foods

Avoiding or retarding spoilage of raw and processed foods but at the same time preserving the sensory and nutritional

Table 3 Main filamentous fungi involved in the spoilage of specific food groups

Types of food	*Main groups responsible for spoilage*	*References*
Salted fish and similar products	*Wallemia*, *Hortaea*, *Aspergillus*, *Penicillium*, *Polypaecilum*, *Eurotium*, *Basipetospora*, *Cladosporium*, and *Scopulariopsis*	Pitt and Hocking (1999)
Cheeses	*Penicillium*, *Cladosporium*, *Byssochlamys nivea*, *Talaromyces avellaneus*, *Neosartorya fischeri* var. *spinosa*, and *Eupenicillium brefeldianum*	Hocking and Faedo (1992); Pitt and Hocking (1999)
Yogurts	*Penicillium* and *Aspergillus*	Cousin (2001); Ndagijimana *et al.* (2008)
Meat and meat products	*Aspergillus* spp., *Penicillium* spp., *Mucor* spp., *Cladosporium* spp., and *Eurotium* spp.	Deak and Beuchat (1996); Samson *et al.* (2000)
Fruits and vegetables	*Penicillium*, *Phytophthora*, *Alternaria*, *Botrytis*, *Fusarium*, *Cladosporium*, *Phoma*, *Trichoderma*, *Aspergillus*, *Alternaria*, *Rhizopus*, *Aureobasidium*, and *Colletotrichum*	Hagenmaier and Baker (1998); Nguyen-the and Carlin (1994); Tournas (2005)

Table 4 Methods for controlling the microorganisms involved in food spoilage

Principle of preservation	*Methods*
Prevent access of the microorganism to the food	Good agricultural practices Good manufacturing practices Appropriate hygienic and sanitary conditions
Microorganism removal	Washing of surfaces Centrifugation Filtration by membranes
Growth inhibition	Cooling or freezing Reduce water activity (drying and addition of solutes) Food acidification Addition of inhibitors (weak organic acids, nitrites, nitrates, sulfites, and bacteriocins) Microbial competition Atmosphere modification (vacuum or modified atmosphere packaging)
Microbial inactivation	Thermal treatments (pasteurization, sterilization, blanching, and thermization) Radiation High hydrostatic pressures Pulsed electric field processing Ultrasound

characteristics of foods is a great challenge for the industry. The methods used for controlling microbial spoilage include preventing access of the organisms to the foods, removing their cells or spores, inhibiting their growth, and using thermal and nonthermal methods to inactivate them (**Table 4**).

The good manufacturing and handling practices are very important means of reducing the baseline microbial load and increasing shelf life. They are considered the minimum hygienic requirements for the production of any type of food. These practices should be used throughout the entire food production chain, from production of raw materials to consumer consumption.

Other methods of preventing spoilage include: (1) washing the raw materials before processing, which removes microbial cells from its surface, (2) centrifuging, (3) or using membrane filtration processes, which can only be used on certain food groups. In addition to the above-mentioned methods, foods can also be preserved by manipulating factors that not only influence microorganism growth and survival but are also safe for consumers (Gould, 1995). Control of microbial growth by changing intrinsic and extrinsic factors, also called barrier theory, is the main way of reducing food spoilage. The most important barriers used for food preservation are temperature (high and low), low a_w, acidity (pH), redox potential (Eh), preservatives, and other organisms (microbial competition) (Leistner, 2000). These microbial control methods use changes in food characteristics and storage conditions to prevent or reduce microbial growth. Combining different sublethal conditions to prevent microbial growth is a successful approach mainly because it does not change the sensory characteristics of the foods significantly. The great disadvantage of these methods is that microorganisms can resume growth if favorable growth conditions occur.

Some food preservation methods focus on microbial inactivation. They can be classified as thermal or nonthermal methods of food preservation. The thermal methods, such as pasteurization and commercial sterilization, are widely used methods to efficiently inactivate pathogens and reduce the load of spoilage microorganisms. Despite this, they can also change the nutritional and sensory properties of the food. To

replace these methods and meet the increasing consumer demand for healthier products, many nonthermal methods are being developed and used. The main nonthermal methods are radiation, high hydrostatic pressure, pulsed electric field, and ultrasound. Many of these methods are still difficult to implement because of equipment cost, need of trained personnel, and consumer distrust.

Pathogenic Microorganisms in Foods

Gram-positive foodborne pathogens

Most foodborne illnesses are caused by the ingestion of food or water contaminated with microorganisms or their toxic metabolic products. Some Gram-positive bacteria, especially *St. aureus*, *Cl. botulinum*, *Clostridium perfringens*, *Bacillus cereus*, and *L. monocytogenes*, are considered important foodborne pathogens responsible for foodborne illness outbreaks everywhere in the world (**Table 5**). Most of these microorganisms, except for *L. monocytogenes* and *Cl. perfringens*, can grow on food and produce toxins that will cause food poisoning when ingested. *Clostridium botulinum*, *Cl. perfringens*, and *B. cereus* are capable of forming spores, structures that make them resistant to high temperatures and other adverse conditions.

Among Gram-positive bacteria, *St. aureus* stands out because it can grow in foods with high sodium chloride concentrations (10–20%) and low a_w (0.83–0.86). *Staphylococcus aureus* is heat labile and produces heat-resistant enterotoxins (Adams and Moss, 2008). The disease caused by *St. aureus* is due to consumption of animal-origin and excessively handled foods. *Staphylococcus aureus* have a short incubation period and the intoxication caused is self-limiting. The clinical symptoms associated with *B. cereus* poisoning are very similar to those associated with staphylococcal intoxication. However, *B. cereus* can cause two distinct types of foodborne illnesses, namely emetic and diarrheal syndromes. Emetic syndrome is caused by the ingestion of a preformed toxin (cereulide) in foods, which stimulates the vague nerve and causes nausea and vomiting (Agata *et al.*, 2002; Ehling-Schulz *et al.*, 2004). The diarrheic syndrome is an infection caused by ingesting bacterial cells, which then colonize the small intestine and produce enterotoxins *in loco* (Andersson *et al.*, 1998; Clavel *et al.*, 2004). These two syndromes are also characterized by their rapid onset and self-limiting nature, not requiring therapeutic interventions and hospitalization. Despite this, severe and even fatal cases have been reported (Dierick *et al.*, 2005; Granum, 1994; Lund *et al.*, 2000).

Clostridium botulinum, the causative agent of botulism, is a globally distributed bacterium. It causes a severe disease with high mortality rate (Lund and Peck, 2000; Smith and Sugiyama, 1988) due to ingestion of botulinum toxin. Botulinum toxin is preformed in foods and as a neurotoxin, after absorption in the intestines, reaches the nervous system and blocks the release of acetylcholine by nerve terminals (Montecucco *et al.*, 1996). Despite the severity of the illness, the associated neurotoxins are heat labile and can easily be destroyed by heating the food to 80° C for 20 min or 85° C for 5 min (Siegel, 1993).

Clostridium perfringens is another important spore-forming bacterium widely distributed in nature and capable of producing more than 15 toxins that cause different diseases in humans and animals (Lindström *et al.*, 2011). Food poisoning caused by this bacterium is among the most common foodborne illnesses in the world. Food poisoning by *Cl. perfringens* is caused by the ingestion of at least 10^7 cells of the microorganism, which sporulate in the intestines, releasing the *Cl. perfringens* enterotoxin (McClane, 2001).

Differently from the above-mentioned Gram-positive bacteria, *L. monocytogenes* is characterized by its ability to invade intestinal cells and diffuse to other organs and tissues (Orsi *et al.*, 2011). It is a ubiquitous bacterium resistant to desiccation, low water activity, and low pH and may cause anything from a mild gastroenteritis to severe infections of the central nervous system and abortion, depending on the host's susceptibility (Orsi *et al.*, 2011; Rocourt *et al.*, 2003). Listeriosis, the disease caused by *L. monocytogenes*, is a major concern for those involved in food safety because of its high mortality rates (approximately 50%). *Listeria monocytogenes* is a psychrotrophic pathogenic bacterium of very high importance for processed foods or minimally processed foods that are stored for medium to short periods.

Gram-negative foodborne pathogens

Many Gram-negative pathogenic bacteria can cause foodborne illnesses, including *Salmonella* spp., *Campylobacter* spp., pathogenic *Escherichia coli*, *Shigella* spp., *Y. enterocolitica*, *Vibrio* spp., *Aeromonas* spp., and *Cronobacter sakazakii*, among others (**Table 6**).

Among these, *Campylobacter* spp. has been identified as the main cause of foodborne illnesses and outbreaks in the USA and Europe in the past 5 years. The thermophilic species *Campylobacter jejuni* and *Campylobacter coli* are the main causes of campylobacteriosis in humans, a usually self-limiting gastrointestinal disease that can, nevertheless, cause severe complications, such as Guillain–Barré syndrome and reactive arthritis (Allos, 1997; Zilbauer *et al.*, 2008). *Salmonella* spp. also plays an important role in foodborne illness outbreaks worldwide, being an important public health problem (Payment and Riley, 2002). Most serotypes cause gastroenteritis limited to intestinal infections, but the Typhi and Paratyphi serotypes can cause enteric fevers, which are more severe illnesses and affect other organs and tissues (Crump and Mintz, 2010). Although *E. coli* are considered part of the normal intestinal microbiota of warm-blooded humans and animals, some strains can cause foodborne illnesses. These pathogenic strains can be grouped into at least six different groups: enteropathogenic *E. coli* (EPEC), enterotoxigenic *E. coli* (ETEC), enteroinvasive *E. coli* (EIEC), enteroaggregative *E. coli* (EAggEC), diffuse aggregative *E. coli* (DAEC), enterohemorrhagic *E. coli* (also known as verocytotoxin-producing *E. coli*, VTEC, or Shiga toxin-producing *E. coli*, STEC), and enteroaggregative hemorrhagic *E. coli* (EAHEC). Foodborne illness outbreaks have been particularly associated with VTEC and, to a smaller extent, EPEC, ETEC, and EAggEC. A great outbreak with EAHEC strain *E. coli* 0104:H4 occurred in Europe in 2011, with 320 bloody diarrhea cases, 850 cases of hemolytic-uremic syndrome (HUS), and 82 deaths.

Yersinia enterocolitica is one of the most interesting species within the *Yersinia* genus, and related outbreaks are mainly associated with the consumption of contaminated pork.

Table 5 Main Gram-positive bacteria associated with foodborne illnesses

Pathogen	*Characteristics*	*Symptoms*	*Incubation*	*Foods*	*References*
Staphylococcus aureus	Ingestion of one or more types of staphylococcal toxins	Intense vomiting, diarrhea, abdominal pain, and nausea	0.5–6 h	Milk and dairy products, meat products, confectionary products, and ready-to-eat foods	Adams and Moss (2008); Argudín *et al.* (2010); Gilmour and Harvey (1990); Kim *et al.* (2011); Schelin *et al.* (2011); Tranter (1990)
Clostridium botulinum	Ingestion of botulinum neurotoxin	Initial gastrointestinal symptoms, double vision, dry mouth, difficulty in swallowing and controlling tongue, and flaccid paralysis	12–36 h	Canned foods (vegetables and meats), honey, milk products, fish, and fermented seafood	Lindstrom *et al.* (2006); Lund and Peck (2000); Peck *et al.* (2011)
Clostridium perfringens	Release of *Clostridium perfringens* enterotoxin after intestinal sporulation	Acute abdominal pain, nausea, and diarrhea	8–12 h	Meat products and meat-based ready-to-eat foods	Lindström *et al.* (2011); Liu (2009); McClane (2001)
Bacillus cereus	Ingestion of cereulide toxin (emetic syndrome)	Nausea and vomiting	0.5–6h	Rice and grain-based foods	Agata *et al.* (2002); Ehling-Schulz *et al.* (2004); Shaheen *et al.* (2006)
	Toxin production in the small intestine (diarrheic syndrome)	Abdominal pain and aqueous diarrhea	8–16 h	Meats, pasta, desserts, cakes, sauces, and milk	Andersson *et al.* (1998); Clavel *et al.* (2004); Granum (1994)
Listeria monocytogenes	Invasion of intestinal epithelial cells and diffusion to other organs and tissues	Fever, headache, abdominal pain, diarrhea, chills, and complications (abortion, meningitis, and septicemia)	2 days to 3 weeks	Vegetables and salads, cheeses, milk, beef, chicken, and fish	Abadias *et al.* (2008); Cabedo (2008); Caramello and Vaudetti (1990); Kvenberg (1988)

Table 6 Main Gram-negative bacteria associated with foodborne illnesses

Pathogen	*Characteristics*	*Symptoms*	*Incubation*	*Foods*	*References*
Salmonella spp.	Invasion of intestinal cells (gastroenteritis) Typhoid fever (Typhi and Paratyphi serotypes)	Fever, headache, abdominal pain, diarrhea, and chills	12–36 h	Eggs, meats, milk, and dairy products	Crump and Mintz(2010); D'AOUST (2001); Payment and Riley (2002).
Campylobacter spp.	Invasion of intestinal cells	Fever, headache, muscle pain, diarrhea, abdominal pain, and nausea. Complications: Guillain–Barré syndrome and reactive arthritis	2–10 days	Meat and poultry products, raw milk, and contaminated water	Rao *et al.* (2001); Rautelin and Hanninen (2000); Solomon and Hoover (1999); Zilbauer *et al.* (2008)
E. coli (pathogenic) (EPEC, EIEC, EAggEC, ETEC, EHEC, and DAEC)	Adherence to intestinal cells, electrolyte imbalance, toxin production, and rare invasion of intestinal cells	Fever, abdominal pain, chills, diarrhea, and nausea Complications: hemolytic-uremic syndrome (Shiga toxins)	8 h to 4 days	Meats and meat products, milk and milk products, leafy vegetables, and fish	Abadias *et al.* (2008); Atanassova *et al.* (2008); Brandl and Amundson (2008); Eglezos *et al.* (2008)
Shigella spp.	Invasion of intestinal cells and toxin production	Fever, bloody diarrhea, chills, abdominal pain, and vomiting Complications: Hemolytic-uremic syndrome	12–50 h	Shellfish, crustaceans, fruits, vegetables, and salads	Agle *et al.* (2005); Chanachai *et al.* (2008); Kimura *et al.* (2006); Pinu *et al.* (2007); Warren *et al.* (2006)
Yersinia enterocolitica	Invasion of intestinal cells, penetration in mesenteric lymph nodes, and inflammation	Abdominal pain, fever, diarrhea, sore throat, and joint pain	1–3 days	Beef, pork, poultry, oyster, fish, milk, and milk products	Arnold *et al.* (2006); Fredriksson-Ahomaa *et al.* (2007); Yucel and Ulusoy (2006)
Vibrio cholerae	Cholera toxin production in the small intestine	Abdominal pain, aqueous diarrhea, and dehydration	6 h to 5 days	Contaminated water, vegetables, and seafood	Austin (2010)
Vibrio parahaemolyticus	Colonization of the small intestine and production of adhesins and cytotoxins	Abdominal pain, diarrhea, colic, fever, headache, nausea, vomiting, and chills	4 h to 4 days	Shellfish, raw fish, shrimp, and oyster	Chan and Chan (2008); Davis *et al.* (2007); DePaola *et al.* (2003)
Vibrio vulnificus	Colonization of the small intestine and production of adhesins and cytotoxins	Diarrhea, abdominal pain, vomiting, fever, and may cause infections in wounds	7 h to some days	Shrimp, fish, oysters, and mussels	Colakoglu *et al.* (2006); Gopal *et al.* (2005); Jung *et al.* (2007)
Cronobacter sakazakii	Opportunistic infection	Abdominal pain and bloody diarrhea Complications: septicemia, meningitis, and brain abscess		Infant foods and formulas	Strydom *et al.* (2012); Zhou *et al.* (2008)
Aeromonas spp.	Opportunistic infection	Symptoms similar to those of cholera with aqueous diarrhea and mild fever; in some cases, symptoms similar to dysentery with bloody diarrhea, fever, and abdominal pain		Fish, shrimp, milk, and bottled water	Igbinosa *et al.* (2012)

Shigella spp. are transmitted by the fecal/oral route and ingestion of contaminated food or water. These bacteria are highly infectious and can produce the Shiga toxin, which causes the HUS (DuPont *et al.*, 1989). *Vibrio cholerae*, *Vibrio vulnificus*, and *Vibrio parahaemolyticus* have been associated with foodborne illnesses due to consumption of contaminated water, vegetables, and seafood (DePaola *et al.*, 2003; Drake *et al.*, 2007; Morris, 2003).

Other Gram-negative bacteria, such as *Aeromonas* spp. and *Cr. sakazakii*, are considered opportunistic foodborne pathogens and infect specific population groups, namely newborns, the elderly, and immunocompromised individuals (Igbinosa *et al.*, 2012; Nazarowec-White and Farber, 1997).

Protozoan foodborne pathogens

Protozoans are important etiological agents of human diseases that can be transmitted by contaminated water and foods. Intestinal infections caused by protozoans include toxoplasmosis (*Toxoplasma gondii*), cryptosporidiosis (*Cryptosporidium* sp.), cyclosporiasis (*Cyclospora cayetanensis*), cystoisosporiasis (*Cystoisospora belli*), sarcocystosis (*Sarcocystis* sp.), giardiasis (Giardia sp.), and amebiasis (*Entamoeba histolytica*). More recently, *Trypanosoma cruzi*, the causative agent of Chagas disease, was included in this list because it can be transmitted by foods (Yoshida *et al.*, 2011). Among the abovementioned protozoans, *Giardia*, *Cryptosporidium*, and *Cyclospora* are the main microorganisms responsible for diarrhea in humans (Dawson, 2005). The main transmission route of these protozoans is the fecal/oral route. However, indirect transmission from pets, such as dogs and cats, and ingestion of foods contaminated with oocysts represent a threat (Karanis *et al.*, 2007; Smith *et al.*, 2007). In general, water and certain foods, such as vegetables, fruits, and seafood, which are more likely to have been in contact with diseased individuals, are the main vehicles of intestinal protozoans.

Foodborne viruses

Viruses are small intracellular parasites capable of causing diseases in plants, animals, and human beings. Many viruses can be found in the human intestines, but only some are generally recognized as important foodborne pathogens (Koopmans and Duizer, 2004). Foodborne viruses attack intestinal cells and propagate within them. Later, some types of viruses may attack other cells or invade other organs, such as the liver and the central nervous system (Bajolet and Chippaux-Hyppolite, 1998; Koopmans and Duizer, 2004). The main genera associated with foodborne illnesses are Norovirus, Sapovirus, Enterovirus, Hepatovirus, Astrovirus, Rotavirus, and members of the Adenoviridae family, among others (Vasickova *et al.*, 2005). Norovirus, Rotavirus, and the hepatitis A virus are the ones most related with foodborne illness outbreaks around the world. All these viruses can be transmitted through the fecal/oral route, either by direct contact with infected individuals or by ingestion of contaminated water and foods, such as vegetables, fruits, shellfish, bivalve molluscs, and sometimes beef (Dubois *et al.*, 2002; Keeffe, 2004; Koopmans and Duizer, 2004; Lees, 2000; Richards, 2001).

Although viruses are the most common pathogenic foodborne agents, their identification and association with foods is still difficult in the absence of systematic surveillance and appropriate legislation to establish food safety criteria (Koopmans and Duizer, 2004).

Mycotoxigenic molds

Filamentous fungi can grow in foods and cause chronic disease in humans and animals because of their mycotoxins. Mycotoxins are secondary metabolites that may cause a variety of adverse effects in human beings, such as intestinal symptoms, allergic responses, immunosuppression, mutagenesis, inhibition of protein synthesis and essential metabolic pathways, and cancer (Bennett and Klich, 2003). Mycotoxins may be produced before harvest or during storage, and filamentous fungi need favorable water activity, atmosphere (oxygen), substrates, and temperatures to grow. The main filamentous fungal genera associated with the production of mycotoxins in foods are *Aspergillus* spp., *Penicillium* spp., and *Fusarium* spp.

Aspergillus flavus and *Aspergillus parasiticus* are the main fungi responsible for the production of aflatoxin in peanuts, corn, wheat, rice, and other grains. The main types of toxins isolated from these foods are aflatoxins B_1, B_2, G_1, and G_2. They are characterized by their fluorescence under ultraviolet light. Additionally, toxic metabolites, such as aflatoxins M_1 and M_2, may be present in the flesh and milk of animals fed grains contaminated with type B aflatoxin.

Aspergillus carbonarius, *Aspergillus niger*, *Aspergillus ochraceus*, and *Penicillium verrucosum* are associated with the production of ochratoxins. An important characteristic of this mycotoxin is that it is found in many different products, such as raisins, barley, soybean and coffee products, grapes, and wines, but usually in low levels. These mycotoxins can accumulate in human or animal body tissues and fluids when contaminated foods are consumed regularly.

Citrinin is another mycotoxin produced by *Penicillium citrinum* and by some *Aspergillus* species, such as *Aspergillus terreus* and *Aspergillus niveus*, and industrially important species, such as *Monascus ruber*, *Monascus purpureus*, *Penicillium Camemberti*, and *Aspergillus oryzae*. This nephrotoxic mycotoxin is found mainly in wheat, oat, rye, corn, barley, and rice. Patulin, produced by some species of *Penicillium*, *Aspergillus*, and *Byssochlamys*, is the main mycotoxin found in fruits, such as apple, pear, and cherry, and their derivatives. This toxin may irritate the stomach and cause vomiting and nausea.

Fusarium spp. species are responsible for the production of many mycotoxins, such as fumonisins, zearalenone, and trichothecenes (deoxynivalenol, also known as vomitoxin or DON, and toxin T2); corn is the source of these mycotoxins.

The toxic effects and economic losses caused by mycotoxins are of global concern for public health and agricultural and livestock production. Mycotoxin control should be done in the entire food production chain, taking into account the interactions between toxicogenic fungi and plants, storage manner and conditions, animal contamination and metabolism, detection methods, and mycotoxin elimination from foods.

Controlling and Inactivating Foodborne Pathogens in Foods

Diverse strategies have been used to control and inactivate foodborne pathogens. These methods are used for insuring

that foods are pathogen free or for keeping them within levels that do not jeopardize consumer's health.

Most animal-origin pathogens are transmitted by the oral/fecal route, and good manufacturing practices and hygienic conditions throughout the entire food production chain can reduce the risks of contamination effectively. Use of potable water, prohibition of animals in processing units, pest control, correct hygiene practices by food handlers, and proper hygienic and sanitary conditions are important for reducing the contamination of foods by pathogenic protozoans and intestinal viruses.

Some pathogenic bacteria depend on favorable conditions to grow on foods and produce enough toxins to cause foodborne illness. The inhibition of microbial growth by changing intrinsic and extrinsic factors, especially temperature, water activity, and pH, are ways of reducing foodborne illnesses caused by these bacteria.

Foodborne pathogens have different virulence levels. Sometimes a few pathogenic cells are capable of causing disease, so their elimination is essential for food safety. Among all inactivation methods, heat can be considered the most commonly used. However, consumers' demand for minimally processed foods and essentially unchanged nutritional and sensory characteristics requires nonthermal methods of microbial inactivation. Some of these methods are irradiation, high hydrostatic pressure, pulsed electric field, and ultrasound. However, more studies are required to determine how efficiently these methods can be used in industrial scale, not only to insure inactivation of specific microbial groups but also to minimize losses on the food components and be accepted by consumers.

Technological microorganisms in foods

Microorganisms of industrial importance

Biotechnology is defined as the use of live organisms or biological systems in industrial processes and waste treatment plants (Borem *et al.*, 2003). Today, biotechnology is equally important in food science and technology. Fermentation processes are a link between the old food preparation arts (cheese and wine, among others) that use natural microbiota and the modern food fermentation industry.

There are two types of cells in nature and both types are used in industrial fermentation processes: prokaryotes (bacterial cells) and eukaryotes (fungal, animal, and plant cells). Industrial microorganisms also differ as a function of their oxygen requirement: they may be strictly aerobic, such as *Streptomyces* and most filamentous fungi; strictly anaerobic, such as clostridiums; and facultative, such as industrial yeasts.

The bacteria used in fermentation processes are mainly chemoorganotrophic, that is, they obtain their energy by oxidizing organic compounds. Lactobacilli are bacteria that ferment carbohydrates, producing lactic acid. They can be homo- or heterofermentative. Homofermentative species produce only lactic acid from glucose, whereas heterofermentative species produce ethanol, carbon dioxide, and lactic acid from glucose.

The ability to ferment carbohydrates makes lactobacilli very useful for food production, but they may also cause food spoilage. However, Streptococci, Pediococci, and Lactococci are Gram positive, homofermentative cocci that produce mainly lactic acid. Then, these genera have a major importance for industrial processes.

Molds are also chemoorganotrophic and the most important molds used in industrial fermentation are classified into two groups: (1) Zygomycota, which have nonseptate hyphae and include the genera *Mucor* and *Rhizopus* and (2) Deuteromycota, which have septate hyphae and include the genera *Trichoderma*, *Aspergillus*, *Penicillium*, *Fusarium*, and *Aureobasidium*. Some *Mucor* and *Rhizopus* species are used for the production of cheeses and fermented Eastern foods. Among the Penicillia, *P. camemberti* and *Penicillium roqueforti* stand out because they are used for producing the Camembert and Roquefort cheeses, respectively.

Yeasts are unicellular fungi that reproduce asexually or sexually. The most commonly used yeasts in industrial fermentation processes are the *Saccharomyces*, with the most important species being *Saccharomyces cerevisiae*. *Saccharomyces cerevisiae* is used for many different purposes, such as the production of breads, beverages (beers and wines, among others), alcohol, and glycerol, among other uses in technological processes. *Saccharomyces cerevisiae* does not break down lactose, so the production of alcohol and biomass from whey requires another species, such as *Kluyveromyces lactis*. *Kluyveromyces lactis* has the necessary enzymes to break down lactose. Other important yeasts are: *Candida utilis*, used for processing apple residues (Fellows and Worgan, 1987), and *Endomycopsis fibuligera*, used for ethanol production (Reddy and Basappa, 1996; Chi *et al.*, 2009).

Biotechnological use of lactic acid bacteria in food production

LAB are found in very diverse environments, such as fermented foods and beverages, plants, fruits, soil, and residual water. They are also part of the respiratory and intestinal tracts of humans and other animals (Holzapfel and Wood, 1995).

The manufacturing of fermented meat products intends to continue using a set of microorganisms because they give the product agreeable sensory, hygienic, and sanitary characteristics. This set of LAB are introduced into the product by raw materials or by starter cultures sold frozen or freeze-dried (Patarata, 2002).

From the technological perspective, LAB have many potential uses ranging from control of the fermentation process in the production of fermented foods to their use as probiotics for human and animal health Inês *et al.*, 2008. According to Klaenhammer *et al.* (2002), the main beneficial and nonpathogenic genera used by the food industry are: *Lactococcus* (milk), *Lactobacillus* (milk, meat, vegetables, and grains), *Leuconostoc* (vegetables and milk), *Pediococcus* (vegetables and meat), *Oenococcus oeni* (wine), and *Streptococcus thermophilus* (milk). These microorganisms are generally regarded as safe (GRAS), although some studies in the literature have shown that some strains become opportunistic pathogens in individuals with a weakened immune system Zé-Zé *et al.* (2004).

LAB cultures are an important group of starter cultures used by the food industry for the production of cheeses, yogurts, sausages, sauerkraut, and sourdough (Messens and De Vuyst, 2002). Starter cultures quickly acidify the raw materials and give the final products pleasant sensory characteristics (Leroy *et al.*, 2006).

The quick acidification promoted by LAB prevents the development of other microorganisms that could give the final product undesirable characteristics (Hugas and Monfort, 1997). This inhibitory activity stems from their ability to produce lactic and acetic acids, hydrogen peroxide, bacteriocins, and surfactants (Fernández *et al.*, 2000).

Other microorganisms in this group include the probiotics. The probiotics are defined as "live organisms that, when administered in adequate amounts, confer a health benefit on the host" (Guarner and Schaafsma, 1998). LAB are the most common microorganisms used as probiotics (Cinque *et al.*, 2010).

Within the *Lactobacillus* genus, the most studied strains used as probiotics are *Lactobacillus acidophilus* LA1, *L. acidophilus* NCFB 1748, *Lactobacillus rhamnosus* GG, *Lactobacillus casei shirota*, *Lactobacillus gasseri* ADH, and *Lactobacillus reuteri*. They boost the immune system, help to control pathogenic microorganisms in the intestines by competitive exclusion, and have anticarcinogenic activity Leroy and De Vuyst, 2004. The genus *Bifidobacterium*, including *Bifidobacterium breve*, *Bifidobacterium longum* BB536, and *Bifidobacterium lactis* Bb12, also promotes good intestinal function. These microorganisms reduce intestinal irritation and can be used in the treatment of allergies, improvement of diarrhea caused by rotavirus, and reduction of the incidence of traveler's diarrhea (Ouwehand *et al.*, 2002).

The use of probiotics in animal feed has also been studied (Corcionivoschi *et al.*, 2010). The advantages include the improvement of intestinal disorders, inhibition of pathogenic bacteria, and proliferative stimulation of peripheral blood mononuclear cells (Collado *et al.*, 2007; Schierack *et al.*, 2009; Strompfova *et al.*, 2006). Hence, their use in livestock feed is increasingly desirable because they may dispense with the need of some antibiotics or other pharmaceutical products.

Biotechnological use of acetic acid bacteria in food production

The production of vinegar from alcohol–water solutions has been known for at least 10 000 years since Romans and Greeks obtained vinegar by the spontaneous fermentation of wine exposed to air (Crueger and Crueger, 1989). The process consists of the production of acetic acid.

The oxidation of ethanol into acetic acid is done by a mixed culture of acetic bacteria, preferably, a mixed microbiota of *Acetobacter* with different species or strains of the same species Zancanaro, 2001. However, different *Gluconobacter* and *Frateuria* strains are normally found in the microbiota used by vinegar manufacturers (Ebner *et al.*, 1996).

Although the classification of acetic acid bacteria is very problematic (Ebner *et al.*, 1996), it is estimated that mainly 20 strains of the species *Acetobacter aceti*, *Acetobacter pasteurianus*, *Acetobacter acidophilum*, *Acetobacter polyoxogenes*, *Acetobacter hansenii*, and *Acetobacter liquefaciens* are responsible for submerged acetification in the food industry Zancanaro, 2001.

Vinegars are classified according to the raw materials used in their preparation. For example, distilled vinegar is obtained by the acetification of diluted and distilled alcohol. Wine vinegar is obtained by the acetification of grape wine (Ebner *et al.*, 1996). Nondistilled alcohol–water solutions (fruit wines, grain wines, and others) do not require the addition of nutrients for acetification. These solutions already contain the nutrients required by acetic acid bacteria, as the preceding alcoholic fermentation helped to enrich them. However, the acetification of alcohol–water solutions prepared with distilled alcohol (ethanol or distilled beverages) requires the addition of many nutrients, namely glucose and dietary minerals, including ammonium phosphate (Ebner *et al.*, 1996; Zancanaro, 2001). Finally, if the solution requires dilution, the added water should be potable, of low hardness, and free from sediments and chlorine (Zancanaro, 2001).

Acetic acid bacteria are obligate aerobes. Interruption of aeration during any phase of the submerged fermentation process may impair vinegar production. The degree of impairment increases as the duration of the interruption and the total concentration of ethanol and acetic acid increase. For example, a 2 min aeration interruption in a solution with a total concentration of 5% causes a loss of 34% of the viable cells; the same loss occurs after a 10–20 s aeration interruption in a solution with a total concentration of 12% (Crueger and Crueger, 1989; Ebner *et al.*, 1996).

Additionally, once there is no more ethanol in the solution, acetic acid may be oxidized to CO_2 and H_2O depending on the organisms present in the solution (Ebner *et al.*, 1996). When ethanol reaches a critical concentration of 0.2%, the semicontinuous process must be stopped (Crueger and Crueger, 1989).

Biotechnological use of yeasts and molds in food production

Yeasts are used for processing numerous basic food items. Bread texture is given by the activity of the yeast *Sa. cerevisiae*, which ferments small amounts of sugar and releases carbon dioxide, forming bubbles. The production of beer also depends on yeasts. Beer is a malt beverage resulting from the alcoholic fermentation of an aqueous extract of malted barley and hops. Consequently, beer production is a multiple-stage process involving the biological conversion of fresh raw materials into a final product (Walker, 2000). All traditional brewing yeasts used in beer production consist of *Sa. cerevisiae* strains, which are a diverse group of microorganisms.

Still on beverages, sparkling wines are other gastronomic inventions produced by fungi. Nowadays, most wine is produced industrially by selected *Saccharomyces* sp. strains, and small wineries even select yeasts from their own environment as starter cultures (Ortiz *et al.*, 2013). The selected strains must have the following characteristics: ethanol tolerance, high fermentation activity, ability to grow in the presence of high sugar concentrations, and resistance to certain fermentation by-products (Nikolaou *et al.*, 2006). Even when strains meet these criteria, the starter culture may fail because of the presence of wild yeasts (Capece *et al.*, 2010).

Cheeses also deserve to be highlighted in addition to the above-mentioned products. They have probably been consumed by humans since the domestication of animals because they are an efficient means of storing milk proteins for long periods of time. There are more than 500 different types of cheeses, each one bearing specific characteristics of the location they were originally produced. However, only some cheeses are produced by fungi and these happen to be those with the most appreciated flavor and texture. These cheeses are divided into two categories: Camembert-type cheeses and blue Roquefort-type cheeses. The former includes the world-famous

Camembert and Brie and the less known cheeses Troyes, Thenay, and Vendome. These cheeses are produced by two *Penicillium* species: *camemberti* and *caseiolum* (hyphomycetes).

However, the blue cheeses, namely Roquefort, Stilton, Gorgonzola, Danish Blue, and Wensleydale, are produced with *P. roqueforti*. This fungus oxidizes fatty acids into methyl ketones, producing unique flavors and odors.

Many Asian countries developed a wide range of foods and condiments fermented by fungi. The most widely known fermented Asian food item is undoubtedly shoyu, a Japanese sauce made by fermenting soybeans with *A. oryzae*. Another important Japanese product is miso, a fine paste produced by fermenting soybeans and rice or barley. The fungi used for producing miso are *Saccharomyces rouxii* and *A. oryzae* (Abe *et al.*, 2006).

Assessing the Microbiological Quality and Safety of Foods

Microbiological Sampling Plans

The International Commission on Microbiological Specifications for Foods (ICMSF) has provided guidance on the use of sampling plans and microbiological criteria for international food trade for many decades. Many microbiological criteria have been established by the ICMSF and national surveillance and public health authorities. These criteria may be important in food analysis, including the analysis of raw materials and ingredients of unknown origin. Microbiological criteria are an important part of the food protection and public health systems, and they assist in determining whether foods meet required safety needs.

Two types of sampling plans, by attribute and by variable, are used for performing microbiological analysis and making decisions on food safety and quality (ICMSF, 1986). Attribute sampling plans assess data quality and detect the occurrence of changes, without determining their degree, i.e., they provide a qualitative assessment. However, variable sampling plans assess quality characteristics quantitatively by making measurements.

Variable sampling can be used when the numbers of microorganisms in the food follow a log-normal distribution. The implementation of such a plan requires making many decisions. The first decision regards the establishment of an acceptable limit for the microbiological quality of the study lot and a maximum proportion of the lot that may exceed said limit. Furthermore, an α (standard deviation of the log-normal distribution) should be chosen to represent the maximum probability of accepting the nonconformity of the lot, so 1α is the desired probability for rejecting the nonconformity of the lot (Schothorst *et al.*, 2009). The disadvantages of this plan include the calculations required for lot assessment and for each variable and the fact that the probability distribution of each measurement must be known or assumed. The transformation that insures a normal distribution may not be known, and the estimates of variance are often different for each measurement. For these reasons, variable sampling plans are not widely used in the food industry for microbiological measurement (Midura and Bryant, 2001).

Attribute sampling plans are used when the microbiological distribution in the food is unknown or when the counts of microorganisms do not follow a log-normal distribution (Forsythe, 2000). The ICMSF describes two attribute sampling plans (ICMSF, 1986): a two-class plan and a three-class plan (**Figure 1**). The two-class plan consists of specifying *n*, *m* and *c*, where *n* is the number of units sampled from a lot, *m* is the maximum acceptable number of microorganisms per gram, and *c* is the maximum number of units that may exceed *m* (the lot is rejected if *c* is exceeded).

A sampling plan may approve a relatively bad lot of food and reject a good lot. This can be illustrated by the operating characteristic curve (OC) (**Figure 2**), where the probability of acceptance on the *y*-axis is the expected proportion of times that a lot with a certain quality is accepted, and the proportion of defective sampled units of the lot is on the *x*-axis.

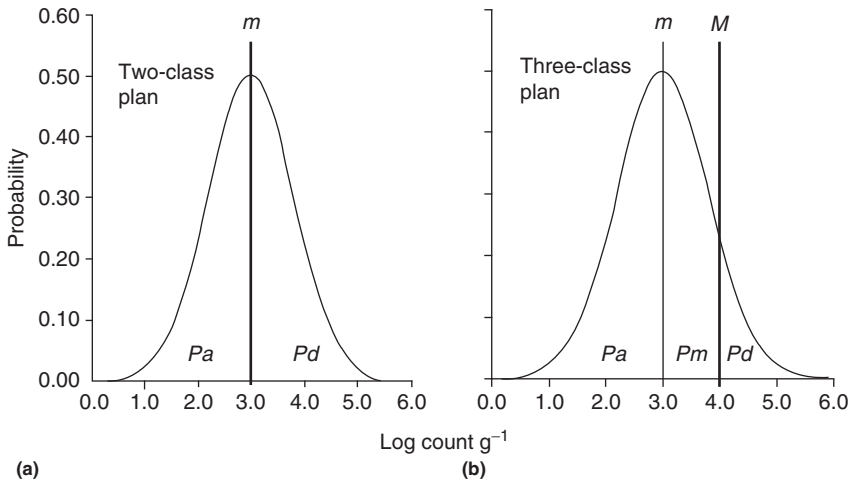


Figure 1 The relationships between acceptable and defective log concentrations for a two-class plan and acceptable and defective concentrations for a three-class plan when $m=3.0$, $M=4.0$, and distribution of organisms has mean$=3.0$ and $\sigma=0.8$. *Pa* is the proportion of acceptable material, *Pm* is the proportion marginally acceptable, *Pd* is the proportion defective, *m* is the maximum acceptable number of microorganisms per gram, and *M* is the upper bound on the marginally acceptable concentration. Adapted from Legan, J.D., Vandeven, M.H., Dahms, S., Cole, M.B., 2001. Determinig the concentration of microrganisms controlled by attributes sampling plans. Food Control 12, 137–147.

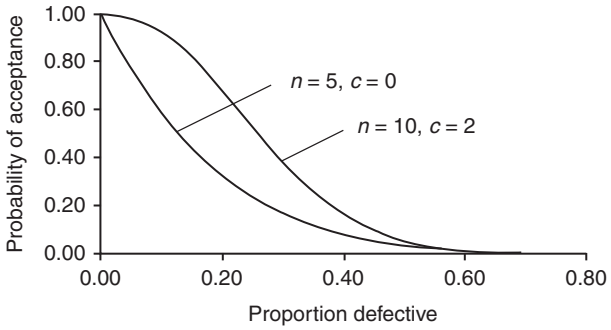


Figure 2 Operating characteristic curves showing the probability of acceptance at different defect rates for two-class plans with $n=10$, $c=2$ and $n=5$, $c=0$. n is the number of units sampled from a lot and c is the maximum number of units that may exceed m. Adapted from Legan, J.D., Vandeven, M.H., Dahms, S., Cole, M.B., 2001. Determinig the concentration of microrganisms controlled by attributes sampling plans. Food Control 12, 137–147.

The ability of a sampling plan to reject or approve the quality of a lot with high probability and the slope of the OC curve depend on n and c. **Figure 2** shows how much these characteristics change when the number of samples increases from 5 to 10 units, resulting in steeper curves and lower probabilities of acceptance, which provides better assurance that lots with high proportion defectives will be rejected (Dahms, 2004).

Three-class plans have an additional parameter called M, which is an amount chosen to distinguish marginally acceptable from unacceptable counts. Any sample with a count greater than M is rejected (**Figure 1**). Hence, a three-class plan is that in which the food may be divided into three classes according to its microbial load (Forsythe, 2010). The sample is acceptable if the counts are below m; marginally acceptable if the counts are greater than m but below M; and rejected if the counts exceed M. The strictness of a sampling plan should be given by the potential hazard of the food or its desired condition by the time it is consumed (ICMSF, 1986).

Overview of Microbiological Methods for Food Analysis

The microbiological analysis of food is part of food safety management and conformity tests that define microbiological criteria or assess the performance of control strategies based on the Hazard Analysis and Critical Control Point.

For microbiological testing of foods, rapid and conventional methods can be used. The conventional methods are called so because they were developed many years ago and have been in use ever since as the official methods of most food microbiology laboratories. These methods are described in the so-called reference publications; they are accepted internationally and recommended, for example, by the American Public Health Association, ICMSF, and the Food and Drug Administration.

The traditional methods have disadvantages associated with excessive laboratory work, time consumption, culture media, and laboratory glassware requirement. Other limitations should also be taken into account, such as technique failures related to high agar temperature and high risk of contamination because of all the stages involved in culture medium preparation and inoculation (Chain and Fung, 1991). The limitations of the traditional methods have encouraged the development of alternative methods for microbiological analysis of foods.

Many techniques for enumerating and identifying bacteria have been studied; they are currently called rapid methods. A rapid method can be defined as any method or system that reduces the time required for obtaining a microbiological test result (Feng, 1996). These include enumeration methods (quantitative methods) and detection methods (qualitative methods), which can be used depending on the objective of the study.

The direct epifluorescent filter technique consists of a rapid way of enumerating viable and unviable microorganisms using microscopy. The sample is pretreated with enzymes and surfactants and filtered with a polycarbonate membrane that traps microorganisms. Detection can be automated by connecting the microscope to an image analysis system (Jasson *et al.*, 2010). Enumeration takes 0.5–1.0 h, but the pretreatment stage may increase the total time required for analysis. The detection limit is 10^4–10^5 cells per ml. This technique has been used to enumerate bacteria in raw milk (Moran *et al.*, 1991; Rosmini *et al.*, 2004) and minimally processed vegetables (Araújo *et al.*, 2009).

Another microscope-related technique is flow cytometry, a powerful technique that uses light scattering for rapidly analyzing cells suspended in a fluid. Flow cytometry measures the optical characteristics of cells. Because most microorganisms are optically very similar, fluorescent stains may be used for verifying the microorganism's viability and their metabolic status (Flint *et al.*, 2006). This technique has been used for monitoring the load of somatic cells in milk (Gunasekera *et al.*, 2003), in wine (Malacrino *et al.*, 2001), and for assessing the microbiological quality of water (Delgado-Viscogliosi *et al.*, 2005).

Another rapid technique developed is the adenosine triphosphate (ATP) bioluminescence assay. This technique measures the light emitted by ATP when ATP reacts with luciferin and oxygen in the presence of the enzyme luciferase and magnesium cations. The amount of light produced (measured as relative light units) is proportional to ATP concentration, and consequently, to the number of microorganisms present in the sample. This technique can be used only if the microbial load is high ($>10\,000$ colony-forming units per gram, CFU g^{-1}). ATP is found not only in bacterial cells but also in any biological material, so ATP bioluminescence is generally used as a rapid indicator of organic load (Jasson *et al.*, 2010). The ATP bioluminescence assay has been used to determine the microbiological quality of food products, such as milk and dairy products, beverages, vegetables, meats, and meat products; to assess the water quality of the public water supply system; and to assess the efficiency of the cleaning and disinfection processes used by the food and pharmaceutical industries and by hospitals (Corbitt *et al.*, 2000; Griffiths *et al.*, 2000; Kennedy and Oblinger, 1985; Velazquez and Feirtag, 1997; Tydrich, 1996).

Classical or modified culture methods and molecular methods, such as enzyme-linked immunosorbent assay

(ELISA), enzyme-linked fluorescent assay (ELFA), fluorescence *in situ* hybridization (FISH), and conventional, real-time, and multiplex polymerase chain reaction, have been developed for detection of foodborne microorganisms. Classical methods are usually used for detecting pathogens in 25 g food samples. These methods require preenrichment stages because pathogens may have been injured in the study food (Wu, 2008; Jasson *et al.*, 2010). Later, other tests are used for confirming the findings.

ELISA is a biochemical technique based on antibody–antigen interaction. Detection may take from 2 to 3 h (Kumar *et al.*, 2008). ELFA is an automated test of the Bio-Mérieux's VIDAS® system that combines immunoenzymatic assay with fluorescence detection. A VIDAS® run may take from 25 to 120 min, depending on the target microorganism (Sewell *et al.*, 2003).

Molecular methods for the detection of bacteria in food, such as FISH, and multiplex and real-time PCR have also been developed and applied in microbiological analysis. FISH uses fluorescent probes to detect small deoxyribonucleic acid (DNA) or ribonucleic acid (RNA) sequences. These probes consist of nucleotide sequences that complement the DNA or RNA sequences; they are designed to identify (Shimizu *et al.*, 2009).

PCR is a rapid, inexpensive, and safe technique based on the exponential amplification of a specific DNA region. This technique has revolutionized the scientific world and its uses are innumerous. PCR success is explained by its ability to amplify a specific DNA sequence and its simplicity, accuracy, high sensitivity, and high specificity. Owing to PCR specificity given by primers, DNA does not need to be isolated even if the DNAs from other species are present. PCR limitations include the synthesis of specific primers requires knowing the DNA sequence of their target region; PCR sensitivity allows it to detect the presence of DNA contamination, inducing incorrect results; the length of the target sequence cannot exceed 5 kb, because it is difficult to use PCR to amplify longer sequences; and incorrect bases may be incorporated into a strand.

Today there are techniques faster than PCR, such as the Bax System, which consists of automated, real-time PCR for the detection of *Salmonella*, *E. coli* 0157:H7, *L. monocytogenes*, *Listeria* spp., *Cr. sakazakii*, *Ca. jejuni*, and *Ca. coli* and some molds and yeasts. The Bax System can perform as many as 96 simultaneous analyses and an analysis takes approximately 3.5 h. This technique assesses the unique genetic structure of the microorganism, greatly increasing the sensitivity and specificity of the method (Yuste and Fung, 2007).

Other innovative techniques for the microbiological analysis of food are being tested, such as microarrays (DNA microchip). This technique consists of the hybridization of messenger RNAs (mRNA) on a surface containing millions of attached sequences of DNA. It is used for specific gene identification, genome comparison, and monitoring of gene expression (Jasson *et al.*, 2010; Ikeda *et al.*, 2006).

Biosensors are another innovative technique that may be used for detecting foodborne pathogens. They consist of biologically active material, such as enzymes, antibodies, antigens, or nucleic acids, attached to a surface. Biosensors reduce the time required for analysis and can be used for analyzing very small samples (Zhang *et al.*, 2009).

See also: Biotechnology Crop Adoption: Potential and Challenges of Genetically Improved Crops. Fermentation: Food Products. Fermented Beverages. Food Engineering. Food Labeling. Food Law. Food Packaging. Food Safety: Emerging Pathogens. Food Safety: Food Analysis Technologies/Techniques. Food Safety: Shelf Life Extension Technologies. Safety of Street Food: Indonesia's Experience

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Codex Alimentarius.

http://www.efsa.europa.eu/
European Food Safety Authority: Committed to Ensuring that Europe's Food is Safe.

http://www.icmsf.org/
International Commission on Microbiological Specifications for Foods.

http://www.fda.gov/
U.S. Food and Drug Administration.

Food Packaging

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Introduction

Food packaging lies at the very heart of the modern food industry and very few foods are sold unpackaged. Good packaging prevents waste and ensures that the food retains its desired quality throughout its shelf life. Despite its importance and the key role that packaging plays, it is often regarded as, at best, somewhat superfluous, and, at worst, a serious waste of resources and an environmental menace. Such views arise because, by the time most consumers come into contact with a package, its job, in many cases, is almost over. However, if the world is ever going to be able to feed 9 billion people, then the quality and quantity of food packaging is going to have to increase considerably.

Requirements of Packaging Materials

Four primary, interconnected functions of packaging have been identified: containment, protection, convenience, and communication (Robertson, 2013). Foods must be contained before they can be moved from one place to another, and the package must contain the product to function successfully. Without containment, product loss and pollution would be widespread.

Protection is often regarded as the primary function of the package: to protect its contents from outside environmental influences such as water, water vapor, gases, odors, microorganisms, dust, shocks, vibrations, and compressive forces. For the majority of foods, the protection afforded by the package is an essential part of the preservation process. For example, aseptically packaged milk and fruit juices in paperboard laminate cartons only remain aseptic for as long as the package provides protection. Likewise, vacuum-packaged meat will not achieve its desired shelf life if the package permits O_2 to enter, and dried foods will deteriorate if the package permits moisture to enter.

Modern industrialized societies have brought about tremendous changes in life styles and created a demand for greater convenience in household products; the packaging industry has had to respond to those changes. Products designed to increase convenience include foods that are preprepared and can be cooked or reheated in a microwave oven, preferably without removing them from their package, and special kinds of packages with dispensing caps, sprays, and other convenience features make products easier to use.

Two other aspects of convenience are important in package design. One of these can best be described as the apportionment function of packaging. The relative cheapness of food is largely because of its production on an enormous scale, leading to the need for effective methods of apportioning the product into consumer-sized dimensions. For a product that is not entirely consumed when the package is first opened, the package should be resealable and retain the quality of the product until completely used.

An associated aspect is the shape (relative proportions) of the primary package with regard to consumer convenience (e.g., easy to hold, open, and pour as appropriate) and efficiency in building into secondary and tertiary packages.

The modern methods of consumer marketing would fail were it not for the messages communicated by the package. The ability of consumers to instantly recognize products through distinctive shapes, branding, and labeling enables supermarkets to function on a self-service basis. By allowing brands to be created and standardized, it makes advertising meaningful and large-scale distribution possible. Other communication functions of the package include a universal product code (UPC) that can be read accurately and rapidly, serving instructions, and nutritional information on the outside of the package.

Packaging Materials

The protection offered by a package is determined by the nature of the packaging material and the format or type of package construction. A wide variety of materials is used in packaging and primary packaging materials consist of one or more of the following materials: glass, metals, paper, and plastic polymers (Robertson, 2013). These are briefly described below.

Glass

Glass is an amorphous, inorganic product of fusion that has been cooled to a rigid condition without crystallizing. Although rigid, glass is a highly viscous liquid that exists in a vitreous or glassy state. A typical formula for soda-lime glass is:

- silica, SiO_2 68–73%
- calcia, CaO 10–13%
- soda, Na_2O 12–15%
- alumina, Al_2O_3 1.5–2%
- iron oxides, FeO 0.05–0.25%

The loss on ignition or fusion loss (generally the oxides of carbon and sulfur) can vary from 7% to 15%, depending on the quantity of cullet (used and scrap glass), there being less fusion loss the greater the quantity of cullet. Soda-lime glass accounts for nearly 90% of all glass produced and is used for the manufacture of containers where exceptional chemical durability and heat resistance are not required.

The two main types of glass containers used in food packaging are bottles (which have narrow necks) and jars (which have wide mouths or openings). Approximately 75% of all glass food containers are bottles and approximately 80% of container glass is clear, the remainder being mainly amber or green. Today's glass containers are lighter but stronger than their predecessors, and through such developments the glass container has remained competitive and

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continues to play a significant although declining role in the packaging of foods.

The container finish (so-called because in the early days of glass manufacturing, it was the part of the container fabricated last), is the glass surrounding the opening in the container that holds the cap or closure. It must be compatible with the cap or closure and can be broadly classified by size (i.e., diameter) and sealing method (e.g., twist cap, cork, etc.). Although glass is an excellent barrier to water vapor, gases, and odors, an incorrectly designed or applied closure may negate the benefits that glass packaging offers in protecting foods from deterioration.

Metals

Four metals are commonly used for the packaging of foods: steel, aluminum, tin, and chromium. Tin and steel, and chromium and steel, are used as composite materials in the form of tinplate and electrolytically chromium-coated steel (ECCS), the latter being somewhat unhelpfully referred to as tin-free steel (TFS). Aluminum is used in the form of purified alloys containing small and carefully controlled amounts of magnesium and manganese.

The term tinplate refers to low-carbon (~0.02–0.3%) mild steel sheet varying in thickness from approximately 0.15–0.5 mm with a coating of tin between 2.8 and 17 gsm (g m^{-2}) (0.4–2.5 μm thick) on each surface of the material. Tinplate is manufactured by electrolytically applying a thin coating of tin to a steel sheet, which, depending on the final application, contains various levels of carbon, silicon, manganese, phosphorous, copper, and sulfur. After plating, the coating is passivated by electrolytic treatment in sodium dichromate to render the surface more stable and resistant, and then lightly oiled. The final structure of the completed coating is shown in Figure 1.

The production of ECCS is very similar to electrotinning. ECCS consists of a duplex coating of metallic chromium and chromium sesquioxide to give a total coating weight of approximately 0.15 gsm, much thinner than the lowest grade of electrolytic tinplate. The surface of ECCS is more acceptable for protective enamel/lacquer coatings, printing inks, and varnishes than tinplate. However, ECCS is less resistant to corrosion than tinplate and therefore must be enameled on both sides.

Aluminum, the earth's most abundant metallic constituent, is used to manufacture both metal cans and thin foil in thicknesses ranging from 4 to 150 μm; foils thinner than 20 μm contain minute pinholes that are permeable to gases and water vapor. In both applications, alloying agents including silicon, iron, copper, manganese, magnesium, chromium, zinc, and titanium are added to impart strength, and improve formability and corrosion resistance.

Paper

Pulp is the fibrous raw material used for the production of paper, paperboard, corrugated board, and similar manufactured products. It is obtained from plant fiber and is therefore a renewable resource. The cell wall of softwoods, which are preferred for most pulp products, typically contain 40–44% cellulose, 25–29% hemicelluloses, and 25–31% lignin by weight. Compared to hardwoods, softwoods have fibers that are generally up to 2.5 times longer. As a result, hardwoods produce a finer, smoother, but less strong sheet.

Pulping refers to the reduction of wood or other fibrous raw materials to a fibrous mass, the purpose being to separate the fibers without damaging them so that they can then be reformed into a paper sheet in the paper-making process. The intercellular substances (primarily lignin) must be softened or dissolved to free individual fibers. Commercial pulping is accomplished by either mechanical, thermal, chemical, or a combination of these treatments. Pulps that retain most of the wood lignin deteriorate in color and strength quite rapidly; most or all of the lignin can be removed by cooking wood with solutions of various chemicals and the pulps thus produced are known as chemical pulps. In contrast, mechanical pulps are produced by pressing logs onto a grindstone when the heat generated by friction softens the lignin so that the fibers separate with very little damage. Mechanical pulps can also be formed by grinding wood chips between two rotating refiner plates. In addition, there are some processes that are categorized as semichemical and chemimechanical. The most prevalent process is chemical pulping, which accounts for

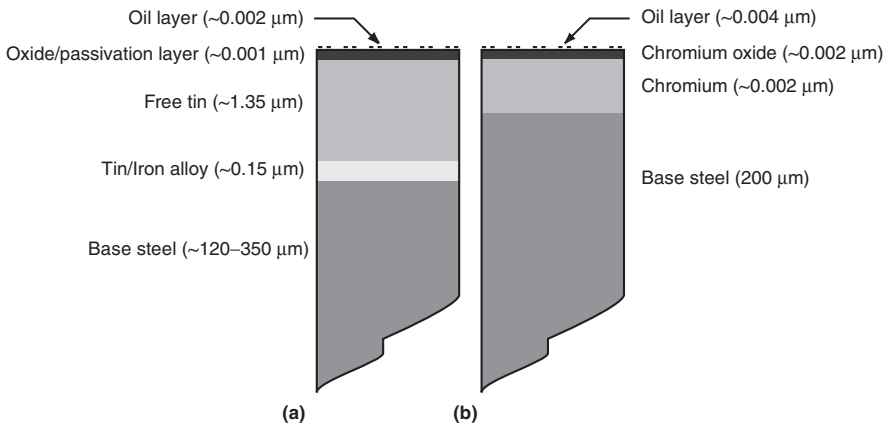


Figure 1 Schematic structure (not to scale) of (a) tinplate and (b) ECCS showing the main functional layers. Reproduced with permission from Robertson, G.L., 2013. Food Packaging: Principles & Practice, third ed. Boca Raton, FL: CRC Press.

>70% of the worldwide production of pulp, of which kraft pulping is the most prevalent at 80%.

Almost all paper is converted after manufacture by undergoing further treatment such as embossing, coating, laminating, and forming into special shapes and sizes such as bags and boxes. Further surface treatment involving the application of adhesives and printing inks are common, depending on the end use.

Paper and paperboard (>250 gsm) are poor barriers to gases and water vapor; uncoated paper packaging provides little more than protection from light and minor mechanical damage. For example, a sized commercial kraft linerboard of 200 gsm has a water vapor transmission rate (WVTR) at 50% RH/ 23 °C of 426 g m^{-2} day^{-1}. In many packaging applications, a barrier is needed against water vapor and/or gases such as O_2. A water barrier can be formed by changing the wettability of the paper surface with sizing agents, whereas coating the paper with plastic polymers provides a good barrier to gases and water vapor. Beverage cartons consist of layers of paperboard coated internally and externally with low-density polyethylene (LDPE), resulting in a carton that is impermeable to liquids and in which the internal and external surfaces may be heat sealed. There may also be a thin layer (6.5 μm) of aluminum foil, which acts as a gas and light barrier.

Plastics

Plastics are organic polymers with the unique characteristic that each molecule is either a long chain or a network of repeating units. The properties of plastics are determined by the chemical and physical nature of the polymers used in their manufacture, the properties of polymers being determined by their molecular structure, molecular weight (MW), degree of crystallinity, and chemical composition (Ebnesajjad, 2013). These factors in turn affect the density of the polymers and the temperatures at which they undergo physical transitions.

Polymer chains can and do align themselves in ordered structures, and the thermodynamics of this ordered state determine such properties as melting point T_m, glass transition temperature T_g, and mechanical and electrical properties. However, it is the chemical nature of the polymer that determines its stability to temperature, light, water, and solvents, and hence the degree of protection it will provide to food when used as a packaging material. A wide range of polymers is used in food packaging and the major categories are briefly reviewed in Section Polyolefins.

Polyolefins

These form an important class of thermoplastics and include low-, linear-, and high-density polyethylenes (LDPE, LLDPE, and HDPE) and polypropylene (PP). The polyethylenes have the nominal formula $-(CH_2-CH_2)_n-$ and are produced with a variable amount of branching, each branch containing a terminal methyl ($-CH_3$) group. Branch chains prevent close packing of the main polymer chains.

LDPE is a tough, flexible, slightly translucent material that provides a good barrier to water vapor but a poor barrier to gases. It is widely used to package foods and is easily heat sealed to itself. LLDPE contains numerous short side chains and has improved chemical and puncture resistance and higher strength than LDPE. HDPE has a much more linear structure than LDPE, is stiffer and harder, and provides superior oil and grease resistance. It is used in both film form where it has a gray, translucent appearance, and as rigid packs such as bottles. PP is a linear polymer with lower density, higher softening point, and better barrier properties than the polyethylenes. In film form it is commonly used in the biaxially oriented state (BOPP) where it has sparkling clarity; it can also be blow- and injection-molded to produce closures and thin-walled containers.

Copolymers of ethylene

For copolymers of ethylene, the other comonomer can be an alkene such as propene, butene, hexene, or octene, or a compound having a polar functional group such as vinyl acetate (VA), acrylic acid (AA), ethyl acetate (EA), methyl acrylate (MA), or vinyl alcohol (VOH). The two most important ethylene copolymers in food packaging are discussed below.

Ethylene-vinyl acetate (EVA) is a random copolymer of ethylene and VA whose properties depend on the VA content and MW. For example, EVA with a VA content of 3–12% is similar in flexibility to plasticized PVC. As the VA content increases, EVA becomes more elastic and less crystalline, resulting in an increase in permeability to gases, water vapor, fats, and oils. EVA has three advantages over LDPE: a lower heat-sealing temperature, better barrier properties, and excellent stretch properties. Thus, it finds use as a cling-wrap and stretch film for food packaging (particularly fresh meat) and has replaced PVC for many stretch-wrapping applications.

Ethylene-vinyl alcohol (EVOH) copolymers are produced by a controlled hydrolysis of EVA copolymer, the hydrolytic process transforming the VA group into VOH; there is no VOH involved in the copolymerization. EVOH copolymers offer not only excellent processability, but also superior barriers to gases, odors, aromas, etc. when dry. It is these characteristics that have allowed plastic containers incorporating EVOH barrier layers to replace many glass and metal containers for packaging food. Generally, as the ethylene content increases, the gas barrier properties decrease and the water vapor barrier properties improve.

Substituted olefins

Monomers in which each ethylene group has a single substituent are called vinyl compounds and the properties of the resultant polymers depend on the nature of the substituent, MW, crystallinity, and degree of orientation. Disubstituted monomers with two substituents on the one carbon are called vinylidene.

Polyvinyl chloride (PVC) has a repeating unit of $(-(CH_2-CHCl)_n-)$ and a range of PVC films with widely varying properties can be obtained from the basic polymer. The two main variables are changes in formulation (principally plasticizer content) and orientation.

Thin, plasticized PVC film was widely used for the stretch-wrapping of trays containing fresh red meat and produce, with the relatively high WVTR of PVC preventing condensation on the inside of the film. Oriented films are used for shrink-wrapping of produce and fresh meat, but in recent years

LLDPE films have increasingly replaced them in many applications.

Unplasticized PVC as a rigid sheet material is thermoformed to produce a wide range of inserts from chocolate boxes to biscuit trays. Unplasticized PVC bottles have better clarity, oil resistance, and barrier properties than those made from HDPE but are softened by certain solvents, notably ketones and chlorinated hydrocarbons. They are used for a wide range of foods including fruit juices and edible oils, but in recent years PVC has been increasingly replaced by PET.

Polyvinylidene chloride (PVdC) has a repeating unit of $(-(CH_2-CCl_2)_n-)$ and the homopolymer yields a rather stiff film, which is unsuitable for packaging purposes. When PVdC is copolymerized with 5–50% (but typically 20%) of vinyl chloride (VC), a soft, tough, and relatively impermeable film results. Although the films are copolymers of VdC and VC, they are usually referred to simply as PVdC copolymer and their specific properties vary according to the degree of polymerization and the properties and relative proportions of the copolymers present. Properties include a unique combination of low permeability to water vapor, gases, and odors, as well as greases and alcohols. They also have the ability to withstand hot filling and retorting and so find use as a component in multilayer barrier containers. As an important component of many laminates, PVdC copolymers can be sealed to themselves and to other materials. The copolymer is frequently used as a shrink film because orientation improves tensile strength, flexibility, clarity, transparency, and impact strength. As well, gas and water vapor permeabilities are lowered and tear initiation becomes difficult.

Polystyrene (PS) has the general formula $(-(CH_2-CHC_6H_5)_n-)$. Crystal grade PS can be made into film but it is brittle unless the film is biaxially oriented. Although a reasonably good barrier to gases, it is a poor barrier to water vapor. The oriented film can be thermoformed into a variety of shapes. To overcome the brittleness of PS, synthetic rubbers (typically 1,3-butadiene isomer $CH_2=CH-CH-CH_2$) can be added during polymerization at levels generally not exceeding 25% w/w for rigid plastics. The chemical properties of this toughened or high-impact polystyrene (HIPS) are much the same as those for unmodified or general purpose polystyrene (GPPS). HIPS is an excellent material for thermoforming and is also injection-molded into tubs, which find wide use in food packaging. Extruded PS foam sheet has high tensile strength, good water resistance, low water vapor transmission, ease of fabrication, excellent thermal insulating capability, low weight, and good cushioning characteristics. This combination of properties leads to a wide spectrum of applications in food packaging.

Polyesters

Polyethylene terephthalate (PET) is a condensation polymer produced by the esterification of ethylene glycol (EG) with terephthalic acid (TPA) or dimethyl terephthalate (DMT) and has the general formula $(-OOC-C_6H_5-COOCH_2-CH_2-)_n$. In contrast to the carbon-carbon links in the polymers discussed previously, polyesters are based on carbon–oxygen–carbon links where one of the carbons is part of a carbonyl group. The outstanding properties of PET film as a food packaging material are its great tensile strength, excellent chemical resistance, light weight, elasticity, and stability over a wide range of temperatures (−60° to 220 °C). PET films are most widely used in the biaxially oriented, heat-stabilized form.

To improve the barrier properties of PET, coatings of LDPE and PVdC copolymer have been used. PET film extrusion-coated with LDPE is very easy to seal and very tough. Two-side PVdC copolymer-coated grades provide a high barrier, and a major application is the single-slice cheese wrap. PET is also used to make 'ovenable' trays for frozen foods and prepared meals, where they are preferable to foil trays because of their ability to be microwaved without the necessity for an outer paperboard carton.

PET bottles are stretch-blow molded, the stretching or biaxial orientation being necessary to get maximum tensile strength and gas barrier, which in turn enables bottle weights to be low enough to be economical.

Polyamides

Polyamides (PAs) are condensation, generally linear thermoplastics made from monomers with amine and carboxylic acid functional groups resulting in amide (–CONH–) linkages in the main polymer chain that provide mechanical strength and barrier properties. Nylon 6 refers to PA made from a polymer of ε-caprolactam; one material is used that has 6 carbon atoms. Nylon 11 refers to PA made from a polymer of ω-undecanolactam, which has 11 carbon atoms. Films from nylon 6 have higher temperature, grease, and oil resistance than nylon 11 films.

Nylon 6,6 is formed by reacting hexamethylenediamine with adipic acid. Both materials each contain 6 carbon atoms. Nylon 6,10 is made by reacting hexamethylenediamine with sebacic acid $(HOOC-(CH_2)_8-COOH)$. The diamine has 6 carbon atoms and is numerically first, followed by the acid that contains 10 carbon atoms.

A relatively new polyamide is MXD6 made from *meta*-xylylene diamine and adipic acid, the 6 indicating the number of carbon atoms in the acid. It has better gas barrier properties than nylon 6 and PET at all humidities, and is better than EVOH at 100% RH, due to the existence of the benzene ring in the MXD6 polymer chain. Biaxially oriented film produced from MXD6 is used in several packaging applications as it has significantly higher gas and water vapor barrier properties, and greater strength and stiffness, than other PAs. Together with its high clarity and good processability, the above properties make MXD6 film suitable as a base substrate for laminated film structures for use in lidding and pouches, especially when the film is exposed to retort conditions.

Biobased plastics

Starch

Starch is the most common annually renewable raw material and is mainly extracted from cereals and tubers. Native starch is not a true thermoplastic but can be converted into a plastic-like material called thermoplastic starch (TPS). In the presence of plasticizers at high temperature (90–180 °C) and under shear, starch readily melts and flows, allowing for its use as an extrusion, injection-molding or blow-molding material, similar to most conventional petroleum-based thermoplastic polymers. Although TPS can be processed in the same way as traditional plastics, its sensitivity to water vapor and poor

mechanical properties make it unsuitable for many applications. TPS properties reach equilibrium only after several weeks.

Commercial water-resistant, starch-based bioplastics are produced by using blends of biodegradable petroleum-derived polymers and starch. These materials are made with gelatinized starch (60–85%) and hydrophilic (e.g., EVOH) or hydrophobic petroleum-derived biodegradable polymers (e.g., polycaprolactone) and compatibility agents. The polyesters form the continuous phase leading to materials having relative water resistance and acceptable barrier and mechanical properties.

Chitosan

Chitin is, after cellulose, one of the most abundant polysaccharides produced in nature and is particularly abundant in the exoskeleton of arthropods and the cell walls of insect cuticles. Chitosan is a hydrophilic polysaccharide derived from chitin by deacetylation with alkalis. Although both chitin and chitosan can be extruded to make films for food packaging applications, their main use is as an edible coating to extend the shelf life of fresh fruits and vegetables. Films made only from chitosan lack water resistance and have poor mechanical properties. Both chitin and chitosan have antimicrobial activity, which can be a useful attribute in many food packaging applications to improve quality and extend shelf life.

Polylactic acid

Polylactic acid (PLA) is a linear, aliphatic polyester synthesized from lactic acid monomers. The ester linkages in the polymer are sensitive to both enzymic and chemical hydrolysis. Lactic acid can be produced cheaply by the fermentation of glucose obtained from the starch in biomass such as corn or wheat, or from lactose in whey, or sucrose in molasses. The properties of PLA are similar to LDPE but its rigidity is much higher due to a higher T_g (58 °C compared to −25 °C for LDPE).

PLA biodegrades at temperatures above the T_g and therefore can only be composted in industrial composters where high temperatures are generated. Degradation of PLA is primarily due to hydrolysis of the ester linkages, which occurs more or less randomly along the backbone of the polymer. Two major challenges to the stabilization of PLA with regard to hydrolysis are that it is quite permeable to water and the hydrolysis reaction is autocatalytic.

Poly(hydroxyalkanoates)

Poly(hydroxyalkanoates) (PHAs) are linear aliphatic polyesters consisting of homo- or co-polymers of β-hydroxyalkanoic acids that can be produced from the fermentation of sugars by, for example, *Cupriavidus necator*. They are produced in the form of intracellular particles that accumulate as a carbon and energy sink when certain microorganisms are grown under nutrient stress in the presence of excess carbon. Poly(hydroxybutyrate) (PHB) is the most common polymer but by manipulating the growth medium, a random copolymer containing both 3-hydroxybutyrate (HB) and 3-hydroxyvalerate (HV) is obtained: poly(hydroxybutyrate *co*-hydroxyvalerate) or PHBV. By changing the ratio of HV to HB, the resulting copolymer can be made to resemble either PP (low HV) or LDPE (high HV) with regard to flexibility, tensile strength, and melting point. PHB/V has good chemical and moisture resistance as well as good O_2 and aroma barrier properties.

Biopolyethylene

Bioethylene is produced by the catalytic dehydration of bioethanol, which can be made by fermentation of various feedstocks including sugarcane, sugar beet, and wheat grain. Biopolyethylene (BioPE) has characteristics equivalent to those of conventional polyethylene and can be used in identical applications. From bioethylene it is possible to produce all the polyethylene types: HDPE, LDPE, and LLDPE.

Biopolyethylene terephthalate

It is now possible to make biopolyethylene terephthalate (bioPET) using EG derived from sugarcane, and TPA or DMT produced from biobased *para*-xylene (PX) by converting fermentation-derived isobutanol into PX using several traditional chemical processes such as dehydration, dimerization, and cyclization. Commercial production is expected by 2015. Of course, the bioPET has identical properties to petrochemical-based PET, i.e., it can be recycled but is not biodegradable.

Regenerated cellulose film

Regenerated cellulose film (RCF) (commonly referred to by the generic term cellophane, which is still a registered trade name in some countries) is manufactured from highly purified cellulose (usually derived from bleached sulfite wood pulp) and is therefore a biobased and renewable material. However, it is not a plastic as it will not melt and cannot be formed by heat and pressure; it can be regarded as transparent paper. For food packaging applications it is plasticized (typically with EG) and coated on one or both sides; the type of coating largely determines the barrier properties of the film. The most common coatings are LDPE, PVC, and PVdC copolymer; it can also be metallized with aluminum particles.

Packaging Material Properties

The ability to quantify the properties of packaging materials and the resulting packages is critical to the design and development of packaging that will serve its intended functions. It is necessary to be aware of just what properties are essential at the package development stage. Although the dangers of underperformance of food packaging are usually well understood, overperformance is equally to be avoided in light of the high costs of packaging materials and societal pressures to reduce the quantity of packaging materials used commercially.

Mechanical Properties of Metals, Glass, Paper, and Plastic Packaging

The mechanical properties of a packaging material, together with the effectiveness of the package closure or seal, determine the ability of a package to maintain integrity, i.e., its protective properties under physical stress. A number of tests are used to assess the packaging material strength under tension, compression, bursting, tearing, or impact forces.

Metals

Carbon is the most important alloying element for steel and affects the strength of cans, a higher carbon content usually being combined with a higher manganese content, resulting in higher strength steel. Lower carbon content improves material formability and weldability. To reduce the possibility of severe fluting, paneling, or creasing, and to impart the desired surface finish, steel is given a final, light cold rolling in a 'temper' mill. This imparts springiness to the steel but changes the temper or surface hardness only slightly. Temper refers to an arbitrary number designation that indicates the forming properties of tin and is the summation of interrelated mechanical properties such as elasticity, stiffness, springiness, and fluting tendency.

The combination of tin and steel produces a material that has good strength, combined with excellent fabrication qualities such as ductility (the capability to undergo extensive deformation without fracture) and drawability (these attributes arise from the grade of steel selected and the processing conditions employed in its manufacture), as well as good weldability, nontoxicity, lubricity, lacquerability, and a corrosion-resistant surface of bright appearance (these latter properties are due to the unique properties of tin). Furthermore, the tin coating adheres sufficiently to the steel base so that it withstands any degree of deformation that the steel is able to withstand without flaking.

Compared with tinplate and ECCS, aluminum is a lighter, weaker, but more ductile material that cannot be soldered. Aluminum has a higher strength to weight ratio but less tensile strength than steel. The high ductility allows aluminum to be shaped and formed with relative ease. Most commercial uses of aluminum require special properties that the pure metal cannot provide. Therefore, alloying agents are added to impart strength, improve formability characteristics, and influence corrosion characteristics. A wide range of aluminum alloys is commercially available for packaging applications, depending on the container design and fabrication method used.

Glass

Because of its amorphous structure, glass is brittle and usually breaks because of an applied tensile stress. It is now generally accepted that fracture of glass originates at small imperfections or flaws, the large majority of which are found at the surface. A bruise or contact with any hard body on the glass surface produces very small cracks or checks that may be invisible to the naked eye. However, because of their extreme narrowness, they cause a concentration of stress that may be many times greater than the nominal stress at the section containing them. Because glass cannot yield, the applied stress (when it is high enough) causes these flaws to propagate. Thus, it is the ultimate tensile strength of a glass surface that determines when a container will break. In practice, a stress concentrator may be a small crack or check induced in the manufacturing process, or a scratch resulting from careless container handling. Therefore, the major step taken to make glass more break-resistant involves the elimination of surface flaws (e.g., microcracks) by careful handling during and after forming and annealing, because the condition of the surface has a great deal to do with its tensile properties.

The mechanical strength of a glass container is a measure of its ability to resist breaking when forces or impacts are applied. Glass deforms elastically until it breaks in direct proportion to the applied stress. Although the mechanical strength of a glass bottle or jar can increase with glass weight, this is at the expense of thermal strength, which decreases with increasing glass weight.

Paper

The strength and mechanical properties of paper depend on the mechanical treatment of the fibers and the inclusion of fillers and binding materials. Paper has a definite grain caused by the greater orientation of fibers in the direction of travel of the paper machine, and the greater strength orientation that results partly from the greater fiber alignment and partly from the greater tension exerted on the paper in this direction during drying. The grain direction is known as the machine direction (MD), whereas the cross direction (CD) is the direction of the paper at right angles to the MD. Most of the physical properties of paper depend on direction, i.e., the MD, CD, and thickness direction (z direction), and these must be taken into account in measuring all physical properties and clearly indicated when reporting test results.

Papers vary in MD:CD strength ratios, and usually there is less variation in paper properties in the MD than in the CD because variations occur slowly in the MD, whereas in the CD they may occur quite suddenly for a variety of process-related reasons. In addition, the CD strength normally varies depending on how far the sample was taken from the edge of the sheet. In general, papers should be used to take greatest advantage of the grain of the paper.

Plastics

The four properties tensile and yield strength, elongation and Young's modulus are usually considered together because the same equipment is used for measuring each of them. It is usual when carrying out tensile tests to plot the stress against the strain, i.e., the load against the elongation. A great deal of information about the material can be obtained from the shape of its stress/strain curve. In addition to the numerical values for tensile strength, Young's modulus, elongation, and so on, it is possible to obtain some idea of the toughness of the material by measuring the area under the curve. Some mechanical properties of plastics are given in Table 1. One problem that arises when considering the strength of thermoplastic polymers is the time and temperature dependence of the changes that occur under mechanical stress.

Optical Properties of Glass and Plastic Packaging

Glass, because it has no crystalline structure, is optically isotropic when it is homogeneous and free from any stresses. The optical properties of glass relate to the degree of penetration of light and the subsequent effect of that transmission, transmission being a function of wavelength. The spectral transmission of glass is determined by reflection at the glass surface and the optical absorption within the glass. In silicate glasses, transmission is limited by the absorption of silica at approximately 150 nm in the UV and at 6000 nm in the IR region. Iron impurities further reduce transmission in the UV and near-IR regions.

Table 1 Mechanical properties of some biobased and petroleum-derived polymers

Polymer	*Melting temperature*	*Glass transition temperature*	*Young's modulus*	*Tensile strength*	*Elongationat break*
	T_m (°C)	*T_g (°C)*	*MPa*	*MPa*	*(%)*
Starch[a]		8	100–400	24–30	200–1000
Starch[b]		–20	200–2000	20–30	20–500
Starch	110–115		600–850	35–80	580–820
PHA	70–170	–30 to –10	0.7–1.8	18–24	3–25
PHB	178	4	1000–2000	25–40	5–8
PHBV[c]	153	5	900		15
PHBV[d]	145	–1	800	20	50
PLA	152	58	2050	40–63	9
PET	267	69	2800–4100	48–72	30–300
PS	240	100	3000–3500	34–50	3–5
LDPE	105–115	–25	300–500	8–20	500–1000
PP	176	–18	1000–2000	30–40	400–900

[a]Film grade.
[b]Injection-molding grade.
[c]7 mol% HV.
[d]20 mol% HV.
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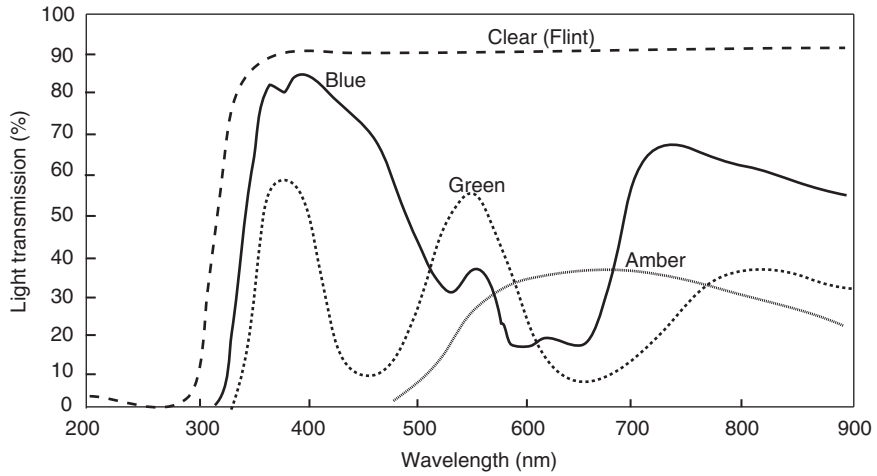


Figure 2 Typical light transmission properties of common container glasses. Reproduced with permission from Robertson, G.L., 2013. Food Packaging: Principles & Practice, third ed. Boca Raton, FL: CRC Press.

Light transmission may be controlled by the addition of coloring additives such as metallic oxides, sulfides, or selenides. Most of the transition metal oxides (e.g., cobalt, nickel, chromium, iron, etc.) give rise to absorption bands, not only in the visible but also in the UV and IR regions of the spectrum. The three main colors of glass used to produce food containers are flint or clear, amber or brown, and green, and the typical light transmission of these glasses is shown in Figure 2.

A light-resistant container is defined as one that passes no more than 10% of incident radiation at any wavelength between 290 nm and 450 nm through the average sidewall thickness. Amber glass provides this degree of light protection quite economically, as shown in Figure 2.

Optical properties of plastics are related to both the degree of crystallinity and the actual polymer structure. Optical properties of importance with thermoplastic polymers include clarity, haze, color, transmittance, reflectance, gloss, and refractive index. The clarity of a film indicates the degree of distortion of an object when viewed through the film, with 'see-through' clarity referring to the ability of the film to resolve fine details of fairly distant images viewed through the film.

Barrier Properties of Plastic Packaging

Unlike metal and glass packages, plastic packages are permeable and the concept of permeability is normally associated with the quantitative evaluation of the barrier properties of a plastic. A plastic that is a good barrier has a low permeability. This section is concerned with aspects of the solution,

diffusion and permeation of gases and vapors ('permeants') in effectively nonporous polymeric materials.

The protection of foods from gas and vapor exchange with the environment depends on the integrity of packages (including their seals and closures), and on the permeability of the packaging materials themselves. The barrier properties of plastics indicate their resistance to sorption and diffusion of substances such as gases and flavor and aroma compounds.

Under steady-state conditions, a gas or vapor diffuses through a polymer at a constant rate if a constant pressure difference is maintained across the polymer. The diffusive flux, J, of a permeant in a polymer can be defined as the amount passing through a plane (surface) of unit area normal to the direction of flow during unit time as follows:

$$J = Q/At \quad [1]$$

where Q is the total amount of permeant that has passed through area A during time t.

The relationship between the rate of permeation and the concentration gradient is one of direct proportionality and is embodied in Fick's first law:

$$J = -D\frac{\delta c}{\delta x} \quad [2]$$

where J is the flux (or rate of transport) per unit area of permeant through the polymer, c is the concentration of the permeant, D is the diffusion coefficient, and $\delta c/\delta x$ is the concentration gradient of the permeant across thickness δx. D reflects the speed at which the permeant diffuses through the polymer and is a function of temperature and may also be of concentration. Equation [2] can be used to calculate the steady-state rate of diffusion assuming that D is constant and the concentration is a function only of the geometric position inside the polymer.

Consider a polymer X mm thick, of area A, exposed to a permeant at pressure p_1 on one side and at a lower pressure p_2 on the other as shown in Figure 3. The concentration of permeant in the first layer of the polymer is c_1 and in the last layer c_2.

When steady-state diffusion has been reached, J=constant and eqn [2] can be integrated across the total thickness of the polymer X, and between the two concentrations, assuming D to be constant and independent of c:

$$JX = -D(c_2 - c_1) \quad [3]$$

and

$$J = \frac{D(c_2 - c_1)}{X} \quad [4]$$

By substituting for J using eqn [1], the quantity of permeant Q diffusing through a polymer of area A in time t can be calculated:

$$Q = \frac{D(c_2 - c_1)At}{X} \quad [5]$$

Rather than the actual concentration, it is more convenient when the permeant is a gas to measure the vapor pressure p, which is at equilibrium with the polymer, rather than measure the actual concentration. Henry's law applies at low

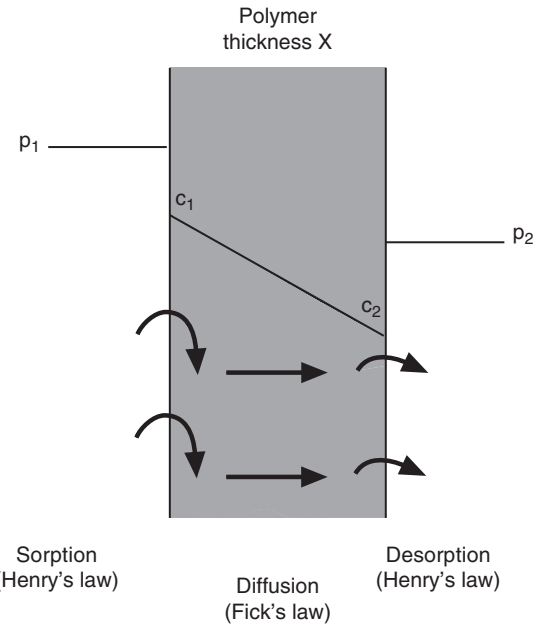


Figure 3 Permeability model for gas or vapor transfer through a polymer. Reproduced with permission from Robertson, G.L., 2013. Food Packaging: Principles & Practice, third ed. Boca Raton, FL: CRC Press.

concentrations and c can be expressed as:

$$c = Sp \quad [6]$$

where S is the solubility coefficient of the permeant in the polymer (it reflects the amount of permeant in the polymer). By combining eqns [5 and 6],

$$Q = \frac{DS(p_1 - p_2)At}{X} \quad [7]$$

The product DS is referred to as the permeability coefficient or constant and is represented by the symbol P:

$$P = DS \quad [8]$$

Thus, the permeability coefficient is the product of a kinetic term (D), which reflects the dynamics of the penetrant-polymer system, and of a thermodynamic term (S), which depends on the penetrant-polymer interactions. P represents the ease with which a gas permeates through a polymer when subjected to a pressure gradient.

$$P = \frac{QX}{At(p_1 - p_2)} \quad [9]$$

or

$$\frac{Q}{t} = \frac{P}{X}A(\Delta p) \quad [10]$$

The term P/X is called the permeance; it is not a property of the material but a performance evaluation indicator.

Although steady-state is usually attained in a few hours for small molecules such as O_2, larger molecules in barrier polymers (especially glassy polymers) can take a long time to reach steady-state, with this time possibly exceeding the anticipated

Table 2 Broadly representative permeability coefficients of various polymers and permeants at 25 °C and 0% RH unless indicated otherwise in barrer (10^{-10} cm^3 (STP) cm cm^{-2} s^{-1} (cm Hg)$^{-1}$)

Polymer	*O_2*	*CO_2*	*N_2*	*H_2O (90% RH)*
Linear low-density polyethylene	1.3–3.0	13	1.5	
Low-density polyethylene	3.0–6.7	13–28	0.6–1.9	80
High-density polyethylene	0.6–1.1	1.7–4.5	0.14–0.33	13
EVA copolymer	3.0–4.2	13.1–17.3		29
Polypropylene	0.9–2.3	9.2	0.44	57
Polyvinyl chloride film	0.005–0.12	0.03–1.0	0.04	156–275
Polystyrene film (oriented)	1.1–2.7	8.8–10.5	0.29–0.78	11–1800
Nylon-6	0.012–0.038	0.04–0.16	0.01	700 (0% RH)
Nylon MXD6	0.001–0.003	0.009 3		
Polyethylene terephthalate (amorphous)	0.055–0.075	0.21–0.30	0.005	
(40% crystalline)	0.018–0.030	0.12–0.16	0.006	130–183
PVdC/PVC copolymer	0.000 6	0.002 2–0.003 6	0.000 9	1.4–4.5
EVOH copolymer				
32% ethylene	0.000 12	0.000 36	0.000 012	
44% ethylene	0.000 48	0.001 4	0.000 05	
Polylactic acid	0.11–0.56	1.88	4.99	3000

Source: Reproduced with permission from Robertson, G.L., 2013. Food Packaging: Principles & Practice, third ed. Boca Raton, FL: CRC Press.

shelf life. Although D and S are independent of concentration for many gases such as O_2, N_2, and, to a certain extent, CO_2, this is not the case where considerable interaction between polymer and permeant takes place (e.g., water and hydrophilic films such as EVOH and PAs, or many solvent vapors diffusing through polymer films).

Although the chemical structure of a polymer can be considered to be the predominant factor that controls the magnitude of P, it also varies with the morphology of the polymer and depends on many physical factors such as density, crystallinity, and orientation.

Consideration of eqn [9] suggests that the dimensions of P are:

$$P = \frac{(\text{quantity of permeant under stated conditions})(\text{thickness})}{(\text{area})(\text{time})(\text{pressure drop across polymer})} \quad [11]$$

The quantity of permeant can be expressed in mass, mole, or volume units. For gases, volume is preferred, expressed as the amount permeating under conditions of standard temperature and pressure (STP: 273.15 K and 1.013 25×10^5 Pa). Although more than 30 different units for P appear in the scientific, commercial, and patent literature, the American Society for Testing and Materials (ASTM) has adopted a single unit for P called the *barrer* (B) after the New Zealander Richard Maling Barrer (1910–1996), a pioneer in gas transport through membranes. It is defined as 10^{-10} cm^3 (STP) cm cm^{-2} s^{-1} (cm Hg)$^{-1}$. The SI units of kg m m^{-2} s^{-1} Pa^{-1} are found occasionally in the scientific literature where the exponential term is 10^{-18}. Broadly representative permeability coefficients for a number of polymers to several gases and water vapor are presented in Table 2.

The above treatment of steady-state diffusion assumed that both D and S are independent of concentration but in practice deviations do occur. Equation [9] does not hold for heterogeneous materials such as coated or laminated films, or when there is interaction between polymer and permeant. The property is then defined as the transmission rate (TR) of the material, where:

$$\text{TR} = \frac{Q}{At} \quad [12]$$

where Q is the amount of permeant passing through the polymer, A is the area, and t is the time. Permeabilities of polymers to water and organic compounds are often presented in this way, and in the case of water and O_2, the terms WVTR and oxygen transmission rate (OTR) are in common usage.

It is critical that the thickness of the film or laminate, the temperature and the partial pressure difference of the gas or water vapor are specified for a particular TR.

Typically, units of (g m^{-2} day^{-1}) are used for WVTR and (ml m^{-2} day^{-1}) for OTR. Often the WVTRs are given for so-called tropical conditions of 38 °C/90% RH but sometimes for so-called temperate conditions of 25 °C/75% RH; OTRs are often given for 23 °C/0% RH. Such data for a variety of polymer films of 25 μm (2.5×10^{-3} cm) thickness are given in Table 3.

TR is related to P as follows:

$$P = \frac{QX}{At\Delta p} = \text{TR}\frac{X}{\Delta p} \quad [13]$$

Factors Affecting Permeability

Both compositional and environmental factors affect permeability. Compositional factors include permeant size and shape, polymer morphology, polymer additives, and permeant-polymer interactions. A major environmental factor is temperature, which influences both the solubility and diffusion coefficients as follows:

$$P = DS = D_o S_o \exp\{-(E_d + \Delta H_s)/RT\} = P_o \exp(-E_p/RT) \quad [14]$$

where ΔH_s is the heat of sorption of the permeant in the polymer, E_d is the activation energy for the diffusion process, and E_p is the apparent activation energy for permeation. For all known permeant-polymer pairs, P increases with temperature.

Table 3 Oxygen transmission rate (OTR) and water vapor transmission rate (WVTR) of some plastic films

Polymer (25 μm thick)	*OTR*	*WVTR*	
	(23 °C/0% RH) ml m^{-2} day^{-1}	*(38 °C/90% RH) g m^{-2} day^{-1}*	*(25 °C/75% RH) g m^{-2} day^{-1}*
Low-density polyethylene	7400	12.50	4.00
High-density polyethylene	1600	3.70	1.45
Polypropylene (cast)	3040	8.20	3.30
Polypropylene (oriented)	1550	5.00	1.35
Polypropylene (oriented & metalized)	35	1.00	
Polyvinyl chloride (rigid)	120	32.00	12.00
Polyvinyl chloride (oriented)	27	17.50	7.00
Polyvinyl chloride (plasticized)	190–3100	85.00	32.70
PVdC/PVC copolymer	1.25–14.5	0.6–3.20	0.25
Polyethylene terephthalate	55	20.00	7.00
Polyethylene terephthalate (metallized)	0.65	1.00	0.40
Nylon-6	40	280	80–110
Nylon-6 (oriented)	18	130	28
Nylon-6,6	35	90	15–30
EVOH copolymer (32% ethylene)	0.2	80.0	32.0
Cellulose film MXXT/A (PVdC/PVC copolymer coated)	8.75	8.60	3.40

Source: Reproduced from Mathlouthi, M., 2003. Packaging/packaging of solids. In: Caballero, B., Trugo, L.C., Finglas, P.M. (Eds.), Encyclopedia of Food Sciences and Nutrition, second ed., vol. 7. London, England: Academic Press, p 4314.

Many foods require more protection than a single material can provide to give the product its intended shelf life. Where increased barriers to gases and/or water vapor are necessary, it is more economical to incorporate a thin layer of barrier material than to simply increase the thickness of a monolayer. Provided that the permeability coefficients of the individual layers are independent of the permeant partial pressure, the permeability coefficient of the multilayer film, P_T, can be calculated using the equation:

$$P_T/X_T = (P_1/X_1) + (P_2/X_2) + \ldots\ldots(P_n/X_n) \qquad [15]$$

where X_T is the total thickness of the multilayer film, and the permeability coefficients and thickness of the individual layers are designated by 1,2,……,*n*.

Food Packaging and Shelf Life

The quality of most foods and beverages decreases with storage or holding time, from which it follows that there will be a finite length of time before the product becomes unacceptable. This time from production to unacceptability is referred to as shelf life and includes the time in warehouses and the distribution chain, as well as time on the retailer's shelf and in the consumer's home. The shelf life of a food is controlled by:

- formulation and processing parameters (intrinsic factors);
- the environment the product is exposed to during distribution and storage (extrinsic factors);
- the properties of the package.

Examples of intrinsic factors include pH, water activity a_w, enzymes, microorganisms, and concentration of reactive compounds. Many of these factors can be controlled by selection of raw materials and ingredients, as well as the choice of processing parameters. Examples of extrinsic factors include temperature, relative humidity, light, total pressure, and partial pressure of different gases, and mechanical stresses including consumer handling. Many of these factors can affect the rates of deteriorative reactions that occur during the shelf life of a product (Robertson, 2010).

The properties of the package can have a significant effect on many of the extrinsic factors and thus indirectly on the rates of the deteriorative reactions. In summary, the shelf life of a food can be altered by changing its composition and formulation, processing parameters, packaging system, or the environment to which it is exposed.

Moisture-Sensitive Foods

When a food is placed in an environment at a constant temperature and relative humidity, it eventually comes to equilibrium with that environment. The corresponding moisture content at steady-state is referred to as the equilibrium moisture content (m_e). When a range of moisture contents (expressed as mass of water per unit mass of dry matter) is plotted against its corresponding relative humidity or a_w at constant temperature, a moisture sorption isotherm (MSI) results. Such plots are very useful in assessing the stability of moisture-sensitive foods and selecting effective packaging.

The expression for the steady-state permeation of a gas or vapor through a thermoplastic material was derived previously (see eqn [9]) and can be rewritten as:

$$\frac{\delta w}{\delta t} = \frac{P}{X} A(p_1 - p_2) \qquad [16]$$

where $\delta w/\delta t$ represent the rate of gas or vapor transport across the film, the latter term corresponding to Q/t in the integrated form of the expression (eqn [9]).

The prediction of moisture transfer either to or from a packaged food requires analysis of the above equation given certain boundary conditions. If it is assumed that P/X is constant, that the external environment is at constant temperature and humidity, and that p_2, the vapor pressure of the water in the food, follows some simple function of the moisture content, then a simple analysis can be made.

However, because external conditions do not remain constant during storage, distribution, and retailing of a packaged food, P/X is not constant. If the food is being sold in markets in temperate climates, then WVTRs determined at 25 °C/75% RH can be used. A 'worst-case' analysis can be made using WVTRs determined at 38 °C/90% RH. A further assumption is that the moisture gradient inside the package is negligible, i.e., the package should be the major resistance to water vapor transport, which is the case for most films under high humidity conditions.

Consideration of eqn [16] indicates that the internal vapor pressure is not constant but varies with the moisture content of the food at any time. Consequently, the rate of gain or loss of moisture is not constant but falls as Δp gets smaller. Thus to be able to make accurate predictions, some function of p_2, the internal vapor pressure, as a function of the moisture content must be inserted into the equation. Assuming a constant rate results in the product being overprotected.

In low and intermediate moisture foods, the internal vapor pressure is determined solely by the MSI of the food. In the simplest case when the isotherm is treated as a linear function:

$$m = b\,a_w + c \qquad [17]$$

where m, moisture content in g H_2O per g solids; a_w, water activity; b, slope of isotherm; c, constant.

The moisture content can be substituted for water gain and after some mathematical manipulation the following expression is obtained:

$$\ln\frac{m_e - m_i}{m_e - m} = \frac{PAp_o}{XW_s b}t \qquad [18]$$

where m_e, equilibrium moisture content of the food if exposed to external package RH; m_i, initial moisture content of the food; m, moisture content of the food at time t; p_o, vapor pressure of pure water at the storage temperature (not the actual vapor pressure outside the package); W_s, weight of dry solids inside the package.

The end of product shelf life is reached when $m = m_c$, the critical moisture content, at which time $t = \theta_s$, the shelf life.

Equations such as eqn [18] have been extensively tested for foods and found to give excellent predictions of actual weight gain or loss (Robertson, 2011). These equations can be used to calculate the effect on shelf life of changes in the permeability of the packaging film, external conditions such as temperature and humidity, the surface area:volume ratio of the package, and variations in the initial moisture content of the product.

Oxygen-Sensitive Foods

Oxygen is the gas of major importance in packaged foods because it plays a crucial role in many reactions that affect shelf life (e.g., microbial growth, color changes in fresh and cured meats, oxidation of lipids and consequent rancidity, and senescence of fruits and vegetables). The transfer of gases and odors through packaging materials can be analyzed in an analogous manner to that described for water vapor transfer, provided that values are known for the permeance of the packaging material to the appropriate gas, and the partial pressure of the gas inside and outside the package.

The principal difference between predominantly water vapor-sensitive and O_2-sensitive foods is that the latter are generally more sensitive by two to four orders of magnitude. Thus, the amount of O_2 present in the air-filled headspace of O_2-sensitive foods must not be neglected when predicting their shelf life. A further complicating factor with O_2-sensitive foods is that a concentration gradient occurs much more frequently than in moisture-sensitive foods.

Assuming that resistances of headspace and food to O_2 diffusion are negligible, the unsteady-state material balance for oxygen content of the headspace is (Krochta, 2007):

$$\frac{\delta p_{O2}}{\delta t} = \frac{PA(p_{O1} - p_{O2})}{VX} - r_O W \qquad [19]$$

where p_{O1} is the O_2 partial pressure outside the package (constant at 0.21 atm), p_{O2} is the O_2 partial pressure inside the package, t is time since the packaging of the food, V is the package headspace volume, W is the weight of the food, r_O is the O_2 reaction rate per unit weight of food, and P, X, and A are as defined earlier. The simplest solution is obtained when r_O can be related to p_{O2} with a linear equation, permitting r_O to be integrated over time and the shelf life θ_s calculated when the quantity of O_2 (Q_O) permeating into the food has reached the limit of acceptability. An even simpler approach that does not require an equation relating r_O to p_{O2} is to assume that O_2 reacts immediately on entering the package, that p_{O2} is zero, and that steady-state is reached rapidly. Equation 19 can then be simplified to

$$\frac{PA(p_{O1})}{X} = r_O W \qquad [20]$$

Given that

$$r_O = Q_O/\theta_s \qquad [21]$$

Then

$$\theta_s = \frac{Q_O WX}{PAp_{O1}} \qquad [22]$$

This approach gives a conservative estimate of shelf life.

Packaging Systems

Modified Atmosphere Packaging

Modified atmosphere packaging (MAP) is being successfully used around the world to extend the shelf life and retain the quality of a wide variety of foods. MAP is the enclosure of food in a package in which the atmosphere inside the package is modified or altered to provide an optimum atmosphere for increasing shelf life while maintaining food quality. Modification of the atmosphere may be achieved either actively or passively. Active modification involves displacing the air with

a controlled, desired mixture of gases, and is generally referred to as gas flushing. Passive modification (also known as commodity-generated MA) occurs as a consequence of the food's respiration and/or the metabolism of microorganisms associated with the food; the package structure normally incorporates a polymeric film and so the permeation of gases through the film (which varies depending on the nature of the film and the storage temperature) also influences the composition of the atmosphere that develops.

In vacuum packaging, elevated levels of CO_2 can be produced by microorganisms or by respiring fruits and vegetables. Thus vacuum packaging of respiring foods or foods containing viable microorganisms such as flesh foods is a form of MAP because after initial modification of the atmosphere by removal of most of the air, biological action continues to alter or modify the atmosphere inside the package.

With the exception of baked goods, MAP is always used in association with chill temperatures (usually taken as $-1°$ to $+7$ °C). The preservative effect of chilling can be greatly enhanced when it is combined with modification of the gas atmosphere because many deteriorative reactions involve aerobic respiration in which the food or microorganism consumes O_2 and produces CO_2 and water. By reducing O_2 concentration, aerobic respiration can be slowed. By increasing CO_2 concentration, microbial growth can be slowed or inhibited.

The normal composition of air by volume is 78.08% nitrogen, 20.95% oxygen, 0.93% argon, 0.03% carbon dioxide, and traces of nine other gases in very low concentrations. The three main gases used in MAP are O_2, CO_2, and N_2, either singly or in combination. Although the literature on their application and benefits is limited, noble or 'inert' gases such as argon are being used commercially for a wide range of products. Argon is 1.43 times denser than N_2 and can thus be made to flow like a liquid through air spaces whereas N_2 cannot. Use of carbon monoxide (CO) and sulfur dioxide (SO_2) has also been reported for specific foods.

The gas mixtures used for MAP of different foods depend on the nature of the food and the likely spoilage mechanisms. Where spoilage is mainly microbial, the CO_2 levels in the gas mix should be as high as possible, limited only by the negative effects of CO_2 (e.g., package collapse when CO_2 is absorbed by the food) on the specific food. Typical gas compositions for this situation are 30–60% CO_2 and 40–70% N_2. For O_2-sensitive products where spoilage is mainly by oxidative rancidity, 100% N_2 or N_2/CO_2 mixtures (if microbial spoilage is also important) are used. For respiring products it is important to prevent anaerobic respiration by avoiding too high a CO_2 level or too low an O_2 level.

The recommended concentrations of O_2 and CO_2 for fruits and vegetables can be found in the published literature, and a very effective way of plotting this data with CO_2 concentration as the ordinate and O_2 concentration as the abscissa is presented in **Figure 4** for fruits (Kader *et al.*, 1998). The windows represent the boundary of recommended gas concentrations; the smaller the window the more rigid the design requirement.

The permselectivity β of plastic films is defined as the ratio of the permeability coefficients of CO_2:O_2. For air β is approximately 0.8; this is represented by the line A–D in **Figure 4**. An otherwise impermeable package with a few small holes can be used to create atmospheres along this line that passes through the window for berry fruits and figs. Line A–B is plotted for a β of 5.0, which is approximately the value for LDPE and PVdC copolymer films. This line bisects several windows indicating that these films could be used successfully for some fruits. However, PVdC copolymer is suitable only for produce with very low respiration rates because it has such low gas permeabilities (*see* **Table 2**). The CO_2–O_2 atmospheres that lie between the lines A–B and A–D may be created by using packages made from LDPE film with microperforations or microporous windows. However, the permselectivity ratios are not constant for a given polymer but increase as the temperature is lowered. For example, β for LDPE has been reported to range from 5.08 at 0 °C to 3.45 at 20 °C, and β for PVC from 6.0 at 5 °C to 4.0 at 40 °C. Line A–C is plotted for a β of 3.0.

Equipment for MAP must generally be capable of removing air from the package and replacing it with a mixture of gases. Three types of packaging equipment are generally used for MAP: chamber machines using preformed pouches or trays; snorkel machines using preformed bags or pouches; and horizontal or vertical form-fill-seal (FFS) machines using pouches or trays.

The main characteristics to be considered when selecting packaging materials for MAP are the package permeability to gases and water vapor, mechanical properties, heat sealability, and transparency. For nonrespiring products, all the common high gas barrier structures have been used in MAP, including laminates and coextruded films containing PVdC copolymer, EVOH, and PAs as a barrier layer. To provide a good heat seal and water vapor barrier, the inside layer is usually LDPE.

The choice of suitable packaging materials for the MAP of respiring produce such as fruits and vegetables is much more complex and no easy solutions are available due to the dynamic nature of the product. Ideally the packaging material should maintain a low O_2 concentration (3–5%) in the headspace and prevent CO_2 levels from exceeding 10–20%. As discussed earlier, few plastic polymers are able to do this. One solution to this problem is the use of microperforated films where the number and diameter of the perforations is related to the food being packed.

Aseptic Packaging

Aseptic packaging is the filling of sterile containers with a commercially sterile product under aseptic conditions, and then sealing the containers so that reinfection is prevented; that is, so that they are hermetically sealed. The term aseptic implies the absence or exclusion of any unwanted microorganisms from the food, container, or other specific areas, whereas the term hermetic (strictly air-tight) is used to indicate suitable mechanical properties to exclude the entrance of microorganisms into a package and gas or water vapor into (or from) the package. The term commercially sterile is generally taken to mean the absence of microorganisms capable of reproducing in the food under nonrefrigerated conditions of storage and distribution, thus implying that the absolute absence of all microorganisms need not be achieved.

The three major reasons for the use of aseptic packaging are (1) to take advantage of high temperature-short time (HTST)

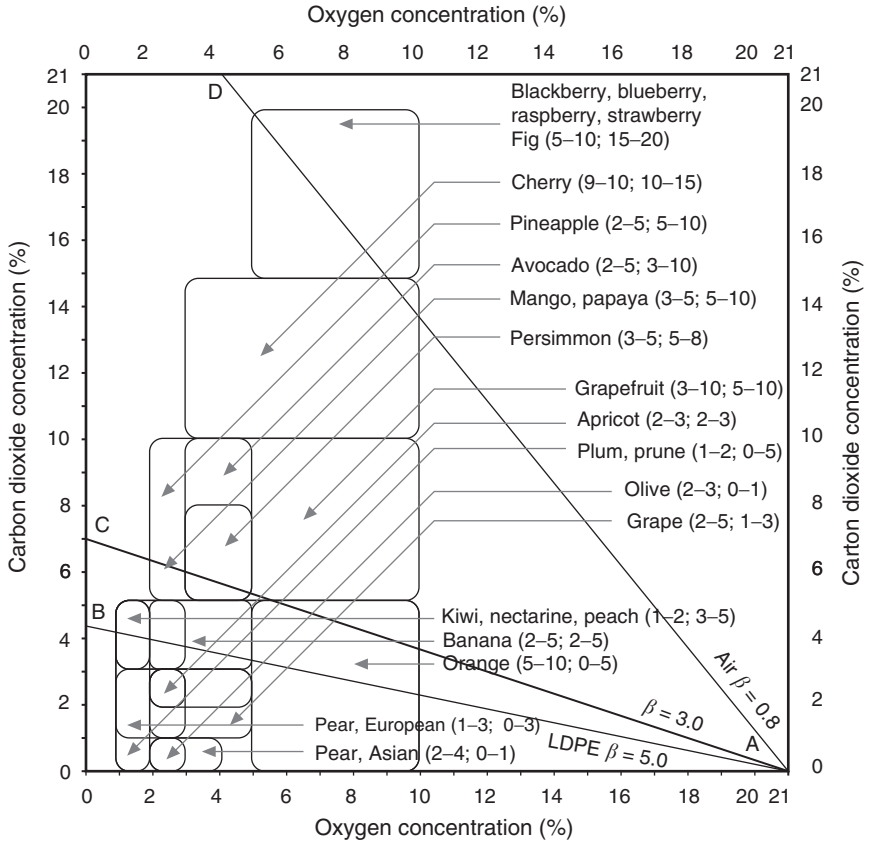


Figure 4 Recommended modified atmospheres for storage of fruits. Reproduced with permission from Kader, A.A., Singh, R.P., Mannapperuma, J.D., 1998. Technologies to extend the refrigerated shelf life of fresh fruits. In: Taub, I.A., Singh, R.P. (Eds.), Food Storage Stability. Boca Raton, FL: CRC Press, pp. 419–434.

sterilization processes, which are thermally efficient and generally give rise to products of a superior quality compared to those processed at lower temperatures for longer times, (2) to enable containers to be used that are unsuitable for in-package sterilization, and (3) to extend the shelf life of products at normal temperatures by packaging them aseptically.

Three main sterilization processes for packaging material are in common use, either individually or in combination: irradiation, heat, and chemical treatments. Irradiation involves ionizing radiation using gamma rays from cobalt-60 or cesium-137. The use of intense and short-duration pulses of broad-spectrum 'white' light (200–1000 nm) that generate high power levels can also sterilize aseptic packaging material and has recently been commercialized. UV radiation is most effective in terms of microbial destruction between 248 and 280 nm (the so-called UV-C range), with an optimum effectiveness at 253.7 nm. However, UV-C irradiation is generally only used commercially in combination with hydrogen peroxide (H_2O_2) as discussed below.

Heat sterilization processes can involve either steam (moist heat) or dry heat. For example, saturated steam at 165 °C and 600 kPa for up to 2 s is used to sterilize plastic containers. Hot air at a temperature of 315 °C has been used to sterilize paperboard laminate cartons where a surface temperature of 145 °C for 180 s is reached. A mixture of hot air and steam has been used to sterilize the inner surfaces of cups and lids made from PP, which is thermally stable up to 160 °C.

The lethal effect of H_2O_2 on microorganisms (including resistant spores) has been known for many years and is widely used to sterilize food packaging materials. When UV irradiation and H_2O_2 are used together they act synergistically, and the overall lethal effect is greater than the sum of the individual effects of peroxide and irradiation; the optimum effect is at a relatively low peroxide concentration of between 0.5% and 5%. Peracetic acid (PAA) is a liquid sterilant, which is particularly effective against spores. It is used for sterilizing filling machine surfaces as well as packaging materials such as PET bottles before aseptic filling, with the PET bottles being rinsed with sterile water rather than hot air.

The most widely used package is the paperboard laminate carton; it consists of layers of unbleached and/or bleached paperboard coated internally and externally with polyethylene, resulting in a carton that is impermeable to liquids and in which the internal and external surfaces may be heat sealed. There is also a thin (6.3 μm) layer of aluminum foil that acts as an O_2 and light barrier. The structure of a typical paperboard carton is shown in **Figure 5**.

Metal cans and glass bottles are used to a very limited extent for aseptic packaging. Blow-molded plastic bottles have been used for many years as a cheaper alternative to glass for nonreturnable containers. HDPE and PP were the two most

common thermoplastics used, sometimes with pigments added so that the contents are better protected from light. In recent years the use of PET has increased dramatically. Sachet and pouch systems are increasingly common, a typical material being a laminate of LLDPE with a center layer of EVOH copolymer and carbon black to give the pouch the required shelf life. Aseptic bag-in-box systems ranging in size from 1.5 to 1400 L are used for packaging UHT products. The bags contain EVOH and metallized PET as barrier layers and are manufactured fully sealed with minimum air content and then sterilized using gamma radiation. Preformed plastic cups are usually made from HIPS, PP or coextruded, multilayered polymers such as an outer layer of HIPS, a laminating adhesive, a barrier layer of PVdC or EVOH copolymer, a laminating adhesive, and finally LDPE. FFS cups are also available.

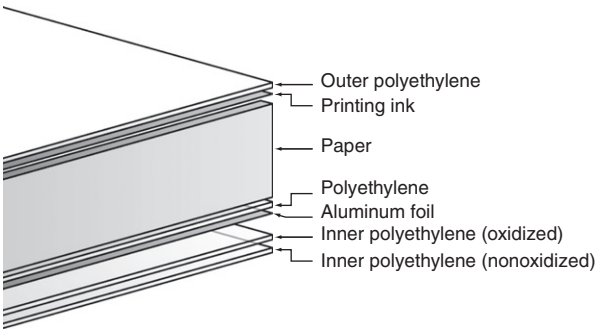


Figure 5 Typical structure of a paperboard laminate carton for aseptic filling. Reproduced with permission from Robertson, G.L., 2013. Food Packaging: Principles & Practice, third ed. Boca Raton, FL: CRC Press.

Assessment of package integrity is one of the most critical issues in the aseptic packaging of foods, and it is imperative that package integrity be maintained to ensure the safety and quality of the product. There is increasing interest in nondestructive (or noninvasive) package integrity testing, which allows the on-line testing of every package produced, while leaving both product and package intact. However, the availability of commercially viable, nondestructive package integrity testing equipment is still very limited.

Active Packaging

Active packaging is packaging in which subsidiary constituents have been deliberately included in or on either the packaging material or the package headspace to enhance the performance of the package system (Robertson, 2013). The two key words are deliberately and enhance. Implicit in this definition is that performance of the package system includes maintaining the sensory, safety, and quality aspects of the food. Selected examples of active packaging systems are given in Table 4.

A common type of active packaging involves the absorption or scavenging of O_2 inside the package. The most widely used O_2 scavengers consist of small sachets containing various iron-based powders together with an assortment of catalysts that scavenge O_2 within the food package and irreversibly convert it to a stable oxide. Water is essential for O_2 absorbents to function and in some sachets the water required is added during manufacture, whereas in others moisture must be absorbed from the food before O_2 can be absorbed. The iron powder is separated from the food by keeping it in a small sachet (labeled *Do not eat*) that is highly permeable to O_2 and,

Table 4 Selected examples of active packaging systems

Active packaging system	*Mechanisms*	*Food applications*
Oxygen absorbers	Iron-based, metal/acid, metal (e.g., platinum) catalyst, ascorbate/metallic salts, enzyme-based, nylon MXD6	Bread, cakes, cooked rice, biscuits, pizza, pasta, cheese, cured meats and fish, coffee, snack foods, dried foods, and beverages
Carbon dioxide absorbers/emitters	Iron oxide/calcium hydroxide, ferrous carbonate/metal halide, calcium oxide/activated charcoal, ascorbate/sodium bicarbonate	Coffee, fresh meats and fish, nuts and other snack foods, and sponge cakes
Ethylene absorbers	Potassium permanganate, activated carbon, activated clays/zeolites	Fruits and vegetables
Antimicrobial packaging	Organic acids, silver zeolite, spice and herb extracts, BHA/BHT antioxidants, vitamin E antioxidant, chlorine dioxide, sulfur dioxide	Cereals, meats, fish, bread, cheese, snack foods, fruits, and vegetables
Ethanol emitters	Encapsulated ethanol	Pizza crusts, cakes, bread, biscuits, fish, and bakery products
Moisture absorbers	Poly(vinyl acetate) blanket, activated clays and minerals, silica gel	Fish, meats, poultry, snack foods, cereals, dried foods, sandwiches, fruits, and vegetables
Flavor/odor adsorbers	Cellulose triacetate, acetylated paper, citric acid, ferrous salt/ascorbate, activated carbon/clays/zeolites	Fruit juices, fried snack foods, fish, cereals, poultry, dairy products, and fruits
Self-heating and self-cooling	Quicklime/water, ammonium nitrate/water, calcium chloride/water	Ready meals, beverages
Changing gas permeability	Side chain crystallizable polymers	Fruits and vegetables

Source: Reproduced from Day, B.P.F., 2008. Active packaging of food. In: Kerry, J., Butler, P. (Eds.), Smart Packaging Technologies for Fast Moving Consumer Goods. New York: John Wiley & Sons, Ltd., pp. 1–18.

in some cases, to water vapor. The overall reaction proceeds as follows:

$$Fe + \tfrac{3}{4}O_2 + 1\tfrac{1}{2}H_2O \rightarrow Fe(OH)_3 \quad [23]$$

O_2 scavengers have been used for a range of foods including sliced, cooked, and cured meat and poultry products, coffee, pizzas, specialty bakery goods, dried food ingredients, cakes, breads, biscuits, croissants, fresh pastas, cured fish, tea, powdered milk, dried egg, spices, herbs, confectionery, and snack food.

Sachets that contain $Ca(OH)_2$ in addition to iron powder absorb CO_2 as well as O_2 (sachets that absorb only CO_2 are rare). They find a niche application inside packages of roasted or ground coffee as fresh roasted coffee releases considerable amounts of CO_2 (formed by the Maillard reaction during roasting) that can cause swelling or even bursting of the package unless removed.

Attempts have been made to incorporate O_2-scavenging systems in a container lid or closure, with ascorbates or isoascorbates, either alone or in combination with sulfite, being the preferred O_2 scavengers. These compositions may be in a liquid or meltable form for application to a closure or as a component of a gasket. The scavenging properties of these compounds are activated by pasteurizing or sterilizing the container after sealing (de Abreu *et al.*, 2012).

During the ripening of fruits and vegetables the plant hormone ethylene (C_2H_4) is produced; it can have both positive and negative effects on fresh produce. Many C_2H_4-adsorbing substances have been described in the patent literature but those that have been commercialized are based on potassium permanganate, which oxidizes C_2H_4 in a series of reactions to acetaldehyde and then acetic acid, which can be further oxidized to CO_2 and H_2O, the overall reaction proceeding as follows:

$$3C_2H_4 + 12KMnO_4 \rightarrow 12MnO_2 + 12KOH + 6CO_2 \quad [24]$$

Other systems are based on the ability of certain materials to absorb ethylene, either alone or with an oxidizing agent such as finely divided and dispersed minerals, for example, zeolites, silicates, and activated carbon (de Abreu *et al.*, 2012).

Liquid water can accumulate in packages as a result of transpiration of horticultural produce, temperature fluctuations in high moisture packages, and drip or tissue exudate from flesh foods. This water can lead to the growth of molds and bacteria as well as fogging of films if allowed to build up in the package. Drip-absorbent pads consisting of granules of a superabsorbent polymer sandwiched between two layers of a microporous or nonwoven polymer have been used in the packaging of flesh foods to absorb liquid water. Polyacrylate salts, carboxymethyl cellulose, and graft copolymers of starch are the most frequently used polymers and they can absorb up to 500 times their own weight of liquid water.

Antimicrobial agents such as ethanol, silver ions, chlorine dioxide, sulfites, antibiotics, organic acids, enzymes, bacteriocins such as nisin, essential oils, and spices have been incorporated into packaging materials and used to prevent the growth of microorganisms on the food surface, leading to an extension in shelf life and/or improved microbial safety of the food. The burgeoning interest in antimicrobial food packaging is driven by increasing consumer demand for minimally processed, preservative-free foods. The use of antimicrobial films ensures that only low levels of preservative come into contact with the food compared to the direct addition of preservatives to the food.

Ethanol exhibits antimicrobial effects even at low concentrations and sachets containing ethanol (55%) and water (10%) adsorbed onto SiO_2 powder (35%) and filled into a paper/EVA copolymer sachet are available commercially. The sachet contents absorb moisture from the food and release ethanol vapor.

Despite considerable research over the past 20 years to develop and test films with antimicrobial properties to improve food safety and shelf life, few such systems are commercially available. Nisin is the antimicrobial most commonly incorporated into films, followed by acids and salts, chitosan, plant extracts, and the enzymes lysozyme and lactoperoxidase. A comprehensive quantitative analysis of the effectiveness of antimicrobial films for food applications revealed that the majority of results centered around 2 $\log_{10}$ reductions, suggesting that antimicrobial films still face limitations and are perhaps best viewed as part of a hurdle strategy to provide safe foods (Joerger, 2007). The legislative status of antimicrobials is also a limiting factor in their commercialization.

Intelligent Packaging

Intelligent is defined as 'having or showing understanding; clever, quick of mind' and the primary meaning intended when the word is applied to packaging is 'showing understanding.' Intelligent packaging is defined as packaging that contains an external or internal indicator to provide information about the history of the package and/or the quality of the food (Robertson, 2013). The key word in this definition is 'indicator' and includes indicators for gases, ripeness, and temperature including radio frequency identification (RFID) sensors but not RFID tags or labels because the latter do not indicate the history of the package or the quality of the food but merely its location. In summary, intelligent packaging senses some properties of the food it encloses or the environment in which the package is kept and is able to inform the manufacturer, retailer, or consumer about the state of these properties.

Quality or freshness indicators are used to indicate if the quality of the product has become unacceptable during storage, transport, retailing, and in consumers' homes. Intelligent indicators typically undergo a color change that remains permanent and is easy to read and interpret by consumers. Despite many attempts and several innovative approaches, no quality indicators are in widespread use by the food industry at present. Most have been based on detecting volatile metabolites such as diacetyl, amines, ammonia, and H_2S produced during the aging of foods. Others have responded to organic acids or volatile biogenic amines formed by microbial degradation of protein-containing foods such as putrescine from arginine, cadaverine from lysine, and histamine from histadine.

Time–temperature indicators (TTIs) are devices that integrate the exposure to temperature over time by accumulating

the effect of such exposures, and their response is usually expressed in a visually quantifiable identifier in the form of mechanical deformation, color development, or color movement (Taoukis, 2011). TTIs are based on irreversible physical, chemical, enzymic, or microbiological changes and the visible response reflects the cumulative time–temperature history of the package on which they are placed.

Many TTIs have been developed and the patent literature contains designs of more than 300 such devices. Maschietti (2010) reviewed the most relevant, recent patents based on the commercial success of the TTIs or their potential commercial viability, and the originality of the fundamental principles of the inventions. Although the majority of these devices were developed specifically for frozen foods, there is now widespread interest in TTIs for most categories of food, especially those where the rate of quality deterioration is highly temperature sensitive. An overview of the major types of TTIs, together with their application to food quality monitoring, has been presented by Taoukis (2011).

In developing an application of TTIs to shelf life monitoring, it is necessary to be able to define and measure quantitatively the key deteriorative reactions that contribute to quality loss in the particular food, and to integrate the expression for quality loss with the TTI response. Paramount to the success of any TTI is recognition of the fact that unless it has the same or similar E_A as the quality-determining deteriorative reaction in the food it is monitoring, it will overestimate or underestimate the loss of shelf life. The underlying requirement for the reliable prediction of food shelf life using a TTI is that the E_A of the TTI should be within ± 25 kJ mol^{-1} of the E_A of the key deteriorative reaction (Taoukis, 2011).

For many MAP applications (both gas flushing and vacuum packaging), it is helpful to know the gas concentration inside the package headspace and whether or not it is changing over time. Any changes can be as a result of enzymic activity in the food such as respiration of fruits and vegetables, deliberate absorption or generation of gas by added absorbers or generators as discussed in the Section Active Packaging, or loss of package integrity due to faulty seals or pinholes. The two gases of most interest are O_2 and, to a lesser extent, CO_2. Several types of gas indicators are available commercially, based on either colorimetric changes or luminescence. Many patents exist for colorimetric O_2 indicators and some have been commercialized, but they suffer from high costs and a lack of reliability due to their reversible nature (Mills *et al.*, 2012).

To date, most RFID tags have been used to increase convenience and efficiency in supply chain management and traceability, and are normally applied to secondary or tertiary packaging. To qualify as intelligent packaging, they must contain an indicator that provides information about aspects of the history of the package (e.g., its temperature) and the remaining shelf life or the quality of the food, and such intelligent RFID tags are now being commercialized. This provides for intelligent inventory management, and creates an opportunity to dramatically reduce the amount of expired product by first selling those products that the reader shows have the least shelf life left. An increasing number of systems are now available commercially. If costs can be reduced significantly, then they could find application on individual consumer packages although it is unclear what benefits they might provide to the consumer because a special reader is required to interpret them. However, such readers may be developed as applications for smart phones.

Recently, Potyrailo *et al.* (2012) demonstrated the applicability of passive (battery-free) RFID sensors for monitoring different aspects of food quality including freshness, aging, and spoilage. The electric field generated in the RFID sensor antenna extends from the plane of the RFID sensor and is affected by the ambient environment, thus providing the opportunity for sensing. This environment may be in the form of a food sample within the electric field of the sensing region or a sensing film deposited onto the sensor antenna.

To determine the milk spoilage rate, which is related to the changes in the dielectric properties of milk during storage, noninvasive determinations with RFID sensors were done directly through the walls of the original milk cartons. RFID sensors for monitoring fish freshness were constructed by draw-coating a polyaniline polymer to form a sensing film onto the antenna; such sensors had a detection limit of 500 parts per trillion (ppt) for ammonia gas. For monitoring bacterial growth, the RFID sensors measured the resonance impedance of the antenna circuit with the increase in response due to the accumulation of bacteria in the sensing region. To be accepted for diverse practical application scenarios, RFID sensors should have the ability for self-calibration and self-correction for variable ambient conditions such as temperature and repositioning.

Food Packaging and Sustainability

In its simplest sense, sustainable means to maintain or keep going continuously and it has been used in connection with forest management for more than a century. It is now accepted that sustainability has three dimensions or pillars: economic, environmental, and social. These three dimensions are also referred to as the triple bottom line or profits, planet, and people. Sustainable business practices integrate environmental concerns with social and economic ones. The metrics used for the measurement of sustainability are evolving and include indicators, benchmarks, standards, and certification systems.

There is no industry consensus as to what constitutes 'sustainable packaging' and the debate has been dominated by a narrow focus on reducing packaging weight and arguments around whether one material is more or less sustainable than another. However, the concept of sustainable packaging is more complex, and what may be the most sustainable solution for one product or particular market might not be the same elsewhere (Robertson, 2009).

The US-based Sustainable Packaging Coalition (SPC) defined sustainable packaging by listing eight criteria that relate to the activities of the packaging value chain and defined the areas in which they actively seek to encourage transformation, innovation, and optimization; the latest version is presented in **Table 5**. It is intended as a 'target vision' for companies to strive toward through continuous improvement and will evolve over time with new materials and technologies, leading to more sustainable packaging systems. The SPC claims quite correctly that their criteria blend broad sustainability objectives with business considerations and strategies that address

Table 5 Sustainable packaging criteria[a]

Is beneficial, safe, and healthy for individuals and communities throughout its life cycle
Meets market criteria for performance and cost
Is sourced, manufactured, transported and recycled using renewable energy
Optimizes the use of renewable or recycled source materials
Is manufactured using clean production technologies and best practices
Is made from materials healthy throughout the life cycle
Is physically designed to optimize materials and energy
Is effectively recovered and utilized in biological and/or industrial closed loop cycles

[a]No ranking is implied by the SPC in the order of criteria.
Source: Reproduced from Sustainable Packaging Coalition, 2011. Available at: http://www.sustainablepackaging.org/content/?type=5&id=definition-of-sustainable-packaging (accessed 29.10.13).

the environmental concerns related to the life cycle of packaging and the activities of the SPC membership. The SPC members believe that by successfully addressing these criteria, packaging can be transformed into a closed loop of packaging materials in a system that is economically robust and provides benefits throughout the life cycle – a sustainable packaging system.

The European Organization for Packaging and the Environment (Europen) believes it makes much more sense to talk about packaging and sustainability rather than sustainable packaging, which in the view of its members cannot be an end in itself. They recommend that packaging suppliers tell their customers how their packaging helps them to achieve their corporate sustainability goals. In the context of overall sustainability, packaging should (in their view) be regarded as part of the solution, not part of the problem, and as a net contributor to achieving the broad sustainability goal of resource optimization and waste minimization. In their view, packaging makes a valuable contribution to economic, environmental, and social sustainability through protecting products, preventing waste, enabling efficient business conduct, and providing consumers with the benefits of the products it contains.

Trying to reconcile 'sustainable packaging' and 'packaging and sustainability' is difficult if not impossible and is more than simply an exercise in semantics. How can the food industry expect the public to understand what it is doing to become more sustainable when the language and metrics are so confusing? Reaching a broad consensus on what may constitute sustainable packaging would provide the packaging industry with a platform from which to influence regulation as well as customer and consumer attitudes and expectations. One useful tool to compare different packages and assist in the development of more sustainable packaging is life cycle assessment (LCA).

Life Cycle Assessment

LCA is an environmental management tool that attempts to consider the resource and energy use, as well as the environmental impacts, over the entire life cycle of a package, product, or service from extraction of the raw materials through manufacture/conversion, distribution and use, to recovery or disposal. It is sometimes referred to as 'cradle to grave' analysis and typically compares two or more products that provide the same function or equivalent use. Thus an LCA makes it possible to isolate the stages in the life cycle of a process or product that make the most significant contribution to its environmental impacts. The ISO 14040 and 14044 international standards provide a framework for conducting LCAs.

Despite the increasing popularity of LCAs among both industry and governments, the technique does have significant limitations, which are often overlooked. One is that LCAs are not able to assess the actual environmental effects of emissions and wastes from the product or package because the actual effects depend on when, where, and how they are released into the environment.

Another is that LCAs take no account of economic factors such as the costs of raw materials, manufacturing, transport, and recovery or disposal. Furthermore, the conclusions from LCAs are specific only for the precise system under study and cannot be extrapolated to provide universal generalizations that, for example, one particular package is always better than another in every situation, or that reusable packaging is always better than single-use packaging.

Notwithstanding the limitations described above, LCA can be a very useful tool in two major areas. First, package design, development, and improvement all benefit from having LCA results available, which can help identify where significant resource use, wastes, and emissions occur, and thus suggest where significant changes or improvements can be made. Second, LCA can help decision-makers select the product or process that results in the least impacts to the environment. This information can be used with other factors, such as cost and performance data, to select a package or process. Third, LCA is a useful tool for assessing waste management options and planning integrated solid waste management systems on a case-by-case and regional basis.

In recent years, the carbon footprint (CFP) has been used to describe the greenhouse gas (GHG) emissions caused by a particular activity or entity, and thus a way for organizations and individuals to assess their contribution to global warming and climate change. Understanding these emissions, and where they come from, is necessary to reduce them. In this context, manufacturers are asking for the CFP associated with the manufacture, distribution, and disposal of products provided to them such as packaging. The CFP is expressed as CO_2 equivalents (abbreviated CO_2e).

Recently, Amienyo *et al.* (2013) presented the full life cycle impacts of carbonated soft drinks manufactured and consumed in the UK. Two functional units were considered: 1 l of packaged drink and total annual production of carbonated drinks. The system boundary was from 'cradle to grave' and the different packages considered were glass bottles (750 ml), aluminum cans (330 ml), and PET bottles (500 ml and 2 l). The study followed the ISO 14040/44 LCA methodology. Packaging was the main hotspot for most environmental impacts, contributing between 59% and 77%. The ingredients accounted for 7–14% (mainly due to sugar) and the manufacturing stage contributed 5–10%, largely due to the energy for filling and packaging. Refrigeration of the drink at retailers increased global warming potential (GWP) by up to 33%. Transport contributed up to 7% of the total impacts.

Table 6 Environmental profiles for the different life cycle stages of beverages

	Juice	*Beer*	*Water*
	1000 ml Aseptic carton	*330 ml Aluminum can*	*1500 ml PET bottle*
GWP[a] (g CO_2e)			
Beverage	29	713	6
Transport	35	36	34
Packaging	57	858	83
Recycling	−7	−780	−45
Total	113	826	78
CED[b] (megajoule)			
Beverage	0.20	17.26	0.03
Transport	0.58	0.60	0.57
Packaging	2.36	13.93	2.21
Recycling	−0.46	−12.73	−1.29
Total	2.68	19.06	1.53

[a]Global warming potential.

[b]Cumulative energy demand.

Source: Reproduced from Pasqualino, J., Meneses, M., Castells, F., 2011. The carbon footprint and energy consumption of beverage packaging selection and disposal. Journal of Food Engineering 103, 357–365.

Drinks packaged in 2 l PET bottles were the most sustainable option for most impacts, including the CFP, whereas drinks in glass bottles were the worst option. However, reusing glass bottles three times would make the CFP of the drink in glass bottles comparable to that in aluminum cans and 500 ml PET bottles. If recycling of PET bottles increased to 60% (currently 24%), the glass bottle would need to be reused 20 times to make their CFPs comparable. At the sectoral level, carbonated drinks in the UK are responsible for over 1.5 million tonnes of CO_2e emissions per year. This represented 13% of the GHG emissions from the whole food and drink sector or 0.26% of the UK total emissions in 2010.

Pasqualino *et al.* (2011) assessed the environmental impacts of the most common packaging options on the Spanish market for juice (aseptic cartons, glass, and HDPE bottles), beer (aluminum cans, glass, and HDPE bottles), and water (PET and glass bottles). The production of different packaging materials and sizes was evaluated, together with their method of final disposal (landfilling, incineration, and recycling). Recycling was found to be the most environmentally friendly disposal option for all the packaging alternatives compared, and either incineration or landfilling was considered the second best option depending on the packaging material. The packaging options with the lowest environmental impacts were aseptic cartons and plastic bottles (for sizes greater than 1 l). The environmental profiles of the whole beverage life cycles in terms of the GWP in g CO_2e and cumulative energy demand (CED) in megajoule (MJ) are summarized in **Table 6**. The impacts of beer packaging were similar to the impacts of beer production and these were the highest impact stages in the life cycle of beer. Packaging was found to have the highest environmental impacts in the life cycles of water and juice.

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Food Safety: Emerging Pathogens

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Glossary

Biofilms Multicellular communities (i.e., cell aggregates) that provide bacteria with the ability to grow adhered to biotic and abiotic surfaces.
Clones (or clonal groups) Genetically related (identical or similar) isolates of an organism derived from a single common ancestor.
Genotype The genetic information dictating a particular trait.
Phage type A set of bacterial strains susceptible to the same bacteriophages.
Phenotype Visible, expressed trait influenced both by the genetic information and the environment.
Quorum sensing Cell-to-cell communication in the context of which gene expression is regulated in response to changes in cell population density.
Serotype Group of isolates distinguished from others by the type of expressed surface antigens.
Shiga toxins Family of related toxins that inhibit protein synthesis, originally described to be produced by *Shigella dysenteriae*.
Strain An isolate (or group of isolates) that can be distinguished from other isolates of the same species by phenotypic or genotypic characteristics.
Zoonosis Any disease that can be transmitted from animals to humans.

Introduction

The appearance (or emergence) of new or unexpected pathogens in foods have been identified as one of the most important trends likely to affect food safety in the next 50 years (Tauxe *et al.*, 2010). Different, and often confusing, definitions have been proposed for 'emerging pathogens.' For instance, an emerging pathogen has been defined as a pathogen that is linked to a novel and serious to public health disease (Smith and Fratamico, 1995). In other cases, the term 'emerging' has been used to describe the appearance of microbial strains that have developed enhanced resistance to stresses and have adapted to new environments (Mor-Mur and Yuste, 2010). It has been proposed that, with particular reference to foodborne pathogens, the terms 'new,' 'evolving,' 'emerging,' and 'reemerging' should be differentiated and considered separately. In this sense, 'new foodborne pathogens' are serious hazards for public health and important causal agents of outbreaks that have not been previously described, whereas 'evolving foodborne pathogens' are those that become more potent (i.e., increased involvement in foodborne outbreaks) or more associated with other food products as well as those that were already known but not recognized as agents of human illness (Mor-Mur and Yuste, 2010). Finally, 'emerging foodborne pathogens' are foodborne pathogens that have newly arisen, meaning that they may have been recognized as pathogens but only recently are associated with foodborne transmission, whereas the 'reemerging' had been known for some time, but had fallen to low levels and are now showing increasing trends (Mor-Mur and Yuste, 2010; Sofos, 2008).

The emergence (or reemergence) of foodborne pathogens is a complex process and depends on the interaction of multiple factors including the following: (1) changes in agricultural practices (e.g., increased use of antibiotics in animal production); (2) microbial adaptation and evolution (e.g., enhanced virulence); (3) technological changes in the food industry (e.g., production, processing, packaging, and handling); (4) changes in human behavior and particularly in people's eating habits (e.g., increased consumption of raw/undercooked or minimally processed foods); (5) changes in demographics (e.g., migration, urbanization, aging of the population, and increasing number of people with conditions that result in immunosuppression); (6) health care and public health infrastructure; (7) environmental parameters (e.g., climate changes); (8) the global trade in foods leading to greater interdependence on the food safety systems of different countries; and (9) development of improved and more sensitive methodologies for the isolation, detection, and identification of foodborne pathogens (Miller *et al.*, 1998; Smith and Fratamico, 1995; Schofield, 1992; Tauxe *et al.*, 2010). In general, virtually any change affecting directly or indirectly the food chain is expected to create a selection pressure that will ultimately result in the emergence of foodborne pathogens (Miller *et al.*, 1998; Smith and Fratamico, 1995).

This article describes the characteristics, epidemiology, prevalence in foods, transmission routes to humans, and means of control of pathogens that are foodborne or have the potential to be foodborne, with a particular emphasis being placed on bacterial pathogens.

Bacteria

Aeromonas spp.

Aeromonas spp. are Gram-negative, rod-shaped, facultatively anaerobic, catalase-positive, chemoorganotrophic, nonspore-forming bacteria, and most of them are motile by polar flagella (Igbinosa *et al.*, 2012; Isonhood and Drake, 2002). This genus is characterized by considerable phenotypic variation, with gas

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production being variable and often temperature dependent, whereas marked differences can also be observed in cellular morphology (Forsythe and Varnam, 2009). Aeromonads are easily differentiated from the bacterial species of the family Enterobacteriaceae, with which they share many biochemical characteristics, based on their positive oxidase reaction (Igbinosa *et al.*, 2012). The taxonomy and nomenclature of the genus *Aeromonas* have been complex and have undergone several changes over time (Igbinosa *et al.*, 2012; Janda and Abbott, 2010). Although formerly positioned in the family Vibrionaceae, the genus *Aeromonas* is now officially classified within the family Aeromonadaceae (Igbinosa *et al.*, 2012; Merino *et al.*, 1995). Furthermore, four *Aeromonas* species were originally identified: *Aeromonas hydrophila*, *Aeromonas sobria*, *Aeromonas caviae*, and *Aeromonas salmonicida*. However, distinct biochemical and genetic (i.e., deoxyribonucleic acid (DNA) hybridization) groups, referred to as phenospecies and genospecies, respectively, were later identified, resulting in significant reconsiderations on species designation and classification (Isonhood and Drake, 2002; Janda and Abbott, 2010). Currently, the genus comprises more than 15 species, with the latest research data indicating the existence of 13 phenospecies and 19 genospecies (Janda and Abbott, 2010).

Extensive variability in the optimum growth temperature of *Aeromonas* spp., with the latter growing optimally at temperature ranges between 22 and 35 °C (Igbinosa *et al.*, 2012; Isonhood and Drake, 2002). Indeed, optimum growth temperature has been one of the phenotypic markers (along with motility, production of indole, and elaboration of a melanin-like pigment on tyrosine agar) traditionally used for the differentiation of species of the genus into two major groups based on physiological properties and host specificity: (1) motile aeromonads, which grow optimally at 35–37 °C, are predicted to cause human infections and are represented by *Ae. hydrophila* and (2) nonmotile aeromonads, which grow optimally at 22–28 °C, are associated primarily with fish infections and are represented by *Ae. salmonicida* (Igbinosa *et al.*, 2012; Joseph and Carnahan, 2000). A few species can exhibit growth at a wide temperature range; for instance, *Ae. hydrophila* is capable of growing at temperatures ranging from 1 to 42 °C (Isonhood and Drake, 2002). The ability of many strains of the genus to grow at refrigeration temperatures (4–5 °C) has been well-established and long acknowledged as one of the most important factors contributing to the public health significance of aeromonads in foods (Buchanan and Palumbo, 1985; Kirov, 1993; Knøchel, 1990). Most *Aeromonas* spp. tolerate high pH well and can resist pH values ranging from 4.5 to 9.0, with the optimum pH being in the range 5.5–9.0 (Igbinosa *et al.*, 2012; Isonhood and Drake, 2002; Merino *et al.*, 1995). In general, aeromonads do not tolerate NaCl concentrations higher than 5% (Knøchel, 1990), whereas the lowest water activity (a_w) value allowing growth varies with the humectant (Merino *et al.*, 1995).

Aeromonas spp. are ubiquitous organisms, having the potential to be isolated from a wide range of environmental niches including aquatic habitats (surface water, groundwater, chlorinated, and nonchlorinated drinking water), natural soils, fish, foods, domesticated pets, invertebrate species, birds, and insects (Igbinosa *et al.*, 2012; Janda and Abbott, 2010). They are also found in raw sewage, sewage effluents, and sewage-contaminated waters and activated sludge (Dumontet *et al.*, 2001; Igbinosa *et al.*, 2012). Aeromonads have long been considered as opportunistic pathogens of both aquatic (warm- and cold-water fish) and terrestrial animals (Harikrishnan and Balasundaram, 2005; Isonhood and Drake, 2002; Queiroga *et al.*, 2012). Nonetheless, the motile mesophilic aeromonads, and particularly *Ae. hydrophila*, have been recently identified as emerging human pathogens, gaining continuously increasing public health recognition as potential causative agents of both gastrointestinal and extraintestinal infections, primarily in immunocompromized individuals (Cabral, 2010; Igbinosa *et al.*, 2012; Isonhood and Drake, 2002; Janda and Abbott, 2010; Merino *et al.*, 1995; Senderovich *et al.*, 2012).

Although not supported by the findings of volunteer human feeding studies, epidemiological data (i.e., presence of the organisms in the stools of individuals with diarrhea, in the absence of other known enteric pathogens) have frequently suggested aeromonads as putative enteropathogens (Forsythe and Varnam, 2009). Most human pathogenic strains are now recognized as being grouped into three genospecies: *Ae. hydrophila* hybridization group (HG) 1, *Ae. caviae* HG 4, and *Aeromonas veronii* biovar sobria HG 8 (Forsythe and Varnam, 2009). Gastroenteritis associated with aeromonads may vary in severity from mild, self-limiting diarrhea to dysentery or cholera-like illness with the latter being potentially life threatening (Forsythe and Varnam, 2009; Igbinosa *et al.*, 2012). Although *Aeromonas* spp. have been recognized as emerging human pathogens, their exact role as enteric pathogens has not been definitely established; their mechanisms of pathogenicity remain vague and their infectious dose is unknown (Forsythe and Varnam, 2009; Igbinosa *et al.*, 2012; Isonhood and Drake, 2002). Several putative virulence factors of *Aeromonas* spp. that can be associated with gastroenteritis have been identified including hemolysins, invasins, adhesins, endotoxin (or lipopolysaccharide), proteases, fimbriae, pili, capsular polysaccharides, S-layers, siderophores, and various extracellular enzymes (Igbinosa *et al.*, 2012; Isonhood and Drake, 2002; Merino *et al.*, 1995). Extraintestinal human infections associated with aeromonads include septicemia, meningitis, cellulitis, myonecrosis, peritonitis, hepatitis, pancreatic abscesses, respiratory, urogenital and eye infections, endocarditis, osteomyelitis, and septic arthritis (Forsythe and Varnam, 2009; Janda and Abbott, 2010; Roberts *et al.*, 2006; Talon *et al.*, 1998). At greatest risk for *Aeromonas* infections are people with predisposing conditions (e.g., deficient immune system, leukemia, and liver disease) as well as young (6 months to 2 years old) children (Forsythe and Varnam, 2009; Gracey, 1994).

The most common routes of infection suggested for *Aeromonas* spp. are the ingestion of contaminated water (drinking or natural mineral water) or food, and contact of the organisms with a break in the skin (e.g., when swimming in contaminated water) (Cabral, 2010; Igbinosa *et al.*, 2012). Despite the fact that the relative importance of water and food in *Aeromonas* infections has been the subject of considerable discussion, these two sources are most likely interrelated; given the strong association of aeromonads with water, it has been suggested that risk of human exposure is greatest through consumption of contaminated water, or food processed with contaminated water (Forsythe and Varnam, 2009). With particular reference to foods of animal origin, also significant in

the transmission of aeromonads to humans is expected to be the contribution of aeromonad-contaminated animals (symptomatic or not), with animal feces appearing to be the major source of contamination of foods (Igbinosa *et al.*, 2012). Furthermore, given their wide environmental distribution in conjunction with their ability to form biofilms, which may provide increased resistance to conventional bactericidal treatments, *Aeromonas* spp. may establish niches in food-processing equipment, with the latter potentially serving as a source of cross-contamination of foods in the absence of sufficient cleaning and sanitation (Cotton and Marshall, 1998; Isonhood and Drake, 2002).

Aeromonas spp. have been isolated from a wide range of foods of both plant and animal origin including fresh vegetables, fish, shellfish, meat, poultry, and dairy products (**Table 1**). Despite their frequent presence in foods, *Aeromonas* isolates may be nontoxigenic questioning their foodborne pathogen potential (Kirov, 1993). Indeed, *Aeromonas* spp. occur commonly on minimally processed produce items as well as on fresh fish, meat, and poultry as part of their normal spoilage microflora (Forsythe and Varnam, 2009; Jacxsens *et al.*, 1999; Samelis, 2006). Although potentially pathogenic, genospecies of *Aeromonas* have been occasionally isolated from food samples (Neyts *et al.*, 2000; Forsythe and Varnam, 2009), the link between food contamination and human disease can be definitely established only via confirmed epidemiological data. Nevertheless, such data are limited as only few foodborne outbreaks associated with *Aeromonas* spp. have been documented with the majority of them involving seafood (Altwegg *et al.*, 1991; Ghenghesh *et al.*, 2008; Isonhood and Drake, 2002; Kirov, 1993). A recent foodborne outbreak of *Ae. hydrophila* was reported in a college in China; more than 200 students were reported to be sick with acute diarrhea and, as supported by the findings of the conducted epidemiological investigation, the most probable source of the organism was salad ingredients washed in contaminated tank water (Qian *et al.*, 2012).

In continuation to its initial recognition as an agent of human illness, the genus *Aeromonas* is being considered as a pathogen of emerging importance due to a number of special features, including its ubiquitous presence in water and food, the abundance of virulence factors, and the psychrotrophic nature of many of its isolates (Smith and Fratamico, 1995; Vivekanandhan *et al.*, 2005). Another issue of major importance for the public health significance of *Aeromonas* spp. is the increasing documentation of isolates exhibiting resistance to several antimicrobial agents (Queiroga *et al.*, 2012). Hence, in the context of basic control procedures common for all foodborne pathogens (i.e., prevention of contamination, reduction of contamination, and prevention of microbial growth), the aforementioned issues need to be particularly addressed with regard to aeromonads. Water used for washing of food, and particularly of food products intended to be consumed raw such as fresh or minimally processed produce items, should be chlorinated or otherwise disinfected and care should be taken to ensure that water distribution systems are not colonized by *Aeromonas* spp. (Forsythe and Varnam, 2009). Although managing their growth in biofilms can be very difficult, the entry of aeromonads into water distribution systems can be significantly reduced through effective treatment and maintenance procedures, such as maintaining temperatures below 14 °C, providing free-chlorine levels above 0.1–0.2 mg l^{-1}, and limiting the levels of organic carbon compounds in the water (Igbinosa *et al.*, 2012). Regarding the control of the organisms in aquaculture systems, and, thus, in fish and seafood, proper disposal of diseased animals, maintaining high standards of water quality, temperature control, and disinfection of equipment are expected to be useful and effective approaches (Igbinosa *et al.*, 2012). Moreover, disease prevention by means of vaccination and immunostimulation of fish in aquaculture has been shown to be successful against several bacterial pathogens, including *Aeromonas* spp. However, alternative control approaches in aquaculture such as the application of probiotics and herbals may also be promising, while allowing at the same time for reduced cost of disease management compared with the use of antibiotics, chemicals, and vaccinations, as well as for reduced incidence of multidrug-resistant (MDR) *Aeromonas* strains (Harikrishnan and Balasundaram, 2005). Given that aeromonads are not particularly heat or acid resistant, they do not exhibit unusual resistance to conventional food-processing procedures (Isonhood and Drake, 2002), whereas nonthermal processing technologies such as irradiation are also expected to be effective against these organisms on various types of foods (Nagar and Bandekar, 2011). Therefore, as also supported by the findings of epidemiological investigations, particular emphasis needs to be placed on the prevention of contamination/recontamination of foods with the organisms via the implementation of appropriate sanitary measures such as proper food handling practices and efficient sewage disposal systems (Igbinosa *et al.*, 2012; Qian *et al.*, 2012). Furthermore, the implementation of improved diagnostic and detection procedures appears to be essential for proper surveillance of water, food, and sanitation facilities, as well as of human infections which may be considerably underestimated particularly in developing countries (Igbinosa, *et al.*, 2012; Qian *et al.*, 2012). The development of novel or the improvement of existing molecular-based techniques is expected to be very useful toward this direction, allowing for an enhanced detection of aeromonads and, thus, for clarification of their true role as pathogens (Ghatak *et al.*, 2012; Tichoniuk *et al.*, 2010). Finally, given that the pathogenesis of *Aeromonas* spp. is multifactorial, with a large number of virulence genes being identified and quorum-sensing signal molecules being potentially associated with the expression of virulence determinants, research on these fields of study will provide a better understanding of the mechanism(s) underlying the emergence of these organisms as human pathogens and help to develop effective diagnostics and novel therapeutics (Chan *et al.*, 2011; Yu *et al.*, 2005).

Arcobacter spp.

Arcobacter species are Gram-negative, spiral, curved to S-shaped, fastidious, and nonspore forming microorganisms belonging to the family Campylobacteraceae (Vandamme and De Ley, 1991). They are motile by a single unsheathed polar flagellum, exhibiting darting or corkscrew movement (Blackburn and McClure, 2009). The organisms were first isolated from aborted bovine and normal porcine fetuses, sows with

Table 1 Prevalence of certain emerging bacterial pathogens in some foods

Bacterial agent	*Food*	*Country*	*Prevalence (%)*[a]	*Reference*
Aeromonas spp.	Chicken	Turkey	86.9	Yucel and Çitak (2003)
	Fish	India	33.6	Vivekanandhan *et al.* (2005)
		India	26.6; salted and dried finfish	Udgata *et al.* (2009)
		Nigeria	67.0; fresh fish	Igbinosa *et al.* (2006)
			70.0; smoked fish	
	Meat	Nigeria	54.0	Igbinosa *et al.* (2006)
		Turkey	67.7; minced meat	Yucel and Çitak (2003)
	Meat products	Nigeria	80.0	Igbinosa *et al.* (2006)
	Milk	Nigeria	85.0; raw milk	Igbinosa *et al.* (2006)
		Turkey	47.7; raw milk	Yucel and Çitak (2003)
			16.1; pasteurized milk	
	Poultry	Nigeria	80.0	Igbinosa *et al.* (2006)
	Prawns	India	17.6	Vivekanandhan *et al.* (2005)
	Shrimp	Nigeria	60.0	Igbinosa *et al.* (2006)
	Vegetables	Nigeria	35.0	Igbinosa *et al.* (2006)
Arcobacter spp.	Beef	Belgium	31.3	Collado *et al.* (2009)
		Malaysia	38.0	Shah *et al.* (2011)
	Chicken	Belgium	64.3	Collado *et al.* (2009)
		Korea	21.1	Lee *et al.* (2010)
		Malaysia	39.0	Amare *et al.* (2011)
	Clams	Belgium	100.0	Collado *et al.* (2009)
	Duck meat	Belgium	40.0	Collado *et al.* (2009)
	Ground beef	Belgium	9.0	De Smet *et al.* (2010)
		Turkey	37.0	Aydin *et al.* (2007)
	Milk	Belgium	3.2	Pianta *et al.* (2007)
		Northern Ireland	46.0	Scullion *et al.* (2006)
	Mussels	Belgium	41.1	Collado *et al.* (2009)
	Pork	Belgium	21.0	Van Driessche and Houf (2007a)
			53.0	Collado *et al.* (2009)
	Rabbit meat	Belgium	10.0	Collado *et al.* (2009)
	Turkey meat	Belgium	33.3	Collado *et al.* (2009)
Clostridium difficile	Chicken	Canada	12.8	Weese *et al.* (2010)
		The Netherlands	2.7	De Boer *et al.* (2011)
	Fish	Canada	9.1	Metcalf *et al.* (2011)
	Ground beef	Canada	20.8	Rodriguez-Palacios *et al.* (2007)
		Canada	6.7	Rodriguez-Palacios *et al.* (2009)
		US	50.0	Songer *et al.* (2009)
	Ground meats	Austria	3.0	Jöbstl *et al.* (2010)
	Ground pork	US	42.9	Songer *et al.* (2009)
	Ground turkey	US	44.4	Songer *et al.* (2009)
	Ground veal	Canada	14.3	Rodriguez-Palacios *et al.* (2007)
	Lamb	The Netherlands	6.3	De Boer *et al.* (2011)
	Pork	Canada	1.8	Metcalf *et al.* (2010)
		US	9.5	Harvey *et al.* (2011)
	Pork sausage	US	23.1	Songer *et al.* (2009)
	Salads	Scotland	7.5	Bakri *et al.* (2009)
	Scallops	Canada	33.3	Metcalf *et al.* (2011)
	Shrimp	Canada	15.4	Metcalf *et al.* (2011)
			33.3 (frozen)	
			10.0 (cooked)	
	Summer sausage	US	14.3	Songer *et al.* (2009)
	Veal chops	Canada	4.6	Rodriguez-Palacios *et al.* (2009)
	Vegetables	Canada	4.5	Metcalf *et al.* (2010)
Cronobacter spp.	Cereals/cereal products	Czech Republic	15.1	Hochel *et al.* (2012)
		The Netherlands	4.9	Kandhai *et al.* (2010)
	Cereal-based follow-up formula	South Korea	6.0	Kim *et al.* (2011)
	Cheese products	UK	3.2	Iversen and Forsythe (2004)
	Dried infant foods	UK	10.2	Iversen and Forsythe (2004)
	Eggs	Czech Republic	10.0	Hochel *et al.* (2012)
	Grains	South Korea	18.0	Chon *et al.* (2012)
	Herbs and spices	Czech Republic	13.5	Hochel *et al.* (2012)

(*Continued*)

Table 1 Continued

Bacterial agent	*Food*	*Country*	*Prevalence (%)*[a]	*Reference*
		The Netherlands	3.6	Kandhai *et al.* (2010)
		South Korea	19.2	Chon *et al.* (2012)
		UK	32.8	Iversen and Forsythe (2004)
	Legumes	Czech Republic	27.5	Hochel *et al.* (2012)
	Marine products	South Korea	7.5	Chon *et al.* (2012)
	Minced meats	The Netherlands	3.2	Kandhai *et al.* (2010)
	Powdered infant formula	South Korea	5.3	Kim *et al.* (2011)
		The Netherlands	2.3	Kandhai *et al.* (2010)
	Powdered infant formula milk	UK	2.4	Iversen and Forsythe (2004)
	Powdered milk	Czech Republic	10.0	Hochel *et al.* (2012)
		The Netherlands	4.0	Kandhai *et al.* (2010)
		UK	4.2	Iversen and Forsythe (2004)
	Seeds	Czech Republic	41.2	Hochel *et al.* (2012)
	Vegetables	The Netherlands	4.3	Kandhai *et al.* (2010)
		South Korea	30.0	Chon *et al.* (2012)

[a]Percentage (%) of positive samples.

reproductive problems, and asymptomatic pigs (Ellis *et al.*, 1977, 1978; Neill *et al.*, 1978, 1979). The genus *Arcobacter* was proposed by Vandamme *et al.* (1991) to describe those organisms formerly designated 'aerotolerant campylobacters,' was classified along with the genera *Camplylobacter* and *Helicobacter* within the ribosomal ribonucleic acid (rRNA) Superfamily VI, and currently includes 12 recognized species: *Arcobacter butzleri*, *Arcobacter cryaerophilus*, *Arcobacter skirrowii*, *Arcobacter nitrofigilis*, *Arcobacter cibarus*, *Arcobacter halophilus*, *Arcobacter molluscorum*, *Arcobacter defluvii*, *Arcobacter marinus*, *Arcobacter trophiarum*, *Arcobacter mytili*, and *Arcobacter thereius* (Shah *et al.*, 2011). *Arcobacter* spp. can grow at temperatures ranging from 15 to 42 °C, at pH values between 5.5 and 9.5, and under both aerobic and anaerobic conditions with their optimal, however, growth occurring under microaerophilic conditions (i.e., 3–10% oxygen) (Blackburn and McClure, 2009; Vandamme *et al.*, 1991). The ability of arcobacters to grow at 15 °C under aerobic conditions is the basis for their differentiation from campylobacters with which they have similar morphological, metabolic, and several other phenotypic and genotypic features (Blackburn and McClure, 2009; Shah *et al.*, 2011).

Livestock animals, and primarily poultry and swine, constitute significant reservoirs of *Arcobacter* spp. (Phillips, 2001; Snelling *et al.*, 2006; Van Driessche *et al.*, 2004). Arcobacters have commonly been isolated from feces and rectal swabs of clinically healthy cattle, sheep, and horses at prevalences ranging from 3.6% to 41.7% (Shah *et al.*, 2011). According to the findings of De Smet *et al.* (2011), healthy small ruminants (i.e., primarily sheep and to a smaller extent goats) are important carriers of these organisms. In general, the presence of *Arcobacter* spp. in the feces of healthy livestock at slaughter poses an important risk of carcass, meat, and possibly milk (in the case of ruminants) contamination (De Smet *et al.*, 2011; Van Driessche *et al.*, 2003). Nevertheless, and despite their frequent isolation from poultry carcasses, organisms of the genus *Arcobacter* have rarely been isolated from the intestinal content of poultry, rendering the fecal origin of carcass contamination questionable and suggesting that contamination may occur at the postslaughter level (Houf and Van Driessche, 2007; Phillips, 2001; Van Driessche and Houf, 2007b; Van Driessche *et al.*, 2003). As demonstrated by the results of a study assessing the distribution of arcobacters in chickens, the organisms were isolated from neck skin samples but not from the intestinal tract or from the feathers; however, the way of sample collection and the time period for sample processing were identified as crucial parameters for the interpretation of such findings (Houf and Van Driessche, 2007). In addition to livestock, *Arcobacter* spp. have been isolated from wild and nondomesticated animals (e.g., raccoons, rhinoceroses, and gazelles) as well as from pets such as dogs and cats (Fera *et al.*, 2009; Houf *et al.*, 2008; Shah *et al.*, 2011). In spite of their natural occurrence in healthy animals, arcobacters have also been associated with animal infections, with their main clinical manifestations including abortion, mastitis, and enteritis (Phillips, 2001; Wesley, 1997). *Arcobacter* spp. have also been found in different water sources (e.g., sea, lake, river, canal, and groundwater), with the latter assumed to play a significant role in the transmission of the organisms to both animals and humans (Phillips, 2001; Snelling *et al.*, 2006; Shah *et al.*, 2011). More specifically, *Ar. butzleri* has been isolated from canal water, from well-water sources, as well as from water samples in water treatment plants from all stages of processing (Phillips, 2001). However, given the organism's sensitivity to chlorine, its presence in water is probably the result of either inadequate chlorination or posttreatment contamination (Phillips, 2001; Wesley, 1997). Furthermore, *Ar. butzleri* has been found in various types of sewage sludge (Phillips, 2001).

For a long time, the importance of *Arcobacter* spp. as human pathogens was uncertain, and still, very little is known about the epidemiology, pathogenesis, and real clinical significance of these organisms. The lack of a standard protocol for primary isolation and of routine screening procedures, as well as the similarity of the symptoms of *Arcobacter* infections with campylobacteriosis (i.e., *Campylobacter jejuni* infection) have hindered the assessment of infection rates (resulting in underestimation of infections) and the establishment of a definitive association between human illness and the pathogenicity of these organisms (Phillips, 2001; Shah *et al.*, 2011). On the basis of the findings of studies undertaken in Belgium and

France, *Ar. butzleri* was the fourth most common *Campylobacter*-like organism isolated from human stools, whereas *Arcobacter* presence has also been recorded in other countries such as Thailand and South Africa (Shah *et al.*, 2011). Indeed, predominantly *Ar. butzleri* and to a smaller extent *Ar. cryaerophilus* and *Ar. skirrowii* are the species with the strongest association with human disease (Shah *et al.*, 2011; Vanderberg *et al.*, 2004; Wesley, 1997). *Arcobacter* infections are mainly manifested in the form of enteritis with its main clinical symptoms being persistent and watery diarrhea with abdominal pain (at a higher frequency compared with campylobacteriosis), nausea, vomiting, and fever (Snelling *et al.*, 2006; Vanderberg *et al.*, 2004). In addition to its association with enteritis, it has been suggested that *Ar. butzleri* has the potential to invade other parts of the body and cause considerable complications. Indeed, the organism has been isolated from patients with liver cirrhosis and acute gangrenous appendicitis, from septicemic patients, as well as from the blood of uremic patients with hematogenous pneumonia (Shah *et al.*, 2011). Certain factors such as health status, age, and hypertension may predispose a person to *Arcobacter* infection (Shah *et al.*, 2011). The currently available knowledge regarding the dose response and pathogenicity of *Arcobacter* spp. is still very limited. Although some potential virulence factors have been identified, very little is known about the genes involved in the pathogenesis of these organisms (Houf and Stephan, 2007; Shah *et al.*, 2011; Snelling *et al.*, 2006). With regard to potential infection routes, these mainly include drinking of contaminated water (particularly in developing countries with inadequate water supplies), and consumption and handling of contaminated food (primarily raw or undercooked meat) (Ho *et al.*, 2006; Taylor *et al.*, 1991; Wesley, 1996, 1997). Nevertheless, contact with pets and person-to-person transmission have also been suggested as potential risk factors for human infections (Fera *et al.*, 2009; Houf *et al.*, 2008; Vandamme *et al.*, 1992).

Although the lack of a standard isolation method may result in considerable underestimation of their true occurrence in foods, *Arcobacter* spp. have been frequently isolated from products of animal origin with the highest prevalence being reported in poultry meat, followed by pork and beef (Blackburn and McClure, 2009; Cervenka, 2007; Shah *et al.*, 2011). The prevalence of the organisms in chicken can be as high as 100%, whereas the detection rates in beef, pork, mutton, and milk have been shown to range from approximately 1% to 50% (Cervenka, 2007; Shah *et al.*, 2011). However, arcobacters have not been found in eggs, and only rarely their incidence has been reported in seafood such as clams and mussels (Cervenka, 2007; Collado *et al.*, 2009). It was the isolation of arcobacters (and particularly *Ar. butzleri*, *Ar. cryaerophilus*, and *Ar. skirrowii*) over the last decade from various foods of animal origin that resulted in their classification as emerging foodborne pathogens by the International Commission on Microbiological Specifications for Foods (ICMSF, 2002), despite their very poor association with human foodborne diseases. Although an outbreak of recurrent abdominal cramps in a nursery and primary school in Italy in 1983 was associated with *Ar. butzleri*, with the successive timing of the cases suggesting a person-to-person transmission, no specific food vehicle was identified (Vandamme *et al.*, 1992). Only recently were arcobacters associated with an outbreak of foodborne illness; *Ar. butzleri* was identified as the most likely cause of a foodborne outbreak among attendees of a wedding reception in Wisconsin, US, with the collected epidemiological data demonstrating that rigorous investigation of outbreaks of undetermined etiology is valuable for enhancing one's understanding of emerging agents of foodborne diseases (Lappi *et al.*, 2013).

Arcobacters can easily be inactivated by heating food to an internal temperature of 70 °C as well as by chlorination (Shah *et al.*, 2011). Hence, the risk of transmission to humans of *Arcobacter* spp. via properly cooked foods and chlorinated water should be regarded as negligible (Wesley, 1996, 1997). With particular reference to poultry products, given that arcobacters are probably not normal inhabitants of the poultry intestine (Houf and Van Driessche, 2007; Phillips, 2001), control measures should be focused on preventing contamination of, and proliferation in, the broiler environment as well as at the postslaughter level (Blackburn and McClure, 2009). Although *Ar. butzleri* is believed to be more resistant to irradiation than *Ca. jejuni* (Phillips, 2001; Shah *et al.*, 2011; Wesley, 1997), irradiation with approximately 0.3 kGy for 10 s is sufficient for their inactivation (Shah *et al.*, 2011); thus, irradiation doses currently allowed for pork in the US (i.e., 0.3–1.0 kGy) should provide an effective means of reducing, if not completely eliminating, this organism from pork (Phillips, 2001). Furthermore, organic acid solutions, including those used widely in meat decontamination (e.g., acetic and citric acids at concentrations higher than 0.2%), have demonstrated considerable effectiveness and, therefore, application potential for controlling arcobacters on meat and poultry surfaces (Cervenka, 2007; Shah *et al.*, 2011; Skrivanova *et al.*, 2011; Snelling *et al.*, 2006). Being organisms of recent interest, there are no standard widely accepted methodologies for the detection, isolation, and typing of *Arcobacter* spp. (Blackburn and McClure, 2009). Although several methods using both aerobic and microaerophilic conditions and based on media for *Campylobacter* have been proposed, the currently available methods need to be improved in terms of specificity and sensitivity, with the development and application of molecular techniques gaining increasing interest (Blackburn and McClure, 2009; Douidah *et al.*, 2010; Shah *et al.*, 2011). Robust and reliable molecular typing methods along with basic research on the virulence characteristics of arcobacters are expected to contribute significantly to the accurate identification of this emerging foodborne pathogen as well as to a better understanding of its epidemiology and distribution both in the environment and in foods (Douidah *et al.*, 2010; Shah *et al.*, 2011; Snelling *et al.*, 2006). *Arcobacter* spp. exhibit susceptibility to aminoglycosides (e.g., kanamycin and streptomycin) and thus, the latter antibiotics may be regarded as suitable for the treatment of *Arcobacter* infections when adequate control of their use in veterinary and human medicine is in place (Snelling *et al.*, 2006). Nevertheless, due to the fact that there is evidence of acquired resistance of *Arcobacter* spp. to antimicrobials generally prescribed as first-line drugs for the treatment of campylobacteriosis (e.g., erythromycin, tetracycline, chloramphenicol, and ciprofloxacin), future research trends include studies on the number and diversity of antibiotic-resistant *Arcobacter* strains, as well as assessment of the transfer potential of antibiotic resistance genes among

Arcobacter spp. and between *Arcobacter* and *Campylobacter* (Blackburn and McClure, 2009; Snelling *et al.*, 2006).

Clostridium difficile

Clostridium difficile is a Gram-positive, spore forming, and anaerobic bacillus that has been relatively recently identified as a human pathogen (Dawson *et al.*, 2009; Gibbs, 2009). The first confirmed case of *Cl. difficile* infection (CDI) was reported in 1977 (Larson *et al.*, 1978), when the use of clindamycin was introduced and resulted in a rapid increase in the number of pseudomembranous colitis cases (Dawson *et al.*, 2009). *Cl. difficile* grows optimally at 35–40 °C, ferments amino acids in order to create adenosine triphosphate as an energy source, and can also utilize sugars (Gibbs, 2009). Extensive research on the genome of this bacterium has been carried out aiming at elucidating its mechanisms of infection and pathogenicity. Pathogenic strains of the organism produce two distinct toxins, both of which are high-molecular weight proteins capable of binding to specific receptors on the intestinal mucosal cells: (1) toxin A, an enterotoxin and (2) toxin B, a cytotoxin (Gibbs, 2009). Colonization of the gut by *Cl. difficile* and toxin production results in an acute inflammatory response and severe damage to the intestinal epithelium, particularly following treatment with broad-spectrum antibiotics (Dawson *et al.*, 2009; Rupnik, 2007). The organism, which may be naturally present in the gastrointestinal tract of healthy adults and infants, is usually kept under control by the normal intestinal microflora (Gibbs, 2009; Warren and Guerrant, 2011). When, however, certain antibiotics disrupt the protective gut microflora, indigenous or ingested spores of *Cl. difficile* germinate, multiply rapidly, colonize the gastrointestinal tract, and produce toxins (Dawson *et al.*, 2009; Gibbs, 2009; Warren and Guerrant, 2011). Although any broad-spectrum antibiotic can be associated with CDI, the latter has been primarily linked to clindamycin, cephalosporins, penicillins, and fluoroquinolones (Warren and Guerrant, 2011).

Since its initial recognition, the incidence and severity of CDI has considerably increased and *Cl. difficile* currently constitutes one of the most frequent causative agents of nosocomial diarrhea worldwide (Dawson *et al.*, 2009; O'Donoghue and Kyne, 2010; Rupnik, 2007). Symptoms of CDI may vary from mild diarrhea to life-threatening pseudomembranous colitis, and in addition to patients on antimicrobial treatment, the population at risk for the infection includes patients on other therapies that may also alter the balance of the gut microbiota (e.g., antacid/proton pump inhibitors and nonsteroidal antiinflammatory drugs), as well as the immunocompromized and the elderly (Dawson *et al.*, 2009). As a result of the worldwide increase in the incidence of CDI in the past decade, several molecular typing approaches have been developed in order to enhance the understanding of the epidemiology of *Cl. difficile*, including pulsed-field gel electrophoresis, restriction endonuclease analysis, toxinotyping (i.e., using sequencing data of toxins A and B), multilocus sequence typing, and polymerase chain reaction (PCR)-ribotyping (Dawson *et al.*, 2009). Recent changes in the epidemiology of *Cl. difficile* that have contributed to its characterization as a 'continually evolving pathogen' include (1) the emergence of new groups of highly virulent strains (e.g., strains with PCR-ribotype 027) causing outbreaks of increased disease severity, high relapse rate, and significant mortality in North America, Japan, and Europe (Dawson *et al.*, 2009; Gould and Limbago, 2010; Kuijper *et al.*, 2007; O'Donoghue and Kyne, 2010) and (2) the onset of community-acquired cases involving low-risk population groups (i.e., young individuals, not subjected to antibiotic therapy or previous hospitalization) (Gould and Limbago, 2010; Rupnik, 2007).

The increasing rate of community-associated cases of CDI has raised questions with regard to the routes of transmission of *Cl. difficile* to humans, with foodborne acquisition through consumption or handling of contaminated food products being hypothesized as a possible source of such infections (Gould and Limbago, 2010). In addition to constituting an important pathogenic organism for humans, *Cl. difficile* has also been recognized as an emerging animal pathogen (Rupnik, 2007; Songer and Anderson, 2006), and although a definitive link between the organism's carriage by animals and human disease has not been established, it has been suggested that food animals are likely to play an important role in the transmission of this pathogen to humans through food (Gould and Limbago, 2010). Indeed, there are several reports suggesting that food animals (both healthy and symptomatic) can be reservoirs for *Cl. difficile* (Dawson *et al.*, 2009; Simango and Mwakurudza, 2008; Thitaram *et al.*, 2011), whereas a marked overlap between isolates from animals and humans (including highly virulent outbreak subtypes) has also been documented (Keel *et al.*, 2007; Rupnik, 2007; Zidaric *et al.*, 2008). The organism can also be recovered from a wide variety of environmental sources including soil, seawater, and freshwater (Gould and Limbago, 2010). Hence, food products may become contaminated with *Cl. difficile* via multiple routes. With particular reference to meat and meat products, the organism could be either introduced during processing or be initially present in the muscle tissue (Rupnik, 2007). The presence of *Cl. difficile* spores in the feces of swine or beef cattle, for instance, may result in contamination of pork and beef products during slaughter (Thitaram *et al.*, 2011). In addition to meat and meat products, *Cl. difficile* has been isolated from a diverse set of foods such as chicken, produce, fish, and seafood (**Table 1**).

Given that broad-spectrum antibiotics exacerbate CDI, treatment of the disease is complicated with the administration of very few antibiotics, such as metronidazole and vancomycin, appearing to be effective (Kuijper *et al.*, 2007). As antibiotic resistance constitutes one of the most important virulence factors for *Cl. difficile*, attempts to prevent infections should focus on controlling the overall use of antibiotics, and particularly high-risk antibiotics such as cephalosporins, clindamycin, and fluoroquinolones (Dawson *et al.*, 2009; Kuijper *et al.*, 2007). However, it has been suggested that with the development of more potent antibiotics for other resistant bacterial pathogens, the problem of CDI is expected to continue (Warren and Guerrant, 2011). Therefore, despite the fact that new treatment options (both antibiotic and nonantibiotic alternatives) are becoming available (Kuijper *et al.*, 2007; O'Donoghue and Kyne, 2010), the antibiotic susceptibilities of *Cl. difficile* isolates need to be assessed and known; although such knowledge might not be relevant to the infection's treatment per se, it is expected to

facilitate the identification of the predisposing and prevailing antibiotic pressure to which this pathogen is subjected (Warren and Guerrant, 2011). In addition to classical virulence determinants such as toxin production and antibiotic resistance, the evaluation of other factors (e.g., increased gut colonization, increased resistance to bile salts, and increased motility/chemotaxis) should be very useful in explaining the emergence of epidemic *Cl. difficile* strains (Dawson *et al.*, 2009). Moreover, given that *Cl. difficile* spores can survive on surfaces for long periods of time and are resistant to many disinfectants, research on spore germination would provide useful information for controlling the spreading and persistence of this organism (Dawson *et al.*, 2009). With particular reference to community-associated cases of CDI, in order to understand the dynamics of and risk factors for the development of human disease, including the true occurrence and importance of foodborne transmission, more research covering the following areas is required (Gould and Limbago, 2010; Rodriguez-Palacios, *et al.*, 2010; Thitaram *et al.*, 2011): (1) determination of the infectious dose of *Cl. difficile*, which is currently unknown, and comparison of it with the microbial load typically present on contaminated foods at the time of consumption; (2) surveillance for human and animal infections utilizing standard subtyping systems capable of discerning common sources of these infections; (3) detailed strain typing and epidemiological investigations aiming at establishing the relationship between food animals and human isolates and, thus, determining the true potential for acquisition of foodborne disease; (4) development of consensus best practice methods for food testing; and (5) improving our understanding of the effects of heating (and assessment of the need for revising current cooking recommendations) and surface decontamination on *Cl. difficile* spores.

Cronobacter spp.

Cronobacter spp. are Gram-negative, facultatively anaerobic, and motile with peritrichous flagella rods, which are members of the family Enterobacteriaceae (Iversen *et al.*, 2008). The genus *Cronobacter*, formerly known as *Enterobacter sakazakii* (Farmer *et al.*, 1980), consists of five species, plus a possible sixth species: *Cronobacter sakazakii*, *Cronobacter malonaticus*, *Cronobacter turicensis*, *Cronobacter muytjensii*, *Cronobacter dublinensis*, and Genomospecies 1 (Forsythe and Varnam, 2009; Iversen *et al.*, 2008). *Cronobacter* species differentiation is primarily based on DNA sequence analysis, supported by biochemical differentiation (Forsythe and Varnam, 2009). *Cronobacter* spp. are considered emerging opportunistic pathogens and the etiological agents of life-threatening infections among infants (Bowen and Braden, 2006; CDC, 2009; Drudy *et al.*, 2006), with the first reported outbreak referring to neonatal meningitis in England in 1958 that resulted in the deaths of two infants (Urmenyi and Franklin, 1961). Few virulence factors have been identified so far (Pagotto *et al.*, 2003; Townsend *et al.*, 2008), though there is evidence of considerable virulence variability among different subtypes of these organisms (Townsend *et al.*, 2008). Owing to their isolation from neonatal infections, the species *Cr. sakazakii*, *Cr. malonaticus*, and *Cr. turicensis* are of particular interest (Forsythe and Varnam, 2009). Despite its low incidence, *Cronobacter* infection, whose main clinical manifestations include meningitis, septicemia, and necrotizing enterocolitis, is associated with significant morbidity (i.e., irreversible neurological sequelae resulting in quadriplegia, developmental impedance, and impaired sight and hearing) and with mortality rates as high as 80% (Drudy *et al.*, 2006). Powdered infant formula (PIF) products have been epidemiologically linked to several cases of *Cronobacter* infection (Bowen and Braden, 2006; CDC, 2009; Himelright *et al.*, 2002; Van Acker *et al.*, 2001), and premature/low-birth-weight infants and those aged less than 28 days are more at risk than older infants due to their underdeveloped immune status and lack of competing intestinal flora (Drudy *et al.*, 2006; Forsythe and Varnam, 2009). Infants of more than 3 months appear to be at considerably less risk for fatal infections (O'Brien *et al.*, 2009), though the few available reports of *Cronobacter* infections in adults usually refer to individuals with underlying diseases (e.g., malignancies) (Drudy *et al.*, 2006). *Cronobacter* spp. are naturally resistant to all macrolides, lincomycin, clindamycin, streptogramins, rifampicin, fusidic acid, and fosfomycin, and the infections associated with these organisms have been traditionally treated with a combination of ampicillin with gentamicin or chloramphenicol (Drudy *et al.*, 2006).

Specific natural reservoirs of *Cronobacter* spp. have not been established yet, with the distribution of these organisms appearing to be ubiquitous. On the basis of their presence in dry herbs and spices, it has been hypothesized that the natural habitat of *Cronobacter* spp. may be plant materials (Chon *et al.*, 2012; Drudy *et al.*, 2006; Hochel *et al.*, 2012; Iversen and Forsythe, 2004). Nonetheless, organisms of the genus *Cronobacter* have also been isolated from animal sources, a wide range of clinical sources (e.g., cerebrospinal fluid, blood, bone marrow, urine, intestinal and respiratory tracts, wounds, and feces), hospital settings, food-processing, and household environments, as well as from multiple food sources (Drudy *et al.*, 2006). *Cronobacter* spp., and primarily *Cr. sakazakii*, have been detected in various food products mainly of plant origin and dried food ingredients (**Table 1**). However, strong association has been observed only with PIF in which the pathogen can be introduced either intrinsically (i.e., at some stage during the manufacturing process) or extrinsically (i.e., during preparation of PIF at hospital neonatal units or at home) (Drudy *et al.*, 2006). As supported by molecular typing data, production facilities may serve as points of continuous entry and dissemination of *Cronobacter* spp. into milk powder products (Lehner *et al.*, 2010). Indeed, studies assessing the occurrence and distribution of the pathogen within milk powder-processing plants have revealed a number of potential reservoirs as well as of practices/events that may compromise the safety of the final product. Potential sources of *Cronobacter* spp. in manufacturing environments are the supply air, spray-drying towers, roller dryers, textile filters for exhaust air, vacuum cleaners, and the filling line of the processing units (Hein *et al.*, 2009; Jacobs *et al.*, 2011; Reich *et al.*, 2010). Long-term persistence of certain *Cronobacter* subtypes in milk powder processing units has been observed in some cases (Craven *et al.*, 2010; Hein *et al.*, 2009). On the basis of the findings of Craven *et al.* (2010), the most prevalent and persistent *Cronobacter* clones were isolated from external roofs above spray dryers, in air treatment areas and where high foot traffic occurs. Practices/events that may result in

contamination of the final milk powder include reintroduction of filtered powder into the product flow, passing of contaminated milk concentrated through the process unheated, and failure of established hygiene measures (e.g., cleaning-in-place events and heat treatments) to completely eliminate *Cronobacter* spp. from all areas of the processing line (Hein *et al.*, 2009; Jacobs *et al.*, 2011). In addition to food-processing facilities, *Cronobacter* spp. have been isolated from various sites in domestic environments (Kilonzo-Nthenge *et al.*, 2012; Molloy *et al.*, 2009). Hence, given this and that the organisms can also be present in the feces or on skin of healthy individuals (Kandhai *et al.*, 2010), in the absence of good hygiene and food handling practices, PIF contamination may also occur during preparation at home.

To reduce the risk of PIF contamination with *Cronobacter* spp., control measures should be in place throughout the food chain. Manufacturers should implement strategies aiming at controlling the initial populations of these organisms and reducing the risks of PIF contamination both during production and at the postprocessing level. PIF products should be formulated in accordance with the Codex Alimentarius Commission Standards (CCFH, 2008), although manufacturers are being encouraged to develop a greater range of commercially sterile alternative formula products specifically targeting high-risk groups (i.e., premature/low-birth-weight infants) (Drudy *et al.*, 2006). With regard to the development and application of control interventions at the manufacturing level, research data suggest that gamma irradiation may be effective against *Cronobacter* spp. in PIF (Osaili *et al.*, 2007), whereas organic acids such as propionic acid and acetic acid may possibly be used as preservatives to inhibit the survival and growth of these organisms in liquid foods (Back *et al.*, 2009). In addition to PIF manufacturers, caregivers in hospital neonatal units as well as food handlers at home are also responsible for the safety of this product, and should be continuously alerted that PIF is not a sterile product, and that, therefore, the use of hygienic measures during preparation is essential (Drudy *et al.*, 2006). Furthermore, given that infant formula can support prolific bacterial growth, appropriate temperature control of reconstituted product is of vital importance for its safety (Forsythe and Varnam, 2009). The World Health Organization (WHO) and the United Nations Children's Fund recommend that, where possible, infants should be exclusively breastfed for the first 6 months of life (WHO/UNICEF, 2003). Furthermore, the WHO in collaboration with the Food and Agriculture Organization (FAO) of the United Nations have issued recommendations regarding the safe preparation, storage, and handling of PIF in both care settings and the home. According to these recommendations, PIF should be reconstituted at 70 °C and either used within 2 h after preparation or stored in the refrigerator ($\leq$5 °C) for up to 24 h; feed that has not been consumed within 2 h should be discarded (FAO/WHO, 2007). Finally, as certain procedural and environmental factors within neonatal intensive care units may have an important effect on infant formula contamination (Steele and Short, 2008), increasing the awareness of the potential threats posed by *Cronobacter* spp. among medical personnel and caregivers via continuous education is of vital importance for protecting high-risk infants (Drudy *et al.*, 2006). With reference to future trends, given that since its initial recognition the incidence of *Cronobacter* in PIF on the market has appeared to decrease, though improvement of hygiene measures has been associated with reduction of reported outbreaks, it has been opined that of particular interest are also powdered nutrition formulas frequently consumed as dietary supplements by the elderly and other immunocompromized individuals, population groups which are also susceptible to *Cronobacter* infections (Forsythe and Varnam, 2009).

Escherichia coli

There are a number of different enteropathogenic groups of *E. coli* that have been shown to cause various types of gastrointestinal infections, with enterohemorrhagic *E. coli* (EHEC) being recognized as an etiological agent of serious illness and mortality in outbreaks of foodborne illness involving a large variety of foods and proceeding to hemolytic uremic syndrome (HUS) (Viazis and Diez-Gonzalez, 2011). A common characteristic of all EHEC strains is their ability to produce shiga toxins, and as such, they are commonly referred to as shiga toxin-producing *E. coli* (STEC) (Viazis and Diez-Gonzalez, 2011). STEC cause sporadic or epidemic foodborne or waterborne illness, whose clinical spectrum involves diarrhea, hemorrhagic colitis, and the potentially fatal HUS (Karmali, 2005). The most common serotype implicated worldwide as the major cause of hemorrhagic colitis and HUS is *E. coli* O157:H7, whose detection and diagnosis is based on its inability to ferment the carbohydrate sorbitol (Bielaszewska and Karch, 2000; Karmali, 2005; Viazis and Diez-Gonzalez, 2011). Since the initial association of *E. coli* O157:H7 with epidemic foodborne disease in 1982, and the consequent definition of a new foodborne zoonosis (Riley *et al.*, 1983), more than 200 different O serogroups of *E. coli* have been shown to produce shiga toxins, and more than 100 of these STEC have been linked to human disease (Johnson *et al.*, 2006). STEC strains capable of fermenting sorbitol have also been isolated from patients and associated with an increasing number of outbreaks and sporadic cases of diarrhea and HUS (Bielaszewska and Karch, 2000). Although their linkage to human disease is not as well understood as that of *E. coli* O157:H7 and their true occurrence is most likely underestimated, the rising public health significance of sorbitol-fermenting STEC has been acknowledged (Bielaszewska and Karch, 2000; Gerber *et al.*, 2002).

Non-O157 shiga toxin-producing Escherichia coli

Non-O157 STEC are a heterogeneous group of organisms consisting of more than 100 serogroups (Bielaszewska and Karch, 2000). The clinical diagnosis of non-O157 STEC can be very challenging because, similar to *E. coli* O157:H7, they are capable of inducing a range of illnesses, including diarrhea, hemorrhagic colitis, and HUS, either as sporadic cases or in the form of outbreaks (Johnson *et al.*, 2006). However, despite the similarities of their clinical manifestations, genomic studies suggest that O157 and non-O157 STEC have different evolutionary histories (Smith and Fratamico, 2012). Although cattle are regarded as the major reservoir for clinically significant non-O157 STEC, other animals such as sheep, goats, deer, and swine may also be carriers of these organisms (Monaghan *et al.*, 2012; Smith and Fratamico, 2012). Outbreaks caused by

this group of STEC have been associated with ingestion of contaminated food and water, as well as with person-to-person contact (Kaspar *et al.*, 2010; Smith and Fratamico, 2012). Non-O157 STEC strains have been linked to major foodborne outbreaks in the USA, Europe, Australia, Japan, and other countries, being often responsible for a considerable portion of the total reported STEC foodborne infections (Kaspar *et al.*, 2010; Scallan *et al.*, 2011; Smith and Fratamico, 2012). Foods that have been associated with illness caused by these organisms include raw and pasteurized cow's milk, ice cream, cheeses, fermented sausages, ground beef, cider, and vegetables (Mathusa *et al.*, 2010; Smith and Fratamico, 2012).

Serogroups that have emerged as significant etiological agents of human disease (both diarrhea and HUS) in several parts of the world include O26, O45, O103, O111, O121, and O145 (Bielaszewska and Karch, 2000; Bielaszewska *et al.*, 2007; Brooks *et al.*, 2005; Brown *et al.*, 2012; CDC, 2013; Gerber *et al.*, 2002; Patton *et al.*, 1996; Vally *et al.*, 2012). Indeed, approximately three-fourths of the disease-inducing non-O157 STEC isolates reported to the Centers for Disease Control and Prevention of the United States Department of Health and Human Services belonged to the above-mentioned six O serogroups (Brooks *et al.*, 2005). Hence, as a result of their increasing public health impact, these six serogroups were declared by the United States Department of Agriculture's Food Safety and Inspection Service as adulterants if present in raw nonintact beef products (USDA-FSIS, 2011). Molecular subtyping data indicate that strains of serogroups O26, O103, and O111 belong to their own clonal lineage and exhibit unique virulence profiles (Bielaszewska and Karch, 2000). Additional non-O157 STEC serogroups that have been reported to emerge in Europe are O100 and O127 (Orth *et al.*, 2006). It has been suggested that certain non-O157 STEC strains (e.g., strains producing shiga toxin 2 (Stx2)) may be more likely to precipitate HUS than others (e.g., strains producing shiga toxin 1 (Stx1) alone) (Brooks *et al.*, 2005; Johnson *et al.*, 2006). Nevertheless, due to the generally limited information that is currently available with regard to the virulence and stress responses of non-O157 STEC, it is difficult to draw solid conclusions on their pathogenicity or their behavior when exposed to stress in the environment, in food, and during food processing (Smith and Fratamico, 2012). It has been opined that the incidence, distribution, and pathological spectrum of these emerging agents is expected to be elucidated only through improved surveillance, with the latter requiring a number of individual conditions to be met including increased clinical suspicion, improved laboratory isolation through the development and use of rapid, sensitive, accurate, and inexpensive techniques, as well as continued serotyping of isolates in public health laboratories (Brooks *et al.*, 2005; Johnson *et al.*, 2006).

Sorbitol-fermenting shiga toxin-producing Escherichia coli *O157:H*$^-$

Sorbitol-fermenting STEC O157:H$^-$ (H$^-$ indicates nonmotility) strains have been identified as agents of severe human disease, such as HUS, with the organisms being isolated throughout Europe including the Czech Republic, Hungary, Finland, and the UK, as well as in Australia (Orth *et al.*, 2009). The first isolation of these organisms was reported during a HUS outbreak investigation in Bavaria, Germany, in 1988; nonmotile *E. coli* strains, harboring the *stx2* gene, and fermenting sorbitol within 24 h of incubation were isolated from the stools of two out of six affected children (Karch *et al.*, 1990). This group of organisms appears to represent a new clone within the *E. coli* O157 serogroup, having its own typical combination of virulence factors (Bielaszewska and Karch, 2000). Indeed, it has been observed that illness associated with sorbitol-fermenting STEC O157:H$^-$ is rarely confined to diarrhea and usually progresses to life-threatening HUS, and that patients infected with these organisms tend to develop HUS more frequently than patients infected with other EHEC strains, indicating a potential hypervirulence of this group of STEC (Nielsen *et al.*, 2011; Orth *et al.*, 2009). Although some epidemiological data indicate potential existence of differential reservoirs of and vehicles of infections caused by STEC O157:H$^-$ in comparison to STEC O157:H7 (Karch and Bielaszewska, 2001), the reservoir and transmission routes of the former organisms are still largely unknown (Orth *et al.*, 2009). Evidence that bovine animals may constitute a reservoir of sorbitol-fermenting STEC O157:H$^-$ and, thus, a source of human disease, has been provided in some cases (Bielaszewska *et al.*, 2000; Orth *et al.*, 2006). Moreover, it has been hypothesized that these pathogens might be adapted to the human intestine and that humans may constitute their primary reservoir; however, the role of person-to-person transmission, which is assumed to be the major route of spreading of STEC O157:H$^-$ infections, still needs to be established (Karch and Bielaszewska, 2001). To properly assess the epidemiological significance of STEC O157:H$^-$ and to better understand its epidemiology, microbiological detection of this pathogen and HUS surveillance need to be improved (Karch and Bielaszewska, 2001; Nielsen *et al.*, 2011). Given that detection of all HUS-causing strains, including the sorbitol-fermenting STEC O157:H$^-$, cannot be assured on the basis of phenotypic characteristics, screening for shiga toxins (e.g., by enzyme-linked immunosorbent assay (ELISA), or shiga toxin genes (e.g., by PCR) is strongly recommended (Orth *et al.*, 2009).

Sorbitol-fermenting shiga toxin-negative Escherichia coli *O157:H*$^-$

Serogroup O157:H$^-$ strains capable of fermenting sorbitol, but not producing shiga toxins, have also been identified as agents of diarrhea and HUS in different countries such as Austria, Germany, and India (Allerberger *et al.*, 2000; Chakraborty *et al.*, 2003; Schmidt *et al.*, 1999). Although their origin, pathogenic mechanisms, and role in human disease warrant clarification, the following hypotheses have been postulated regarding sorbitol-fermenting Stx-negative *E. coli* O157:H$^-$ (Karch and Bielaszewska, 2001): (1) they might have emerged from sorbitol-fermenting STEC O157:H$^-$ organisms by losing their *stx* genes during infection, isolation, or subculture; (2) they might be progenitors of sorbitol-fermenting STEC O157:H$^-$, with the latter arising by transduction with *stx*-converting bacteriophages; and (3) they might be inherently Stx-negative and cause the underlying diseases through the potential possession of additional, as yet unidentified, virulence factor(s).

Mycobacterium paratuberculosis

Mycobacterium avium subspecies *paratuberculosis* (MAP) was first described by Johne and Frothingham in 1895 in the context of an investigation of the cause of chronic diarrhea in cattle, and it has been classified as a member of the family Mycobacteriaceae with the latter consisting of Gram-positive, strictly aerobic, nonmotile, and acid-fast rod-shaped bacteria with fastidious growth requirements (Griffiths, 2009; Legrand *et al.*, 2000). MAP is the etiological agent of paratuberculosis, a chronic granulomatous enteritis in ruminants, also known as Johne's disease, which results in diarrhea, weight loss, and ultimately death (Griffiths, 2009; Skovgaard, 2007). Johne's disease is widespread in dairy cattle and its prevalence is increasing in food-producing animals globally, causing significant financial losses (Greenstein and Collins, 2004; Skovgaard, 2007). Owing to the remarkable clinical, epidemiological, and pathological similarity of Johne's disease to Crohn's disease in humans, a chronic inflammatory disease most commonly affecting the terminal ileum, MAP has also been proposed as the etiological agent of Crohn's disease (Greenstein and Collins, 2004; Griffiths, 2009; Skovgaard, 2007). It has been suggested that multiple interacting factors (genetic predisposition, infectious agents like MAP, alteration of intestinal microflora, and immune-mediated tissue damage) are involved in the development of this disease, with the relative importance of each one of them not being determined (Griffiths, 2009; Pistone *et al.*, 2012). Despite the fact that since the first proposal of a possible link of MAP with Crohn's disease (Chiodini *et al.*, 1984) a considerable amount of data indicating such association has been generated (Feller *et al.*, 2007), a definitive causal relationship has yet to be established (Pistone *et al.*, 2012). Nevertheless, the precautionary principle approach has been advocated until the role of the organism has been definitively determined (Griffiths, 2009), and potential vehicles of transmission of the organism from animals to humans include milk and dairy products as well as raw meat contaminated via feces during slaughtering (Kim and Griffiths, 2011; Skovgaard, 2007). As MAP has been isolated from both raw and pasteurized milk, the efficacy of routine pasteurization against the organism has been questioned (Greenstein and Collins, 2004; Griffiths, 2009; Skovgaard, 2007). However, based on the findings of certain studies, among the numerous studies assessing the ability of MAP to survive pasteurization, it has been concluded that the organism is unable to survive high-temperature short-time (HTST) pasteurization (Griffiths, 2009). Other issues of concern with regard to food safety that warrant further investigation are the ability of MAP to survive the low-temperature thermization processes used in manufacturing of many cheeses, as well as its prevalence and evolution during cheese ripening (Skovgaard, 2007). Additional possible means of transmission of MAP to humans include contaminated water and animal contact (Greenstein and Collins, 2004). The rising concerns regarding the putative zoonotic and foodborne transmission potential of MAP, in conjunction with the difficulties associated with the culture of this organism, render the development of rapid and sensitive methods for its detection and characterization essential (Griffiths, 2009; Kim and Griffiths, 2011; Skovgaard, 2007). Information regarding the relationship between MAP and Crohn's disease, the prevalence and survival of this emerging pathogen in foods and in the environment, as well as potential control approaches has been reviewed in detail by Griffiths (2009).

Salmonella enterica

Salmonellosis, the infection caused by the bacterium *Sa. enterica*, is an illness known for more than 100 years (Bailey *et al.*, 2010). Among the so-called 'host-restricted' *Sa. enterica* serotypes, the ones that are associated with animal hosts (e.g., Gallinarum and Abortusovis) usually elicit very mild symptomatology in humans, whereas, the 'human-restricted' *Sa. enterica* serotypes Typhi, Paratyphi A, and Paratyphi B (which are not usually pathogenic to animals) commonly cause severe systemic disease such as typhoid or enteric fever in humans (Velge *et al.*, 2005). Widespread *Sa. enterica* serotypes, such as Enteritidis and Typhimurium, generally cause gastrointestinal infection to humans, known as nontyphoidal salmonellosis which, however, may also be associated with serious clinical outcomes (e.g., bacteraemia, endovascular infections, and focal infections), particularly in susceptible individuals (Hohmann, 2001; Velge *et al.*, 2005). In addition to host-related factors (e.g., health status, immunosuppresion, age, and genetic defects), the exact clinical outcome of nontyphoidal salmonellosis depends on the virulence traits of the *Sa. enterica* strains responsible for the infection, as certain serotypes of the pathogen are more likely than others to cause systemic infections not only in susceptible hosts, but also in people with no identifiable predisposing conditions (Fierer and Guiney, 2001).

Nontyphoidal *Salmonella* has been a leading cause of foodborne illness in many countries (Adak *et al.*, 2005; Scallan *et al.*, 2011). The emergence of human foodborne infections caused by *Salmonella* Enteritidis and by multiple-antibiotic-resistant strains of *Salmonella* Typhimurium constituted two major changes in the epidemiology of nontyphoidal salmonellosis in the European Union and the USA in the second half of the twentieth century (Velge *et al.*, 2005). Although *Sa. enterica* serotypes Enteritidis and Typhimurium are the serotypes most commonly associated with human infections (CDC, 2011a; EFSA-ECDC, 2012), the emergence and potential connection to human disease of rare serotypes of the organism during the last decades has attracted the attention of the scientific community. For instance, the prevalence, among human clinical cases, of *Sa. enterica* serotype 4,5,12:i:, a serotype antigenically similar and genetically closely related to *Salmonella* Typhimurium, has increased considerably in many countries in the last decade (Soyer *et al.*, 2009). This emerging *Sa. enterica* serotype, which represents multiple distinct clones, has been responsible for a number of human salmonellosis outbreaks (e.g., in Spain, Luxemburg, and the USA) and has been isolated from different foods and animals over the last decades (Soyer *et al.*, 2009). *Salmonella enterica* serotype Cerro has been identified as a potentially emerging pathogen of cattle; given the fact that other *Sa. enterica* serotypes important to bovine health have emerged to become leading causes of human foodborne disease, close monitoring of *Salmonella* Cerro is warranted (Cummings *et al.*, 2010). According to the

findings of a study assessing the association of *Sa. enterica* with foodborne and waterborne diseases in Korea during 1998–2007, although the three most prevalent serotypes were Typhi, Enteritidis, and Typhimurium, there were also remarkable outbreaks caused by rare serotypes such as Othmarschen, London, and Paratyphi A (Kim, 2010). *Salmonella enterica* serotype Napoli is another emerging serotype in Italy, France, and Switzerland; characterization of strains of this serotype isolated in Italy from human cases, foods of animal origin, and the environment showed an array of virulence genes similar to those of other serotypes of public health significance, demonstrating its ability to cause infection in humans (Graziani *et al.*, 2011). Lastly, *Sa. enterica* serotype Weltevreden, which has long been associated with meat products in Southeast Asia, is an emerging serotype associated with meat and particularly with plant products in Western countries (Brankatschk *et al.*, 2012; Emberland *et al.*, 2007). Nonetheless, to enhance one's understanding of the ecology and risk factors for human infection of the aforementioned emerging serotypes, further studies are required.

Streptococcus suis

Streptococcus suis is an encapsulated Gram-positive, facultatively anaerobic coccus which is emerging as an important threat to human health (Segura, 2009; Wertheim *et al.*, 2009). The organism's main reservoir is swine, with its natural habitat being the upper respiratory, genital, and alimentary tracts of pigs (Ma *et al.*, 2008; Segura, 2009). *Streptococcus suis* was first described by veterinarians in 1954 as the etiological agent of outbreaks of meningitis, septicemia, and purulent arthritis among piglets (Field *et al.*, 1954). The first human cases of *St. suis* infection were reported in 1968 in Denmark (Perch *et al.*, 1968), and since then numerous cases have been reported worldwide including the UK, France, Germany, The Netherlands, Sweden, New Zealand, Thailand, Singapore, Taiwan, and Hong Kong (Ma *et al.*, 2008). On the basis of composition of the polysaccharide capsule, 35 serotypes of the organism have been identified, with serotype 2, however, being associated with the majority of cases of human infections (Lun *et al.*, 2007; Wertheim *et al.*, 2009; Segura, 2009). Despite the fact that most reports refer to sporadic cases of infection, an outbreak of acute disease in humans in Sichuan Province, China in 2005, involving 215 cases and 38 deaths, highlighted the importance of *St. suis* as an emerging zoonotic pathogen (Yu *et al.*, 2006). The epidemiology of *St. suis* infections in humans remains largely undefined (Segura, 2009). Nonetheless, and in concordance with the pathogen's natural distribution in the environment, human cases are most frequently reported from countries where pig-rearing is common (particularly in Southeast Asia), and the majority of them are associated with cutaneous contact with infected pigs or with handling or consumption of uncooked or undercooked pork (Segura, 2009; Wangsomboonsiri *et al.*, 2008; Wertheim *et al.*, 2009). *Streptococcus suis* causes systemic infection in humans affecting several organ systems, with its most common clinical manifestation being meningitis, while patients are also likely to develop skin problems (e.g., petechiae, purpura, and ecchymoses) (Wertheim *et al.*, 2009). Less common manifestations of the infection include endocarditis, acute pyogenic arthritis, endophthalmitis and uveitis, peritonitis, rhabdomyolysis, and spondylodiscitis, whereas a striking feature that may be reported by up to one-half of patients is subjective hearing loss (Segura, 2009; Wertheim, *et al.*, 2009). Simple control measures, embraced by both workers with occupational exposures and the general public, should be adequate to prevent the majority of cases of *St. suis* infection. Such measures include cautious handling of pigs or raw pork (e.g., wearing gloves during swine slaughtering or processing of pork meat, hand washing after handling of raw pork meat, and avoiding cross-contamination between raw and cooked pork) and thorough cooking of pork meat (Ma *et al.*, 2008; Segura, 2009; Wertheim *et al.*, 2009). Future research shedding light on the virulence factors, the selective pressures resulting in virulence enhancement, as well as the geographical localization of emerging highly virulent types of *St. suis*, is expected to improve significantly one's understanding of the complex evolution of this pathogen (Segura, 2009).

Antimicrobial-Resistant Strains

The appearance of antimicrobial-resistant bacteria has been promoted by the extensive use or misuse of antimicrobial agents, not only in the treatment of infected humans and animals but also as growth-enhancing or health-promoting agents in livestock, seafood, and plant production (Helmuth, 2000; Hur *et al.*, 2012). The overuse of antimicrobials in animal husbandry may result in a long-lasting, strong selective pressure on bacteria prevalent in intensive production units, leading to the emergence of antimicrobial-resistant strains in food animals, which are then transmitted to humans either directly or through the food supply (Angulo *et al.*, 2000; Fey *et al.*, 2000; Helmuth, 2000). A growing concern over the past 30 years is the worldwide emergence and increasing prevalence of MDR phenotypes among bacterial strains, and particularly among *Sa. enterica* serotypes, exhibiting resistance to several clinically important antimicrobial agents traditionally used to treat bacterial infections in human and veterinary medicine (Hur *et al.*, 2012). The first reports on resistant *Salmonella* date back to the early 1960s and refer mainly to monoresistant strains of the organism (Helmuth, 2000). Widespread resistance of *Sa. enterica* serotypes Typhi and Paratyphi A to chloramphenicol, ampicillin, and cotrimoxazole was documented at the end of the 1980s and early 1990s with MDR isolates of these serotypes causing significant outbreaks, particularly in Asia (Parry *et al.*, 2002). Nonetheless, the declining resistance levels as observed and reported in the following years suggested that drugs such as chloramphenicol may be used again as first-line therapy for enteric fever (Parry, 2003). Low-level resistance to ciprofloxacin in the aforementioned serotypes has been reported in areas of Central, South and Southeast Asia, frequently resulting in fluoroquinolone treatment failures (Aarestrup *et al.*, 2003; Parry *et al.*, 2002). With reference to nontyphoidal *Salmonella*, MDR strains have been found to be of various serotypes including Agona, Anatum, Choleraesuis, Derby, Dublin, Heidelberg, Kentucky, Newport, Pullorum, Schwarzengrund, Seftenberg, Typhimurium, and Uganda (Hur *et al.*, 2012; Wasyl and Hoszowski, 2012). Antimicrobial

resistance has generally been less of a problem in *Sa. enterica* serotype Enteritidis (Hur *et al.*, 2012; Parry, 2003). An event of major public health significance has been the emergence and clonal spread of certain MDR genotypes, with the most characteristic example being the global epidemic spread of *Sa. enterica* serotype Typhimurium definitive type 104 (DT104) (Butaye *et al.*, 2006). This phage type commonly exhibits the following pentaresistance pattern (i.e., resistance to five antimicrobial agents): ampicillin, chloramphenicol, streptomycin, sulfamethoxazole, and tetracycline (R-type ACSSuT) (Helmuth, 2000; Hur *et al.*, 2012; Parry, 2003). Additional resistance to trimethoprim and low-level resistance to ciprofloxacin have also been occasionally observed among *Salmonella* Typhimurium DT104 isolates (Parry, 2003; Velge *et al.*, 2005).

The ability to produce β-lactamases (i.e., enzymes that hydrolyze β-lactams) constitutes one of the most important resistance mechanisms of Gram-negative rods, and the emerging resistance related to the production of extended-spectrum β-lactamases (ESBLs) has been identified as a significant problem with regard to handling of bacterial infections (Gniadkowski, 2001; Paterson, 2006). ESBLs are mainly found in strains of *E. coli* and *Klebsiella pneumoniae*, but are also reported in other members of the family Enterobacteriaceae as well as in *Pseudomonas aeruginosa*, and infections with ESBL-producing bacterial strains are mainly encountered, sporadically or in outbreaks, in critical care units in hospitals (Shah *et al.*, 2004). ESBLs are typically plasmid, rather than chromosomally mediated enzymes, and the majority of them have evolved from class A β-lactamases, namely TEM-1, TEM-2, and SHV-1, which are frequently expressed in Gram-negative bacteria and confer resistance to ampicillin, amoxicillin, and other penicillins, as well as to early generation cephalosporins (Paterson, 2006; Shah *et al.*, 2004). TEM- or SHV-type ESBLs are typically not active against cephamycins or carbapenems, and can generally be inhibited by β-lactamase inhibitors (e.g., clavulanate, sulbactam, or tazobactam) (Paterson, 2006). Persistent exposure of bacterial strains to a multitude of β-lactams has induced dynamic and continuous production and mutation of β-lactamases of certain strains, expanding their activity even against newly developed β-lactam antibiotics (Shah *et al.*, 2004). For instance, mutations of the genes encoding TEM-1, TEM-2, or SHV-1 gave rise to new β-lactamases, capable of hydrolyzing third-generation cephalosporins and aztreonam (Paterson, 2006). Additional families of ESBLs that may also be expressed by Enterobacteriaceae include the CTX-M-type (cefotaximases) and OXA-type (primarily in *P. aeruginosa*) enzymes as well as novel unrelated β-lactamases (Jin and Ling, 2006; Paterson, 2006; Shah *et al.*, 2004). In addition to ESBLs, other β-lactamases capable of hydrolyzing extended-spectrum cephalosporins are: (1) class C cephalosporinases (AmpC) which, unlike ESBLs, are also active against cephamycins and resistant against β-lactamase inhibitors and (2) carbapenemases that have a broader range of activity and are also active against carbapenems (Gniadkowski, 2001; Paterson, 2006).

There is ample evidence of person-to-person transmission with regard to β-lactamase producers (Paterson, 2006). Furthermore, although β-lactamase-producing bacterial strains are mainly prevalent in hospital settings, there is evidence suggesting that they also are emerging and spreading in the community, with community-acquired cases of infections including both urinary tract and gastrointestinal infections (Paterson, 2006). β-lactamase-producing bacteria that have been associated with drug-resistant gastroenteritis include *Sa. enterica*, *Shigella* spp., *Vibrio cholerae*, and STEC (Paterson, 2006). With reference to *Sa. enterica*, both ESBLs and AmpC β-lactamases have been identified, and the resistance of this pathogen to third-generation cephalosporins is of great concern as ceftriaxone constitutes the antimicrobial of choice for treating invasive salmonellosis caused by MDR strains in children (i.e., where the use of quinolones is not indicated) (Butaye *et al.*, 2006; Paterson, 2006; Velge *et al.*, 2005). The emergence and worldwide increase of ESBL (particularly of the CTX-M group) producers among *Sa. enterica* serotypes, including the serotypes Enteritidis, Typhimurium, and Virchow, has been acknowledged as an important public health issue during the last years (Bonalli *et al.*, 2011; Jin and Ling, 2006; Riano *et al.*, 2009). Although more research is required in order to track the evolution of ESBLs in *Sa. enterica* isolates from different environments, some findings do support the potential for clonal spread of CTX-M-type ESBLs among animals and humans (Riano *et al.*, 2009). Furthermore, *Sa. enterica* serotype Newport isolates resistant to multiple antimicrobials, including extended-spectrum cephalosporins via the production of AmpC, known as serotype Newport MDR-AmpC isolates, have recently emerged. The common recovery of MDR-AmpC isolates of *Salmonella* Newport from food animals and humans suggests their potential transmission to humans through the food chain (Zhao *et al.*, 2003). Indeed, as supported by epidemiological data, infections with such isolates appear to be acquired through the food supply, most likely from bovine and perhaps poultry sources, and particularly among individuals already taking antimicrobial agents (CDC, 2002; Varma *et al.*, 2006). The emergence and worldwide dissemination of multiresistant *E. coli* producing ESBLs, particularly of the CTX-M-type, as an important cause of both nosocomial and community-onset infections have also been acknowledged (Oteo *et al.*, 2010; Pitout *et al.*, 2004). Similar to the case of *Sa. enterica*, the rising trend of antimicrobial resistance and the high prevalence of β-lactamase determinants in *E. coli* strains of animal origin (Li *et al.*, 2010) dictate the development and implementation of effective control interventions.

Surveillance programs, at both national and international levels, have been proven to be valuable tools for ensuring prudent use of antimicrobials in livestock and veterinary medicine as well as for monitoring the appearance of antimicrobial resistance (Hur *et al.*, 2012; Parry, 2003). In addition to appropriate antibiotic management, improved vaccines and diagnostics as well as adherence to infection control measures (e.g., use of gloves and adequate hand hygiene in health care settings) may also be needed in order to address this public health and food safety issue (Hur *et al.*, 2012; Oteo *et al.*, 2010; Paterson, 2006). Moreover, continued research on the genetic determinants of antimicrobial resistance (e.g., plasmid sequencing projects) and on the ecology, epidemiology, and evolution of MDR strains is expected to provide a better understanding of the emergence and distribution of antimicrobial resistance, and, therefore, to allow for the design of improved control measures (Alcaine *et al.*, 2007; Louden *et al.*, 2012).

Other Bacteria

Although its foodborne pathogen status has been well-established, constituting the leading cause of sporadic bacterial gastroenteritis, *Ca. jejuni* has also been recognized as one of the most prevalent and serious emerging bacterial pathogens of meat, poultry, and derived products (Mor-Mur and Yuste, 2010). Its low infectious dose (i.e., less than 100 cells can cause disease) and its ability to survive refrigeration and freezing delineate the relevance of this organism to food safety and public health, with raw or undercooked poultry being the primary source of campylobacteriosis (Mor-Mur and Yuste, 2010). Complications of campylobacteriosis include reactive arthritis, pancreatitis, meningitis, endocarditis, and the Guillain–Barré syndrome, a disorder of the peripheral nervous system, with the latter being primarily associated with serotypes O:19, O:4, and O:1 of the pathogen (Mor-Mur and Yuste, 2010). Owing to difficulties associated with culturing of *Ca. jejuni*, it has been opined that the incidence of campylobacteriosis in the past was most likely underestimated, with foodborne outbreaks being erroneously identified as caused by other organisms such as *Salmonella* spp. (Mor-Mur and Yuste, 2010).

Bacterial species belonging to the genus *Helicobacter* have also been identified as potentially emerging foodborne pathogens. One such example is *Helicobacter pylori*, which, since its initial recognition in 1982, has been implicated as the etiological agent of gastritis and as a major contributing factor in the development of peptic gastroduodenal ulcers (Gracey, 1994; Meng and Doyle, 1998). Although humans were originally thought as the only natural host of *H. pylori*, the organism has also been isolated from nonhuman primates, suggesting that it may be a zoonotic pathogen with its transmission occurring from animals to humans (Meng and Doyle, 1998). Additional modes of *H. pylori* transmission that have been proposed include fecal–oral transfer and person-to-person spread (Gracey, 1994), though there is also evidence supporting the hypothesis of waterborne transmission (Meng and Doyle, 1998). Nevertheless, the significance of this organism as a foodborne pathogen has not been firmly established yet. *Helicobacter pullorum* is another species of potential importance as an emerging foodborne pathogen; it has been associated with diarrhea, gastroenteritis, and liver diseases in humans, to which it may be transmitted via consumption of undercooked poultry products (Skovgaard, 2007).

In addition to the aforementioned bacterial pathogens, attention should be paid to well-established foodborne pathogens, which, however, appear to reemerge exhibiting additional characteristics/abilities (e.g., higher virulence or lower infectious dose) or being associated with other, frequently unexpected, food vehicles. Examples of such foodborne pathogens are *Sa. enterica* and *Listeria monocytogenes*. Recent salmonellosis outbreaks have been associated with unexpected food products such as microwavable, ready-to-cook foods, breaded (sometime prebrowned) chicken nuggets, and chicken entrees, as well as peanut butter, demonstrating that the landscape of foodborne infections is in flux (Tauxe *et al.*, 2010). Furthermore, both *Sa. enterica* and *L. monocytogenes*, as well as other established foodborne pathogens, have been increasingly associated with illness outbreaks linked to consumption of fresh produce (CDC, 2011b, 2012; Tauxe *et al.*, 2010). For instance, an unusually large listeriosis outbreak associated with cantaloupe was reported in 2011 in the US (CDC, 2011b); this was the first epidemiologic association of *L. monocytogenes* with melon, whereas a novel serotype 1/2a outbreak strain and two novel epidemic clones of the pathogen were identified during the outbreak investigation (Lomonaco *et al.*, 2013).

Viruses

Various groups of viruses are well recognized as important agents of waterborne and foodborne illness. Among these, the gastroenteritis-causing noroviruses (NoVs) and hepatitis A virus have been identified as the most important foodborne pathogens on the basis of their highly infectious nature, and the large numbers of outbreaks and people affected (Duizer and Koopmans, 2009; Koopmans and Duizer, 2004). Despite the well-established foodborne pathogen status of certain viral agents, such as the above two groups, foodborne viruses can be regarded as an emerging problem as a whole, due to the decrease in immunity of populations in countries with high standards of hygiene observed in recent years (Koopmans and Duizer, 2004). In general, a definitive association of direct or indirect animal contact with foodborne infection in humans has not been established, and most documented foodborne viral outbreaks can be traced to foods that have been manually handled by infected food handlers (symptomatic or not) and not heated or minimally processed afterwards (Koopmans and Duizer, 2004). Although most frequently observed at the end of the food chain, viral contamination of food can occur anywhere in the process from farm to fork, and a wide variety of food items have been associated with epidemic disease including deli meats, sandwiches, bakery products, berries, dishes containing fresh (or fresh frozen) fruits and vegetables, and, most importantly, shellfish (Koopmans and Duizer, 2004). Given that viruses, unlike bacteria, are strict intracellular pathogens (i.e., cannot replicate in harvested or processed food), and, thus, viral contamination of food is not expected to increase during processing, transport, or storage, the emphasis with regard to their control should be placed on prevention of contamination by proper implementation of good hygiene practices, good manufacturing practices, and Hazard Analysis and Critical Control Points programs (Koopmans and Duizer, 2004). With reference to recommended areas for future research, these include development of simple, efficient, and reproducible detection methods of viruses in foods, assessment of viral survival on different food commodities, and determination of the duration and levels of shedding of viral pathogens in people with and without symptoms (Koopmans and Duizer, 2004).

As viruses causing gastroenteritis have been well recognized as among the most common causes of foodborne illness worldwide, with NoVs ranking number one in many industrialized countries (Duizer and Koopmans, 2009), they will not be further discussed in this article. The information provided in the following sections refers to viral pathogens that are or have the potential to be foodborne, and that would better fit the term 'emerging.'

Hepatitis Viruses

The enterically transmitted hepatitis viruses are transmitted by the fecal–oral route, either directly from person to person or indirectly when water or food contaminated with fecal material is ingested, and replicate and cause disease in the liver (Mattison *et al.*, 2009). The hepatitis A virus (HAV) is a member of the Picornaviridae family, in the genus Hepatovirus, and consists of nonenveloped, icosahedral capsids of approximately 30 nm in diameter enclosing a 7.5 kb single-stranded, polyadenylated RNA genome (Mattison *et al.*, 2009). The incidence and severity of HAV infection may vary considerably both among and within countries. In many developing regions of the world where hygienic standards (i.e., clean water, sewage systems, and proper hygiene practices) may be below acceptable standards, HAV infection is endemic, with the majority of people being infected in early childhood and virtually all adults appearing to be immune; in these areas, HAV transmission occurs primarily from person to person, and outbreaks are not that common as most infections occur among children, who generally remain asymptomatic (Koopmans and Duizer, 2004; Mattison *et al.*, 2009). In contrast, in the developed countries, where HAV endemicity is low, the majority of adults are susceptible to HAV infection, and HAV constitutes a serious and increasing public health concern (Koopmans and Duizer, 2004; Mattison *et al.*, 2009). Viral hepatitis, which is generally an acute infection but its resolution provides life-long immune protection against future infections, is characterized by fever, jaundice, light-colored stools, dark-colored urine, abdominal pain, and occasional diarrhea (Mattison *et al.*, 2009). As virus shedding may start 10–14 days before the onset of symptoms, HAV spreading can be extensive (Koopmans and Duizer, 2004). Although the accurate identification of foodborne sources of HAV infection is frequently difficult due to the long incubation period between infection and symptomatic disease, foodborne outbreaks of HAV have been associated with many different food types, and primarily with shellfish (due to fecal contamination of shellfish growing waters) and fresh or frozen produce (Mattison *et al.*, 2009).

Hepatitis E virus (HEV) is a member of the genus Hepevirus in the Hepeviridae family, with its particle being a nonenveloped icosahedron of approximately 30 nm in diameter and its genome a 7.5 kb single-stranded RNA molecule (Mattison *et al.*, 2009). Although HEV is known for its ability to cause acute clinical hepatitis, primarily as waterborne outbreaks and sporadic infections, in young adults throughout the developing world, there are recent reports on zoonotic foodborne autochthonous HEV infections in developed countries (Khuroo and Khuroo, 2008; Nicand *et al.*, 2009). In this sense, hepatitis E is regarded as an emerging concern in western countries (i.e., Western Europe, North America, Japan, and Australia), and considerable advances have been successful in understanding its epidemiology (Mattison *et al.*, 2009; Khuroo and Khuroo, 2008). Emerging HEV infections in the developed world have been more frequently associated with people of advanced age (i.e., more than 50 years) (Mattison *et al.*, 2009; Nicand *et al.*, 2009). In addition to its well-established waterborne transmission, HEV may be transmitted to humans via the following routes: (1) consumption of raw or undercooked meat of naturally infected wild (e.g., boar and deer) and domesticated (e.g., pigs) animals; (2) occupational exposure to infected animals; (3) parenteral transmission; and (4) vertical transmission from mother to child (Khuroo and Khuroo, 2008; Nicand *et al.*, 2009). The incubation period of HEV varies from 15 to 45 days, and the typical clinical symptoms of the infection are similar to those associated with HAV infection and include jaundice, dark urine, enlarged tender liver, elevated liver enzymes, abdominal pain, and tenderness accompanied by nausea, vomiting, and fever (Khuroo and Khuroo, 2008). Nevertheless, the disease may vary in severity and is often complicated by protracted coagulopathy and cholestasis, whereas chronic HEV infection, chronic hepatitis, and cirrhosis have been frequently reported in organ transplant recipients (Khuroo and Khuroo, 2008). High rates of fulminant hepatitis and fatality have been documented for classical HEV infections in pregnant women, particularly in the third trimester (Mattison *et al.*, 2009).

Other Viruses

In addition to the discussion above in Section Hepatitis Viruses, there are also some emerging viruses that, although not usually transmitted via the fecal–oral route, may infect via the gastrointestinal tract and have the potential to emerge as food safety concerns. These viruses are avian influenza viruses, the coronavirus, and the tick-borne encephalitis virus (Mattison *et al.*, 2009).

The avian influenza virus A genus is classified in the family Orthomyxoviridae and is characterized by pleomorhpic, enveloped virions with a segmented single-stranded RNA genome. The viruses of this genus are classified into subtypes based on the two envelope glycoproteins, the hemagglutinase (H type) and the neuraminidase (N type), and there are 16 known H types and 9 known N types (Mattison *et al.*, 2009). All of the known subtypes of influenza A viruses have been found in birds, and viruses containing combinations of the H1, H2, H3, N1, and N2 types are considered to be established in the human population, whereas viruses of the H5, H7, and H9 subtypes have been associated with sporadic human infections (Mattison *et al.*, 2009). Humans acquire avian influenza viruses primarily through direct contact of the mucous membranes with infectious secretions and excreta from infected birds or contaminated poultry products (Doyle and Erickson, 2006). An avian influenza virus subtype that has recently attracted the attention of public health authorities is the highly pathogenic H5N1 virus, which has been detected in poultry from more than 50 countries and it has infected humans in Vietnam, Thailand, Indonesia, Cambodia, China, Turkey, Iraq, Azerbaijan, Egypt, and Djibouti (De Jong and Hien, 2006; Mattison *et al.*, 2009). This virus replicates to extremely high levels in the upper respiratory tract, causing an intense inflammatory response, and is associated with a particularly high case fatality rate, frequently more than 60% (De Jong *et al.*, 2006). Despite its limited ability to spread from person to person, there is concern that H5N1 virus could acquire the ability to spread effectively in humans and result in a worldwide pandemic (Mattison *et al.*, 2009). Although almost all H5N1 infections of humans have been linked to close contact with infected poultry (De Jong and Hien, 2006), given that the virus has been isolated from various parts of infected

poultry such as the blood, bones and meat, the consumption of raw or undercooked poultry products as a potential source of infection cannot be renounced (Mattison *et al.*, 2009).

Although coronaviruses typically cause mild respiratory disease, a particularly virulent strain, known as the 'sudden acute respiratory syndrome coronavirus,' emerged in 2003, causing more than 8000 cases of systemic infections as well as respiratory illness, and being associated with an approximately 10% case fatality rate (Mattison *et al.*, 2009; Wang and Chang, 2004). The fact that this virus was isolated from the digestive tract, as well as from feces and sewage, raises the possibility that it may have had the potential to be transmitted through the fecal–oral route and food products (Mattison *et al.*, 2009). The tick-borne encephalitis virus is considered endemic to Europe, and is usually transmitted to humans by tick bites; nonetheless, some cases have been linked to the consumption of raw milk from infected cattle or goats (Mattison *et al.*, 2009). Finally, additional emerging viruses of interest are the gastroenteritis-causing parvoviruses, toroviruses, and picobirnaviruses (Mattison *et al.*, 2009).

Parasites

Waterborne and foodborne parasitic infections have received considerable attention in the last decade. Despite the fact that many of these infections are well recognized for many years, they are considered emerging as a result of either true higher incidence or higher detection (Dorny *et al.*, 2009). Factors that can be associated with increased human exposure to foodborne parasites and, thus, with the emergence or reemergence of many foodborne parasitic diseases as this has been documented recently on a worldwide basis, include changing eating habits (e.g., increased demand for exotic and raw food), population growth and particularly increase of population of highly susceptible people, increased international travel, globalization of food supply, changes in food production systems, climate changes, and improved diagnostic tools (Broglia and Kapel, 2011; Dorny *et al.*, 2009). A characteristic example is that of the increasing development of certain farming practices such as aquaculture, driven by the rising global demand for protein of animal origin, in developing countries where the existing health monitoring practices may not be sufficient or adequately implemented (Broglia and Kapel, 2011). It has been acknowledged that there is an urgent need for better monitoring and control of foodborne parasites, and some of the suggested means for achieving this are the use of new risk assessment tools, the development and utilization of new monitoring technologies (both serological and molecular), as well as health education (Dorny *et al.*, 2009). In general, given that foodborne parasitic infections are actually reflecting a complex system of interconnected biological, economic, social, and cultural variables, it has been proposed that their control should be based on a holistic approach, with the latter, however, requiring a large amount of high-quality data as well as systematic collaboration across sectors and disciplines (Broglia and Kapel, 2011). The information provided below refers to emerging parasites that have been associated with human infections and are or have the potential to be foodborne.

Cyclospora cayetanensis

Cyclospora cayetanensis is a single-cell coccidian protozoan, which has been implicated as the etiological agent in cases of watery diarrhea, nausea, vomiting, fatigue, and anorexia in humans and other primates (Dorny *et al.*, 2009; Rose and Slifko, 1999). Despite the fact that the infection is generally treatable with none or mild symptomatology in the immunocompetent, it may be associated with a profuse and prolonged (lasting for several months) diarrhea in immunocompromized individuals (Rose and Slifko, 1999). Outbreaks of *Cy. cayetanensis* infection have been increasingly observed since the 1990s, particularly in North America and Asia (Dorny *et al.*, 2009). Although traditionally regarded as a waterborne parasite, outbreaks of *Cy. cayetanensis* infections have also been linked to various fresh fruits, vegetables, and herbs such as blackberries, raspberries, strawberries, lettuce, and basil (Dorny *et al.*, 2009; Rose and Slifko, 1999; Smith and Evans, 2009).

Cryptosporidium and Giardia

The parasites of the genera *Cryptosporidium* and *Giardia* are well-recognized causes of protozoan waterborne diseases known as cryptosporidiosis and giardiasis, respectively. Owing to their extensive genetic diversity, the taxonomy of these parasites has frequently been a matter of debate (Dorny *et al.*, 2009). In spite of the fact that these parasites have been primarily associated with waterborne outbreaks and with infections contracted via animal handling or contact with children, they may also contaminate food commodities (e.g., soft fruits and vegetables, and shellfish) and cause infections in humans by these routes (Dorny *et al.*, 2009).

Cryptosporidium is a coccidian parasite that infects a wide range of vertebrate hosts including mammals, rodents, birds, reptiles, and fish (Smith and Evans, 2009). This parasite has emerged as an important pathogen of humans in the last 25 years, with eight described and five undescribed species potentially infecting immunocompetent and immunocompromized humans. Among these species, *Cryptosporidium hominis* and *Cryptosporidium parvum* are the most commonly detected, though the latter is the best studied species and has been identified as a major zoonotic pathogen and a significant contributor to environmental contamination with oocysts (Smith and Evans, 2009). Cryptosporidiosis is a cholera-like disease, its main symptoms are large volumes of fluid loss, fever, and abdominal pain, and its mortality rate can be high (i.e., 50%–60%) in the immunocompromized population (Rose and Slifko, 1999). Foods that have been (or suspected to be) linked to foodborne outbreaks of cryptosporidiosis include apple cider, chicken salad, and cow's milk (Smith and Evans, 2009).

The genus *Giardia* includes species that are host specific (infecting rodents, amphibians, birds, great blue herons, the prairie vole and mammals), as well as species that have zoonotic potential. The parasites that infect humans belong to the species *Giardia duodenalis*, formerly also known as *Giardia intestinalis*, and *Giardia lamblia* (Smith and Evans, 2009). The most common symptoms of giardiasis are diarrhea followed by flatulence and cramps (Rose and Slifko, 1999). Examples of foodstuffs that have been associated with documented outbreaks of giardiasis are Christmas pudding, fruit salad,

home-canned salmon, ice, noodle salad, raw sliced vegetables, sandwiches, and tripe soup, and food handlers have been identified in most of the cases as the most likely source of food contamination (Smith and Evans, 2009).

Toxoplasma gondii

Toxoplasma gondii is a coccidian protozoan parasite of man and animals with a worldwide distribution, constituting one of the most significant parasitic pathogens in Europe and the USA (Mead *et al.*, 1999; Vaillant *et al.*, 2005). Although it has a disease burden similar to that of salmonellosis and camplylobacteriosis, toxoplasmosis (i.e., the disease caused by *T. gondii*) is still regarded as a considerably underreported disease (Dorny *et al.*, 2009). On the basis of multilocus restriction fragment length polymorphism techniques, there are three genotypes within *T. gondii* (genotypes I, II, and III) which correlate with different patterns of human disease, with, however, the majority of human toxoplasmosis cases being associated with genotype II (Smith and Evans, 2009). Toxoplasmosis in immunocompetent hosts is either asymptomatic or associated with nonspecific clinical symptoms such as pyrexia, lymphadenopathy, malaise, and myalgia (Smith and Evans, 2009). Nonetheless, the disease can be severe and is generally considered as a serious health problem in pregnant women, who can pass the infection to the fetus, as well as in immunocompromized people (e.g., acquired immunodeficiency syndrome patients, organ and bone marrow transplant recipients, those with malignancies and on anticancer chemotherapy) (Dorny *et al.*, 2009; Smith and Evans, 2009).

Human toxoplasmosis can be contracted by the ingestion of sporulated oocysts present in cat feces and the environment (Dorny *et al.*, 2009). Furthermore, *T. gondii*, by being a zoonotic parasite present worldwide, has been detected in many animals used for meat production; viable parasites have been isolated from the meat of game, sheep, goat, horse, chicken, and pig (Dorny *et al.*, 2009; Smith and Evans, 2009). With particular reference to swine, a reemergence of toxoplasmosis has been observed in pigs raised in organic farms with outdoor access (Kijlstra *et al.*, 2004). Hence, *T. gondii* can also be transmitted to humans by consumption of raw or undercooked meat contaminated with tissue cysts of the parasite (Dorny *et al.*, 2009; Smith and Evans, 2009). Indeed, foodborne outbreaks of toxoplasmosis have been frequently linked to raw or rare meat, whereas additional food products associated with human infections include raw liver, goat's milk and ice cream (Smith and Evans, 2009). Nevertheless, as supported by epidemiological data, consumption of unwashed fresh vegetables or fruit has also been identified as an important risk factor with regard to toxoplasmosis (Dorny *et al.*, 2009).

Trichinella spp.

Trichinella spp. are zoonotic pathogens with widespread distribution and have been recognized as important agents of meat-borne parasitic infections in humans for a long time. The disease caused by the nematodes of the genus *Trichinella*, referred to as trichinellosis, is contracted in humans by the ingestion of larvae of the parasite that are encysted in muscle tissue of domestic or wild animal meat, with the domestic pig being identified as the most important source of the infection worldwide (Dorny *et al.*, 2009). Although, until recently, all cases of infections in both animals and humans were attributed to the species *Trichinella spiralis*, eight species and four genotypes are today recognized in the genus *Trichinella* (Dorny *et al.*, 2009). Clinical disease in humans is characterized by an intestinal phase and a subsequent parenteral (tissue) phase. Adult worms in the intestine may cause diarrhea, nausea, vomiting, fever, and abdominal pain, whereas the parenteral phase is usually accompanied by heavy muscle pains, fever, and eosinophilia (Dorny *et al.*, 2009; Murrell and Crompton, 2009). Potential complications attributed to larvae of the parasite during the early parenteral phase include facial edema, skin rash, convulsions, weight loss, meningitis, encephalitis, and vertigo, whereas death may also occur in heavily infected individuals (Murrell and Crompton, 2009).

Other Parasites

In addition to the parasites mentioned above, the taeniid tapeworms of the genus *Taenia* are also important zoonotic pathogens likely to be transmitted by food, and particularly by meat, to humans. More specifically, the species *Taenia saginata* (main reservoir: cattle), *Taenia saginata asiatica* (main reservoir: swine), and *Taenia solium* (main reservoir: swine) are the species that have been associated with human infections, and the terms cysticercosis and taeniosis refer to infections with larval and adult tapeworms, respectively (Dorny *et al.*, 2009). *Taenia saginata* is a cosmopolitan parasite found in both industrialized and developing countries; whereas *T. saginata asiatica* (which, although genetically is considered a subspecies of *T. saginata*, has distinct morphological and biological characteristics) is restricted to Asian countries (Dorny *et al.*, 2009). Intestinal taeniosis is usually contracted as the result of consumption of raw or undercooked meat, liver, or viscera, and may cause abdominal discomfort, nausea, weight loss, and occasionally more severe symptoms such as intestinal perforation and peritonitis (Dorny *et al.*, 2009).

Additional emerging parasites with a foodborne transmission potential are the intestinal trematodes of the genera *Fasciola* and *Fasciolopsis*. These parasites, and particularly the species *Fasciola hepatica*, *Fasciola gigantica*, and *Fasciolopsis buski*, may have a significant impact on the livestock sector, and cause infections in humans that are usually acquired by consumption or handling of freshwater aquatic plants (e.g., watercress and water chestnut) (Dorny *et al.*, 2009; Murrell and Crompton, 2009). Moreover, parasites that have recently gained interest are *Trypanosoma cruzi* and *Echinococcus* spp. (especially *Echinococcus granulosus* and *Echinococcus multilocularis*); infective stages of these parasites may be shed in the environment via feces and contaminate foods such as vegetables, fruits, or fruit juices (Dorny *et al.*, 2009). Finally, there is a wide variety of parasites including trematodes, cestodes, nematodes, and pentastomides that can be transmitted to humans by fish, crustaceans, reptiles, amphibians and snails when the meat of these animals is consumed raw or undercooked. Although, traditionally, such parasitic zoonoses are

most common in Asian countries (due to their particular culinary habits and the importance of aquaculture), some of them may emerge in other countries as a result of aquaculture, improved transportation and distribution systems, and tourism (Dorny *et al.*, 2009).

Concluding Remarks

Emerging foodborne pathogens, including bacteria, viruses, and parasites, are undoubtedly one of the most important food safety concerns for the food industry and public health authorities. As proposed by Buchanan (1997) several years ago, there are three research areas of interest with regard to emerging pathogens, which are still relevant and include: (1) research seeking improvements or alternatives to detect and control emerging pathogens; (2) research aiming at reducing the response between the emergence of a pathogen and its control; and (3) research identifying factors that will allow new food safety threats to be anticipated. In general, the challenge of foodborne pathogen emergence is expected to be successfully handled primarily via the development and implementation of robust and effective surveillance programs; such programs will allow for early detection and investigation of emerging (or reemerging) foodborne diseases and for the use of effective strategies for their control and prevention. Furthermore, food safety education of food handlers and consumers and prudent use of antimicrobials also are important for the control of emerging pathogens. Finally, the development and utilization of novel molecular techniques for studying foodborne pathogens, as this has been observed in the past decade, is expected to provide information that will improve one's understanding of the factors underlying the emergence of foodborne pathogens.

See also: Food Microbiology

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Food and Agriculture Organization of the United Nations.

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Food Safety and Inspection Service, United States Department of Agriculture.

www.who.int
World Health Organization.

Food Safety: Food Analysis Technologies/Techniques

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Introduction

In recent years, consumers have become increasingly concerned about the safety and quality of their food supply. To ensure that food supplies meet the highest standards of safety and nutritional quality, robust and state-of-the-art analytical methods are essential for all food products. The rapid growth of novel raw materials and ingredients, and new processes in the food industry has also brought new challenges to food scientists. The progresses in food science and technology have driven analytical methods toward those that heavily rely on instrumentation and biochemistry, which provide higher sensitivity and accuracy. Advances in modern food analysis technologies have allowed scientists in food safety and quality to meet such new challenges and demands.

Food analysis is particularly complex due to the intricate food system, which includes key physicochemical and biological characteristics of raw materials, potential existence of microorganisms, different contaminants and additives, and the processing techniques used. For these reasons, various analytical methods have been required for the quality control of foods and selection of appropriate techniques and methodologies are required to obtain the best results. In general, the choice of an analytical technique depends on the purposes of the analysis and the properties of the food. This article attempts to cover the recently developed technologies, as well as traditional instrumentation, techniques, and applications in food analysis.

Food Composition

Food, a highly complex system, contains essential nutrients such as water, carbohydrates, lipids, proteins, vitamins, minerals, and dietary fibers (Eastwood and Kritchevsky, 2005; Williams, 1995). Recent findings about the beneficial roles of nonessential micronutrients, such as polyphenols and carotenoids, to health have led to greater needs for more sophisticated analytical methods. In addition to chemical components, live microorganisms, such as those in fermented foods like probiotic yogurt, can also be a target of the analysis. All these contribute to the increased complexity of the food systems that are analyzed. To gain a meaningful insight into the analysis of these compositions, the aforementioned macronutrients and micronutrients are briefly discussed in this section.

Water

Water, the most abundant substance in nearly all food, plays an important role in the food system. Even pure substances such as sugar and salt contain a small amount of water absorbed on the surface of the crystal. Moisture content is one of the quality factors for food products, especially for dried goods such as milk powder, dehydrated vegetables and fruits, and flours. A reduced moisture content is beneficial for the packing and transportation of food (Slade *et al.*, 1991), as it inhibits microbial growth. However, certain amount of water is essential to make a food fresher and tender.

Moreover, water may be present in the food system as free liquid in which nutrients are dissolved, hydrated, imbibed in gels, or adsorbed on the surfaces of other materials (Levine and Slade, 1991). A method for moisture analysis must therefore depend upon the form of the water present as well as the amount in a particular food.

Carbohydrates

Carbohydrates are an important nutrient that supplies abundant energy and serves as a source of many physiologically active compounds. In general, carbohydrates are divided into three subgroups: monosaccharides, oligosaccharides, and polysaccharides. Carbohydrate analysis is a key quality assurance tool for food processing, not only because it ensures that the amount of ingredients added into the food meet the standards or claims on the label, but it is also a means to detect food deterioration. Moreover, low-caloric sweeteners, such as sugar alcohols and rare sugars, D-psicose and D-tagatose, became increasingly important to consumers and the need for specific analytical methods for these carbohydrates has also been recognized. Another significant outcome of carbohydrate analysis is calorie calculation.

Proteins

Like other biological macromolecules such as polysaccharides and nucleic acids, proteins are vital to the metabolism of all living organisms. Proteins play an essential role in the tissue of live animals and carry out various functions, such as actin and myosin, which are contractile proteins essential for movement and locomotion.

Proteins consist of one or more chains of amino acids, and they differ from one another primarily in the sequence of amino acids. Proteins can be hydrolyzed into polypeptides or amino acids by proteases. Amino acids are essential nutrients, and some are supplemented in foods in both natural and synthetic forms (Ikeda, 2003). Quantitative and qualitative analyses of amino acids are important to the food industry in general, but are especially critical for quality assurance in the amino acid industry.

However, for protein molecules their function depends on the specific three-dimensional structures that are easily altered by physical, chemical, and biological factors like heat,

presence of organic solvents, and microorganisms. Functional properties of proteins are, therefore, also an important element of protein analysis (Hall, 1996). Methods commonly used to analyze protein structures and functions included those based on site-directed mutagenesis, nuclear magnetic resonance, X-ray crystal diffraction, and mass spectrometry (MS) (Cavanagh *et al.*, 2010; Ladd and Palmer, 2003; Whitford, 2005; Zhang and Smith, 1993). As such, proteins are often purified using a wide range of techniques such as ultracentrifugation, precipitation, chromatography, and electrophoresis (Janson, 2012).

Nutritive value of a protein also needs to be evaluated apart from amino acid composition, protein content, and protein structure and function. The most commonly evaluated parameters are the amino acid score (AAS), net protein utilization (NPU), true digestibility (TD), and biological value (BV) (Owusu-Apenten, 2002).

Lipids

Lipids are essential to living organisms because they contribute to vital metabolic processes in cells. Fats such as butter and lard are derived from animal products such as milk and meat, whereas oils such as soybean oil, peanut oil, and olive oil are derived from plants. Lipids can be categorized into two classes: saturated and unsaturated, which are dependent on the fatty acid backbone of the triacylglyceride. Melting points of saturated fatty acids are higher than those of unsaturated fatty acids. Therefore, most animal fats with a high content of saturated fatty acids are in the solid form at room temperature, whereas lipids from plants such as olive oil are liquid on account of the higher content of unsaturated fatty acids.

The taste, flavor, and nutritional value of food, as well as the health of humans, are affected by the variety and quantity of the lipids, because of the potentially toxic oxidation byproducts of lipids (Kubow, 1992). In addition, some mono- and polyunsaturated fatty acids can help reduce the risk of human chronic diseases beyond their basic nutritional functions (Jew *et al.*, 2009). An accurate and precise analysis of total and individual lipids is essential for the development of safe and high-quality foods and functional foods.

Minerals

What makes minerals different from organic nutrients is that minerals cannot be synthesized or decomposed in a biological system like the human body. According to the requirement of minerals by living organisms, they can be categorized into macrominerals such as calcium, potassium, phosphorus, and trace minerals like iron, iodine, and zinc (Faller *et al.*, 2004). Although the requirement of trace minerals is low, they are very important for metabolism. Minerals are obtained through food, and those necessary in maintaining healthy metabolism are called essential microelements. In some cases, fortification is allowed in the diet. Mineral analysis is of great significance but highly challenging for evaluating the nutritional value, potential toxicity, and food safety, especially for the trace elements in food. Modern instrumentation plays an important role in obtaining accurate, precise, and sensitive results in mineral analysis.

Vitamins

A vitamin, including fat-soluble and water-soluble vitamins, is defined as an organic compound present in minute amounts in natural foodstuffs that are required by humans or any other organisms as a vital nutrient at low concentrations (McDowell, 2008). Insufficient levels of vitamins result in hypovitaminosis or avitaminosis.

Many vitamins are lost or decomposed during food processing. Monitoring the stability and reducing the loss of vitamins in raw and prepared foods or food supplements thus requires accurate and sensitive analytical methods. Such methods are also important for assessing dietary adequacy.

Dietary Fibers

Dietary fibers, including soluble and insoluble ones, have special physiological functions such as protecting against colon cancer, lowering the cholesterol absorbed, reducing the risk of obesity, and cardiovascular diseases. Research has shown that dietary fibers changed the microbial contents of the gastrointestinal tract in favor of the growth of beneficial bacteria against the pathogenic ones (Eastwood and Kritchevsky, 2005).

Physicochemical and Biological Properties

Energy

Food energy is defined as the energy released from carbohydrates, fats, proteins, and other organic compounds. When the three major calorigenic nutrients (carbohydrates, fats, and proteins) in a food are burnt entirely with sufficient amounts of oxygen, it releases energy or food calories that are expressed in kilojoules (kJ) or kilocalories (kcal). Food energy is usually measured by a bomb calorimeter based on the heat of combustion (Insel *et al.*, 2012).

Energy released by a particular food is a critical parameter in nutrition. Several chronic diseases such as obesity, diabetes, and cardiovascular disease have been considered to be caused by excess energy intake. All food manufacturers are now required to label the energy of their products to help consumers control their energy intake. Fats have the greatest amount of food energy per mass, up to 9 kcal g^{-1}. Most of the carbohydrates and proteins have approximately 4 kcal g^{-1}, whereas fibers have less due to its low digestibility and absorbance in human bodies (Insel *et al.*, 2012). Restricting long-term consumption of high-energy foods rich in fats and sugar can reduce the incidence of obesity and other diseases.

pH and Acidity

There are two indicators of food flavor and quality: pH and acidity. Most common organic acids in foods are just partially ionized. In food processing, optimization of flavor and taste, and improvement of formulations are often done by controlling the pH and the acidity, which are also important for effectively inhibiting the activities of enzymes and the growth of microorganisms, ultimately improving the food quality and

prolonging the shelf-life of the product (Brown, 2010; Vaclavik and Christian, 2003).

Texture

The texture of the food is its physical and chemical interaction in the mouth and can directly correlate to food rheology. Food texture encompasses hardness, smoothness, thickness, and other mouth-feel characteristics (Lawless and Heymann, 2010). Food is constantly evaluated, from the initial impression when the product touches the palate, until the aftertaste. Physical properties that contribute to the texture of a food are now widely used to represent the state and taste of that respective food. The collective expression of food texture through such properties at present is measured using mechanics and by visual and auditory methods.

Food texture has been used to: (1) explain food structural characteristics; (2) explain changes of physical properties of a food during processing and cooking processes; (3) improve food quality and unique characteristics; (4) explore the relationship between sensory analysis and the instrumental measurement(s).

Rheological Properties

Like texture, rheological properties are also one of the significant assessment criteria of food quality. The rheological properties of food, such as consistency, viscosity, and elasticity, are very important factors and are used to evaluate the stability of a food during processing, and the shelf-life during storage (Herh *et al.*, 2000). A proper design of food formulation can therefore improve the shelf-life and sensory characteristics by measuring the rheological properties.

Foods can be classified into solid, liquid, emulsion, and gel according to their rheological state (Rao, 2007). However, due to the complex structural features of different food components, a food often appears to be a mixture of solid and fluid with varying properties. Rheological properties of a complex food matrix are obtained through disciplinary approaches, using theoretical and experimental information to gain a better understanding of various properties of food materials.

Color

Whether or not people decide to buy a food depends, to a large extent, on the appearance of the product, among which the most important factor is color, and seems to have an innate allure that gives people the first impression and the greatest influence on our judgment (Potter and Hotchkiss, 1998). For consumers, the most intuitive feeling for products is the color.

Improving and maintaining color stability is one of the most important practices in food processing. Colorants are often added into products in the food industry to enhance the appeal of foods. Natural pigments are normally not required to be certified before they are added to foods because they are generally considered to be safe (Ronzio, 2003). Naturally derived pigments are typically more expensive than certified synthetic colorants and may add unintended flavors to foods. However, certified colorants are synthetically produced and are used widely because they are less expensive, as well as they impart an intense, uniform color, and blend more easily in food to create a variety of hues (Potter and Hotchkiss, 1998). Under these circumstances, the levels of colorants added should be monitored to ensure that appropriate regulatory guidance is complied with.

Flavors

People enjoy the products with good flavor which can, in turn, affect the digestion and absorption of nutrients. Flavor is just the sensory impression of a food mainly caused by the chemical senses. In general, the chemical senses are divided into two types: taste and smell. Sour, sweet, bitter, piquant, salty, umami, and metallic are the seven basic tastes, whereas smell is only limited to fragrance and stink (Jeleń, 2011; John, 1995).

A flavor is determined by a mixture of several compounds in most foods. If one or several compounds represent the characteristic flavor of a particular food, these are considered as the characteristic or key compound(s). These substances have the properties of poor stability, small quantity, and vulnerability (Philippe *et al.*, 2003).

Flavoring can be practices that are used to prevent undesirable flavors produced during treatment, storage, and processing of food, or to create desired flavors for specific products such as candies and other snacks. Natural or artificial flavorants alter the taste of the food itself. Most commercial flavorants used in the food industry are chemically synthesized rather than extracted from native materials, as artificial flavorants are much less expensive and more available (Chandrashekar *et al.*, 2006). As a result, in food industries, flavor analysis must be performed to ensure food quality and safety.

Sampling and Sample Preparation

Sampling

Food analysis always starts with sampling which is the process of taking a representative fraction from a large collection of a particular product or item, for example, a small quantity from a full production batch.

Before sampling, the objective and target analytes or properties of a food must be well established and understood, so an appropriate sampling method is determined for reliable results. There are two methods of sampling: random sampling and representative sampling. Opportunities for drawing any individual sample from the population in the process at random must be equal (Rana, 2008).

Sample Preparation

To eliminate the interference of other components, and increase the concentration of the target components, samples are often pretreated before analysis. Sample preparation also increases uniformity thus leading to better extraction

efficiency. Below are some commonly used sample preparation methods:

Methods for removal of organic compounds

These methods are mainly used for the determination of inorganic elements. The inorganic elements of the food often bind tightly with organic compounds such as proteins. Therefore, organic compounds are removed to reduce/eliminate potential interference. The details are discussed in the Section Ash Content Analysis.

Solvent extraction

Solvent extraction is commonly used to remove unwanted components by taking the advantage of significantly different solubilities between the analytes and interfering compounds. Solvent extraction methods include lixiviation, supercritical fluid extraction (SFE), ultrasonic extraction, microwave-assisted extraction, and solid phase extraction.

Chromatography

Although modern chromatography has been largely instrumentalized and automated for analytical purposes, some manual are still widely used in sample cleanup and preparation, and more details are discussed in the Section Chromatography.

Grinding

For sample preparation before analysis, grinding is important. It reduces the particle size of solids and semisolids, and improves the uniformity and increases extraction efficiency of the sample. Various mills are available for reducing the particle size to achieve sample homogenization.

Other methods

Concentration: Concentration reduces sample size and enriches the target components to make the samples easier to be analyzed. Concentration of liquid samples is done by evaporation under vacuum or atmospheric pressure.

Distillation: Distillation, including air distillation, reduced pressure distillation, and steam distillation, separates analytes from the interfering components based on their different boiling points. Usually, no reagents are needed during this process.

Precipitation: The appropriate chemical agents, such as basic copper sulfate, isolate the target components or interfering compounds by settling them out of solution. Filtration or centrifugation is carried out to either recover the precipitate or the supernatant for analysis.

Masking: A masking agent is added to bind selectively to an interfering component; therefore, only the analytes are available for extraction or further analysis.

Sulfonation and saponification: These two methods are used to remove lipids from samples.

Sample Preservation

Ideally, all samples should be analyzed upon arrival at the laboratory. However, more often than not, samples are stored before analysis. In the latter case, samples must be kept under appropriate conditions. Light, oxygen, temperature, and moisture are the major factors that cause deterioration of the sample and the analytes. Exposure to light and oxygen (air) leads to oxidation including photodegradation of compounds, for example, riboflavin and carotenoids. Temperature and moisture affect microbial growth and enzyme activity in the samples. Preservatives and antioxidants can be added into the samples on the condition that they will not affect the analysis results. Freeze-drying and ultralow temperature are good preservation techniques for samples that cannot be analyzed timely. Proper preservation methods must be chosen based on the probability of contamination, storage time, and the target analytes.

Enzyme inactivation

Raw food material often contains endogenous enzymes, which may decompose the primary elements, that is, proteins, thereby leading to interference upon analysis. Therefore, these enzymes must be eliminated or controlled. In general, thermal treatment is the most common method to inactivate enzymes. Sometimes, samples are frozen during storage to limit enzyme activities. However, activities of some enzymes are more effectively regulated by changing the ionic strength or pH.

Lipid oxidation protection

Unsaturated lipids are protected through storage in vacuum or under nitrogen, as they are sensitive to oxidative degradation. Lipids may be stabilized by antioxidants that could be used upon analysis (Kadoya, 1991). Low-temperature storage is suitable for protecting most foods. Light-initiated photooxidation of unsaturated lipids are avoided by being stored in the dark. Containers for lipid samples should be free of any transition metals as these ions are catalysts for lipid peroxidation.

Microbial growth inhibition

Microbial contamination can occur during sampling and even processing for analysis; therefore, efforts must be made to avoid exposure to microorganisms at each step between sampling and analysis. Freezing, drying, and chemical preservatives are effective controls and often a combination of these are used (Nielsen, 2010b).

General Analysis Methods

Moisture Analysis and Water Activity Measurement

Oven drying: The moisture content of the samples is calculated by the loss of weight. The loss of moisture from a sample is a function of time and temperature in the process of analysis. Sometimes, the components in the food may be decomposed at a higher temperature; while the volatile constituents, such as acids, alcohols, and other flavor compounds, may also be lost. Moisture content can be calculated using oven drying procedures, such as the following (Nielsen, 2010b):

$$\%\ \text{Moisture content (wt/wt)} = \frac{\text{wt } H_2O \text{ in sample}}{\text{wt of wet sample}} \times 100 \quad [1]$$

$$\%\ \text{Moisture content (wt/wt)} = \frac{\text{wt of wet sample} - \text{wt of dry sample}}{\text{wt of wet sample}} \times 100 \quad [2]$$

Oven-drying methods generally include air, vacuum, microwave, and infrared drying. Drying under reduced pressure leads to more efficient and complete removal of water and volatiles, less decomposition, and reduced drying time. Microwave drying, in which the samples must be uniform, centrally located and evenly distributed in order to prevent uneven heating of the sample, has the advantages of rapidity and accuracy. Infrared drying techniques are more suited for qualitative online processes, because of the rapidity of analysis: however it has not yet been approved by Association of Official Analytical Chemists.

Distillation: The principles have been discussed in the Section Sample Preparation. Distillation causes less thermal decomposition of some foods compared with oven drying at high temperatures.

The Karl Fischer Method: The principle of the Karl Fischer method is schematically based on the following oxidoreduction reaction:

$$SO_2 + I_2 + 2H_2O \rightleftarrows 2I^- + 4H^+ + SO_4^- \quad [3]$$

Others: Infrared (IR) spectroscopy (see Section Infrared spectroscopy) has been successfully used in the laboratory and in online applications. For water, the –OH stretching at 1400–1450 nm and 1920–1950 nm (near-IR (NIR) bands) are characteristic (Ozaki *et al.*, 2006; Workman and Weyer, 2007). Dielectric method is used to determine the moisture content by the electrical properties of water. Hydrometry is still widely used for routine analysis of moisture (or solids) content of numerous products. Refractometry is used commonly to measure the content of moisture in liquid sugar products with the characteristics of convenience, rapidity, and surprising accuracy. It is also used online to monitor the Brix of products in real time.

Water activity: Water activity (a_w) is one of the most important physicochemical properties for predicting the growth and the survival of microorganism in foods. In addition, it significantly affects lipid oxidation, endogenous enzyme activity, and nonenzymatic browning reactions. a_w is a thermodynamic concept, defined as the vapor pressure of a liquid divided by that of pure water at a given temperature. More details are in the reference (Barbosa-Cánovas *et al.*, 2008).

There are various techniques to measure a_w, among which are the portable water activity meters. As shown in **Figure 1**, the developed portable water activity meters that are widely used in the food industry can yield accurate measurements in less than 5 min, where the reading is directly displayed on the screen of the instrument.



Figure 1 AquaLab 4TEV water activity meter.

Ash Content Analysis

Ash is the inorganic residue after all organic components of a food sample are burnt. Two major types of ash analysis are used: dry ashing, which is primarily used for specific mineral analyses and wet ashing, a method based on completely oxidizing organic compounds using chemical agents. Before ashing, drying and degreasing must be done, especially for high-fat products. The ash content of foods is expressed on either a wet or a dry weight basis.

Dry ashing refers to the method of burning organic substances completely in the presence of oxygen by using a muffle furnace capable of maintaining temperatures of 500–600 °C, at which water and volatiles are vaporized (Sharma, 2006). Most minerals are converted into oxides, sulfates, and other inorganics. This method requires no reagents, as well as, little attention during combustion, but the drawback is that it is time consuming and losses may occur for some volatile elements and mineral components that may interact with crucibles. Strong acids or other oxidizing agents, or their combinations are used in wet ashing. During the procedure of wet ashing, minerals are solubilized in a solution, and because it is done at an ambient temperature, no loss occurs from volatilization (Aras *et al.*, 2006). This is a faster method because of the quick oxidation time.

Recently, a novel method called microwave ashing has been developed (Nollet and Toldrá, 2012). Assisted by a microwave instrument, both dry ashing and wet ashing can be done. The microwave-assisted method is mainly used for accelerating the digestion of samples.

Carbohydrate Analysis

Total carbohydrates

Carbohydrates can be destroyed by the addition of a strong acid and/or high temperature, where various furan derivatives are produced. The furan derivatives react with phenols to produce reaction products that can be conveniently measured by a spectrophotometer. This method, namely, phenol-sulfuric acid method, is rapid, simple, sensitive, accurate, and specific for carbohydrates, and widely applied (Chandrasekaran, 2012). The reagents are also readily available, inexpensive, and stable.

Total reducing sugar

Reducing sugars naturally existing in foods or released by enzymes are determined by the dinitrosalicylic acid method. In this reaction, 3,5-dinitrosalicylate is changed to the reddish monoamine derivative, which can be measured by a spectrophotometer. This reaction is not stoichiometric and must be determined with a standard curve of D-glucose (Robyt, 1998). Another often used is the Somogyi–Nelson method. It is also used for the determination of oligo- and polysaccharides (Chandrasekaran, 2012).

Mono- and oligosaccharides

Mono- and oligosaccharides such as D-psicose, difructose anhydride III and oligofructose are commonly analyzed using high-performance liquid chromatography (HPLC) (Zhang *et al.*, 2009; Zhao *et al.*, 2011, Hocine *et al.*, 2000). HPLC identifies individual sugars with specific retention times and gives quantitative results with peak integration. It is a rapid, precise, and accurate method for a wide range of samples.

Ionic-exchange, normal-phase and reversed-phase chromatography are widely used for the analysis of sugars in different foods such as honey, beverage, cakes, and ice creams. In anion-exchange chromatography, the general elution sequence is alditols, monosaccharides, disaccharides, and higher oligosaccharides (Nielsen, 2010b). The elution order is reversed in cation-exchange chromatography (Rassi, 1994). In normal-phase chromatography, the stationary phase is the silica gel derivatized with amino groups, and acetonitrile water (50–85% acetonitrile) is a commonly used mobile phase. The elution order is monosaccharides and sugar alcohols, disaccharides, and higher oligosaccharides. In the reversed-phase chromatography, the hydrophobic stationary phase is silica gel with alkyl chains or phenyl group, such as a C18 column or phenyl column. It is used for the analysis of mono-, di-, and trisaccharides (Nielsen, 2010b).

Thin-layer chromatography (TLC) has been used for the analysis of mono- and oligosaccharides. Although it provides both quantitative and qualitative information of the sugars, TLC is not as sensitive and accurate as HPLC. More information in detail is provided in the reference (Sherma and Fried, 2003).

Starch, food gum, and dietary fiber

The starch content is determined by the amount of D-glucose released from the hydrolysis reaction by purified enzymes specific for starch. The enzymes for starch hydrolysis must be purified to prevent the release of D-glucose by other enzymes. For example, cellulose can be converted into D-glucose by cellulases. The presence of nonstarch specific enzymes can cause an overestimation of the total starch content.

The degree of gelatinization of starch is measured by a combination of pullulanase and β-amylase, which is particularly sensitive and only able to act on gelatinized or pasted starch. The determination of the content of food gum, like pectin, is discussed in detail in the reference (Nielsen, 2010b). Dietary fiber is usually determined gravimetrically. The Prosky method is the principal procedure, which measures both soluble and insoluble fiber. The Englyst-Cummings method is used for the chemical measurement of dietary fiber (Shils, 2006).

Protein Analysis

Kjeldahl method: In the Kjeldahl procedure, after digestion in concentrated sulfuric acid, the total organic nitrogen is converted to ammonium sulfate. Ammonia is formed and distilled into boric acid solution under alkaline conditions. The borate anions formed are titrated with standardized hydrochloric acid, by which is calculated the content of nitrogen representing the amount of crude protein in the sample. Most proteins contain 16% of nitrogen, thus the conversion factor is 6.25. However, the nitrogen from nonprotein additives or contaminants in the food, such as melamine in milk, is also measured.

Biuret method: Under alkaline conditions, peptide bonds react with cupric ions to produce a violet-purplish color, the intensity of which at 540 nm is correlated to the protein content of the sample (Owusu-Apenten, 2002). This method is quick and simple with little interference from nonpeptide or nonprotein sources.

Lowry method: The Lowry method is developed based on the biuret method. Proteins react with Folin–Ciocalteu phenol reagent to produce a blue conjugate at 750 nm. The intensity of color is proportional to the protein content of the sample (Owusu-Apenten, 2002). Although this method is very sensitive, it is interfered by sucrose and lipids.

Ultraviolet 280 nm Absorption Method: Proteins, at 280 nm, show strong absorption primarily for tryptophan and tyrosine residues. This technique is mainly applied in a purified protein system, because absorbance will be falsely increased if particulates or other substance like nucleic acids are in the solution (Scopes, 1994). This method is noninvasive; thus samples can be used for other analyses after protein determination.

Other methods: In addition to the aforementioned methods, the Dumas, IR spectroscopy, bicinchoninic acid, anionic dye-binding, Bradford dye-binding, Ninhydrin, and immunological methods are some other techniques commonly used for protein analysis (Nielsen, 2010b; Owusu-Apenten, 2002; Ozaki *et al.*, 2006). Choosing an appropriate method depends on the properties of proteins present in the samples as well as the characteristics of analytical approaches.

The nutritional value of a protein is determined by the amino acid composition and the digestibility of that protein. The most common parameters for protein quality are the AAS, BV, TD, and NPU. The procedure for calculation is further elaborated in the reference Owusu-Apenten (2002).

Lipid Analysis

Solvent extraction method: The total lipid content of a food is commonly determined by its organic solvent extract. The choice of solvents is highly critical for total fat analysis. The most commonly used solvents are ethyl ether and petroleum ether, but pentane and hexane are used for extracting oil from soybeans. In addition, lipids in food may be conjugated with proteins and polysaccharide; thus, a successful extraction requires that the lipids be freed by alkaline or acid hydrolysis and then extracted into the organic solvents. The Goldfish method is commonly used as a continuous solvent extraction approach. In this procedure, solvent from a boiling flask continuously flows over the sample. Fat content is measured by the weight of fat loss of the sample. Soxhlet method is a semicontinuous solvent extraction approach. In this procedure, the sample is soaked completely for 5–10 min in a solvent and then siphoned back into the boiling flask. A commercial Soxhlet apparatus is shown in **Figure 2**. The Mojonnier test is an example of the discontinuous solvent extraction method. SFE (Anklam *et al.*, 1998) is a relatively

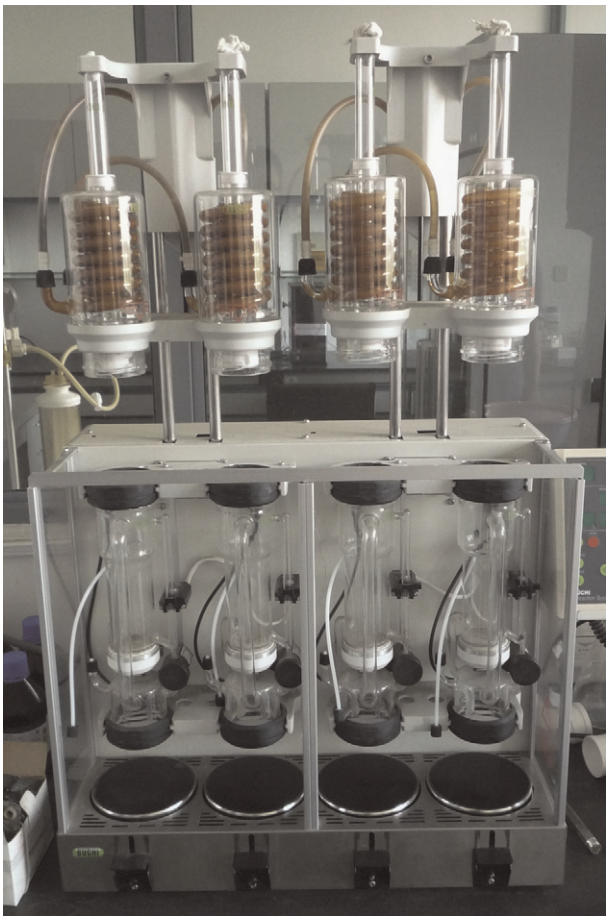


Figure 2 Soxhlet extraction apparatus.

new solvent-free technology developed to replace or reduce the use of toxic organic solvents.

Nonsolvent wet extraction methods: The Babcock method and Gerber method are commonly used for milk fat analysis. In these procedures, carbohydrate and protein are removed by centrifugation after addition of H_2SO_4. Milk fat is separated and measured volumetrically, and the result is expressed as a percentage of fat by weight.

Gas chromatography (GC): GC is the most sensitive and accurate method for fat analysis. A triglyceride, triundecanoin (C11:0), is added as an internal standard. More information is in the Section Gas chromatography.

Other methods: Details of some other methods such as IR, specific gravity, nuclear magnetic resonance, and ultrasonic method can be found in the reference (McDonald and Mossoba, 1997).

In addition to the total lipid content, physicochemical properties of the lipids in a foodstuff, such as stability and safety of fats, are also important to be characterized. Refractive index, melting point, smoke point, flash point, fire point, and cloud point are commonly measured. Degree of unsaturation of fats or oils is indexed by the iodine value. Higher iodine value is indicative of a higher degree of unsaturation. Saponification is an alkaline hydrolysis process by which neutral fats (triglycerides) break into glycerol and fatty acids. Saponification value is an index of the mean molecular weight of the triacylglycerides in the samples. The amount of fatty acids hydrolyzed from triacylglycerides is reflected by the acid value. Peroxide value tests the peroxide products after lipid oxidation. The thiobarbituric acid test measures the secondary products of lipid oxidation, primarily malondialdehyde. Details on these and other indexes also can be found in the reference (Nielsen, 2010b).

Mineral Analysis

Atomic absorption spectroscopy is the most commonly used method for mineral analysis, and it will be discussed in detail in the Section Atomic absorption and emission spectroscopy. Inductively coupled plasma MS (ICP-MS) is introduced in the Section Raman spectroscopy. Only traditional titration methods are briefly introduced here.

Gravimetric analysis: This method is only for insoluble minerals. The mineral content of the sample is weighed after proper precipitation, washing, and drying. It is not suitable for the determination of trace elements.

Ethylenediamine tetraacetic acid complexometric titration: Ethylenediamine tetraacetic acid (EDTA) forms stable 1:1 complexes with numerous mineral ions except alkali metals, and this principle has been the basis of the widely used complexometric titration. The endpoint of a complexometric EDTA titration is the color change from pink to blue using either Calmagite or Eriochrome black T as the indicator (Nielsen, 2010a).

Precipitation titration: It is well suited for any foods that may be high in chlorides (Dieter and Multon, 1997). However, it ultimately has few applications in the analysis of food.

Colorimetric methods, redox reaction, and ion-selective electrodes may also be used in mineral analysis (Nielsen, 2010b). These procedures generally require only inexpensive chemicals and equipment readily available in an analytical laboratory.

Vitamin Analysis

HPLC, owing to its simplicity, and good accuracy and precision, is a preferred method for vitamin analyses (Leenheer and Lambert, 2002; Nollet, 2012). HPLC is suitable for most lipid-soluble and water-soluble vitamins such as vitamins A, C, D, and E and the B vitamins, respectively. Liquid chromatography (LC) in combination with MS is particularly useful for vitamin analysis. Detection by LC–MS leads to increased sensitivity as well as unequivocal identification and characterization of vitamins. In addition to the UV/Vis or diode array detector, fluorescence spectroscopy detector is also used in HPLC, especially for B vitamins such as thiamin (vitamin B_1).

Physicochemical Analysis

pH and Acidity

In food analysis, pH is different from titratable acidity, but there is a close relationship between them. Titratable acidity indicates the total acidity contained within a food, whereas pH only means the free H_3O^+ concentration. Total acids, which give

more impact on flavor, are determined by exhaustive titration of the intrinsic acids with a standard base. The growth of microorganisms is more dependent on pH than total acids. In nature, the value of pH can span from 1 to 14 orders of magnitude.

pH is usually determined using a pH meter or pH indicator. Titratable acidity is determined by neutralizing the bases present in the sample using a standard acid. When the color of a pH-sensitive dye changes suddenly, the titration reaches the endpoint. The endpoint of the target pH is identified by the pH meter. The advantage of the potentiometric method is that the precise equivalence point is identified. The titration of acids or bases is also determined by the conductometric method, which is also applied for the determination of halides, sulfides, and mercaptans (Paré and Bélanger, 1997).

Thermal Analysis

A set of physical properties of foodstuff and food products, such as texture and storage stability, can be analyzed by thermal analysis, which provides information on the structures and qualities of the material. Thermogravimetric analysis (TGA) and differential scanning calorimetry (DSC) (Nielsen, 2010b; Pomeranz and Meloan, 2002) are two typical methods in thermal analysis.

Thermogravimetric analysis: TGA measures the thermal or oxidative stability of the components of the samples. When samples are heated from room temperature to 1000 °C or higher, even small weight changes due to the decomposition of components are detected by TGA instruments (**Figure 3**). However, it does not identify the gaseous compounds evolved from the sample.

Differential scanning calorimetry: DSC can measure structures such as amorphous, crystalline, or semicrystalline components of food, based on the fact that structural changes occur as a result of heat absorption or release (**Figure 4**). It is perhaps one of the most useful of the thermal techniques for identifying the structures and their changing characters.

Texture and Rheological Analysis

There are no better ways to quantify the sensory properties of a product in the mouth than by measuring the physical properties related to the sensory texture of foods. These properties are determined by rheological methods and texture analysis. Instrumental and physiological methods are used to determine a food's quality and structural characteristics, thus providing a more accurate description of a product, which subsequently can help control the quality and structure of food.

Viscosity and other rheological properties of materials are determined by rheometers. Viscosity for fluids is the most important parameter, providing rapid and fundamental information. Some common foods exhibit ideal Newtonian flow: however, the majority of fluid foods exhibit pseudoplasticity. If the viscosity of a material increases in response to increased rate of shear strain, such as cornstarch slurry, the material is called a dilatant (Rao, 2007; Steffe, 1996). The rheological properties of solid foods are determined by extending, compressing, or twisting the samples. The process, by which samples are significantly deformed, strained, damaged, or possibly fractured by mechanical forces, simulates the process of chewing resulting in the change of food texture in the mouth (Bourne, 2002).

Texture profile analysis (TPA) is an important technique using the texture analyzer. Numerous sensory parameters, including hardness, springiness, and cohesiveness, are determined by the TPA test (Bourne, 2002). For example, sample hardness has been strongly related to the highest force fracturing the sample. **Figures 5** and **6** show rheometer and texture analyzer, respectively.

Color Analysis

The concept of color is defined as the sensation that can be interpreted by our brain. In chromatology, the Munsell system is probably the best known and the most widely used one (John, 1995; Lawless and Heymann, 2010). A food color can be mathematically represented by the International



Figure 3 TGA Spirit Drinks Trade Act (SDTA) 815.



Figure 4 DSC Q2000.



Figure 5 ARES-G2 rheometer.

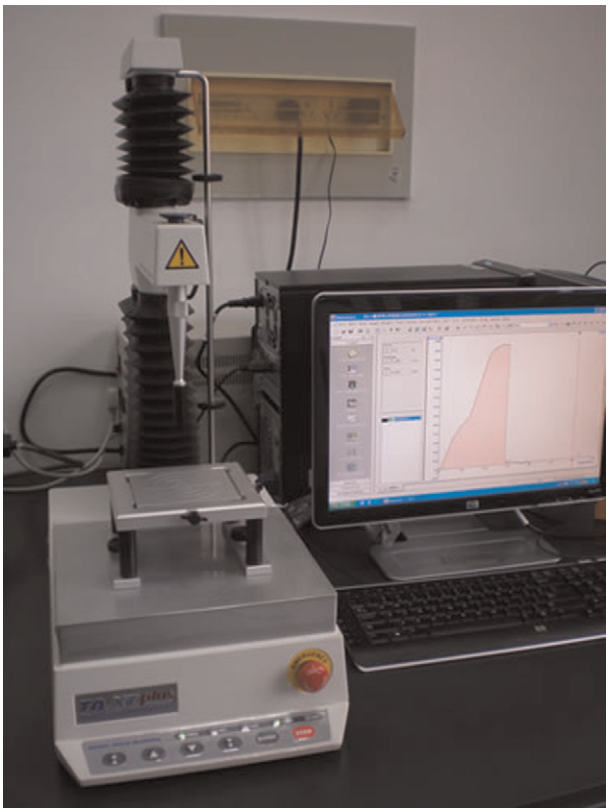


Figure 6 TA XT plus texture analyzer.

Commission on Illumination tristimulus values, although such values are difficult to be directly related to the observed color.

The colorimeters are commercially available today. They are portable, online for process control, and specialized for specific commodities. However, quantitative analysis of artificial and natural colorants has been a great challenge in food processing. The properties of colorants and their derivatives and the interaction between colorants and other components make the qualitative and quantitative analysis very complex. Sometimes, especially in thermal processing, colorants are difficult to be extracted. In addition, they are also sensitive to oxygen, heat, light, and metal ions. The common methods for colorant analysis are stand-alone UV–Visible spectrophotometry and HPLC using a UV–vis detector. More details are discussed in MacDougall (2002).

Sensory Analysis

Sensory analysis combines experimental methods and statistical analysis for the purpose of evaluating food products using human senses (sight, taste, smell, touch, and hearing). It greatly depends on the sensation of the assessors, which is related to the psychological factors at that time (Carpenter *et al.*, 2000). It is possible to make inferences about the quality of products under test by applying statistical methods to the results.

The sensory testing environment is vital to the perception of analysts, because they more or less cause specific physiological sensations/ characteristics. According to standardized procedures, sensory specialists need to be very careful in experimental design, selection of protocols, and preparation of samples before testing. The visual appearance, such as size, shape, the quantity, and even the container of the samples should be decided carefully. There are many methods for designing experiments; the experimental design is divided into two basic structures, namely treatment structure and design structure (Lawless and Heymann, 2010).

In the process of testing, people's sensory opinions of food is collected and described. Normally, the number of experts should not be less than five. Further details regarding sensory analysis can be found in these references (Carpenter *et al.*, 2000; Chambers, 1996; Lawless and Heymann, 2010).

Biological Analysis

Enzyme Application

Enzymatic analysis involves the measurement of the activity of specific added commercial enzymes and/or endogenous enzymes, which can be used to indicate the quality of food. The enzyme reactions require less reaction time and cost less in contrast to complicated chromatographic separation techniques.

There are several uses of enzymes in food science and processing. For instance, peroxidase and lipoxygenase, two endogenous enzymes found in vegetable products, are used as a measure of adequacy of blanching (Fennema, 1996). In addition, glucose content in the presence of other reducing sugars can be determined by the combination of the glucose oxidase (GOX) and catalase in a food system (Aehle, 2007). It

is a useful tool in determining the amount of glucose because of the GOX specificity for glucose.

Immunoassays

Immunoassays are widely used for food toxins such as pesticide residues, mycotoxins, process-induced toxins and drugs, identification of bacteria and viruses, and detection of allergens in food, which attribute to their high specificity, sensitivity and simplicity (Tothill, 2003).

Enzyme-linked immunosorbent assay (ELISA) is a common immune analytical technique based on the high and specific affinity binding of particular target antigens with antibodies. Horseradish peroxidase and alkaline phosphatase are most commonly used in immunoassays, because these enzymes can convert colorless substrates to colored soluble products in order to generate the detectable signals for the assay. Western blot is another common method that combines two techniques: polyacrylamide gel electrophoresis (PAGE) and immunoassay.

Food Contaminants and Residues Analysis

Microbiological Analysis

Food products may be exposed to potential risks of microbial contamination during the process of production, transportation, and at the point of sale.

Traditional methods for the detection and identification of microorganisms in food largely depend on the culture method. A general strategy to detect specific microorganisms is to identify first the target organism and determine the nutritional requirements for the optimal growth of the target microorganism. Optimum incubation conditions including temperature, time, and atmosphere are then established (Lund and Baird-Parker, 2000). Finally, assessment of the performance against an established method using contaminated foodstuff is carried out.

In recent years, with the rapid advancement in molecular biology and microelectronics technology, faster, more accurate and specific testing methods have emerged as novel alternative tools for the identification of microorganisms. The following is a few examples of the new technologies:

Electrical impedance method: During the growth of bacteria, the inert macromolecules such as carbohydrates, proteins, and lipids in the culture medium will degrade into electrically active small molecules such as lactate and acetate, which can increase the conductivity of the medium, causing changes in the impedance of the medium. Detection of such changes can be used as an indicator of the growth and characteristics of the corresponding bacteria in the medium (Harrigan, 1998). It has been used for the detection of the total number of bacteria, fungi, yeast, *Escherichia coli*, *Salmonella*, and *Staphylococcus aureus*.

Nucleic acid probe technology: The nucleic acid probe, marked with specific deoxyribonucleic acid (DNA) fragments, is used to hybridize with target DNA, specifically. The probe can be labeled using either radioactive or nonradioactive labeling. The nonradioactive labels can be biotin, digoxigenin, fluorescence labeling, and immunolabeling (Harrigan, 1998; Jay, 1996). This method has been successfully used in the detection of *Salmonella* and *Listeria*.

Polymerase chain reaction technology: It can detect *Salmonella*, *E. coli* O157, and *Listeria monocytogenes* (Patel, 1994): Although it requires special equipment, polymerase chain reaction is a novel technology that has the advantage of being rapid, sensitive, accurate, and is the promising method for detecting microorganisms in the future.

Enzyme-linked immunosorbent assay: The principal of ELISA, in detail, is given in the Section Immunoassays. The amount of aflatoxin is usually measured by this technology.

Pesticide and Veterinary Drug Residue Analysis

Pesticides in food can be herbicides, insecticides, fungicides, acaricides, molluscides, nematicides, pheromones, plant growth regulators, repellents, and rodenticides. Results of pesticide residue analyses are influenced by several factors including food components, the physical and chemical properties of the pesticides, and the interaction between the food matrix and the pesticide molecules. A wide range of analytical methods has been used in pesticide analysis. The enzyme inhibition assays and immunoassays are commonly used for the measurement of pesticides. Testing kits are also commercially available. Pesticides with enzyme-inhibitory activities will develop color; thus their residues can be quickly detected using these methods. Chromatographic techniques, including TLC, GC, HPLC, GC–MS, and LC–MS, are widely used in the analysis of pesticides. Details of these techniques are discussed in Sections Mass Spectrometry and Chromatography.

Veterinary drugs are used to reduce the risk of disease outbreak in the animal population. In addition, they are used to promote animal growth and increase feed conversion in animals (Picó, 2008). A wide variety of analytical methods have been developed and optimized for the analysis of the drugs including antibiotics. Microbial growth inhibition assay is usually used for quantitative measurement of the veterinary drugs. If the drugs are present in samples, the microbial growth is inhibited. Enzyme substrate assays, immunoassays, HPLC, LC–MS, and LC–MS/MS have all been applied for the analysis of feed additives and veterinary drugs in foods.

Other Chemical or Biological Contaminants

Genetically modified organisms: The safety of genetically modified foods (GMFs) is a concern not only to the general public but also to the food industry and government regulatory agents. Currently, soybeans, corn, and canola have been implicated in genetically modified organisms (GMO) products. In addition to these common GMO field crops that are modified for pesticide and herbicide-tolerance, other GMO foods from both flora and fauna have been developed for improved or enhanced quality and nutritional value (James, 2001). For example, genetically modified fruits have better taste and potentially a longer/ extended shelf-life. Another example is 'golden rice,' which has been engineered to produce vitamin A precursor (Paine *et al.*, 2005). In general, there are two methods for detecting GMO. Immunoassays, for detecting the proteins of GMO, are highly specific methods because they are based on the use of antibodies. However, detection of the transgenic

DNA itself, such as the promoter sequence is another effective method for the identification of GMFs (Nielsen, 2010b).

Melamine: Melamine was added illegally to milk products and animal feed to falsify the protein content, which caused illness and death of infants. LC–MS is commonly used for melamine analysis. However, several rapid and less expensive methods such as near- and mid-IR technologies and immunoassays have also been developed (Picó, 2012; Hui *et al.*, 2006; Vail *et al.*, 2007).

Residues of Packaging Materials: The health risks of novel plastic food packing materials or the plasticizers/additives thereof have become an increasingly serious food safety issue in recent years (Robertson, 2012). Chemicals such as bisphenol A and 4-methylbenzophenone are used in plastics, but their residues can migrate into food. To ensure food safety, residue levels of packing material in food are highly regulated and monitored using GC–MS, GC–MS/MS, LC–MS, and LC–MS/MS. Other analytical methods include uses of commercially available immune-affinity columns and ELISA kits.

Modern Instrumental Analysis

Spectroscopy

Ultraviolet and visible spectroscopy

Ultraviolet and visible spectroscopy (UV–vis) is one of the most commonly encountered techniques in food analysis. The wavelength of UV light ranges from 200 to 350 nm, and that of Vis light ranges from 350 to 700 nm in the spectrum (Frost and Russell, 1993). Many food components that have no or weak UV or visible absorption are analyzed with UV/Vis spectrophotometric methods after color generation through derivatization. Analyses of total phenolic, total flavonoid, total anthocyanin, and total carotenoid contents in food are good examples (Tsao and Li, 2013).

The concentration of analyte in a given sample solution can be determined by the quantitative absorption spectroscopy based on the observation that the concentration is proportional to the amount of light absorbed from a reference beam as it passes through the sample solution. The relationship between the absorbance of a solution and the concentration of the analyte is known as Beer's law (Nielsen, 2010b).

In spectroscopy or spectrophotometry, the solution of the sample must be uniform, clear, and transparent. The reference solution for food samples is normally the sample solvent, namely, water or an aqueous buffer. For good quality results, the cuvette for the measurements within the UV range should be quartz, whereas that for the Vis range can be silicate glass or inexpensive plastic cells. The best results are obtained when the wavelength is the maximum UV/Vis absorbance of the analyte and the absorbance is stable at that wavelength.

Fluorimetry

During the past 20 years, the fluorescence spectroscopy is primarily considered to be a research tool in biochemistry. The use of fluorescence now has been expanded. The fluorescence spectroscopy is similar to UV–vis, but more sensitive. The instrumentation is also similar to that of the UV–vis absorption spectroscopy, except for the optical system. In a fluorometer, there is a need for two wavelength selectors, one for the emission beam and the other for the excitation beam. Similarly, the quantitation is also based on the direct linear relationship between the fluorescence intensity and the concentration of the targeted compound in the solution. For example, the content of certain vitamins such as thiamin is determined by this method (Ball, 2005). In addition, conformation changes of a protein in a solution is studied qualitatively or quantitatively using fluorimetric methods (Lakowicz, 2009).

Infrared spectroscopy

IR spectroscopy refers to the measurement of the absorption of different frequencies of IR radiation by any food component in a solid, liquid, or gaseous state (Settle, 1997). IR spectroscopy can be categorized into near-IR of which the wavelength is 0.8–2.5 μm; mid-IR of which the wavelength is 2.5–15 μm; and far-IR of which the wavelength is 15–100 μm. The near- and mid-IR regions of the spectrum are both useful for qualitative and quantitative analysis of foods.

For food industry, the most important is attenuated total reflectance in conjunction with Fourier transform IR (FTIR) technology. It is available for the analyses of fats and oils, meats, butter, milk, even sweetened condensed milk, and juices (Downey, 1998; Van de Voort, 1992). FTIR (**Figure 7**) is convenient, rapid and automatable, and has dramatically simplified sample handling.

NIR spectroscopy is more widely used for quantitative analysis of foods than mid-IR. This technique requires much less time and is widely used throughout the production of grain and cereal products, meat and fish products, and in oilseed processing industries. NIR spectroscopy has also been used to analyze specific chemical constituents in a food, such as the total sugar content in fruit (Li-Chan *et al.*, 2011; Ozaki *et al.*, 2006), for monitoring changes that occur during processing, transportation, and storage.

Atomic absorption and emission spectroscopy

Atomic spectroscopy is widely used for accurately measuring the trace amounts of minerals in food. Although traditional



Figure 7 FTIR spectroscopy Nicolet iS10.

chemistry titration methods for mineral analysis, such as iron, chloride, calcium, and phosphorus, remain in use today, it has been largely replaced by atomic spectroscopy. In theory, virtually all of the elements in food can be measured by atomic spectroscopy.

There are two types of atomic spectroscopy, namely atomic absorption spectroscopy (AAS) and atomic emission spectroscopy (AES). AAS is based on the absorption of ultraviolet or visible radiation by free atoms in the gaseous state. Figure 8 is the photograph of AAS provided by the State Key Laboratory of Food Science and Technology of Jiangnan University. In contrast to AAS, the source of radiation in AES is the excited atoms or ions in the sample rather than an external source (Lajunen and Perämäki, 2004; Wilson and Walker, 2010).

AES has been revolutionized by adding an apparatus called ICP torch. The samples are made into an aerosol and carried into the plasma. They atomized and are excited into various higher energy levels (Clugston and Flemming, 2000; Lajunen and Perämäki, 2004). ICP–AES has a much larger analytical working range and are suitable for more elements.

Raman spectroscopy

Raman spectroscopy, a vibrational spectroscopic technique, is complementary to IR spectroscopy. It is commonly used for organic analysis. In general, the fingerprint region of organic molecules is approximately in the wavenumber range of 500–2000 cm^{-1}. Another application of this technique is in studying the changes in chemical bonding, such as when a substrate is added to an enzyme (Li-Chan *et al.*, 2011). In contrast to IR, low concentrations of organic molecules in an aqueous solution are allowed to be measured due to the weak Raman scattering of water. The instrument is shown in Figure 9.

Mass spectrometry

Mass spectrometry (MS), different from the above discussed spectroscopic techniques, is based on the detection of charged molecules or fragments of a molecule. The generated ions are separated in the electrostatic field and then finally detected according to their mass-to-charge ratio (m/z). The results from ion generation, separation, fragmentation, and detection are manifested as a mass spectrum that can be interpreted to yield molecular weight or structural information of a compound. There are different ionization methods, but electrospray ionization and atmospheric-pressure chemical ionization are two of the most frequently used methods, and both can be in either positive or negative mode (Hoffmann and Stroobant, 2013). MS is now interfaced with GC and HPLC, and the hyphenated analytical methods are powerful tools and now widely used for analyzing various food components in a mixture. Structural information for the identification of unknown compounds separated and eluted from the HPLC column can be obtained using an MS detector (McClatchey, 2002). LC–MS has played important roles in the screening and identification of bioactive compounds such as polyphenols and carotenoids in fresh foods, and in functional foods and nutraceuticals (Paré and Bélanger, 1997; Li *et al.*, 2011; Li *et al.*, 2012).

ICP-MS is a multielement analysis technology with excellent sensitivity. Atoms are first ionized and then driven into a mass spectrometer, which accelerates the ions, and separates them according to their m/z. The resolution of modern mass spectrometers is sufficient to separate ions with m/z differences (Nielsen, 2010b; Ötleş, 2011; Thomas, 2008). On the basis of the above principals, it can simultaneously measure most elements in the periodic table. In addition, even ultratrace concentrations of the samples can be detected and analyzed.

Nuclear magnetic resonance

Nuclear magnetic resonance (NMR) spectroscopy provides important structural information for a wide variety of food components. NMR instruments (Figure 10) may be configured to analyze samples in a solution or in a solid state. It may be used for the elucidation of the complete structure of complex molecules (only NMR), the 3D-imaging of fresh tissues, and the simple ingredient assays for quality assurance. The nuclei of protons (^{1}H) and the ^{13}C isotopes have a characteristic charge and spin and are most commonly used in NMR of food components. The principles and the latest applications of NMR in food analysis can be found in detail in the reference (Picó, 2012).

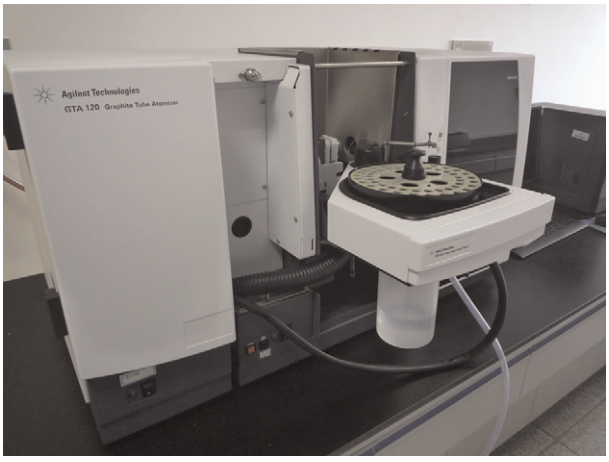


Figure 8 Atomic absorption spectroscopy spectra 240FS AA.



Figure 9 Nexion 300 ICP-MS. Photo by PerkinElmer Instruments (Shanghai) Co. Ltd. Copyright © 2013.



Figure 10 AVANCE III 400 MHz Digital NMR spectrometer.

X-ray methods

X-ray diffraction is mainly used to identify the structure of lipids, starch, as well as proteins and enzymes. The phases of lipids can also be determined by X-ray diffraction measurements. Trace amounts of metal ions in food are detected by X-ray fluorescence, whereas X-ray adsorption spectrometry is used to determine the structural environment around the metal ions in crystalline and amorphous structures (Pomeranz and Meloan, 2002).

Chromatography

Column chromatography

Chromatography has found its use in nearly all areas of food analysis. Chromatography with a very high flow rate is known as flash chromatography (FC) (Sensen, 1999). Several FC systems have been commercially available. The FC technology makes the separations easier and faster, and has been used for semipreparation of food components.

High- or ultrahigh performance liquid chromatography

Compared with conventional column chromatography, HPLC is much faster. It is a convenient and widely used technology for sugar content, pesticide residues, amino acids, toxins, organic acids, lipids, vitamins, and various phytochemicals in foods. The types of separation modes and its application in the field of carbohydrate analysis have been described in the Section Mono- and oligosaccharides. Many hydrophilic food components such as vitamin C, amino acids, phenolic compounds, and many bioactive foods are analyzed by reversed-phase HPLC, whereas both normal and reversed HPLC are used for lipophilic compounds such as vitamin E and carotenoids (Nollet, 2012; Li *et al.*, 2012). The average molecular weight of proteins and molecular weight range of polysaccharides are rapidly determined by size-exclusion chromatography. Many glycoproteins are purified using affinity chromatography (Nollet, 2012).

It is worth noting that in the past several years, two revolutionary technology advancements, the development of ultrahigh pressure pumps and sub-2-micron packing particles, have led to the state-of-the-art ultrahigh performance liquid chromatography (UPLC or UHPLC) (Waksmundzka-Hajnos and Sherma, 2011; Xu, 2013; Li *et al.*, 2012). UHPLC not only significantly reduces the sample size, analytical run time, and the solvent usage, but also produces exceptionally high sensitivity and better resolution. UHPLC is now also interfaced with MS.

Gas chromatography

GC is a separation method used to analyze thermally stable volatile substances. For example, GC has been used for the determination of fatty acids, triglycerides, flavor compounds, and many other food components, as well as pesticides, aroma compounds, polychlorinated biphenyls, and other volatile contaminants. Sample preparation is a critical step in GC analysis. It generally involves grinding, homogenization, and isolation of analytes from food samples, which may be achieved by headspace analysis, distillation, preparative chromatography, or solvent extraction. More details are mentioned in the reference (Poole, 2012).

Paper and thin-layer chromatography

Although paper chromatography is no longer widely used, TLC, because of its ease of use, relatively low cost, and greater sensitivity and reproducibility, is still used to analyze a variety of compounds in food including lipids, carbohydrates, vitamins, amino acids, and natural pigments. TLC plates with fluorescent indicators are commercially available. Compounds with UV absorption are directly detected under a UV lamp.

Other Methods

Biosensors

A biosensor is a device composed of a biological sensing element coupled to a suitable transducer. Enzyme–substrate, antibody–antigen, DNA–DNA, and aptamer–target are the most well-known interactions used in biological biosensor design. The transducers include electrochemical, optical, or a combination of the two. A wide range of biosensors has been developed for the detection of many food components such as glucose and starch, or contaminants such as carbamate, pesticides, and herbicides. The references (Joshi and Joshi, 2006; Mutlu, 2010) provide more details.

Electronic nose and tongue

Electronic nose (e-nose) and electronic tongue (e-tongue) are widely used for flavor, aroma, or odor analysis. Both techniques use different sensors for detection, and the components are grouped through pattern recognition using data analysis tools. e-Nose may use either a metal oxide semiconductor or conducting polymer as sensors that can be selective and sensitive, whereas taste sensors for e-tongue are often chemical sensors with cross-sensitivity to different components, thus lacking the sensitivity and selectivity. It should be pointed out that none of these techniques provide compositional information of a food sample, but rather profiles of different types of compounds. Using a solid-phase microextraction probe, the headspace gas can be absorbed onto the fiber and injected to a GC or GC–MS for compositional analysis. Some applications

of e-nose and e-tongue in food analysis are discussed in the references (Berger, 2007; Deisingh *et al.*, 2004).

Ultrasound

Ultrasound is a nondestructive testing method for characterizing food composition, monitoring some unit operations during production, and elucidating molecular processes in foods. Ultrasound is highly flexible and can be applied in an online environment allowing real-time observation of the changes in the product structure under processing conditions. More examples are described in the reference (Irudayaraj and Reh, 2008).

Electrophoresis

Electrophoresis is a technology that separates proteins according to the migration of charged molecules in a solution through an electric field. Each protein separated in a nondenaturing system has a characteristic mobility determined by a combination of the intrinsic charges located on the protein surface combined with physical characteristics such as shape and molecular weight (Walker and Rapley, 2008). Unlike nondenaturing electrophoresis, sodium dodecyl sulfate-PAGE is used to separate protein subunits only by size.

Modern instrument such as capillary electrophoresis has been developed and used for protein separation and analysis, as well as for some artificial sweeteners and preservatives in soft drinks. Niacin in food is determined by capillary zone electrophoresis (Perrett, 2002). More examples of instrumental analysis are described in the reference (Pomeranz and Meloan, 2002).

Conclusion

Advances in food science and technology have brought innovations and improvements in the analytical methods or techniques used to ensure food safety, quality, and nutrition-related research and actual applications along the food production chain. Fundamental discussions such as those on the comprehensive reviews on well-established conventional chemical, physical, and microbiological methods were included in this article; furthermore, recent advances in sensorial, bioanalytical, and instrumental analysis techniques and their applications have also been addressed. Applications and their pros and cons of these novel technologies in the analysis of the food components and additives including carbohydrates, proteins, lipids, trace elements, vitamins, toxins, contaminants, and residues have been discussed. Technologies related to the physical and chemical properties of food such as texture, rheology, and color are also important aspects for food-related research and development. Introduction to novel technologies and approaches, such as the noninvasive and nondestructive methods such as NMR, ultrasound, biosensor and e-nose and e-tongue, is believed to provide insights into future trends in food analysis.

See also: Advances in Pesticide Risk Reduction. Analyses of Total Phenolics, Total Flavonoids, and Total Antioxidant Activities in Foods and Dietary Supplements. Food Microbiology. Food Packaging. Food Safety: Emerging Pathogens. Food Safety: Shelf Life Extension Technologies. Food Security, Market Processes, and the Role of Government Policy. Food Toxicology. Regulatory Challenges to Commercializing the Products of Ag Biotech

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Food Safety: Shelf Life Extension Technologies

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Glossary

Electroporation Pore formation in the membrane of biological cells caused by the application of an external electric field.

Hurdle concept The principle of applying combined methods in order to have a series of preservation methods resulting in multitarget effects for microbial inactivation.

Plasma Quasi-neutral gas generated by coupling energy to a gaseous medium in order to dissociate the gaseous component molecules into a collection of ions, electrons, charge-neutral gas molecules, and other species.

Protective culture Target microorganisms inoculated to food matrix with consequent *in situ* production of inhibitory molecules or competitive effect against pathogen and spoilage bacteria.

Volumetric heating Heat generation inside a product rather than conduction from the outside due to dissipation of electrical energy (Ohmic heating) or electromagnetic energy (Microwave heating).

Needs and Principles for Food Safety and Food Preservation

The production of safe food with improved sensorial and nutritional quality at low cost remains the key challenge within food processing. Shelf life extension technologies play a major role in order to achieve this task. The avoidance of unnecessary overprocessing requires the design of improved processes and process conditions need to be controlled with much greater precision.

In general, pasteurization is used to inactivate vegetative germs. Therefore, usually continuous heat treatment between 65 and 90 °C for 0.5 s and 30 min, respectively, is needed (Wilbey, 1996, 2003). To inactivate heat-resistant forms of microorganisms, like bacterial endospores, thermal sterilization is used. Sterilization in food preservation describes a technique to provide commercial sterility meaning that the product has to be free from microorganisms that are either capable of producing food poisoning toxins or cause food spoilage during the product's shelf life (Ababouch, 1999). To realize these conditions, it is understood that a treatment is needed, which insures atleast an inactivation effect similar to 3 min holding time at 121 °C. Therefore, packaged products are treated discontinuously at temperatures ranging from 120 to 125 °C for 5–20 min (Berry and Pflug, 2003; Ramesh, 1999), whereas modern out-of-pack ultrahigh temperature (UHT) treatments usually combine rapid continuous flow steam heating (130–150 °C), short holding periods (2–15 s), and subsequent aseptic packaging (Kumar *et al.*, 2012; Swartzel, 2003).

However, excessive thermal treatments indeed cause remarkable losses in sensory and nutritional quality and affect noticeably structural and rheological product properties (James and James, 2003; Nicoli *et al.*, 1997). For these reasons it is aimed to apply as less heat as possible in a preservation treatment, by insuring the necessary level of food safety at the same time.

To find appropriate heat treatments, liquid and high-moisture foods are divided by definition into low-acid foods (pH > 4.6) and acid foods (pH < 4.6). The basis for this classification is the inability of *Clostridium botulinum* to germinate, grow, or produce toxin below pH 4.6. Yet, in products of pH between 4.6 and 4.0 the survival and growth of some spore-forming Bacillaceae (*Bacillus coagulans*, *Bacillus macerans*) and butyric anaerobes like *Clostridium butyricum* have to be controlled. Therefore, products with pH of 4.0 or higher, such as dairy products or vegetable juices, are usually sterilized. Microorganisms, which are able to germinate in acidic environments of pH lower than 3.7, are commonly inactivated by pasteurization (Berry and Pflug, 2003). Examples are lactic acid bacteria, yeasts, or molds (Rajashekhara *et al.*, 2000). Owing to these facts, acidic products with pH of 4.0 or below are usually pasteurized, which preserves valuable product compounds in comparison with sterilization (Ababouch, 1999). Nevertheless, some heat-resistant molds produce ascospores, which can outlive standard pasteurization processes and additionally are able to grow out at pH levels lower than 4.0 (Taniwaki, 1995). These abilities make them a high risk, especially in production of fruit-based products (Beuchat and Rice, 1979; Houbraken *et al.*, 2006; Nguyen, 2012), and therefore are the reason for further extension of the applied thermal load.

Many different preservation techniques are applied. Each of the used technologies is based on certain preservation factors or inactivation mechanisms. These preservation factors can be biological, chemical, or physical. The most important preservation factors for foods to extend the shelf life during storage are high or low temperatures, acidity, water activity, chemical agents, or redox potential. Traditional preservation techniques, such as dehydration or salting of food, as well as the common practice of refrigerated storage target at one of those preservation factors in order to avoid the growth of microbial population in food as well as to minimize chemical reactions. Traditional preservation techniques are mainly based on a single preservative effect, are used in high intensity, and are especially an issue for thermal sterilization treatments, which are excessively used for preservation of ambient liquid foods. Owing to these facts, the

idea of the so-called hurdle concept is a promising concept in order to lower losses in sensory and nutritional quality by raising safety of processed foods at the same time.

To lower the mentioned high treatment intensities, the so-called hurdle effect can be used. In detail the hurdle effect describes the synergetic effect of combined preservation technologies using different mechanisms for inactivation or inhibition of undesirable microorganisms (Leistner, 1978). Based on this effect, the hurdle technology was developed. The hurdle technology describes a concept for planned microbial spoilage control, shelf life extension, and quality improvement of preserved food. The main assumption is that the treatment intensity of each applied preservation technique can be lowered by use of the right combination of hurdles. For these reasons the application of the hurdle concept can help to apply gentler preservation treatments, especially by use of nonthermal preservation techniques (Ross *et al.*, 2003), possibly in combination with mild thermal energy inputs. Hereby applicability, effectiveness, and combination of hurdles are dependent on target organisms, product, process, and raw materials (Leistner, 1992, 1994, 2000; Leistner and Gorris, 1995).

Hence, the below sections aim to give an overview on existing technologies with a focus on inactivation and decontamination processing technologies as indicated in **Table 1**. Intrinsic hurdles, such as modification of pH or water activity, in order to avoid the growth of microorganisms are also potential concepts to extend the shelf life of foods but are not discussed in this article.

Microbial Inactivation Indices and Inactivation Kinetics

Inactivation indices as well as inactivation kinetics can be used to describe a given process. As an example, thermal pasteurization is defined as a food that is free of vegetative microorganisms, excluding thermoresistant. This condition or requirement can be achieved by a reference heat treatment of, i.e., 62.8 °C for 30 min for milk and up to 68.3 °C for 30 min for eggnog and frozen dessert mixes. In case of pasteurization of juice, for example, apple juice from concentrate, a treatment of 71 °C for 6 s should be applied (FDA, 2013). Depending on the target pathogenic microorganism to be eliminated and on the food matrix, alternative process conditions may be applied. Alternative thermal treatments can then be estimated on the basis of the following two thermal indices, *D*- and *z*-values. *D*-value is defined as the time required to reduce 90% of a given microorganism at a given temperature; *z*-value is the temperature variation giving a 10 times variation of *D*-value. Both parameters, *D*- and *z*-values, allow estimating alternative process conditions as defined by a linearity between temperature and time. Because the elimination of pathogenic microorganisms depends not only on temperature and time but also on food matrix, the microbial characteristics and process design and the use of inactivation kinetics have facilitated the estimation of adequate processes conditions. In addition, the nonlinearity inactivation phenomena (mainly due to hurdles combination, nonthermal inactivation effects, and food in-homogeneities), and several chemical reactions affecting quality attributes of the food have made from kinetics a valuable tool to design tailored food processes.

Numerous experimental results have been fitted to proposed kinetic models, mainly to describe the evolution of the microbial inactivation as a function of process parameters, i.e., temperature, pressure, electric field strength, etc. The main mechanism of microbial inactivation is related to several chemical or physical mechanisms depending on the inactivation technology applied. Mechanistic models for the microbial inactivation have rarely been combined with kinetic models to give one single predictive model that is capable of describing the expected microbial inactivation based on the mechanism of inactivation. In contrast to this, several empirical models have been developed, which can be widely found in the literature. A detailed description of the main inactivation kinetics can be found in the following sections. Empirical models based on Huelsheger *et al.* (1981) and Peleg (1995) and those that follow a Weibull distribution (Van Loey *et al.*, 2002; Weibull, 1951) have preferably been used to model the microbial inactivation by the various emerging technologies. An example of different models is given next:

First-order exponential decay:

$$S(t) = e^{-kt} \quad [1]$$

Table 1 Examples of preservation technologies depending on the state of food

Product type	*Liquid*	*Semisolid*	*Solid*
Pasteurization	Conventional thermal	Conventional thermal	Conventional thermal (e.g., baking and frying)
	Pulsed electric field	Microwave	Microwave
	High pressure (HP)	Ohmic heating	
	Filtration	HP	
Sterilization	Ultrahigh temperature (direct/indirect)	Retort	Retort
	Filtration	Pressure-assisted thermal sterilization (PATS)	PATS
		Ohmic heating	Cold plasma (surface)
		Microwave	Irradiation
Product examples	Dairy/Juices	Paste and puree with/without pieces	Meat/seafood Fruit and vegetables Cereals/herbs

Huelsheger model (Huelsheger *et al.*, 1981):

$$S(t) = \left(\frac{t}{t_c}\right)^{\frac{-(\phi-\phi_c)}{k}} \quad [2]$$

where S is the survival rate (survival microbial concentration/initial microbial concentration), t is the treatment time, t_c the critical treatment time, ϕ is a process parameter (i.e., temperature or pressure), ϕ_c is the value of the previous selected process parameter at the extrapolated survival fraction of 100%, and k is a constant characteristic of each microorganism.

Peleg model (Peleg, 1995):

$$S(t) = \frac{1}{1 + \exp\left[\frac{\left(\phi-\phi_{c(n)}\right)}{k_{(n)}}\right]} \quad [3]$$

$\phi_{c(n)}$ is a process parameter (i.e., temperature or pressure) at which the survival level is 50% and $k_{(n)}$ is a kinetic constant describing the steepness of the sigmoid curve.

Weibull distribution (Weibull, 1951):

$$S(t) = \left(-\frac{t}{\delta}\right)^{\alpha} \quad [4]$$

where δ is the time needed for the first decimal reduction, α is a shape parameter, and t is the processing time. Additionally, δ and α depend on process parameters and an additional equation may be needed to describe the behavior of both as a function of the most influent process parameter.

The existence of two populations of microorganisms (sensitive and resistant subpopulations) or the existence of inhomogeneities of process parameters within a given treatment chamber has made it difficult to describe the inactivation rate with a single equation. Instead, several equations have been modified in order to fit the obtained experimental results. Special attention should be paid when considering single models as it is not possible to easily distinguish between the inactivation mechanisms and the inhomogeneities of the process parameters. Weibull, *n*th-order, exponential and Churchill models, and modifications of them have been adapted in order to account both populations, the resistants and the weak ones. An example of a modified model is an extension of the exponential equation (Amiali *et al.*, 2004; Pruitt and Kamau, 1993):

$$S(t) = \beta_1 + (1-\beta_1)e^{-\beta_2 t} \quad [5]$$

$$S(t) = \beta_1 e^{-\beta_1 t} + (1-\beta_1)e^{-\beta_2 t} \quad [6]$$

where $S(t)$ is the fraction of total survivors; t, the treatment time; β_1, the fraction of survivors in population 1 (generally related to the sensitive population); β_1, the specific death rate of subpopulation 1; and β_2, the specific death rate of subpopulation 2.

Another widely used model is the modified Weibull equation:

$$\log_{10}(S) = \beta_1\left(\frac{t}{\delta_1}\right)^{\alpha_1} - (1-\beta_1)\left(\frac{t}{\delta_2}\right)^{\alpha_2} \quad [7]$$

To validate the accuracy of a given kinetic model, the degree of fit for the obtained equations can be analyzed according to the coefficient of determination (R^2), root mean square error (RMSE), bias factor (B_f), and accuracy factor (A_f).

The RMSE is defined as an error between predicted and experimental microbial survival values. The RMSE is a statistical measure of the differences between values predicted by a model and the values actually observed from experiments and can be expressed by an absolute value. The B_f is a measure of overprediction ($B_f > 1$) or underprediction ($B_f < 1$) of the predicted values by the empirical model in comparison with the experimental values. The accuracy factor (A_f) indicates how the predictions differ from the observed data. An A_f of 1 indicates perfect agreement between all predicted and observed values. An A_f value higher than 1 (e.g., 1.13) shows that the prediction is on an average either 13% smaller (if $B_f < 1$) or 13% larger (if $B_f > 1$) than the observed values (Ongeng *et al.*, 2010). The A_f should thus be analyzed always in combination with the B_f.

According to the best fitting parameters, the best kinetic models should be chosen. However, differences in the experimental setup and enzymes or microorganisms from varying sources make it difficult to validate existing kinetic models. Thus, it is worth mentioning that a kinetic model should be elaborated and used for a specific case and not for similar applications.

Food Quality Aspects during Preservation and Shelf Life Considerations

The shelf life of a food product can be defined as the period during which the product is still acceptable for human consumption. The shelf life is determined by microbial, chemical, and physical aspects. As a result of these aspects, consumers may reject the product based on its sensory characteristics. The shelf life is in most cases determined by a combination of raw material quality, product formulation, processing, packaging, and storage conditions. Special attention should be paid to storage conditions, as temperature and oxygen content may faster or delay chemical reactions as well as microbial growth. The storage temperature directly affects enzymes. Enzyme activity in food may result in a change of the chemical composition of the product, resulting in changes in flavor, odor, color, and texture. The amount of oxygen may gather chemical reactions and thus cause oxidation.

Thermal treatments are the most used methods to extend the shelf life of liquid foods by inactivation of microorganisms and enzymes; however, heat causes irreversible losses of nutritional compounds, undesirable changes in physicochemical properties, and alteration of their antioxidant properties (Plaza *et al.*, 2006; Wang and Xu, 2007). Thus, the application of nonthermal technologies or the combination of modified atmospheres and active packaging has been widely used. The application of any thermal or nonthermal pasteurization technology requires accurately defined treatment intensity, followed by a predictable microbial inactivation as well as a minimal impact on heat-sensitive compounds. The development of each single chemical, physical, or microbiological change can additionally be described by mathematical models,

i.e., growing of microorganisms and vitamin degradation during the whole storage period. A mathematical model can thus be used to predict the shelf life or for determination of the conservation conditions that result in the desired shelf life.

The microbial growing of microorganisms, yeast, and molds during the shelf life can be fitted to the Gompertz's equation. Zwietering *et al.* (1990) reported that the Gompertz's model was statistically sufficient to describe microbial growth data:

$$\log_{10}\left(\frac{N}{N_0}\right) = A\exp\left(-\exp\left(\frac{\mu_m e}{A}(\lambda - t) + 1\right)\right) \quad [8]$$

where μm [Δlog10(CFU ml^{-1})/day] represents the maximum specific growth rate, λ(day) represents the stage adaptation of the microorganism to the environment in which it is, A is the maximum diameter reached by the colony (mm), and e is a constant (2.7182). The longer the adaptation phase and the lower the maximum specific growth rate, the better for the industry (Zimmermann *et al.*, 2011).

The above-described equation is a potential tool in order to determine the shelf life of a certain product as a function of spoilage microorganisms, but it does not give any indication about how to control or design the process variables of the killing step. A good approach for determining best process conditions followed by the best storage conditions is the combination of microbial inactivation kinetics models with the Gompertz's model, as described by Boon *et al.* (2010), in which a predictive shelf life model for orange juice treated by high pressure (HP) and pulsed electric field (PEF) processing was described by combining inactivation and shelf life kinetics. The model can be applied to predict the shelf life based on microbial and enzymatic spoilage and to determine the processing conditions to obtain the desired shelf life. The model combines microbial inactivation and growth with enzyme inactivation, enzyme rest activity, and quality.

Food Preservation Technologies

Thermal Food Preservation

One of the oldest industrial sterilization of food is canning (Prescott and Underwood, 1897; Prescott and Underwood, 1898). Canning involves heating hermetically sealed containers to at least 121 °C for low-acid foods, which requires a pressure vessel or retort (Larousse and Brown, 1997). High-acid foods are sterilized at lower temperatures after filling or may be hot filled. Packaging formats for retorting are metal cans, glass jars, and plastic or paperboard composite containers. Compared with other preservation techniques, canning is relatively inexpensive and the quality of meats, fruits, and vegetables is adequate for most consumers (Lopez, 1987). Products are shelf stable and ready to eat. Process improvements have been achieved by hydrostatic retorts, rotary or shaking retorts, or packaging innovations, such as two-piece cans or the use of pouches.

Pouches for retort were developed by Natick Labs of the US Department of Defense as an improved military ration, replacing small, single-serve metal cans. The retort pouch is a flexible container made of laminated polymer films with an aluminum foil barrier layer to protect against light and oxygen. The critical development was a sealant layer of polypropylene that could withstand the elevated temperatures of pressure cooking. The narrow profile of the package was also presumed to provide improved flavor and texture quality compared with a cylindrical can of the same volume due to reduced overcooking.

The limited strength of these flexible packages represents an engineering challenge because internal pressure develops inside the packages during thermal processing as a result of internal water vapor pressure and the expansion of entrapped gases with increasing temperature. This internal pressure will become greater than the saturation pressure of the steam in the retort and can cause packages to burst unless an overriding air pressure is applied in the retort. Profiles of overriding air pressure required during the retorting of foods in flexible packages are largely determined by trial and error. Recently, online detecting devices are in use in order to allow an accurate control of air pressure. Recent developments in retorting mainly concern improved methods for calculating optimum retort process conditions of time and temperature as well as the introduction of automation and robotics in materials handling operations on the cook room floor in major food plants.

As an in-pack sterilization process, canning has some limitations with regard to the heat transfer, especially for larger cans that lead to some overprocessing until the cold spot has reached the targeted sterilization conditions. Out-of-pack sterilization represents a more gentle option in order to better maintain the product quality when assuring food safety. Aseptic processing and packaging involves sterilizing foods and containers separately before filling the sterile containers in a sterile environment. Because foods are cooled before filling, containers do not need the strength to resist high temperatures and pressures, as do containers used in canning. This makes packaging less expensive and a larger diversity of packaging materials exist – lightweight plastics, paperboard laminates, and large polymer bags, for instance. Containers are sterilized in a variety of ways: by chemicals (hydrogen peroxide) for paperboard, by irradiation for bags, and by the heat of thermoforming for plastic tubs. The sterile environment is created by steam or chemical sterilization and maintained by sterile air filtration.

Depending on the type of food, the concentration and size of particles, and the viscosity, foods are sterilized by heat in scraped surface heat exchangers, tubular heat exchangers, or plate heat exchangers and cooled with similar equipment. Low-viscous products are suitable for direct UHT heating methods, such as steam injection and steam infusion. Foods with particulates require special care in sterilization to ensure that the center temperatures reach the minimum required for the type of food (Ramaswamy *et al.*, 1997). The flavor and texture of aseptically processed foods may be superior to that of postpackage-processed foods, due to a less severe heat treatment, but the big advantage of in-pack processing is low-cost packaging. Capital cost is higher than that for equivalent canning capacity because filling rates are generally slower for aseptics and the equipment controls are more complex.

Both of the above-discussed technologies, canning as well as conventional aseptic UHT processing, have some limitations with regard to the speed of heating as well as with regard to the processing of high viscous food containing large

particles. To overcome these constraints, volumetric heating methods are gaining interest for pasteurization and sterilization. Ohmic heating and microwave heating represent promising solutions.

Ohmic heating involves the conversion of electrical energy into thermal energy. The food is exposed to the electric field in direct contact with electrodes. Depending on the electric field strength, electrical conductivity of the product, and electrode configuration, an electrical current flows that causes volumetric heating based on the Joule effect. Ohmic heating is commonly applied in a continuous system where the product is pumped through a set of electrodes. The fast heating can be used for pasteurization as well as for sterilization of products depending on the energy input. In-pack application of Ohmic heating is also under development and involves the use of packaging materials with electrically conductive parts in order to transfer the electrical current into the product. To avoid electrochemical reactions, an alternating current with a frequency >20 kHz is favorable and currently used in the available industrial equipment. With regard to product composition, the distribution of the electrical conductivity is the key property in order to allow a homogeneous heating. Product fractions with a higher electrical conductivity due to higher salt content heat faster. Therefore, adaptation of the electrical conductivity of the solid and liquid phase and between different particle fractions is required. Otherwise, hot spots and cold spots will occur at locations of high and low electrical conductivity, respectively (Larkin and Spinak, 1996; Parrott, 1992).

Microwave heating is a common method for heating food in the kitchen, although industrial applications for food pasteurization and sterilization are also emerging. Recently, microwave heating has been investigated as a fast heating method for pumpable foods in a continuous system. In addition, in-pack sterilization concepts using microwave heating are developed. Microwaves and radio frequencies are forms of electromagnetic energy that interact with water molecules and ions in the food and heat material from the inside as compared with other forms of heat transfer in which energy is supplied from the surface. The result can be very fast and selective heating. However, some desirable reactions in cooking, such as browning, may not occur.

Nondirect Thermal Preservation

To lower the thermal load of preserved food products, several approaches for nonthermal inactivation of microorganisms have been introduced over the past 20 years. In general nonthermal technologies are able to inactivate microorganisms at sublethal temperatures by use of alternative inactivation methods. Among proposed techniques, pulsed electric fields, high hydrostatic pressure, ionizing irradiation, pulsed light, or cold plasma have to be mentioned (Butz and Tauscher, 2002; Knorr *et al.*, 2011a). However, most of these techniques still require very high treatment intensities, depending on the treated product and the expected target organisms (Ross *et al.*, 2003). The effectiveness concerning spore inactivation in particular has to be considered very carefully for each of the mentioned technologies and methods, as possible inactivation mechanisms are not yet totally understood in most cases.

High pressure processing

High pressure processing (HPP) is often regarded as the leading nonthermal preservation technology. During the past decade, HPP has emerged as a viable commercial alternative for pasteurization of value-added fruits, vegetables, meat, ready-to-eat food, and seafood products. This cold pasteurization process is used in more than 190 industrial-scale installations worldwide, which produce more than 300 000 tons of product per year (Tonello Samson, C. 2012, NC Hiperbaric, Spain, personal communication). In most cases HPP is used for food safety reasons or to extend the shelf life (Knorr *et al.*, 2011b), but there are numerous other interesting applications of HP, such as food structure engineering and the reduction of the allergenic potential of, for example, rice (Knorr *et al.*, 2006; Sharma and Yadav, 2008).

However, the primary aim of treating foods with HPP is to reduce or eliminate relevant foodborne microorganism and pathogens (Patterson *et al.*, 2007). Typically, ambient temperatures, pressures up to 600 MPa, and treatment times from a few seconds to several minutes are used to kill bacteria while preserving quality related factors like vitamins, pigments, and flavor components (Oey *et al.*, 2008). During the inactivation of microorganisms and quality-related enzymes, changes in the functionality of food proteins as well as in the structure of food system or texture can occur (Knorr, 2002).

The reasons for these phenomena are diverse; in general the primary structure of low molecular weight molecules, like peptides, lipids, vitamins, and saccharides, is rarely affected by isostatic HP because of the very low compressibility of covalent bonds at pressures below 2 GPa (Cheftel and Culioli, 1997; Gross and Jaenicke, 1994; Oey *et al.*, 2008). Conversely, the native structure of macromolecules, such as starch, can be changed by HP, and thermally induced structural changes can also occur. Pressure, as a basic thermodynamic parameter, affects these biomolecules and can change the state of molecular organization (e.g., crystallization of fats or phase changes of phospholipids) (Macdonald, 1992). In food systems such changes can be either positive (e.g., inactivation of microorganisms or gel formation) or negative (e.g., texture defects). These HP effects are governed by three general principles, which are outlined below:

1. The principle of Le Chatelier and Braun states that if a chemical system at equilibrium experiences a change, the equilibrium will shift in order to minimize that change. If this change is an increase of pressure, any phenomenon that is accompanied by a decrease in reaction volume (e.g., chemical reactions, phase transitions, or changes in the molecular configuration) is enhanced and vice versa (Cheftel, 1995). Hence, HP will shift the equilibrium toward the system with the lowest volume. Moreover, when the activation volume (ΔV^*) of an activated complex is smaller than that of the initial reactants, a pressure increase and a temperature decrease will increase the reaction rate constant k_{kinetic} and therefore also the reaction rate, according to Equation 9

$$\ln k_{\text{kinetic}} = \ln k_0 - \Delta V^* \frac{p}{RT} \qquad [9]$$

where p is pressure, T is temperature, and R is the molar gas constant. However, an increase in temperature also

increases the rate of reaction according to the Arrhenius law (Cheftel, 1995).
2. The isostatic principle implies that pressure is instantaneous and uniform and is transmitted independently of the geometry and size throughout the whole biological sample (Balny, 2004).
3. The microscopic ordering principle means that at a constant temperature an increase of pressure increases the degree of the molecular ordering of a substance (Urrutia Benet, 2005).

The main reason for the dynamic behavior of biomolecules under pressure is the free volume of the system, which is expected to decrease with increasing pressure (Heremans, 2002).

HP can, therefore, induce reversible or irreversible changes in the native structure of proteins, starches, and other macromolecules, which are similar to changes occurring at heat and in the presence of chemicals, but the residual molecular structure after a pressure treatment can vary significantly. In this regard, Knorr *et al.* (2006) published a detailed review of pressure-induced changes in the structure of proteins, and Jaeger *et al.* (2012) reviewed the impact of these on food structure.

The specific pressure effects on microorganism are more complex and several different mechanisms leading to cell death interact if HPs at ambient temperatures are applied. Primarily, HP at a sufficient high level can induce enzyme inactivation and cell membrane rupture caused by a phase transition of the membrane (Abe, 2013; Ananta *et al.*, 2005; Winter and Jeworrek, 2009). The pressure level needed to achieve a 5 $\log_{10}$ reduction of pathogenic microorganism in different food products range from 300 to 800 MPa (Hendrickx and Knorr, 2002) and often a synergism between pressure and temperature is reported (Buckow and Heinz, 2008). By increasing the process pressure, it is possible to decrease the needed temperature level to achieve the same inactivation. According to Smelt *et al.* (2001) the pressure-induced effects leading to cell death of vegetative microorganisms can be attributed to four factors:

1. Protein and enzyme unfolding, including partial or complete denaturation
2. Cell membranes undergo a phase transition and solidify under pressure
3. Disintegration of ribosomes in their subunits and
4. Intracellular pH changes, which are related to the inactivation of enzymes and membrane damage (Knorr *et al.*, 2011b).

Bacterial endospores show in this regard a much higher pressure and temperature resistance. The process conditions used for the cold pasteurization of solid, semisolid, and liquid foods are insufficient to achieve a sterilization and hence an extended shelf life at ambient temperatures. A combination of HP (>500 MPa) and elevated initial product temperatures ($>80\ ^{\circ}C$) can be a promising approach to produce high-quality low-acid foods (Reineke *et al.*, 2013).

Pulsed electric field

PEF treatment is a nonthermal alternative to conventional thermal pasteurization for liquid products. Other applications of PEF are the disintegration of plant or animal raw materials or the induction of stress responses in biological cells. According to several studies, the quality of a PEF-pasteurized food product is closer to that of the fresh product than to that of the heat-pasteurized product, and the safety of the fresh product is enhanced by the inactivation of vegetative pathogenic microorganisms. The first commercial PEF application was installed in 2005 in the United States for fruit juice preservation. Clearance of the FDA was already available since 1996, indicating the techniques potential for safe and gentle preservation (Barbosa-Cánovas *et al.*, 1999).

PEF technology can be used to induce nonthermal permeabilization of cell membranes. Depending on the treatment intensity (external electric field strength, number, and duration of the electric pulses) and cell properties (size, shape, orientation, and conductivity), the pore formation may be permanent or temporary (**Figure 1**).

The treatment consists of the application of very short electric pulses (1–100 μs) at electric field intensities in the range of 0.1–1 kV cm^{-1} (reversible permeabilization for stress induction in plant cells), 0.5–3 kV cm^{-1} (irreversible permeabilization of plant and animal tissue), and 15–40 kV cm^{-1} for the irreversible permeabilization of microbial cells. The aforementioned field intensities lead to the formation of a critical transmembrane potential, which is regarded to be the precondition for cell membrane breakdown and electroporation (Rubinsky, 2010).

The temperature at which the cells are exposed to the electric field has a significant influence on membrane fluidity properties and therefore on physical stability of the cell membrane. The liquid crystalline structure of the phospholipid bilayer at elevated temperature facilitates pore formation and increases PEF treatment effectiveness, leading to a synergetic effect of PEF and elevated temperature (Lelieveld *et al.*, 2007; Raso and Heinz, 2007).

High-intensity electric pulses can be generated by the switched discharge of a suitable capacitor bank. A schematic drawing of an electrical circuit for the generation of high-intensity electric field pulses is given in **Figure 2**. The characteristics of the discharge circuit determine the shape of the time-dependent potential in the treatment chamber. Exponential decay pulses represent a complete discharge of the capacity. A rectangular shape of the pulse can be produced by using special switches, capable of interrupting the current at high potentials, or by the implementation of a pulse forming network. If an additional capacitor is used together with a parallel switch, bipolar pulses can be obtained (Loeffler, 2006).

The geometry of the treatment chamber has a considerable effect on the electric field distribution and on the total resistance and therewith on the discharge circuit. The treatment chamber design needs to be optimized, taking also into account a homogenous distribution of the electric field strength as well as the characteristics of the fluid flow, the viscosity, and the particle sizes.

Various treatment chamber designs, such as parallel plates, coaxial cylinders, or colinear configurations, have been used for PEF processing and some modifications of these basic designs have been proposed. A comprehensive overview of different treatment chamber configurations can be found in Huang and Wang (2009).

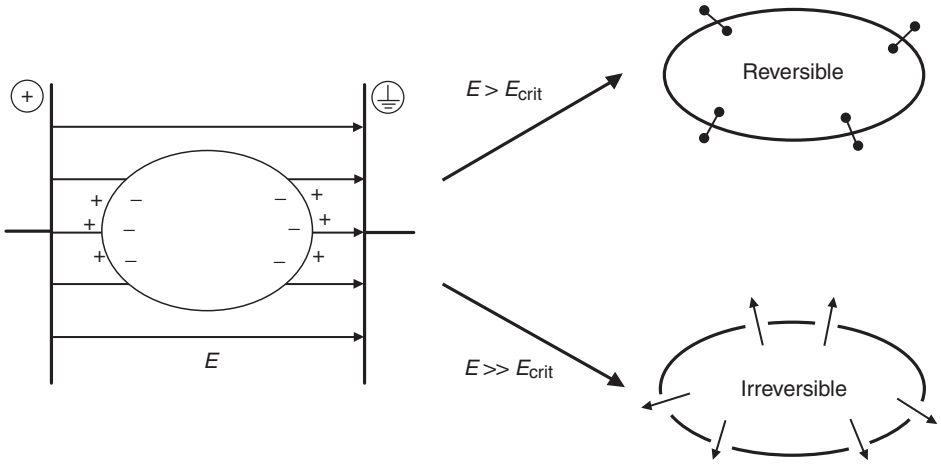


Figure 1 Exposure of biological cells to an external electrical field that results in reversible or irreversible pore formation.

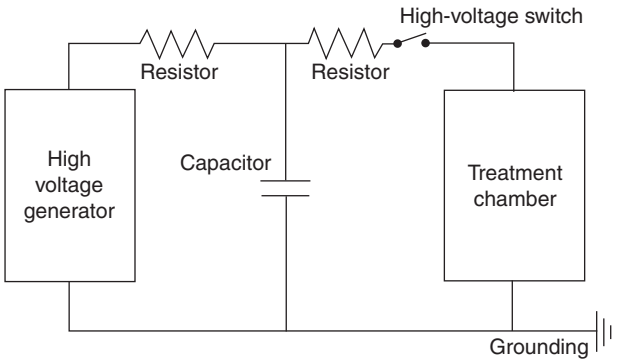


Figure 2 Schematic drawing of an electrical circuit for the generation of high-intensity electric field pulses.

Although the PEF treatment is considered as a nonthermal food processing technology with the electroporation being the main inactivation mechanism, there is a significant temperature increase during high-intensity PEF treatment, as applied for pasteurization purposes due to Ohmic heating effects. Many authors have described the temperature distribution in a PEF treatment chamber and reported the occurrence of high local temperatures due to inhomogeneous field distribution of the electrical field, limited flow velocity, and recirculation of the liquid (Gerlach *et al.*, 2008; Jaeger *et al.*, 2009a; Lindgren, 2001; Lindgren *et al.*, 2002). This is of particular importance when discussing PEF effects on functionality of heat-sensitive compounds, such as proteins, or when conducting inactivation kinetic studies. Additional thermal effects may occur in case of application of high total energy inputs, insufficient temperature control, or unfavorable treatment chamber design. Treatment homogeneity and the avoidance of overprocessing of the product, including the occurrence of local high temperatures due to Ohmic heating effects, are the key aspects to guarantee predictable microbial inactivation while maintaining heat-sensitive food constituents.

Effective inactivation for most of the spoilage and pathogenic microorganisms has been shown and colony count reductions depending on treatment intensity, product properties, and type of microorganism in the range of 4–6 log-cycles are comparable to traditional thermal pasteurization. Most of the studies conducted in the past showed that PEF is effective only against vegetative microorganisms, yeasts, and molds as well as mold ascospores but ineffective against bacterial endospores and viruses (Lelieveld *et al.*, 2007).

The factors that affect microbial inactivation during PEF treatment are process factors, such as electric field intensity, pulse width and shape, treatment time, and temperature; microbial factors, such as type, shape, size, concentration, and growth stage of microorganism; and media factors, such as pH, antimicrobials and ionic compounds, electrical conductivity, and medium ionic strength.

Membrane damage and inactivation of microorganisms due to PEF was at first considered as an all-or-nothing event, but a differentiated approach is required even if the critical parameters for the electrical breakdown of cell membranes are exceeded. Membrane damage and sublethal injury was found to be repairable under certain conditions and the extent to which cells repair their injuries was reported to depend on the treatment intensity, the microorganism, and the treatment medium pH. On the one hand, sublethally injured cell fractions are a risk from a food quality and safety point of view, because these cells may recover and regain their initial vitality. On the other hand,

sublethally injured fractions have a potential for subsequent complete inactivation by the application of additional hurdles, such as suboptimal storage conditions or the application of other inactivation methods, such as the application of antimicrobials or other food preservation technologies (Garcia *et al.*, 2005; Jaeger *et al.*, 2009b; Somolinos *et al.*, 2008).

The microbial inactivation rates differ considerably between inactivation in simple media and inactivation in a complex matrix. This was partly attributed to the protective effect of some food compounds, such as xanthan (Ho *et al.*, 1995), proteins (Jaeger *et al.*, 2009b; Sampedro *et al.*, 2006), or fat (Grahl and Märkl, 1996). In addition, model microorganisms used in most of the studies and the way of sample preparation differ significantly from the native state of the microbial population present in the real food system. The diverse and heterogeneous microbial flora present in real foods is not comparable to inoculated microorganisms in most cases due to strong variability of microbial species and physiological state of microorganisms. The consideration of microbial growth state, adaptation to the treatment media, and the existence of inhomogeneous microbial populations with less sensitive subpopulations seem to be the most challenging aspects when transferring inactivation results to real products and industrial implementation.

The evaluation of the effect of PEF on food compounds is complex. Available reports are limited and different experimental setups and processing parameters make them difficult to compare. The consideration of electric field side effects, such as temperature increase and temperature hot spots due to Joule heating effects within a nonuniform electric field and the occurrence of electrochemical reactions and pH shifts, is the most challenging aspect within this context. The nonthermal inactivation of microorganisms by PEF is based on the electroporation of membrane structures. High-intensity electric fields are unlikely to affect covalent chemical bonds, but the electric field application and related side effects may show an impact on food compounds; moreover, process modifications toward the inactivation of microorganisms and enzyme structures are also possible. Owing to the application of PEF, changes in the conformational state of proteins might cause changes in protein structure and enzyme activity. A comprehensive overview of PEF effect on food material properties can be found in Van Loey *et al.* (2002) and Jaeger *et al.* (2012).

Irradiation

Electromagnetic waves of high frequency and corpuscular rays have bactericidal effects. In the past century extensive research has been carried out to evaluate the use of irradiation for sterilizing food. Possible process applications range from influencing the ripening process of fruit and vegetables to a nonthermal sterilization of food. Hence, the irradiation of food is gaining more and more attention in the past few years. Today, health and safety authorities in more than 45 countries have approved irradiation of more than 70 different foods, ranging from spices to grains, from deboned poultry meat to ground beef, over to fruits, nuts, and vegetables (Sommers and Fan, 2006). The irradiation process involves exposing the food matrix, either packaged or in bulk, to controlled amounts of ionizing radiation for a predetermined time. During the process and in dependence on the irradiation dose, microorganisms, vegetative bacteria, bacterial spores, viruses, and insects that might be present in the food are inactivated. The irradiation process does not increase the normal radioactivity level of the treated food (Kessler, 2002).

The main lethal effect of irradiation is the induction of structural changes in the DNA. Irradiated microorganisms can no longer proliferate and cause food spoilage. Insects do not survive or become incapable of proliferation (CAST, 1989). Plants are unable to continue the natural ripening or aging process. The specialty of processing food by ionizing radiation is that the energy density per atomic transition is very high; it can cleave covalent bonds in molecules and induce ionization, which is not achieved by mere heating. This is the reason for both new effects and new concerns. The treatment of solid food by ionizing radiation can provide an effect similar to heat pasteurization of liquids, such as milk or fruit juice (Kessler, 2002; Lakritz *et al.*, 1989).

For food irradiation electron beams and gamma rays are used. Gamma radiation is radiation of photons in the gamma part of the electromagnetic spectrum. The radiation is obtained through the use of radioisotopes, generally cobalt-60 or, in theory, cesium-137. The advantage of gamma rays with regard to food irradiation is the deeper penetration depth compared with electron irradiation. For electron irradiation, electrons are accelerated in an electric field to a velocity close to the speed of light. Electrons are particulate radiation and hence have cross-section many times larger than photons, so that they do not penetrate the product beyond a few inches, depending on product density. Electron beams are, therefore, more suitable for flat thin products (up to 5 cm) and gamma rays for larger size bodies up to 30 cm thickness (Kessler, 2002).

The dose of radiation is measured in the SI unit known as Gray (Gy). One Gy dose of radiation is equal to 1 J of energy absorbed per kilogram of food material. In radiation processing of foods, the doses are generally measured in kGy (1000 Gy). 'Dose' is the physical quantity governing the radiation processing of food.

The application is generally divided into three main categories based on the dose (Kessler, 2002):

Up to 1 kGy: Low-Dose Applications

- Sprout inhibition in bulbs and tubers 0.03–0.15 kGy,
- Delay in fruit ripening 0.25–0.75 kGy,
- Insect disinfestation, including quarantine treatment and elimination of foodborne parasites 0.07–1.00 kGy.

1–10 kGy: Medium-Dose Applications

- Reduction of spoilage microbes to prolong shelf life of meat, poultry, and seafood under refrigeration 1.50–3.00 kGy.
- Reduction of pathogenic microbes in fresh and frozen meat, poultry, and seafood 3.00–7.00 kGy.
- Reducing the number of microorganisms in spices to improve hygienic quality 10.00 kGy.

Above 10 kGy: High-Dose Applications

- Sterilization of packaged meat, poultry, and their products that are shelf stable without refrigeration. 25.00–70.00 kGy.
- Sterilization of Hospital diets 25.00–70.00 kGy.

Table 2 Membrane filtration technologies and its possible applications

Filtration technology	*Application for separation*	*Pore size (nm)*
Microfiltration I	Microorganisms fat globules	10^3–10^4
Microfiltration II	Casein micelles	25–130
Ultrafiltration	Proteins	3–5
Nanofiltration	Sugars (mono- and disaccharides)	~0.8
Reverse osmosis	Mineral salts, cations, and anions	~0.4
	Water	~0.3

Source: Compiled from Kessler, H.G., 2002. Food and Bio Process Engineering – Dairy Technology. Munich: Verlag A Kessler.

Pathogenic microorganisms, such as *Escherichia coli* O157: H7, *Salmonella*, *Campylobacter jejuni*, *Listeria monocytogenes*, and *Vibrio*, are sensitive to low levels of ionizing radiation. With increasing irradiation dose the lethal effect on microorganisms is more intense, but a higher dose, although not creating any harmful products, may simultaneously introduce changes in sensory qualities. Therefore, a balance must be attained between the optimum dose required to achieve the desired objective with a minimum impact on the sensory quality of the processed food (Sommers and Fan, 2006).

With the combination of low-dose irradiation and refrigeration, the shelf life of several fruits and vegetables, meat, poultry, and fish can be prolonged considerably without altering the flavor or texture of the food. Spoilage microorganisms, such as *Pseudomonas* spp. and *Salmonella*, are relatively sensitive to irradiation at a dose of 2.5 kGy applied to fresh poultry carcasses processed according to good manufacturing practices (FDA, 1997). When properly refrigerated, the meat shelf life can double (provided it is kept below 5 °C). Further the short shelf life of some fruit can be increased by slowing down the ripening. For example, ripening in bananas, mangoes, and papayas can be delayed by irradiation at 0.25–1 kGy. However, the extension achieved depends on the initial quality of the fresh food. The time of harvest and the physiological state also affects the response of fruits and vegetables to irradiation. Indeed, not all fruits and vegetables are suitable for irradiation because they undergo undesirable changes, like off-flavors or changes in texture and color (Kessler, 2002; Sommers and Fan, 2006).

Filtration

The filtration process is a mechanical or physical operation, that is used for the separation of solids from fluids or fluids from a gas phase by interposing a medium through which only the fluid/gas can pass. Oversize solids in the fluid are retained in the so-called retentate and the filtrated fluid that passes through the filter membrane is called permeate. Based on the particle size, which is retained in the retentate, one could distinguish between microfiltration, ultrafiltration, nanofiltration, reverse osmosis/hyperfiltration, electrolysis, and ion exchange. With regard to shelf life extension of liquid food, microfiltration is the common filtration process to remove most of the microorganisms, whereas the other membrane filtration technologies can be used to remove food constitutes (Table 2).

In the case of microfiltration, the main purpose is the removal of microbial cells from solutions and is hence operated with pore diameters larger than those required by ultrafiltration. This ensures higher permeation rates, without compromising the retention of microorganisms. The membranes employed have mean pore diameters of 0.05–5 μm and are made of zirconium and aluminum oxides, which makes them mechanically and thermally more stable (Kessler, 2002). Hence, they can be heat sterilized and can handle the whole pH range of liquid foods and cleaning agents.

For the separation of microorganisms from beverages, like wine, cider, mineral water or soft drinks, and milk, pore sizes in the range of 0.8–1.4 μm are commonly used. For the processing of milk in particular, a strong interest for minimally processed products with extended shelf life is present. Whereas high-temperature short-time pasteurized milk has a storage quality of approximately a week at cold storage, ultra-high temperature (UHT) milk can be held at room temperatures for several months. However, the UHT processing of milk is accompanied with undesired thermally derived product alterations, like cook flavor, off-flavor, and caramel flavor (Mehta, 1980). Therefore, the extended shelf life (ESL) milk with taste like fresh milk, but a prolonged shelf life of up to 4 weeks in the cold chain distribution, was introduced into the market by a combination of microfiltration and heat pasteurization. By applying this method, raw milk is separated into skimmed milk and milk fat. The skimmed milk is microfiltrated through ceramic membranes and subsequently pasteurized. The milk fat, together with the germ-enriched skim milk retentate, is processed by ultrahigh heat treatment and then reverted into the skimmed milk (Schmidt *et al.*, 2012). By microfiltration, bacterial counts can be reduced by 4–6 $\log_{10}$ (Elwell and Barbano, 2006; Schmidt *et al.*, 2012). Interestingly, microfiltration can lead to a shift of the microbial population of the ESL milk compared with heat pasteurized milk, because of a disproportionately high retention of Gram-negative bacteria, which may be due to generally larger cell size of Gram-negative compared with that of Gram-positive or lactic acid bacteria (Schmidt *et al.*, 2012).

Consequently, the combination of microfiltration and heat pasteurization has a remarkable potential for the production of high-quality ESL milk. With regard to other beverages, like beer or fruit juice, a microfiltration alone could be sufficient to achieve a 'cold' pasteurization (Kessler, 2002).

Antimicrobials in Food Preservation

In the past years, an increased consumer's demand for sophisticated foods, with an additional health-promoting benefit

above basic nutrition, has been seen. To fulfill this goal and to ensure the consumers safety and provide food with an acceptable shelf life, the addition of antimicrobials could be a part of a hurdle concept. This includes not only traditional methods for food preservation, such as salting and smoking, but also the bioconversion of raw products during the fermentation or the addition of natural or artificial antimicrobials.

Natural antimicrobials

Most perishable food are stored at low temperature and are often packaged under modified atmosphere in order to extend their shelf life. However, these hurdles for microbial growth do not eliminate undesirable microorganisms from the product. Besides the technologies introduced above to control and inactivate pathogens, a wide range of food grade chemicals could be added during the food manufacturing process to extend the shelf life by stabilizing chemical changes in the food or by preventing or inhibiting microbial growth. These secondary preservatives include traditional and natural antimicrobials with potential or current value for its use in foods (Holley and Patel, 2005; Naidu, 2000). Because of the consumer awareness regarding synthetic chemical additives, foods preserved with natural additives have become popular and led researches to look for natural food additives with a broad antimicrobial spectrum.

Natural antimicrobials are derived from animal, plant, or microbial sources and until now more than 1340 plants with defined antimicrobial compounds have been identified. The antimicrobial compounds present in these plants were identified as phenols, alcohols, aldehydes, ketones, ethers, and hydrocarbons (Tajkarimi *et al.*, 2010). Antimicrobials from plant origin are obtained by various methods, which include steam distillation and hydro distillation as well as supercritical fluid extraction. Hence, the extracted essential oil fraction is often a mixture of several compounds. However, traditional food ingredients, like some spices and herbs, also have antimicrobial effects on human pathogens (Brandi *et al.*, 2006). The antimicrobial effects of clove, mint, ginger, garlic, cinnamon, and mustard have been known for centuries and are still in use as an antimicrobial hurdle. Further, bay leaf, coriander, cumin, oregano, rosemary, sage, and thyme have been reported to have significant bacteriostatic properties (Tajkarimi *et al.*, 2010). Despite its contribution to taste and flavor, plant extracts and spices can act against Gram-positive pathogens, such as *L. monocytogenes*. Essential oils derived from plants and spices showed antimicrobial activity against *L. monocytogenes*, *Salmonella typhimurium*, *E. coli* O157:H7, *Shigella dysenteriae*, *Bacillus cereus*, and *Staphylococcus aureus* at levels between 0.2 and 10 $\mu l\ ml^{-1}$ (Burt, 2004). For example, a combination of mild heat treatment and the addition of cinnamon and clove essential oils to apple cider significantly reduced the time to achieve a 5 $\log_{10}$ inactivation of *E. coli* O157:H7 (Knight and Mckellar, 2007). Further, Mosqueda-Melgar *et al.* (2008) achieved a pasteurization (>5 $\log_{10}$ reduction of *Salmonella enterica*) of tomato juice by a combination of 2.0% of citric acid or up to 0.1% of cinnamon bark oil and a PEF treatment.

A promising recent development for the use of natural antimicrobials is its incorporation into packing materials, rather than in the food itself, to protect the food surface. The advantage of this approach is, among others, that the sensory and chemical compatibility of the antimicrobial with the target food plays a secondary role.

Fermentation and protective cultures

A special case of an antimicrobial hurdle is the fermentation of food, where microorganisms produce lactic or acetic acid, which lowers the pH value of the product and hence extends its shelf life. The mankind uses fermentation to increase the hygiene and storability of food for more than 10 000 years. Hence, the food fermentation process underwent continuous improvements and microbial cultures became an essential component in food production.

In modern food production, fermentation is defined as a process of biotransformation carried out by microorganisms or their enzymes, irrespective of whether it is based on fermentation in the classical sense (with an anaerobic catabolism of organic substrates without the involvement of exogenous electron acceptors) or oxidative metabolism (respiration) (Vogel *et al.*, 2011). For fermentation, thermally treated or untreated food raw materials from plant or animal origin are used. By addition of certain microorganisms or mixtures of microorganisms to the food, its appearance odor and color are significantly changed and the shelf life is extended (Kessler, 2002). Fermented foods cover a broad range of products, including fermented dairy products, like yoghurt and cheese, vinegar, alcoholic beverages, sourdough, pickles and sauerkraut, fermented olives, or soy sauce. In total, approximately one-third of all food currently being consumed is fermented.

Fermented products have some unique features and a number of advantages, compared with the untreated raw product or the product treated with other preservation technologies. This includes a high degree of hygienic safety, because of, for example, the production of alcohol or a decrease of the pH value, which significantly increases the shelf life. Raw materials are refined by improving quality-determining properties. Further, harmful or toxic substances derived from raw materials, such as cyanides, goitrogens, proteinase inhibitors, phytic acid, oxalic acid, glucosinolates, and indigestible carbohydrates, are partly degraded (Vogel *et al.*, 2011). Moreover, fermented products meet the demand for natural and organic foods and they have low energy consumption during production, whereby it could be regarded as an ecologically friendly preservation technology.

The development of fermented foods was determined by the fact that originally a special microbial community developed under the ecological conditions present in the respective substrate. Such spontaneous fermentations are still in use for the production of olives, pickles, sauerkraut, or kimchee. For the industrial-scale formation of, for example, beverages and dairy products, defined cultures/starter cultures are used, which allow a greater control of the fermentation process. In this regard, starter cultures are defined as preparations of live microorganisms or their resting forms, whose metabolic activity has desired effects in the fermentation substrate/food

(Vogel *et al.*, 2011). Mäyrä-Mäkinen and Bigret (1998) further specified starter cultures into:

- Single strain cultures: contain one strain of a species.
- Multistrain cultures: contain more than one strain of a single species (e.g., a mixture of different *Lactobacillus* strains).
- Multistrain mixed cultures: contain different strains from different species.

The use of starter culture has some benefits, compared with spontaneous fermentation or an 'old-new inoculation' with in-house strains, which, for example, entails the risk of selecting *Listeria* in red smear cheeses (Bockelmann *et al.*, 2005). Starter cultures allow a uniform and high-quality food production in large scale, with controlled fermentation times and a reduced hygienic risk (Vogel *et al.*, 2011).

A special case of food fermentation is the use of protective cultures, for example, for fermented sausages like salami. The discovery that certain strains are competitive, and in particular that they can also inhibit pathogenic and toxigenic microorganisms, opens up the possibility that these strains can be used for food production. Hence, protective cultures are added to food with the aim of reducing risks by pathogenic microorganisms. Its effectiveness follows two principles. The first is the competitive exclusion, for example, through a competition for nutrients and binding sides/space for growth on the substrate or through a better adaption to the oxygen content. The second is the formation of antagonistically active substances, for example, the formation of organic acids (e.g., lactic, acetic, propionic, and formic acids) by lactobacilli or the production of ethanol, CO_2, and bacteriocins (compounds like Nisin) as well as antibiotics or other antimicrobial substances (Kessler, 2002; Vogel *et al.*, 2011).

Modified atmosphere packaging

Food packaging serves to protect a product against deteriorative effects, protects it against mechanical stress, communicates to the consumer as a marketing tool, and provides the consumer with ease of use and convenience (McMillen, 2008). To increase the shelf life of packaged food, different techniques can be applied. However, one of the most interesting application is the modified atmosphere packaging (MAP), because of the high demand of additive-free products.

MAP packaging is the removal or replacement of the atmosphere surrounding the product before sealing in vapor barrier materials (McMillin *et al.*, 1999). The proportion of gas inside the package can be changed passively, by properly using semipermeable materials, or actively, by using specific gas mixtures, together with semipermeable or impermeable packaging materials (Amanatidou, 2001). MAP can as well be a vacuum packing, which removes most of the air before the product is enclosed in barrier materials.

During active modification of the packaging atmosphere, first the air is removed by vacuum or flushing and later replaced with another gas mixture before sealing the package. The main gases used in mixture are CO_2, N_2, and O_2, but the potential of other gases (i.e., CO, Ar, or O_3) has been investigated as well (Zagory and Kadar, 1988). The optimal gas composition and storage conditions depend on the type of product and desired effect, which is often a slowing down of the respiration rate to reduce produce metabolism and maturation. For example, in fresh-cut vegetables the respiration rate is reduced by employing a gaseous atmosphere with an O_2 level low enough to maintain basic produce metabolism and using refrigeration temperatures as low as possible (often between 2 and 8 °C). The final shelf life of these MAP-packed products could be extended by 5–7 days (Amanatidou, 2001). High concentrations of O_2 (60–85%) are recommended for the MAP storage of poultry and fresh meet. The positive effects of high O_2 concentrations in muscle products is related to color retention of red meat, minimized drip losses, and inhibition of anaerobic microorganisms (McMillen, 2008). However, the shelf life of meat products further depends on the presence of CO_2. To minimize the risk of growth of anaerobic pathogens (i.e., *C. botulinum*) in fish products, lower O_2 concentrations ($\sim$30%) are recommended often in combination with higher CO_2 concentrations. On the contrary, it has been suggested to exclude O_2 for fatty fish products to minimize rancidity caused by lipid peroxidation.

Hence, the MAP packaging has to be adapted to the product, but if done correctly it could be a significant part of a hurdle concept to extend the shelf life of minimally processed products.

Surface Decontamination

Cold atmospheric plasma

Plasma is an ionized gas and also called the fourth state of matter. For the formation a plasma, a gas can be heated or an excess of free electrons is needed to displace electrons in the atoms and molecules of the bulk gas. The plasma can be described as a quasineutral particle system in the form of gaseous or fluid-like mixtures of free electrons and ion, frequently containing neutral particles (atoms and molecules), activated and metastable species (NO_x*), and free radicals like reactive oxygen species and reactive nitrogen species (Knorr *et al.*, 2011a; Rutscher, 2008). In the field of plasma research one can find a complex nomenclature considering the temperature of the electrons and the bulk gas and the surrounding pressure (Roth, 1995). In nonthermal plasmas, the electron temperature is much higher than the bulk gas temperature. Although the electron can reach several ten thousands K, the gas temperature remains at temperature levels below 40 °C (Knorr *et al.*, 2011a; Mastwijk and Nierop Groot, 2010). Most plasma source are operated in a vacuum; however, the most suitable system for food processing is an atmospheric pressure plasma device where no extreme conditions are required, low process temperatures are possible, and no evaporation of water from high-moisture food products occurs.

The industrial use of applied plasma technology in the nonfood sector is diverse (e.g., cost-effective light sources, high-definition large flat panel displays, and plasma-improved printability of foils). Much work has already been done in the field of plasma medicine and related topics, like tissue sterilization or blood coagulation (Fridman *et al.*, 2006). However, the first approaches in the field of food surface decontamination are published in the past years. These studies primarily focus on the inactivation of unwanted microorganisms on

heat-sensitive foods, such as fresh fruit and vegetables, meat, and eggs, where conventional thermal decontamination methods are more or less unsuitable. Plasma treatment is also regarded as a potential alternative to other chemical (e.g., chlorine treatment) or physical methods (e.g., HP, PEF, and ionizing irradiation). Advantages of plasma processes are high efficiency at low temperatures (generally $<70\ ^{\circ}C$); precise generation of plasmas suitable for the intended use; just in time production of the acting agent; low impact on the internal product matrix; application free of water or solvents; absence of residues; and their being resource efficient (Schluter *et al.*, 2013).

The presence of UV-emitting species, charged particles, and free radicals is associated with the antimicrobial effect of the plasma (Laroussi, 2005). The capability of nonthermal atmospheric plasmas to inactivate vegetative cells, including Gram-negative and Gram-positive bacteria, yeast, fungi, biofilm formers, and endospores, was shown in various studies (Moreau *et al.*, 2008). Recent interest is focused mainly on the inactivation efficiency of cold plasma with respect to contaminated pericarps of mangoes, melons, bell pepper, freshcut fruit surfaces, almonds, and eggs (Ragni *et al.*, 2010). However, the inactivation mechanisms of different plasmas are not yet fully understood. Depending on the plasma source, process parameters, and process gases the reactive species vary within the plasma, which makes inactivation mechanisms difficult to compare.

Recent research activities focus mainly on inactivation of microorganisms, but little is known about the effect of plasma on food matrices. Emitted reactive species not only react with bacteria but also affect food components, such as water, lipids, proteins, and carbohydrates (Keener, 2008), and have an effect on phenolic compounds, at least in lamp lettuces (Grzegorzewski *et al.*, 2010).

In the past decade, concerted research efforts were expended to understand and to apply atmospheric pressure plasmas as surface decontamination and sterilization method. Modular and selective plasma sources were developed. These combine the technological advantages of atmospheric pressure plasmas (avoidance of vacuum devices and batch processing) with the flexibility and handling properties of modular devices (Ehlbeck *et al.*, 2008). This technological progress may enable plasma applications in food processing in the near future. However, further investigations are required to characterize the plasma applied and to better understand the interactions of reactive species with organic surfaces as well as vital biosystems (Mastwijk and Nierop Groot, 2010). This will allow us to control the effects of plasma and to design highly specified and efficient plasma processes.

Steam

Natural microbial contamination in dried food, such as almonds, nuts, spices, seeds, cocoa beans, and cereal products, is found mainly at the surface of those foods. Microorganisms are not able to grow in low water activity environments; however, cells may survive. In addition, significant food safety risk may occur when contamination takes place after a lethal processing step, cross-contamination being one of the main causes of *Salmonella* contamination (Podolak *et al.*, 2010). Application of inactivation technologies is a powerful tool to eliminate or reduce the level of natural microbial contamination. However, without the implementation of good manufacturing practices, well hygienic designed equipment, and postcontrol lethality areas, the use of inactivation technologies could not guarantee a safe food production.

Commonly used processes for the decontamination of dried products are hot air, microwaves, radiofrequencies, or Joule-heating treatments. The application of heat on dried food often induces organoleptic degradation or achieves only a low destruction rate. It has also been well documented that heat resistance of microorganisms significantly increase with a decrease in water activity (McCann *et al.*, 2009; Staack *et al.*, 2010). The heat resistance at low water activity contents may correlate with the presence of a specific microflora adapted to harsh environment conditions. In addition, proteins become more stable when in a dry state during heat treatment (Hansen and Riemann, 1963). Moreover, water availability has also a great impact on the transfer of heat to microorganisms (Laroche *et al.*, 2005). The increase in resistance of vegetative cells to heat as a function of water activity has been studied by several authors (Bera *et al.*, 1998; Brown and Melling, 1971; Corry, 1973; Daemen, 1981; Laroche *et al.*, 2005).

In the case of pasteurization of almonds, all pasteurization technologies are evaluated by the ABC's technical expert review panel for their ability to provide a minimum 4-log reduction in *Salmonella* contamination and to demonstrate no significant degradation to the sensory, quality, and nutritional characteristics of almonds. Based on a risk assessment conducted for the ABC and reviewed by the FDA, it has been determined and implemented in 1 September 2007 that a 4-log reduction is an appropriate level of control (Almond Board of California, 2012).

The use of steam may help increasing the microbial inactivation of dried food products. The underlying mechanism of steam inactivation is based on increasing the water activity where bacteria are located: at the surface of the food. However, in order to avoid excess of steam condensation and an increase of final food moisture, the application of steam should be carefully done and thus the design of processes should allow a controlled steam condensation only at the surface of dried foods.

The processing of particulate food crops consists of several process steps. As an example, the following steps describe the adequate application of steam and its controlled condensation at the surface of dried foods (Perren and Fischer, 2009):

1. First, the product surface temperature is increased to a level right below the equilibrium temperature of the subsequent process step. To preheat, it is appropriate to use dry heat. This step allows conditioning the food and avoiding an excessive water condensation. If no preheating is applied, risks of increasing the food moisture and a larger heat impact on food quality properties might occur.
2. Second, the product is transferred into a preheated pressure vessel. In this vessel, a default pressure below atmospheric pressure is established and steam is induced into the product, whereas the pressure is maintained constant. To equilibrate the surface temperature of the product to the evaporation temperature of the system, a minor quantity of water condenses on the surface forming a surface water film. This water film allows increasing the water activity and

thus creating an environment adequate to transfer heat and faster bacterial inactivation.

3. Third, after equilibrium is achieved, the process continues for a given duration, until the desired inactivation of the microorganisms is accomplished.
4. Finally, the steam injection is stopped and the system pressure is further reduced in order to evaporate excessive surface moisture. Thus, the food is restored to its initial condition as it was before the controlled condensation process.

Minimized treatment times are possible only on the basis of the unique combination of HP, high temperature, and high humidity. An optimized combination of the above parameters may allow the inactivation of pathogenic and even thermophilic vegetative microorganisms and their spores within a very short time to below detection limits.

Conclusion

The tailored preservation of food involves the selection of a suitable processing technology according to the characteristics of the food as well as according to processing targets, such as relevant spoilage microorganisms and desired shelf life conditions. It was shown that available technologies differ widely in their ability to inactivate vegetative cells and spores inside or on the surface of a food product. Traditional thermal processing was often found to negatively affect food quality of sensitive products, which led to the development of more gentle processing technologies applying advanced heating principles or using nonthermal inactivation mechanisms. Process validation remains the key challenge in order to assure the suitable selection of processing conditions and the consideration of food characteristics covering aspects such as the presence of particles as well as the distribution of salt affecting the heating properties during Ohmic or microwave sterilization. The profound knowledge of the relevant process–product interactions will allow the successful application of existing processing concepts and will lead to further innovations toward a targeted food preservation.

See also: Energy and Greenhouse Gases Footprint of Food Processing. Food Engineering. Food Microbiology. Food Safety: Emerging Pathogens. Food Safety: Food Analysis Technologies/Techniques

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Food Security: Development Strategies

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Rice and Food Security in Asia

Rice, a staple for nearly half of the world's seven billion population, is grown in more than 100 countries. However, more than 90% of rice is produced and consumed in Asia, where it constitutes the basic staple for majority of the population, including the region's 560 million hungry people. As a poor man's food, rice is a sensitive topic in many countries; governments can 'make or break' with the fall and rise of rice prices. In many of these countries, rice is deeply engraved into their rich culture and tradition. Asian countries also take immense pride in having a vibrant rice farming system, and the reaffirmation of many countries after the 2008 rice crisis to revamp domestic rice sector and achieve food security through rice self-sufficiency is a good example of what rice means to many countries in the region.

The introduction of high-yielding varieties in the late 1960s, which marked the beginning of the Green Revolution, has more than tripled Asian rice production in the past four decades, from 200 million tons (paddy equivalent) in early 1960s to above 600 million tons in 2010. This has been possible with the introduction of modern varieties in tandem with assured irrigation, subsidized inputs (such as fertilizer, fuel, and pesticide), and guaranteed prices. During this period, more than 1000 modern varieties have been released to farmers in Asian countries with the adoption from 30% in 1970 to approximately 70% in 1990 (IFPRI, 2002).

The success of the Green Revolution in the early 1960s witnessed steady rise in Asia's per capita rice consumption from 85 kg in the early 1960s to approximately 100 kg by 2010; however, global per capita consumption rose from 50 to 65 kg during the same period (Figure 1). The rising per capita consumption in combination with growing population resulted in tripling of total Asian rice consumption during this period from 150 to 450 million tons (milled equivalent).

In line with rising rice consumption, per capita calorie intake also increased by more than 40% from 1891 in 1960 to 2706 in 2009. Similarly, life expectancy and infant mortality also witnessed significant improvements during the post-Green Revolution era. Although the contribution of rice to total calorie intake has dropped in Asia during this period (from 38% in 1970 to 29% in 2009), it still accounts for 45–70% of total calorie intake in many rice-consuming countries in the region including Bangladesh, Cambodia, Vietnam, Indonesia, and many other Asian countries (Figure 2).

Changing Consumption Patterns

Since the early 1990s, strong economic growth in many Asian countries, particularly in China and India, snapped the upward trend in Asian per capita rice consumption as consumers diversified their diet from rice to high-value products, such as meat, dairy products, fruits, and vegetables. Between 1992 and 2005 per capita rice consumption in Asia declined from 103 to 96 kg. Similarly, per capita rice consumption in India also declined after economic liberalization in the early 1990s. In both these countries, per capita consumption declined by 10 and 8 kg, respectively, during this period. Despite such decline in per capita consumption in heavyweights like China and India, the total consumption in Asia has continued to rise on the basis of population growth and rising per capita consumption in other Asian countries.

However, the declining trend in per capita rice consumption in heavyweights like China, India, and Indonesia has been snapped in recent years and per capita consumption has started rising again (Figure 3). This reversal in trend has contributed to the recent surge in total Asian global consumption: 40 million tons in 7 years. Household consumer expenditure data collected by India's National Sample Survey Organization also confirm the flattening in per capita consumption in recent years from the declining trend in the 1990s in all four regions in India.

In other Asian countries, such as Bangladesh and the Philippines, per capita consumption remains strong across income groups both in urban and rural areas. National representative household consumption survey data collected between 2000 and 2010 both from the Philippines (Family Income and Expenditure Survey) and Bangladesh (Household Income and Expenditure Survey) confirm the trend. Even high-income group population both in rural and urban areas is found to consume more rice with rise in income. Unlike the Philippines and Bangladesh, per capita rice consumption is on a downward trend in few other Asian countries including Thailand, Vietnam, and Malaysia.

Future Consumption Trends

As one looks ahead, income growth, urbanization, and other long-term social and economic transformations are likely to influence the composition of food basket in the future. Normally, one would expect diversification away from rice to more high-value products, such as meat, dairy products, fruits, and vegetables in the diet as the income rises. But the diversification rate in many Asian countries will also be influenced by the extent of government interventions in price control and subsidized food grain distribution.

India is a good example, where the government has rolled out an elaborate food subsidy program to provide highly subsidized food grains (rice and wheat) for 65 million below-poverty-line households, including nearly free food grains to 20 million Antyodaya Anna Yojna (AAY) households, the poorest of the poor households. Each of the 65 million households is provided 35 kg of grains every month at 74–86% below the procurement cost (Sharma, 2012). The above poverty line (APL) families are also given 15–35 kg of grain every month depending on the availability at less subsidized

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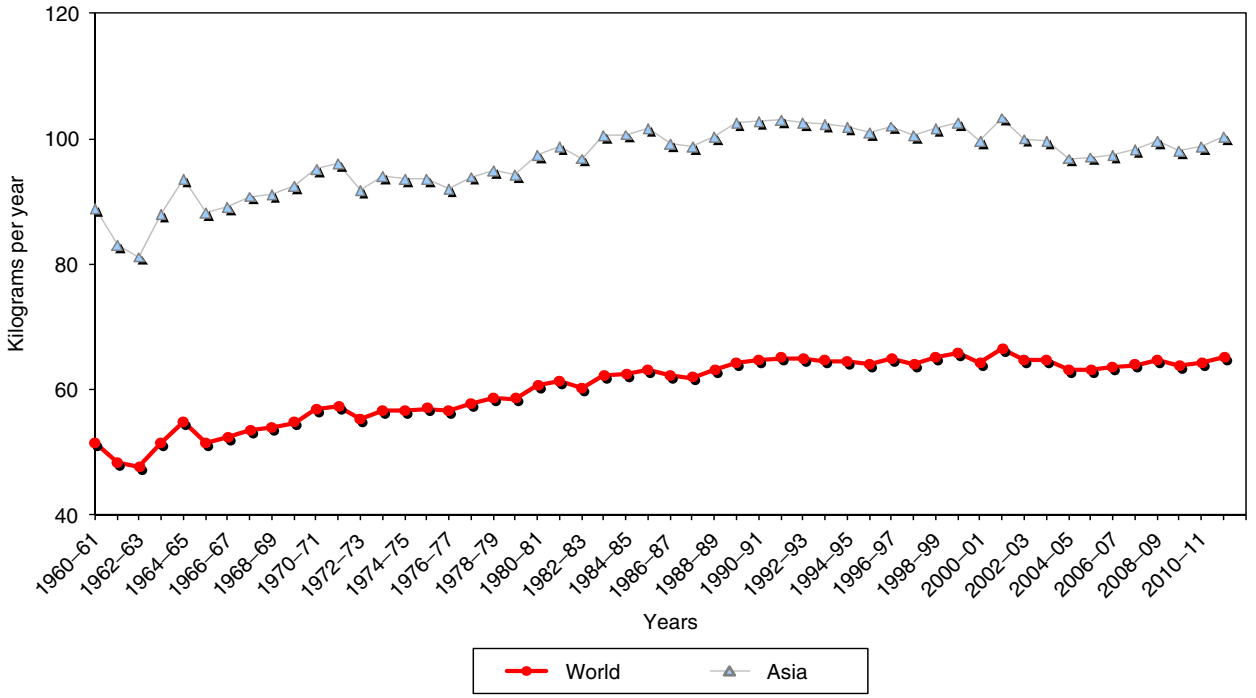


Figure 1 Global and Asian per capita rice consumption. Reproduced from PSD online database (USDA) and FAOSTAT population database (FAO).

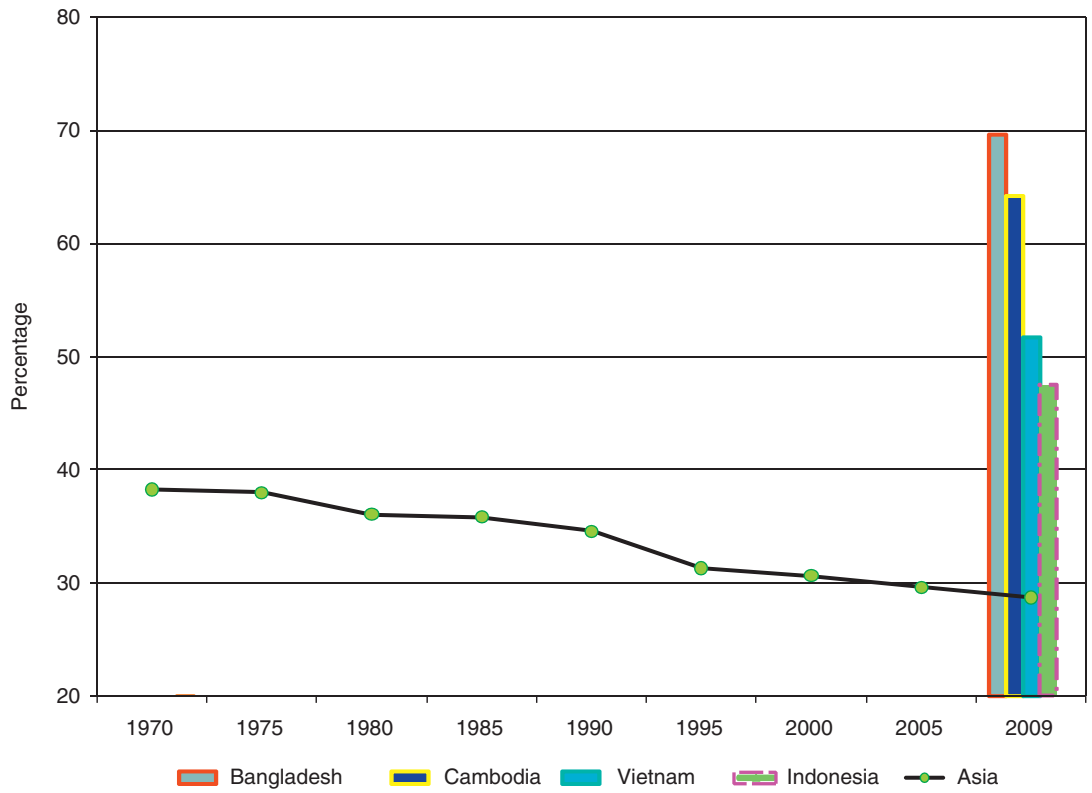


Figure 2 Share of rice in total calorie intake in Asia.

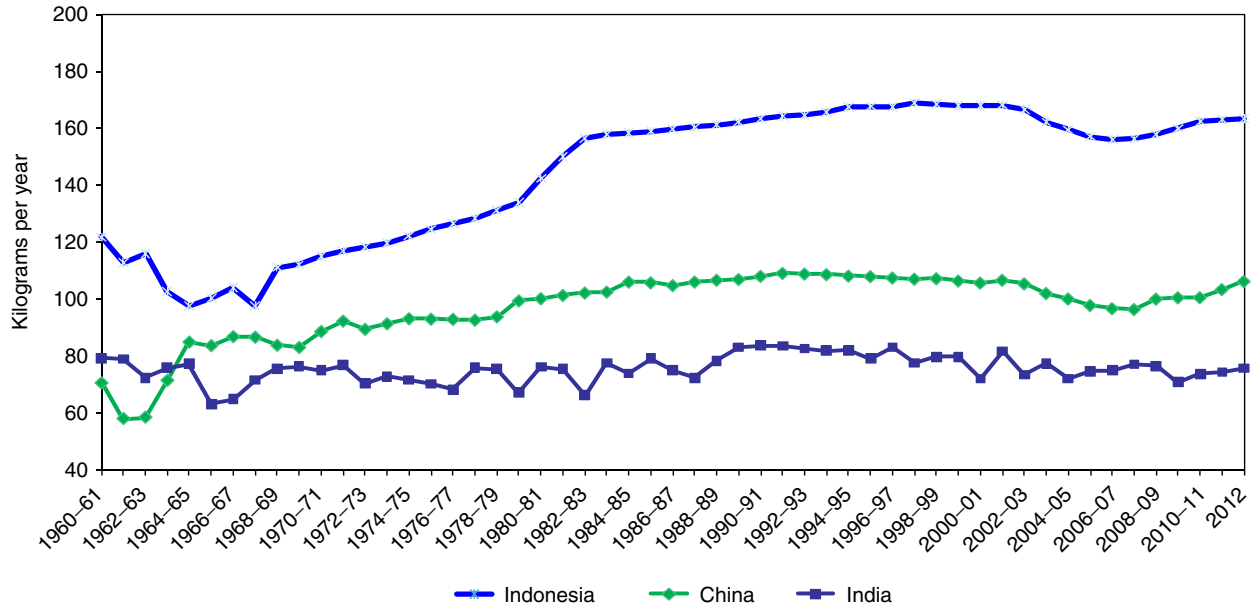


Figure 3 Per capita rice consumption in the top three countries. Reproduced from PSD online database (USDA) and FAOSTAT population database (FAO).

prices. In 2011/12, the food subsidy bill amounted to approximately Rs 72 823 crores (US$14 billion) (Sharma, 2012).

Thus it would be a mistake to bundle all Asian countries together and project them to behave like Japan and South Korea as they get wealthier. Each Asian country will be unique in the way it diversifies its consumption pattern as incomes rise. For a country such as India with a large number of vegetarians, it is unrealistic to assume that their rice consumption will follow the patterns of the Korean, Japanese, and Taiwanese populations with rising standards of living. Even other developing Asian countries, such as Bangladesh, the Philippines, and Vietnam are likely to adopt consumption patterns different from what has been witnessed in the past. Overall, it may be reasonable to assume that the diversification away from rice will be slow in many Asian countries and the minimum threshold level of rice consumption for each country will be different.

Additionally, 700 billion mouths will have to be fed in the next 30 years, based on United Nation's 2010 population projections, when the Asian population reaches close to the 5 billion mark in 2035 and 5.15 billion by the mid-century. If Asian per capita rice consumption follows the trend it has seen in the past two decades, then total consumption will grow at the rate of population growth. The total consumption growth may even exceed population growth if the recent uptrend in per capita consumption in 'big three' countries (China, India, and Indonesia) continue in the future.

The bottom line message is that if diversification in Asia is slow and not widespread then it is almost certain that the total demand for rice in Asia will continue to rise in the future. However, the opposite will be true and total Asian consumption may start declining if Asian countries follow rapid diversification path. A recent study by Seck *et al.* (2012) projected global rice consumption to rise from 439 million tons (milled rice) in 2010 to 496 million tons in 2020, and it will further increase to 555 million tons in 2035. Among the various rice-consuming regions, Asian rice consumption is projected to account for 67% of the total increase, rising from 388 million tons in 2010 to 465 million tons in 2035.

Future Supply Prospects

In the first three decades of the Green Revolution, the higher productivity growth of more than 2% annually provided incentives for farmers to bring in additional areas into rice production. Part of the area expansion has been possible due to greater cropping intensity through the adoption of short-duration varieties. A combination of productivity growth and area expansion provided the needed production growth to keep rice prices affordable and meet the global needs. However, in the past decade, yield growth has significantly slowed down: less than 1% in recent years. The effect is already evident with two food price spikes in the past 5 years and steady rise in rice prices in the past decade. From 2001 to 2007, rice prices nearly doubled, primarily because of the supply–demand imbalance. Between November 2007 and May 2008, the rice market witnessed the tripling of international rice prices. Although prices went down quickly after May 2008, they have settled at a much higher level of US$500–600 per ton as compared with US$300–400 per ton before the crisis.

The current rice area is at an all time high at approximately 160 million hectares as compared to 120 million hectares in the early 1960s. Further expansion of rice area in the future is not a viable option for most Asian rice-growing countries, where additional land is no longer available and pressure on the existing rice land from urbanization and other non-agricultural uses is growing rapidly. This is particularly true for China, India, Indonesia, Thailand, the Philippines, and Bangladesh, which account for approximately 70% of global rice

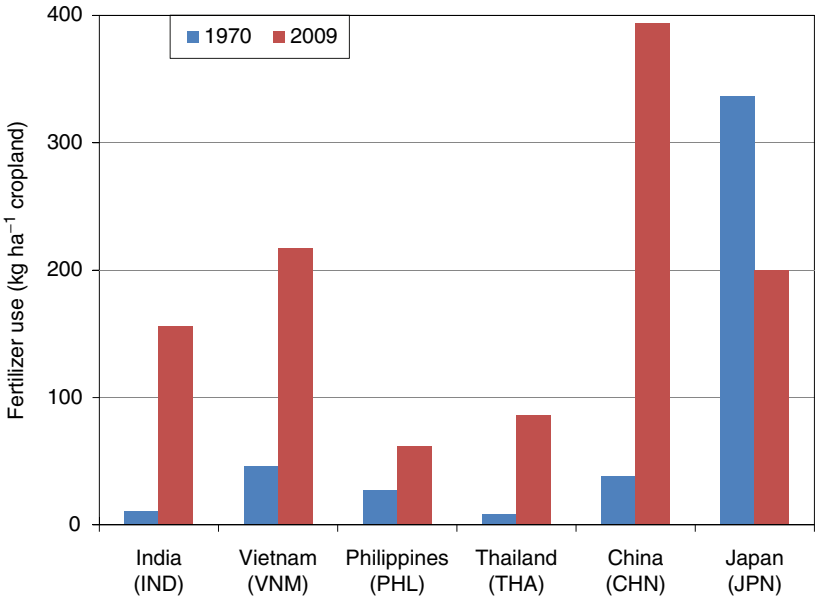


Figure 4 Fertilizer (NPK) use in agriculture, 1970–2009. Reproduced from International Fertilizer Industry Association (IFA) and FAO.

production and consumption. For example, China's rice area has declined by more than 5 million hectares (15%) in the past 3 decades and the downtrend may continue in the future. Although a similar downtrend has not been evident in other rice-growing countries in the region because of government interventions, it is hard to foresee how governments can continue with such interventions in the face of rising costs, water shortages, and growing pressure from competing sectors.

The few exceptions could be countries such as Cambodia and Myanmar, which were left out of the Green Revolution for varying reasons but they could be stimulated to expand rice production by developing infrastructure and providing better market linkages.

Without the possibility of further area expansion in the future, yield growth will have to be revamped to approximately 1.5% annually to be able to meet growing global needs and keep prices affordable. But unfortunately, the approaches adopted that led to the success of the first Green Revolution may not be applicable now. During the first Green Revolution, many Asian countries provided incentives to the farmers through subsidized inputs and assured markets for their products to expand rice production. Farmers responded by adopting input–responsive high-yielding modern varieties and bringing additional land into crop production.

Fertilizer use in Asian countries has increased markedly in the past four decades (Figure 4). In China, fertilizer application per hectare in NPK equivalent has increased from 38 kg in 1970 to approximately 400 kg in 2009. Similarly, Vietnam has witnessed a five-fold increase in fertilizer use during this period from 46 kg in 1970 to 217 kg in 2009. Fertilizer use in India has gone up significantly during this period but still remains low as compared to China and Vietnam at 156 kg ha^{-1}. However, the variations among Indian states are still very large. The problem is much more severe in frontline Green Revolution states of Punjab and Haryana where NPK use per hectare is 200 kg ha^{-1} as compared to 50 kg for Orissa and 10 kg for Arunachal Pradesh, the states mostly left behind by the Green Revolution.

Similarly, use of ground water for irrigation purpose has also increased in many Asian countries, more notably in India, Indonesia, and Bangladesh. In case of India, water withdrawal for agriculture increased by more than 70% in the past three decades (Figure 5). Similarly, agricultural water withdrawal has gone up by approximately 25% in Indonesia between 1990 and 2000. In a recent study published in *Nature*, Rodell *et al.* (2009) concluded that groundwater use for irrigation in northwestern India is not sustainable. According to this study, the water table in this part of India is declining by 4 cm $year^{-1}$. Thus, yields improvements in the future needs to be achieved in the face of these emerging constraints including land and water scarcity, environmental degradation, and rising input prices.

Climate Change

Apart from various constraints described above, the anticipated change in global climate in the form of rising temperature, increasing amount of carbon dioxide in the atmosphere, greater frequency of extreme weather events (e.g., floods and droughts), and greater incidence of pest and diseases are likely to make things more complicated for rice production in the future. A large share of rice production is already lost to various abiotic (flood, drought, and salinity) and biotic stresses (pests and diseases). Among abiotic stresses, drought is the largest constraint, affecting nearly a third of the total rice area in Asia (Venuprasad *et al.*, 2008) and causing significant economic losses to poor rice producers in the region. According to Pandey and Bhandari (2007), average production loss due to drought in three regions: eastern India, northeast Thailand, and southern China adds up to US$200 million annually. Similarly, flood is another abiotic stress that

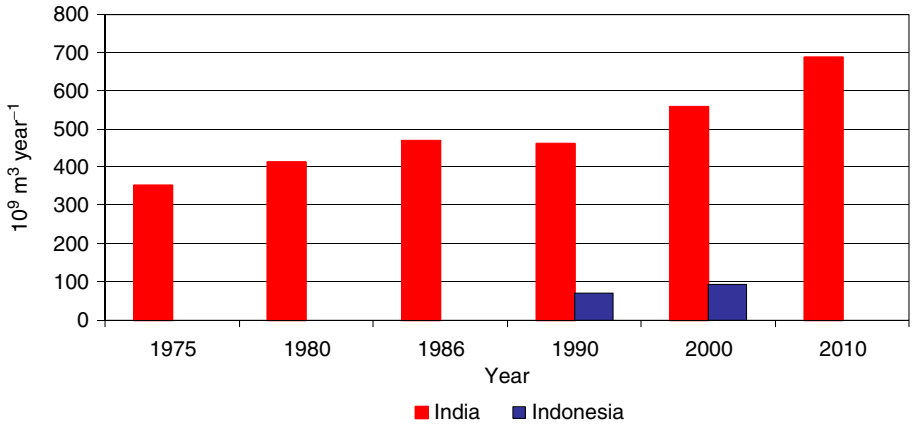


Figure 5 Agricultural water withdrawal. Reproduced from FAO AQUASTAT database.

regularly causes severe rice yield damage on 16 million hectares of flood-prone rice area in Asia (Johnson *et al.*, 2012). The annual loss in rice production in South Asia alone is estimated to be 4 million tons (IRRI, 2010). Salinity, though not as big a stress as drought and flood, still affects 10 million hectares of coastal and inland areas (Johnson *et al.*, 2012). But growing rice is the only option available to farmers in the saline-prone coastal regions where nothing else can be grown; this crop is critical to the food security of these resource-poor farmers.

Crop losses are likely to be lot greater in the future with changing climate that will make flood, drought, and salinity more frequent and severe. In addition, rising sea levels due to climate change are expected to spread the salinity problem to a wider growing area where rice is presently cultivated under favorable conditions. The rice area in some deltas may also be affected by salinity. For example, the Mekong River delta, which accounts for nearly half of Vietnam's total rice production, is also vulnerable to sea-level rise in the future. Salinity may also spread beyond the coastal areas and deltas to some groundwater irrigation agriculture in the interior regions. The excess withdrawal could increase salinity in groundwater, making it unsuitable for rice production (Mohanty *et al.*, 2012). Similarly, drought losses would be much greater in the future, with many rainfed areas experiencing more intense and more frequent drought spells (Mohanty *et al.*, 2012).

In addition to higher production losses caused by more frequent and more severe droughts, floods, and salinity, rising temperatures will also negatively affect yield and grain quality in the future (Fitzgerald and Resurreccion, 2009). This is true if temperature becomes higher during the reproductive phase, particularly during flowering (Jagadish *et al.*, 2010). In the past three decades, nighttime minimum temperature has been rapidly rising and the current trend is expected to continue in the future. Studies by Welch *et al.* (2010) and Peng *et al.* (2004) have estimated that a 1 °C rise in nighttime temperature above critical temperature (>24 °C) would reduce yield and biomass by 10%.

Apart from direct production losses due to actual occurrence of extreme weather events and rising temperature, farmers in stress-prone environments also practice less intensive agriculture by applying less input. They end up getting lower yield, even in normal years. The rise in frequency of extreme weather due to climate change is likely to make these farmers even more risk-averse, causing further decline in yields in normal years.

Nelson *et al.* (2009) estimated the impacts of climate change on global agriculture using the IMPACT model developed by the International Food Policy Research Institute. The model includes a hydrology model and links crop simulation model to the Decision Support System for Agrotechnology Transfer (DSSAT). The study also looked at additional investments that would be required to offset the negative consequences of climate change on global food security. The results suggest that climate change will have varying impacts on rice production across regions. But the overall global rice production in 2050 under two climate scenarios (Commonwealth Scientific and Industrial Research Organisation and National Center for Atmospheric Research) is projected to decline by 12–14% relative to the 2000 level. The production effect accounts for both changes in area, yield, and farmers' adaptation due to climate change. Sub-Saharan Africa and South Asia would be the two hardest regions in terms of decline in rice production, followed by South Asia and East Asia and the Pacific. In terms of absolute change in rice production, South Asia would be the worst affected region: Rice production is projected to change from 169 million tons in 2050 under the no-climate-change scenario to slightly above 100 million tons under a climate-change scenario, a difference of more than 65 million tons of rice. The decline in production would result in higher prices and lower consumption, which eventually would lead to lower calorie intake and increase in child malnutrition. Overall, the study suggests that developing countries would be worse off than developed countries for all crops, including rice.

Similarly, a study by Agarwal (2008) estimated approximately 18% decline in Thailand's rice yield in 2020 because of climate change. Another study by Srivastava *et al.* (2009), focusing on three major rice ecosystems in India (Odisha, Kerala, and Tamil Nadu) found varying impacts of climate change on rice production. They found that in Kerala and Odisha, the decrease in yield due to rising temperature is likely to be offset by the increase in yield due to high atmospheric CO_2 concentration. However, that is not the case in Tamil Nadu, where

currently grown varieties show much greater decline in yield due to the higher temperature. It makes Tamil Nadu more vulnerable to climate change.

In addition to the above-mentioned abiotic stresses, many biotic stresses, such as pest and disease incidence and weed infestation would also be triggered by climate change. Sparks *et al.* (2012) estimated yield loss for Asia due to pest and diseases under current climate condition by combining yield loss estimates obtained by simulating a rice yield loss model 'RICEPEST' due to sheath blight, brown spot, sheath rot, bacterial leaf blight, brown planthoppers, defoliating insects, deadhearts, and whiteheads caused by stem borers, and weeds with estimates of area under two most common rice ecologies, i.e., intensive irrigated monoculture system and rainfed system. Average yield loss due to major pest and diseases was at a staggering 37% and ranged between 24% and 41%, depending on the production system. These losses would be bigger with climate change that would bring about frequent extreme weather, water scarcity, and uneven rainfall. This is particularly true for brown spot and blast, which are expected to intensify with water shortage and irregular rainfall (International Rice Research Institute). In addition, weed infestation is also predicted to rise with climate change and would represent a major challenge for sustainable rice production.

One of the most important adaptation strategies is to develop varieties that can withstand extreme weather conditions to enable them to perform better than current modern high-yielding, varieties. The future efforts should be directed in developing varieties that withstand multiple stresses such as drought and flood in the same season. This is extremely important for rainfed lowland areas where the likelihood of both flood and drought occurring in the same season is expected to be higher in the future with the changing climate.

Apart from planting stress-tolerant varieties, farmers need to modify their management practices to counter the negative effects of climate change on rice production. First and foremost, water-saving technologies, such as alternate wetting and drying, land leveling, improved tillage, bound preparation, and direct seeding, among other things, can make a significant difference in keeping the plant standing in the face of water shortage and irregular rainfall. Similarly, farmers should be educated on pest dynamics and the benefits of diverse ecosystems to keep pest at a distance in order to minimize pesticide overuse. This cannot happen without active participation of government agencies that can make policy reforms to prevent excessive use of pesticides.

Market Distortions

Historically, rice production in Asia has been subjected to extensive market distortions because of its strategic and political importance. For decades, governments in major rice-growing countries in the region have attempted to minimize market risk faced by farmers through various policy measures such as subsidized inputs (fertilizer, seed, fuel, pesticide, machinery, etc.) and guaranteed price for paddy. The goal was to support farm income and at the same time keep rice affordable for millions of urban poor. To make domestic programs work, majority of Asian countries have tried to insulate the domestic market from global uncertainty through a slew of trade measures including state trading, export ban, import ban, import tariffs, import tariffs, export quota, and others. However, since the recent rice crisis in 2007, countries have revamped their efforts to expand rice production by raising support prices at a much faster rate than what has been witnessed in the past. For example, as shown in **Figure 6**, the minimum support price (the price at which the government purchases crops from the farmers) for rice has gone up by 75% between 2007 and 2011, whereas it took 12 years, from 1994 to 2006, for the minimum support price to increase by a similar proportion.

This has resulted in a global rice market that is very small with only 5–7% of the total production as compared to 20% for wheat, 13% for maize, and 30% for soybeans. For most rice exporters in the region, trade is an afterthought when domestic need and an adequate buffer stock are achieved. However, the volume of global rice trade increased by 150% between 1990 and 2010 due to trade liberalizations by many countries in the late 1980s and the General Agreement on Tariffs and Trade in 1994 after remaining stagnant for three decades before that.

The recent rice crisis in 2007 has forced many rice-growing countries to take measures to achieve food security through self-sufficiency and move away from their dependence on imported rice. If this trend continues then the global rice market, which is already small may even get smaller in the

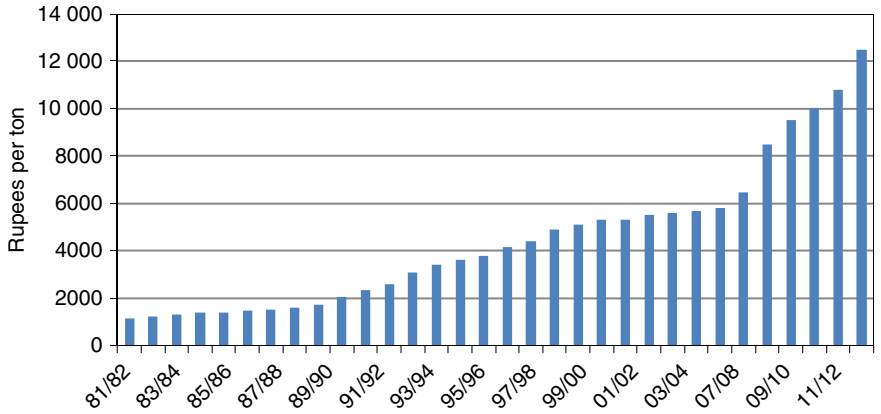


Figure 6 Indian paddy minimum support price (common varieties). Reproduced from Department of Agriculture and Cooperation, India.

future. This would push exporters such as Thailand, Vietnam, and Pakistan to cut back on their production to reduce exportable surplus and use their land for planting other profitable corps. The smaller market will lead to greater price volatility with rapid rise in rice prices in years of low production and vice versa. This will particularly affect the food security of poor countries who cannot afford to buy rice at higher prices from the international market.

Toward a Food-Secured Asia

Rice continues to remain a political commodity in Asia. Countries in the region are still bogged down with rice food security and treat it very differently from other food commodities. Despite economic boom in the region in the past three decades and rise in income and prosperity, rice consumption remains high across countries, with some diversification away from rice in a few selected countries. Interestingly, per capita rice consumption in India, China, and Indonesia, which account for more than 65% of total Asian consumption, have started rising again after steady decline in the past decade. Overall, rice consumption in Asia is projected to rise in the next two decades even with the slow down in population growth and diversification in some Asian countries.

The future supply growth, however, seems to be on shaky ground with several emerging uncertainties including possible rice area decline, slowdown in productivity growth, and climate change. The Asian rice productivity growth that has fallen below 1% in the past decade is definitely a serious matter of concern for food security in the region as further area expansion is unlikely to continue in the future. As a matter of fact, most experts feel that Asian rice area is likely to fall in the future because of population pressures, water shortage, and also competition from other crops. In addition, the ongoing structural transformation of Asian agriculture with aging farmers and out-migration of rural youths may also influence rice farming in the future. Ultimately, the onus falls on policy makers to adequately fund agricultural research and on scientists to develop technologies that are climate proof and enable farmers to grow more with less inputs and smaller environmental footprint.

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Food Security: Food Defense and Biosecurity

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Glossary

Biosecurity It is the reduction in intentional or unintentional spread of infectious disease, pathogens, or invasive pests.

Economically Motivated Adulteration (EMA) It is surreptitious addition of nonauthentic substances, unwarranted substitution of ingredients, or mislabeling of food products to gain inequitable financial advantage.

Food defense It is the reduction in the occurrence and impact of intentional acts of contamination or tampering intended to cause physical or economic harm on the food system and consumers.

Food protection The combined efforts of food safety and food defense.

Food safety It is the reduction in exposure of food to naturally occurring, unintentional hazards or failures.

Food security It is the access by all people to enough readily available, nutritionally adequate, and safe food for an active, healthy life. This includes the ability to acquire acceptable foods in a socially acceptable way.

Food terrorism The deliberate (or threat of) contamination of food with hazardous agents (biological, chemical, physical, or radionuclear) for the purpose of causing injury or death and/or disrupting social, economic, or political stability.

Introduction

Food safety programs focus on reducing unintentional contamination of the food system, whereas food defense programs are designed to reduce intentional contamination of the food system. A common goal for both food safety and food defense programs is to prevent foodborne illness; however, "foodborne illness from intentional contamination results not from system failure (as in food safety), but instead from intentional attacks on a system that defeat the in-place controls" (Kennedy and Busta, 2013, p. 93). The unique challenge of food defense is that the adversaries are not just pathogens routinely finding niches to survive and grow along the food processing chain but can also be intelligent humans with the ability to craft a method that will evade detection and will overcome control systems in order to deliver a deleterious agent to consumers. Therefore, food safety systems such as Hazard Analysis and Critical Control Points (HACCP) are a start, and only a start, to a well-defended food system.

Motivations for an individual or group to contaminate the food system may include extortion, political assassination or coercion, a disgruntled employee, interpersonal conflict, or to use food as a means of terrorism. Food terrorism is the intentional contamination of food to harm people, animals or plants, or otherwise create terror, panic, or economic disruption. However, food terrorism is distinguished from nations attacking other nations. Food terrorism is generally attributed to nonnation actors attempting to disrupt the stability of a nation or the food supply (World Health Organization, 2008).

Food defense contributes to the overarching goal of food security: the accessibility of adequate nutrition to support a healthy, active lifestyle and the ability to obtain that nutrition through socially acceptable means, that is, food security cannot be achieved without the food being safe from intentional contamination. See **Figure 1** for relationships between the various food system programs.

The first step in creating a food defense plan is risk assessment. The goal of risk assessment is to identify the highest hazard and most likely vulnerabilities to be exploited in a food defense incident. The analysis informs how resources can be used commensurately to the vulnerabilities, addressing highest priority vulnerabilities first. Intentional contamination of food could involve sundry biological, chemical, physical, or radiological threat agents. There were more than 350 confirmed malicious contamination of food from 1950 to 2008, and there have been 169 separate recorded incidents of economically motivated adulteration (EMA) around the world since 1980. Examples of each type of incident are highlighted here in the following sections.

Before, during, and after a food defense incident, best practices must be used to design effective risk and crisis communication messages to the public. Risk and crisis communication could mean the difference between public outrage and public collaboration when addressing a food defense incident. The most recent, most impactful official policies on food defense include the Food Safety Modernization Act (FSMA), US Presidential Policy Directive 8 (PPD-8), and the International Health Regulations (IHRs). Official policy serves as a driving force to develop food defense systems in the food supply.

The importance of food defense is evident by its potential for catastrophe: "Intentional contamination of the food system has the potential to result in disastrous and far-reaching effects, including direct morbidity and/or mortality, disruption of food distribution, loss of consumer confidence in government and the food supply, business failures, trade restrictions, and dramatic ripple effects on the economy" (Busta and Kennedy, 2011, p. 120). The fact that the food system is an extraordinarily complex network of supply chains creates a twofold challenge: there are many points along the supply chain that could be contaminated, and it is exceedingly difficult to monitor and protect every step and transfer. Globalization of the food system adds greatly to this challenge

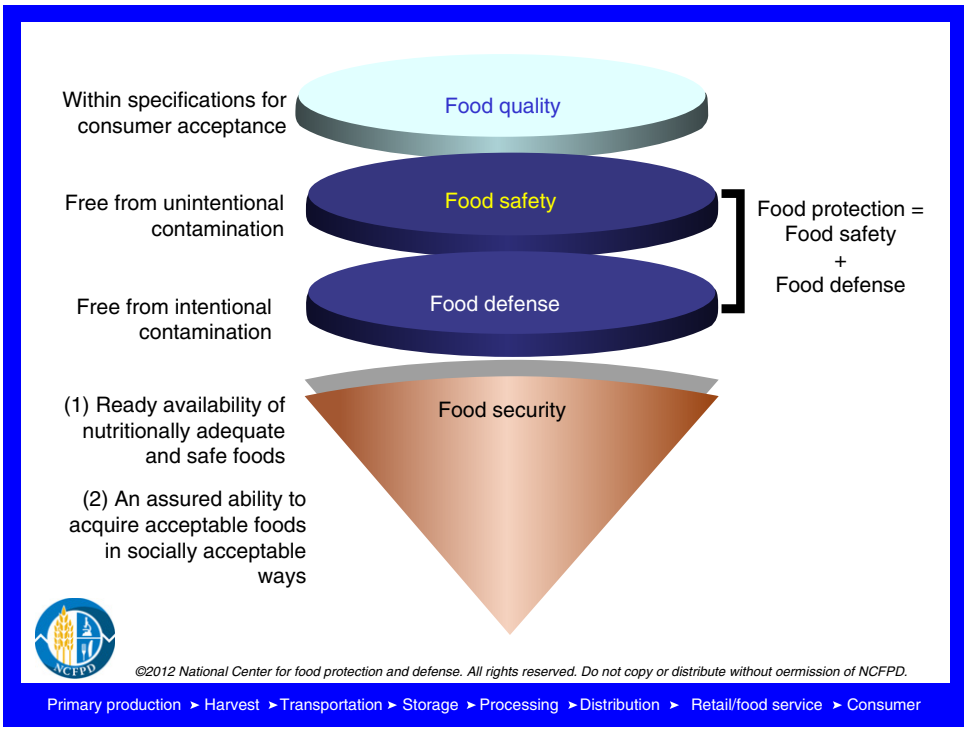


Figure 1 Relationships between food system programs. Reproduced with permission from Figure 7.1 in Busta, F.F., Kennedy, S.P., 2011. Defending the safety of the global food system from intentional contamination in a changing market. In: Hefnaway, M. (Ed.), Advances in Food Protection, NATO Science for Peace and Security Series A: Chemistry and Biology 1. Dordrecht, The Netherlands: Springer Science & Business Media B.V., p. 121.

because vulnerability existing in one nation traces into another nation through trade. The entire farm-to-table food system must invest in infrastructure to prevent, rapidly identify, and respond to intentional contamination or threatened intentional contamination; moreover, transnational collaboration is essential for complete food system defense.

Global Food System Defense

Today's food system is a vast and incredibly complicated network of supply chains. Each supply chain is also an elaborate concert of producers, processors, suppliers and buyers, exporters and importers, and retailers and distributors. The food system is literally complexity compounded on complexity which creates a problem in the realm of food defense: "The transition of the agriculture sectors in the developing world from subsistence agriculture to agribusiness... directed at commodity and value-added exports has dramatically increased access to the food supply chain and consequently increased vulnerabilities" (Busta and Kennedy, 2011, p. 124). Specifically, vulnerabilities arise when food products are created from disparate global sources as well as when they are produced and distributed rapidly and widely.

Given the magnitude and interconnectedness of the modern global food trade, "an attack on one country's food supply cannot be seen in isolation" (World Health Organization, 2008, p. 11), and the contamination may spread to other countries through trade. For example, staphylococcal toxin contamination in canned mushrooms from China caused illness in the US in 1989 (World Health Organization, 2008). Therefore, the World Health Organization (WHO) explains that thorough collaborative relationships between nations are imperative for global food defense: "cross collaboration with governments, global cooperation in surveillance and outbreak preparedness, alert and response, open sharing of knowledge, technology and materials and capacity building in health security is necessary by Member States" (World Health Organization, 2008, p. 3). Since the 55th World Health Assembly in 2002, WHO has worked to provide tools and support for Member States to prepare for and respond to food defense threats. The role of the WHO in a food terrorism event is to act as the directing coordinating agency, implementing the IHR and assisting in other varied emergency response action capacities.

A bioterrorism incident in the food system would also have enormous economic impact on the food industry domestically and internationally. In 1998, a company in the US recalled 14 million kilograms (30.9 million pounds) of sausages, frankfurters, and luncheon meats potentially contaminated with *Listeria*. The company closed the plant and estimated their total loss to be US$50–70 million (€38–54 million) (World Health Organization, 2008). This example is a demonstration of the vast economic impact of contamination in the food supply. The losses are exacerbated when such an incident causes nations to bar trade from the nation experiencing the contamination. The UK 's multiyear Bovine Spongiform Encephalopathy (BSE) crisis caused an estimated loss between £740 and £980 millions (€0.8–1.1 billion, US$1.1–1.5 billion) in 1 year alone. The crisis also caused the European Union and other countries to ban the export of British beef,

and once the suspected link between BSE and variant Creutzfeldt–Jakob Disease was announced, public confidence in the beef industry and the government was greatly diminished (Atkinson, 1999).

Closing borders as a response to a global food defense incident is perhaps too little, too late – the food system is too globalized, and products move too rapidly for that to be an effective response to prevent the movement of contaminated food. The systems necessary to prevent and efficiently respond to an international food defense incident are not yet in place, and many countries may not have the public health service capacity to effectively address the illnesses resulting from a catastrophic food defense incident. Food defense as a threat to public health is not theoretical. There have been real cases of intentional contamination of the food supply to cause harm to public health. For these reasons, international collaboration is needed to improve global food defense.

Highlighted Food Defense Incidents

Biological warfare dates back to ancient history and is still timely today. One of the earliest records of intentional contamination of a food or water supply is when the Athenians contaminated the city of Kirrha's drinking water circa 600 BC to lay siege to the city easier while its citizens suffered from gastroenteritis. In more recent history, Japan experimented during World War II with food as a vehicle for pathogens (Kennedy and Busta, 2013). The difference between warfare and food defense is that warfare involves one nation versus another nation, but malevolent nonstate actors working to disrupt order or cause physical harm carry out food defense incidents.

Intentional contamination incidents have been recorded at every major point along the farm-to-fork continuum: preharvest, processing, transportation, retail, and consumer levels. Figure 2 shows a map of the more than 350 confirmed malicious contaminations of food by different countries from 1950 to 2008. There is a difference between intentional contamination to cause harm to an individual or group of people (malicious contamination) and intentional contamination for economic gain (EMA), but both cases may lead to catastrophe. For example, 20 000 injuries and 800 fatalities in 1981 were the result of 'toxic oil syndrome' from EMA of cooking oil with industrial rapeseed oil in Spain (Dalziel, 2009). This example is one of many alarming instances that show just how easy it is to contaminate the food system despite

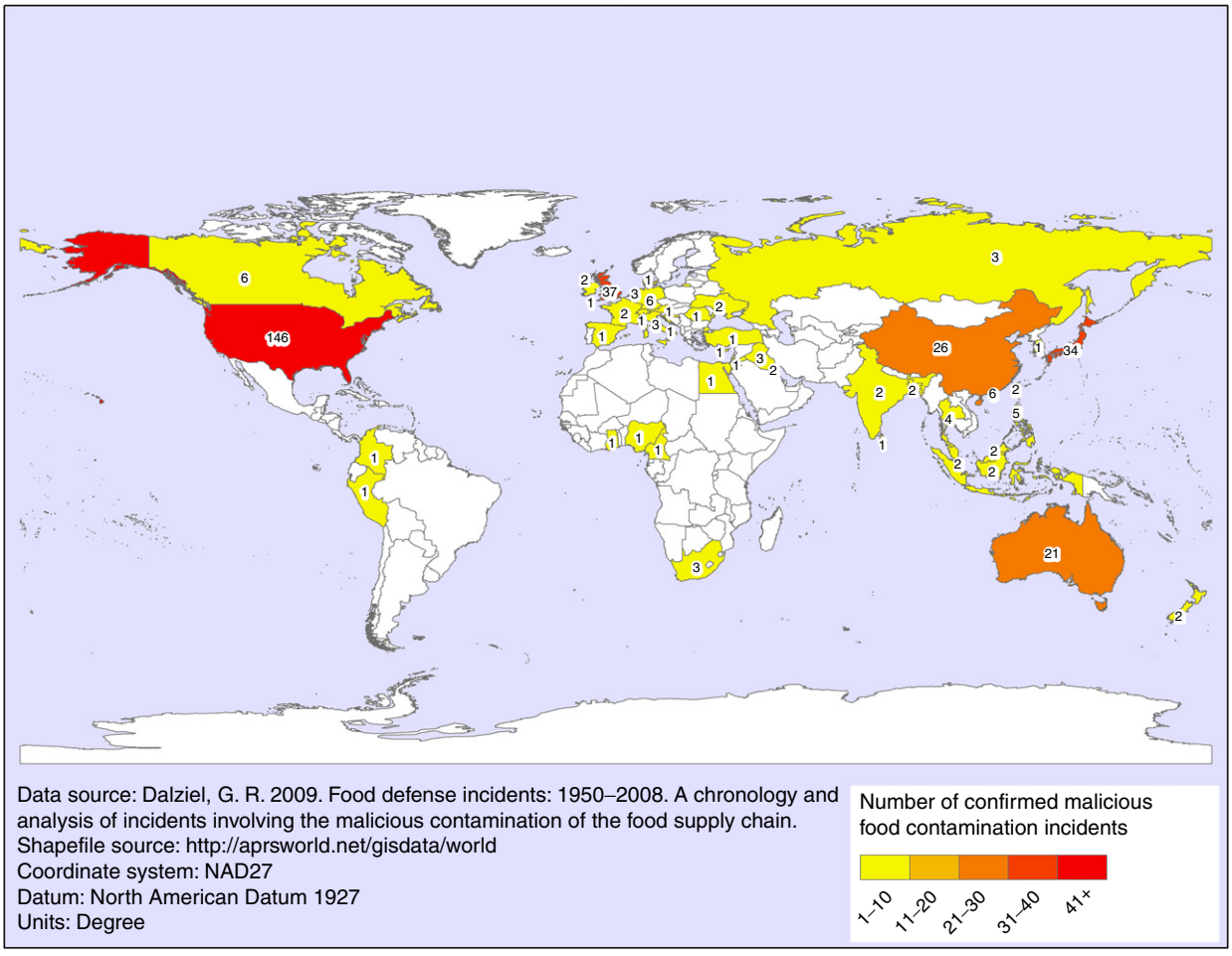


Figure 2 Confirmed malicious contaminations of food around the world.

the food safety and quality systems in place. If contamination can occur at a large scale for unfair economic gain, it can also occur just as easily as a malicious attack, so food defense systems should be in place to reduce that vulnerability. EMA is discussed more in the Section Economically Motivated Adulteration. There is also a difference between contaminating foodstuffs with deleterious agents and destroying or vandalizing food industry infrastructure (buildings, crops, shipping vehicles, etc.). Vandalism on food system infrastructure is not discussed here. Other motivations to contaminate the food supply include extortion, political assassination or coercion, a disgruntled employee, interpersonal conflict, or to use food as a means of terrorism. Extortion incidents are typically underreported by law enforcement in order to minimize copycat incidents and damage to consumer confidence in the food system (Dalziel, 2009).

There have been seven cases of water supply contamination from 1950 to 2008. These incidents caused a total of three fatalities and fewer than 100 other injuries. Most water supply incidents involve pesticides and insecticides with limited toxicity. Given the comparatively few events and small impact, it could be concluded that widespread hazard of intentional water supply contamination is unlikely (Dalziel, 2009).

Preharvest contamination events have also been relatively rare. Pesticide was once used to contaminate the tank of a crop duster in Australia; the contaminated food was brought to market, but a subsequent recall was issued, so the incident resulted in no injuries or fatalities. Incidents that resulted in harming animals or crops that never made it to market are more common. In 1970, the water supply for a cattle farm was contaminated with cyanide, killing 30 cattle in AL, USA, and 500 000 fish were killed when a Northern Ireland fishery was contaminated in 2001. The economic effects of events at this point in the food chain are the preponderant result rather than human health consequences. A famous historical example is when Chilean grapes were allegedly found to have trace levels of cyanide in 1989. The resulting trade bans caused US$300 million (€232 million) in losses. However, laboratory results were disputed, so this instance serves as a demonstration of the impact public perception can have in the event of potential food contamination and the importance of good risk and crisis communication (Dalziel, 2009).

A total of three incidents have been confirmed during assembly, processing, packaging, or storage. When combined, the incidents resulted in 125 injuries but no fatalities. The largest incident occurred in China. A total of 120 citizens fell ill from eating noodles that had been contaminated with rat poison at the factory. At the time, the factory was undergoing a property–leasing dispute (Dalziel, 2009). This example shows the importance of fostering a food defense culture at processing plants to help protect the food system from contamination, especially during times of disorder.

With a wide variety of agents used (e.g., arsenic, *Salmonella typhimurium*, pesticide, etc.), 85 instances of contamination have been confirmed occurring at the retail and food service level of the food system. These incidents resulted in 123 deaths and 3304 other injuries during 1950–2008 (Dalziel, 2009). Incidents at this part of the food supply chain caused the heaviest casualties with an average of 40 casualties (fatalities plus injuries) per incident. The most famous case is when the Rajneeshee clan contaminated salad bars in Oregon with *Salmonella typhimurium* in 1984. The final illness count was 751, 45 of whom were hospitalized (Dalziel, 2009; Török *et al.*, 1997). This incident is the only "instance in which a terrorist group operating in the US employed a chemical or biological weapon" to contaminate the food system (Carus, 1998, p. 7 cited in Dalziel, 2009, p. 19). Another widespread incident occurred in 1992 when flour at the College of Finance and Taxation cafeteria in Zhengzhou, China was contaminated with arsenic, resulting in 788 illnesses (Dalziel, 2009).

The majority of intentional contamination incidents happened at the consumer and home level of the food system. There have been 263 cases of intentional contamination causing 265 fatalities and 670 other injuries or illnesses. Although most cases happen at this level, the large majority (70%) of these cases caused only 1–4 casualties per case (Dalziel, 2009). The challenges of preventing and detecting incidents at this level are that each incident usually affects only a few people, and without detection systems at the consumer level other than organoleptic detection, many incidents could go unnoticed until the adverse effects take place. This is especially true for chemical or biological agents that create no noticeable organoleptic effects in the food. The incidents at this level often involve household cleaners and chemicals or readily available pharmaceuticals making threat agent control especially challenging.

Only nine out of all the confirmed incidents during 1950–2008 involved biological agents such as pathogenic microorganisms, toxic plant matter, and fecal matter (Dalziel, 2009). Radiological agents (e.g., phosphorus-32, iodine-125, and polonium-210) were used in only 8 of the incidents. Radiological agents account for a single fatality and 36 injuries. The single fatality was the 2006 poisoning of Soviet KGB officer and spy, Alexander Litvinenko, with polonium-210 allegedly placed in food at a restaurant. A common thread between the radiological and biological agents is that several cases in each category involved an adversary that worked in a laboratory setting and had direct access to the agents. The remainder of the recorded incidents involved chemical agents – mostly chemicals that are readily available to the public.

In summation, 98% of confirmed intentional contamination incidents occurred late in the food supply chain (e.g., consumer and retail), but incidents earlier in the food chain have much larger impact per event. There have been 391 deaths and 4355 illnesses from malicious food contamination during 1950–2008 (Dalziel, 2009). Nonmalicious contamination of the food system is also a common occurrence. These events are called EMA.

Economically Motivated Adulteration

EMA is substituting or diluting foodstuffs with lesser value ingredients, mislabeling food, counterfeiting, or otherwise masking the true origin or quality of a food in order to unfairly gain access to a market or to obtain a higher price for the food than it is worth. As opposed to intentional contamination for bioterrorism, EMA is executed with the intention of never being discovered. The intention for a malicious adversary is to

Table 1 Potential food defense threat agents

Threat agent	*Oral lethal dose (LD_{50})*
Abrin	0.04 μg kg^{-1} in mice[a]
Bacillus anthracis	$>10^8$ spores in rabbits[b]
Botulinum neurotoxin	0.001 μg kg^{-1} in mice[a]
Clostridium perfringens epsilon toxin	0.1–5.0 μg kg^{-1} in mice[a]
Cyanide	30 μg kg^{-1} in rats[c]
Fluoroacetic acid	5 μg kg^{-1} in rats, 7 μg kg^{-1} in mice[d]
Ricin	3–5 μg kg^{-1} in mice[a]
Saxitoxin	263 μg kg^{-1} in mice[d]
Shiga-toxin producing *Escherichia coli*	0.002 μg kg^{-1} in mice[a]
Staphylococcal enterotoxin	1–25 μg kg^{-1} in humans[e]
Strychnine	2350 μg kg^{-1} in rates, 20 μg kg^{-1} mice[d]

[a]Darling and Woods (2004), cited in Kennedy and Busta (2013), p. 94–95.
[b]Lincoln *et al.* (1967), cited in Kennedy and Busta (2013), p. 94.
[c]Centers for Disease Control and Prevention Agency for Toxic Substances and Disease Registry, cited in Kennedy and Busta (2013), p. 94.
[d]National Library of Medicine 'TOXNET', cited in Kennedy and Busta, (2013), p. 94–95.
[e]Burows and Renner (1999), cited in Kennedy and Busta (2013), p. 94.

Table 2 Incidents of economically motivated adulteration (EMA) in food since 1980

Food category adulterated	*Number of incidents recorded*
Fish and Seafood	66
Dairy	14
Alcoholic beverages	13
Oils and fats	11
Grains and grain products	11[a]
Spices and extracts	9
Fruit juices and concentrates	8
Meat and meat products	8
Produce	7[a]
Honey and other natural sweeteners	6
Eggs (duck and chicken)	5
Other	4
Coffee and tea	3
Infant formula	3
Other beverages (soft drinks)	2

[a]One incident included adulteration of both produce and grains products.
Source: National Center for Food Protection and Defense (NCFPD), 2012a. NCFPD EMA Incidents Database. Saint Paul, MN: National Center for Food Protection and Defense. Available at: https://www.foodshield.org/ (accessed 28.03.13).

cause harm and disruption, and the actor wants the act to be recognized as terrorism rather than a routine foodborne illness outbreak. However, fraudulent food producers do not want to be discovered, so they may continue selling their adulterated product as long as possible. Global trade has created uniquely multilateral opportunities for EMA: transshipment to avoid duties or specific embargoes or port shopping to find a port that will accept previously rejected food or avoid inspections (Busta and Kennedy, 2011). Incidents of EMA demonstrate times when regulatory and quality controls currently in place in the food system were evaded. If the controls can be evaded for economic gain, then they may be evaded for bioterrorism too (**Table 1**).

If the fraudulent food itself or the adulterant added causes unintended health consequences in consumers, the resulting health effects are often the trigger to signal an intentional contamination incident. For example, toxic oil syndrome in Spain in 1981 and melamine contamination in Chinese milk and wheat gluten during 2006–08 were all instances of EMA that were discovered only after the catastrophic public health consequences. There have been 169 separate recorded incidents of EMA around the world since 1980 (NCFPD, 2012a). These incidents are summarized in **Table 2**, organized by what category of food was adulterated.

According to the NCFPD (2012a), the most often adulterated category is fish and seafood. The seafood supply chain includes many producers and complicated handling transfers, and after the fish has been disassembled, it is very difficult to identify. Those combined factors make fish and seafood particularly vulnerable to mislabeling. For example, a restaurant or seafood retailer may list red snapper, grouper, or flounder, but the consumer may not notice that the fish that is served is actually a different (and often of lesser value) fish such as tilapia, cod, or swai. Many cases of seafood mislabeling are not dangerous to public health, so the major concern is that consumers are being deceived and overcharged for low-value fish and seafood. However, there are some cases where substitution or mislabeling of fish may cause harm. For example, the Food and Drug Administration (FDA) warns against consuming the fishes escolar and oilfish: "In some people, eating even small amounts of these fish can cause oily diarrhea... abdominal cramps, nausea, vomiting and headache" (Fry Jr., 2012, p. 220). There have been two confirmed incidents when escolar was served instead of the white fish named on the menu (NCFPD, 2012a).

The second most adulterated food category for unfair economic gain is the dairy. The most relevant and impactful example occurred in China between 2007 and 2008. Milk was contaminated with melamine, a toxic industrial chemical, to increase the nitrogen content of the milk. The protein content of milk is determined by the total nitrogen content, using the Kjeldahl method (FDA, 2011). Melamine is high in nitrogen, so adding melamine to the milk artificially increased the protein content analysis readout. The consequences of this EMA were disastrous: 300 000 illnesses and 6 infant deaths from kidney complications (Gossner *et al.*, 2009; NCFPD, 2012a).

In addition to the potential for negative health consequences, EMA is a concern for profitability of honest food production firms. It has been estimated that EMA and counterfeiting costs the food industry US$10–15 billion (€7.7–11.6 billion) per year (GMA and A.T. Kearney, 2010). It is agreed that this complex of a problem will require collaboration between industry partners and the government. Some industry-wide solutions to EMA have been proposed: an information-sharing clearinghouse to disseminate EMA-related information to the industry, a shared audit program and ingredient analysis library to reduce costs, and relationship building for sharing information through trade associations (GMA and A.T. Kearney, 2010). A database of the susceptibility of food ingredients to EMA has been published (NCFPD, 2012b; Moore *et al.*, 2012) to help spread information about

the susceptibility of common food ingredients to EMA. Given the occurrence of intentional contamination, malicious and not, there have been new official policies written to address this problem.

Food Defense Policy

Strengthening food defense programs around the world requires national policies and resources to support food defense infrastructure. The role of food defense policy is to ensure that food monitoring and surveillance, inspection, foodborne disease surveillance, education and training, and food handlers' food defense plans are adequate and up to date. Much of the officially adopted policy with explicit or implicit language on food defense has been written in the US, but the topic of food defense policy is growing in popularity around the world. Intergovernmental organizations such as the WHO have written guidelines and recommendations to improve food defense globally.

In response to the terrorist attack on the World Trade Centers on 11 September 2001, the US passed the Public Health Security and Bioterrorism Preparedness and Response Act of 2002 (aka The Bioterrorism Act of 2002). Title III of the act is entitled 'Protecting Safety and Security of Food and Drug Supply,' and it describes the actions that the US government and food system will take to ensure that the food and drug supply is protected from bioterrorism (107th US Congress, 2002). To implement this act, the US FDA requires that all food facilities be registered with the FDA and that all importers shipping food to the US must give the FDA 24 h advance notice of their arrival to a port of entry (see list of relevant web pages for more information).

In 2004, George W. Bush's Homeland Security Presidential Directive 9 (HSPD-9) called for the establishment of university-based centers of excellence to address various homeland security challenges (Bush, 2004). The food system was one of the critical infrastructures identified and many university consortia competed to be selected as a center of excellence. In June of 2004, a consortium led by the University of Minnesota was identified as the winner of the competition, and the National Center for Food Protection and Defense (NCFPD) was established. NCFPD is still highly active today pursuing its vision: "defending the safety of the food system through research and education." See the list of relevant websites for NCFPD's homepage URL.

In FDA's 2007 Food Protection Plan, the FDA requested authority to require mandatory controls in the food system for both unintentional and intentional contamination. This request came to fruition when the US FSMA passed in 2011 (see list of relevant web pages for more information). The FSMA requires organizations to "identify and evaluate hazards that may be intentionally introduced, including by acts of terrorism" (111th US Congress, 2011, Section 103(b)(B)(2)). Although this law was passed in 2011, regulations are still being written.

US President Barack Obama's PPD-8 describes a vision for a national preparedness goal for the US at large, and critical infrastructure like the food system are topics affected by this directive. Interpolated from the overarching language in PPD-8, there are 5 frameworks of planning for food defense: prevent, protect, mitigate, respond, and recover. The plans for each framework should be designed to coordinate with each other in order to create a fluid preparedness system.

- *Prevent*: The capability to avoid or stop an intentional contamination event from happening in the first place. Prevention capabilities for the food system include information-sharing environments and employee screening.
- *Protect*: The capability to halt an intentional contamination event that is underway. This includes fostering a food defense culture so that individuals keep a watchful eye on activity at their certain part of the food system. More technical capabilities include locks on food containers and trucks, limited access to production floors, and fences and surveillance at the proximity of sensitive nodes in the food chain.
- *Mitigate*: The capability to reduce morbidity, mortality, and economic loss after an incident occurs. In the food system, mitigation strategies include rapid threat agent detection, recall procedures, and high-quality crisis communication.
- *Respond*: Response capabilities include emergency management systems, healthcare systems, and recalls to save lives after an incident has occurred.
- *Recover*: Recovery capability of the food system involves regaining market access, public trust, and business continuity of the food products that were contaminated in the food defense incident (Obama, 2011).

Around the world, government has many roles in fostering food defense for a nation. Overall, the role of government is to oversee the food system from a broad perspective so that the producers can put their focus on the quality of their production. The government should collaborate with the food industry to perform risk assessment, create response and recovery plans, and ensure that preventive controls are in place. The government also has a role with the general public, especially in risk and crisis communication. See Section Risk and Crisis Communication for more on that topic.

The WHO IHR have a role in establishing food defense practices around the world. The Regulations are a framework for international public health surveillance, assessment, and response for the WHO and its member states (World Health Organization, 2008). The purpose of these international policies is to prevent and respond to public health risks that could cross borders. As discussed above in the Section Global Food System Defense, a food defense incident could easily spread to other nations due to the vast international trade network that characterizes today's globalized food system (World Health Organization, 2013). The State Parties that decide to abide by the IHR must create a centralized authority for communicating and guiding the implementation of the IHR, follow reporting protocols, and complete assessments all for the goal of improving international public health (World Health Organization, 2013). See the list of relevant web pages for more information.

Threat Agents and Detection

Threat Agents

There are four general classes of threat agents that could be used to maliciously contaminate foodstuffs: biological, chemical,

physical, and radiological. Biological agents include infectious pathogenic bacteria, viruses, or parasites. Chemical agents of concern include man-made or natural toxins, industrial cleaning agents or lubricants, pesticides, allergens, etc. Agents used for EMA mostly fall under the chemical (either toxic or nontoxic) and physical classes. EMA is not intended to harm the consumer, but the agent used may cause unintended harm. The history of food defense incidents show that chemical agents are the most common adulterant probably because of their availability: "the most commonly used compounds for poisoning were those that were either at hand or readily available on the market" (Dalziel, 2009, p. 6). Another reason that chemical agents are the culprit most often is because 100 or more years of food safety and food quality program development, research, and regulation have focused on controlling microorganisms (especially pathogens) rather than chemical agents. Toxins extracted from biological sources (e.g., ricin and Shiga toxin) are the intersection of the biological and chemical categories. Physical agents include glass, needles, metal shards, etc. Fortunately, many food manufacturing lines not only include magnetic or X-ray detectors originally included in the food safety program but also serve food defense goals. Radioactive chemicals are also a concern because of their availability in research laboratories and their heightened hazard when ingested. The Centers for Disease Control (CDC) and Prevention National Select Agent Registry shows agents that are of particular biosecurity concern because of their potential for high mortality (see list of relevant web pages). An additional hazard that characterizes the agents on this list is that many physicians are not familiar with diagnosing them, so accurately identifying the problem may be severely delayed in a food defense incident. **Table 1** lists highlighted food defense threat agents and their oral lethal doses.

A key to threat agent analysis is the understanding that the context (e.g., delivery method, heat stability, lethal or infectious dose, availability of the agent, etc.) in which a certain agent is most hazardous can help in determining which agents are of greatest concern for certain parts of the food system. Current research explores the reaction kinetics and viability of threat agents in certain food matrix contexts (Lumor *et al.*, 2012; He *et al.*, 2011). To be a threat, an agent must be stable in the particular food matrix and must survive the control steps (thermal treatment, washing, etc.) it will undergo. To cause harm to the consumer, a toxin will have to outlast inactivation, and microorganisms may have to survive in great enough numbers to be infectious. If an agent produces noticeable organoleptic changes (e.g., turbidity, color change, and off-odors and flavors), the public may not consume the contaminated food, and illness may be prevented. Understanding the contextual toxicity of threat agents in food matrices will inform risk assessment decisions and prioritize countermeasure implementation.

Pasteurization kinetics can be used to the advantage of food defense. Increasing the total heating schedule will help to control certain microbial and toxic contaminants. Certainly, if the agent was particularly heat resistant (e.g., Bacillus anthracis spores), the organoleptic effects of additional thermal processing needed would make the product unacceptable to consumers. Some nonthermal processing methods are now also effective at delivering 5 log cycle microbial population reductions such as high-pressure processing and ionizing radiation (Kennedy and Busta, 2013).

Detection

There are three general methodologies for detecting a food defense incident in the food system: detect to prevent, protect, and recover. Detect to prevent means detecting the contamination before the food leaves the facility. This method prevents any chance of public health consequences, but the food producer incurs all costs of testing and detection. Detect to protect means detecting contamination of the food after processing but before sale to the final consumer, so all public health impact is again avoided. This is the method intended during a recall, and this method is even more expensive for the production firm because it has already paid for the food to be moved down the supply chain. There may also be indirect losses from a drop in consumer confidence in the brand during and after a recall. Detect to recover (or detect to mitigate) means the contamination was not identified before consumption of the food, and now the deleterious product must be removed from the supply chain and retrieved from consumers as quickly as possible to limit the public health impact (Kennedy and Busta, 2013).

Currently, it is most likely that detection of a food defense incident would be based on illness data due to the contaminated food – a detect to recover method. However, this is a difficult task because it can be analogous to finding a needle in a haystack: "The main requirement for rapid detection of an epidemic is a surveillance system that is sensitive enough to identify small clusters of illness" (World Health Organization, 2008, p. 20). Surveillance systems that detect contamination incidents based on cases of foodborne illness are passive systems, relying on reporting from physicians and laboratories to detect outbreaks. The disadvantage of this method is that it is not proactively searching for contaminated food, and there is a delay from the time of contamination to the time of consumption up to several days, that is, enough time for the food to be widely distributed and consumed, especially if the food has short shelf life and is consumed quickly after purchase (e.g., milk and produce). A key factor for the magnitude of public health impact from an intentional contamination incident is the speed of distribution and consumption after processing. A food that is distributed and consumed quickly would have more intense public health effect if it were contaminated than a food that is held at a location before reaching the consumer. There is a better chance that in the latter case the food would be recalled before consumers ate it.

Some existing surveillance and detection systems are FoodNet, C-EnterNet, OzFoodNet, and PulseNet. The CDC and Prevention's FoodNet, the Public Health Agency of Canada's (PHAC) C-EnterNet, and the Australian Government Department of Health and Ageing's OzFoodNet are consortia of sentinel site clinical laboratories that track and disseminate information on instances of illness for select foodborne pathogens. PulseNet, also CDC-coordinated, is a collaborative database and sharing environment of pathogenic bacteria's 'fingerprints' based on pulsed-field gel electrophoresis (see list of relevant web pages for more information on each of these systems). Detection at the laboratory requires the laboratory to have the necessary test on hand and the ability to interpret the results. Communication lines between laboratories and

emergency managers must be efficient for rapid response. Many countries, however, do not maintain a surveillance system that detects foodborne illnesses, so the event may go undetected for even longer. New opportunities for food defense surveillance include mining other sources of information that are potentially indicative of a foodborne disease outbreak: unusually high demand at pharmacies for certain drugs, veterinary surveillance systems, consumer complaint hotlines in the food industry, unusual coroner's reports, and mass absentees in large facilities.

Innovations in detection methods for nefarious biological or chemical agents are being developed in laboratories around the world. Methods in development include Raman spectroscopy, nanoparticles, immunoassays, biological cell bioassays, and more (Kennedy and Busta, 2013). Laboratory detection methods may be expensive, so vulnerability assessment is useful to determine which methods and other interventions are the highest priorities.

Vulnerability Assessment

The purpose of food defense vulnerability assessment is to identify and weigh the hazard and likeliness (risk) of particular intentional contamination incidents at a food processing facility or along an entire supply chain. The end goal of the analysis is to commensurately allocate resources to achieve the highest level of security for the resources available. The challenge is in finding which nodes in the system are the highest priorities to protect and if the chosen intervention is fiscally justified. Terrorism scholar Brian Michael Jenkins writes, "the danger arises when speculation becomes the basis for launching costly efforts to prevent 'what ifs'" (Lesser *et al.*, 1999, p. xi).

The food system may be contaminated at any of many points in the complex network of supply chains. Risk assessment involves identifying the agents that could be used and the places the agents could be introduced in a food chain. Some supply chains may be more susceptible to certain agents at certain points than others. Therefore, one role of risk assessment is to elucidate which agents and nodes are of particular concern for a certain supply chain. Case-by-case assessment is necessary to understand the unique risk profile for each part of the food system.

Food production firms are responsible for evaluating any work process that could be vulnerable to a food defense incident. Certainly, that includes the manufacturing floor, but the facility utilities (water, air, etc.) should also be included in the assessment (Biegel and Beach, 2010). Similar to hazard analysis for HACCP, the first goal of vulnerability assessment is to identify potential hazards and points of entry for intentional contamination. For each hazard and at each entry point, a judgment is made on the level of risk and the level of hazard. Hazard is the degree to which the event can do harm, and risk is the probability of the particular vulnerability being exploited. Highest hazard and risk vulnerabilities should be addressed foremost.

Determining the hazard of a potential food defense event is particularly challenging and unfortunately subjective. One method is to judge the potential impact of an intentional contamination incident based on the impact from unintentional contamination events in the past. Some key events have caused hundreds of thousands of illnesses. For example, unintentionally contaminated clams in China caused 300 000 hepatitis cases in 1989 (Manning *et al.*, 2005 cited in Dalziel, 2009). The contrary theory says that comparing the potential hazard of intentional contamination with actual reports of unintentional events is spurious because it does not take into account an adversary's ability to orchestrate the attack to evade systems in place designed for food safety. The impact of a designed attack with a carefully chosen agent could be catastrophic, but such events have been very rare. Therefore, foolproof risk assessment is not possible without actual events to base the claims on stochastic statistics. Considering centralized food processing, wide distribution, and that aggressive pathogens and high toxicity agents exist, there is potential (although rarely realized) for incidents even more hazardous than food safety incidents from the past.

The severity of a threat agent is determined by: (1) public health impact potential for delivery to a large population through the food system, (2) availability of the agent or possibility of its production, (3) interpersonal transmissibility of the agent, (4) public perception of the agent (an agent may be chosen because of its shock factor), (5) healthcare system's response capacity (e.g., antiserum stockpiling), and (6) difficulty of detection before consumption. In the US, the Department of Homeland Security biennially performs the Biological Terrorism Risk Assessment and the Chemical Terrorism Risk Assessment considering "aggressor intent and capabilities, ease of agent acquisition, ease of agent introduction, probability of agent survival through to target populations and probable public health (primarily) consequences" (Kennedy and Busta, 2013, p. 100).

Based on historical evidence, the closer the food gets to the consumer, the higher is the risk of intentional contamination. (Dalziel, 2009). However, the hazard for large-scale health impact is highest at the centralized points in the supply chain where large amounts of food may be contaminated all at once and then widely distributed. Perhaps the greatest risk of intentional contamination are the scenarios that the food industry sees as so unlikely that they do not need to invest in controlling them. It is in these unexpected blind spots in security that a malicious attack could take the industry by surprise.

Compared with the occurrence of food safety incidents at the processing plant level, food defense incidents are very rare. Because there are no routine food defense incidents like there are food safety incidents, food manufacturers are understandably not as motivated to invest in preventive methods specifically for food defense, that is, the return on investment for food defense infrastructure is more difficult to rationalize than the return on investment for food safety precautions. Furthermore, food safety programs are required by policy, but food defense programs are not yet.

Developed by the US National Air and Space Agency and Department of Defense, the US FDA has adopted Operational Risk Management for some risk assessment tasks. The method follows a typical hazard analysis process: Risks are identified and assessed for their relative hazard level, and

then interventions specific for each risk are identified and implemented. The final step is to assess the success of the intervention made. After interventions are implemented, the risk assessment process is reiterated to achieve acceptable levels of vulnerability. Each vulnerability is assessed on the basis of the intensity of the hazard it poses and on the probability that it may be exploited. The highest hazard and highest risk vulnerabilities are the top priority for intervention. For food defense, the severity of a hazard is relatively well understood compared with the probability of the hazard; large-scale intentional contamination events resulting in public harm are not common enough for sound statistics to be performed under the assumption that these events are stochastic.

Another risk assessment tool currently used is CARVER +Shock. This method assesses risk in a system based on seven elements. The initial letter of each element makes up the acronym 'CARVER,' and 'Shock' includes psychological or other hazards. The US Department of Agriculture and the FDA use 10-point scales to rate a node in the food system on each of these elements. Higher scores mean greater vulnerability or hazard (see list of relevant web pages for more). The seven elements are:

- *Criticality*: The degree of public health or economic consequence.
- *Accessibility*: Ability of the perpetrator to gain access and egress from the point of contamination.
- *Recuperability*: The delay required to bring the system back into operation. Higher scores mean longer recovery times.
- *Vulnerability*: The potential for a successful attack. In the food system, this means the ability to introduce enough of a deleterious agent to cause harm and for the agent to survive control steps to reach the consumer.
- *Effect*: Direct loss from the attack as measured by lost production of that product in the food system.
- *Recognizability*: Ease of target identification by an adversary.
- *Shock*: The combined health, economic, and psychological impacts of the attack. Economic and psychological impacts of an attack may not cause morbidity or mortality, but they may result in substantial loss of public confidence in the food system or the government (Kennedy and Busta, 2013; Catlin and Kautter, 2007).

The first task of a CARVER+Shock analysis is to identify the nodes of a given processing plan. Each node represents a change in the vulnerability of the system to contamination. When combined, the nodes represent the entirety of the process under examination. For example, each unit operation (receiving, mixing, thermal processing, etc.) and every transfer between unit operations in a food processing facility count as nodes. Next, each node is evaluated on each of the seven CARVER+Shock elements. The sum of the element scores for each node is used to identify which nodes are most vulnerable. One limitation of this method is that if many parts of a diverse system are compared, the method becomes less valid to quantitatively compare the node scores. Therefore, extrapolation of this method to cover an entire supply chain may not result in a valid vulnerability assessment. More information on CARVER+Shock can be found on the FDA's web page named below in the list of relevant web pages.

Food Defense Preparedness

A critical design aspect of a successful food defense plan is that is has redundant protection: "The goal of the Food Defense Plan is to implement procedures in layers, like that of an onion, so that each time a layer of defense is peeled back there is another layer in place to discourage or prevent an incident from occurring" (Biegel and Beach, 2010, p. 12). Ideally, there would be layers of defense at every node along the food supply chain. A similar metaphor is the hurdle philosophy in food safety: a pathogen may be able to survive and grow when one aspect of the food environment is unfavorable, but the probability of the pathogen's success diminishes with the number of hurdles. For example, the pathogen may be able to grow in low pH, but it would be unable to grow in low pH plus high salinity. By the same token, an adversary may successfully design a way for his/her contamination to survive the thermal processing step, but he/she may not be able to also overcome key card-restricted access to the processing floor.

Creating a food defense plan and implementing security interventions follows directly after the risk assessment process. Resources to implement mitigation strategies and preventive methods should be allocated commensurately to the severity and likelihood of the vulnerabilities found, that is, the highest hazard and the highest risk vulnerabilities deserve the foremost intervention to protect, and lesser vulnerabilities can be addressed subsequently. Note that the solutions implemented for the highest priority vulnerabilities may generate, modify, or reorder lesser vulnerabilities, so reassessment is needed to find the new highest priority vulnerability in the new system. Ideally, any interventions made will build on existing food safety and food quality systems instead of jettisoning them. Be aware, however, that improved or bolstered policies and strategies that principally serve food quality goals may not also serve food defense goals. "HACCP and other food safety systems designed to control naturally occurring microbial pathogens cannot anticipate and protect against individuals committed to using the food system as a means of public health or economic terrorism without significant modification" (Kennedy and Busta, 2013, p. 103).

An inhibition to the motivation an organization needs to create a food defense plan is that justifying the return on investment is difficult until it can be seen retrospectively. Basically, food defense preparation is brand protection. Unfortunately, once the food defense incident has occurred, it is too late to create plans for efficient mitigation, response, and recovery: "the effectiveness of a response depends to a great extent on the... preparedness plans that are developed and implemented long before any event occurs" (World Health Organization, 2008, p. 23).

According to PPD-8, a food defense emergency preparedness plan should include five frameworks: prevention, protection, mitigation, response, and recovery (Obama, 2011). Below are some of the strategies that organizations could implement for each of these frameworks. In the current status of food defense, the prevention, protection, and mitigation goals lie mostly in the hands of the food industry. Incident detection, rapid response, and public health services goals are currently the government's responsibilities. Collaboration on all emergency preparedness frameworks between the food

industry and the government agencies is promoted to advance the overall security of the food system. "The purpose of preparedness planning is to build a response system that links all the players needed for effective management of an emergency and to develop coordination, communication and integration among local, regional and national resources" (World Health Organization, 2008, p. 26).

Prevent

The goal of the prevention framework is to avoid or minimize the possibility of an intentional contamination event from happening. "Prevention, although it can never completely be effective, is the first line of defense" (World Health Organization, 2008, p. 1). The intelligent adversary theory says that no matter how many preventive measures there are in place, the complexity of the food system is such that there will always be another vulnerability, and the adversary will find it. Prevention is achieved by industry action with government direction. One key step the food industry can take is training employees in food defense. The NCFPD has created a curriculum framework for trainers to create food defense training materials (Fredrickson *et al.*, 2012).

Perhaps one of the most valuable ways to ensure food protection is to first focus on the people involved. The WHO recommends employers to screen employee backgrounds for security concerns, and all staff should be trained to identify and address suspicious behavior or unexpected visitors (World Health Organization, 2008). Creating a food defense culture among the food industry's employees is a way to utilize human resources to achieve food defense goals. Trained personnel may be more effective at stopping a perimeter breach or other suspicious activity than sampling methods, access restriction methods, or locked doors. The FDA's ALERT model can be used to train employees in food defense, and FDA's 'See Something, Say Something TM' campaign is one tool to establish a food defense culture. The human resources department of a company can assist greatly in screening employee applications to exclude aggressors attempting to gain access to the production line and to address any reasons that may motivate a current employee to undermine the security measures in place. Similar to that of a food quality program, food handlers should roll food defense goals into their supplier quality control program. Chemical cleaners and other industrial chemicals should be stored behind a locked door, and use of these chemicals should be documented so that anomalies and missing chemicals can be investigated.

Protect

Protecting the food system means halting an intentional contamination event that is currently underway. This involves restricting access to the foodstuffs themselves. At the processing plant, sensitive production floors (i.e., finished product with no further control step, open vats, or conveyers that give direct access to the production line) should have controlled access so that only authorized personnel may access them. Any visitor should be documented and easily identified so that personnel on the production floor can easily identify unauthorized people in the plant. Have a visitor agreement policy that each visitor must agree to the company's food defense goals. Outside of the production plant, surveillance cameras, physical barriers, and guards can deter any adversaries from entering the plant.

At the food product level, tamper-evident or -resistant packaging should be used and consumers should be informed not to consume any food that has been tampered with. It is critical to maintain the integrity of the food product after processing because if contamination occurs after the final control step, there may be no subsequent treatments to eliminate the contaminant before the consumer eats the food. Firms should ensure that contamination after this point in the supply chain is extremely unlikely and could be reliably detected before sending the product to consumers.

Mitigate

The goal of mitigation is to reduce morbidity, mortality, and economic loss after an incident occurs. A robust recall plan could remove contaminated products from distribution centers and shelves before it reaches consumers. A strong recall plan is founded in reliable tracing mechanisms for where the inputs for a product come from and where the product goes after processing. Rapid communication with a network of emergency response agencies and all nodes of the supply chain will be very important for the success of a recall. According to the Institute of Food Technologists, creating a product tracing plan relies on identifying critical tracking events (e.g., transfers of products to other handlers and processing steps) and recording and communicating key data elements (e.g., unique item identification codes) at each critical tracking event (Institute of Food Technologists, 2011). Creating a consistent system of monitoring tracking events and key data elements will drastically improve the food system's ability to minimize morbidity and mortality after a food defense incident.

Respond

The response to a food defense emergency is intended to save lives after an incident has occurred and contaminated product has already been consumed. Emergency response is when the critical tracking events and key data elements established in the mitigation planning are put to use. A response plan includes protocols to notify appropriate groups of the incident (including government, food industry, and the public), and how each potential scenario, including attacks on other facility utilities, will be handled (Biegel and Beach, 2010). It is essential that a response plan be in place before an attack happens so that the ensuing response is efficient and effective. Outlining the collaboration plan with local, tribal, state, and national emergency response agencies beforehand will ensure that the response itself will run as smoothly as possible. Depending on the magnitude of the threat, the capacity of municipal healthcare systems may be tested to respond to a large number of illnesses in a short period of time.

Decontamination and disposal of the contaminated food is necessary after it has been identified. The appropriate decontamination method is dependent on the threat agent used and the characteristics of the food matrix. In some cases, thermal processing can inactivate toxins and chemical sanitizers may be appropriate for other cases. The presence of the threat agent and these interventions, certainly, render the food inedible, and it must be disposed of safely after decontamination.

Recover

The challenge of food system recovery is regaining market access, public trust, and business continuity. Economic loss due to tarnished confidence in the safety of a particular food product is one of the lasting impacts of an intentional contamination incident. In 2008 and 2009, Peanut Corporation of America's (PCA) *Salmonella* outbreak resulted in the largest recall in US history and eventually forced PCA out of business. The total industry loss is an estimated US$1 billion (€778 million) (Kennedy and Busta, 2013). If a malicious contamination event could impact as many products as the PCA *Salmonella* outbreak, the economic impact could be devastating. The Chilean grape controversy discussed above in the Section Highlighted Food Defense Incidents demonstrates that economic losses extend to the global stage if countries impose trade limitations due to an incident in another country, and "intentional contamination of a particular food becomes more attractive as a target as the magnitude of various economic consequences increases" (Kennedy and Busta, 2013, p. 97).

Detailed food defense plans that include multiple layers of security help to prevent and protect against a food defense incident. Rapid recall systems and swift emergency management are needed to mitigate the hazard and respond efficiently. Business continuity plans and best practice public risk and crisis communication (discussed further in the Section Risk and Crisis Communication) are the key to maintaining a business market and public trust. See the list of relevant web pages for the US Department of Agriculture and FDA guidance documents for stakeholders in the food system on their respective 'Food Defense and Emergency Response Guidance' websites.

Risk and Crisis Communication

In addition to the direct impacts malicious contamination of the food system may cause, a food defense incident will have social and political impacts as well. Such an event may cause the public to lose confidence in the government's ability to keep its citizens safe and in the food industry's ability to make safe food. The purpose of good public risk communication before, during, and after a food defense incident is to mitigate public panic, dispel false information, and minimize the impact on public trust of the government and food industry.

Mass communication can serve as a double-edged sword during risk and crisis communication. The ability to deliver accurate information quickly is an advantage over misinformation, but the torrent of perceptions of risk can spread unnecessary panic just as quickly. Public media contributes to the 'available heuristic' – everyone remembers the extremes of the experiences while putting little importance on the much more common normal conditions of the day-to-day life. Cass Sunstein says that this phenomenon "can lead to a grossly overestimated sense of risk" (Sunstein, 2004 cited in Dalziel, 2009, p. 4) because one's panicked perception of the risk is much greater than its statistical reality. Some channels of public communication may intensify or exaggerate the status of a risk or a crisis, causing unnecessary outrage and anxiety.

There are risk and crisis communication best practices for government and industry in the literature. When an organization creates food defense policies, it is best to also determine communication methods at the same time. Note that food defense policies and communications are best when proactively determined before the incident occurs, not reactively after a crisis. Communication methods should be designed to align well with other policies, and designing both of them concurrently is an effective way to achieve that. Viewing risk and crisis communication as a constantly adapting process gives organizations the freedom to react accordingly to contextual dynamics of the particular scenario. New information about a given risk or crisis is constantly coming in, and often in unpredictable ways, so communication policies that allow for dynamic adaptation will serve best. Overall, risk communicators can trust that the public will receive honest, approachable, and transparent communication most positively. Risk communicators should also collaborate with credible and trusted sources to ensure that the information shared is accurate (Sellnow *et al.*, 2009).

Drafting risk and crisis communication messages requires a keen understanding of the particular audience that will receive the message. "Perceptions of risk are socially and culturally constructed" (Sellnow *et al.*, 2009, p. 23), so messages should be crafted with demographics such as age, gender, education, and culture considered. Risk communicators should also know that the public may have diverse interpretations of the risk, not just one. The diversity in perception should be acknowledged instead of ignored because the social implications of accusing the public of adopting a single perception will complicate risk communication in the future. Risk communication will be most effective if there is a relationship between the communicating parties. Relationships between parties should be built by including the public in risk assessment and communication questions (aka 'risk sharing') so that the public has a role in understanding the risk at hand.

Ethics are intimately involved in communicating with the public about potential health hazards. The NCFPD recommends listening to the public's needs and communicating with compassion, concern, and empathy during crises (NCFPD, n.d.). In addition, goals related to the ethical treatment of people should be paramount over economic concerns: "goals such as consumer safety must be prioritized over secondary goals of monetary gain or reputational maintenance" (Anthony and Sellnow, 2011, p. 441).

Because of the globalized food system, food defense is a global issue. To maintain the safety and trustworthiness of the global food supply, the food industry, all levels of government, and academia must collaborate to create robust preparedness systems for food defense.

See also: Analyses of Total Phenolics, Total Flavonoids, and Total Antioxidant Activities in Foods and Dietary Supplements. Critical Tracking Events Approach to Food Traceability. Food Law. Food Microbiology. Food Safety: Emerging Pathogens. Food Safety: Food Analysis Technologies/Techniques. Food Safety: Shelf Life Extension Technologies. Food Toxicology

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Food Security, Market Processes, and the Role of Government Policy

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Introduction

Modern analyses of food security list five essential components: availability of food on farms and in markets, access to that food by all households, effective utilization of the food within the household (a function of food safety, nutritional status, and health), the sustainability of the food system that delivers these components, and its stability (Timmer, 2012). This definition stresses the elements that individuals and households require to be food secure, but food security is also an important objective at the national level, where political leaders can be held responsible for failures and successes in maintaining accessible supplies of staple foods at stable prices, especially in major urban markets where many consumers procure their food. (This will be chapter 33 in the *Encyclopedia of Agricultural Sciences* to be published by Elsevier. It draws on much of my research and writing over the past several decades, and especially on Timmer (2000 and 2013). David Dawe and Casey Friedman provided very helpful comments, but are not responsible for the arguments here).

At the global level, considerable attention is focused on both short- and long-run balances between food production and food consumption. Rising food prices suggest that the production race is being lost to rapid gains in food consumption – a 'Malthusian' world where population growth and higher incomes cause food demand to outstrip the resource base for food production. Falling food prices, however, suggest that expanded agricultural land, better water control, and improved technologies are generating food surpluses. In this 'Sen-ian' world, access becomes the limiting factor for household food security, not availability (Sen, 1981).

In both worlds, food prices are a key signal about what is happening to food security. Two dimensions of food prices are important: their average level and their volatility. Price spikes and collapses can create risks and poverty for consumers and farmers even when average prices are affordable to the poor and create adequate incentives for farmers. Although highly unstable food prices have negative consequences at the micro level for household-level decision makers, food price instability also has a deeper and more insidious impact: it slows down economic growth and the structural transformation that is the pathway out of rural poverty (Timmer, 1989, 2009a). Thus, food price instability really hurts the poor in both the short run and the long run.

To see this, consider a very simple model of food security that focuses on the short run versus the long run, and on the macro level (of policymakers) versus the micro level (of household decision makers) (see **Figure 1**). When the global economy is reasonably stable, and when food prices are well behaved, policymakers at the national level can concentrate their political and financial capital on the process of long-run, inclusive growth. Keeping the poor from falling into irreversible poverty traps is easier and less costly in a world of stable food prices, and the poor are able to use their own resources and entrepreneurial abilities to connect (via the small horizontal arrow) to long-run, sustainable food security for themselves.

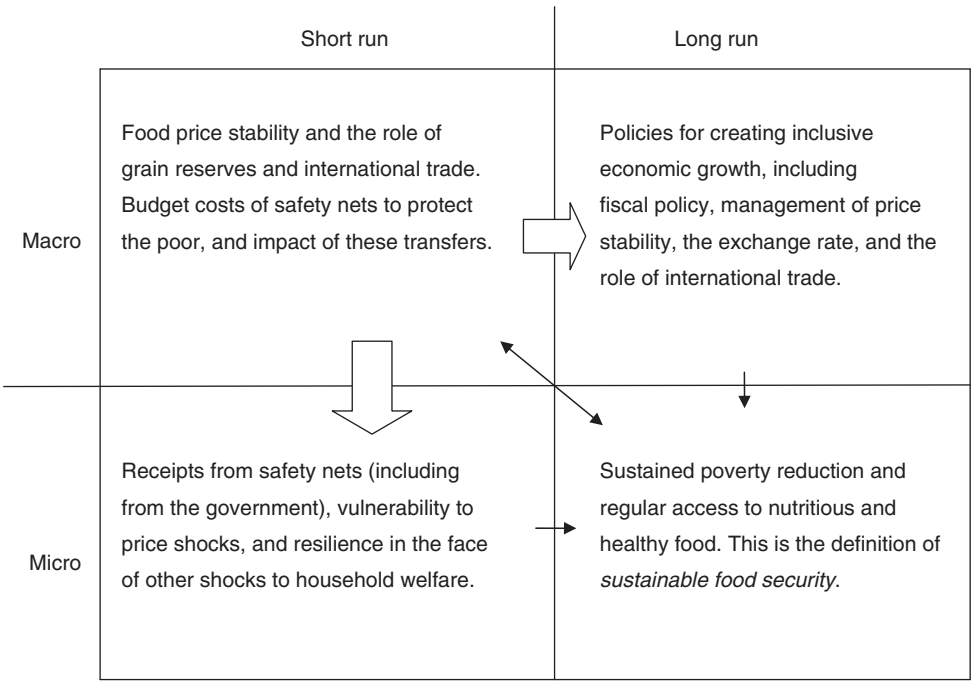


Figure 1 Basic framework for understanding food security issues.

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If the food economy is highly unstable, constantly in crisis, policymakers spend all of their time and budget resources in the 'upper left' box, trying to stabilize food prices and provide safety nets for the poor. During food crises, vulnerable households often deplete their human and financial capital just to stay alive. This is the world of poverty traps and enduring food insecurity. One is also trapped in short-run crisis management, both macro and humanitarian. Donors such as United States Agency for International Development can be trapped in crisis mode as well as governments, and end up spending their human and financial resources on emergency relief rather than longer-run development strategies and investments.

With success in achieving the objectives in the upper right and lower left boxes, market forces gradually – over decades – bring the poor above a threshold of vulnerability and into sustained food security (connecting macro to micro and short run to long run). The goal is to get to the 'lower right' box where households have sustainable access to food in the long run. That is, they are food secure.

This result is achieved by using a 'food policy perspective' (Timmer, Falcon and Pearson, 1983). This perspective stresses the need for analytical and policy flexibility to cope with market instability. Such flexibility is not a natural feature of domestic policymaking, in the food sector or elsewhere, and providing the analytical tools for understanding how to create flexible responses to both high and low price environments is a real challenge. The starting point is usually to understand the food marketing system, which transforms commodities in a farmer's field in time, place, and form, into food on the table. It is impossible to understand the challenges facing efforts to eliminate hunger without understanding the role of markets and how the food marketing system operates. This is the food policy perspective.

The food policy agenda includes rapid and sustained poverty reduction. There are four basic food policy objectives, and all four are important:

1. Faster economic growth (the 'efficiency' objective),
2. More equal distribution of income from that growth (the 'welfare' objective'),
3. A guaranteed nutritional floor for the poor (the 'safety net' objective), and
4. Secure availability and stable prices in food markets (the 'food security' objective).

There are many trade-offs (and overlap) among these objectives, and substantial analysis of a country's food system is necessary to understand, if even roughly, the magnitudes of the trade-offs. The central organizing theme of the analysis is the 'food price dilemma,' an explicit recognition that a single market-clearing food price cannot satisfy all four objectives simultaneously – a 'pure' market solution does not work. Additional policy instruments are needed, but they all need to operate compatibly with market prices. The most important lesson is the centrality of food prices – and the signals they send to farmers, traders, consumers, and finance ministers. The behavior of these decision-making agents dictates market outcomes, but also responds to those market outcomes. The 'macro' food system that food policy analysts need to understand encompasses micro behavior on the farm and in the household, market-level behavior by traders, processors and retailers, and macroeconomic responses by policymakers.

In a market economy (the only kind of economy with a successful track record of raising labor productivity, and hence living standards, over many generations), markets play three key roles: First, as stressed by technical planners, they play an engineering role by moving inputs to farmers and food to consumers. Even socialist, planned economies have to use markets in this role.

However, there are two deeper roles for markets that provide market economies their distinguishing strengths (and often harsh outcomes). First is the role of markets in price discovery – what is a commodity (or service) 'worth' in monetary terms? These terms dictate the rate of exchange and determine such important values as the price of rice or of wages for unskilled labor. Price discovery is about scarcity, the distribution of incomes, and who gets what.

However finally, markets serve as the arena for allocating society's scarce resources to meet the virtually unlimited needs and desires of consumers. This allocation process, when joined to reasonably efficient price formation, is the reason market economies have outperformed other forms of economic organization over the long haul. Efficiency in resource allocations is simply critical to raising economic output in a sustainable fashion, and thus to reducing poverty and hunger.

Simply 'getting prices right' in markets will not solve the problem of hunger. However, it is also not possible to 'plan' one's way out of hunger by making markets do one's will. The trick, and only a few countries (mostly in East and Southeast Asia) have managed it smoothly, is for government policy and markets to work together to bring poor households into a growing economy that is based on a productive, sustainable, and stable food system. Only then can one end hunger, and keep it ended.

From this policy perspective, food security as a global issue presents an enormous paradox. At one level, steady progress has been made in the past half century in bringing much of the population out of poverty and hunger. Measured by the key determinants of food security – improved availability, access, utilization, and stability – food security has been improving. Large pockets of food insecure populations remain, especially in Sub-Saharan Africa and South Asia, but because of rapid economic growth, aggressive food price stabilization efforts, and/or safety net programs that deliver food to the poor, the rest of Asia and Latin America are coping reasonably well with their food security challenges.

At the same time, food security strategies and policies are in almost total disarray. A fundamental disconnect exists between what most countries say their food security strategies are, and what policies they are actually pursuing. The disconnect is most manifest with rice policy in Asia, where high prices for rice farmers are implemented to 'reduce poverty,' when in fact most of the poor and hungry in the region are net rice buyers, and thus suffer more hunger and poverty from high rice prices. However, many countries do not have coherent strategies to improve their food security. An important reason for this disconnect is a basic misunderstanding in the political arena of

the interconnected role of markets and government policies in providing sustainable food security.

An Overview of Food Security Dynamics

The Food and Agriculture Organization's (FAO's) flagship publication, The State of Food Insecurity in the World 2012, provides a sophisticated new methodology for estimating the prevalence of undernutrition and uses it with the latest data to present the best indicators available on the state and dynamics of food security at the country level between 1990–92 and 2010–12 (FAO, WFP and IFAD, 2012). **Table 1** summarizes the key data for the world, Latin America, Sub-Saharan Africa, and the subregions of Asia, for comparative purposes. For each region, data are shown for 1990–92, 2000–02 and 2010–12, with changes calculated between decades.

Four food security indicators are shown for each region. First is the 'prevalence of undernutrition,' the 'headline' indicator used to measure progress on the Millennium Development Goals (goal 1, target 1.9). It is the proportion of the population at risk of caloric inadequacy and is the traditional FAO measure of hunger. Second is a new measure of average dietary energy supply adequacy. This indicator expresses each country's or region's average supply of food calories available for consumption (including imports) as a percentage of average dietary energy requirements for the population, as calculated by FAO. Third is a measure of the depth of the food deficit facing the undernourished, also as calculated by FAO. It indicates how many calories would be needed to lift the undernourished from their status, normalized by total population, everything else held constant. The measure shown in **Table 1** uses the 'depth of the food deficit in kilocalories per capita per day' as a percentage of the minimum dietary energy requirement (MDER), so that it is on a similar scale as the food supply measure.

Finally, a 'food security gap' is calculated for this article to indicate the rough balance between food supplies available and the depth and extent of hunger. This gap is simply the

Table 1 Food Security Indicators

Region/Indicator	*Time period (and change from previous time period)*				
	1990–92	*2000–02 (change)*		*2010–12 (change)*	
World					
Prevalence[a]	18.6	14.9	(−3.7)	12.5	(−2.4)
Food supply[b]	114	117	(+3)	121	(+4)
Food deficit[c]	7.2	5.8	(−1.4)	5.1	(−0.7)
Food security gap[d]	6.8	11.2	(+4.4)	15.9	(+4.7)
Sub-Saharan Africa					
Prevalence	32.8	29.7	(−3.1)	26.8	(−2.9)
Food supply	100	104	(+4)	109	(+5)
Food deficit	13.7	12.7	(−1.0)	11.8	(−0.9)
Food security gap	−13.7	−8.7	(+5.0)	−2.8	(+5.9)
Latin America					
Prevalence	14.6	11.2	(−3.2)	8.3	(−2.9)
Food supply	117	121	(+4)	125	(+4)
Food deficit	5.4	4.1	(−1.3)	3.2	(−0.9)
Food security gap	11.6	16.9	(+5.3)	21.8	(+4.9)
South Asia					
Prevalence	26.8	21.3	(−5.3)	17.6	(−3.7)
Food supply	106	104	(−2)	107	(+3)
Food deficit	10.2	8.6	(−1.6)	7.1	(−1.5)
Food security gap	−4.2	−4.6	(−0.4)	−0.1	(+4.5)
Southeast Asia					
Prevalence	29.6	19.2	(−10.4)	10.9	(−8.3)
Food supply	100	107	(+7)	120	(+13)
Food deficit	12.3	7.4	(−4.9)	4.3	(−3.1)
Food security gap	−12.3	−0.4	(+11.9)	15.7	(+16.1)
Developing East Asia					
Prevalence	20.8	14.3	(−6.5)	11.5	(−2.8)
Food supply	107	117	(+10)	124	(+7)
Food deficit	8.2	5.2	(−3.0)	4.0	(−1.2)
Food security gap	−1.2	11.8	(+13.0)	20.0	(+8.2)

[a]Prevalence of undernourishment.

[b]Average dietary energy supply adequacy.

[c]Food deficit is the 'depth of the food deficit in kilocalorie per capita per day' as a percentage of minimum dietary energy requirement (MDER).

[d]Food security gap = (Supply − 100) − Food deficit = FSgap. When FSgap = 0, there is exactly enough 'surplus' food supply to offset the entire food energy deficit.

Source: Reproduced from FAO, WFP, IFAD, 2012. Economic growth is necessary but not sufficient to accelerate reduction of hunger and malnutrition. The State of Food Insecurity in the World 2012. Rome: FAO.

'surplus' food supply available (food supply – 100) minus the food deficit, as calculated and reported in Table 1. A negative gap means the food deficit is larger than the food surplus, with the inevitable consequence that people will be hungry even with equitable distribution. Sharply positive levels of the gap mean there is plenty of food for all. (Note that the 'supply' variable makes no allowance for the state of nutrition of the population. The 'population normalized' food deficit measure indicates how much food energy would be needed per capita to bring the undernourished population up to the minimum energy requirement. Both indicators need to be examined together to gain an understanding of the relative importance of food availability and food access in driving the extent of undernutrition. The 'food security gap' measure does this in a simple (if crude) way. Substantial hunger (high 'prevalence') in these environments suggests a highly unequal distribution of economic resources. This measure of the food security gap is a particularly sensitive indicator of progress (or lack thereof) in reducing undernourishment, and whether availability or access is the limiting factor.

It is clear from the data in Table 1 that substantial progress in reducing food insecurity has been made over the past two decades. Prevalence of undernutrition at the global level has fallen from 18.6% in 1990–92 to 12.5% in 2010–12, a decline of 6.1% points (almost a third).

Both Southeast Asia and Developing East Asia have made enormous progress in lowering food insecurity in the past two decades, with prevalence dropping by 18.7% points and 9.3 points, respectively. Most remarkably, both regions moved from negative food security gaps to sharply positive ones. In Southeast Asia, a very large negative gap of −12.3% was transformed into a very large positive gap of 15.7 points in just 20 years. Improved supplies (up 20%) and sharply lowered food deficits (down 8%) contributed to this amazing performance.

Significant challenges remain, of course. The prevalence of undernutrition in Sub-Saharan Africa remains very high, 26.8%, although the trend is for modest improvements. In South Asia the rate has fallen by 9% points, although it remains relatively high at 17.6% undernourished in 2010–12.

As noted, the most sensitive indicator of changes in food security status is the 'gap' measure. Only Sub-Saharan Africa and South Asia continue to have negative gaps, indicating an overall shortage of food available in the countries in each region, and even these negative gaps have narrowed significantly. At one level, the relationship between an improving food security gap and reductions in prevalence of malnutrition is obvious. More food and smaller deficits translate into less hunger. However, there are nuances to the relationship. In particular, the relationship is not linear – there are clear diminishing returns to improving the food security gap in terms of lowering the prevalence of undernutrition. (The statistical relationships used to calculate the rate of diminishing returns are based on annual data for individual countries in each of the regions.) Food insecurity becomes less a problem of food availability and general poverty, and more a structural problem of people 'left behind.' Structural poverty and hunger require a much more sophisticated and targeted approach than the 'propoor growth with stability' approach that has worked so well in the past, especially in Asia (Timmer, 2004).

The Three Fundamental Transformations Needed to Ensure Food Security

Three basic transformations drive the link between economic development and food security (Timmer, 2009a): Structural, agricultural, and dietary. Especially in Asia and Latin America, accompanying these three basic transformations have been rapid changes in the entire food marketing system (led by the 'supermarket revolution,' see Reardon and Timmer, 2012), and in the growing importance of urban consumers as drivers of a country's food system. The 'endpoint' of the structural transformation – the full integration of factor markets between rural and urban areas – is now within sight in the richest transition countries, but remains a challenge to poor- and middle-income countries.

Structural Transformation

The structural transformation involves declining shares of agriculture in gross domestic product (GDP) and employment, almost always accompanied by serious problems closing the gap in labor productivity between agriculture and nonagriculture. The basic cause and effect of the structural transformation is the rising productivity of agricultural labor. Figure 2 presents an especially graphic illustration of the structural transformation in 86 countries between 1961 and 2000. Each red square represents the share of agriculture in total employment for a particular country and year. Similarly, each blue circle represents the share of agriculture in economic output, or GDP, for the same country and year. Finally, each green cross is the difference between these two shares measured so that the value, which is simply the gap in labor productivity between agriculture and nonagriculture, is negative

The historical path of structural transformation has been accompanied by falling food prices, leading to a 'world without agriculture' (Timmer, 2009a). However continued financial instability, coupled with the impact of climate change, could lead to a new and uncertain path of rising real costs for food. Such a path would lead to a reversal of structural transformation (Timmer and Akkus, 2008). Management of food policy, and the outlook for sustained poverty reduction, will be radically different depending on which of these alternatives materialize.

The structural transformation involves four main features:

1. A falling share of agriculture in economic output and employment,
2. A rising share of urban economic activity in industry and modern services,
3. Migration of rural workers to urban settings, and
4. A demographic transition in birth and death rates that always leads to a spurt in population growth before a new equilibrium is reached.

These four dimensions of the historical pathway of structural transformation are experienced by all successful developing economies; diversity appears in the various approaches governments have tried to cope with the political pressures generated along that pathway. Finding efficient policy mechanisms that will keep the poor from falling off the

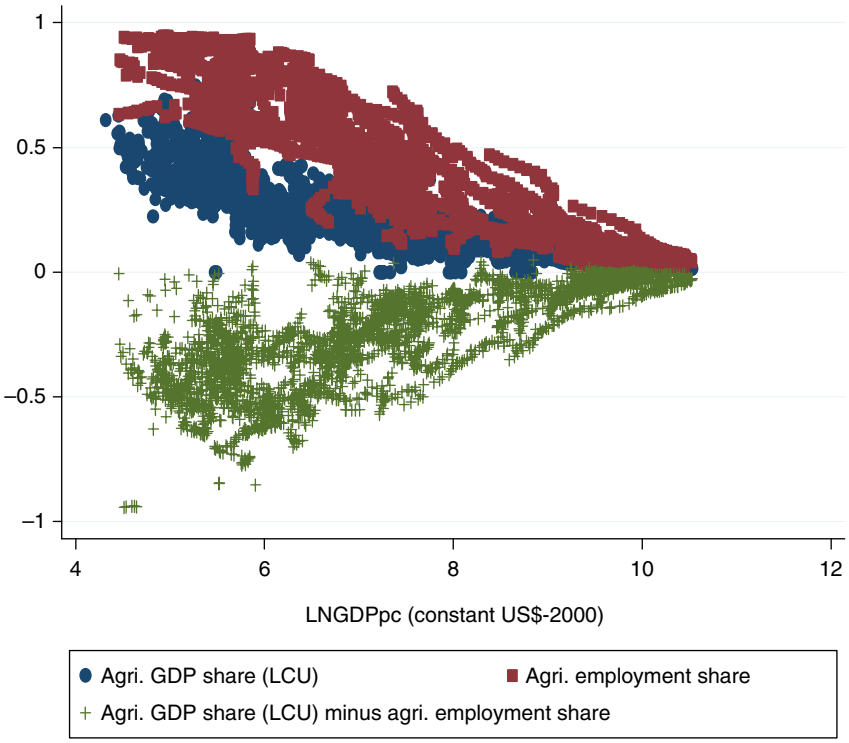


Figure 2 The structural transformation in 86 countries from 1965 to 2000. Reproduced from Timmer, C.P., Akkus, S., 2008. The structural transformation as a pathway out of poverty: Analytics, empirics and politics. Working Paper 150. Washington, DC: Center for Global Development.

pathway altogether has occupied the development profession for decades. There are three key lessons.

First, the structural transformation has been the main pathway out of poverty for all societies, and it depends on rising productivity in both the agricultural and nonagricultural sectors (and the two are connected). The stress on productivity growth in both sectors is important, as agricultural labor can be pushed off the farms into even lower productivity informal service sector jobs, a perverse form of structural transformation that has generated large pockets of urban poverty, especially in Sub-Saharan Africa and India. (Both of these cases have been documented in the Stanford Symposium Series on Global Food Policy and Food Security in the twenty-first century (Badiane, 2011; Binswanger-Mkhize, 2012).) It is no accident that these are the two regions of the world where food insecurity remains severe.

Second, in the early stages, the process of structural transformation widens the gap between labor productivity in the agricultural and nonagricultural sector – a process shown in Figure 2. This widening puts enormous pressure on rural societies to adjust and modernize. These pressures are then translated into visible and significant policy responses that alter agricultural prices. The agricultural surpluses generated in rich countries because of artificially high prices then cause artificially low prices in world markets and a consequent undervaluation of agriculture in poor countries. This undervaluation over the past several decades, and its attendant reduction in agricultural investments, is a significant factor explaining the world food crisis in 2007–08 and continuing high food prices.

Third, despite the decline in relative importance of the agricultural sector, leading to the 'world without agriculture' in rich societies, the process of economic growth and structural transformation requires major investments in the agricultural sector itself. This seeming paradox has complicated (and obfuscated) planning in developing countries as well as donor agencies seeking to speed economic growth and connect the poor to it. Owing to active policy concerns about providing food security to their citizens, countries in East and Southeast Asia largely escaped much of this paradox, but Sub-Saharan Africa has not.

For poverty-reducing initiatives to be sustainable over long periods of time, the indispensable necessity is a growing economy that successfully integrates factor markets in the rural with urban sectors, and stimulates higher productivity in both. That is, the long-run success of poverty reduction, and with it, improvements in food security hinge directly on a successful structural transformation. The historical record is very clear on this path.

Managing the ingredients of rapid transformation and coping with its distributional consequences have turned out to be a major challenge for policymakers. 'Getting agriculture moving' in poor countries is a complicated, long-run process that requires close, but changing, relationships between the public and private sectors. Donor agencies are not good at this. More problematic, the process of agricultural development requires good economic governance in the countries themselves if it is to work rapidly and efficiently. Aid donors cannot hope to contribute good governance themselves – and may well impede it.

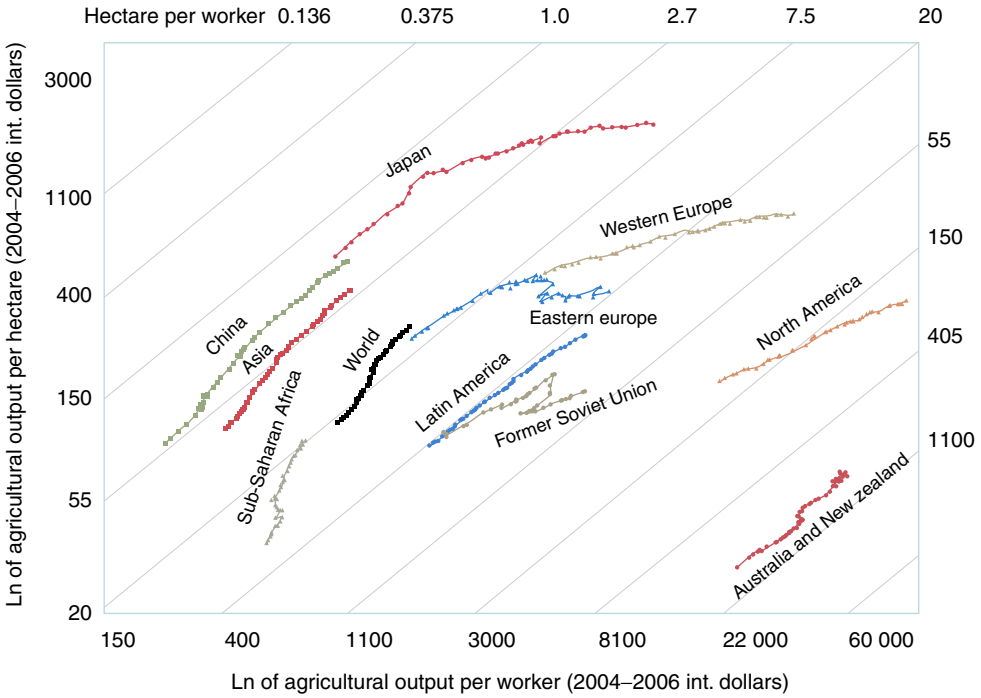


Figure 3 Land and labor productivity in agriculture, 1961–2010. Reproduced from Philip, P., 2011. African agricultural productivity growth and R&D in a global setting. Stanford Symposium Series on Global Food Policy and Food Security in the 21st Century, October 6, Stanford University.

The strong historical tendency toward a widening of income differences between rural and urban economies during the initial stages of the structural transformation is now extending much further into the development process. Consequently, with little prospect of reaching quickly the turning point, where farm and nonfarm productivity and incomes begin to converge, many poor countries are turning to agricultural protection and farm subsidies sooner rather than later in their development process. The tendency of these actions to hurt the poor is then compounded, because there are so many more rural poor in these early stages.

Agricultural Transformation

Although the structural transformation is a general equilibrium process that is not easily visible from inside the agricultural sector, the changing demand and productivity patterns induce significant change within the sector itself (Timmer, 1988). This agricultural transformation is driven by changing domestic demand, opportunities for international trade, commercialization of decision making, and technical change that is both commodity specific; for example, 'green revolution' varieties of wheat and rice; and sector-wide-better inputs, improved knowledge, communications, infrastructure, and financial intermediation. Nonstaple commodities, such as palm oil, and nonfood commodities such as coffee and rubber, play larger roles in certain circumstances. The potential for commodities to be grown as raw materials for biofuel production – especially maize, palm oil and cassava – might be a future driver of the agricultural transformation (with highly uncertain consequences for food security).

No single measure of the pace and extent of agricultural transformation captures the complexity and heterogeneity of the process – much is country and time specific. The most graphic and general representation of the process of agricultural transformation is the 'Ruttan-a-gram,' which measures productivity per hectare on the vertical axis and productivity per worker on the horizontal axis (see Figure 3). This two-dimensional perspective on agricultural development was developed by Hayami and Ruttan (1985), where it was used as a powerful tool to demonstrate the multiple paths to successful agricultural transformation. The 'Asian Path' relied heavily on new biological and chemical technologies to raise yields in land-scarce, labor-surplus environments, whereas mechanical technologies were used to raise labor productivity in land-abundant, labor-scarce environments. Japan characterized the former approach for raising agricultural productivity; the United States, Canada, and Australia/New Zealand characterized the latter. Western Europe was, appropriately, in between these two more extreme approaches.

Figure 3 shows the pathways of productivity change in the agricultural sectors of major regions, as well as the world total. Two things are striking. The first is the rapid pace of gain in most regions (indicated by the overall length of the line for each country or region because both axes are measured in logarithms). Japan and China have both seen major gains in labor and land productivity over the past half century, although average farm size has only started to increase in Japan in the past several decades; most of Europe has seen gains in labor productivity via larger farm size, although Eastern Europe and the Former Soviet Union suffered severe reversals after the fall of communism. The most striking feature of Figure 3, however, is the stagnation of growth of labor

productivity in Sub-Saharan Africa. Although yields per hectare are increasing slowly, there has been virtually no gain in labor productivity in agriculture in half a century.

The second striking feature is that land consolidation has barely begun at a global level. Indeed, farm size continues to get smaller on average, driven by the gradually shrinking farms in Asia and the more quickly falling farm size in Africa. Farm size has been virtually constant in Latin America. Uncertain land ownership and tenancy laws in Asia and Sub-Saharan Africa may account for some of this 'stickiness' in reported farm size. Outmoded statistical definitions may also be a factor: workers may be counted in the agricultural labor force even if most of their income is derived from off-farm sources.

Dietary Transformation

The basic drivers of changed dietary patterns are Engel's Law (the share of food in budget expenditures falls with higher incomes, thus providing a buffer against the welfare impact of sudden changes in food prices) and Bennett's Law (the share of starchy staples in the diet falls with higher incomes, as a deep, perhaps 'hard-wired,' desire for diversity in the diet can be expressed), but long-run changes in relative prices, changing demographics, as well as exposure to 'foreign' eating patterns also seem to have an impact.

As with the agricultural transformation, no single measure captures the complexity of dietary changes, and much is specific to local customs and tastes. As one example of the complex changes that are underway in a rapidly developing part of the world, Figure 4 presents several important dimensions of the dietary transformation that is underway in Southeast Asia, with the area of each pie chart proportional to average energy intake per capita for each of the 6 years depicted. Four things are striking. First, total caloric intake has risen steadily over the past half century, by 0.8% per year. In 1961, average food availability per capita, as measured by FAO Food Balance Sheet data, was just 1814 cal per day. Most citizens of Southeast Asia would have been chronically hungry then. By 2009, the most recent year for which data are available, food available per capita per day reached 2657 cal. At that level, hunger will not be common and obesity will be a rising problem.

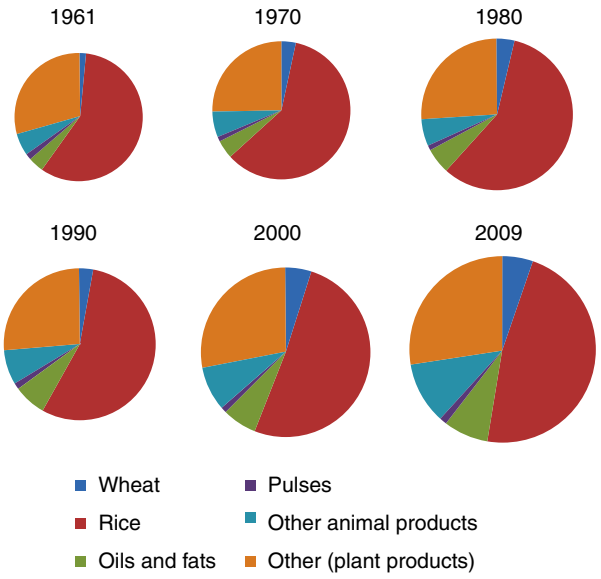


Figure 4 The dietary transformation in Southeast Asia. FAOSTAT, 'Food Balance Sheets,' FAO of the United Nations.

Second, the starchy staple ratio – the share of calories coming from cereals and starchy roots – fell from 74.8% to 62.1%. Intake of animal protein nearly tripled. The quality of the diet in nutritional terms has improved markedly, although the doubling of fat in the diet is a worrisome sign.

Third, rising consumption of animal products will require a modern feed industry to supply domestic producers of poultry, livestock, and aquaculture products, unless imports of final goods increase drastically. Domestic farmers have a rapidly growing market for feedstuffs, but at the moment a very large proportion of Southeast Asia's feed ingredients, especially maize and soy meal, is imported.

Finally, wheat calories are increasing 8% per year and wheat consumption is more than a 10th of rice consumption. Southeast Asia imports all of its wheat – Indonesia will surpass Egypt in 2013 as the world's largest importer of wheat. A volatile world market for wheat will increasingly be seen as a threat to food security in Southeast Asia, but national agricultural development strategies cannot be used to cope with that threat. With rice becoming less important to food security in the region, and wheat and feed grains becoming more important, management of food security will increasingly be a trade and macroeconomic issue rather than an agricultural issue.

The Changing Food Marketing System

The food marketing system is changing rapidly, especially as modern supply chains evolve to provision supermarkets (see Figure 5), and as concerns for food safety and origin are reflected in the purchasing decisions of increasingly affluent consumers. Modern supply chains and supermarkets change the nature of farm–market–consumer interactions. The spread of modern supply chains has the potential to be a real problem for food security.

Increasingly, modern supply chains are transmitting demand signals from consumers who are shopping in supermarkets, back up the food system, level by level, to processors, farmers, and input suppliers. Traditionally, each cell in the food system depicted in Figure 5 was connected locally by small traders operating with minimal capital and primitive technology (Reardon and Timmer, 2007, 2012). Modern supply chains are far more integrated into the farm-level procurement systems of supermarkets and are coordinated by these firms as they seek to 'drive costs out of the system.'

Four important trends emerge from the '10-wheeler' perspective in Figure 5, when it is overlaid with changing food consumption patterns in a given country or region. First, the vertical boxes are increasingly connected by market and nonmarket forces. One key conclusion for suppliers of technology in the private sector is that there can be no effective demand for inputs unless farmers are able to sell surpluses into the market. This market is increasingly controlled by procurement officers for supermarket chains, and their tendency to

	Food grain economy (starchy staples)	Non staple commodities (Fruits and vegetables, meat/ dairy, processed foods)
Farm inputs/ supplies	Smaller area possible higher yields, stress tolerance consumer quality	More value/hectare, but what role for small farmers (what 'assets' do they need to stay in ?)
Farm production (management and knowledge)	Very knowledge-intensive for good management practices; Access to inputs by farm size	Knowledge intensive; can there be effective extension for new technologies? Role of farm assets
Procurement/ logistics and wholesalers	Less rural consumption as workers leave; more transportation and storage; greater production instability with climate change	High transaction costs of dealing with small farmers; issues of quality control and product traceability
Processing and value added	Milling technology How to add value; branding?	Large share of consumer food expenditure is spent in this box
Retail/consumer welfare and health dimensions	Supermarkets as suppliers of food grains? Increased price stability through private actions? Problems of access by the poor?	Modern supply chains are funneling consumer demand back up the system. The food system is less supply driven.

Figure 5 Modernizing food supply chains: The '10-Wheeler' Model. Author design.

consolidate suppliers may counter the effort by governments seeking to include small farmers. However, successful efforts to reduce the transactions costs of incorporating small farmers into modern supply chains may simultaneously pay dividends by making these same farmers more accessible to modern input suppliers.

Second, there is a clear and rapid shift from the left side column of Figure 5 to the right side – from the 'starchy staple' sector to the 'diversified foods' sector. This shift reflects Bennett's Law (Bennett, 1954). This dietary diversification tends to improve the nutritional quality of the diet, although more processed foods and highly industrialized meat production raise nutritional, environmental, and food safety concerns.

Third, this increasingly diversified, market-driven food economy is more reflective of supply chain dynamics and consumer demand than in the past, which makes it more sensitive to rapid income growth and somewhat less sensitive to population growth. Especially where population growth is slowing quickly and income growth continues at a rapid pace, understanding the 'Engel elasticities' of the various items in the food shoppers' baskets (i.e., how demand for individual items responds to income growth), as well as other factors shaping consumer demand for food such as advertising, age structure, urbanization, and globalization of tastes, will be necessary for effective planning all the way back the chain to input supply.

Fourth, as consumers increasingly use supermarkets as the source of their purchased food staples, some surprising implications arise for food security. Traditionally, staples have been purchased in small retail shops with multiple grades and varieties available. Prices fluctuated according to local supply and demand conditions and often changed daily during periods of instability. The concentration of purchasing power into a handful of supermarket chains raises the possibility that procurement officers for food staples will encourage (force) their suppliers to maintain large enough stocks so that supplies will be reliable and that prices can be kept reasonably stable. Indeed, it is easy to imagine supermarkets, especially in East and Southeast Asia, where unstable rice prices are a threat to food security, beginning to compete for customers with a

promise of 'safe, reliable rice supplies, at a stable, fair price.' Rice price stability could become a private good rather than the public good it has been historically (Timmer, 1989, 2010). The whole debate over how to provide food security in settings where volatile food prices can threaten it will be transformed when most food is purchased in supermarkets. We are a long way from that situation in 2013, but supermarkets are increasingly important as a supplier of basic food staples in developing countries.

What Is Driving Food Security? The Changing Global Environment

The international context for domestic food policy decision making with respect to food security has changed substantially since the mid-twentieth century. Six basic trends stand out, especially with respect to expectations in the early 1980s:

1. Surprisingly rapid economic growth occurred, especially in Asia, with hundreds of millions of people pulled out of poverty. The strong connection between inclusive economic growth, especially in rural areas, and rapid reduction of poverty was simply not apparent in the empirical record in the early 1980s. The East Asian Miracle (World Bank, 1993) did not appear for another decade. This rapid growth validated the central theme of the food policy perspective, which is the unsustainability of poverty reduction efforts without higher economic productivity of unskilled, especially rural, labor. That theme remains powerfully relevant.
2. A communications revolution at both the household and international levels has radically reduced transactions costs and increased access to knowledge. Again, the centrality in the food policy perspective of markets and price formation to understanding food policy design and implementation was boosted because marketing margins narrowed under improved and more informed competition. Consumers and farmers both benefited from more competitive local food markets. The 'supermarket revolution' has merely accelerated these changes (Timmer, 2009b; Reardon and Timmer, 2012).
3. Global financial markets became interested in 'emerging economies.' The early 1980s were an era of fixed exchange rates, tight controls on the flow of foreign capital, and virtually no financial intermediation beyond state banks. At first, the influx of foreign capital in the 1990s was welcomed as a sign of confidence, but except for foreign direct investment in 'real' assets such as factories and real estate, the global financial interest in emerging economies was a two-edged sword. A rapid influx could cause currency appreciation and a loss of competitiveness; its rapid exit when the economy started to decline or foreign investors saw better opportunities elsewhere caused a crisis in local financial markets. Global financial integration came with very poorly understood risks, and 2009 demonstrated them clearly. The growth of foreign investments in land to produce food and/or biofuels for export – the so-called land-grabs – is controversial, but at least the capital cannot leave the country quickly. The injection of new capital into agriculture in poor countries may not be all bad. Much will depend on who benefits from the new production – foreigners or local farmers.
4. The rapid emergence in the 1990s of China and India as global growth engines meant a gradual shift in the drivers of demand for commodities and natural resources. Advanced economies had become more knowledge-driven and less dependent on energy, metals, and other basic commodities – including food commodities – to fuel their economic growth. The price depression for nearly all commodities in the 1980s and 1990s reinforced the view that the future depended on value added from skills and knowledge, not from exploitation of natural resources. However industrialization, especially as practiced by China and India, is a very intensive user of natural resources (and producer of greenhouse gases). By the turn of the millennium it was increasingly clear that the growth path of developing countries was the primary driver of commodity prices, starting with energy prices but quickly extending to food prices. The Malthusian challenge was back, but with two decades of neglected investments in raising agricultural productivity (because of the low agricultural prices), the challenge is turning out to be hard to meet.
5. High energy prices have turned out to be a 'game changer' for agriculture and the food economy. Once oil prices were high enough to justify using sugar, maize, cassava, or vegetable oils to produce gasoline or diesel substitutes, agricultural commodity prices became directly linked to oil prices. The concern to reduce emissions of greenhouse gases to mitigate climate change provided ample motivation to the US and European legislatures to mandate the use of domestic food crops to produce liquid fuels. The combination of legislative mandates, which provided essential risk coverage to investors in biofuel facilities, and high oil prices, which provided market-based incentives, led to a new set of linkages between agriculture and the energy sector. (The link between biofuel policies and food prices is complicated and depends on fundamentals in energy and food markets as well as on policies. This complexity has become the topic of intensive research, for examples, see de Gorter and Just (2010), de Gorter and Drabik (2012), and Naylor (2012).) There had long been a link on the supply side, as energy prices affected fertilizer costs, fuel costs for tractors and trucks, and the economics of global supply chains. The new link was through the demand side. Higher prices for energy translated directly into greater demand for food commodities to convert into liquid fuels. There is no way that agriculture can meet the nearly insatiable demand globally for liquid fuels, and having the food–fuel price linkage puts poor food consumers at serious risk.
6. Climate change is imposing itself as a reality on the increased probability of extreme weather events in general, and also on both global and localized food security outcomes in particular. The ecosystem services provided by the climate are a *sine qua non* for all agricultural production – photosynthesis remains the most efficient way to capture solar energy for human use. The most important effects of climate change on agriculture are likely to include a net global loss of agricultural land, changing crop suitability,

and an increase in the frequency of natural disasters. It will also have negative effects on other areas of agriculture broadly interpreted; climate change will reduce the carrying capacity of many rangelands and pose threats to fisheries and aquaculture production systems.

Climate change is expected to have highly variable effects on different regions; tropical and equatorial regions will bear the heaviest burdens, with Sub-Saharan Africa probably facing the greatest challenges, with some gains in yields and land availability in temperate regions. As rural poverty is concentrated in tropical and, in South and Southeast Asia, coastal areas, climate change is expected to have a disproportionate effect on the already vulnerable. The growing urbanization of poverty, the result of dysfunctional structural transformations (especially in Africa and India), may change the geographic incidence of the impact of climate change on the poor, but probably not the overall level (Ravallion, Chen and Sangraula, 2007; Badiane, 2011; Binswanger-Mkhize, 2012).

Agriculture also plays an important role in driving climate change, accounting for 14% of global greenhouse gas emissions, and this figure more than doubles when deforestation and other land-use changes are included. Forests, thus, are a crucial global natural resource for climate change mitigation. At the global level, the challenge of climate change for the international architecture in agriculture is to continue pushing toward an overarching global climate deal, while contributing to other schemes that support and provide incentives to the absorption and reduction of emissions at the country level. In-country 'climate-smart agriculture' adaptation projects and programs now form part of the food policy agenda. The challenge is to design, analyze, and implement these projects and programs.

The Way Forward

Several policy approaches to improving food security are under consideration. Which is best will depend on which global food price regime is likely to drive policy formation in the coming quarter century. The historical path of structural transformation with falling food prices, leading to a 'world without agriculture' is an obvious possibility (Timmer, 2009a). However, continued financial instability, coupled with the impact of climate change, could lead to a new and uncertain path of rising real costs for food with a reversal of structural transformation (Timmer and Akkus, 2008). Management of food policy, and the outlook for sustained poverty reduction, will be radically different depending on which of these global price regimes plays out.

Policy Approaches to Food Security in a Volatile Price Environment

There are three basic approaches to coping with the impact of high food prices once they hit world markets: domestic price stabilization; increasing supplies available in local markets; and providing safety nets to poor consumers. All three are directed at and must be managed by individual countries themselves, but donors and international agencies can play a substantial role as well in coordinating activities and providing resources, both financial and technical assistance.

The first approach is for individual countries to use market interventions to stabilize their domestic food prices. Such stabilization requires some capacity to isolate the domestic rice market from world markets and can only be implemented through government actions (although private traders can handle most of the actual logistics. Isolation from the world market does not, of course, guarantee more stable prices. Indeed, for most countries, open borders to world markets lead to greater price stability, as local shortages and surpluses can be accommodated through trade). Such isolation runs directly against the spirit and, for many countries, the letter of WTO agreements. However, it is a very widespread practice. Demeke, Pangrazio, and Maetz (2009) count 36 countries that used some form of border intervention to stabilize their domestic food prices during the 2007–08 crisis.

Such policies can have a large impact on the level of food insecurity, even at a global level. India, China, and Indonesia stabilized their domestic rice prices during the 2007–08 food crisis by using export bans (or at least very tight controls), thus protecting well over 2 billion consumers from sharply higher prices. The policies pursued by these three countries demonstrate the importance of understanding local politics in policy formation, especially food policy. Although the end results were similar – food prices remained stable throughout the crisis – the actual policies pursued in each country were quite different (Slayton, 2009; Dawe, 2010a). (The 'pass through' of price increases in world markets to the domestic economies of China, India, and Indonesia from early 2007 to early 2008 were 4%, 8%, and 3%, respectively. In each case, however, domestic rice prices were already higher than world prices, before the crisis hit (Dawe, 2010a).)

India, Indonesia, and China are big players in the global rice market, even if their actual trade is limited. As Dawe (2010b) emphasizes, there is a case to be made simply in terms of aggregate global welfare that stabilizing domestic rice prices in these large countries using border interventions might be both an effective and an efficient way to cope with food crises, even after considering the spillover effects on increased price volatility in the residual world market. Dawe points out that unstable supply and demand must be accommodated somewhere, and passing the adjustment to the world market may be both equitable and efficient in a second-best world where fast-acting and well-targeted safety nets are not available. One important advantage of successful price stabilization efforts in Asia is that they also stabilize price expectations among the many participants along the entire rice supply chain, and thus prevent the disastrous hoarding behavior that can generate extreme market shortages and severe price spikes (Timmer, 2010, 2012).

The second basic approach to coping with a food crisis is to stimulate additional supplies through fast-acting programs. Nearly all countries tried to do something along these lines during the 2007–08 crisis, whether by subsidizing fertilizer to get a quick production response or encouraging planting of short-season crops, even urban gardens. If the high prices

for food seen in the crisis actually get to farmers, they have strong incentives to search out these options themselves, but government assistance in gaining access to inputs or proper seed varieties can also help. In Asia, the short-run response of rice farmers to high prices was surprisingly vigorous, partly because of the availability of short-duration rice varieties and irrigated farming systems with multiple-cropping potential (Slayton, 2009). In Vietnam, for example, which has three distinct cropping seasons for rice, production increased by 6.3% in 2007 and by 5.3% in 2008, compared with average annual increases of just 3.3% per year between 2005 and 2011. All of this increase in production, a total of 1.2 mm, was put on the export market.

Countries can also hold emergency food stocks as part of a broader strategy for providing food security to their citizens. Expectations of higher and more volatile food prices in the future should lead authorities to invest in larger food stocks than in the past. The 'design rules' for adding to and disposing of these stocks, and their day-to-day management to avoid large storage losses, will be essential to making emergency food stocks a sustainable and cost-effective approach (Timmer, 2009c). Clear rules on management of public stocks minimize the displacement of private storage.

One critical element of these rules will be to use international trade in the commodity as part of the provisioning mechanism, thus avoiding the extraordinarily high costs that can come from a strategy of total self-sufficiency. Even in countries as large as Indonesia, India, and China, where a high degree of food self-sufficiency is required simply because of the limited size of world grain markets, some interaction with these markets through a managed trade regime can lower the costs of food security. Managed trade regimes can be open and transparent, with clear rules on the nature of interventions, thus allowing the private sector to handle actual trade logistics.

The third approach to coping with a food crisis is to provide safety nets to poor consumers, either in cash or through the direct provision of food aid. This was the immediate, and almost only, response of the donor community to the food crisis in 2007–08. The safety net approach figures prominently in 'best practice' recommendations from the World Bank, FAO, and the World Food Program (World Bank, 2005). The logic is clear: let high prices be reflected in local markets to signal the necessary changes in resource allocations to both producers and consumers, but protect the very poor from an irreversible deterioration in their food intake status. Efficiency is maintained, and the poor are protected.

The difficulty is that food crises are relatively short-lived events (as opposed to chronic poverty). Effective safety nets take a long time to design and implement, and they are very expensive if the targeted poor are a significant proportion of the population. Unless a well-targeted program with adequate fiscal support is already in place when the crisis hits, it is virtually impossible for a country to design and implement one in time to reach the poor before high food prices threaten their nutritional status. Even when a program is in place, and can be scaled up quickly, as with the Raskin program of rice distribution to the poor in Indonesia, operational inefficiencies and simple corruption in deliveries may mean that the poor are reached only at exceptionally high cost (Olken, 2006).

Improving the Supply Outlook

A number of chapters in this Encyclopedia treat various dimensions of increasing agricultural output and food supply. The cursory discussion in this section focuses mostly on the challenges facing that task as they relate to food security. In keeping with the basic framework of the chapter, there are short-run and long-run dimensions, and issues at the micro, macro, and global level. Only the global and long-run topics are treated here.

The long-run issue is whether supply responses can meet the outlook for rapid growth in demand, especially at the global level (although this will obviously be made up of varied national responses). In the past, when food prices spiked and talk of an impending Malthusian crisis arose, output responded to bring world food prices back to their long-run downward trend, though with a lag. Now, expectations are that such a benign output response may not be forthcoming, for three basic reasons: limited land available for expanding area; stagnant yields; and high-cost inputs.

A quarter of a century ago Hayami and Ruttan (1985) pointed out that area expansion as a source of increased agricultural production was drawing to a close, with future increases needing to come from higher yields on existing farmland. More than a decade into the twenty-first century, it is clear that there is little high-quality, unutilized agricultural land now available for farming. Even existing agricultural land is under threat in many regions from overexploitation and degradation, expanding recreational use, urbanization, even speculative demand from investment funds. Where there is good land available for expansion, especially in Africa and a few areas in Southeast Asia, vigorous competition, especially from foreign companies and sovereign investment funds ('land grabs'), is making that land inaccessible to local farmers.

Yields at research stations of existing agricultural technologies have essentially been unchanged for decades because of the paucity of investment in research during this time. Thus raising yields from actual farmer practices to the present technology potential is the only source of increased output until new agricultural technologies are developed. New technologies, however, are at least a decade away. Moreover, the yield gap to full potential has largely been closed except for Africa.

The costs of essential inputs – fuel, fertilizer, and water – to obtain greater yields are both high and growing rapidly. In addition, prolonged periods of high grain prices are likely to raise land rents and rural labor costs.

Managing Demand: Biofuels and Food Policy

Biofuels are not new. Although coal was known in China in prehistoric times, and was traded in England as early as the thirteenth century, it was not used widely for industrial purposes until the seventeenth century. Until then, biofuels were virtually the only source of energy for human economic activities, and for many poor people they remain so today. However, the widespread use of fossil fuels since the Industrial Revolution has provided a huge subsidy to modern economic activities as coal and later petroleum were so cheap – a subsidy which seems to be nearing an end.

The role of biofuels going forward, and the impact on agriculture, will depend on the structure of agriculture in individual countries. In the extreme, the demand for biofuels in rich countries to power their automobiles has the potential to raise the price of basic agricultural commodities to such a level that the entire structural transformation could be reversed. If so, the growing use of biofuels has two alternative futures: it could spell impoverishment for much of the world's population because of the resulting high food prices, or it could spell dynamism for rural economies and the eventual end of rural poverty. Which future turns out to be the case depends fundamentally on the location, technology, economics, and politics of biofuel production (and whether new energy sources and technologies, such as cheap natural gas or more efficient batteries to store solar and wind energy, come on stream).

The potential devastating effects of biofuels are easy to conceptualize (Naylor, 2012). The income elasticity of demand for starchy staples (cereals and root crops for direct human consumption) is less than 0.2 on average, and falling with higher incomes – it is already negative in much of Asia. Adding in the indirect demand from grain-fed livestock products brings the average income elasticity to approximately 0.5, and this is holding steady in the face of rapid economic growth in India and China. Potential supply growth seems capable of managing this growth in demand.

However, the demand for biofuels is almost insatiable in relation to the base of production of staple foods. The income elasticity of demand for liquid fuels for automobile and truck fleets, not to mention power generation, is greater than one in developing countries. The average for the world is rising as middle class consumers in China, India, and beyond seek to graduate from bicycles to motorbikes to automobiles. One simple calculation shows the dimension of the problem: if all the corn produced in the US were used for ethanol to fuel automobiles, it would replace just 15% of current gasoline consumption in the US. Something has got to give.

If this were a market-driven process, it is easy to see what will give. High grain prices will make ethanol production uneconomic, driving down the demand (and returns on investments in ethanol processing plants). Greater profitability of grain production will stimulate a supply response, although this may take several years if improved technologies are needed. Grain prices will reach a new equilibrium, with demand from the biofuel industry having only a modest impact.

This is not the scenario most analysts see. Instead, political mandates to expand biofuel production in many countries will continue to drive investments in processing facilities and the need to keep these profitable in the face of high raw material prices will require large public subsidies. Rich countries will be able to afford these more easily than poor countries, so a combination of inelastic demand for fuel and a willingness to pay large subsidies will keep grain prices very high (Naylor, 2012; de Gorter and Just, 2010).

If this scenario plays out, the consequences for economic growth, poverty reduction, and food security in developing countries depends on the role of agriculture in individual countries, the pattern of commodity production, and the distribution of rural assets, especially land. It is certainly possible to see circumstances where small farmers respond to higher grain prices by increasing output and reaping higher incomes. These incomes might be spent in the local, rural nonfarm economy, stimulating investments and raising wages for nonfarm workers. In such environments, higher grain prices could stimulate an upward spiral of prosperity.

An alternative scenario seems more likely however, partly because the role of small farmers has been under so much pressure in the past several decades. If only large farmers are able to reap the benefits of higher grain prices, and their profits do not stimulate a dynamic rural economy, a downward spiral can start for the poor. High food prices cut their food intake, children are sent to work instead of school and an intergenerational poverty trap develops. If the poor are numerous enough, the entire economy is threatened, and the structural transformation comes to a halt. The share of agriculture in both employment and GDP starts to rise, and this reversal condemns future generations to lower living standards. There will be much more 'structural' poverty, and countries determined to cope with it will find themselves supporting expensive and long-term safety nets for the poor.

A reversal of the structural transformation as the regular path to economic development and reduced poverty will be a historical event, countering the patterns generated by market forces over the past several centuries. Such an event is likely to have stark political consequences, as populations do not face the sustained prospect of lower living standards with equanimity. It is possible, of course, that new technologies will come onstream and lower energy costs across the board and thus allow the biofuel dilemma to disappear quietly – the natural gas revolution in the US certainly holds significant potential. However, it looks like a rocky couple of decades before renewable energies are available and competitive with fossil fuels.

A Food Policy Response to Climate Change

The biofuel challenge to food policy analysts stems from efforts to mitigate climate change. Equally challenging will be efforts to adapt agriculture to the dual effects of climate change – higher temperatures and greater variability in rainfall. In pulling together their final thoughts on the impact of climate change on food availability, food access, and food utilization – the three main factors that determine food security – Lobell and Burke make the following observation:

> …one thing appears almost certainly true in the twenty-first century; if agriculture and food security are to thrive, they will have to do so in a constantly warming world. The level of climate stability that has been experienced since the dawn of agriculture is a thing of the past; the future will be one of constant change. This need not spell disaster for food security, but we would be wise not to underestimate the enormity of the challenge at hand (Lobell and Burke, 2010, p. 1960).

Food policy analysis that understands this challenge and offers insights into how best to cope with it will be a key driver of how successfully society adapts to climate change.

Behavioral Dimensions to Food Security

Perhaps the most important element of food security in the minds of most citizens is the fear of a food crisis, when prices spike or staple foods (especially rice) disappear from the

market. Accordingly, preventing food crises through better understanding of their fundamental causes, thus allowing implementation of better food policies, should be a high priority for food policy analysts. Once a food crisis hits, coping with its consequences becomes the main task at hand, with emergency food aid and other forms of safety nets hastily brought into play. However, preventing food crises in the first place, especially by preventing sharp spikes in food prices, is obviously a superior alternative if a way can be found to do it. Understanding the behavioral dimensions of food security is an important step in learning how to prevent food crises. New insights from behavioral economics explain why governments should stabilize basic food grain prices (Timmer, 2012). With a better understanding of 'why,' it is possible to suggest better approaches to 'how.'

It is conceptually possible to hedge the risks from unstable food prices, or to mitigate their welfare consequences for the poor using safety nets, but there are no markets in which to purchase stability in food prices directly. The message is clear. Citizens would willingly go to the market to buy food price stability, but such a market does not exist, no doubt because the private coordination costs are too high. Food price stability is a public good, not a market good. Understandably then, citizens turn to the political market instead, although the costs of providing price stability as a public sector activity can also be very high, especially if public food agencies are poorly managed and become highly corrupt. However, only political action and public response from governments can provide stable food prices. Thus, food becomes a political commodity, not just an economic commodity, and a 'behavioral political economy' is needed to understand how food policy can achieve and sustain food security.

Understanding the behavioral foundations of formation of price expectations will be critical to building this new political economy. In particular, the dynamics of herd behavior and the tendency of bad news – about terrorism, wild fires, or a sudden rise in rice prices in local markets – to serve as a 'focusing event' in stimulating simultaneous, spontaneous behavior that results in panics, provide robust insights into how individuals form price expectations and respond to them (Tversky and Kahneman, 1986).

Governments that fail to stabilize food prices have failed in the provision of a quite basic human need that is rooted in behavioral psychology – the need for a stable environment. Governments that are successful in stabilizing food prices are usually rewarded politically; witness the landslide victories of Prime Minister Manmohan Singh in India and of President Yudhoyono in Indonesia in early 2009. Both candidates campaigned openly on their ability to bring their countries through the world food crisis with minimal impact on domestic food prices. Clearly, other factors contributed to the electoral success in both countries, but it is equally clear that the governments' abilities to provide stable food prices when the rest of the world was experiencing a food crisis were politically popular.

The trick, of course, is to provide stability in domestic food prices at low cost to economic growth, participation by the poor, and government finances. By and large, Asia has figured out how to do this as a domestic endeavor, but with large negative spillovers to world markets (Timmer, 2009c). African countries do not have a viable strategy for stabilizing their domestic food prices, and the continent suffers even more from the instability in world markets transmitted from the Asian approach to food price stabilization (Jayne, 2009). Indeed, the resource riches of Africa are attracting sizable investments from Asia (and elsewhere), but there seems to be little linkage between these investments, especially in land to produce food crops for export, and local food security.

The food security challenge is thus twofold: (1) to help Asia find more efficient ways to stabilize their domestic food prices, especially for rice, with fewer spillovers to world markets (and now including investment spillovers as well as price spillovers) and (2) to help Africa find a way to stabilize their domestic food prices without introducing serious distortions to their food economies or retarding the development of an efficient private food marketing sector. Neither of these challenges can be met without a basic rethinking of development approaches by academics, government policy circles, NGOs and community leaders, and citizens themselves. Ending hunger is hard because it is so complicated, deeply entwined with how we organize economic activities and regulate them through public policies. However, it is not impossible either, with better understanding of these complications and concerted efforts to resolve them.

See also: Agricultural Labor: Demand for Labor. Agricultural Labor: Gender Issues. Agricultural Labor: Labor Market Operation. Agricultural Labor: Supply of Labor. Agricultural Mechanization. Agricultural Policy: A Global View. Changing Structure and Organization of US Agriculture. Climate Change: Agricultural Mitigation. Climate Change: Cropping System Changes and Adaptations. Climate Change, Society, and Agriculture: An Economic and Policy Perspective. Computer Modeling: Policy Analysis and Simulation. Consumer-Oriented New Product Development. Economics of Natural Resources and Environment in Agriculture. Food Chain: Farm to Market. Food Marketing. Food Security: Food Defense and Biosecurity. Food Security: Postharvest Losses. Food Security: Yield Gap. From Foraging to Agriculture. Global Food Supply Chains. Government Agricultural Policy, United States. Green Revolution: Past, Present, and Future. Human Nutrition: Malnutrition and Diet. Industrialized Farming and Its Relationship to Community Well-Being. International and Regional Institutions and Instruments for Agricultural Policy, Research, and Development. International Trade. Investments in and the Economic Returns to Agricultural and Food R&D Worldwide. Land Use, Land Cover, and Food-Energy-Environment Trade-Off: Key Issues and Insights for Millennium Development Goals. Markets and Prices. Policy Frameworks for International Agricultural and Rural Development. Production Economics. Root and Tuber Crops

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Relevant Website

http://foodsecurity.stanford.edu/events/series/global_food_policy_series
Center on Food Security and Environment.

Food Security: Postharvest Losses

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Glossary

Relative humidity The ratio of the amount of water vapor present in the air expressed as percent of the greatest amount possible (saturation) at the same temperature.

Introduction

There are two kinds of food security that require completely different approaches to resolution:

Type 1: Postharvest loss covers the technologies needed to preserve food in safe and edible condition between the time of harvest and the moment it is prepared for consumption by people. The time can range from minutes to years. It is the subject of this article.
Type 2: Food biosecurity or food defense describes intentional contamination or destruction of the food system for warfare, political coercion, unfair economic gain, or exacting revenge. This topic will be covered in the accompanying article by N. Fredrickson.

The world production of food is enormous and the amount increases every year because of great efforts by many in the agricultural production sector. Some illustrative data are given in Table 1, which lists worldwide production of the major foods in 1989 and 2009.

This is sufficient to provide 100% of the nutritional requirements of every living human being.

It needs to be pointed out that the data in Table 1 lists production, not consumption. A substantial portion of the foods listed in Table 1 is not consumed because it is lost or becomes unfit to eat after harvest. These are known as 'postharvest food losses.'

Another aspect of world food production statistics is that the production is not evenly distributed among populations.

Table 1 World production of major foods 1989 and 2009

World food production (million tons) in 1989 and 2009		
Year	*1989*	*2009*
Cereals	1880	2489
Starchy roots and tubers	599	753
Vegetables	438	941
Fruits	345	588
Cow milk	471	697
Beef and buffalo	52	62
Pork	68	106
Eggs	36	67

Source: Data taken from FAO, 1990. FAO Yearbook, vol. 44. Rome: Food and Agriculture Organization of United Nations and FAO, 2010. FAO Statistical Yearbook. Rome: Food and Agriculture Organization of United Nations. Available at http://www.fao.org/docrep/015/am081m/am081m00.htm (accessed 29.10.13).

Developed countries have abundant food at reasonable cost. It is easy for their people to overeat, which leads to obesity and associated medical problems such as high blood pressure, diabetes, and coronary heart disease. In these countries large quantities of good edible food are discarded because of the demands for convenience and perfect appearance. These losses are defined as 'food waste.' In contrast most developing countries have insufficient food and food is high in cost in relation to income. Their problem is undernutrition, which leads to stunted growth, impaired ability to fight infectious diseases and starvation. There are approximately a billion people in this category. Families in developed countries typically spend 15–25% of their income on food whereas families in developing countries (DCs) spend 50–80% of their income on food. In DCs a food loss is a huge economic blow whereas in a developed country wasting food has a trivial cost. Insufficient food and high cost of food is a major contribution to the elevated rate of morbidity and mortality in developing countries.

The publication '2012 Global Hunger Index' jointly produced by The International Food Policy Research Institute in Washington, DC, Welt Hunger Hilfe in Bonn and Concern Worldwide in Dublin describes in detail the severity of hunger around the world (http://www.ifpri.org/publication/2012-global-hunger-index). A brief history of the development of postharvest food loss reduction activities can be found in Bourne, 2013.

Increasing Food Supply

The projected increases in the world population in the next 50 years means that there must be concomitant growth in food production. There are four main avenues by which the supply of food can be increased:

1. Increase the area of production: This includes activities such as clearing and developing new land, introduction of irrigation systems, developing salt-tolerant cultivars of crops, etc.
2. Increase the yield of crops harvested per unit area: This includes activities such as the development of higher-yielding cultivars, greater use of fertilizers, breeding plants and animals that are resistant to diseases, and controlling field losses resulting from insects, rusts, and rodents.
3. Produce more crops per year: Multiple cropping systems in which several crops per annum are harvested are activities that can be utilized where length of growing season and water availability are suitable.

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4. Reduce postharvest loss and waste: It is wasted effort to increase food production if this increase does not fulfill its nutritional destiny by getting into the stomach. This fourth avenue to increase food availability has never received the attention and resources that have been directed to the first three items mentioned above. Spurgeon (1976) has aptly called the reduction of postharvest food losses the 'hidden harvest.' This fourth avenue is a less obvious strategy than increasing production but it is an essential, and often overlooked part of ameliorating hunger in the world.

There are good reasons to concentrate on increasing food production because these avenues have an 'open-end' potential – increases of 50%, 100%, or more are possible. In contrast, postharvest food loss reduction has a 'closed-end' potential. For example, if postharvest losses are 15% then the maximum increase that can be obtained from this avenue is 15%. Although this may seem to be a small item, it carries more weight than appears at first sight as the formula to calculate the increase in production needed to affect a postharvest food loss shows:

$$\text{Production increase needed to offset postharvest loss} = \text{amount of consumable grain} \times \frac{100\%}{100 - \%\ \text{postharvest loss}}$$

Suppose 100 tons of grain are harvested and there is a loss of 20 tons (20%) in the postharvest system. There are two ways to regain 100 tons of consumable grain:

1. Eliminate the 20% postharvest loss.
2. Increase production to 125 tons (a 25% increase) so that after losing 20% of the 125 tons there will remain 100 tons for consumption. In other words, it requires a 25% increase in production to offset a 20% postharvest loss. Similarly, it would require a 100% increase in production to offset a 50% postharvest loss.

Some Definitions

It is necessary to precisely define what is meant by the term 'postharvest food loss' in order to prevent confusion and to establish boundaries so the term does not cover every aspect of the food chain. The following three-part definition from Bourne (1977) has been widely used.

'Postharvest' means after separation from the medium and site of immediate growth or production of the food.

Postharvest begins when the process of collecting or separating food of edible quality from its site of immediate production has been completed. The food need not be removed any great distance from the harvest site, but it must be separated from the medium that produced it by a deliberate human act with the intention of starting it on its journey to the table. The postharvest time ends when the food enters the mouth; it does not cover inefficiencies in human metabolism and utilization of the food.

'Food' means wholesome edible material that would normally be consumed by humans.

Inedible portions such as hulls, stalks, leaves, skins, bones, and shells are not food. Two critical nutrients, oxygen and water, are excluded because they are normally not considered as foods. Potential food (e.g., mycoprotein or leaf protein) are not foods; they do not become food until they are accepted and consumed by large populations. Feed (intended for consumption by animals) is not food. Crops grown for fuel production are not food. The method of measuring the quantity of food in the postharvest chain should be on the basis of weight expressed on a moisture-free basis or a specified moisture basis because changes in moisture content are not a food loss or food gain. For example, if 100 tons of rice at 20% moisture is dried to 90 tons at 10% moisture there is no food loss because only water is lost.

There will be times when information on losses in nutritional units and economic losses will also be needed but these are not the primary means of measuring postharvest food losses.

'Loss' means any change in the availability, edibility, wholesomeness, or quality of the food that prevents it from being consumed by people.

Food losses may be direct or indirect. A direct loss is disappearance of food by spillage, or consumption by rodents or birds. An indirect loss is the lowering of quality to the point where people refuse to eat it. If the food is consumed by people it is not lost; if it is not consumed by people for any reason at all then it is considered a postharvest food loss.

'Food waste' was originally defined as edible material intended for human consumption, arising at any point in the food supply chain that is instead discarded, lost, degraded, or consumed by pests (FAO, 1981). Over the past decade or so the term 'food waste' has come to mean wholesome edible food that is thrown out because of consumer demand for perfect appearance and convenience. This has become a problem in affluent countries where the cost of food in relation to income is low and people can afford to discard wholesome food if they are sated or it does not meet their high expectations for appearance, texture, or flavor. This meaning is in contrast to food loss, which means the food is unavailable or has become unfit to eat. A 2011 report from FAO gives extensive data on food loss and food waste (FAO, 2011). It shows that food waste is high and food loss low in developed countries whereas food waste is low and food loss is high in developing countries.

The motivation to reduce food waste is to reduce stress on the environment and requires a modification of human behavior. In contrast, reducing food loss requires the application of food preservation technologies and the motivation is to bring more food to those who are malnourished and poor. This article addresses the problems of food loss and how to reduce them. It will not address the problems of food waste and their reduction. Recent articles addressing food waste can be found in Parfitt *et al.* (2010), Gunders (2012), Beddington *et al.* (2012), and Institution of Mechanical Engineers (2013).

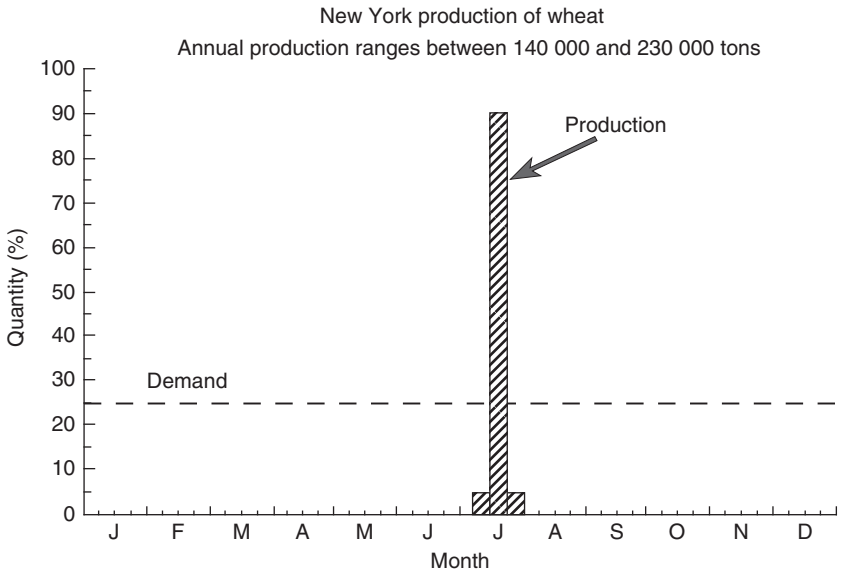


Figure 1 Production of wheat in New York state – a year's supply is harvested in a 3-week period.

Nature of the Problem

Within a given region the daily demand for food is constant over the course of a year (excluding any changes in population) but the supply of food for that region is very uneven from day to day over the course of the year. Food preservation, storage, and transportation are the mechanisms by which humankind matches the uneven day-to-day supply of food with the even day-to-day demand for food. This problem of matching the uneven food supply to the even demand has been a problem throughout recorded history.

The problem is that although humankind grows or hunts food for their own personal consumption, there are many other living organisms that try to use this food. This includes organisms ranging from large animals, through small forms of life such as insects down to microscopic forms of life such as bacteria. These produce direct losses – the food is no longer there.

Moreover, there is a natural tendency for food, which is built up principally from inorganic carbon, nitrogen, and water sources into complex energy-rich organic compounds, to degrade again to the simple inorganic compounds from which it was produced in the first place. These biochemical and chemical reactions occur spontaneously and lower the quality of the food. These produce indirect losses – the food is no longer fit to eat.

These problems are illustrated in Figure 1, which shows the production of wheat in New York State for each month of the year. The farms in New York produce no wheat from January to June or from August to December. All the wheat is harvested in the month of July as shown by the vertical bars. In fact, 90% of the wheat is harvested in 1 week, usually the third week of July. However, the demand for bread, macaroni, donuts, and all other nice foods made from wheat is very uniform throughout the year as shown by the dashed line parallel to the horizontal axis of Figure 1.

Most of the world food supply is seasonal – cereals, legumes, fruits, vegetables, roots, and tubers produce a large crop over a short period of time and then nothing until the next crop matures. The time when the harvest is ready can be any month of the year depending on the climate and nature of the crop but the pattern of a large harvest followed by a period of no harvest is the common feature. In some locations, where climate and water supply permit there is more than one harvest per year. In those cases there are two or more peaks of production with nothing in between.

Foods obtained from domestic animals are not seasonal. With good management, the time of harvest can be controlled to become uniform throughout the year. Milk and eggs can be harvested daily. Animals and birds can be kept alive and slaughtered as needed. Some fish harvests are seasonal because wild fish cannot be managed like domestic animals. Therefore, apart from fish, foods of animal origin are not given attention in postharvest loss reduction programs (but they do receive a lot of attention in food waste prevention programs).

Causes of Losses

There are many causes of postharvest food losses and they can be grouped under the headings of primary and secondary causes. Examples of loss are given for each cause.

Primary Causes

1. Biological and microbiological: Consumption or damage by insects, mites, rodents, birds, larger animals, and by microbes such as fungi and bacteria.
2. Chemical and biochemical: Undesirable reactions between chemical compounds that are present in the food such as the Maillard reaction, fat oxidation, and enzyme-activated reactions; contamination with harmful substances such as pesticides, or obnoxious substances such as lubricating oil.
3. Mechanical: Spillage, abrasion, bruising, excessive polishing, peeling or trimming, puncturing of containers, defective seals on cans, or other containers.

4. Physical: Excessive or insufficient heat or cold, improper atmosphere.
5. Physiological: Sprouting of grains and tubers, senescence in fruits and vegetables, and changes caused by respiration and transpiration.
6. Psychological: Human aversion, such as "I don't fancy eating that today." This is the major cause of food waste, but is a minor cause of food loss.

Some of the causes of losses interact. For example, respiration generates heat which if not dissipated will accelerate biochemical and chemical changes. If the temperature continues to rise the point is reached in stored grain where the grain blackens and eventually burns (spontaneous combustion).

In some cases more than one of these causes may be responsible for food loss. Multiple causes may work simultaneously or sequentially. Simultaneous action is the growth of mold and insects at the same time. An example of sequential action would be first the growth of mold which is stopped by drying, followed by biochemical reaction caused by the enzymes elaborated by the mold that results in unacceptably soft texture, rancid flavor, or inferior color.

Secondary Causes

Secondary causes lead to conditions that enable a primary cause of loss to occur. These usually are the result of inadequate human input. Examples include

1. inadequate drying equipment or poor drying season;
2. inadequate storage facilities to protect food from insects, rodents, birds, rain, and high humidity;
3. inadequate transportation to get the food to market before it spoils;
4. inadequate refrigerated or frozen storage (for perishables);
5. marketing system that fails to connect potential buyers with producers; and
6. legislation: The presence or absence of legal standards can affect the eventual retention or rejection of a food for human use.

There are times where it is possible to use a primary cause to offset a secondary cause and vice versa. For example, the problem of a poor transportation system can be partially overcome by drying of grain so that it does not become moldy so quickly, or by growing a variety of a tuber that has longer keeping properties. Conversely, insufficiently dried grain can be rushed to market and sold before it molds if good transportation and marketing services are available.

Cause – Commodity Link

The causes of food loss depend on the type of food, which are summarized below:

Cereals – fungi, insects, vertebrate pests, and poor milling.
Fruits and vegetables – bruising, rotting, senescence, and wilting.
Roots and tubers – sprouting, rotting, senescence, and wilting, insects.
Meat, milk, poultry, and fish – growth of microbes.
Dry fish – fungi and insects.

Food preservation technologies that control each of these causes of food loss are well known in developed countries. Unfortunately, the technologies are not so well known in developing countries nor are the equipments for storage, transport, and handling facilities readily available and reasonable in cost. Societies that suffer the worst hunger and malnutrition are the ones with the least knowledge of food preservation technologies and have the poorest infrastructure to preserve their food.

Factors Affecting Losses

Nature of the Product

Moisture content

Foods with high-moisture content (fruit, vegetables, foods of animal origin) generally have higher perishability and suffer higher losses than foods with a lower moisture content (e.g., cereal grains)

Texture

Hard items such as cereal grains do not bruise easily whereas soft items do bruise easily (mangoes, peaches). Items with a tough or thick outer skin (coconut, grapefruit) are more resistant to invasion by rotting organisms than those with a thin or tender skin (tomatoes, plums). Brittle foods fracture more easily than nonbrittle foods. For example, wheat at 25% moisture is somewhat pliable and does not fracture easily during handling but when dried to 10% moisture it becomes brittle and fractures easily.

Respiration rate

Much of our food is still living when harvested and, therefore, respiring by absorbing oxygen from the surrounding air and giving off carbon dioxide and water vapor. High respiration rates shorten shelf life. For example, asparagus (respiration rate at 9700 BTU ton^{-1} day^{-1} at 0 °C and 49 000 BTU ton^{-1} day^{-1} at 21 °C) has a much shorter shelf life than onion (respiration rate 650 BTU ton^{-1} day^{-1} at 0 °C and 3650 BTU ton^{-1} day^{-1} at 21 °C) (see Table 2).

Table 2 Heat generation vs. storage temperature for some fruits and vegetables

Heat generation by fresh fruits and vegetable (B.T.U. per ton per day)

	0 °C	*5 °C*	*15 °C*	*21 °C*	*27 °C*
Apples	700	1 350	4 900	5 700	–
Asparagus	9 700	18 000	39 000	49 000	92 000
Lettuce	2 500	3 650	8 500	12 200	18 100
Cantaloupes	1 200	2 100	7 900	12 000	14 700
Onions	650	750	2 400	3 650	6 200
Green peas (shelled)	13 500	19 400	–	99 500	–

Source: Reproduced from Hardenburg, R.E., Watada, A.E., Wang, C.Y., 1986. The commercial storage of fruits, vegetables, and flowers and nursery stock. US Department of Agriculture Handbook Number 66. Washington, DC: United States Department of Agriculture.

Table 3 Comparison of cereals with horticultural crops

Comparison of horticultural crops vs. cereals	
Cereals and oilseeds	*Horticultural crops*
Low moisture content, typically 10–15%	High-moisture content, typically 80–95%
Small unit size, typically less than 1 g	Large unit size, typically from 5 g to 10 Kg
Very low respiration rate with very small generation of heat. Heat production, typically 0.05 MJ ton^{-1} day^{-1} for dry grain	High to very high respiration rate. Heat production, typically 0.5–10 MJ ton^{-1} day^{-1} at 0 °C and 5–70 MJ ton^{-1} day^{-1} at 20 °C
Hard texture	Soft texture, easily bruised
Stable, natural shelf life, several years	Perishable, natural shelf life, several days to several months
Losses usually caused by molds, insects, and rodents	Losses usually caused by senescence, sprouting, rotting (bacteria and fungi), and bruising
Losses in DCs usually 10–20%	Losses in DCs usually 15–50%

Cereals have a very low respiration rate. However, the respiration of mold or insects within the grain mass releases carbon dioxide, water vapor, and heat which can damage the grain quality. Table 3 summarizes differences between cereal grains and horticultural crops.

Perishability

The inherent perishability of food as harvested determines what technologies are needed to maintain it in excellent condition. Perishable foods are prone to higher losses than stable foods. The level of perishability can be assigned to three levels:

- Highly perishable foods remain in edible condition for a few hours to a week unless some preservation technology is promptly applied. Foods such as milk, meat, fish, poultry, and some fruits and vegetables fall into this class.
- Perishable foods remain in edible condition for a week to several months unless treated. Some fruits and vegetables, tubers and roots, and oils are in this class.
- Stable foods remain in edible condition for several months to many years. This class includes cereal grains, oilseeds, many nuts, and honey.

Preservation technologies stabilize, safeguard, and maintain the harvest from land and sea in a condition suitable and safe for human consumption. The technologies selected for any food depend on the level of perishability and how much extension of shelf life is required. Refrigeration and pasteurization bring highly perishable foods into the perishable class whereas freezing, dehydration, and thermal sterilization enable them to be kept for months or years. Similarly, refrigeration, controlled or modified atmosphere storage, and chemical preservatives convert perishable foods into stable forms.

Processing technologies convert edible food materials into another form with higher acceptability and they usually make the food more perishable. For example, wheat is stable and keeps for years but when made into flour it becomes a perishable product because of oxidation. However, when flour is made into bread it becomes highly perishable because of staling and/or molding. However, bread can be changed from highly perishable to perishable by including preservatives and antistaling agents, or even back to stable condition by freezing. Similarly, barley is stable but when made into beer it becomes highly perishable. Refrigerating beer moves it from highly perishable to perishable.

Changes in perishability are shown schematically in Figure 2, where preservation technologies shown by the arrows on the left side decrease perishability and many processing technologies shown by the arrows on the right side increase perishability.

Climate

Temperature

During storage changes in food may be caused by

- microbial action (yeasts, fungi, bacteria);
- chemical reactions within the food (fat oxidation, browning);
- biochemical reactions from enzyme activities;
- physiological changes (respiration, sprouting); and
- biological agents (insects, rodents, birds).

All of these cause deterioration of quality (appearance, flavor, texture, nutritional value) and sometimes complete loss of the food. Most of these deteriorative changes occur at a faster rate as the temperature increases.

Example 1

Microbial growth: Table 4 shows the effect of temperature on the rate of increase in the number of bacteria in unpasteurized milk. At 0 °C the total count slowly decreases. The count increases at all temperatures above zero until at 30 °C (a normal day in a tropical country) the count becomes enormous within 24 h.

Example 2

Chemical reactions: Most foods naturally contain hundreds of different chemical components, most of which have reactive groups such as alcohols (–OH), aldehydes (–CHO), amines ($–NH_2$), carboxylic acids (–COOH), ketones (–CO), thiols (–SH), and double bonds (=). These allow numerous chemical reactions to occur many of which are not well understood but the rate of these reactions accelerates as the temperature increases.

The Q10 factor expresses the rate of change of a chemical reaction caused by a 10 °C increase in temperature. Chemical reactions performed in the chemistry laboratory frequently have a Q10 of approximately 2, that is, a 10 °C increase in

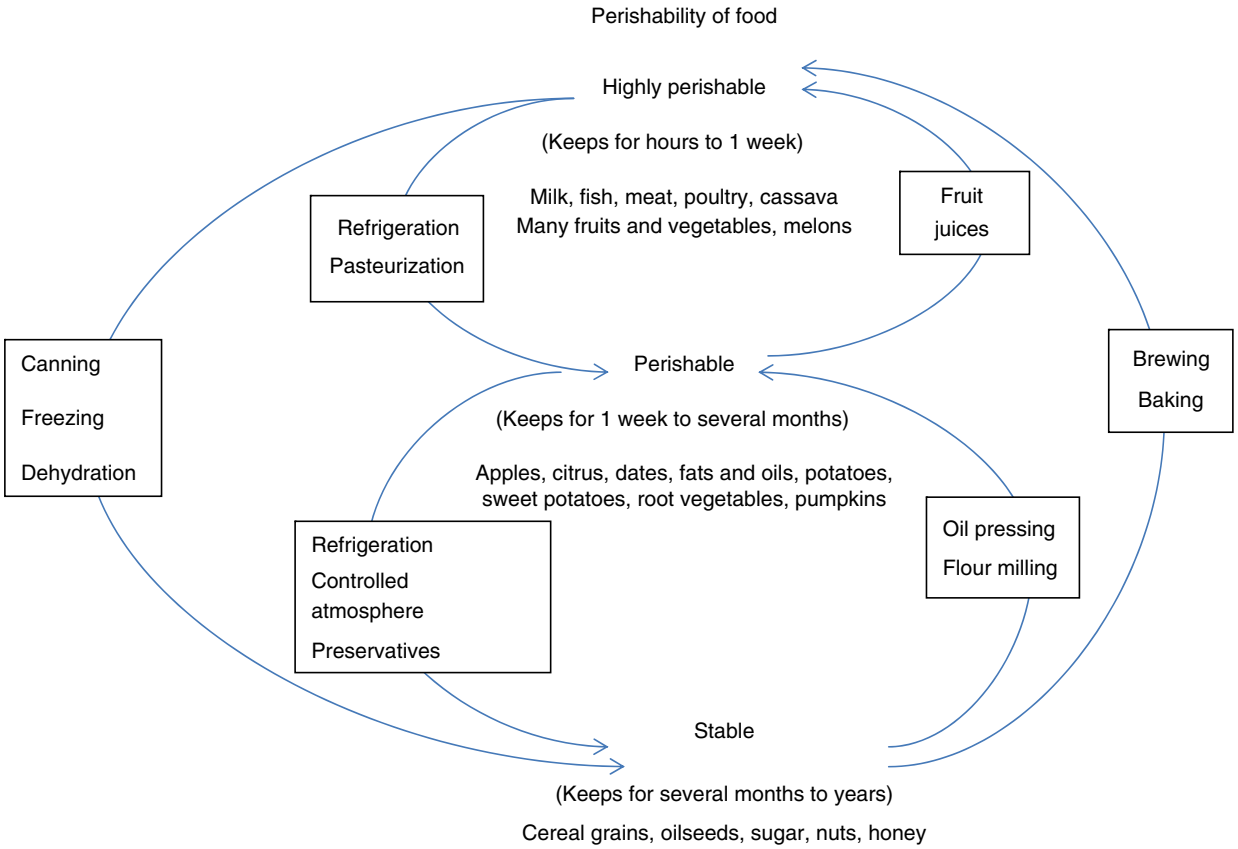


Figure 2 Levels of perishability in foods and changes caused by preservation technologies (LHS arrows) and processing technologies (RHS arrows).

Table 4 Growth of bacteria in unpasteurized milk

Growth of bacteria in unpasteurized milk (number of organisms per milliliter of milk)

Temperature (°C)	*24 h*	*48 h*	*96 h*	*168 h*
0	2 400	2 100	1 850	1 400
4	2 500	3 600	218 000	4 200 000
8	3 100	12 000	1 480 000	–
10	11 600	540 000	–	–
15	180 000	28 000 000	–	–
30	1 400 000 000	–	–	–

Source: Personal communication from F. Shipe.

temperature will double the rate of the chemical reaction. Chemical reactions occurring in foods usually have a higher Q10 in the 3–8 range. That is, a 10 °C increase in storage temperature will increase the rate of the chemical reactions that are spontaneously occurring three-fold to eight-fold.

A more fundamental description of the effect of temperature on reaction rates is the Arrhenius equation:

$$\log_{10} K = A - \frac{Ea}{4.6T}$$

where K equals the rate constant, A equals a constant, Ea equals the activation energy, and T equals the absolute temperature in Kelvin A Q10 factor of 10 is equal to Ea 12 800 cal mol^{-1}. Activation energies for reactions in food are often much higher than 12 800 cal mol^{-1}. The accepted rule that chemical reaction rates double for every 10 °C in temperature usually underestimates the rate of loss caused by deteriorative chemical reactions in foods. Even a small increase in temperature will markedly increase the rate of most deteriorative chemical reactions in foods.

Figure 3 shows the rate of nonenzymatic browning of freeze-dried onion measured as the absorbance of a water extract measured in a spectrophotometer. Onion stored at 5 °C showed no browning after 160 days whereas onion stored at 45 °C showed considerable browning.

Figure 4 shows the loss of thiamine in canned meats stored for 3 years at 0 °F (−18 °C), 32 °F (0 °C), 70 °F (21 °C), and

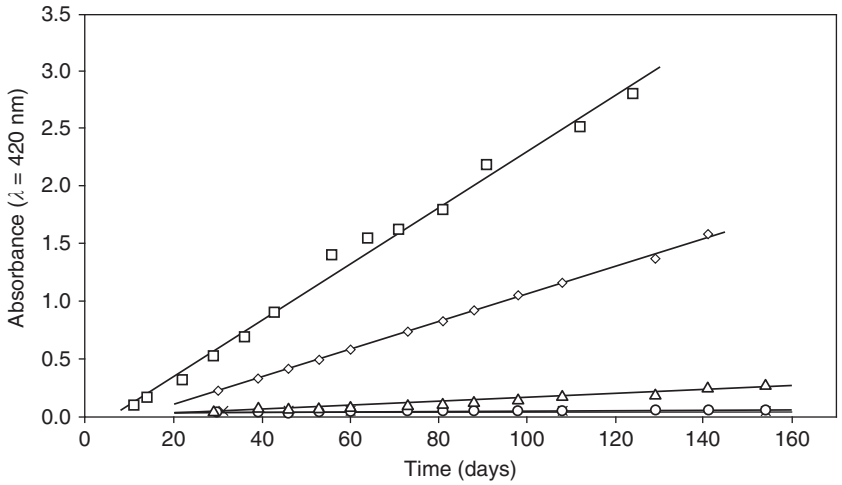


Figure 3 Nonenzymatic browning of freeze-dried onion equilibrated to Aw = 0.53 and stored at 0°, 15°, 25°, 35°, and 45 °C. Reproduced with permission from Sá, M.M., Sereno, A.M., 1999. Kinetics of browning measured during the storage of onion and strawberry. International Journal of Food Science Technology 34, 343–349.

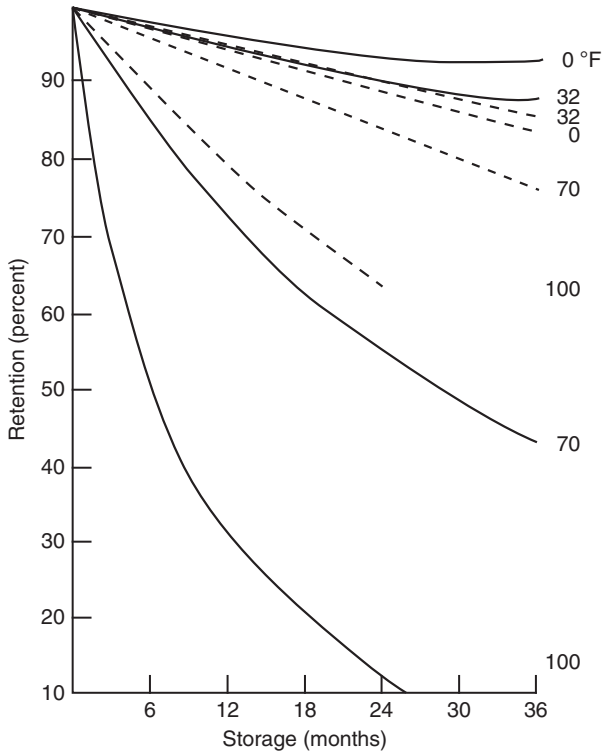


Figure 4 Retention of thiamine (solid line) and sensory quality (broken line) of canned meats stored for 3 years at four different temperatures. Reproduced with permission from Cecil, S.R., Woodroof, J.G., 1963. The stability of canned foods in long-term storage. Food Technology 17, 131–138.

100 °F (38 °C). Note how much faster thiamine and sensory quality are lost as the storage temperature increases.

Example 3

Arthropods (insects): Table 5 shows the minimum, optimum, and maximum growth temperature for insects commonly found in stored food. None of these insects grow below 15 °C (except mites) and the optimum temperatures are typical of the temperatures found in the tropics.

To sum up

- High storage temperatures accelerate most deteriorative changes that occur in stored food. Even stable foods such as cereal grains deteriorate more quickly as the temperature increases.
- Hence, tropical zones have a more difficult problem in maintaining food quality than do temperate zones. Arctic zones have little problem with food spoilage other than freezing injury. The rapid growth of plants in the humid tropics is matched by a rapid rate of decay.
- Shelf life for all foods is shorter in the tropics than in the temperate zones. One cannot expect to get as long a shelf life in a hot climate as in a cold climate.
- All foods, even stable foods, should be stored in the coolest place possible. Always store away from heat such as direct rays of sun, near boilers, or cooking stoves.

Exposing foods or storage structures to direct sunlight increases the temperature and the activity of all spoilage vectors. In temperate climates, most foods are stored out of the sun. In contrast, in tropical climates one often sees food products exposed to the sun. Figure 5 shows the effect of exposing vegetables to direct sunlight all day in Geneva, NY (latitude 42°53′ N, longitude 77°02′W, elevation 220 m). Single whole vegetables were supported on a thin wire mesh raised 60 cm off the ground on a wooden frame and the temperature measured by copper–constantan thermocouples inserted into the geometric center of each item. The experiment was conducted in July; close to the time of the summer solstice when solar radiation is at its peak in the Northern Hemisphere although not as high as in tropical latitudes.

The ambient temperature was measured by the official weather station #3031840 of the US Department of

Table 5 Temperature requirements for growth of some stored product insects

Species	*Typical foodstuffs infested*	*Temperature for growth (°C)*		
		Minimum	*Optimum*	*Maximum*
Sitrotroga cerealella (Angoumous grain moth)	Whole cereals	16	32	35
Cadra cautella (tropical warehouse moth)	Cereals and oilseeds	15	30	38
Sitophilus oryzae (rice weevil)	Whole cereals	17	28	34
Rhizopertha dominica (lesser grain borer)	Cereals and cassava	18	34	39
Tribolium confusum (confused flour beetle)	Flour and meals	20	33	38
Oryzaephilus surinamensis (saw-toothed grain beetle)	Cereals and meals	18	35	38
Cryptolestes ferrugineus (flat grain beetle)	Damaged cereals	20	33	42
Acanthoscelides obtectus (dry bean beetle)	Dry beans	16	30	35
Callosobruchus maculatus (cowpea beetle)	Cowpeas and other pulses	18	30	35
Trogoderma granarium (Khapra beetle)	Peanuts and cereals	20	37	41
Dermestes maculatus (hide beetle)	Dried fish	18	32	37
Lasioderma serricorne (cigarette beetle)	Cocoa, coffee, and pulses	20	30	37
Acarus siro (mites)	Meals, cheese, and dried fruits	4	20	31

Source: Reproduced from Hall, D.W., Jamieson, M.F.S., 1970. Food Storage Manual (3 volumes). Slough: Tropical Stored Products Centre.

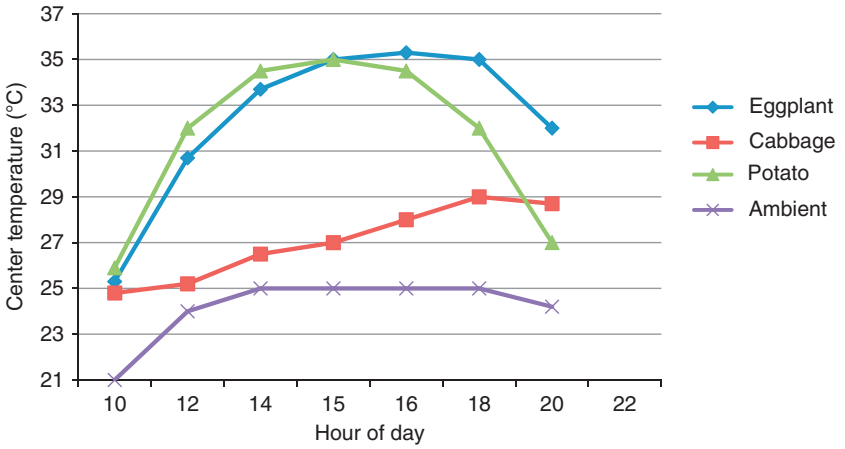


Figure 5 Internal temperature of three vegetables exposed to direct sunlight on a summer day. Reproduced with permission from Unpublished data of Marlett and Bourne.

Commerce National Oceanic and Administration Network and the temperature of the vegetables was measured approximately 1 m away from the weather station. The ambient temperature was at 21 °C at 10 am, rose to 25 °C in the middle of the day, and fell to 24 °C by 8 pm. Eggplant and potato had a dark skin and the internal temperature rose to 36 °C, some 12° higher than ambient. The temperature of the large head of pale-green cabbage rose to 29 °C.

Providing shade to food is a simple technology and should be universally used in developing countries. Comparing Figure 5 with the data in Table 2 shows that shade is effective in lowering the temperature and therefore the respiration rate thus extending the shelf life of the produce.

Climate data enable one to understand why food-spoilage rates are higher in some regions than in others and why it is more difficult to prevent losses in certain regions. Figure 6 shows the mean monthly temperature in three cities lying in the tropics and one city in a temperate zone. Medellin, Colombia, latitude 6° N, altitude 1498 m, has a mean monthly temperature of 22–23 °C all year long. From Table 5 one can expect to have problems controlling insects in stored grain throughout the year in Medellin. Panama, latitude 9° N, altitude 61 m, has a mean monthly temperature of 26–28 °C throughout the year and as this is close to the optimum temperature for insect growth one can expect to have more difficulty in controlling insects in stored grains than that in Medellin. In contrast, Bogota, Colombia, latitude 4.5° N elevation 2645 m, has a mean monthly temperature of 14–16 °C throughout the year and one can expect few problems with insects because it is too cold for insects to grow. These three cities lie in the tropics where there is little change in temperature throughout the year.

These three cities are relatively close together in the tropics. The differences in their temperature profile are caused by altitude. Ambient temperature decreases by approximately 5 °C for every 1000 m increase in altitude.

Cipoletti, Argentina, latitude 39° S, altitude 270 m, shows mean monthly temperatures typical of temperate climates; the monthly temperature is high in summer and low in winter. From Table 5 one can expect to have no problems with insects in stored grain from April through October when the temperature is below 15 °C, but insect problems can occur early (January

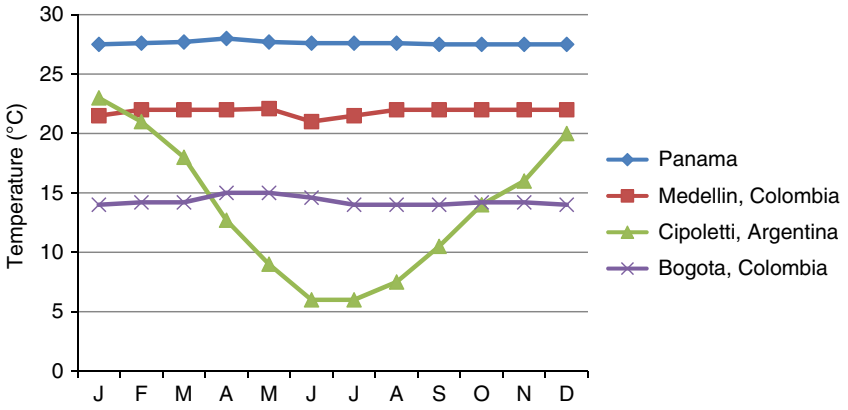


Figure 6 Mean monthly temperatures in Panama (latitude 9° N, elevation 61 m), Medellin (latitude 6° N, elevation 1498 m), Bogota (latitude 4.5° N, altitude 2645 m), and Cipoletti (latitude 39° S, altitude 270 m).

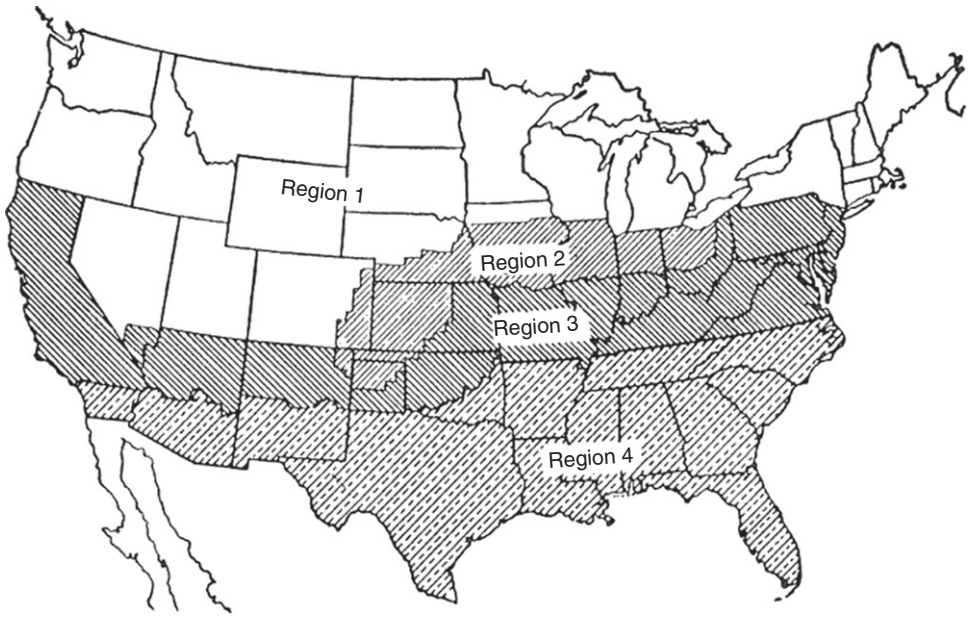


Figure 7 Stored grain risk across the US. Reproduced with permission from Cuperus, G., Noyes, R.T., Farg, W.S., *et al.*, 1993. Reducing pesticide use in wheat postharvest systems. Cereal Foods World 38, 199–203.

through March) and late (November through December) in the year when the ambient temperature is above 15 °C.

Figure 7 shows another example of the effect of temperature on storage stability of grains. Region 1 comprising northern states in the US has the lowest risk, and as one moves south into regions 2, 3, and 4 the risk increases as the average temperature rises. The dip in region 1 on the left side of the map is caused by the low temperatures experienced in the high mountains of the Sierra Nevada and the Rockies.

Relative humidity

Air always contains water vapor. It is usually expressed as the amount of water vapor in the air as a percentage of the amount that would be in the air if the air were saturated. The amount of water vapor at saturation increases as the temperature increases and many handbooks give tables for the saturation vapor pressure of water at different temperatures. The amount of moisture in any stored food will eventually equilibrate with the surrounding air. It is called the equilibrium relative humidity (ERH).

Dry foods are not sterile. They resist mold growth and other forms of microbial spoilage because their moisture content is too low to support growth. This statement applies to all dry foods – cereal grains, flours, spaghetti, dry fish, dry fruit, dry vegetables, dry milk, etc. The moisture content at which the foods begin to grow mold varies widely. For example, tea becomes moldy when its moisture content exceeds 7%, but unsalted dry fish does not mold until the moisture content exceeds 12%, whereas cereal grains will mold when moisture content exceeds 14%, and raisins do not mold until the moisture level exceeds 25%.

ERH, an old term, has been replaced by water activity (Aw), which is defined by the equation: Water activity $(\mathrm{Aw}) = \frac{P}{P_o}$; where P equals the water vapor pressure exerted by moisture in a food, P_o equals water vapor pressure exerted by pure water at

Table 6 Conditions for growth of some common fungi

Species	Temperature (°C)			Aw	
	Minimum	Optimum	Maximum	Minimum	Optimum
Aspergillus ruber	5	24	38	0.72	0.93
A. amstelodami	10	30	42	0.70	0.94
A. flavus	12	35	45	0.80	0.99
A. fumigatus	12	40	52	0.83	0.99
A. niger	10	35	45	0.77	0.99
Penicillium martensii	5	24	32	0.80	0.99

same temperature. For example, if a food has a water vapor pressure of 12.5 mm Hg at 20 °C, what is its water activity? Vapor pressure of pure water at 20 °C is 17.54 mm Hg (obtained from tables). Then $\text{Aw} = \frac{12.5}{17.54} = 0.71$.

The relationship between water activity and ERH is: $\text{Aw} = \frac{\text{ERH}}{100}$ or ERH = 100 Aw.

Example 1

If ERH is 71%, what is the water activity?

$$\text{Aw} = \frac{71}{100} = 0.71$$

Example 2

If water activity is 0.71, what is the ERH?

$$0.71 \times 100 = 71\%\ \text{ERH}$$

As Aw and ERH have the same numerical value it is easy to convert from one to the other; just move the decimal point two places. For a thorough description of water activity, consult any of the following references, Barbosa-Cánovas *et al.* (2007), Iglesias and Chirife (1982), or Bourne (1999).

The limiting water activity for most bacteria is approximately Aw = 0.90, for most yeasts approximately Aw = 0.88, for most molds (fungi) approximately Aw = 0.80, and for xerophilic molds Aw = 0.65. Conditions for growth of some common fungi are shown on the right-hand side in **Table 6**.

The moisture content of grains and other dried foods is such that there is seldom any problem with the growth of bacteria and yeasts but there are frequently problems with the growth of molds (fungi). Unless the Aw is reduced to below approximately 0.7, molds will grow on any food and as the relative humidity in the humid tropics is generally more than 70% almost all dry foods will become moldy when stored in the humid tropics unless the moisture content is reduced to an Aw of less than 0.70, followed by storage that will protect that food from absorbing moisture from the high-humidity environment.

Water vapor always moves from a region of high Aw to a region of low Aw until equilibrium is reached. Moist food will always give up water to dry air whereas dry food will always absorb moisture from high relative humidity air. The only way to prevent the invisible flow of water vapor from a high Aw region to a low Aw region is to place a barrier between the food and the air that will move through it. The design of storage structures for bulk commodities such as cereal grains, and packaging technologies for retail foods to prevent migration of water vapor are the subject of other articles in this encyclopedia.

Table 7 Moisture content for safe storage of paddy is inversely related to temperature

Water content – temperature – Aw for paddy rice		
Temperature (°C)	Aw	% H_2O (as-is)
7	0.70	14
27	0.70	13
43	0.70	12
57	0.70	11

Table 8 Moisture content and temperature effect on storage life of barley

Maximum number of weeks of mold-free storage of barley			
% H_2O	5 °C	15 °C	25 °C
16	>100	>100	10
18	80	12	2
20	9	3	1
22	4	1.5	0.5

Source: Personal communication from R. L. Obendorf.

As the saturation point of moisture in air increases with rising temperature, the safe moisture content for storage of grain becomes lower as the storage temperature increases. **Table 7** demonstrates how the moisture content of paddy rice needs to be reduced in order to maintain a safe Aw not greater than 0.70. Another example is that wheat with 14.0% water has an Aw equal to 0.75 at 30 °C and will mold, whereas the same wheat stored at 10 °C has an Aw equal to 0.68 and will not mold.

Table 8 shows how temperature and moisture content affect the safe storage life of barley.

There are two ways to express moisture content:

1. Wet basis or 'as-is' basis is the percentage of moisture in the food as it is, (partly solids + partly water).
2. Dry basis or dry matter basis (DMB) is the percentage of moisture expressed on the basis of solids only.

Example: 100 g food contains 80 g dry matter and 20 g water.

% moisture as-is = 20/100×100 = 20%
% moisture DMB = 20/80×100 = 25%

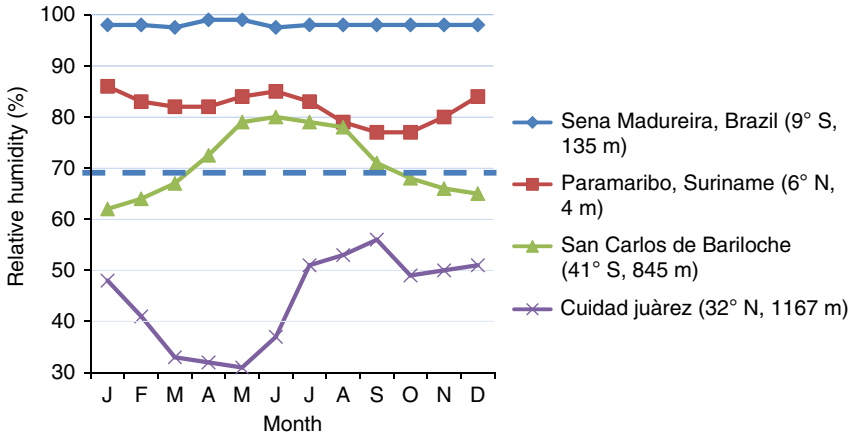


Figure 8 Mean monthly relative humidity in Sena Madureira (latitude 9° S, elevation 135 m), Paramaribo (latitude 6° N, altitude 4 m), San Carlos de Bariloche (latitude 41° S, elevation 845 m), and Cuidad Juárez (latitude 32° N, altitude 1167 m).

Both systems of expressing moisture content are widely used and both are effective. Remember to specify whether the percentage of moisture is on the as-is or DMB.

Conversion equations:

$$x\%\ \text{moisture as is} = \frac{x}{100 - x}\%\ \text{DMB}$$

$$y\%\ \text{moisture DMB} = \frac{y}{100 + y}\%\ \text{as-is}$$

Figure 8 shows the mean monthly relative humidity for four cities. As observed, cereal grains and other dry foods need to be stored at Aw < 0.70 to prevent mold growth. If the ambient relative humidity is less than 70%, the grain, if properly dried, will not absorb moisture to a level that will permit the growth of mold. The city of Cuidad Juárez in Mexico, latitude 32° N, elevation 1167 m, has a low relative humidity all year long and should experience no mold problems in stored cereal grains. San Carlos de Bariloche in Argentina (latitude 41° S, altitude 845 m) will not experience mold problems from January through March or October through December but will experience mold from April through September unless some protection against uptake of water vapor is in place. Paramaribo in SurÏnam (latitude 6° N, elevation 4 m) has a relative humidity well above 70% all year long and will need all year long protection against uptake of water vapor from the atmosphere. Sena Madureira in Brazil (latitude 9° S, altitude 135 m) has a very high relative humidity throughout the year, which means tremendous efforts are needed to prevent mold from growing in its stored dry food.

High-moisture foods

The discussion thus far has been about keeping dry foods sufficiently dry to prevent mold growth. Fruits and vegetables have a high-moisture content, typically 80–95% and a very high Aw, typically Aw > 0.98. They are vulnerable to spoilage by growth of many microorganisms. It is the skin that protects them from microbial spoilage. Therefore, maintaining intact skin to prevent invasion by microflora is necessary for preservation of horticultural crops.

Owing to their high Aw, horticultural crops easily lose water into the air causing wilting which results in a lowering of quality and loss of weight. For these products, a high humidity storage atmosphere is necessary, in contrast to cereal grains and other dry foods where low humidity atmosphere is required.

Most developing countries lie within the tropics and their high ambient temperatures make preserving the quality of stored foods considerably more difficult than in temperate climates because the naturally occurring deteriorative chemical reactions are accelerated in the tropics. In addition, the year-round high temperatures of tropical countries allow pests such as rodents and insects to feed and multiply throughout the year, whereas the cold winters of temperate zones slow down or stop reproduction and reduce the feeding activities of these pests. The low temperatures in very cold climates kill many of the pests.

Even if tropical countries had the same per capita income as the developed countries the continual high temperatures at which food must be stored pose a much more difficult set of problems than is found in temperate zones. The high relative humidity in the humid tropics compounds this problem.

Magnitude of Losses

A major question is: "How much food overall is lost in the postharvest food chain?" The honest answer to this question is that there is little reliable data. It is known that the losses are highly variable depending on the commodity, the climate, the conditions in which the food is being handled, and the length of time the food is stored. One would expect to find higher losses in perishable foods than in stable foods, and the extent of loss increases with time of storage. It is possible to find individual losses ranging from 0% to 100%, but what is of primary interest is an overall average loss figure. However, little hard data based on meticulous scientifically designed observation is available.

Harris and Lindblad (1978) developed a standard methodology to assess losses in stored cereal grains. This is the only loss assessment procedure that has a standard method. Other loss

measurements each use their own procedure and wide variations in methodology are used even for the same class of food.

A number of figures for the extent of loss quoted in scientific literature and by the communications media are unreliable because the amount of loss has been estimated and not been obtained by actual measurements. Sometimes 'worst case' figures are used to dramatize the problem. For example, care must be taken when looking at one lot of food and seeing extensive insect infestation not to assume that all food in the country is just as heavily infested. Extrapolation of loss from a limited sample to all food of a country is an unsound procedure.

Sometimes cited figures are manipulated for various reasons. There is the temptation to exaggerate loss figures when high loss figures might prompt donor aid or grants. In other cases, actual loss figures may be understated to avoid embarrassment, or for political, financial, pride, or trading reasons.

Another way loss can be exaggerated is found in the case of the subsistence farmer who harvests one crop a year and stores most of it for personal use. If the grain is properly dried most of his losses will come from insect infestation and perhaps rodents. During the first few months loss percentage is low. As storage continues, the number of insects increases exponentially and there is a very high percentage loss just before the next harvest season. However, this high loss at the end of the storage period applies only to a small fraction of the year's supply of grain. Inspection of this grain in the second month might show 2% loss which is not a great concern. By the sixth month a loss of 8% might be found which would cause some anxiety, whereas by the 10th month the loss could be 36% and cause for alarm. In this case the actual loss for the year would probably be approximately 12% of the total crop which is too high but not nearly as high as the 36% just before the next harvest. An example of time effect is given by Mushi (1978), who reported postharvest loss of maize in Tanzania at 9% after 3 months, 14% after 6 months, and 67% after 9 months storage.

Another precaution that needs to be taken in reporting losses is to ensure that the arithmetic of loss figures is correctly calculated. In quoting loss figures at various steps along the postharvest chain there is a common error of adding the percentage of loss at each stage to obtain the total loss. This leads to overall loss figures that are too large because it assumes that each loss figure is a percentage of the original weight of material. As each loss is expressed as a percentage of the amount in the previous step, the percentage is being applied to a diminishing base. An actual example of this error is shown in Table 9, which shows the apparent loss and actual loss that occurs in 1000 kg rice.

Table 9 Faulty arithmetic in assessing losses in rice

	Loss (%)	*Weight loss (kg)*	*Remainder (kg)*
Start	–	–	1000
Harvest	15	150	850
Threshing	15	128	722
Transport	10	72	650
Storage	30	195	455
Milling	20	91	364
Distribution	15	54	310
Totals	105	690	

Adding the percentage loss at each step as shown in the first column would lead to the conclusion that 105% loss occurred. Column 2 shows what the actual weight loss is at each step. The harvest loss of 15% of 1000 kg rice is 150 kg but the threshing loss of 15% is 128 kg because it represents 15% of 850 kg not 15% of 1000 kg and at the distribution end of the chain 15% loss represents only 54 kg. In this example, the overall weight loss is 690 kg or 69%, not 105%.

The 1978 US National Academy of Sciences report, 'Postharvest Food Losses in Developing Countries' summarizes the problem of assessing the magnitude of losses in these words:

> It is very difficult to estimate postharvest food losses with precision. Partly, this is due to their inherent variability. But it is also a result of many cultural and economic factors that frustrate the smooth, efficient flow of food through the postharvest system from producer to consumer….loss estimates – unlike production estimates, which are based on the measurable genetic potential of crops – are location – and season specific to a degree that makes the concept of average levels of loss almost meaningless. The low accuracy of loss survey techniques on the one hand, and the limitations of extrapolating from even a specific well characterized loss situation on the other, make reliable, economic loss estimates very difficult to obtain.

This problem is still with us in the twenty-first century.

Some Old Loss Figures

The 1978 National Academy of Sciences report gives the most extensive and best documented figures for postharvest loss up to that time. Although this is old data, it is likely that most of these loss figures are still close to the mark today. A small sample of loss data is given in Table 10 for losses of maize and Table 11 for losses in roots and tubers, fruits and vegetables.

Table 10 Reported postharvest losses of maize

Reported losses of maize in the postharvest system

Country	*Total percentage of weight loss*
Belize	20–30
Benin	8–9
Brazil	15–40
Ghana	7–14
Honduras	20–50
India	6.5–7.5
Indonesia	4
Ivory Coast	5–10
Kenya	10–23
Malawi	6–14
Mexico	10–25
Nicaragua	15–30
Nigeria	1–5 or 5.5–70
Pakistan	2–7
Paraguay	25
Rwanda	10–20
Tanzania	20–100
Togo	5–10
Uganda	4–17
Venezuela	10–25
Zambia	9–21

Source: Data from NAS, 1978. Postharvest Food Losses in Developing Countries. Washington, DC: National Academy of Sciences.

Newer Loss Figures

The 2011 FAO Report, 'Global Food Losses and Waste. Extent, Losses, and Prevention' is the most recent publication that gives postharvest loss figures. FAO hired the services of the Swedish Institute for Food and Biotechnology (SIK) to carry out two studies on the extent and effects, as well as causes and prevention of food losses and food waste, one for high/medium-income countries, and one for low-income countries. The two studies highlighted food losses occurring along food chains, and made assessments of the magnitude of these losses, focusing on quantitative weight losses. They compiled, analyzed, and assembled data and reports about global food loss and waste during recent years. Where information was not available, assessments and assumptions were made.

Table 11 Reported postharvest losses of roots and tubers, fruits and vegetables

Losses in roots/tubers and fruit/vegetables reported by region and country

Region/country	*Roots/tubers (percentage of loss)*	*Fruits/vegetables (percentage of loss)*
Africa		
Ghana	10–20	30–35
Nigeria	10–50	10–50
Rwanda	5–40	5–40
Sudan		50
Asia/Far East		
India		20–30
Indonesia	10	15–25
Iran	5–100	5–28
Jordan		2–3
Malaysia		20
Philippines		10–50
Sri Lanka		20–40
Thailand		23–28
Latin America		
Bolivia	24	17–30
Brazil	5–30	8–10
Chile	30	30
Dominican Republic	17–26	25
Peru	20–50	

Source: Reproduced from NAS, 1978. Postharvest Food Losses in Developing Countries. Washington, DC: National Academy of Sciences.

Table 12 lists some of the data found in this report. The full report lists estimated/assumed losses for five segments of the food supply chain: (1) agricultural production, (2) postharvest handling and storage, (3) processing and packaging, (4) distribution, and (5) consumption. It should be noted that this report puts more emphasis on food waste (edible food that is discarded) than on food loss. Table 12 only lists the item 2 segment, postharvest handling, and storage.

Although many of these figures may seem low, when applied to huge quantities of food that are produced (see Table 1) the amount in tons is substantial. For example, the report 'Global Food. Waste Not, Want Not' published by the Institution of Mechanical Engineers in 2013 notes:

> Ghana, one of the more developed of the emerging West African economy, recently experienced a 50% loss rate of stored maize from a total 2008 production of one million tons. Considerably greater levels of tonnage loss exists in other larger developing nations, such as India for example, where about 2 million tons of wheat annually perish due to inadequate storage and distribution. In the neighboring Pakistan, losses amount to approximately 16% of production, or 3.2 million tons annually, where inadequate storage infrastructure leads to widespread rodent infestation problems.

Postharvest losses need not be so high. A good example of control of postharvest losses is found in the Australian wheat industry that has invested heavily in storage structures, handling practices, and insect control. Most Australian wheat is harvested during the hot dry summer months and drying to prevent fungal growth is not a problem. Analysis for the crop years 1961/62–1971/72 show that the average quantitative loss in storage is 0.249% per annum with a range of 0.138–0.675% during that decade (Bourne, 1977). This close control of all aspects of wheat handling and storage continues to this day. The 2013 report of the Institution Mechanical Engineers cited above comments, "in a developed country such as Australia, wastage of 0.75% in stored grain is at the upper end of acceptability."

Loss Reduction Activities

A wide range of activities is needed in any comprehensive program of postharvest food loss reduction activity; and because there are so many different types of foods and so many different spoilage vectors it is necessary to select an appropriate remedial activity for each specific food-spoilage combination. Table 13 lists the major causes of loss for the different food

Table 12 FAO report on losses and waste

Estimated/assumed postharvest handling and storage losses (percentage)

Region	*Cereals*	*Roots and tubers*	*Fruits and vegetables*
Europe	4	9	5
North America and Oceania	2	10	4
Industrialized Asia	10	7	8
Sub-Saharan Africa	8	18	9
North Africa, West and Central Asia	8	10	10
South, Southeast Asia	7	19	9
Latin America	4	14	10

Source: Reproduced from FAO, 2011. Global Food Losses and Food Waste, Extent, Causes and Prevention. Rome: Food and Agriculture Organization.

Table 13 Causes of loss and control of loss in foods

Commodity	*Major causes of loss*	*Methods for reducing loss*
Grains, cereals, and legumes	Fungi	Adequate drying, prompt drying, and dry stores
	Insects	Good sanitation, use of insecticides and fumigants, and gas-tight stores
	Rodents	Good housekeeping, rodent-proof stores, baits, traps, and fumigation
	Inefficient handling and processing	Better equipment, maintenance of equipment, and knowledgeable management
Fruits and vegetables	Bruising	Gentle harvesting and handling and protective packaging to maintain intact skin
	Rotting by bacteria and fungi	Good sanitation, cool storage, and use of fungicides
	Senescence	Cool storage, prompt marketing, and processing into stable forms
	Wilting	Maintenance of high-humidity surroundings
Roots and tubers	Rotting by bacteria and fungi	Maintenance of intact skin, promotion of suberization and wound cork formation, good sanitation, cool storage, and application of fungicides
	Sprouting	Cool storage and application of antisprout agents
	Bruising	Gentle harvesting and handling and protective packaging
	Senescence	Prompt marketing, cool storage, and processing into stable forms
	Insects	Good sanitation and use of insecticides
Fresh fish, meat, poultry, and milk	Bacterial spoilage	Refrigeration, good sanitation, pasteurization, and processing into stable forms
Dry fish	Insects	Good sanitation and use of insecticides
	Fungi	Adequate drying and prompt drying

Source: Reproduced from Bourne, M.C., 1981. United Nations Environment Programme. Industry and Environment Newsletter 4 (1), 3–5.

types and the technologies needed to preserve unprocessed or minimally processed agricultural commodities.

The resources needed include:

- grain handling and drying equipment;
- storage structures of all sizes for grain and oilseeds;
- dehulling and milling equipment for grains;
- cold stores/freezer storage;
- equipment that handles horticultural crops gently;
- fumigation and other sanitation equipment;
- extraction equipment that achieves the maximum yield of sugar from cane or oil from oilseed; and
- packaging to protect the food from water vapor, oxidation, or light exposure.

All of the above items are described in other articles in this encyclopedia and require no elaboration here.

See also: Agricultural Policy: A Global View. Food Security: Development Strategies. Food Security, Market Processes, and the Role of Government Policy. Food Security: Yield Gap. Human Nutrition: Malnutrition and Diet. Policy Frameworks for International Agricultural and Rural Development

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Food Security: Yield Gap

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Glossary

Allocative efficiency Occurs when the quantities of variable inputs are chosen such that net value is maximized.
Allocatively efficient yield The yield that maximizes the net value of production at a particular location and point in time given existing technology and input constraints.
Maximum limiting yield The maximum yield that can be achieved at a particular location and point in time given the best existing technology for that location and time, and nonlimiting inputs other than the amount of land.
Partial factor productivity The ratio of output to the amount of a single input (e.g., land) used to produce it.
Production possibilities frontier The maximum amount of output that can be produced for each quantity of input.
Technical efficiency Occurs when the maximum amount of output is produced for a given amount of inputs.
Total factor productivity The ratio of output to an aggregation of all inputs used to produce it.

Introduction

In the past half-century, agricultural science achieved a great deal. From 3.1 billion in 1961, the world's population more than doubled to just over 7.0 billion in 2012 (an average compound rate of growth of 1.6% per year). Over the same period, total production of cereals grew faster than population (from 877 million MT in 1961 to 2546 million MT in 2012, or approximately 2.1% per year), and this increase resulted largely from unprecedented increases in crop yields (FAOSTAT, 2013; Pardey *et al.*, 2012). (Cereals include wheat, rice, maize, and other agronomic crops that are primarily used for their edible grain.) The fact that the Malthusian nightmare has not been realized in our lifetime is attributable in large part to improvements in agricultural productivity achieved through technological change enabled by investments in agricultural R&D (Alston *et al.*, 2013).

Looking forward, however, some early warning signs suggest that the period of global agricultural abundance may be coming to an end, if it has not ended already. Certainly, after decades of rapid (but slowing) decline, in real (inflation-adjusted) terms farm commodity prices have not trended down appreciably since 2000 (and have recently risen), and in recent times proportional crop yield growth rates have been slowing (Alston *et al.*, 2009). The prospect of continuing population growth and rising per capita incomes, combined with additional demand for biofuels, implies a significant increase in global demand for farm output over the decades to come. These prospects have contributed to a revival of concerns over the future capacity of the world to feed a growing population at affordable prices, giving rise to questions about the prospects for agricultural production and, in particular, crop yields. How and where will this additional output be produced with ever-tighter supplies of arable land and water, and in the face of a changing climate?

The issue of 'yield gaps' comes up in this context, in particular. (The concept of yield gaps in crops can be applied with equal force to livestock. Productivity or 'yield' gains in livestock are often delineated in terms of increases in pounds of meat produced per animal, or milk per cow, or eggs per laying hen. This is akin to tracking the amount of grain produced per plant, which is typically conceived as a harvest index (i.e., the proportion of the plant's biomass that is realized in grain rather than straw and other plant parts) rather than crop yield per se. A more natural concept of 'livestock yield' that parallels crop yields is the amount of meat, eggs, or milk produced per unit of feed or energy or some other input.) One concept of a yield gap is the difference between yields achieved by farmers in high-income countries and their counterparts in low-income countries. Can we bring up the yield of poor farmers in, perhaps, marginal areas, and by closing this yield gap reduce poverty while at the same time addressing the world food problem? (For example, a 2011 *New York Times* article by Justin Gillis defined the yield gap as "[t]he enormous gulf between the crop yields obtained by the most successful farmers and the least successful," noting that US maize yields are often five times those of small farmers in Africa. A recent *Time* magazine article (Walsh, 2012) used the term to describe "…parts of the planet where agricultural yield is lagging," with reference to "under-performing regions." This notion of yield gaps is also present in some NGO, government, and scholarly publications, such as reports from the US Department of Agriculture (e.g., Rosen and Shapouri, 2012) and the US Agency for International Development (e.g., Collier, 2012) who use a similar concept, noting the yield gap between grain yields in sub-Saharan Africa and the rest of the world.) Another concept of a yield gap is the difference between the commercial yield achieved by farmers and the experimental yield achieved by researchers. Davidson and Martin (1965), for example, report that average experiment station yields can be as much as 75% higher than average farm yields, depending on the crop and location. Can we close this gap? Should we try to do so? A third type of yield gap is the difference between experimental or commercial yields and some concept of a biological maximum potential yield. Is this gap shrinking in a way that limits our scope for increasing experimental or commercial yields in the future?

Many people are interested in closing yield gaps primarily as they relate to food security – in the sense of producing enough food at affordable prices to meet the caloric and other

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nutritive requirements of a growing population – especially by increasing yields for subsistence farmers. But this is only one dimension of yield gaps, and closing yield gaps for subsistence farmers is only one of the many approaches for improving food security. Indeed, UN projections indicate that in the next 5–10 years the majority of the developing world's population will be urbanized, shifting attention to urban poverty and the food insecurity status of urban consumers versus subsistence producers (United Nations, 2012). Hence, rather than closing yield gaps by increasing the lowest yields, the more important concept for increasing global food security may be to increase total production by lifting the entire distribution of yields, even if that might mean making gaps larger in some cases.

In this article the issue of yield gaps is explored, primarily from an economic perspective, giving due regard to food security concerns but not at the expense of the broader considerations. Yield is an object of choice for a farmer or a researcher, determined by decisions made about technology, inputs, and management, conditioned by uncontrolled elements in the natural environment. From this perspective, yield gaps reflect differences in choices, as well as other differences in the circumstances of production that cannot be fully controlled, and attention appropriately focuses on the sources of these differences and what they imply. In the Section Economic Conception of Yields and Yield Gaps, some economic concepts are introduced. These concepts are applied to show why yield gaps might exist. The Section Measurement of Yields and Yield Gaps reviews the variety of ways in which researchers have attempted to quantify yields and yield gaps, with particular attention paid to the challenges facing such an exercise. Next, an interpretation of yield gaps in the context of global food security and agricultural science and technology policy is provided. The article ends with some concluding remarks regarding the virtue of framing the potential for global food security in terms of yield gaps.

Economic Conception of Yields and Yield Gaps

Crop yield and yield gaps are purely agronomic measures, and provide information on the outcome of a season-long production process. (There are, of course, interseasonal factors that affect yields, such as soil nutrient or water carryover, or the timing of cropping operations.) But crops involve more than agronomy: they are cultivated by farmers who make decisions about what, when, and where to plant, and the quality and quantity of inputs used to foster crop growth. Economics offers a number of conceptual and empirical tools for considering the production process in more detail, allowing one to think not only about yields and yield gaps, but also why yield gaps might exist, and whether it might be advantageous to close them. Thus, an economic perspective can add significant insight and nuance to consideration of yield and yield gaps.

Several concepts are useful for understanding yields and yield gaps from an economic perspective. First is the relationship between what is produced (i.e., the output, such as the amount of maize, wheat, or rice grain), what is used to produce it (i.e., the quantities of inputs, such as land, labor, fertilizer, water from rain or irrigation, solar radiation, pesticides, seed, and services from oxen and tractors), and how it is produced (i.e., the technology of production, which prescribes the different ways inputs can be combined to produce output). This output, input, and technology relationship characterizes the 'production possibilities.' Figure 1(a) illustrates hypothetical production possibilities for maize as more or less fertilizer is used holding other inputs constant. (Any other variable input besides fertilizer could be used to illustrate these concepts, e.g., labor, seed, irrigation water, or agricultural chemicals.) The shaded area in the figure reflects all the different combinations of maize and fertilizer that are possible given the available technology. The solid curve denoting the upper boundary of these production possibilities is known as the production possibilities frontier (PPF).

Technically, efficient production occurs where the greatest possible amount of output is produced from a given quantity of inputs or, equivalently, the least possible amount of inputs is used to produce a particular amount of output. Combinations of maize and fertilizer below the PPF (e.g., point a) are technically inefficient because more maize can be produced with the same amount of fertilizer (point b) or the same amount of maize can be produced with less fertilizer (point c). Alternatively, combinations of maize and fertilizer on the PPF

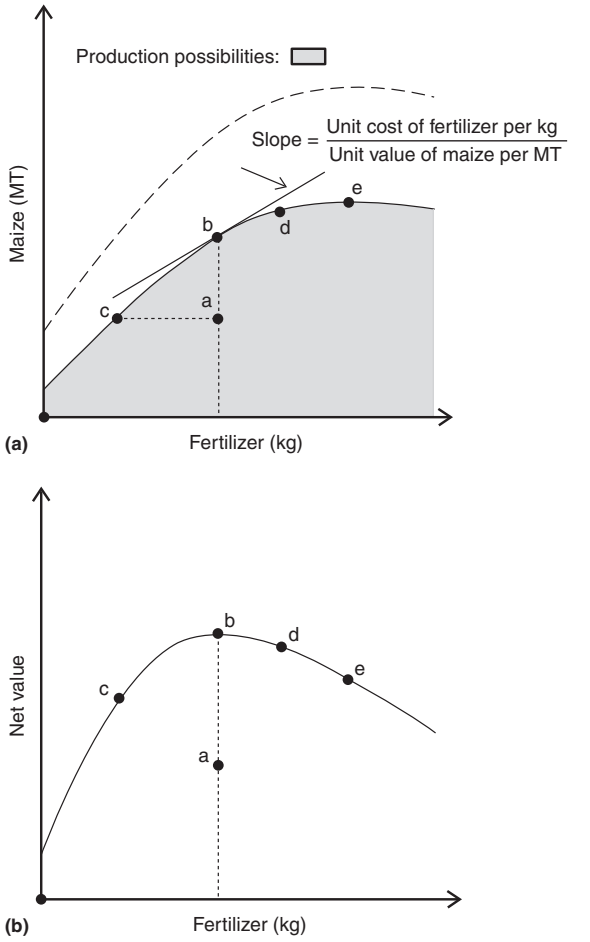


Figure 1 Hypothetical example of maize and fertilizer. (a) Production possibilities and production possibility frontiers. (b) Maximum net value of production.

(points b and c) are technically efficient because it is impossible to produce more maize with the same amount of fertilizer or the same amount of maize with less fertilizer.

Technical efficiency is one of two types of economic efficiency that are relevant in this context. If production is not technically efficient, then resources are being wasted. But as the PPF in **Figure 1(a)** illustrates, many (possibly infinite) combinations of maize and fertilizer avoid this wastefulness, and therefore technically efficient farmers or scientists could choose many different input–output combinations. For example, a scientist might set up an experiment to identify the maximum yield for a given maize variety by using an exorbitant amount of fertilizer to produce output at point e. But this ignores the second type of efficiency of interest to economists, allocative efficiency. Allocative efficiency is accomplished when inputs and outputs are combined to achieve their highest possible net value. In standard economics texts, profit is used as the relevant measure of net value, so allocative efficiency implies profit maximization. However, farmers often have objectives other than simple profit maximization. Other benefits and costs that might be viewed as important include food security for subsistence farmers, the risk of adverse health consequences from using pesticides for cash grain farmers, the risk of losses of production to pests and diseases, or business risk arising from market volatilities. Regardless of how a farmer perceives the net value of production activities, the same analytical approach can be used with appropriate adjustments to the measures used.

The solid curve in **Figure 1(b)** illustrates the maximum net value from maize production for a range of quantities of fertilizer per hectare. Points a–e in this figure correspond to points a–e in **Figure 1(a)**. The highest point on this curve is at point b, which is where production is both technically and allocatively efficient. All other input–output combinations are allocatively inefficient. Net value is lower at point a than at point b because at point b more maize is produced with the same amount of fertilizer; similarly, net value at point a is less than at point c because at point c the same amount of maize is produced with less fertilizer. Point a is technically inefficient, and technical efficiency is a necessary (but not sufficient) condition for allocative efficiency. Points c–e are technically efficient but allocatively inefficient. Points on the PPF to the left of point b (point c) are allocatively inefficient because too little fertilizer is used, whereas points on the PPF to the right of point b (points d and e) are allocatively inefficient because too much fertilizer is used given the relative cost of fertilizer and value of maize. An equivalent way to determine allocatively efficient combinations of maize and fertilizer is to find the point on the PPF where its slope equals the ratio of the unit cost (or price) of fertilizer to the unit value (or price) of maize, which is illustrated in **Figure 1(a)** at point b.

Maize cannot be produced exclusively with fertilizer. Maize seed, a place to plant the seed and other inputs are also required. The relationship illustrated in **Figure 1(a)** embodies an assumption that quantities of all other inputs being used to produce maize do not change as the amount of fertilizer changes. This assumption explains why the PPF in **Figure 1(a)** becomes flatter as the amount of fertilizer increases and eventually begins to decline. Holding the amount of seed and land constant, plant growth can be severely nutrient limited without any fertilizer, so little will be produced. As the amount of fertilizer increases, crop growth becomes more vigorous and more is produced. (This is a hypothetical example. Of course, application of fertilizer does not always increase crop yields. For example, Sileshi *et al.* (2010) found that the addition of enough fertilizer could actually reduce maize yields in some parts of sub-Saharan Africa in some years.) Eventually, with enough fertilizer, growth will no longer be nutrient limited and the amount produced will be as great as possible given other available inputs. Continuing to increase fertilizer beyond this point can become detrimental, leading to a decrease in output. This flattening of the PPF and its eventual decline as the variable input increases is known as diminishing marginal returns – each additional kilogram of fertilizer increases the amount of maize produced by less than what the previous kilogram did. If the amount of seed or land used to produce maize is doubled, the relationship between the amount of maize produced and fertilizer changes, which is illustrated in **Figure 1(a)** by the higher dashed curve. Similar shifts in the PPF could result from changes in quantities of other inputs, such as labor, or the addition of irrigation or some other change in technology, such as switching from landrace to improved seed varieties. Upward shifts in the PPF could also result from changing where maize is produced to a place with more productive soils or more favorable weather.

Considering these additional inputs, the farmer is free to vary more than one, and potentially all of them. Those inputs that the farmer can freely vary are referred to as variable inputs; those that the farmer cannot freely vary are referred to as fixed inputs. In the ultimate long run, all inputs are variable, but over shorter planning horizons, some inputs are better treated as fixed. Thus, within a season, hired labor, irrigation water, fertilizer, and pesticides are typically regarded as variable inputs, whereas capital inputs (such as the available machinery), land, and its attributes (terrain, rainfall, and solar radiation) are regarded as fixed. In this context, allocative efficiency more generally refers to farmers choosing all variable input quantities, not just the quantity of fertilizer, such that net value is as high as possible. Economists use the net value function to represent the highest net value that could be earned from freely choosing the quantities of all variable inputs. These inputs are chosen in response to the unit cost of inputs and unit value of outputs, and the quantities of fixed inputs. (These ideas apply both to commercial or subsistence farmers. Even if farmers do not directly participate in output (or input) markets, they do make optimizing decisions based on the opportunity cost (or shadow prices) of inputs and outputs. As Schultz (1979) observed in his Nobel Prize lecture: "Farmers the world over, in dealing with costs, returns and risks, are calculating economic agents. Within their small, individual, allocative domain they are fine-tuning entrepreneurs, tuning so subtly that many experts fail to recognize how efficient they are.")

The net value function shows how the maximum net value varies as farmers choose allocatively efficient combinations of variable inputs and output. As the technology of production is embodied in the net value function, it can be used to derive the allocatively efficient quantity of output given the unit costs of variable inputs, the unit value of output, and the quantities of any fixed inputs. Likewise, the net value function can be

used to derive the demand for land (when it is a variable input) as a function of the same variables. Thus, both the allocatively efficient quantities of output produced and land used can be expressed as functions of the unit cost of inputs and the unit value of output, technology and the quantities of fixed inputs, and therefore the allocatively efficient yield can also be derived as the ratio of these quantities. (In practice, when some production decisions are made farmers do not know the ultimate realization of some variables, such as rainfall, solar radiation, and output prices. For example, the farmer typically does not know the final output price when deciding on the amount of fertilizer to apply or the area to plant. Thus, decisions are based on expectations of likely realizations and distribution of these uncertain variables.)

The important point is that even in the more general multi-input case, the allocatively efficient yield depends on the unit cost of inputs and the unit value of output, the quantities of fixed inputs, technology, and the quantities of other factors over which producers have no choice in a given cropping season, and all these factors vary across farms and over time. As a result, even if farmers are making technically efficient, or even allocatively efficient use of land and other inputs, 'yield gaps' could be observed across farms insofar as input unit costs, output unit values, or the quantities of other fixed inputs also vary, dictating different choices. Enduring 'gaps' in yields between any two farmers, such as one in the US mid-West and one in Malawi, may reflect persistent differences in their constraints and opportunities as indicated by differences in their economic or agroecological circumstances, reflected, for example, in input unit costs, output unit value, pest pressure, access to public infrastructure, or weather.

Yield as a Productivity Measure

Yield, defined as the output of a crop (e.g., amount of grain or other crop product) per unit of land used to produce it (e.g., metric tons of maize per hectare), is one of the most common measures of crop productivity. (In **Figure 1(a)** there is a one-to-one correspondence between the quantity of maize output (as plotted) and maize yields, that is output per unit area, because in this example all other inputs, including land area, are fixed – only the rate of fertilizer used on that given area varies. Similarly, and for the same reason, there is a one-to-one correspondence between the amount of fertilizer used (as plotted) and the rate of fertilizer application, that is the amount of fertilizer used per unit area. Yield is considered a 'partial productivity' measure because land is not the only input used in production. Partial productivity could also be measured in terms of crop output per unit of any of the other inputs used to produce it, such as fertilizer, labor, seed, or irrigation. Different partial productivity measures can lead to different conclusions. For example, averaging 2010 production at the continental scale, US farmers produced approximately 9.6 MT ha^{-1} of maize using 152 kg ha^{-1} of nitrogen fertilizer and sub-Saharan African (SSA) farmers produced 1.9 MT ha^{-1} of maize using approximately 9.7 kg ha^{-1} of nitrogen such that 61 kg of maize per kg of nitrogen was produced in the United States whereas 194 kg of maize per kg of nitrogen was produced in sub-Saharan Africa. (United States values were derived using area and output data from FAOSTAT (2013) along with USDA fertilizer use data (USDA, ERS 2011). SSA values were estimated using area and output data from FAOSTAT (2013), an estimate of average SSA nutrient application on maize (Smale *et al.*, 2011), and applying typical NPK shares from Alexandratos and Bruinsma (2012).) By these measures, US farmers appear more productive than SSA farmers in terms of land, but not as productive in terms of nitrogen, which highlights the perils of naïve interpretation of partial productivity measures like yield; namely, productivity with respect to any single input (e.g., land or fertilizer) could easily lead to inaccurate conclusions about the overall productivity of a system.

Furthermore, a difference in crop yield between countries or regions is not, in itself, sufficient for drawing definitive conclusions about productivity. The 2011 average Australian wheat yield (2.0 MT ha^{-1}) was less than one-third of the national average wheat yield of France (6.5 MT ha^{-1}), but this difference mainly reflected relatively low land quality and rainfall in the growing environments of Australia rather than any technical or allocative inefficiency in Australian wheat production. (This yield difference might also reflect the influence of differences in incentives for producers provided by European Union subsidies and other policy differences. The 2011 yields are from FAOSTAT (2013).) Even within a country, crop yields differ substantially over space: The 2007 US Census of Agriculture reports that nonirrigated maize yields were 2.5 times higher in Illinois than in Alabama. Although these yield differences can reflect regional differences in the environment, they can also reflect differences in socioeconomic circumstances such as opportunities for off-farm employment of farm family members and other dimensions of input costs, educational attainment, family structure, cultural norms, social and public infrastructure and related services, the nature of markets for farm outputs, and other determinants of the unit value of farm output. Such differences exist in market-driven agricultural systems as well as in subsistence agricultural systems.

Ideally, analyses of production, yields, or yield gaps would consider the production from the entire crop rotation of an enterprise or region and not focus on individual crops (Siebert *et al.*, 2010). Additionally, taking account of inputs other than land would allow for a more complete accounting of productivity and the sources of output growth. One way to take account of crop rotations, cropping intensity and multiple inputs is to apply total factor productivity (TFP) metrics to measure the relationship between all outputs and the amount and quality of all inputs used in production, rather than measure yield, which is a partial factor productivity (PFP) metric considering only the ratio of output to the amount of a single input (e.g., land) used to produce it. (Multifactor productivity (MFP) metrics include only some inputs and outputs, whereas TFP metrics ostensibly include all inputs and outputs. Some argue that TFP is a misnomer insofar as it is impossible to capture and properly measure all of the inputs to production (Alston *et al.*, 2010).) But even an increase in TFP does not guarantee that either yield or output has increased. Although TFP is closely related to the notions of efficiency discussed in this article, changes in TFP for a region over time can also reflect changes in the economic scale of

farm operations or changes in technology. Nonetheless, changes in TFP give a more complete accounting of the sources of growth than do changes in yields or yield gaps.

Total output equals total land under production multiplied by the corresponding yield such that increases in production can be thought of in terms of extensification, increasing the amount of land under production, and intensification, increasing the yield per unit of land. (Focusing on output per unit of land puts undue emphasis on land as a limiting factor in economic growth. For example, Schultz (1951) pointed to the declining economic importance of agricultural land; not only because the agricultural share of economic output has declined, but also because "… the value added by land … declined relative to all inputs used in farming" (p. 735). Although there are prospects for extensification (Pardey *et al.*, 2014), scientists and policymakers often emphasize intensification options as a means to increase crop production because, among other reasons, it is supposed that increasing the land area under production might exact a higher environmental cost than does increasing yields (Garnett *et al.*, 2013). Indeed, approximately 76% of the increase in aggregate crop production worldwide from 1980 to 2010 resulted from intensification, with only 24% attributable to extensification. (This figure is an approximation and is intended for illustrative purposes. The measure of total output is derived by aggregating crops by weight based on data from FAOSTAT (2013).) Thus, it seems, both the historical importance of and policy preference for intensification have led many researchers to focus on the limits to intensification in terms of yield gaps and the potential for closing these gaps as a means for feeding an increasing world population.

Yields, Yield Limits, and Yield Gaps

Because yield measures output per unit of land, it embodies the assumption that production is land constrained, making it subject to diminishing marginal returns and some absolute limit. The gap between this limiting yield and the observed yield bounds how much intensification can potentially increase production. Many conceptualizations and strategies for quantifying the limiting yield have emerged in the yield gap literature with a notable lack of standardization. The quantification of observed yields has also varied. Despite this lack of consistency, key ideas emerging from the literature can be parsimoniously framed from an economic perspective using four quantities:

- Actual yield (Y^{A}) – the measured yield at a particular location and point in time.
- Allocatively efficient yield (Y^{AE}) – the yield that maximizes the net value at a particular location and point in time given existing technology and input constraints.
- Limiting yield (Y^{L}) – the maximum yield that can be achieved at a particular location and point in time given existing technology and input constraints.
- Maximum limiting yield (Y^{ML}) – the maximum yield that can be achieved at a particular location and point in time given the best existing technology for that location and time, and nonlimiting inputs other than the amount of land.

The terminology used here intentionally differs from that used in previous studies to reduce the confusion that would come from having multiple definitions for the same terms. The terms are also defined relative to the economic concepts previously developed and illustrated in Figure 1 to further promote clarity. These four quantities make it possible to carefully define the yield gap as well as to identify distinct reasons for its existence.

The maximum limiting yield is the most that can be produced assuming land is the only constraining factor, given existing technology. This is illustrated in Figure 2 as Y^{ML} where the dashed curve represents the PPF for fertilizer and maize yield assuming the best available technology of the time is used, and inputs other than fertilizer and land are not limiting yields. The maximum limiting yield occurs where this dashed PPF reaches a maximum because fertilizer is also no longer limiting. It is important to remember that the maximum limiting yield is both location- and time-specific. As new technologies are developed over time the maximum limiting yield will also change, resulting in shifts in the dashed PPF.

The limiting yield, illustrated in Figure 2 as Y^{L}, falls short of this maximum limiting yield because of constraints on technology or inputs other than land. For example, farmers may not have access to pesticides, certain improved seed, or other inputs or technologies, owing to a range of socioeconomic and institutional factors. Therefore, the limiting yield occurs at the maximum of the PPF that reflects these technology and other input constraints as illustrated by the solid curve. An upward shift in this solid PPF can be accomplished by alleviating various constraints, though, by definition, the solid PPF could never exceed the dashed PPF. The difference between the maximum limiting yield and limiting yield results in one type of yield gap: $Y^{ML} - Y^{L}$.

The actual yield, illustrated by Y^{A} in Figure 2, typically falls short of the limiting yield. This can occur because input use is technically efficient, but not high enough to achieve the

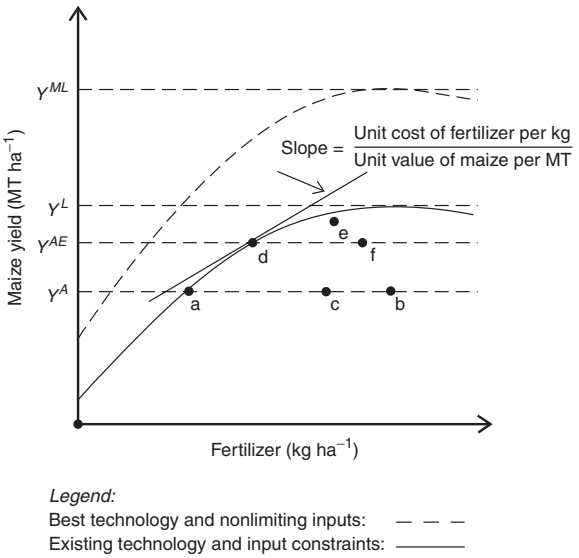


Figure 2 Hypothetical example of maximum limiting Y^{ML}, limiting, allocatively efficient, and actual yields when fertilizer is used to produce maize.

limiting yield (point a). It can also occur even if enough of the input is used to reach the limiting yield, but input use is technically inefficient (point b), or because not enough of the input is used to reach the limiting yield and what is used is technically inefficient (point c). The difference between the limiting yield and actual yield results in a yield gap: $Y^L - Y^A$.

The gap between limiting and actual yields can be decomposed into the gap between limiting and allocatively efficient yields and the gap between allocatively efficient and actual yields: $Y^L - Y^A = (Y^L - Y^{AE}) + (Y^{AE} - Y^A)$. The allocatively efficient yield occurs where the slope of the PPF with existing technology and input constraints equals the ratio of the unit cost of fertilizer to the unit value of maize, represented by point d in Figure 2. A gap between limiting and allocatively efficient yields is inevitable whenever inputs are costly to use or farmers have a limited ability to secure the input (e.g., because of poorly functioning credit markets or lack of public infrastructure). For example, if the unit cost of fertilizer in Figure 2 were zero, then the fertilizer-to-maize unit cost-to-value ratio would also be zero, such that the limiting and allocatively efficient yields would coincide (at Y^L). A gap between allocatively efficient and actual yields is not inevitable. Indeed, some economists argue it is nonexistent because the actual yield ultimately reflects the choices of farmers based on their own objectives and perceived values and costs, so it must be allocatively efficient. (That is, Y^A, corresponds to the output of maize that maximizes the value of production to farmers (point b in Figure 1(b)). The core of the argument is that any difference between Y^A and Y^{AE} results because the analysis has failed to properly incorporate the constraints faced by the farmer, the farmer's technology or the farmer's values.) Others argue that a gap between allocatively efficient and actual yields can and does exist for many farmers. Typically, this gap is presumed to be positive as is the case with the difference in yield between points d and a, b, or c illustrated in Figure 2, but this need not be the case if, for example, the observed yield actually corresponded to point e. Moreover, such gaps arise from either allocative inefficiencies (e.g., the difference in yields between points d and a) or technical inefficiencies (e.g., the difference in yields between points d and c or b).

Production at point f in Figure 2 further illustrates the drawbacks of using partial productivity measures like yield and yield gaps as a focus of policy discussions on food security. The yield corresponding to point f is identical to the allocatively efficient yield corresponding to point d. However, production at point f is technically and allocatively inefficient because too much fertilizer is used. Therefore, it is possible for production to be inefficient even if there were no gap between the allocatively efficient and actual yields.

The relationships illustrated in Figure 2 show how the overall gap between the maximum limiting and actual yields can be decomposed into the gaps between maximum limiting and limiting yields, limiting and allocatively efficient yields, and allocatively efficient and actual yields: $Y^{ML} - Y^A = (Y^{ML} - Y^L) + (Y^L - Y^{AE}) + (Y^{AE} - Y^A)$. How each of these gaps can be closed and whether it should be closed requires very different policy considerations.

Closing the gap between maximum limiting yield and limiting yield requires addressing the factors that are hindering access to better technology and inputs. In sub-Saharan Africa, for example, in many places the provision and adoption of improved technologies that would allow higher yields and lower costs of production for maize have been hampered by a lack of public infrastructure or by incomplete or nonexistent markets for credit, fertilizer, or other inputs, or by poor intellectual property rights applicable to agricultural technologies. In contrast, in the United States and other high-income countries, the comparable infrastructure, markets, and institutions function comparatively well and market-based incentives are much more effective (although that has not always been so, most notably if US crop yield performance is considered in a long-run historical context). If yields in sub-Saharan Africa could be lifted toward their US counterparts by improving markets for inputs or building better infrastructure, farmer (and consumer) welfare would be improved, but other ways of improving welfare may be more economical.

The gap between limiting and allocatively efficient yields can be closed by policies that reduce the unit cost of inputs or increase the unit value of output to farmers – whether these are measured using market prices or implicitly in terms of the opportunity cost for farmers, such as the value of their time or the value of at-home consumption of their products. But, if the market prices of outputs and inputs accurately capture their social value and costs, policies that interfere in the market may hurt other groups more than they benefit farmers. Thus, such policies might only be warranted if they are aimed at correcting some market distortion. (For example, consider the environmental costs (damages) imposed on society through the use of certain chemicals in agricultural production. If farmers are not liable for such damages, they may use more of the chemicals than they would if they were liable for environmental damages. A policy that lowers the price of such inputs might increase these external costs.)

Closing the gap between allocatively efficient and actual yields, if one exists, requires policies that promote the technical and allocative efficiency of farmers, so their input and output choices are less wasteful and capture as much of the value of production as possible, which could be of benefit to farmers and society as a whole. Such policies might include funding of educational extension programs and dissemination of market information to aid farmers in selecting efficient input mixes, or reducing distortions in market prices and the incentives they convey to farmers, such as, for example, in high-income countries that encourage the overuse of fertilizer and other agricultural chemicals by subsidizing output and failing to tax agricultural pollution.

Measurement of Yields and Yield Gaps

The quantification of yield gaps requires the measurement or estimation of a limiting yield as a counterfactual point of comparison for the actual yield. (Crop yields are usually defined in terms of the primary product of the crop. So, for example, maize output is typically measured in tons of grain, not in tons of total biomass produced. Traxler and Byerlee (1993) analyzed the uptake of semidwarf wheat varieties in the context of the demand for the joint (straw and grain) products from growing this crop.) The theoretical maximum yield based on crop physiology independent of realized

genetic improvements attracted interest in the 1960s and 1970s in relation to maximum limiting yields, especially from Dutch researchers, such as de Wit (1967) and Linneman *et al.* (1979) (as cited in Plucknett, 1995). However, although the theoretical maximum yield is referenced in the yield gap literature, it has not been widely adopted to either conceptualize or quantify the maximum limiting yield. Instead, the notion of potential yield, defined by Evans (1993, p. 26) as "the yield of a cultivar when grown in environments to which it is adapted, with nutrients and water nonlimiting, and with pests, diseases, weeds, lodging and other stresses effectively controlled," has been used more consistently to conceptualize the notion of a maximum limiting yield. A feature of this definition that distinguishes it from the theoretically maximum yield of a crop species is that it is defined relative to the best adapted cultivar for a particular environment. As land is heterogeneous across space and time in terms of soil and weather, and cultivars have continuously improved and become more highly adapted to specific environments, potential yield is a spatially and temporally varying concept. Although Evans-type definitions are most common, it is not clear that that they are actually quantifiable; as Cassman (1999) notes, such potential could not be measured in the field because it is impossible to completely mute all crop stress.

Potential yield as defined by Evans is location- and time-specific, which makes it most appropriate for quantifying yield gaps at the scale of a farm (or even farm field) in a particular year. Other notions of limiting yield for comparison to actual yield have cropped up in studies that attempt to quantify yield gaps at a landscape scale. These landscape studies rely on empirically based definitions of limiting yields, though they still maintain some notion of time- and location-specificity through the use of reference years and climate homologs. Although the empirical nature of these landscape definitions makes them easier to quantify, they are conceptually different from definitions like that of Evans. To better understand some of the key differences between perspectives on yield gaps at the farm level and at broader spatial scales, it is useful to briefly review the different strategies that have been employed in these two strands of literature. (Another way yield gaps have been measured is as the difference in yields between countries or regions (Trueblood and Arnade, 2001; Gillis, 2011; Walsh, 2012; Rosen and Shapouri, 2012; Collier, 2012) or production systems (De Ponti *et al.*, 2012; Yang *et al.*, 2008; Paez, 1973). These strategies for yield gap measurement are distinct from the more common field/farm and landscape scale studies because they ignore the location specificity of the production environment.)

Farm Yield Gap Measurement

The early literature on yield gaps relied heavily on measures of yields from intensively managed experiments on farmers' fields or experiment stations to quantify the maximum limiting yield, though researchers recognized that the limiting yields achievable by farmers in practice would likely differ from these experimental yields because of differences in environmental, socioeconomic, or other constraints faced by farmers, but not researchers (Davidson *et al.*, 1967; Gomez, 1977). (It is common in the yield gap literature to view economics as a 'constraint.' This reveals an agronomic point of view in which the counterfactual ideal yield is the limiting yield, even though the limiting yield is unlikely to be economic.) This distinction between the yield achievable in experiments and the yield achievable on the farm led Gomez (1977) and subsequent researchers to define different types of yield gaps; for example, Yield Gap I equal to the difference between the achievable and experimental yields and Yield Gap II equal to the difference between the achievable and actual farm yields. The International Rice Agroeconomic Network, an International Rice Research Institute (IRRI)-led consortium, measured achievable yields by conducting on-farm experiments to reduce the gap associated with potential environmental differences between farms and experiment stations, and thus the achievable yield roughly corresponds to the farm-level limiting yield defined in this article. The early multidisciplinary work at IRRI showed exceptional bio-economic clarity in its framing of yield gaps. This work includes Herdt and Wickham (1975), IRRI (1977 and 1979), De Datta *et al.* (1978), Herdt and Mandac (1981) and others. Our economic conceptualization of yield gaps draws from and repositions these foundational works.

The lines drawn between limiting and allocatively efficient yields and between allocatively efficient and actual yields are motivated by distinctions like those between Yield Gaps I and II proposed by Gomez (1977). However, these early yield gap distinctions did not always clearly delineate between gaps resulting from technical inefficiencies, rational economic behavior, and more fundamental social, cultural, institutional, or economic constraints, making it difficult to understand the practical and policy implications of alternative gaps.

Herdt (1988), as cited in Pingali and Heisey (1999), found that experiment station yields decreased markedly when the objective of the experiment was changed from yield maximization to profit maximization, which led Pingali and Heisey (1999) to argue that differences between farm yields and experiment station yields designed to maximize profits provide a measure of the "exploitable yield potential" (p. 21). This notion of exploitable yield potential is analogous to allocatively efficient yields, assuming farmers are primarily interested in profit maximization. Alternatively, if farmers are also concerned with risk avoidance as argued by Herdt and Wickham (1975), the analogy between exploitable yield potential and allocatively efficient yield begins to wither.

Duvick and Cassman (1999) assert that contest winning yields provide another and better approximation of farm-level limiting yields, whereas Specht *et al.* (1999) warned that contest winning yields "… arise from favorable confluences of genotype, management, soil type, rainfall, weather, etc." (p. 1568) that are unlikely to be scalable across large production areas. Crop growth models offer another way to quantify the maximum limiting yield (e.g., Becker *et al.*, 2003) that has not been as widely adopted because critics have worried about how well such yields capture what farmers can achieve (Lobell *et al.*, 2009), the need to frequently update the models to reliably capture a changing genetic landscape (Fischer and Edmeades, 2010), and the potential for errors and uncertainties in the modeled yields to exceed the actual yield gap (Neumann *et al.*, 2010).

Yield Gap Measurement at Landscape Scales

More recently, the literature has turned to assessments of yield gaps at broader spatial scales than the farm level, including regional and global assessments; these 'landscape scale' assessments generally are undertaken with a view to better targeting productivity-enhancing interventions and investments. Although the details of these assessments vary across studies, the general approach is to represent actual yields using global estimates such as those found in Monfreda *et al.* (2008). In these datasets, the world is partitioned using a grid of pixels (i.e., a raster), with estimates of the actual average yield for each pixel in which the crop is likely to be grown. These global methods also differ in how the limiting yield is estimated for comparison to the actual yield. Using raster data on weather (moisture and temperature), Licker *et al.* (2010) divided the world into 100 climate zones such that each zone ostensibly has a similar temperature and moisture profile (measured using growing degree days and a soil moisture index). The authors then constructed a cumulative distribution of yields across the constituent pixels in each zone and took the 90th percentile (e.g., the minimum yield of the top ten percent of yielding pixels in each zone) as the limiting yield of the zone given its temperature and moisture profile. (The choice of the 90th percentile by Licker *et al.* (2010) was apparently somewhat arbitrary, although the authors expressed concern that higher values in the yield dataset might be "erroneous or overestimated" (p. 774). Others have used the 95th percentile and one could argue for use of the maximum yield for a climate zone as the limiting yield for that zone.) The yield gap of each pixel was then calculated as the difference between the limiting yield in the corresponding zone and the estimated actual yield in the pixel. Foley *et al.* (2011) and Mueller *et al.* (2012) similarly define the limiting yield for each pixel as the 95th percentile of the yield distribution for pixels with similar rainfall and temperature regimes. It is worth emphasizing that defining limiting yields as an arbitrary percentile of a yield distribution is conceptually different from defining limiting yields based on simulated or experimental yields. As the yields in these distributions are actually observed, they will tend to generate conservatively small estimates of limiting yields. (This is especially true when the yield distribution is made up of pixel-level yields because pixel yields are already a spatial average yield (and in some cases, a temporal average as well).)

The coarse measures of temperature and rainfall used in climate homolog methods do not fully describe the growing environment. Indeed, intraseasonal patterns of rainfall and temperature, and the occurrence of weather events relative to the lifecycle of the crop are extremely important in explaining yields (Beddow *et al.*, 2012). As the methods abstract from the intraseasonal extremes of temperature and drought that generate crop stress, they do not generate estimates of potential yield that are in the spirit of Evans (1993). Further, the binning procedures – whereby pixels are grouped into homologs based entirely on some selected agroecological attributes – do not embed spatially sensitive information on input costs or output values and other socioeconomic factors. Thus, both the limiting and allocatively efficient yields may be different for each pixel even if pixels are in the same climate homologs.

This strand of literature does not tend to employ concepts analogous to the maximum limiting yield, though in some sense the maximum yield observed within the distribution of yields in a climate homolog might be interpreted as such. The distinction of allocatively efficient yields is also not typically quantified. Neumann *et al.* (2010), who estimate a stochastic production frontier based on global pixelated yield data, provide an exception to some extent. This stochastic production frontier method incorporates monthly temperature deviations, monthly precipitation, solar radiation, and a measure of soil fertility as inputs in an attempt to quantify the source of technical inefficiencies. Therefore, the method does not explicitly quantify allocatively efficient yields, but it does measure part of the gap between allocatively efficient and actual yields. However, because the set of inputs employed by the authors is limited, what appear to be technical inefficiencies may actually reflect differences in unmeasured inputs related to farmers' management choices or other environmental factors, which could bias the results.

Practical Challenges to Measuring Yield

To quantify yield gaps well requires access to accurate and meaningfully comparable measures of actual yields; whether they are used directly in forming estimates of gaps in yields or indirectly as a basis for calibrating modeled crop yields. However, estimating crop yields that are statistically accurate (or 'true' in ISO parlance) and precise is difficult. Survey-based methods are typically used to estimate average yields (which are usually derived from estimates of planted or harvested area and corresponding estimates of grain production) at county, state, or national scales, but the nature, accuracy, and comparability of these surveys vary markedly over time, across countries, and among crops.

For example, in the United States, objective measures of average maize yields at county scales and above begin by establishing an 'area frame,' from which a probability-proportional-to-size sampling of farm fields is taken. Two parallel, 15 ft. sections of rows within each sampled maize field are then surveyed by trained enumerators who collect the information required to estimate the number of ears per acre and the (standardized moisture content) grain weight per ear that in turn are used to estimate total crop production and average yields (USDA-NASS, 2012). Remotely sensed data coupled with an array of modeling methods are increasingly being used in conjunction with ground-truthed data to generate (georeferenced) crop area, yield, and production landscapes (Bailey and Boryan, 2010).

In other, often developing-country contexts, crop cut or farmer estimates have been the primary means by which crop production, area, and yields are estimated. ('Crop cut' refers to a set of methods for estimating crop quality and yield by harvesting or sampling small portions of fields. Procedures differ, but in general the goal is to scale up the yield of the sampled area to estimate a yield for the entire field or farm.) These estimates are prone to substantial sampling biases and measurement error. This is especially so in the complex

cropping systems characterizing many smallholder operations in low-income countries. The inability to assure a spatially representative sampling of farms, perhaps stratified by size, production systems (e.g., irrigated vs. rainfed), and other relevant attributes, is just the first of many sources of measurement error. Smallholder farms are often subdivided into plots, wherein crops are grown in pure stands as well as multi- or intercropped systems involving two or more crops planted on the same plot in a season, and in many instances involving at least two and in places three cropping seasons per year (Dalrymple, 1971; Poate and Casley, 1985; Fermont and Benson, 2011). In these circumstances, subplot crop cutting methods are often used to estimate yields (and production), introducing a host of potential estimation errors. For example, Poate and Casley (1985) suggest crop cutting methods tend to overestimate yield via a combination of 'edge effects' (plants that lie fractionally outside the subplot are included in the count), 'border bias' (location methods may over- or underestimate the boundaries of a plot), and nonrandom location of the subplot (enumerators tend to avoid bare or sparsely populated parts of the plot) (Also see FAO, (1982) and Murphy *et al.*, (1991)). The timing of the crop cuts matters too; especially for cropping systems in which individual plants within a particular crop stand, or different crops within each (sub-)plot, mature at different times.

Crop cuts generate estimates of the quantity of production, which carry with them problems of standardization by form – fresh or processed, shelled or unshelled, with or without stalk, polished or unpolished, in the cob or seeds only, or some other form – standardization by moisture content, and standardization by type (e.g., Durum vs. winter or spring wheat). To report yields (or to upscale crop-cut or farmer estimates of plot-level yields to estimate total production) at larger spatial scales also requires commensurate measures of planted or harvested area. A host of conventional area measurement techniques are used (e.g., Poate and Casley, 1985; Poate, 1988), increasingly complemented by handheld PDA devices (Keita *et al.*, 2010). None of these area estimation approaches is without error. Newer GPS aided devices are imprecise on very small plots (say less than 0.01 acres), but are more accurate on larger plot sizes, where they reveal a seemingly systematic tendency for farmers to overestimate the size of small plots (by upwards of 90%) and underestimate the size of large plots (by upwards of 59%) (Carletto *et al.*, 2013).

The comparability of yields taken at a point (say on-station yields, or on-farm experimental yields taken from one or a few farms) versus the estimated average yield in the surrounding or adjacent region is also problematic. Crop yields are typically much more variable at the field level than at the regional level (e.g., Lobell *et al.*, 2007) and farm yields are often not symmetrically distributed even within a field (e.g., Hurley *et al.*, 2004), so that a regional average yield may not represent the yield of a typical farm, and thus the calculated yield gap may not be representative of the region being studied. That point estimates of limiting yield (e.g., from an experiment station or highest yielding farm) are essentially incomparable with regional or national average yields was noted by Barker (1979), who deemed such comparisons "… newsworthy (but scientifically worthless)…" (p. 10).

Interpretation of Yield Gaps

Meaningfully measuring the magnitude of a yield gap is one challenge. Another challenge is drawing actionable insights with meaningful scientific, farm management, economic, or policy implications.

Are Yields Gaps Good, Bad, or Irrelevant?

Two somewhat contradictory views of the importance of yield gaps to food security might be taken. One view is that yield gaps are necessary for improvements in farm yield, and as the yield gap decreases, because the actual yield is approaching the limiting yield, it is increasingly difficult for farmers to improve yields such that yield growth rates slow (Grassini *et al.*, 2011; Cassman, 1999; Pingali and Heisey, 1999; Cassman *et al.*, 2003). The natural conclusion is that small yield gaps are a bad omen for future food prospects, and that a robust way to address food security concerns is to increase yield gaps by raising the limiting yield through breeding programs for example. However, the evidence to support a relationship between smaller yield gaps and slower yield growth is not entirely clear (Evans and Fischer, 1999).

A second view is that yield gaps are indicative of potential problems that could be addressed by changing farmer behavior, natural environments or markets. From this viewpoint, 'closing' the yield gap is a way forward to sustainably increase agricultural output (Mueller *et al.*, 2012; Foley *et al.*, 2011). In this context, yield gaps show where output gains might be realized by tackling the biotic, abiotic, and socioeconomic constraints to yields. For example, Herdt and Wickham (1975) first discuss constraints that lead to the gap and then suggest research and investment as a way to relax these constraints. Still, whereas yield gaps might show where improvement is technologically possible, this does not necessarily imply improvement is economically or socially feasible or desirable.

Closing yield gaps is not a necessary condition for increasing output via agricultural intensification. A historical example from the United States serves to illustrate. The improvement in maize output over the past century in the United States is an example of a successful intensification effort, especially from the perspective of increasing global food and feed supplies. Consider the period 1889 through 1954. In the earlier years conditions in US agriculture were comparable to current conditions in many low-income regions, with smaller farms, poor rural infrastructure, comparatively limited use of off-farm inputs, and so on (e.g., Gardner, 2002). But the average maize yield in the United States grew significantly. It increased from just over 1.8 MT ha^{-1} in 1899 to approximately 2.5 MT ha^{-1} in 1954. Over the entire period 1889–2007, the average US maize yield increased to 9.3 MT ha^{-1} such that output sextupled even though the amount of US harvested land devoted to maize increased by only approximately 20%. Using county-level annual yields, the authors approximated the methods of the global yield gap studies (e.g., Foley *et al.*, 2011 and Mueller *et al.*, 2012) and measured yield gaps as the difference between the yield for a particular county in a particular year and the 95th percentile of the yield distribution for that year. (These yield gaps (G) were calculated

for each county, i, and year, t, as $G_{i,t} = \max(Y_t^L - Y_{i,t}^A, 0)$, where Y_t^L is the 95th percentile of the county yield distribution for time t and $Y_{i,t}^L$ is the reported ('actual') yield for the corresponding county and year. The area-weighted mean gap, $\sum_i G_{i,t} a_{i,t} / \sum_i a_{i,t}$ was used as the national yield gap, which was expressed as a percentage of Y_t^L. It is worth noting that slight variations in the way in which the yield gap is calculated or presented can change the results. One could argue effectively for use of unweighted, area-weighted or output-weighted yield gaps, gaps as a percentage of farm yield, calculating the limiting yield using various percentiles of the yield distribution, and so on. In the present data, the absolute yield gap increased between 1889 and 2007, whereas the yield gap expressed as a percentage of Y_t^L decreased (from ~31% to 19%). The gap decreased substantially more (from 80% to 29%) when expressed as a percentage of farm yields.) Although the national yield improved markedly during both periods, this measure of yield gaps increased between 1889 and 1954, and decreased between 1954 and 2007.

More particularly, increases in regional yields do not necessarily imply decreases in the region's yield gap. Figure 3 shows the spatial distribution of US maize yields for 1889, 1954, and 2007, along with the cutoff for the limiting yield (estimated as the 95th percentile of the county yield distribution). The average yield increased between 1889 and 1954, but the larger yield increases tended to be seen at the high end of the distribution, thus increasing the national yield gap. By 2007, the distribution had become much more symmetric, decreasing the yield gap. Thus, changes in the distribution of yields can affect yield gaps, even causing the yield gap to increase while average yields are improving. Indeed, a region's yield might be distributed such that the yield gap could change between two years even if the same amount of output were produced in both years using the same amount of land (and thus the regional yield would not change). (Many distributions exhibit this phenomenon. For example, consider a simple case in which, in a given year, half of a country's hectares had a yield of 7 MT ha^{-1} and the other half yielded 8 MT ha^{-1}. The national yield in that year was 7.5 MT ha^{-1}. Suppose that the country's yield distribution changed the following year, such that half of the hectares yielded 5 MT ha^{-1} and the other half yielded 10 MT ha^{-1}. Again, the national average yield was 7.5 MT ha^{-1}. Using the 95th percentile of the yield distribution as the limiting yield, the first time period had a yield gap of 6.25%, whereas the second year had a yield gap of 25% even though the same amount of output was produced on the same amount of land.)

Lack of Standardization and Potential for Manipulation

Yield gaps often entail the comparison of some observed yield with a counterfactual limiting yield. The preceding discussion noted several ways in which the limiting yield might be estimated. Because the measure of the limiting yield can differ across studies, ostensibly similar 'yield gap' studies may actually be measuring very different things. Thus, care must be taken in interpreting yield gaps – namely, it is important to understand exactly what is being measured. It has been shown empirically that different methods of estimating the limiting yield can produce markedly different results. For example, Singh *et al.* (2009) estimate state-level Indian yield gaps for several crops using both simulated yields and experimental yields as alternative measures of the limiting yield. In most

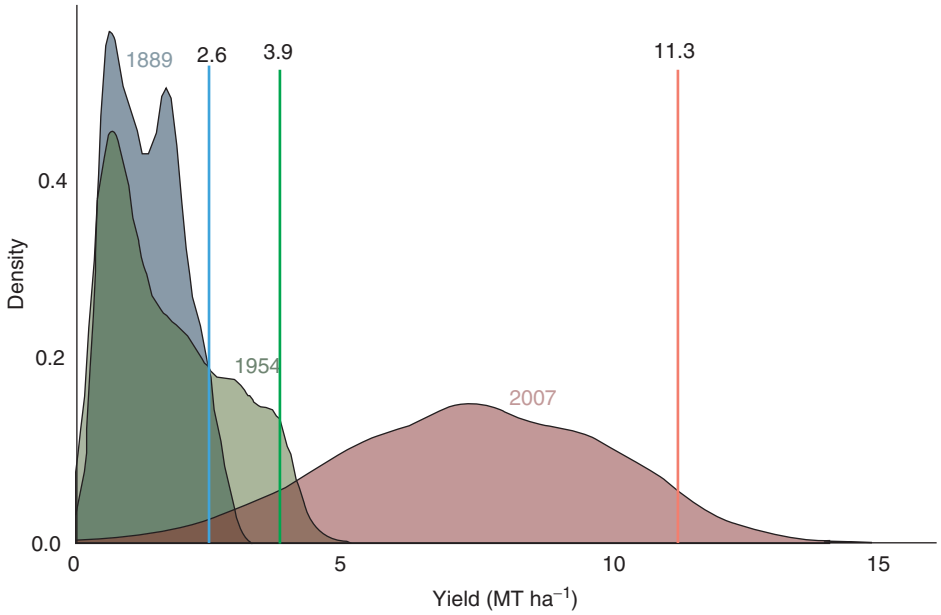


Figure 3 County-level maize yield distribution, 1889, 1954, and 2007. The limiting yield for each year was calculated as the 95th percentile of the unweighted county-level yields for all counties that harvested maize in the corresponding year. This limiting yield is shown as a vertical line for each distribution (with the value indicated at the top), in a color corresponding to the color of the distribution. Created by the authors using data from Beddow, J.M., 2012. A Bio-Economic Assessment of the Spatial Dynamics of U.S. Corn Production and Yields. Ph.D. Dissertation. Department of Applied Economics, University of Minnesota.

cases, the limiting yield implied by crop simulation models was markedly higher than the limiting yield implied by experimental results. Aggarwal *et al.* (2008) present a similar study including yield gaps derived using three methods to estimate the limiting yield: simulation models, experiments, and on-farm demonstrations.

Lack of standardization in the measurement of yields must also be carefully considered in the interpretation of yield gaps. This is particularly true when comparing yield gaps across farm versus landscape analyses, but is also true for comparisons across farm-level analyses or across landscape-level analyses. For example, global analyses of yield gaps rely on aggregate estimates of yields over geo-politically defined statistical regions. The mere process of this aggregation will tend to mute the spatial variability of yields and the size of yield gaps when compared with more disaggregate measures such as those constructed based on farm- or field-level yield observations. This can be illustrated using pixelated estimates of global maize yields on a 5 arc min (approximately 10×10 km) grid. (The production, area and yield data used for this illustration come from the Spatial Production Allocation Model 2000 v3.0.6 (You *et al.* 2000).) **Table 1** reports descriptive statistics for the global distribution of yield gaps calculated in two ways. The first distribution is based on the difference between the 95th percentile yield estimate for all pixelated yields within an agroecological zone (data for the agroecological zones are from Sebastian (2006)) and the pixelated yield estimate, which reflects yield gaps derived from disaggregate data and is to some extent analogous to using farm- or field-level yield estimates in a landscape-scale study of yield gaps. (Yield gap distributions were calculated using area weights as described in the Section Are Yields Gaps Good, Bad or Irrelevant?) The second distribution is based on the difference between the 95th percentile yield estimate for the country average yields in an agroecological zone and the country average yield for a pixel, which reflects yield gaps derived using methods analogous to those typically employed in landscape scale assessments of yield gaps. With the more disaggregated yield estimates, the mean, median, maximum, and standard deviation of the yield gap distribution are 65.2, 148, 44.7, and 8.5% higher, respectively, than with the country aggregated data. Therefore, simple differences in spatial aggregation across studies can result in noncomparable yield gap estimates.

The lack of standardization in the measurement of actual and limiting yields can lead to some confusion, particularly in the policy arena. Sumberg (2012) argues strongly that the yield gaps used in policy arguments are often specified such that they are as large as possible or that they justify the analyst's preferred policies, concluding with a warning that yield gaps are "seldom what they appear" (p. 517).

Yield Gaps with Multiple Enterprises

Diversification is a common strategy in farming used to manage risk and to better utilize lumpy assets and farm family labor resources for which different farm enterprises have different seasonal demands. It is accomplished by growing multiple crops, raising livestock in addition to crops, or being employed off as well as on the farm. With multiple enterprises, the allocation of scarce inputs to one enterprise inevitably affects the output in other enterprises. Van Ittersum *et al.* (2013) note that agronomically optimal sowing dates might not be economically optimal when multiple crops are planted each year (e.g., the optimal harvest date of one crop might conflict with the optimal planting date of a follow-on crop). Von Braun (1988) demonstrated that there may be complex interactions in multicrop systems, such that adoption of a yield-increasing technology for one crop may decrease yields of other crops Von Braun (1988) reported on the effects of an improved rice production scheme in The Gambia, finding that, on average, 390 kg of cereals and 400 kg of groundnuts are foregone for each additional ton of rice. This result was influenced both by the expected substitution of labor into the now more productive rice production along with a complex household and farming structure. Von Braun warns that "[t]he more complex the household structures and production organization in agriculture are, the less straightforward the predictions are on how technological change may impact on nutritional improvement (p. 1095)." The importance of such tradeoffs is not easily accounted for when focusing exclusively on individual crop yields and yield gaps.

Figure 4 illustrates how yield gaps emerge from a farmer's choice of activities. In the illustrated case, a farmer is allocating his (limited) time between maize production and off-farm work that pays an hourly wage. (The off-farm production example used here could easily be replaced by the production of an additional on-farm output, such as a second (or more) crop(s), with no change in the yield-gap implications of the example.) The shaded area shows the production possibilities for maize yields and off-farm work, given existing technology

Table 1 Descriptive statistics for disaggregated pixelated and aggregated country average yield gaps by agroecological zones (AEZ)

	Disaggregated pixelated yield gaps by AEZ (MT ha^{-1})	*Country aggregated yield gaps by AEZ (MT ha^{-1})*
Mean	3.81	2.30
Median	3.38	1.36
Standard deviation	2.58	2.38
Maximum	13.27	9.17
Minimum	0.0	0.0

Note: Disaggregated pixelated yield gaps were constructed as the difference between the 95th percentile of pixelated yields in an agroecological zone (AEZ) and the pixelated yield. Country aggregated yield gaps were constructed as the difference between the 95th percentile of the country average yield in an agroecological zone and the average yield of each country's constituent pixels.

Source: Created by the authors using data from Sebastian, K., 2006. Global Agroecological Zones Dataset. Washington, DC: HarvestChoice (Unpublished data) and You, L., Crespo, S., Guo, Z., *et al.*, 2000. Spatial Production Allocation Model (SPAM). Version 3 Release 2. Available at: http://MapSPAM.info (accessed 20.08.13).

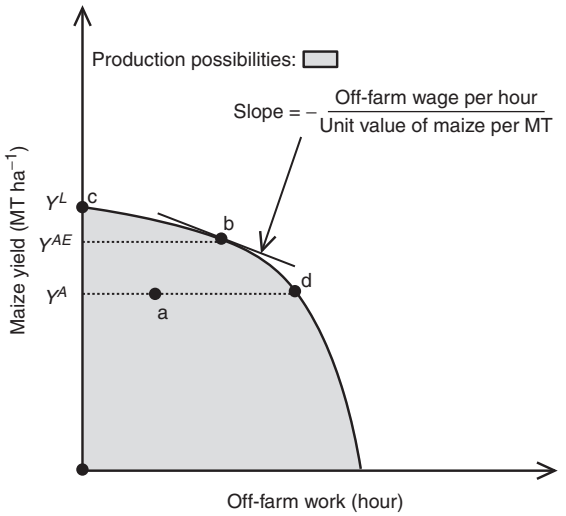


Figure 4 Hypothetical example of limiting, allocatively efficient, and actual yields when maize and off-farm work are produced.

and input constraints. The upper boundary of this region denoted by the solid curve is the PPF. Point a is inefficient because more maize can be produced without decreasing off-farm work (and thus, off-farm income) or more off-farm income could be acquired without decreasing maize production. Allocative efficiency requires equality between the value of an additional ton of maize and the value of the off-farm work that would be given up to produce the additional maize, which occurs where the slope of the PPF equals the negative of the ratio of the wage to the unit value of maize (point b). The negative sign reflects the fact that some maize must be given up to do more off-farm work when production is technically efficient.

The limiting yield, Y^L, occurs at point c where off-farm work is at a minimum so the farmer can devote as much time as necessary to the production of maize to maximize yield. The actual yield, Y^A, could be technically, but not allocatively, efficient (point d). Alternatively, it could be technically and allocatively inefficient (point a). The allocatively efficient yield corresponding to point b maximizes the sum of the value of maize production and off-farm work. The gap between the limiting and allocatively efficient yield is once again inevitable if off-farm work is valuable to the farmer, so trying to close it is not economical. Thus, yield gaps can emerge from economical choices over what to produce (e.g., maize or off-farm work) as well as over how it is produced (e.g., with more or less fertilizer). The gap between the allocatively efficient and actual yield is technically or allocatively inefficient because what the farmer is choosing to produce is wasteful given the value of maize and the wage rate.

Conclusion

Making progress on food security requires more than a biological view. Yields are lower or higher depending on the unit costs of inputs, the unit value of output, and other socioeconomic constraints faced by producers. An important economic constraint, particularly in low-income countries, is the inadequate state of transportation infrastructure. Poor road and rail networks increase the cost of getting output to markets and inputs to farms, and thus change the relative unit costs of inputs and the unit values of output at the farm gate, with (often negative) consequences for the allocatively efficient yield. Other constraints also hinder farmers: poor storage facilities require that output be sold rather than stored when market prices are low; trade restrictions can reduce domestic prices; and missing or poorly functioning markets for credit, insurance and labor all serve to reduce a farmer's allocatively efficient yield.

Yield gaps are the wrong metric if the primary concern is food security, which is fundamentally about the capacity of agriculture to supply affordable food efficiently and sustainably to subsistence farmers and nonfarm consumers alike. Closing yield gaps is neither necessary nor sufficient for improving food security. Indeed, as demonstrated above, a region's yield and output could improve even though yield gaps are increasing. Further, targeting the closure of yield gaps as a policy in order to feed more people may have unintended consequences. For example, idling either less-productive land (thus decreasing the gap directly) or idling the most productive land (thus reducing the limiting yield) would close the yield gap, but would also reduce total output. Output is the primary determinant of the availability and affordability of food, and efforts to increase output will tend to improve the lot of nonfarmers as well as farmers. Thus, in many cases, policies might best be focused on increasing the output of a region or the world as a whole – such as investments that enhance farmer productivity and participation in markets – rather than on simply decreasing yield gaps, which is not guaranteed to improve food security and often will be uneconomic.

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Food Toxicology

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Glossary

Adulterant A chemical substance deliberately added to food to deceive others in some manner.
Food toxicology The science that sets the limits of safety for chemical substances in foods.
Mycotoxin A potentially toxic chemical produced by molds growing on agricultural crops or foods.
Phycotoxin A potentially toxic chemical produced by dinoflagellate algae that is ingested by fish or shellfish.
Toxicology The science of poisons.

Introduction

Foods contain a myriad of chemicals, including the nutrients needed to sustain life. Food toxicology could be defined as the science that establishes the basis for judgments about the safety of foodborne chemicals. The central axiom of toxicology as set forth by Paracelsus in the 1500s states: "Everything is poison. Only the dose makes a thing not a poison." Thus, all chemicals in foods, whether natural or synthetic, inherent, adventitious, or added, are potentially toxic. Although all chemicals are toxic, many fewer pose a risk under typical circumstances of exposure, including the dose and frequency of exposure. The vast majority of foodborne chemicals are not hazardous because the amounts of each foodborne chemical in the typical diet are not sufficient to cause injury. The age-old wisdom about the benefits of eating moderate amounts of a varied diet protects most consumers from any harm. Foodborne chemicals that are considered to be toxicants are those chemicals where the dose and frequency of exposure can, in at least some circumstances, be sufficient to elicit adverse reactions. Unusual dietary practices can sometimes result in intoxications from chemicals that would normally be considered safe and desirable. Examples would include several of the polar explorers who experienced toxic responses to excessive intake of vitamin A as the result of consuming large amounts of polar bear liver and, more recently, the ingestion of copious quantities of water in a misguided radio contest that resulted in the death of a contestant.

Toxic reactions to food encompass all food-associated illnesses that are caused by chemicals in food. Foodborne chemicals vary greatly in toxicity. All consumers are susceptible to most food intoxications, although differences exist primarily related to the dose of exposure and body weight (infants vs. adults). Food allergies and metabolic food disorders, for example, lactose intolerance, are a subset of food intoxications that affect only certain individuals in the population. For the purposes herein, only those foodborne chemicals that are potentially hazardous to humans under known (though sometimes atypical) circumstances of exposure are discussed. These foodborne chemicals are divided into categories based on source – naturally occurring, food contaminants, processing-induced toxicants, and food additives. In recent decades, the science of food toxicology has emerged as an approach toward understanding and assessing the risks posed by the various chemicals in food.

Acute adverse reactions to foods are those adverse reactions occurring within hours to a few days following exposure to the particular foods/foodborne chemicals. Acute foodborne intoxications usually result in a rapid onset of symptoms. Chronic foodborne intoxications involve more prolonged exposures with symptoms that develop more slowly. With chronic toxicity, the attribution of the cause-and-effect relationship to a specific foodborne chemical is often quite difficult due to the existence of many confounding variables. The toxic characteristics of various foodborne chemicals are based either on investigations of incidents where humans developed adverse reactions (more often the situation with acute intoxications) or on the results of controlled feeding trials conducted with laboratory animals, usually rats or mice. In the following sections, examples of foodborne chemicals from various sources are described with the focus on examples of chemicals that do have a realistic potential of eliciting adverse reactions under at least some circumstances of exposure. Clearly, it is impossible to discuss all of the many thousands of chemicals in foods. The examples are selected because the toxic potential is recognized, although the listing is not intended to be comprehensive among chemicals fitting that criterion.

Food Additives

Food additives are chemical substances that are knowingly added to foods to provide a wide variety of technical benefits, including nutrients (Table 1). Thousands of food additives exist, although many are used in rather small amounts. In the United States, food additives can be classified on the basis of their regulatory status: (1) generally recognized as safe (GRAS) substances, (2) flavors and extracts, (3) direct additives, and (4) color additives. Because food additives are intentionally added to foods, these chemicals are carefully evaluated for safety often using feeding trials in laboratory animals. Only those chemicals that are shown nonhazardous under normal circumstances of exposure or those that have a long history of safe use are permitted to be used as food additives.

Many food additives were in common use long before the passage of comprehensive food laws, such as the 1958 Food, Drug and Cosmetic (FD&C) Act in the United States. These substances are considered as GRAS based on their history of safe use. More than 600 chemicals are on the US Food & Drug Administration (FDA) GRAS list, including sucrose, salt,

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Table 1 Categories of food additives

Category	*Example*
Acidulents	Acetic acid
Anticaking agents	Magnesium silicate
Antimicrobial agents	Sodium benzoate
Antibrowning agents	Sodium bisulfite
Antioxidants	Butylated hydroxyanisole
Emulsifying agents	Lecithin
Nutrients	Ascorbic acid
Sequestrants	Citric acid
Stabilizers	Guar gum
Spices	Cinnamon
Oleoresins and extracts	Fennel oil
Flavorings	Ethyl butyrate
Enzymes	Glucose isomerase
Colorants, artificial	FD&C Yellow #5
Colorants, natural	Annatto
Sweeteners	Sucrose
Nonnutritive sweeteners	Aspartame

butylated hydroxytoluene, spices, and many nutrients. From a legal standpoint, GRAS substances are not actually additives, but that distinction is seldom made by the consumer. Although GRAS substances are considered to have a history of safe use, that does not necessarily imply that substantial toxicological data exist for all of these substances. New concerns can periodically arise regarding GRAS substances. For example, the concerns around sodium levels in the diet and hypertension ensued long after the placement of sodium chloride on the GRAS list. Substances, or certain uses of substances, can be removed from the GRAS list if the FDA acquires evidence of some hazard to consumers.

In addition, in the United States new substances can be affirmed as GRAS based on the judgment of a panel of expert scientists qualified by experience and training to make such judgments. In such GRAS affirmation situations, the experts evaluate the safety of the substance based on its characteristics, composition, history of safe use, and toxicological properties. A substance can be affirmed as GRAS based on a documented history of safe use or on the basis of scientific studies that are published in the peer-reviewed scientific literature. Substances are affirmed as GRAS for specific uses, thereby controlling exposure within the limits that might be imposed by the available evidence. The FDA is often notified of GRAS affirmation decisions and has the authority to object if it disagrees with the expert panel.

Internationally, the Joint Expert Committee on Food Additives of the World Health Organization periodically reviews the existing toxicological data on food additives, including long-standing food additives, and establishes Acceptable Daily Intakes (ADIs) for their use. ADIs can be readjusted as new information becomes available.

Flavors and extracts represent a large percentage of the total number of food additives. The Flavor and Extract Manufacturers Association (FEMA) keeps a list of accepted flavors and extracts. The FEMA has established a GRAS list for flavors and extracts and is largely responsible for evaluating the safety of the chemicals on the list; the FEMA has an expert panel that conducts the safety assessments of these chemicals. More than 1000 chemicals are on the FEMA list, although some of these chemicals and extracts are no longer used.

In the United States, direct food additives are those new chemicals that have been approved by the FDA since 1958. Few approvals for new food additives have been granted in recent years. Extensive and costly safety data are required to gain such FDA approval. Aspartame, a nonnutritive sweetener, is one of the most notable direct food additives in use in the United States (and many other countries). Aspartame was approved as a nonnutritive sweetener for certain types of uses some years ago and the consumption of this new additive has become substantial. More recently, Olestra, a noncaloric fat replacer, was approved for certain uses, such as the deep-fat frying of chips.

Color additives are regulated separately in the United States. Any new artificial color additive must be approved by the FDA in much the same way that new direct food additives are approved. Several artificial color additives have been banned since 1958 because of concerns about their possible chronic toxicity. A good example is FD&C Red #2, now banned in the United States but allowed in Canada and other countries. Conversely, FD&C Red #40 is allowed for use in the United States but banned in Canada.

The degree of hazard associated with the presence of additives in foods is quite low. The level of exposure to most food additives, especially flavoring ingredients, is rather low, which diminishes the potential hazard. Additionally, the oral toxicity of food additives tends to be extremely low, especially with regard to acute toxicity. Some concerns have arisen about the chronic toxicity of a few food additives, including saccharin, FD&C Red #2, cyclamate, and others. Furthermore, the safety of many additives is well established through controlled feeding trials conducted in laboratory animals. The toxicity of food additives is low but also well known, and exposure can be limited to levels far below any dose that would be hazardous. By contrast, the toxicity of naturally occurring chemicals in foods is often not known. With naturally occurring chemicals, concerns exist that hazards could exist under certain conditions of exposure.

Despite their long history of safe use and the existence of data from animal feeding trials, the safety of some food additives has been called into question. With FD&C Red #2 and cyclamate (a nonnutritive sweetener), the questions have revolved around evidence for weak carcinogenic activity in laboratory animals. FD&C Red #2 and cyclamate were banned in the United States as a result of such evidence. Other concerns also exist, such as the role of sugar in dental caries and abnormal behavioral reactions, the role of monosodium glutamate (MSG) in asthma, the role of aspartame in headaches and other behavioral and neurological reactions, and the role of Olestra in gastrointestinal complaints. The concerns range from acute toxicity, such as aspartame and headaches or MSG in asthma, to chronic toxicity, such as cyclamate and bladder cancer or sugar in dental caries. Although a detailed discussion of all these issues is beyond the scope of this article, it may suffice to say that many of these assertions have been questioned and remain controversial.

Several illustrative examples are discussed for food additives. For acute intoxications, the examples include situations involving adverse reactions occurring as a result of excessive

consumption of an additive, misuse of an additive by the processor or consumer, and abnormal sensitivities of certain types of consumers to specific food additives. With respect to chronic intoxications, saccharin is discussed briefly. Many other examples could be cited for chronic toxicity concerns, including cyclamate and FD&C Red #2.

Sorbitol and Hexitols

Sorbitol and various other hexitols are alternative sweeteners, frequently used in candies and chewing gum, because they do not support formation of dental caries. Dietetic food diarrhea has been associated with these polyol food additives and serves as a good example of intoxication resulting from the excessive consumption of a food additive. These sugar alcohols are not as easily absorbed as sugar, but they are equally as caloric as sugar, once absorbed. Because of their slow absorption, these sweeteners can cause an osmotic-type diarrhea if excessive amounts happen to be consumed. Several cases have been reported where consumers were ingesting more than 20 g of these sweeteners per day (Taylor and Byron, 1984; Taylor, 2002). The levels of hexitols or sorbitols used in foods vary, but in one case the ingestion of 12 pieces of hard candy over a short period of time provided 36 g of sorbitol and resulted in diarrhea (Taylor and Byron, 1984). Infants are more susceptible than adults to this osmotic diarrhea effect.

Sulfites

Sulfites (sodium and potassium metabisulfte, sodium and potassium bisulfite, sodium sulfite, and sulfur dioxide) are widely used as food additives that serve multiple important technological functions, including antimicrobial agent, inhibitor of enzymatic and nonenzymatic browning, and bleaching agent. A small percentage of the population is known to be highly sensitive to ingestion of sulfites that elicit asthma if sufficient doses are ingested (Taylor *et al.*, 2008).

Tartrazine (FD&C Yellow #5)

Tartrazine, also known as FD&C Yellow #5, is an approved artificial food color that has been widely used in foods and pharmaceuticals for many years. Ingestion of tartrazine is associated with adverse reactions (asthma and chronic hives) in a sensitive subpopulation of consumers (Lockey, 1959). However, unlike the situation with sulfite-induced asthma, the association of tartrazine in the provocation of asthma and chronic uriticaria is controversial. The effects noted in some studies could not be reproduced in others (Bush and Taylor, 2009). Both asthma and chronic urticaria are chronic illnesses whose symptoms tend to flare-up at unpredictable times. In some of the clinical trials on tartrazine, key pharmaceutical agents have been withdrawn from the human subjects before initiation of the tartrazine challenges. If the study is not designed carefully, the flare-up of the asthma or urticaria in such a trial could be due to either the administration of tartrazine or the withdrawal of the medication that controls symptoms. The plethora of poorly designed clinical trials on tartrazine has led several groups to conclude that tartrazine may not actually elicit asthma or chronic urticaria (Bush and Taylor, 2009; Stevenson, 2003).

Olestra™

Olestra, a fat replacer, received food additive approval more recently. Olestra is poorly absorbed and is not metabolized, so it does not provide the calories that would be obtained with fat in similar products. However, ingestion of Olestra has been associated with acute gastrointestinal complaints, including anal leakage in some consumers (Cheskin *et al.*, 1998). The prevalence and seriousness of such complaints is a matter of some controversy (Cheskin *et al.*, 1998). Obviously, many consumers occasionally experience postprandial gastrointestinal maladies that makes the association of such complaints with a particular ingredient rather challenging.

Saccharin

Saccharin was one of the first nonnutritive sweeteners approved for food use. Subsequently, high doses of saccharin were shown to cause bladder cancer in laboratory animals (Munro, 1989). However, the extrapolation of these results to humans, who typically ingest much lower levels of saccharin, has stimulated controversy. Thus, the carcinogenicity of saccharin to humans at typical levels of intake is, at best, uncertain, and saccharin remains on the market in the United States.

Niacin

Niacin is a nutritional additive widely and appropriately viewed as beneficial. But even nutrients can occasionally be associated with adverse reactions. In fact, the Dietary Reference Intakes developed by the U.S. National Academy of Science include tolerable upper intake levels for many of the common micronutrients (Food and Nutrition Board, 1998). Such intake levels are rarely exceeded with foods alone but can be exceeded with dietary supplements.

Excessive consumption of the B vitamin, niacin, can cause an acute onset of flushing, pruritis, rash, and burning or warmth in the skin, especially on the face and upper trunk (DiPalma and Ritchie, 1977), although gastrointestinal discomfort is noted in some patients (Press and Yeager, 1962). Outbreaks have occurred from the excessive enrichment of flour used to make pumpernickel bagels (Campana *et al.*, 1983) or corn meal (Press and Yeager, 1962). These episodes occurred as a result of inaccurate or inadequate labeling of food ingredient containers. The amount of niacin required to elicit such adverse reactions is at least 50 times the recommended dietary allowance (RDA) (Campana *et al.*, 1983; Press and Yeager, 1962). The symptoms of niacin intoxication are acute, self-limited, and without sequelae.

Vitamin A

Vitamin A is also a nutrient additive with well-documented benefits. But excessive intake can elicit adverse reactions. In addition to the example with polar bear liver, the toxicity of

vitamin A can also be illustrated by other more conventional, but also unwise, dietary choices. Vitamin A intoxication occurred in twin infants who were provided a diet consisting largely of pureed chicken livers, pureed carrots, milk, and vitamin supplements (Taylor, 2002). Apparently, the mother of these infants initiated this diet because of her distrust of commercial baby foods. After ingesting this diet for several weeks, both infants began to vomit and developed a skin rash. The symptoms disappeared with institution of a more normal diet. The estimated intake of vitamin A and carotene was 44 000 IU per day compared with the RDA of 1500–4500 IU per day for infants.

Intentional Food Adulterants

Although food additives either have a history of safe use or have been assessed for safety and are approved for use in foods by some regulatory agencies, chemical food adulterants are not approved and their addition is illegal and unscrupulous. Adulterants have not been tested for safety or have not had a long history of safe use. Thus, adulterants have a much higher potential to be hazardous. Although many examples exist from ancient to modern times regarding intentional adulteration of foods (Everstine *et al.*, 2013), a few noteworthy examples, including the toxic oil syndrome, that occurred in Spain several decades ago, the more recent melamine adulteration of infant formula and pet foods in China, and the more mysterious pine mouth syndrome are described here.

Toxic Oil Syndrome

In Spain, in the early 1980s, an epidemic occurred involving more than 10 000 cases and more than 300 deaths that were ultimately linked to the ingestion of unlabeled, illegally marketed cooking oils (Kilbourne *et al.*, 1983; Posada de la Paz *et al.*, 1996). The illicit cooking oil contained denatured oil that was intended for industrial rather than food uses. Apparently, the denaturing process caused the formation of some chemical substance(s) that was responsible for the syndrome. The causative toxin in the oils remains unknown. Fatty acid anilides resulting from the denaturation process are suspected to be at least partially responsible (World Health Organization, 1992).

Toxic oil syndrome was associated with a range of clinical manifestations involving multiple organ systems (World Health Organization, 1992). In the initial phase of the illness, affected individuals experienced fever, chills, headache, tachycardia, cough, chest pain, and pruritis. Physical examinations revealed various skin exanthema, splenomegaly, and generalized adenopathy. Pulmonary infiltrates were noted in 84% of the affected individuals, probably as the result of increased capillary permeability. The intermediate phase of the illness persisted from the second week after onset through the eighth week postingestion and involved gastrointestinal symptoms, primarily abdominal pain, nausea, and diarrhea. At this stage, marked eosinophilia was apparent in 42% of patients accompanied by high IgE levels, thrombocytopenia, abnormal coagulation patterns, and evidence of hepatic dysfunction with abnormal enzymes. Some individuals became jaundiced, and many had hepatomegaly. The late phase of the illness developed in 23% of cases and began after 2 months of illness. The late phase was initially characterized by neuromuscular and joint involvement with later development of vasculitis and a scleroderma-like syndrome. Affected individuals complained of intense muscular pain, edema, and progressive muscular weakness. Some individual experienced muscular atrophy. Neurological involvement included depressed deep tendon reflexes, anesthesia, and dysesthesia. Respiratory problems developed due to neuromuscular weakness and progressed to pulmonary hypertension and thromboembolic phenomena. The scleroderma-like symptoms included Raynaud's phenomenon, sicca syndrome, dysphagia, and contractures due to thickening skin collagen. Vascular lesions were noted in all organs apparently resulting from endothelial proliferation and thrombosis. In the late phase, all patients had antinuclear antibody, and many had antibodies against smooth muscle and skeletal muscle (Rodriguez *et al.*, 1982). These pathological and clinical features point to an autoimmune mechanism for the illness. Since the precise causative agent has not been identified, the prevention of future recurrences of toxic oil syndrome is more difficult to assure. Furthermore, it is unknown whether the toxin might be present in small amounts in other foods and thus might be producing or aggravating other clinical conditions.

Melamine

Melamine (2,4,6-triamino-1,3,5-triazine, **Figure 1**) has been used as an industrial chemical for the manufacturing of plastics, adhesive, fabrics, and flame retardants for many years. Melamine was used as an intentional adulterant of pet foods and dairy products, including infant formula several years ago in China to increase the 'apparent' protein content of these products (Dobson *et al.*, 2008; Ingelfinger, 2008). When analytical methods for nitrogen determination, such as the Kjehdahl and Dumas methods, are used for estimating the protein content of foods, melamine gives a strong positive result. In 2007, wheat gluten from China was adulterated with melamine and that wheat gluten was subsequently used in North America to manufacture pet foods. Because of the exposure to melamine and the related substance, cyanuric acid, a large number of pets suffered renal toxicity and renal failure; many pet dogs and cats died as a result (Dobson *et al.*, 2008). When melamine and cyanuric acid are consumed together, crystals of melamine cyanurate form readily in the kidney tubules leading to acute renal failure (Dobson *et al.*, 2008). The second known instance of melamine adulteration in China occurred in 2008, involving infant formula and other milk products; cyanuric acid was not detected in this episode. As many as 294 000 infants and young children in China were affected by the

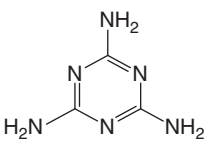


Figure 1 Structure of melamine.

contaminated formula and dairy foods (Ingelfinger, 2008; Wu and Zhang, 2013) leading to 50 000 hospitalizations and at least 6 fatalities. As in the pet food episode, renal toxicity was the primary manifestation. Apparently, melamine alone under some conditions can also lead to the formation of crystals in the renal tubules leading to nephrolithiasis (Wu and Zhang, 2013).

Pine Mouth Syndrome

Pine nuts have been regularly consumed in many countries, although their popularity in North America has increased over the past decade. The Food and Agricultural Organization of the United Nations (FAO) has recognized a list of several dozen species of pine trees that can be considered as suitable sources of pine nuts for food use. Recently, rare cases of an illness called pine mouth syndrome have been reported (Munk, 2012). In this unusual syndrome, affected consumers report losing their sense of taste for several days to weeks after the ingestion of pine nuts. The substance responsible has not yet been identified. However, evidence has emerged that pine nuts from pine trees that are not on the FAO list are implicated in these incidents. Although these incidents are not as deliberate as the toxic oil syndrome or melamine adulteration, pine mouth syndrome serves as a good example of the unintended consequences that can ensue from the use of foods or ingredients that are not well documented as suitable for food use.

Food Contaminants

Foods may also be contaminated with potentially hazardous chemicals from a variety of sources, including natural contaminants, agricultural chemicals, industrial contaminants, and processing-induced contaminants. Mycotoxins from molds, phycotoxins from marine algae, and bacterial toxins serve as the primary categories of natural contaminants. Other contaminants are manmade chemicals that have useful purposes, although they are not intended to occur in foods. These contaminants can include both agricultural and industrial chemicals.

Agricultural Chemicals

Many chemicals are used in modern agricultural practices for a variety of purposes, including insecticides, herbicides, fungicides, fertilizers, and veterinary drugs including antibiotics. Residues of these agrichemicals can be present in raw and processed foods. Public health agencies in various countries evaluate the safety of such chemicals and regulate and monitor their use on plant food products and in food-producing animals (Taylor, 2002).

Insecticides

Insecticides are applied to crops to control insect pests. Several categories of insecticides are used, including organochlorine compounds (dichlorodiphenyltrichloroethane (DDT), chlordane, and others – many of which are now banned), organophosphate compounds (e.g., parathion and malathion), carbamate compounds (e.g., carbaryl and aldicarb), botanical compounds (e.g., nicotine and pyrethrum), and inorganic compounds (e.g., arsenicals).

Low residual levels of insecticides occur in foods. Accordingly, insecticide residues in foods are not particularly hazardous, especially on an acute basis when these chemicals are used properly. Certainly, large doses of insecticides can be hazardous to humans. Several categories of insecticides, such as the organophosphates and carbamates, are neurotoxic. These chemicals are cholinesterase inhibitors and act by blocking synaptic nerve transmission. However, these chemicals dissipate quickly in the environment. Thus, the primary risk involves agricultural workers (pesticide applicators) and that risk can be minimized by use of appropriate protective measures. Insecticide residues in foods pose a low degree of hazard for several reasons: (1) the level of exposure is very low, (2) some insecticides are not very toxic to humans, (3) some insecticides decompose rapidly in the environment, and (4) many different insecticides are used, which limits exposure to any one particular insecticide (Taylor, 2002). Most of the rather rare acute food poisoning episodes attributable to pesticide have resulted from the misuse of pesticides, including contamination of foods during storage and transport, the use of pesticides in food preparation due to their mistaken identity as common food ingredients such as sugar and salt, and their misuse in agricultural practice on crops for which they are not intended to be used (Ferrer and Cabral, 1991).

The agricultural misuse of aldicarb serves as one of the best examples of an acute food poisoning episode associated with pesticides. An outbreak of aldicarb intoxication from watermelons occurred on the West Coast in 1985 (Green *et al.*, 1987). However, the use of aldicarb on watermelons is actually illegal because excessive levels of aldicarb become concentrated in the edible portion of the melon. In this episode, several farmers misused aldicarb by applying it to watermelons. Subsequently, consumers became acutely ill from eating those watermelons. The illegal aldicarb residues were discovered, leading to a watermelon recall and the destruction of thousands of watermelons. The outbreak involved a total of 1373 illness reports with 78% classified as probable or possible aldicarb poisoning cases, making this episode the largest known outbreak of pesticide poisoning in North America (Green *et al.*, 1987; Goldman *et al.*, 1990). The symptoms of aldicarb intoxication include nausea, vomiting, diarrhea, and mild neurological manifestations, such as dizziness, headache, blurred vision, and loss of balance (Green *et al.*, 1987; Goldman *et al.*, 1990; Goes *et al.*, 1980). Although the watermelon episode was larger, aldicarb has also been involved in a smaller outbreak associated with the ingestion of hydroponically grown cucumbers (Goes *et al.*, 1980).

Although acute intoxications from insecticide residues in foods are rare, long-standing concerns have been raised about the possible chronic toxicity associated with pesticide residues in foods (Concon, 1988). DDT, for example, is a known animal carcinogen. Furthermore, organochlorine insecticides, such as DDT, are quite persistent in the environment and have been associated with undesirable environmental consequences, including eggshell thinning in birds. Because of the

health and environmental concerns, many organochlorine pesticides have been banned or allowed for use only under very restricted conditions. Despite the concerns, the evidence that the low residual amounts of insecticides on foods present a carcinogenic risk to human consumers is not particularly strong.

Recently, genetically engineered, insect-resistant crops, especially corn, have been developed. These crops contain a novel gene that produces a naturally occurring insecticidal protein toxin from *Bacillus thuriengensis* (Bt). Bt toxins have been externally applied to crops, especially in organic agriculture for decades. In the case of the genetically engineered Bt corn, the Bt proteins are expressed within the corn plant. The Bt proteins produced by the genetically engineered crops have been thoroughly examined and appear to be quite safe for human consumption (Sanders *et al.*, 1998).

Herbicides

Several categories of herbicides are applied to agricultural crops to control the growth of weeds, including chlorophenoxy compounds (e.g., 2,4-D), dinitrophenols (e.g., dinitroorthocresol), bipyridyl compounds (e.g., paraquat), substituted ureas (e.g., monuron), carbamates (e.g., propham), and triazines (e.g., simazine).

Herbicides tend to be selectively toxic to plants or even certain types of plants. Consequently, herbicide residues in foods do not present any hazard to consumers in the vast majority of circumstances. Food poisoning incidents have never resulted from the proper use of herbicides on food crops. The lack of hazard from herbicide residues is associated with the low level of exposure, their low degree of toxicity to humans and selective toxicity toward plants, and the use of many different herbicides that limits exposure to any particular herbicide (Taylor, 2002).

Although most herbicides are selectively toxic to plants, the bipyridyl compounds are an exception. The bypryridyl herbicides including diquat and paraquat are not selectively toxic to plants and are actually rather toxic to humans. In humans, the bipyridyl herbicides tend to exert their toxic effects on the lungs (Taylor *et al.*, 1992). However, no food poisoning incidents have ever been attributed to inappropriate use of the bipyridyl compounds.

Fungicides

Fungicides curtail the growth of molds on food crops. Important fungicide categories include captan, folpet, dithiocarbamates, pentachlorophenol, and the mercurials. The hazards from foodborne fungicides are miniscule because exposure is quite low, most fungicides do not accumulate in the environment, and fungicides are typically not very toxic (Taylor, 2002). However, the mercurial compounds and hexachlorobenzene are exceptions and do present some risk to consumers in certain circumstances.

Mercurial fungicides are often used to treat seed grains to prevent mold growth during storage. Seed grains treated with mercurial fungicides are typically colored pink and are intended solely for planting. However, especially in times of famine, consumers are tempted to eat the seed grain. On the occasions where consumers have eaten these mercury-treated seed grains, they have developed mercury poisoning sometimes even resulting in deaths (Ferrer and Cabral, 1991). Mild cases of mercury intoxication are more typical and are manifested in gastrointestinal symptoms, such as abdominal cramps, nausea, vomiting, and diarrhea, and dermal symptoms, such as acrodynia and itching (Ferrer and Cabral, 1991).

Hexachlorobenzene is another fungicide used to treat seed grains to prevent mold growth during storage. A massive outbreak of hexachlorobenzene poisoning affecting more than 3000 individuals occurred in Turkey between 1955 and 1959 (Schmid, 1960). This incident is the most massive outbreak of pesticide poisoning in recorded history. In this episode, the symptoms were quite severe with a 10% mortality rate, porphyria cutanea tarda, ulcerated skin lesions, alopecia, porphyrinuria, hepatomegaly, and thyroid enlargement (Schmid, 1960).

Fertilizers

Fertilizers are widely applied to agricultural crop land and are typically combinations of nitrogen and phosphorus compounds. Nitrogen fertilizers are oxidized to nitrate and nitrite in the soil. Both nitrate and nitrite are hazardous to humans, especially infants, if ingested in large amounts (Taylor, 2002). Fertilizers typically present little, if any, risk to consumers. However, some plants, including spinach, can accumulate nitrate to hazardous levels if allowed to grow on overfertilized fields (Fassett, 1973). Because nitrite is more toxic than nitrate, the situation worsens if nitrate-reducing bacteria are allowed to proliferate on these foods. As an example of the effects of nitrate-reducing bacteria, an incident occurred with carrot juice that was improperly stored allowing the proliferation of nitrate-reducing bacteria and the accumulation of hazardous levels of nitrite (Keating *et al.*, 1973). In low doses, the symptoms of nitrite toxicity include flushing of the face and extremities, gastrointestinal discomfort, and headache; in larger doses, cyanosis, methemoglobinemia, nausea, vomiting, abdominal pain, and collapse can occur (Fassett, 1973). Death can result with an estimated lethal dose of nitrite of approximately 1 g in adults (Fassett, 1973).

Veterinary Drugs and Antibiotics

Veterinary drugs are used to treat a variety of conditions in food-producing animals. If properly used, the levels of veterinary drug residues in foods will typically be quite low, and acute food poisoning incidents would not have occurred as a result of properly used veterinary drugs and antibiotics (Taylor, 2002). However, concerns have arisen especially with respect to the use of antibiotics. Penicillin, a common antibiotic used in both veterinary and human medicine, serves as a good example. Some consumers are allergic to penicillin, having been sensitized as a result of its use in human medicine. Are penicillin-allergic consumers at any risk from exposure to penicillin residues that might exist in the food products obtained from penicillin-treated animals? The likelihood of allergic reactions to the very low levels of penicillin

residues found in animal food products is quite remote (Dewdney and Edwards, 1984).

Chemicals Migrating from Packaging Materials and Containers

Foods are often packaged for convenience, shelf stability, and protection from microbial pathogens and insects. Food packages and containers are made from chemical components. Under certain circumstances, some of these chemicals can migrate from the packaging material into the edible portion of the foods. A variety of chemicals, including plastic monomers, plasticizers, stabilizers, printing inks, and others, do migrate at extremely low levels into foods, but these packaging migrants do not typically pose a significant hazard to consumers. Heavy metals, including lead, zinc, tin, and others, can pose a hazard to consumers under certain circumstances (Hughes *et al.*, 1977). More recently, concerns have arisen about the potential chronic toxicity of bisphenol A migrating from packaging materials into foods (NTP-CERHR, 2008).

Bisphenol A

Bisphenol A (BPA) is a monomer used in the manufacture of plastics. BPA has been used in the production of polycarbonate resins for baby bottles and water bottles and in the epoxy resins used as the internal linings of cans for soft drinks and beer. Residues of BPA can migrate into foods and beverages stored in containers containing BPA (NTP-CERHR, 2008). The National Toxicology Program (NTP) in the United States has indicated that some concerns exist for adverse effects on the brain, behavior, and prostate glands in fetuses, infants, and children at current BPA exposure levels (NTP-CERHR, 2008). Considerable debate exists relative to the magnitude of the risk associated with these levels of exposure and little concern exists for any risk to exposed adults. However, efforts are being made to lessen the extent of exposure to BPA, although the safety and efficacy of alternative products are also of concern.

Lead

Environmental exposure to lead has been a persistent and significant public health concern. However, exposure to lead via foods as a percentage of the overall environmental exposure to lead has always been comparatively modest. Historically, the migration of lead from Pb-soldered cans was a source of some concern, but Pb-soldered cans have been successfully and completely phased out of use in the United States. But some concerns remain, principally the occasional use of lead-based glazes on pottery or paint on glassware that may come in contact with acidic foods or beverages. The acid leaches lead from the glaze or paint into the food or beverage. Lead is a well-known toxicant that can affect the nervous system, kidney, and bone.

Tin

The metal cans used for food storage are primarily constructed from tin plate. These inner surfaces of the tin plate cans are lined with a lacquer material when the cans are used for acidic foods or beverages. If unlacquered cans happen to be used for acidic food products, such as tomato juice or fruit cocktail, tin can be leached into the food or beverage, resulting in cases of acute tin intoxication (Barker and Runte, 1972). Tin is poorly absorbed, so the primary symptoms occur in the gastrointestinal tract (bloating, nausea, abdominal cramps, vomiting, and diarrhea) and occur 30 min to 2 h after consumption of the acidic product (Barker and Runte, 1972).

Zinc

Galvanized containers are inappropriate for the storage of acidic foods or beverages because zinc can leach into the food or beverage, resulting in acute zinc intoxication (Hughes *et al.*, 1977; Brown *et al.*, 1964). Fruit punch and tomato juice have been involved in zinc intoxication episodes (Hughes *et al.*, 1977). Zinc is a potent emetic. The symptoms of zinc intoxication include irritation of the mouth, throat, and abdomen; nausea; vomiting; dizziness; and collapse (Taylor, 2002).

Industrial Chemicals

Occasionally, industrial and environmental pollutants can migrate into foods. Usually, the amounts are rather small and inconsequential from a health perspective. However, the potential exists for hazardous levels of such chemicals to enter the food supply on rare occasions and these incidents can have devastating consequences from both a health and economic perspective.

Polychlorinated Biphenyls and Polybrominated Biphenyls

Polychlorinated biphenyls (PCBs) are frequently used in transformer fluid, whereas polybrominated biphenyls (PBBs) are commonly used as fire retardants. PCBs and PBBs are quite persistent in the environment and are considered as toxic pollutants from industrial practices. These compounds are fat soluble so they tend to accumulate in the fat depots of various organisms; concentrations often magnify upward along the food chain. PCBs and PBBs are not particularly worrisome as acute toxicants. However, because PCBs and PBBs are deposited in adipose tissue, they are only very slowly eliminated from the body. Thus, the chronic effects of exposure to these contaminants in foods are of concern. Food contamination with PCBs and PBBs has occurred on several occasions (Taylor, 2002). PBBs were involved in an infamous industrial contamination incident that involved the accidental contamination of dairy feed in Michigan (Fries, 1985). As PBBs are fat soluble, they would tend to accumulate in fat-containing foods, including whole milk. The incident resulted in the destruction of many cows and their milk. Although some consumers were most likely exposed in the early stages of this incident, no health consequences have been clearly linked to the incident. However, the economic impact was considerable. With PCBs, the most noteworthy incident did involve cases of human illness. The PCB incident was associated with the consumption of contaminated rice bran oil in Japan (Kuratsune *et al.*, 1972). The rice bran oil was contaminated

from a leaking heat exchanger that was used to deodorize the oil. The resulting syndrome was called yusho (meaning 'oil disease') by the Japanese. Yusho was characterized by chloracne, weakness, numbness of limbs, swelling of eyelids, discharges from the eyes, dark skin pigmentation, and liver damage (Kuratsune *et al.*, 1972; Higuchi, 1976). The acute symptoms were evident at exposure doses as low as 0.5 g, but chronic effects were noted in many of the victims and persisted for up to 8 years or more following exposure. The chronic symptoms included chloracne, menstrual disturbances, fatigue, headache, fever, cough, digestive disturbances, and numbness of the extremities (Kuratsune *et al.*, 1972; Higuchi, 1976). Because of the widespread use of PBBs and PCBs, industrial contamination incidents have the potential to continue to occur periodically. Hopefully, few will have the human toll experienced in the yusho episode.

Mercury

Another classic example of food contamination from industrial pollutants was the Minamata episode that also occurred in Japan. The Minamata disease episode occurred over a number of years and resulted from an industrial firm located on the shores of Minamata Bay in Japan that dumped mercury-containing wastes into the bay from 1953 until the early 1960s. Bacteria in the bay sediment converted the inorganic mercury into highly toxic, organic methylmercury. Elemental mercury is poorly absorbed from the gastrointestinal tract, whereas organomercury compounds, including methylmercury, are much more efficiently absorbed and are thus more toxic as food contaminants. The human illnesses occurred from consumption of fish from the bay that had become contaminated with methylmercury. More than 1200 cases of mercury intoxication occurred among consumers of Minamata Bay fish (Kurland *et al.*, 1960). The symptoms of mercury intoxication include tremors, other neurotoxic effects, and kidney failure.

Gulf of Mexico Oil Spill

In 2010, a massive oil spill occurred in the Gulf of Mexico from a ruptured oil well. As the Gulf of Mexico is a very rich source of seafood, concerns arose about contamination of various seafood products with the oil and its component chemicals (Genauldi *et al.*, 2013). Seafood harvests were temporarily halted. No illnesses were documented. However, economic consequences were considerable and demonstrate that even the threat of food contamination with industrial pollutants can be disruptive. Many challenges exist for assessment of the risk/safety of seafoods after an oil spill (Genauldi *et al.*, 2013; Gilroy, 2000).

Natural Contaminants

Natural sources such as toxigenic bacteria, mycotoxin-producing molds, and phycotoxin-producing algae are among the contaminants that have the greatest impact on human health.

Bacterial Toxins

Pathogenic bacteria typically cause foodborne disease by the infectious route. The mechanism of foodborne infectious disease involves invasion of cells and tissues, multiplication, and symptoms occurring as a result of cellular injury, inflammation, and disturbance of key physiological processes. Foodborne infectious agents should be viewed as distinct from food toxicology because the causative agents are living microorganisms. However, some foodborne bacteria are toxigenic and produce exogenous toxins in foods before they are eaten. The ingestion of these toxins initiates the disease process even if the bacteria are destroyed in processing or preparation. Thus, bacterial toxins are properly discussed as part of food toxicology. Several examples of bacterial intoxications are the staphylococcal enterotoxins, the botulinal toxins, histamine, and tetrodotoxin.

Staphylococcal Enterotoxins

The staphylococcal enterotoxins are produced in foods by certain strains of *Staphylococcus aureus* (Hennekinnie *et al.*, 2012) that grow on foods under certain conditions such as temperature between 10 and 45 °C and produce the enterotoxin during growth. Ingestion of the staphylococcal enterotoxins causes nausea and vomiting with a rapid onset time of 1–6 h. Staphylococcal food poisoning is a very common form of foodborne disease. The provoking dose of the staphylococcal enterotoxins is quite low, as ingestion of low microgram levels is sufficient to elicit symptoms (Hennekinnie *et al.*, 2012). Nine distinct, but structurally related, types of enterotoxins have been identified as being produced by various strains of *S. aureus* (Balaban and Rasooly, 2000). The staphylococcal enterotoxins are small proteins with molecular weights of 25 000–29 000 Da. On ingestion, the staphylococcal enterotoxins are resistant to digestion and are able to enter the small intestine without much hydrolysis. The enterotoxins bind to some as yet unidentified sites in the small intestine and transmit a signal to the vomiting center in the brain. The enterotoxins are quite heat resistant. Accordingly, staphylococcal food poisoning is often associated with foods cooked after improper storage that allowed the proliferation of *S. aureus* and enterotoxin production.

Botulism

Botulinal toxins are potent neurotoxins produced in foods under anaerobic conditions during growth of *Clostridium botulinum* (Parkinson and Ito, 2002). Toxin formation occurs in underprocessed canned foods. The commercial canning process is predicated on the destruction of *C. botulinum* and its spores so that the spores will not germinate, grow, and produce toxin on storage of the canned product. Canned foods are especially susceptible because of the anaerobic conditions. Seven different toxin-producing strains of *C. botulinum* have been identified, but types A, B, and E are the strains most commonly associated with foodborne illness (Parkinson and Ito, 2002). The botulinal toxins are proteins with a molecular mass of approximately 150 kDa (Parkinson and Ito, 2002). The botulinal toxins exert their neurotoxic effect by inhibiting the release of acetylcholine at the nerve synapses. Thus, the

peripheral nervous system is affected. Botulinal toxins are among the most potent toxins known to humans. In cases of botulism, clinical symptoms begin to develop 12–48 h after exposure to the toxin with weakness, dizziness, and mouth dryness occasionally accompanied by nausea and vomiting. Neurological symptoms follow, including blurred vision, inability to swallow, aphasia, and weakness of the skeletal muscles. Symptoms can ultimately progress to respiratory paralysis and death. The vegetative cell of *C. botulinum* and the botulinal toxins are easily destroyed by heat, but the spores are heat resistant. When thermal processing (canning) is not properly performed, spores will survive, germinate, and grow if suitable anaerobic conditions exist (Parkinson and Ito, 2002).

Infant botulism is a different but related illness where the spores enter the gastrointestinal system early in life before competitive intestinal microflora are in place to resist their germination and growth (Parkinson and Ito, 2002). The growth of *C. botulinum* ensues in the intestinal tract. Toxin production then occurs in the intestinal tract of the infant and causes severe illness. Infant botulism is avoided by limiting the intake of spores by infants. Honey is a frequent source of the spores in the infant diet (Parkinson and Ito, 2002).

Bacillus cereus Toxins

Bacillus cereus is a spore-forming microorganism capable of producing two types of toxins: emetic and diarrhetic (Schoeni and Wong, 2005). *Bacillus cereus* typically grows in foods, such as rice, soups, and sauces, that are stored improperly at elevated temperatures after cooking. The emetic toxin causes nausea and vomiting with an onset time of 30 min to 6 h after ingestion. The diarrhetic toxin causes abdominal cramping and diarrhea with an onset time of 6–15 h after ingestion.

Histamine or Scombroid Fish Poisoning

Histamine poisoning is an allergy-like intoxication most frequently associated with ingestion of certain types of fish from the families Scomberesocidae and Scombridae, such as tuna, skipjack, mackerel, and bonito (Hungerford, 2010). Hence, the syndrome is often called scombroid fish poisoning. However, scombroid fish poisoning is a bit of a misnomer because certain types of nonscombroid fish are also commonly involved, including mahi-mahi, bluefish, jack mackerel, sardines, yellowtail, anchovies, and herring. Cheese can also occasionally be involved, especially Swiss cheese. Histamine poisoning occurs on a worldwide scale with several hundred cases reported annually to public health agencies (Hungerford, 2010).

Histamine formation in foods is associated with the growth of bacteria possessing the enzyme histidine decarboxylase that is able to convert the amino acid histidine into histamine. Few bacterial species are capable of prolific histamine formation necessary to develop hazardous levels food products. In fish, *Morganella morganii* is often implicated. In fish, histamine formation occurs when fish are not properly frozen or refrigerated. In cheese, histamine formation is associated with the growth of certain species of lactobacilli (Sumner *et al.*, 1985). Swiss cheese is susceptible because milk is often not pasteurized before making that type of cheese.

The symptoms of histamine poisoning resemble those experienced during an allergic reaction. As histamine is a primary mediator released from mast cells during IgE-mediated allergic reactions, the reasons for the similarities are obvious. Gastrointestinal symptoms, such as nausea, vomiting, diarrhea, and abdominal cramps, are common. Tingling, itching, and burning sensations often occur in the mouth. Cutaneous symptoms, including flushing, urticaria, angioedema, and other itchy rashes, appear as well. Hypotension is a common manifestation. Other common symptoms include headache and palpitations. Symptoms of histamine poisoning typically appear within minutes to a few hours after ingestion of the offending food. Histamine intoxication is a self-limited illness and symptoms usually subside within a few hours even without treatment. Treatment with antihistamine drugs leads to prompt resolution.

Tetrodotoxin or Pufferfish Poisoning

Tetrodotoxin poisoning is associated with the ingestion of pufferfish, also sometimes known as blowfish, which belongs mostly to the genus *Fugu* (Hwang and Noguchi, 2007). Because of the frequently encountered toxicity of pufferfish, these species are not allowed for commercial sale in some countries. Pufferfish poisoning occurs primarily in Japan and China, because those are the primary areas of the world where pufferfish are frequently consumed and considered as a delicacy (Hwang and Noguchi, 2007). Although more than 30 species of pufferfish are found worldwide, most species are not considered to be toxic (Taylor, 1988) perhaps because the toxin is episodically present. The toxin is a potent neurotoxin called tetrodotoxin (Taylor, 1988; Hwang and Noguchi, 2007). For many years, tetrodotoxin was thought to be produced by the fish. More recently, new evidence suggests that marine bacteria may be the original source of the toxins (Yasumoto *et al.*, 1986). Tetrodotoxins are heat stable and, like the saxitoxins, act by blocking the sodium channels in nerve cell membranes (Taylor, 1988). The symptoms of tetrodotoxin poisoning usually begin with a tingling sensation of the fingers, toes, lips, and tongue, followed by nausea, vomiting, diarrhea, and epigastric pain progressing to twitching, tremors, ataxia, paralysis, and sometimes death (Mines *et al.*, 1997). A fatality rate of approximately 60% occurs in untreated cases (Mines *et al.*, 1997). The tetrodotoxins accumulate in the liver, viscera, and roe of the pufferfish. Careful cleaning of the fish, before ingestion of the edible muscle, safeguards against tetrodotoxin intoxication (Taylor, 1988). Although tetrodotoxin was once thought to be a single chemical entity (Taylor, 1988), it is now recognized that various bacteria which belong to species such as *Altermonas*, *Vibrio*, and others can produce different but related forms of tetrodotoxin that vary in potency (Yasumoto *et al.*, 1986). Even though tetrodotoxin poisoning is primarily associated with *Fugu* fishes, similar if not identical toxins occur in newts, frogs, marine snails, octopuses, crabs, starfishes, and other marine species (Wakely *et al.*, 1966).

Mycotoxins

A wide variety of molds exist in the environment and many of these molds can grow on foods. Some of the foodborne molds

are able to produce toxic substances called mycotoxins as they grow on foods (Richard, 2007). The toxic properties of mycotoxins are recognized either from their effects on humans or on one or more economically important animal species. In some cases, the toxicity of the mycotoxins has not been clearly established in humans, whereas with others, the toxicity to humans is clearly documented. Aflatoxins and fumonisins serve as the primary examples, although many other mycotoxins have also been identified in foods.

The aflatoxins are produced by certain species of *Aspergillus* molds, primarily by *Aspergillus flavus* and *Aspergillus parasiticus*, molds that often contaminate peanuts and corn (Richard, 2007). Aflatoxins B and G are the forms that have been identified in legumes and cereals. Dairy cows fed aflatoxin-contaminated grains or oilseeds are known to have a related form of aflatoxin, aflatoxin M, in their milk. The aflatoxins are potent carcinogens, especially affecting the liver (Richard, 2007). The significance of aflatoxins in human carcinogenesis remains uncertain, although humans with preexisting liver conditions, such as hepatitis, appear to be among the most susceptible. Aflatoxins are among the most potent animal carcinogens known.

Fusarium molds produce several different mycotoxins, including the trichothecenes, fumonisins, and zearalenone (Richard, 2007). Fumonisins are produced primarily by *Fusarium verticillioides* and several other *Fusarium species* (Richard, 2007), *Fusarium* molds that grow especially well on corn but can also contaminate other grains and soybeans. The effects of fumonisins were first noted in horses where the fumonisins have been implicated in equine leukoencephalomalacia. This fatal neurotoxic syndrome is characterized by extensive necrosis of the white matter in the brain of affected horses (Richard, 2007). Fumonisins are also known rodent carcinogens (Howard *et al.*, 2001). The effects of fumonisins on humans remain unknown, but low-level contamination of grains with fumonisins seems to be fairly common.

Algal Toxins (Phycotoxins)

Marine algae proliferate widely in the ocean and especially in near-shore and reef environments. More than 4000 species of marine phytoplankton are known to exist. It is estimated that 60–80 of these marine algae species are capable of producing phycotoxins (Smayda, 1997). The phycotoxins are ingested by shellfish and fish, and the phycotoxins can be transferred to the edible portions of the seafoods. These marine algae often exist in a dormant state as cysts in the marine sediments. When ideal environmental conditions exist, the algae will bloom creating conditions where the fish or shellfish will become hazardous to ingest. Thus, fish and shellfish may be safe to ingest during certain times and hazardous at other times. The fish and shellfish are only toxic in circumstances where they have the opportunity to feed on toxic marine algae. These algal toxins pass through the food chain from smaller organisms to larger ones. Several acute illnesses are associated with such seafoods, including ciguatera poisoning, paralytic shellfish poisoning, amnesic shellfish poisoning, and tetrodotoxin poisoning (James *et al.*, 2010; Dickey and Plakas, 2010; Taylor, 1988).

Ciguatera Poisoning

Ciguatera poisoning is probably the most common cause of foodborne disease of chemical etiology on a worldwide scale. This foodborne illness is common throughout the Caribbean and much of the Pacific Ocean. However, ciguatera poisoning is now encountered around the world due to the improved distribution of fish (Dickey and Plakas, 2010; Taylor, 1988). In the United States, the illness occurs most frequently in Florida, Hawaii, and the Virgin Islands (Taylor, 1988). Ciguatera poisoning results from the ingestion of fish that have fed on toxic dinoflagellate algae. The toxins involved in ciguatera poisoning are initially acquired by small fish that feed on the poisonous planktonic algae but then pass to larger fishes that feed on the smaller fishes (Taylor, 1988). Several species of dinoflagellate algae appear able to produce toxins of the type associated with ciguatera poisoning; *Gambierdiscus toxicus* is one of the most prominent species (Dickey and Plakas, 2010; Taylor, 1988). Fish that inhabit reef and shore areas in temperate regions, such as grouper, red snapper, barracuda, amberjack, kingfish, Spanish mackerel, mahi-mahi, sea bass, surgeon fish, and eels, are the most commonly implicated species, although many different fish species can likely be involved (Taylor, 1988).

The major toxin involved in ciguatera poisoning is a lipid-soluble, polyether, ionophoric compound with a molecular weight of 1112, known as ciguatoxin (Dickey and Plakas, 2010). However, several toxins have been implicated as well (Dickey and Plakas, 2010). The toxins accumulate principally in the liver and viscera of the fish, but sufficient amounts are found in the muscle tissues to result in ciguatera poisoning among humans ingesting these fish (Taylor, 1988). The toxins are heat stable and thus unaffected by processing or cooking practices (Taylor, 1988).

Ciguatera poisoning can involve variable symptoms that perhaps confirm the role of several different dinoflagellate algae and several different toxins in this syndrome (Taylor, 1988). Gastrointestinal and neurological manifestations predominate (Taylor, 1988; Farstad and Chow, 2001). Gastrointestinal symptoms (nausea, vomiting, diarrhea, and abdominal cramps) predominate in some cases, whereas the neurological symptoms (dysesthesia, paresthesia – especially in the perioral region and extremities – pruritis, vertigo, muscle weakness, malaise, headache, and myalgia) predominate in others (Farstad and Chow, 2001). A peculiar reversal of hot and cold sensations occurs in approximately 65% of all patients (Farstad and Chow, 2001). In severe cases, the neurological manifestations can progress to delirium, pruritis, dyspnea, prostration, brachycardia, and coma (Farstad and Chow, 2001). Many patients do recover within a period of a few days or weeks. However, treatment can be difficult, and some deaths from cardiovascular collapse have been encountered (Taylor, 1988; Farstad and Chow, 2001).

Paralytic Shellfish Poisoning

Paralytic shellfish poisoning occurs with less frequency than ciguatera poisoning but has the potential to be an even more serious illness. Annually on a worldwide scale, an estimated 2000 human cases occur (Van Dolah, 2000). The implicated shellfish become toxic by ingestion of toxic dinoflagellate

algae that belong to three genera: *Alexandrium*, *Gymnodinium*, and *Pyrodinium* (Van Dolah, 2000). Blooms of the toxic dinoflagellates are quite sporadic, so most affected shellfish are hazardous only during the times of the blooms (Taylor, 1988). In most shellfish species, the toxins are cleared from their system within a few weeks after the end of the dinoflagellate bloom (Taylor, 1988). However, a few species, such as the Alaskan butter clam, seem to retain the toxin for long periods (Taylor, 1988). Paralytic shellfish poisoning can involve a range of molluscan shellfish, such as clams, mussels, cockles, and scallops (Taylor, 1988; Van Dolah, 2000). The molluscan shellfish are filter feeders and concentrate the toxins from the dinoflagellate algae as they feed. The causative agents involved in paralytic shellfish poisoning are neurotoxins known as saxitoxins, which act by binding to and blocking the sodium channels in nerve membranes (Shimizu, 1988; Taylor, 1988). Saxitoxins are heat stable, so processing and cooking have no effect on their toxicity (Taylor, 1988).

Saxitoxins are very potent neurotoxins, and the symptoms of paralytic shellfish poisoning are reflective of neurotoxicity with tingling and numbness of the lips, tongue, and fingertips followed by numbness in the legs, arms, and neck; ataxia; giddiness; staggering; drowsiness; and incoherent speech progressing to aphasia, rash, fever, and respiratory and muscular paralysis (Taylor, 1988). Death from respiratory failure occurs with some frequency, usually within 2–12 h depending on the dose ingested (Taylor, 1988). No antidotes exist, but the prognosis is good if the victim survives the first 24 h of the illness (Taylor, 1988).

Amnesic Shellfish Poisoning

Amnesic shellfish poisoning (ASP) is a more recently recognized phycotoxicosis. The first recognized outbreak of ASP occurred in Canada in 1987 from the ingestion of mussels harvested near the shore of Prince Edward Island (Perl *et al.*, 1990). This outbreak involved more than 100 cases and at least 4 deaths (Perl *et al.*, 1990; Teitelbaum *et al.*, 1990). The source of the toxin was a dinoflagellate subsequently identified as *Pseudonitzschia* spp., which was blooming in an isolated area of Prince Edward Island at the time of the outbreak (Jeffery *et al.*, 2004). The toxin was identified as domoic acid, a neuroexcitatory amino acid (Jeffery *et al.*, 2004). ASP is characterized by gastrointestinal symptoms and unusual neurological abnormalities (Perl *et al.*, 1990). The gastrointestinal symptoms (vomiting, abdominal cramps, and diarrhea) occur in the first 24 h after onset of the illness. The neurological symptoms are more severe and ensue within 48 h after onset. These symptoms include severe incapacitating headaches, confusion, loss of short-term memory, and, in a few cases, seizures and coma. Severely affected patients who did not die experienced prolonged neurological sequelae, including memory deficits and motor or sensorimotor neuronopathy or axonopathy (Teitelbaum *et al.*, 1990).

Processing-Induced Toxicants

Potentially toxic substances can form under certain processing conditions, especially heat treatments. As processing treatments prolong the shelf life of foods and guard against microbial hazards, the development of processing-induced toxicants is a classic risk versus benefit puzzle. Several examples of processing-induced toxicants, such as heterocyclic aromatic amines, hydroxymethylfurfural, advanced glycation end products, nitrosamines, and acrylamide, form as a result of food processing and preservation commonly used in the food industry as well as in the home. Processing-induced toxicants tend to raise chronic toxicity concerns. Acute symptoms are not known to occur from this category of foodborne toxicants. Acrylamide formation occurs in foods having high levels of carbohydrates and asparagine residues when heated under certain condition. Acrylamide serves as a good example of processing-induced toxicants.

Acrylamide

Acrylamide (2-propenamide) is colorless and odorless and is used in manufacturing polyacrylamide and acrylamide copolymers employed in the paper and textile industries, as flocculants in wastewater treatment, as soil conditioning agents, and as grouting agents for construction of dam foundations, tunnels, and sewers (Mills *et al.*, 2009; Zhang and Zhang, 2007). In the late 1990s in Sweden, researchers investigating the occurrence of neurotoxic symptoms in railway tunnel makers found high levels of acrylamide hemoglobin adducts in blood samples of the workers. Acrylamide polymer had been used as a sealant in the tunnel and apparently some of this sealant entered a nearby stream, leading to the contamination of the local water. Dead fish and paralyzed cattle were also found in the immediate area and fish and cattle were also found to have higher levels of these adducts (Mills *et al.*, 2009). As the adducts were also found in control samples, the researchers questioned whether cooked foods could be the source of acrylamide exposure in humans. An animal study showed that rats fed fried feed had higher levels of the acrylamide hemoglobin adducts than rats fed a standard diet (Tareke *et al.*, 2000). Subsequently, other researchers detected acrylamide in foods with French fries, potato chips, breakfast cereals, cookies, brewed coffee, breads and toasts, and pies and cakes having among the highest levels (Roach *et al.*, 2003).

Acrylamide forms in foods during heating and as a by-product of the Maillard reaction, which leads to desirable color, flavor, and aroma development in cooked foods. Acrylamide forms due to a reaction between the amino acid, asparagine, and reducing sugars, such as glucose and fructose, under elevated temperatures (above 120 °C) in low moisture conditions. The highest levels of acrylamide are found in fried, baked, and broiled foods (Tareke *et al.*, 2002). Acrylamide does not form in foods that are boiled or microwaved (Tareke *et al.*, 2002). Acrylamide is rapidly absorbed from the gastrointestinal tract, distributed throughout the body, and metabolized to form glycidamide, which is a reactive epoxide thought to be responsible for the genotoxic effects associated with acrylamide exposure (Mills *et al.*, 2009). Acrylamide is neurotoxic and carcinogenic in animal models, which lead the International Agency for Research on Cancer to classify acrylamide as a category 2A carcinogen (probably carcinogenic to humans). Several epidemiological studies have investigated

the association between oral exposure to acrylamide from food sources and the incidence of several types of cancer in humans, but no association has been found (Mills *et al.*, 2009).

Natural Toxicants

Natural constituents of foods from fungi, plants, and occasionally animals may be hazardous under some circumstances of exposure. Of course, some fungi, plants, and animals should not be consumed as food because of their inherent hazards but are accidentally or intentionally consumed on occasion resulting in foodborne illness. Beyond the poisonous species, many other plants and animals contain levels of naturally occurring toxicants that are probably not hazardous to humans except when abnormally large quantities of such foods are ingested. Other naturally occurring toxicants in certain plants are inactivated or removed during processing or preparation of foods before consumption. However, foodborne illness can result from the failure to adhere to such processing and preparation practices.

Poisonous Animals

Few acutely toxic animal species exist with the possible exception of pufferfish, although the toxin in pufferfish is most likely a naturally occurring contaminant. Furthermore, animal tissues and products are not generally hazardous if ingested in abnormally large quantities, at least not on acute basis with the exception of vitamin A (Taylor, 2002; DiPalma and Ritchie, 1977) as previously discussed. Of course, this statement does not take into account the nutritional concerns with cholesterol and saturated fats. Although overconsumption of cholesterol and saturated fat on a chronic basis may be considered as potentially deleterious to health, these substances are not generally regarded as toxicants. Milk can occasionally contain hazardous substances, but these are typically contaminants that are secreted into the milk after the cow has eaten a poisonous plant (Panter and James, 1990). Ovomucoid, an egg white protein, is a trypsin inhibitor, but this activity is diminished by cooking and ovomucoid does not appear to inhibit human trypsin (Feeney *et al.*, 1969). Molluscan shellfish can contain arsenical compounds but typically at levels that are not considered to be especially hazardous (Falio *et al.*, 2006). Additional examples are difficult to find.

Poisonous Plants

In contrast, many poisonous plants exist in nature (Poppenga, 2010). Plants such as water hemlock and nightshade were classically used to poison one's enemies. The risk of ingestion of poisonous plants is rather low as consumers purchasing foods from commercial sources are usually able to avoid their ingestion. However, intoxications can and do occur among individuals who harvest foods in the wild (Huxtable, 1990). For example, foxglove can be mistakenly identified as comfrey, a popular herb for brewing of herbal tea. Foxglove contains digitalis, a potent cardiotoxic substance and serious cardiovascular symptoms can develop when foxglove is ingested (Dickstein and Kunkel, 1980; Lin *et al.*, 2010). The intentional or unintentional ingestion of poisonous plant species such as foxglove (digitalis), *Nicotiana glauca* (anabasine), and jimsonweed (atropine and other tropane alkaloids), to name but a few can even have fatal consequences (Centers for Disease Control and Prevention, 2010; Steenkamp *et al.*, 2002; Steenkamp *et al.*, 2004). Although digitalis and atropine are both useful pharmaceutical agents, their ingestion from natural sources in uncontrolled doses can be fatal.

Plant food products purchased from commercial sources can cause acute intoxications on rare occasions. For example, a commercial herbal tea known as gordolobo yerba sold to the Mexican American population in Arizona was contaminated with *Senecio longilobis*, a well-known poisonous plant (Stillman *et al.*, 1977). The herbal tea was promoted as a cure for colic, viral infections and nasal congestion in infants. Six infants died from ingestion of the contaminated herbal tea, which contained 1.5% of dry weight of pyrrolizidine alkaloids. One of the deceased infants was estimated to have consumed 66 mg of the alkaloids over a 4-day period. *Senecio* plants contain a group of toxicants known as pyrrolizidine alkaloids (Coulombe, 2003). Acute exposures to hazardous doses of pyrrolizidine alkaloids as in the case of the contaminated herbal tea can cause ascites, hepatomegaly, venoocclusive liver disease, abdominal pain, nausea, vomiting, headache, and diarrhea (Stillman *et al.*, 1977). The infants who died experienced liver failure.

Pyrrolizidine alkaloids can also cause chronic symptoms, including liver cancer and cirrhosis, if ingested in smaller quantities over more extended periods of time (Coulombe, 2003). With such chronic, low-level intake, the effects on the liver are cumulative and irreversible. Several pyrrolizidine alkaloids are well-documented carcinogens in laboratory animals. The chronic ingestion of products containing low levels of potentially carcinogenic pyrrolizidine alkaloids presents unknown carcinogenic risks. Several herbal teas commonly contain lower levels of pyrrolizidine alkaloids that are not typically hazardous on an acute basis. For example, comfrey (*Symphytum officinale*) typically contains a total alkaloid level of 0.003–0.02%, including a pyrrolizidine alkaloid symphytine. It is unknown whether chronic intake of comfrey tea would significantly increase the risk of development of liver cancer.

Thousands of other alkaloids with varying degrees of toxicity are known to occur in plants (Koleva *et al.*, 2012; Rietjens *et al.*, 2005). Some, like the pyrrolizidine alkaloids in *Senecio*, are very hazardous, but others are much less hazardous.

Many of the naturally occurring toxicants in plant-derived foods occur at doses that are not acutely toxic at typical levels of consumption, but that can be toxic when large quantities of the food are eaten. Examples include solanine and chaconine in potatoes, oxalates in spinach and rhubarb, furan compounds in mold-damaged sweet potatoes, and cyanogenic glycosides in lima beans, cassava, and many fruit pits (Rietjens *et al.*, 2005). Because there are so many possible examples, the cyanogenic glycosides serve as an illustrative example (Vetter, 2000). Cyanogenic glycosides release cyanide from enzymatic action occurring during the storage and processing of the foods or on contact with stomach acid. Wild varieties of lima beans

contain high and potentially hazardous levels of cyanogenic glycosides, but the commercial lima bean varieties contain minimal amounts of these cyanogenic glycosides. Commercial lima bean varieties have an HCN yield of ≤ 10 mg per 100 g of lima beans (wet weight). As the lethal oral dose of cyanide for humans is 0.5 mg kg^{-1}, a 70 kg adult would have to ingest 35 mg of cyanide, an amount that would require the ingestion of at least 350 g of lima beans. Such high levels of consumption are quite unlikely, so human illnesses from cyanide intoxication have never been reported from ingestion of commercially harvested lima beans. Wild varieties of lima beans contain much higher levels of the cyanogenic glycosides (up to 300 mg HCN per 100 g). Cyanogneic glycosides also occur in other plants. In Africa and South America, cyanide intoxications have occurred from the consumption of abnormally large quantities of cassava (Vetter, 2000; Cliff *et al.*, 2011). Such episodes occur primarily when other foods are in short supply. Acute cyanide intoxication has also occurred from the ingestion of fruit pits (Morse *et al.*, 1976). The symptoms of cyanide intoxication include a rapid onset of peripheral numbness and dizziness, mental confusion, stupor, cyanosis, twitching, convulsions, coma, and death when sufficient doses are consumed (Vetter, 2000).

Some naturally occurring toxicants in plant-based foods are hazardous only when the foods are eaten raw because processing and preparation inactivate or remove the potentially hazardous substances. For example, raw legumes, including soybeans, contain trypsin inhibitors, lectins, amylase inhibitors, saponins, and various antivitamins (Liener, 1994), potential toxicants that are inactivated during the heating and fermentation processes used with legume-based foods. For example, raw kidney beans contain lectins that are typically inactivated during cooking. In cases where kidney beans were eaten in undercooked form, nausea, vomiting, abdominal pain, and bloody diarrhea resulting from the lectins were encountered (Rodhouse *et al.*, 1990).

Poisonous Mushrooms

Mushrooms are often poisonous, so the harvesting of wild mushrooms can be a hazardous practice. Mushroom poisoning incidents occur periodically around the world (Diaz, 2005). Poisonous mushrooms contain a variety of naturally occurring toxicants (Diaz, 2005; Spoerke, 1994).

Amatoxin and phallotoxin are the most hazardous mushroom toxicants. Amatoxin is characteristically produced by *Amanita phalloides*, the death cap mushroom. Acute amatoxin intoxication occurs in three stages. The first stage begins to develop 6–24 h after ingestion of the mushrooms and is characterized by abdominal pain, nausea, vomiting, diarrhea, and hyperglycemia. The second stage is a short period of remission that follows. In the third and often fatal stage, severe liver and kidney dysfunction leads to hypoglycemia, convulsions, coma, and death. Death resulting from hypoglycemic shock occurs 4–7 days after the onset of symptoms.

Hydrazines are another group of mushroom toxins. Gyromitrin, a hydrazine produced by *Gyromitra esculenta* or false morel mushrooms, causes acute symptoms, including a bloated feeling, nausea, vomiting, watery or bloody diarrhea, abdominal pain, muscle cramps, faintness, and ataxia occurring with a 6–12 h onset time.

Fly agaric (*Amanita muscarina*) produces muscarine, a neurotoxic substance that affects the autonomic nervous system. Symptoms appear rapidly after ingestion of fly agaric and include perspiration, salivation, lacrimation with blurred vision, abdominal cramps, watery diarrhea, constriction of the pupils, hypotension, and a slowed pulse.

Ibotenic acid and muscimol are hallucinogenic, ostensibly exerting their actions on the central nervous system. These toxins cause dizziness, drowsiness followed by hyperkinetic activity, confusion, delerium, incoordination, staggering, muscular spasms, partial amnesia, a coma-like sleep, and hallucinations beginning 30 min to 2 h after ingestion. Fly agaric is also a good source of ibotenic acid and muscimol.

Psilocybin and psilocin are also hallucinogenic substances found in Mexican mushrooms, *Psilocybe mexicana*. The symptoms associated with Mexican mushroom toxins include pleasant or aggressive mood, anxiety, unmotivated laughter and hilarity, compulsive movements, muscle weakness, drowsiness, hallucinations, and sleep beginning within 30–60 min after ingestion of the mushrooms. Recovery is often spontaneous in 5–10 h. However, when the dose of psilocybin and psilocin are sufficiently high, prolonged and severe sequelae, even death, can occur.

Coprine is a mushroom toxin that causes symptoms only when ingested with alcoholic beverages. Coprine is produced by *Coprinus atramentarius*. Symptoms begin within 30 min of ingestion of the mushrooms but only if alcoholic beverages are also consumed simultaneously and include flushing of the neck and face, distension of the veins in the neck, swelling and tingling of the hands, metallic taste, tachycardia, and hypotension progressing to nausea and vomiting. Symptoms persist for up to 5 days.

See also: Food Labeling. Food Safety: Food Analysis Technologies/Techniques

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Forage Crops

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Glossary

Browse Edible plant parts (leaves, bark, and stems) of woody species consumed by grazing animals.
Forage and Herbage Any herbaceous plant that is consumed by livestock.
Greenchop Forage chopped and fed fresh to livestock.
Hay Dried forage, typically baled and stored.
Pasture Cultivated crops grazed by livestock.
Rangeland and grazingland Uncultivated areas grazed by livestock.
Roughage General term incorporating all forages, straws, and fibrous materials such as jute.
Silage Forage that is anaerobically fermented and preserved.
Stover Leafy or stalky material of grain-producing plants used as a forage (e.g., corn stover).
Straw Dried stem material remaining after harvest of a grain crop (e.g., wheat and rice straw).

Introduction

Forages are among the most important crops to mankind, even though harvested fruit, vegetable, grain, and oilseed crops are more widely recognized by urban cultures. Forages make possible the harvesting of solar radiation for the benefit of human nutrition by plants that are then converted into foodstuffs by ruminants and nonruminants, forming one of the oldest food-production systems in human history. Forages are often grown at sites and under conditions where it is not possible to cultivate other crops. Forages have an ancient history but remain vital today.

Forage production systems are highly diverse and directly linked to animal agriculture. Formally, forages include rangeland (forested and nonforested), pastureland (managed and nonmanaged, seasonal, and intensively grazed), harvested forage crops including dried products (hay), fermented forages (silages), and fresh-fed harvested forages (greenchop). They include a wide range of species, including cool- and warm-season grasses; legumes such as alfalfa and clovers; forbs; and grain crops, such as corn, sorghum, soybean, and small grains (oats, wheat, barley, and triticale) that are harvested as forages.

Forage crops, the focus of this article, are differentiated from naturally occurring rangeland and pasture by the degree of human intervention and management. Forages, by definition, generally only have economic value through animal products. In partnership with animal enterprises, forages produce many of the staple foods important to mankind: meats, milk, and fibers, such as wool. Closely related to forage crops are cellulose-producing plants, such as switchgrass, grass straws, and stovers, that produce fibers which can be used for cellulosic biofuels, erosion control, feeds, and animal bedding. Forage crops are sometimes perceived as a lower value component of agriculture but often are among the top revenue-producing components of a region's agricultural output through the production of valuable animal products.

Not insignificantly, forage crops, pastures, and rangeland systems also contribute important environmental services (Wedin and Russelle, 2007; Franzluebbers, 2013; Karlen *et al.*, 2007; Putnam *et al.*, 2001). These include contributions such as protection of soil, air, and water quality, sequestration of soil carbon, cycling of nutrients, absorption of excess nitrate from contaminated water, suppression of weeds, and provision of important wildlife habitat (**Figure 1**).

As high-quality cropland diminishes in relationship to expanding human populations in the twenty-first century, the dual roles of forage crops for both food production and provision of environmental services may be important to the future of agricultural systems. The purpose of this article is to provide a broad background on the role and biology of forage crops in agricultural systems, with an emphasis on harvested forage crops and the principles of forage crop production.

History

> and the earth brought forth grass, and herb yielding seed after its kind… and God saw that it was good
>
> –Genesis, 1–12

Forage crops do not have a complete historical archeological record, due to the difficulty of preserving herbaceous plants compared with seed-bearing crop plants, but it is clear that forages were a key primary producer in early human cultures and were the basis of early agriculture (Barnes and Baylor, 1995; Barnes and Nelson, 2003). Although formal animal domestication did not occur until later, forages were the key basis for food production for hunter-gatherer societies for the vast majority of the history of *Homo sapiens*, with coordinated animal harvests leading to semidomestication (Harlan, 1975; Diamond, 2002). The major grasslands of the world, such as the prairies of North America, the pampas of South America, the steppes of Central Asia, and the velds of Africa, form the historical biological basis for forage systems (Williams, 1980). Forages codeveloped with grazing animals and human societies during periods reaching into antiquity. The formal domestication of goats, sheep, and then cattle can be traced to earlier



Figure 1 Deer in a Washington State alfalfa field. Forage crops are a major component of land use in the United States and provide a range of axillary environmental services, such as wildlife habitat (Photo: Sharla Wagoner).

than 10 000 to 9500 BCE and now to probably 12 000 BCE (Zeder, 2008). Thus, range and forage grasses, legumes, browse, and forbes provided the basis for human nutrition throughout much of the history of civilized man.

However, these historical forage crops were largely made up of native, noncultivated range and short-term seasonal pastureland, as animals were moved from place to place. In terms of true 'farming' (controlled animal production), animal domestication may have proceeded plant domestication by many years, or at least evolved simultaneously. Semicultivated agricultural techniques (via burning, weeding, seeding, or other techniques) were likely to have occurred later and simultaneous with settled cultures of the fertile crescent (Zeder, 2008).

The Need for Conserved Feed

> The most important invention of the last two thousand years was hay. …
>
> –Freeman Dyson, 1999, Institute for Advanced Study, Princeton University

Some might question Dyson's hyperbole that forages were the most important development in 2000 years, but his logic is as follows:

> Without grass in winter you could not have horses, and without horses you could not have urban civilization. Sometime during the so-called dark ages, some unknown genius invented hay, forests were turned into meadows, hay was reaped and stored, and civilization moved north over the Alps. So hay gave birth to Vienna and Paris and London and Berlin, and later to Moscow and New York.
>
> –Dyson, 1999

Dyson may be onto something; there is little doubt that conserved forages were a key technical requirement for settled, stable animal agriculture and therefore towns and cities. Seasonally determined 'booms and busts' of forage availability were (and are) the norm in most grazing grassland systems due to seasonal rainfall patterns or winter cold. Thus, the conservation of forages through drying (hay) and fermentation (silage) were important historical advances to stabilize and sustain agriculture and settled communities. Although movement of livestock for seasonal pasture is still widely practiced, the emergence of forages as managed crops created a reliable local supply of feed without moving livestock long distances for seasonal pastures.

Harvested forages as hay and silage have been components of diversified farms in Europe and Asia from the earliest settled farmsteads. In Great Britain, the scythe and the process of haymaking date from 750 BCE (Barnes and Baylor, 1995), belying Dyson's 2000-year time frame, and references to proper curing were described by the Roman writer Columella in AD 50 (Barnes and Nelson, 2003). Red clover (*Trifolium repens*) was cultivated in Southern Europe in the third and fourth centuries AD (Evans, 1976) and was brought to America by early settlers (Gibson and Cope, 1985). As pre-Columbian America lacked significant large domestic grazing animals (cows, sheep, goats, and horses), there is little evidence for harvested forages before European settlement, although the contributions of early Native American farmers to the world's food crop larder is well known (e.g., maize, beans, tomato, and potato). Significant management of grasslands and forested farming systems through burning by Native Americans to increase game populations was common.

Some of the earliest development of forages as crops that were seeded and managed are likely traced to alfalfa (*Medicago sativa* L.) and selected cool-season grasses in the Mediterranean and near Asian agricultural regions. Sometimes very important forage species were carried intentionally or unintentionally by immigrants to their new homes. Bermudagrass (*Cynodon dactylon*), a very important forage in the Southern United States, was apparently brought to the United States inadvertently by African slave ships from its center of origin in Africa. It was stuffed into mattresses as bedding and eventually some of the seed ended up in places where it grew successfully. Kentucky bluegrass (*Poa pratensis*), well-known pasture grass in North America, was apparently introduced to America from England as part of the sweepings of cattle boats.

Alfalfa (*Medicago sativa*), the most important leguminous forage in the United States, is the oldest crop plant which has a name (Russelle, 2001). It originated in the area of modern-day Iran and Turkey and was moved by early Mediterranean civilizations throughout the region and into Europe and Central Asia (Lesins, 1976). The horse was a key factor in its early domestication, as it was transported by nomadic peoples and by early Assyrian and Babylon empires from the seventh century BC (Michaud *et al.*, 1988). Pliny and Strabo, early Roman writers, recorded that alfalfa was introduced into Greece as early as 490 BC by invading Medes and Persians. Alfalfa was often associated with the military might of the Greek, Roman, Persian, and later the Islamic empires through its role in feeding war horses (Lesins, 1976). Alfalfa was introduced into China in the second century CE along with Arabian horses (Russelle, 2001) and into the new world by Spanish colonialists.

The first recorded attempt to grow alfalfa in the United States was in Georgia in 1736, and it was grown by both George Washington and Thomas Jefferson in the 1790s, but it was really only successful after its California introduction

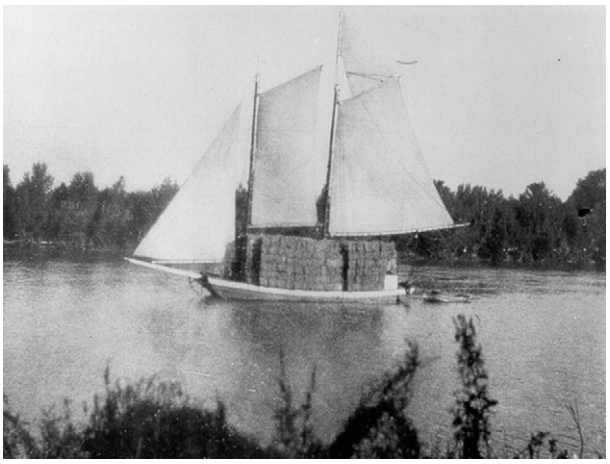


Figure 2 Alfalfa hay was commonly transported by sailing scows in the Sacramento/San Joaquin delta to dairies around San Francisco, c. 1890s. Alfalfa was first introduced in the 1700s in eastern states but was first successful in the United States after California's Gold Rush in the 1850s and quickly moved to eastern states to become the most important hay crop in the United States.

Table 1 Crop values of the top US crops and the value of dairy and beef industries in the United States, 2010–2012

Crop	*2010*	*2011*	*2012*	*Crop rank-US*
	Billions of dollars			
Corn grain	64.6	76.9	77.4	1
Cattle and calves	53.0	65.3	69.6	
Soybean grain	37.5	38.5	43.2	2
Milk and cream	31.3	39.5	37.0	
Hay (all)	14.7	18.2	18.6	3
Hay (alfalfa)	7.7	10.9	10.4	(4)
Wheat (all)	12.8	14.3	17.9	4 (3)
Cotton (all)	7.3	6.9	6.0	5
Potatoes	3.7	4.0	3.9	6
Rice	3.1	2.7	3.0	7
Sugarbeets	2.1	2.0	2.0	8
Sorghum grain	1.6	1.3	1.6	9
All field crops	157.5	175.4	187.8	
All fruit nut crops	21.2	24.2	25.8	

Note: Alfalfa is listed as a subcomponent of all hay. Values in parentheses show the relative ranking of alfalfa and wheat if alfalfa was considered a separate crop rather than a subset of all hay.

Source: Reproduced from USDA-NASS. Available at: http://www.nass.usda.gov/ (accessed 09.01.14).

around 1850 as 'Chilean clover.' Subsequently, alfalfa moved eastward to Utah and other states in the expanding West and later to the colder, wetter climates of the East. The introduction of 'Grimm' cultivar from Germany into Minnesota in 1857 made possible the development of cold-hardy varieties, the descendants of which are grown today in many cold northern regions. Alfalfa and other hays have been transported to dairy and livestock producers for considerable distances in western US states for more than 100 years (Figure 2).

The breeding and production of improved forage crops is a relatively recent phenomenon, occurring mostly during the twentieth century after some early introductions in the 1800s (Michaud *et al.*, 1988). A wide range of improved forages have become available during the latter half of the twentieth century, led by alfalfa; (there are more than 250 cultivars of alfalfa available in North America alone (NAFA, 2014)). However, it is also accurate that the genetic advancements with forage crops have not been as dramatic as with the major grain crops, due in part to the relatively miniscule investment of public or private resources in their improvement in comparison with corn, wheat, soybean, and vegetable crops.

Importance of Forages

By definition, 'forage' is any herbaceous plant species or plant part that is directly consumed by livestock (Barnes *et al.*, 2007). Generally, entire plant parts are consumed, differentiating forages from 'grain' (such as corn, barley, or wheat grain) or by-products such as oilseed meals, which are also major livestock feeds (see Glossary).

Current figures estimate that 26% of the world's land area and 70% of the world agricultural area is covered by grasslands, directly contributing to the livelihoods of more than 800 million people (FAO, 2008). Others have estimated the world's grazing and grasslands, defined as land dominated by grasses, to occupy 52.5% of the world's terrestrial land area (excluding Greenland and Antarctica), making it one of the most important ecosystems worldwide (Reynolds, 2005). However, much of these lands include nonmanaged or partially managed mixed grasses, legumes, and forbs. There are additional millions of hectares of pasture, hay, and silage crops which occupy highly-managed farmland. Typically, world acreage and value of forage crops are not compiled in a complete fashion that includes all forages or even all forage crops, and detailed data are frequently lacking.

In the United States, 'hay' is ranked as the third most important crop in economic value behind only corn and soybean (Table 1). This does not include pasture, rangeland, or silage crops but includes both grassy and leguminous forages harvested as hay. The primary species contributing to the US$14–18 billion year^{-1} hay crop in the United States are alfalfa (*Medicago sativa*), tall fescue (festuca arundinacea), bermudagrass (*Cynodon dactylon*), ryegrass (*Lolium* spp.), orchardgrass (*Dactylis glomerata)*, bromegrass (*Bromus* spp.), timothy (*Phleum pretense*), and various clovers, prominently red clover (*Trifolium pretense*) and white clover (*Trifolum repens*). Alfalfa is the most important hay in the United States and would be ranked fourth in economic value (behind corn, soy, and wheat), if considered by itself (Table 1).

Approximately 870 000 US farms produce hay crops, according to the 2007 USDA Agricultural Census, occupying >65 million acres of farmland (Figure 3). Virtually every agricultural state produces hay crops, with the largest production occurring in the midwestern and western states. Alfalfa production (a subset of hay production), predominately occurs in major dairy and beef-producing states in the west and midwest: the top ranked states are California, South Dakota, Idaho, Montana, Nebraska, Wisconsin, Iowa, North Dakota, Kansas, and Minnesota (USDA-NASS data). Approximately

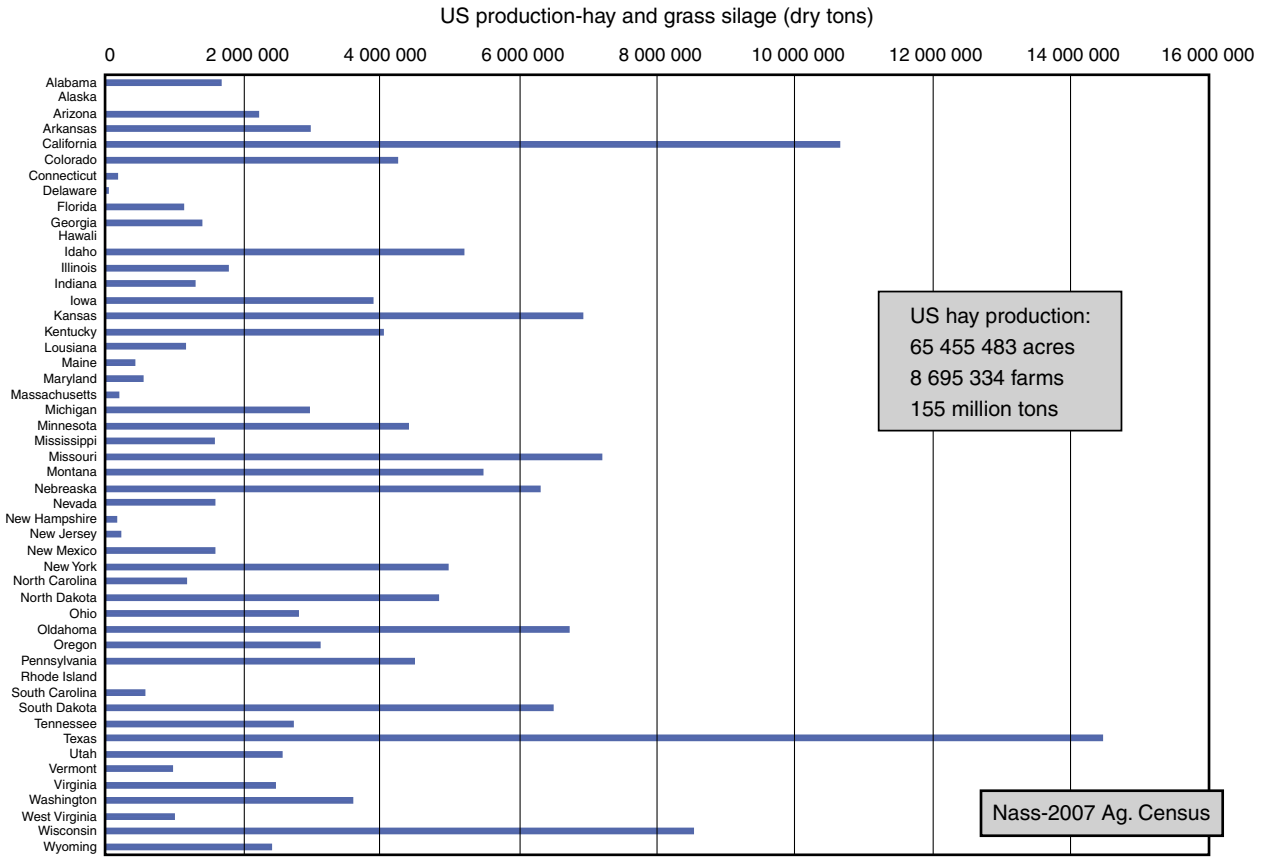


Figure 3 US production of cultivated hay, grass silage, alfalfa haylage, and greenchop (2007). This does not include corn or sorghum (or other) silages, grazed farm pasture, grazed forested lands, or rangeland. Reproduced from USDA-NASS. Available at: http://www.nass.usda.gov/ (accessed 09.01.14).

50% of the US alfalfa is produced in midwestern states, 42% from western states (mostly irrigated), and 8% from eastern states.

Although hay is of economic importance in its own right, forages have economic value primarily through ruminant livestock products. Thus, the value of cattle and calves and the dairy industry, which could not exist without forage crops, is inextricably linked to the value of forages. Dairy and beef are among the top four economic agricultural products in the United States (Table 1). Beef cattle are highly dependent on grazing systems, utilizing seasonal pasture as well as hay and silage crops (primarily during the winter months). Dairy cows are more dependent on stored hay and silage forage crops.

Nationwide, the majority of forages are utilized on-farm, rather than being sold, although there are large east–west differences in this respect. In most western states a vast majority of the alfalfa hay is marketed (sold between farms), whereas this is reversed in eastern and midwestern states, where most of the forage is used on the farm in which it is grown. In both cases, some portion of the economic value of dairy and beef must be attributed to the forage crops that support those industries. For example, in 2011, the value of the sale of hay in California was US$1.7 billion, whereas the value of dairy was US$7.6 billion and cattle and calves US$2.8 billion, with dairy the most important agricultural product in the state (CDFA, 2013). Accounting for 'hay' in these summaries does not include the value of pasture, silage, or greenchop. Forages and livestock are interdependent industries, and this example illustrates how the economic value of forages is frequently underestimated.

Forage Agroecosystems

Forages grown on grazing lands, range, and grazed forestry lands consist of greater than one-third of the total land use in the United States (including cities, water bodies, deserts, agriculture, and other land uses, Table 2). Grazing land use has declined from approximately 50% of land use in 1945, a reduction that is primarily due to a reduction in grazed forested regions. However, forage, grazing, and grasslands remain an important, if not dominant land use, exceeding that of crop production agriculture in its entirety (Nickerson *et al.*, 2011). This estimation does not include harvested hay and silage crops (as per Table 1), which would add approximately 65 million acres to the 'total forages' tally, but reflects pasture, grassland, and grazed areas within forested regions. The importance of animal–forage systems as a primary if not dominant agroecosystem land use in the United States may be a surprise to many.

Table 2 Land use (acres) in United States, 1945–2007

Land use	*1945*	*1974*	*2007*
	(× 1000 acres)		
Cropland (including harvested forages)	450 693	465 084	408 139
Cropland used as pasture	47 448	82 736	35 989
Grassland pasture and range	659 498	597 833	613 733
Forest land grazed	345 000	179 419	127 130
Total US land	2 274 944	2 263 587	2 263 962
Percent used for grazing/pasture	46%	38%	34%

Note: Total land use includes water bodies, cities, agricultural uses, and roads/canals. Cropland includes all harvested hay and silage crops, grain crops, oilseeds, sugar and fiber crops, orchard, and vegetable crops. Cropland used as pasture is cropland in semipermanent pasture, whereas grassland and pasture includes all nonforested grazing areas. Percentage used for grazing does not include hay, silage, and greenchop forage that are included in cropland.

Source: Reproduced from USDA Economic Research Service.

Forage crops can be visualized as key components of a 'food-producing biological system' involving soil, water, climate, plant communities, animal production, and animal-based food and fiber products (**Figure 4**). Energy, minerals, nutrients, carbon, nitrogen, and other minerals are transformed from the abiotic environment (soil, water, air, and sun) through plant and animal production systems, to food products, such as meat and milk, driven by market demand (West and Waller, 2007). Nutrients can also be recycled back to forage crops in the form of manure, municipal waste, and gasses, such as CO_2 from animal respiration. Nitrogen is of special interest because it is in such short supply in the earth's crust for plant growth and a source of contamination in surface and groundwater (Wedin and Russelle, 2007). Extensive systems (grazing and rangeland) are more important for sheep and beef, whereas intensive cultivated forages are more important for dairy animals and horses, but there is considerable crossover. Complex interactions with human input and environmental influences, such as petroleum and fertilizer inputs, management practices, wildlife habitat, climate and seasonal changes, and powerful market forces, influence this system in many ways (**Figure 4**).

Animal production systems are frequently interrelated across species. For example, milk production based on harvested forage systems (primarily alfalfa, corn silage, and grass hays) also influence beef systems through culled dairy cows and bull calves (Putnam and DelCurto, 2007). The primary animals of worldwide importance that are dependent on forages are beef cows, dairy cows, sheep, goats, and horses (**Figure 4**). Chicken and swine are not generally important for forages; an exception is in major poultry production areas, such as Arkansas and Alabama. Poultry wastes are routinely recycled through grassy beef pastures and the same thing happens in swine production regions (West and Waller, 2007). It should be pointed out that most animal production systems in modern times are highly dependent not only on forage crops but also on grain and by-products from grain or seed-producing crops, particularly corn grain, soybean, and other oilseed meals, and by-products, such as fermentation by-products, cottonseed, citrus and sugar beet pulp, etc. Not generally noticed is the service that animal production systems provide in consuming waste products and by-products that would otherwise have no value and end up in landfills.

Modern Concentrated Animal Feeding Operations (CAFOs) provide major challenges to the cycling of nutrients through forage and grain crops in plant–animal production systems. CAFOs are defined by the EPA as either medium (200–699 for dairy and 30–999 for beef) or large (>700 for dairy and >1000 for beef cows) sized. CAFOs have come to dominate animal production systems in many regions worldwide. For example, in California the size of the average dairy is more than 800 mature milking cows, and many of the beef feedlots in Missouri, Oklahoma, and Texas have tens of thousands of cattle concentrated in single units. This trend of increasing operation size is driven primarily by efficiency and cost considerations and the relatively low profitability margins of animal feeding systems. Major challenges of CAFOs include the concentration of nutrients (predominantly N and P), concentration of salts, and the difficulty of cycling nutrients back through forage systems. Compared with traditional, smaller-scale grazing and feeding systems, CAFOs typically have greater environmental challenges associated with the accumulation of excess salts and nutrients imported to small areas from cropland and air quality impacts from animals, manures, and silage.

Classes of Forage Crops

Although ruminants and nonruminants can ingest many types of herbaceous plants, the most important forage crops consist of herbaceous leguminous plants and cool- and warm-season grasses. Perennials and annuals are both widely used, but perennials are more prevalent. The ascendency of various forage species in different regions is dependent on soil type, climate, and adaptation as well as the necessity for high forage quality. The latter factor, in turn, determines the class of animal that can be economically fed. Frequently, the ability or inability to produce certain types of forage crops due to limitations of soil, water, or climate will determine the class of animal that can be raised in a region. Sheep, goats, beef cows, horses, and dairy cows each have different nutrient requirements, with milk-producing animals having the highest quality requirements. Thus, one finds sheep and goat grazing systems more predominantly in regions with extensive rangelands with more coarse forage species and dairy bovine production in regions capable of producing higher quality hay and silage crops.

Conversely, farmers do not always choose to grow the highest yielding forage crop (production per unit area), due to the need to produce quality forage products (nutrients per unit forage) to optimize milk production or daily weight gain. Thus, a farmer may elect to produce alfalfa, ryegrass, or clover compared with higher yielding forages, such as sudangrass, because the former crops are known to improve milk production or growth. However, most animal production systems have uses for all types of forages, from higher quality forage crops to coarser hays, including silage, crop residues, and roughages. Thus, different types of forages are fed to different classes of livestock according to their dietary needs, from

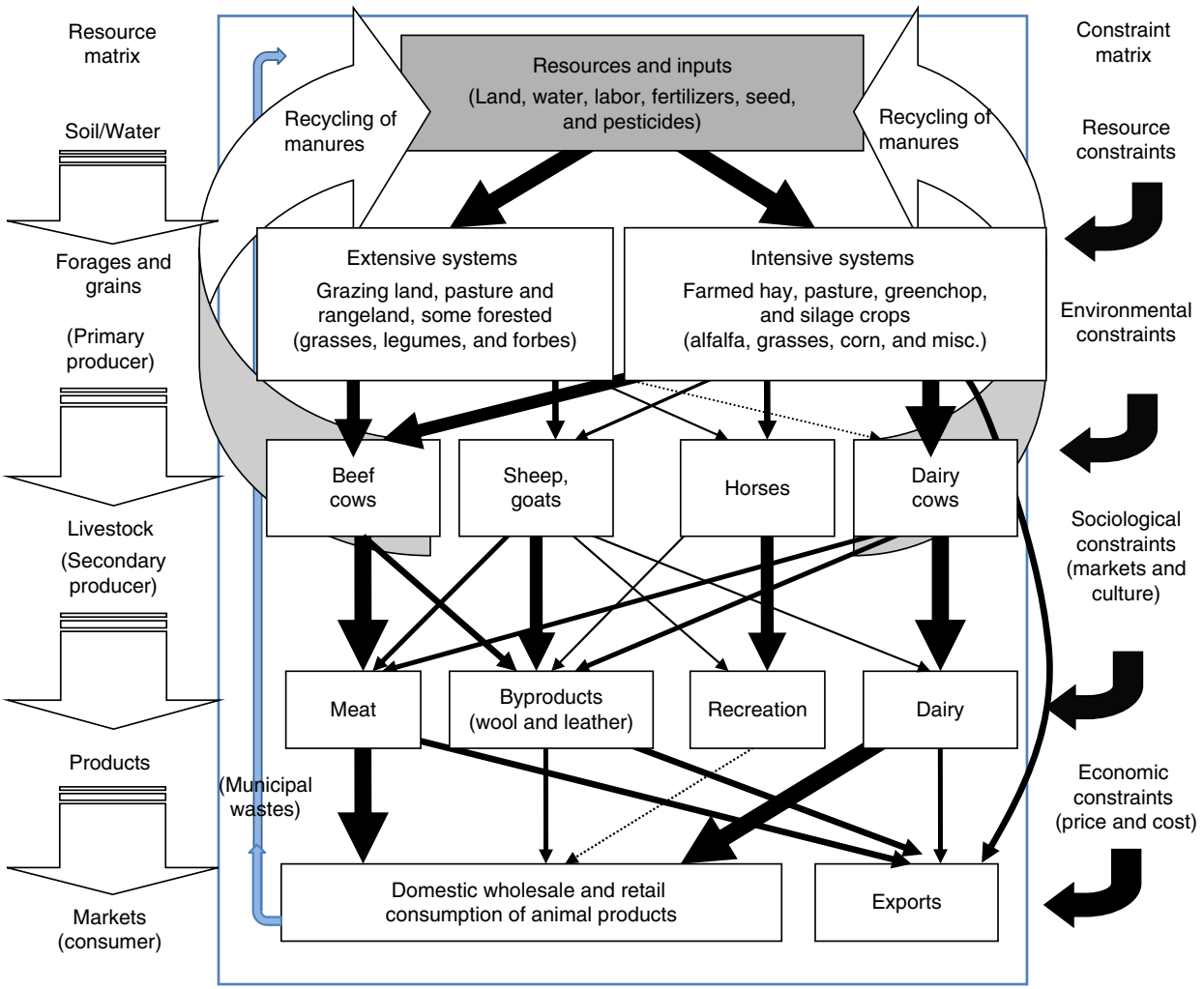


Figure 4 A model of forage food-producing systems consists of the conversion of land and water, through forage crops and grains, with human and other inputs to produce food products under varying constraints. Thickness of arrows indicates importance of flow. Constrains include resource (water and soil), environmental (temperature and environmental impacts), and sociological and economic constraints. Adapted from Putnam, D.H., DelCurto, T., 2007.

high-producing milk cows to heifers and dry cows, horses, beef cows, sheep, and goats.

Here the most important forage crops are discussed, but a wide range of forages can be grown and are important in localized areas, and described in Table 3.

Forage Legumes

There are a wide range of legumes grown as forage crops, both annual and perennial, including alfalfa (*Medicago sativa* L.), various clovers and herbaceous legumes, and seed-bearing crops, such as soybean (*Glycine max*) and cowpea (*Vigna unguiculata*). Forage legumes tend to be higher in protein concentration than grasses and have the advantage of biological N_2 fixation through symbiosis with various *Rhizobia* species, enabling the leguminous forages to be grown without N fertilizers. Worldwide, biological N_2 fixation contributes an estimated 140 million MT of N annually with 85% in agricultural systems coming from pulse and forage legumes (Vance *et al.*, 1988). Forage legumes are frequently highly desired components of forages systems due to the dual benefits of biological N_2 fixation and superior palatability and quality of the forage.

Alfalfa

Alfalfa (*Medicago sativa* L.) or lucerne is the most important forage legume worldwide and frequently called the 'Queen of forages' due to its wide adaptation, high yield, and high quality. This moniker also is due to the fact that it is frequently the most important forage in many regions and is the highest value hay crop in the United States. It is grown from the frozen plains of Southern Canada and Eastern China to the mild climates of Chile's Central Valley to the searing deserts of Mexico and North and South Africa. It is grown as a highly managed cash crop in irrigated regions, such as California

Table 3 Characteristics of many crops commonly grown as forages

Species	*Scientific name*	*Type*	*Life habit*	*Primary use*	*Distinguishing characteristics*
Alfalfa	*Medicago sativa* L.	Legume	Perennial	Principle hay crop in the United States, silage, pasture	Considered the premier forage for dairy production and is the most widely grown hay crop. Called 'Queen of forages' due to high yield and quality
Alsike clover	*Trifolium hybridum* L.	Legume	Short-lived perennial	Pasture	Best adapted to cool climates and tolerates a wide range of soil pH (both acidic and alkaline conditions), poor soil drainage and low fertility
Arrowleaf clover	*Trifolium vesiculosum* Savi	Winter legume	Annual	Hay and pasture	Not tolerant of poor drainage or low fertility. Low bloat potential and naturally reseeds if allowed to mature
Bahiagrass	*Paspalum notatum* Flugge	Warm-season grass	Perennial	Pasture	Subtropical humid grass, well adapted to sandy soils and tolerant of drought, low fertility, close grazing, and continuous stocking. Deep and extensive root system. Little hay potential because of prostrate growth habit
Bermudagrass	*Cynodon dactylon* (L.) pers.	Warm-season grass	Sod-forming perennial	Pasture and hay	Adapted to warm climates but very frost sensitive. Spreads by rhizomes and solons. Propagated by seed and cuttings. Tolerates close grazing
Big Bluestem	*Andropogon gerardii* Vitman	Warm-season grass	Perennial	Primarily summer pasture or hay crop	Native tall grass prairie species well adapted to the Central US. Very cold and drought tolerant. Requires high grazing or cutting height (>6 in.). Used extensively for conservation and wildlife habitat
Birdsfoot Trefoil	*Lotus corniculatus* (L)	Legume	Short-lived perennial	Pasture with some hay	Winter hardy and bloat resistant due to tannin content. Maintains quality after flowering
Brassicas	*Bassica* spp.	Cool-season forb	Annual and biennial	Summer and fall forage for grazing	Includes kale (*B. oleracea* (L), rape (*B. oleracea*), and turnip (*B. rapa* (L). Used primarily as short-season supplemental pasture. Does not tolerate wet soils. High forage quality but may contain toxic compounds if not grazed at the appropriate time. May cause bloat
Bromegrass	*Bromus* spp.	Cool-season grass	Perennial	Pasture with some hay	Primary species include smooth brome, meadow brome, mountain brome, and matua grass. Adapted to well-drained soils. Very winter hardy but does not tolerate flooding. Becomes dormant when stressed for moisture. Can be grazed continuously
Corn	*Zea mays* (L)	Warm-season grasss	Annual	Principle silage crop in the United States	Widely adapted to fertile well-drained soils. High yield and energy content. Stovers can be baled or grazed. High grain component makes for a highly digestible forage. Important for dairies and feedlots as a silage, but stover can be grazed

(*Continued*)

Table 3 Continued

Species	*Scientific name*	*Type*	*Life habit*	*Primary use*	*Distinguishing characteristics*
Crimson clover	*Trifolium incarnatum* L.	Legume	Annual	Pasture, hay, and covercrop	Grown in southern states and the coastal plain. Brilliant red inflorescence
Dallisgrass	*Paspalum dilatutum* Poir	Warm-season grass	Perennial	Pasture	Will tolerate periods of drought, close grazing, and continuous stocking
Elephantgrass	*Pennisetum purpureum* Schumacher	Warm-season grass	Perennial	Pasture	Very tall and high yielding. Adapted to humid tropical and subtropical regions. Extensive root system. Not tolerant of frost or waterlogged conditions
Fescue (tall fescue and meadow fescue)	*Festuca arundinacea* Schreb. *Festuca pratensis*	Cool-season grass	Perennial	Pasture and hay	Predominant forage grass in the United States and widely used for beef cattle production. Very persistent and high yielding. Can be stockpiled in the fall for winter use. Some varieties contain endophytes that improve persistence but produce alkaloids that are toxic to livestock
Kentucky bluegrass	*Poa pratensis* L.	Cool-season grass	Perennial	Pasture	Tolerates flooding and cold conditions. Adapted to northern and temperate regions. Forms extensive sod by rhizomes. Less productive than other taller grasses and rarely seeded alone
Kura clover	*Trifolium ambiguum* Bieb.	Legume	Perennial	Pasture	Persistent winter hardy drought tolerant legume. Spreads by rhizomes. Tolerates close grazing and continuous stocking. Difficult to establish
Lespedeza	*Lespedeza cuneata*	Warm-season legume	Perennial	Used for summer pasture or hay	Low winter hardiness but tolerant of drought, poor drainage, low fertility, and acidity
Medics	*Medicago* spp.	Legume	Annual and perennial	Pasture and cover crop	Prostrate growth pattern, tolerates grazing, reseeds itself
Orchardgrass	*Dactylis glomerata* L.	Cool-season grass	Perennial	Pasture and Hay	Moderate winter hardiness. Relatively easy to establish. Widely used as hay for horses and in pastures. Very shade tolerant
Perennial Peanut	*Arachis glabrata* Benth	Warm-season legume	Perennial	Hay, pasture, and conservation	Grown in subtropical areas. Low cold tolerance. Established with cuttings. Creeping growth habit
Ryegrass	*Lolium perenne* L. and *Lolium multiflorum* Lam.	Cool-season grass	Perennial and annual	Hay and pasture	Highest quality forage grass. Widely used for lactating livestock and for beef prduction. Some perennial varieties contain a fungus that produce alkaloids that can cause disorders in livestock
Reed canarygrass	*Phalaris arundinacea* L.	Cool-season grass	Perennial	Pasture and hay	Very winter hardy and highly adapted to waterlogged conditions. Forms an extensive sod by rhizomes. Difficult to establish but vigorous once established. Some varieties have high levels of alkaloids that reduce palatability and cause health issues

Red clover	*Trifolium pretense* L.	Cool-season legume	Short-lived perennial	Hay and pasture	Widely adapted. Low drought resistance but tolerant of shade and poor drainage. Upright growth habit makes it suitable for hay and pasture
Small grains (oats, barley, wheat, triticale)	*Avena sativa* L., *Hordeum vulgare* L., *Triticum aestivum* L. × *Triticosecale*	Cool-season grasses	Annual	Hay, silage, and occasionally grazing	Used widely as grain crops but can be grown for hay, silage, grazing or greenchop. Small grain forages require moderate to high soil fertility. Very productive under cool conditions and easy to establish. Late harvests include grain component
Sorghum/Sudangrass	Sorghum bicolor L., Sorghum × drummondi	Warm-season grass	Annual	Silage, hay, and grazing	Many cultivars are available, from seed-producing to high-yielding forage types. Sudangrass is a true hay crop whereas most sorghums are silage or grazing types. Adapted to a wide range of soils. More tolerant to low moisture, drought and low soil fertility than corn. Plant during warm periods in spring. Contains prussic acid and may accumulate nitrates which are harmful to livestock at high concentrations
Sweet clover	*Melilotus* spp.	Legume	Biennial	Grazing, hay, or silage	Adapted throughout the United States. Tall legume that reseeds itself. Exceptionally winter hardy and very drought tolerant. Excellent nitrogen fixer. Does not tolerate close grazing. Can cause bloat and contains coumarin, which reduces palatability. Moldy sweet clover should never be fed due to conversion to toxic compounds
Switchgrass	*Panicum virgatum* L.	Warm-season grass	Perennial	Grown as a summer forage for pasture and hay	Native to North America. Good tolerance to drought and heat. Good winter hardiness. Also used as a biofuel
Timothy	*Phleum pretense* (L)	Cool-season grass	Perennial	Hay and some grazing	Produces a storage structure called a haplocorm. Highly valued as a hay for horses. Does not tolerate close grazing or continuous stocking. Very winter hardy
White clover	Trifolium repens (L)	Cool-season legume	Perennial	Used mostly for permanent pasture	Includes Dutch and Ladino types that are larger and more productive than wild types. Low tolerance to heat and drought but tolerates flooding and acid soil conditions. Spreads by stolons. Well adapted for grazing but has high bloat potential
Wheatgrass	Various	Cool-season grasses	Perennials	Grazed or hayed	Various wheatgrass species are adapted to western and northern US. Important range grass for grazing, hay and soil conservation. Most popular species include Western, Intermediate, Crested, Pubescent, and Tall Wheatgrass



Figure 5 Alfalfa production field in Northern California, showing Mt. Shasta in the background (Photo: Steve Orloff).

(Figure 5) but also as a pasture crop for horses and cattle in midsouthern states, and millions of hectares are grown in Argentina in grazing dairy, beef, and sheep operations. Alfalfa is often the most desired forage for dairy production – it is no accident that the primary alfalfa production regions in the United States correspond with areas of high alfalfa acreage, such as Wisconsin, California, and Idaho.

Alfalfa is widely recognized as the oldest forage plant (Michaud *et al.*, 1988) and remains a dominant and highly desired forage in modern times. It originated in Asia Minor, Iran, and the dry highlands of Turkmenistan, regions of hot, dry summers and well-drained soils, which is why it has been highly successful in similar environments in modern times. It was, for many centuries, associated with horses and military might of Indo-European empires from at least 700 BC (Lesins, 1976), and the very word 'alfalfa' has Arabic and Persian roots and connotes 'best horse fodder' (Hendry, 1923). The United States and Argentina are the world's largest alfalfa-producing countries, but significant land area is devoted to alfalfa in Australia, South and North Africa, Southern Europe, Chile, Mexico, Canada, China, and the Middle East.

Alfalfa is a perennial, autotetraploid, partially self-sterile leguminous forage (Rumbaugh *et al.*, 1988). Alfalfa nearly completely lacks antiherbivory compounds that are common in other plants (a factor that makes it a very desirable forage) but accomplishes defoliation survival through the ability to quickly regenerate shoots. The plant has a 'crown' – a toughened top portion of the root that is capable of generating multiple foliar regrowths through new bud formation. This botanical feature enables alfalfa to be harvested multiple times per year for many years. Alfalfa is typically harvested 3–4 times per year but up to 12 times per year in the desert environments of Arizona, Mexico, and California (Putnam *et al.*, 2008a,b).

Alfalfa is best adapted to deep, well-drained, neutral pH soils but can be grown on clay loam soils if subsurface impediments are lacking (Orloff, 2008). Soil pH is a key limiting factor. A soil pH of 6.5–7.5 is considered ideal and lime is required to grow alfalfa on acidic soils. Alfalfa is deep rooted, with roots commonly in the 1.5–3 m range. As a result, alfalfa is not as easily moisture stressed as are more shallow-rooted forages. High-rainfall areas frequently have difficulties growing alfalfa due to saturated soils and low pH as well as root and foliar diseases. Alfalfa often requires irrigation for maximum yield and therefore approximately 35% of US alfalfa is produced under irrigation. Alfalfa requires significant water annually due to its high yield and long growing season, but it is among the most water-use efficient crops grown under irrigation (Putnam, 2012).

Red clover (Trifolium pretense)

'Red Clover' (*Trifolium pretense*) is a forage legume of European origin used for pasture and hay throughout the cool-season forage regions of Europe and North America. It is the most important *Trifolium* species in North America (Taylor, 1985) and is most frequently grown in mixtures with cool-season grasses and other legumes (alfalfa and white clover) for either hay or pasture. It is grown as a winter annual in the south.

Red clover is a short-lived perennial with a prominent short tap root more branched than alfalfa and forms a 'crown' due to contractile growth, similar to alfalfa, except that crowns are not as deep (Smith *et al.*, 1985). It has an upright growth habit. The primary stem does not elongate, but shoots develop from the crown and axillary buds from lower nodes, but stems do not elongate very much until flower formation. Flowers are of rose to magenta color. Leaves are palmately trifoliate, with oblong wedge-shaped leaflets, typically variegated with a white 'watermark.'

There are two types: 'medium' types, which exhibit earlier flowering, and typically multiple harvests, and 'mammoth,' which flowers much later and typically produces one or two harvests. Red clover is adapted to a wide range of soil types, including moderately poorly drained soils, and tolerates low fertility and moderately acid soils but has low drought tolerance. Red clover is susceptible to root and crown diseases in warm regions.

White clover (Trifolium repens)

'White Clover (*Trifolium repens*)' is a perennial legume of Eurasian origin (Evans, 1976). It is widely distributed from the arctic to the tropics but is best adapted to humid temperate climates (Gibson and Cope, 1985). It performs well under irrigation in drier areas of the Western United States as well. Like red clover, it is sometimes grown as a winter annual in the Southern United States and is dominant forage in New Zealand and many parts of Europe. Bloat can be an issue, but it is usually avoided because white clover is most often grown in permanent pastures in combination with cool-season grasses. The forage is most often grazed rather than hayed. White clover is winter hardy and relatively flood tolerant but is susceptible to drought and high temperatures. Its stoloniferous growth habit makes white clover excellent for soil stabilization.

White clover has a prostrate growth habit and is capable of reproducing via 'stolons,' which are underground stems. Like red clover, the leaves are palmately trifoliate with a variegated 'watermark,' which can be white or red. It has a round seed head with typically white flowers that may have a pinkish coloration as well.

White clover is classified as small, intermediate, or large. The wild types of white clover are small – they are lower

yielding, shorter, and have a more prostrate growth habit. Dutch clover, an intermediate type of white clover, is larger than the wild types. Ladino clover is larger still and is more productive but typically less persistent.

Birdsfoot trefoil (Lotus corniculatus)

'Birdsfoot trefoil (*Lotus corniculatus*)' originally comes from the Mediterranean region. It is adapted to humid, temperate regions and is one of the most drought tolerant forage legumes. It is also adapted to a wide range of soil conditions, including acidity and alkalinity, low fertility, and waterlogged conditions. It tolerates poor drainage better than alfalfa because it is not susceptible to Phytophthora (Beuselinck and Grant, 1995). Unlike many other forage legumes, it does not cause bloat. It is grown throughout much of the world, including Europe, the southern part of South America, and in areas of India, Australia, New Zealand, and the United States.

Birdsfoot trefoil can be prostrate or upright depending on the cultivar. Unlike the other forage legumes that are trifoliate, trefoil is pentafoliate with three of the five leaflets attached to the end of the petiole and the other two near the base. Mature plants have several well-branched stems that arise from the crown. The plant has a well-developed branched tap root that is shallower than that of alfalfa. Plants generally survive only for 2–4 years, so plants are often allowed to reseed to regenerate.

Birdsfoot trefoil has gradually replaced some of the red and white clover use because of it wide adaptation, relatively high yield and ability to reseed. It is typically grown as part of a mixture with grasses.

There are a wide range of additional legumes, both annual and perennial types, that are also grown for forage. **Table 3** lists these legumes, their growth habit, and any unique characteristics or uses. These legumes are less commonly grown than the ones mentioned above and some are grown as rotation crops with row crops or as annuals in pastures that are allowed to reseed.

Forage Grasses

> And I will send grass in thy fields for thy cattle that thou mayest eat and be full
>
> –Deuteronomy 11:15

Agricultural grasses are the basis of not only grain-based agriculture (corn, wheat, rice, and barley) but also stable feedstuffs for nearly all ruminant livestock production systems since farming first began some 12 000 years ago (Williams, 1980). There are cool- and warm-season grasses and each type has species with both annual and perennial life cycles.

Cool-season perennial grasses are usually the primary forage used for beef cattle and sheep production in the United States and throughout the world (Moser and Hoveland, 1996). They are sometimes used in dairy rations but to a much lesser degree. Annual cool-season cereals (such as wheat, barley, oats, and triticale) can also be grown for forage and are most often utilized as hay or silage.

Warm-season grasses, although important in tropical regions, are less common in temperate zones. Most warm-season grasses have a C_4 photosynthetic pathway whereby a four-carbon molecule is the first product of carbon fixation compared with a three-carbon molecule for most plants. This is a more efficient form of photosynthesis and warm-season grasses are typically more productive during the warm summer months. However, they are far more frost sensitive and generally have lower forage quality when compared with their cool-season counterparts.

Cool-season grasses

Ryegrass

Ryegrass, both the perennial form (*Lolium perenne* L.) sometimes called English ryegrass and the annual form (*Lolium multiflorum* Lam.) or Italian ryegrass, is one of the most important grass forages worldwide (Jung *et al.*, 1996). It is indigenous to Europe, North Africa, and temperate Asia. It is a vigorously growing productive species in areas where it is well adapted and is the dominant grazing forage for many parts of continental Europe, the United Kingdom, Ireland, and New Zealand. It is typically the highest quality cool-season grass (Jung *et al.*, 1996). However, it is not as winter hardy as some of the other cool-season grasses and does not tolerate low fertility, moisture stress, or heat stress. It is an important forage grass in areas with mild winters and cool summers, but because it cannot withstand harsh winters its area of adaptation in the United States has been confined primarily to coastal areas of the Pacific Northwest and selected areas in the Northeast and mid-South. It is highly palatable and digestible and therefore is often used for dairy pastures, especially in New Zealand, where it is the principal feed source for dairy cows. Perennial ryegrass is commonly grown in mixtures with white clover and may be grazed or fed as silage or hay.

Perennial ryegrass grows most vigorously during the mild temperatures of spring and fall. It is considered a bunch-type grass. Leaves of perennial ryegrass are folded in the bud in contrast to annual ryegrass where the leaves are rolled. Leaf blades are glossy, which often helps to differentiate ryegrass from other cool-season grasses. The inflorescence is a long narrow spike with 5–40 alternate spikelets that are oriented in the same plane as the rachis.

Perennial ryegrass is considered worldwide to be the premier forage grass due to its superior quality compared with other grasses (Balasko *et al.*, 1995). Ryegrass is not as long lived as other perennial grasses and when used in pasture it persists best when rotationally grazed with a rest period of 2–4 weeks.

Tall fescue

Although there are several different species of fescue used as forages, tall fescue (*Festuca arundinacea*) is the most widely used forage type (Sleper and West, 1996). Owing to its wide adaptation and its excellent persistence, it grew from 16 000 ha in 1940 to >12 million ha by 1973 (Buckner *et al.*, 1979). It was introduced from Europe and is well adapted to humid, temperate zones. It is tolerant to a wide range of stresses, including acidic and alkaline soils, poor fertility, drought and flooding, and heat and cold (not well adapted to extremely cold conditions in high-latitude or high-elevation locations). Tall fescue does particularly well with poorly drained, heavy soil types and withstands water logging. Owing to its broad

adaptability, tall fescue is the predominant forage species throughout the humid transition zone in the United States that lies between 32° and 40° north latitude (Moore, 2003).

Tall fescue is considered a tufted bunch grass but does spread via short rhizomes when grazed or mowed frequently (Sleper and West, 1996). The upper surface of the leaf blade is noticeably ribbed and dull in appearance, whereas the underside is somewhat glossy. The inflorescence is a broad to loosely branched panicle.

An endophytic fungus is known to infect the roots of tall fescue. The endophyte is seed transmitted and enables the plant to better tolerate heat and drought stress and improve persistence. However, endophyte-infected tall fescue produces alkaloids that are toxic to livestock and can cause disorders in cattle and is estimated to cost the US livestock industry hundreds of millions in losses annually (Hoveland, 1993). Endophyte-free cultivars have been developed, but they are less productive in areas where the fungus is prevalent. Tall fescue is commonly grown in pasture mixes in combination with legumes, such as white or red clover. Pastures can be hayed or grazed. Tall fescue tolerates continuous grazing better than most other cool-season grasses and it is the most commonly used forage grass for many beef cattle operations.

Orchardgrass (Dactylis glomerata)

Orchardgrass (*Dactylis glomerata*), native to Europe, North Africa, and parts of Asia, is produced throughout much of the world, including Northwestern Europe, Australia, New Zealand, Japan, and the northeastern portion of United States and the Pacific Northwest. It is widely adapted but best adapted to areas with moderate winters and mild summers and relatively high precipitation or irrigation. It is moderately tolerant to cold, heat, and drought but is more shade tolerant than other forage grasses. In the United States, it was found growing within orchards, giving rise to the name orchardgrass; however, it is also called cocksfoot based on the shape of the panicle (Van Santen and Sleper, 1996).

Orchardgrass is a bunch-type grass, and as the stand ages and thins, pastures can become clumpy. Leaves are folded in the bud and appear flat or V shaped at the base of the leaf sheath, a useful feature for identification. Leaves are light green but often become dark blue green when mature, another distinguishing characteristic of orchardgrass.

Timothy (Pleum pretense *L.*)

Timothy (*Pleum pretense* L.) is often the most sought-after forage for horses and is widely grown throughout northern regions where moisture or irrigation is sufficient. It was reportedly introduced by Timothy Hansen (thus its name) to North America from Northern Europe in c. 1720 and rapidly became the predominant pasture and hay grass for New England and northern states and Canada (Berg *et al.*, 1996). It is well adapted to northern regions with severe winters, due partly to the formation of a haplocorm or a swollen portion at the base of the stem that is used as a storage organ. Timothy is frequently grown in mixtures with legumes (alfalfa and red clover) and is fairly tolerant of flooding and acidic condition and very tolerant of freezing conditions, although not very tolerant of heat and drought (Moore, 2003). On variable soils (with some low-lying areas), mixtures of timothy, alfalfa, and red clover are very effective because the timothy and red clover survive in poorly drained areas, whereas alfalfa often does not. Timothy forms a distinctive, compact seed head and is considered a bunch grass with a fibrous shallow root system but has no rhizomes or other sod-forming structures. Regrowth occurs from haplocorms at the base of the stem. Timothy is an excellent hay crop and highly valued for both cattle and horses; significant quantities of timothy are exported from the Pacific Northwest of United States to Japan and the Far East (Putnam *et al.*, 2013).

Warm-season grasses

There are a range of warm-season grasses that are grown extensively throughout the humid Southern United States below 36° N latitude and in similar warmer regions in the world (Redfearn and Jerry Nelson, 2003). Some are also grown in northern regions, particularly corn silage. A distinguishing characteristic of most of these grasses is a C_4 photosynthetic pathway, which enables rapid growth rates even under hot conditions (MacAdam and Nelson, 2003). Generally, warm-season grasses are very productive under warmer and hot conditions but dormant or nonproductive under cool or winter conditions. In southern cropping systems, warm-season grasses are used primarily for grazing beef and cow-calf production (Pitman, 2007). They are frequently overseeded with annual cool-season grasses to improve winter production.

Although a wide range of warm-season grasses are grown as forages (**Table 3**), the principal and most widely grown warm-season perennials are bermudagrass, bahiagrass, and dallisgrass; and the key annual warm-season grasses are corn and sorghum, although others, such as millets, can also be grown as forages. Most are introduced species to North America, with the exception of native Bluestems, Indian grass, and switchgrass.

Bermudagrass (Cynodon dactylon *L.*)

Bermudagrass (*Cynodon dactylon* L.) is well adapted throughout the southernmost portions of the United States and in similar climates worldwide. It appears in early Graeco-Forman pharmacopeias and was (and is) a sacred grass to the Hindu cultures due to its support of cattle (Harlan, 1976). Bermudagrass lacks significant winter hardiness and is sensitive to freezing temperatures, which limits its growth in far northern regions but grows well in some continental climates, such as the mid-South, Texas, Oklahoma, which have cold winters. Typical of warm-season grasses, growth of bermudagrass begins only in the late spring and is maximized under the hot conditions of summer. It is a sod-forming perennial that spreads by multiple stolons and rhizomes and can be closely grazed. It can be established using seed or stolon cuttings. Bermudagrass tolerates continuous grazing and is often oversown with cool-season annual grasses (e.g., ryegrass) to improve pasture production in the fall and winter and early spring periods (Pitman, 2007). Once established, orchardgrass can tolerate salinity and is adapted to a wide range of soil types (Kaffka *et al.*, 2004). Tifton 85 and other improved cultivars have demonstrated higher quality and yields as well as animal

performance compared with traditional coastal Bermuda types (Hill *et al.*, 1993). Although most common in the southern coastal plains and throughout southern US states, it is grown in the Imperial Valley of California for horse hay, export hay, and seed production.

Bhiagrass (Paspalum notatum *Flugge'*)

Bhiagrass (*Paspalum notatum* 'Flugge') is grown on limited acreage in the southeastern United States. It is a perennial warm-season grass well adapted to the coastal plains of the humid subtropics. It is not as productive as bermudagrass on good soils but is very well adapted to sandy soil types due to its tolerance of drought and low fertility. It is extremely competitive when grown in mixtures, thus difficult to grow with legumes. It forms a dense sod from short, thick rhizomes and tolerates close grazing and continuous stocking. Leaf blades are short and flat or folded with hairy margins, and it has a deep and extensive root system. It is not appropriate for hay making due to the short stature and is often used as a turfgrass (Burson and Watson, 1995).

Dallisgrass (Paspalum dilatatum *Poir.*)

Dallisgrass (*Paspalum dilatatum* Poir.) is grown as perennial warm-season pasture forage in southern regions from Texas to North Carolina and mainly used as permanent pasture. It is best adapted to heavier, moist soils in regions with at least 900 mm of annual rainfall and invades streams and riparian areas in regions with low rainfall. It has a clump-type growth habit and grows well in association with other grasses and legumes and persists under heavy grazing (Burson and Watson, 1995). Dallisgrass is often more difficult to establish than other forage grasses due to slow germination and poor seed quality. Ergot (*Claviceps paspali* Stevens & Hall) can affect the flowers and seed of dallisgrass, and this can produce an alkaloid toxic to livestock.

Corn (Zea mays *L.*)

Corn (*Zea mays* L.), or maize, is not only the most widely grown grain crop in North America but also the most important silage crop for dairies and many beef operations. Corn was domesticated by early Native American farmers in what is currently Mexico, possibly as early as 5000 BCE (Goodman, 1976). It is grown in almost every state of the United States and is very important in China, Africa, South America, and Europe. However, its status as a forage crop, especially as a silage crop, has increased in recent years, due primarily to its high productivity and high energy content of the feed. As a very high yielding C4 grass, corn has few rivals with regard to the combination of high biomass yield and forage quality, particularly due to the high grain component. There has been significant investment from the private sector in genetic improvement for grain (less so for silage), and corn grain yields have famously quadrupled since the 1940s (Nielsen, 2012) – silage crops have been the beneficiary of this improvement. Corn is generally the preferred summer annual forage crop for farms with good soils with neutral pH and sufficient heat units in the warm periods of the summer. Corn is particularly important for dairy farms that have a requirement to recycle manures due to its high nitrogen fertilizer requirement. Silage production has become the mainstay of dairy operations nationally, and acreage has been 6–7 million acres (2–3 million ha) nationally, with production in the important dairy states, such as Wisconsin, California, Idaho, New York, and Pennsylvania, leading US production. As a silage forage, corn is particularly high in energy due to the high grain content of the dry matter (typically 45–55%), and thus satisfies a large portion of the energy needs of lactating ruminants. Corn requires high moisture and fertility, especially N fertilizers. Corn residues (stover) are frequently used for grazing or for baling and storage, especially during drought periods. Optimum forage yields and quality of corn harvested for silage are typically harvested when the seed is between 80% milk line and 7–10 days after black layer formation in the maturing seed (Moore, 2003).

Sorghum (Sorghum bicolor *L.*) and *Sudangrass* (Sorghum × drummondii')

Similar to corn, sorghum is grown predominately as a cereal grain crop, primarily in regions where moisture is limiting – the semiarid regions of the world. However, sorghum is also a significant forage option as a summer annual grazing, silage, and hay crop. Sorghum and various hybrids are one of the most important summer annual warm-season grass options appropriate for forage production in water-limiting regions, especially where corn cannot be grown. Sorghum originated in Africa and was fully domesticated by African farmers, possibly as early as 4000 BC (Doggett, 1976). The sorghum group represents a wide genetic resource, ranging from dwarf high seed-producing milo types to medium-height grain types to nongrain-producing forage-type sorghum to tall tropical types and sorghum–sudan hybrids as well as true sudangrass hay-type varieties. Most sorghum races can be crossed successfully, making hybrids possible. The major groups grown for forage are sorghum, sorghum–sudan hybrids (grown for silage and grazing and greenchop), and sudangrass (grown primarily for hay). The sorghum group is very widely adapted, but its production is limited in colder short-seasoned environments (Moore, 2003). The sorghum group has low tolerance to flooding but is adapted to a wide range of soil types and responds well to fertilizers and irrigation. It is sensitive to cold soils, should be planted when soil temperatures exceed 60° F, and thrives in hot environments when moisture is sufficient. Drought tolerance is accomplished by semidormancy, and the sorghum group is considered to have a lower nitrogen and water requirement than corn. Prussic acid, which can cause cyanide poisoning in livestock, is mostly present in young actively growing tissue. Nitrate accumulation, which can poison livestock, is a risk of sorghum and sudangrass forages, particularly under drought stress, freezing, and high nitrogen fertilizer applications. Sudangrass hay can be harvested four times under irrigation in California and Arizona and has recently entered international commerce by being exported to Japan.

Growth Patterns of Forage Crops

Although there are major differences between species, all forage crops share characteristics of growth and development and yield potential that differ significantly from harvested seed-producing and fruiting crops. The primary difference is the

emphasis on vegetative growth, leafy plant parts, and the harvested component, which in most forage plants is equal to nearly the entire above-ground biomass.

Thus, Harvest Index (HI, or ratio of economic yield to above-ground phytomass yield) of forages is nearly 100%, whereas for most orchard, fruiting, and grain-producing plants, harvest indices ranging from 10% to 55% of above-ground dry matter are observed. This is a major efficiency advantage of forage crops in terms of economic solar capture by crop plants, but, of course, conversion of forage crops requires the additional steps of animal conversion into producing utilizable food products.

Annual forage crops differ significantly from perennials in growth and development, and legumes differ significantly from grasses in both biology and management. Additional differences between species are significant – some are warm-season, whereas others are cool-season crops, some are tolerant of flooding or poor soil conditions, others are not. Thus, farmers frequently must consider a range of forage species to maximize production, given their limitations. Annual forage crop production more closely resembles grain crop production, for example, corn, sorghum, oats, barley, vetches, cowpea, soybean, and other annuals that can be used both as forage and grain-producing crops. However, perennials require unique crop production methods.

Stand Establishment and Early Growth

Nearly all perennial forage crops are small-seeded crops that require considerable attention during establishment (Figures 6 and 7). Many grassy pastures and hay fields are seeded only once in a decade or more, whereas alfalfa and perennially legumes, such as red clover, generally have a shorter stand life of 4–7 years.

After stand establishment, forage plants must grow to full canopy before harvesting begins. For perennials, this generally takes a few months or even a half year before full establishment occurs sufficiently to allow harvesting. Well-developed root systems are important to allow plants to be defoliated and regrow successfully.

Growth Patterns of Forage Crops

Forage species differ significantly in dry matter accumulation over the year. Cool-season grasses produce large biomass during spring (Figure 8) but undergo what is known as a 'summer slump' or reduction in yield during the hot summer months. Thereafter, production often increases again in the cool fall period.

This is in contrast to alfalfa or other legumes. These crops also exhibit higher early season yield and some decrease during warm months, but exhibit a more uniform yield pattern across the year (Figure 8), and most species do not exhibit a significant summer slump. Warm-season forages, however, maximize forage production during the hot summer periods and initiate growth later in the spring. Perennial warm-season grasses begin growth earlier than annuals, but often summer growth rates of productive C_4 annual grasses, such as corn or sorghum, exceed that of perennial warm-season grasses.

Forage Quality

Although yield is the primary consideration for forage production, the quality of the forage is a close second. Forage

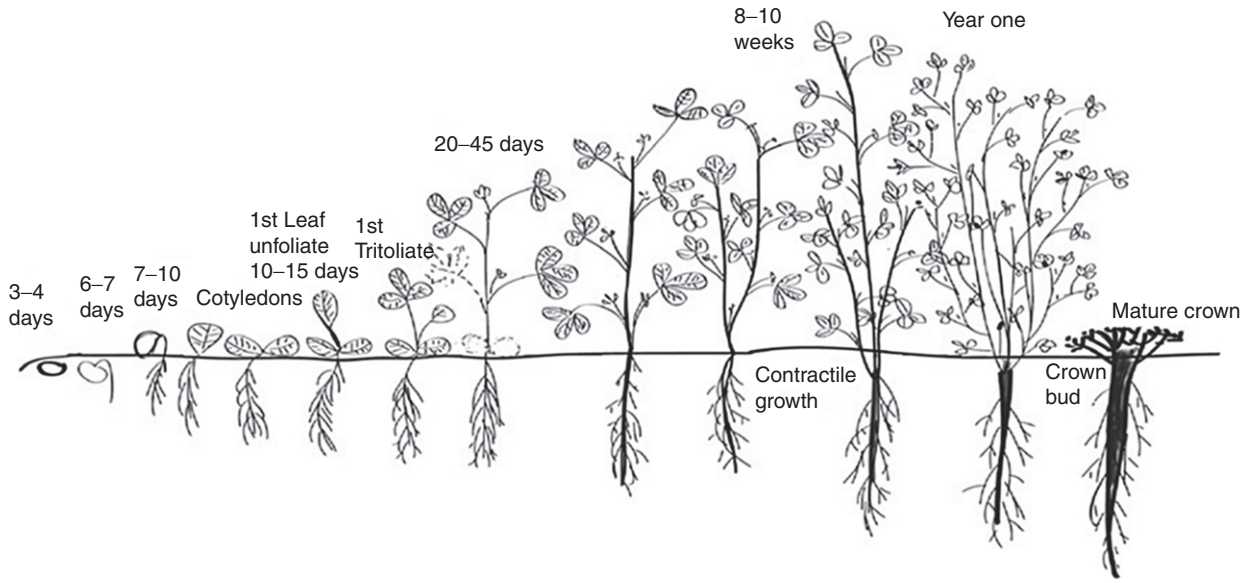


Figure 6 Establishment of an alfalfa plant. Alfalfa develops slowly from a weak annual to a strong perennial over a few months. After seed imbibition (3–4 days) the radicle emerges, pushing downward, after which the first cotyledonary leaves emerge (7–10 days). A single leaf emerges, followed by the emergence of the first true trifoliolate leaves (several weeks). Multiple trifoliolate leaves then emerge, followed by multiple stems from the basal nodes. During contractile growth, the cotyledonary node (2-leaf node) is pulled down into the soil to create the crown, a thickened bud-rich swelling of the root, capable of generating new shoots. The roots must be sufficiently large and deep to store nutrients to sustain frequent harvests (Mohammad Akmal, illustration).

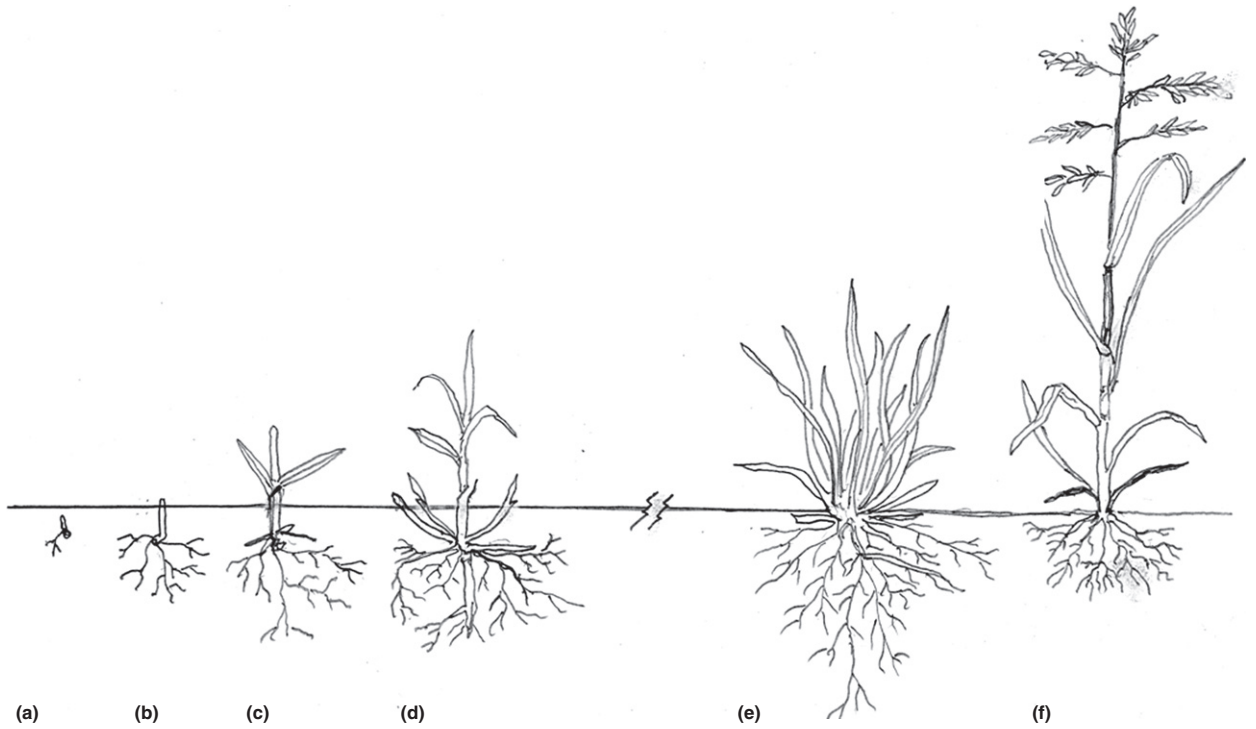


Figure 7 Development of a fescue-type grass. Imbibition of the seed is followed by radicle (root) development (a) and then epicotyl (shoot) emergence. Coleoptile (sheath containing the young shoot) elongation allows emergence from the soil (b), after which the leaf blade extends and the seminal root continues to expand (c). Adventitious roots develop at the coleoptile node (c), followed by the emergence of new tillers developing from basal nodes (d). Adventitious roots develop further, as the seminal root deteriorates. A fully established plant contains numerous tillers, a vigorous adventitious root system, and may produce rhizomes or stolons. During flowering, reproductive tiller growth dominates vegetative growth (f), with new vegetative tillers evident. Adapted from Moser, L.E., Nelson, C.J., 2003.

quality has a large effect on the productivity of forage crops and therefore profitability and economic efficiency of animal production systems. Forage quality impacts animal growth and development and has particular impacts on milk production.

Forage quality has taken on increased importance over the years, particularly for dairy production systems. Average milk production per cow in the United States has improved more than fourfold since the 1920s (**Figure 9**). This is a phenomenal rate of increase in productivity, unmatched by any crop species (with the exception of corn). Although there are many causes for this improvement (animal genetics, veterinary care, cow comfort, management, increased feeding of grains, and concentrated feeds), improvement in forage quality has been a significant factor, accompanied by scientific ration balancing. The process of improvement in animal productivity continues today in the United States (at more than 2% $year^{-1}$ according to USDA-NASS) but is especially apparent in rapidly developing dairy regions of the world that have historically low milk production.

What is Forage Quality?

Although the language of quality is broad, forage quality can be generally defined as the potential to produce a desired animal response from a given intake of forage (Reid, 1994; Ball *et al.*, 2001). As forages are not completely digested by ruminants, the primary considerations are both forage intake (amount consumed per unit time) and digestibility (percent digested – Paterson *et al.*, 1994). Animal response can be measured in the form of milk production, animal growth, meat or wool production, or general health.

Key Attributes of Quality in Forage Crops, listed in approximate order of importance to nutritionists:

- Digestible energy
- Intake potential
- Protein
- Rumen effective fiber
- Minerals
- Lack of antinutritional factors such as noxious weeds and molds

However, forage quality is not an intrinsic characteristic of a plant. The definition and optimization of forage quality depends on both species and class of animal, stage of life, and the mix of feeds in the ration as well as the species and stage of development of the forage plants considered. The best forage for a high-producing lactating dairy cow may not be the best (or most cost effective) forage for a grazing goat, horse, or beef animal. Optimization of quality of oat hay is likely to be different than optimization of quality in red clover. Thus, optimal forage quality is a function of both animal and plant factors.

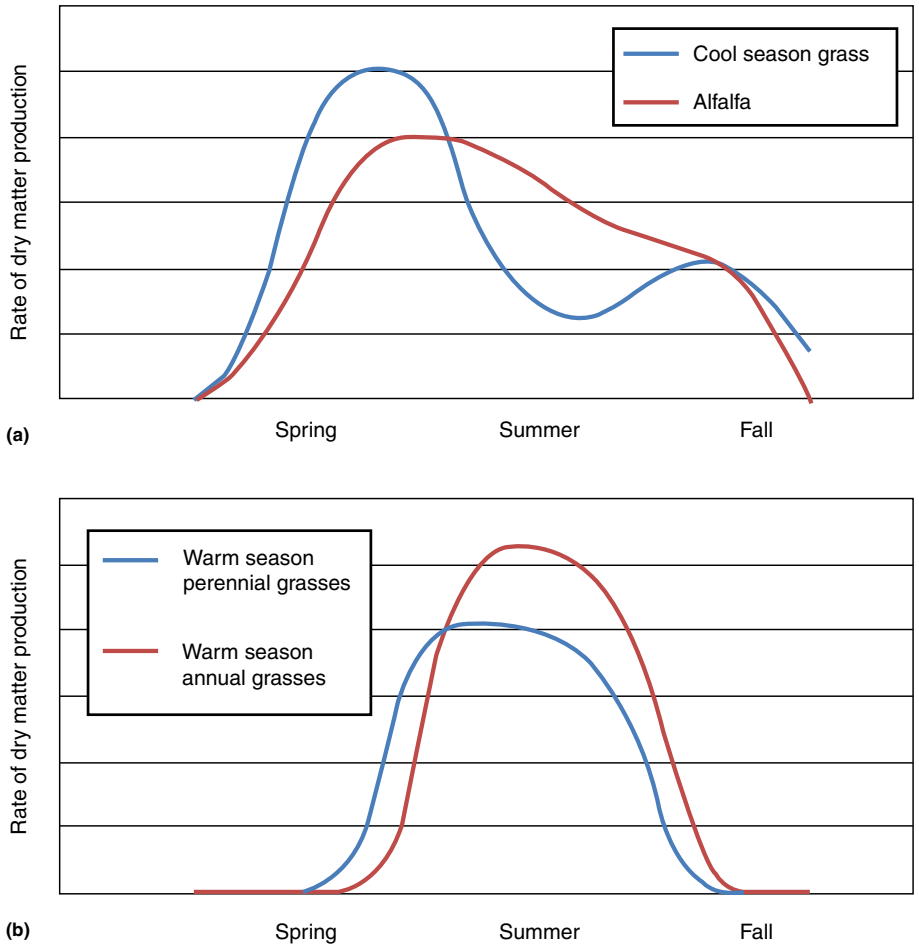


Figure 8 Generalized growth pattern comparison of cool-season forages and alfalfa (a) and warm-season perennial and annual grasses (b). Cool-season grasses typically exhibit very high growth rates, followed by a 'summer slump' and recovery in the fall. Alfalfa yields are highest early but are more even over the season. Warm-season grasses start later, with the highest summer growth rates in the annual C_4 warm-season grasses (e.g., sudangrass, sorghum, and corn).

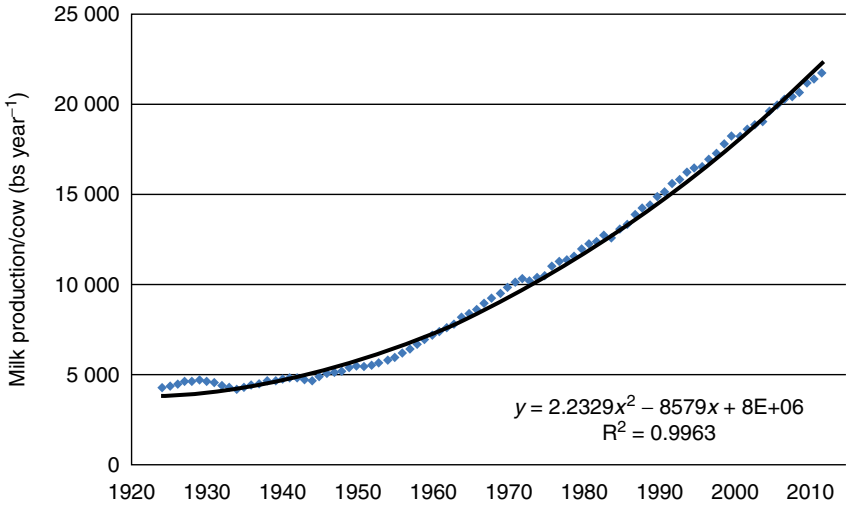


Figure 9 Average productivity of US dairy cows, 1924–2012. The quadrupling of productivity of US dairy cows has necessitated improvement in the quality of forage crops. Reproduced from USDA-NASS. Available at: http://www.nass.usda.gov/ (accessed 09.01.14).

Although it is often tempting to reduce the quantification of forage quality to one or two measurements (e.g., Crude Protein (CP), Metabolizable Energy (ME), Total Digestible Nutrients (TDN) or Relative Feed Value (RFV), see text box for abbreviations), this usually belies a more complicated story. Forage quality is always a complex mix of nutritional traits, including olfactory, chemical, functional, and physical factors. For example, CP concentration is important, but many nutritionists are also interested in the availability (extent and rate of digestion) of the protein. Forages high in digestible soluble carbohydrates and low in fiber (Neutral Detergent Fiber or NDF) are typically desired in forage crops, but NDF itself has important functions in animal nutrition and should not necessarily be minimized, depending on the class of animal and the ration. Furthermore, forages with high-quality analyses may contain toxic weeds or molds with toxins that degrade quality or physical attributes that lower palatability.

Forage quality terminology

Acid detergent insoluble nitrogen (ADIN) The nitrogen fraction in the ADF residue, generally unavailable for digestion by livestock, often due to heat damage.

Acid detergent insoluble crude protein (ADICP) It is calculated from ADIN (ADIN × 6.25).

Acid detergent fiber (ADF) The most difficultly digested fibrous portion of the plant that includes lignin and cellulose and silica, but not hemicellulose. ADF is a subset of NDF.

Ash A measure of the total mineral content of a sample, the residue remaining after burning a sample.

Cellulose A structural carbohydrate, long-chained polymer of glucose with 6 carbons, a major constituent of cell walls.

Crude protein (CP) An estimate of nutritionally important protein calculated from % nitrogen in crop (6.25 × %N).

Dietary cation–anion difference (DCAD) Calculated as a ratio of positively charges and negatively charged, divalent and monovalent mineral ions in a feed.

Digestible energy (DE) The energy in a forage that is not excreted in feces.

Dry matter (DM) The percentage of the crop that is not water. All rations and forage quality are considered on a 100% DM basis.

Ether extract (EE) A laboratory measurement of crude fat (lipid) content of plant material.

Hemicellulose Long chains of 5-carbon sugar compounds, an important component of plant cell walls.

***In vitro* digestible dry matter digestibility (IVDMD)** An *in vitro* bioassay utilizing rumen fluid estimating the amount of forage dry matter which is digestible in a length of time (e.g., 24 or 48 hours).

***In situ* digestibility** Digestibility of a feed determined *in situ* by incubation in a nylon bag within the rumen of an animal for a fixed time period.

Lignin The largely indigestible plant cell wall component, giving the plant stem its strength, reduces digestibility in forages.

Metabolizable energy (ME) The energy in a forage not lost in feces, urine, or rumen gases.

Net energy of lactation (NE_l) An estimate of the energy value of a feed used for maintenance plus milk production.

Net energy for maintenance (NE_m) An estimate of the energy value of a feed to maintain an animal at a stable weight.

Net energy of gain (NE_g) An estimate of the energy value of a feed that may be uses for weight gain above maintenance.

Neutral detergent fiber (aNDF) A fiber measurement which generally includes most of the cell wall material, cellulose, hemicellulose, and lignin (but not pectin); ADF is a sub-set of NDF. aNDF indicates amylose-included NDF procedure.

NDF digestibility (NDFd) An *in vitro* bioassay utilizing rumen fluid estimating the digestibility of the NDF fraction in a given length of time (e.g., 24 or 48 h).

Nonfiber carbohydrate (NFC) An estimate of the rapidly available carbohydrates in a forage (sugars, starches), calculated as a difference (100- ash%, NDF%, CP%, EE%).

Nonstructural carbohydrates (NSC) A measurement of the easily digested starch and sugar components of forages.

Relative feed value (RFV) An index for ranking cool-season grass and legume forages, calculated from ADF and NDF.

Relative feed quality (RFQ) An index for ranking cool season grass and legume forages, based primarily upon NDF, NDFD, ash, CP.

Rumen undegraded protein (RUP) The portion of CP not degraded in the rumen, sometimes called 'bypass protein.'

Total digestible nutrients (TDN) The sum of CP, EE (multiplied by 2.2), nonstructural carbohydrates, and digestible NDF. TDN is often calculated as a linear function of ADF.

Undegraded intake protein (UIP) The amount of forage protein that passes undegraded from the rumen.

There are, however, some major nutritional requirements for animals that are expected from forages that are important for nearly all class of animals. These are listed in approximate rank, but the relative importance will likely change with animal type, stage of life, and feed ration formulation. Forage quality is most often defined in terms of milk production of high-producing dairy cows. However, these factors are relevant to varying degrees to all classes of animals.

Digestible energy

In most cases, the primary consideration for forage quality is the potential DE per unit of forage dry matter. The supply of energy in feeds is a function of digestion and absorption of energy-containing compounds in the plant. This is usually considered very important as biological energy drives all animal functions of maintenance, growth, and milk production.

In forage plants, digestible energy comes from both rapidly and slowly available sources. The rapidly available forms include sugars, starches, and pectins, which are released quickly in the rumen and contribute energy to the animal. However, considerable energy in forages is contained in the cell wall (cellulose and hemicellulose), which is made available only through enzymatic breakdown by rumen microorganisms. These are also subsequently converted into volatile fatty acids and absorbed by the animal. Although starches, sugars, and pectins are essentially 100% digestible, the fibrous energy component in the alfalfa cell wall is typically only 30–70% digestible.

Unfortunately, the total potential biological energy in feeds cannot be easily measured directly with routine analyses, because it is a function of both the forage and the animal but is predicted with equations derived from several laboratory analyses. Energy (TDN), net energy (NE), net energy of lactation (NE_l), or Metabolizable Energy (ME) can be predicted from a linear relationship to a fiber measurement (ADF or

NDF, forage specific) or by summative equations involving a number of measurements. Energy is more accurately calculated from summative equations that use amylose-included NDF (aNDF), neutral detergent fiber digestibility (NDFd), ash, ether extract (EE), CP, and other factors to predict energy. This includes an *in vitro* analysis utilizing a rumen fluid bioassay (NDFd or *in vitro* digestible dry matter (IVDDM)).

Intake potential

Forage intake is one of the most critical quality components of forages and differs significantly between species and within species due to maturity and other factors (Mertens, 1994; Paterson *et al.*, 1994). Of the differences in digestible dry matter among animals and feeds, 60–90% are related to differences in intake (Reid, 1961). Some forages are digested very rapidly in the rumen, whereas other feeds require extended periods for complete digestion. At the extremes, straws have very low rates (as well as extent) of digestion compared with leafy leguminous forages, such as immature alfalfa. These differ greatly in their NDF content and NDF digestibility as well as rate of passage. High-fiber forages may also have slow fiber digestibility – therefore, animals can become 'full' and stop eating. However, NDF content is not highly correlated with NDF digestibility (Putnam and Undersander, 2006). Rumen fill limits intake, which ultimately reduces energy intake (per unit time) and animal performance. However, too low fiber (or NDF) content also creates acidosis and other medical problems in livestock (Mertens, 2010).

There are other factors as well that influence animals' intake of a forage, often termed 'palatability,' which are affected by species, taste, physical condition of the hay, odor, weed content, stem quality, and plant maturity.

There are several approaches to measuring, or predicting, rumen digestibility, including IVDDM, *in vitro* gas production estimates, *in vitro* NDFd, and *in vivo* (in the rumen) fiber disappearance, all of which are bioassays involving digestion of a sample in rumen fluid. Intake potential is one of the most important quality factors for lactating dairy cows (Paterson, *et al.*, 1994).

Protein

As amino acids from proteins are building blocks for muscle, milk, and animal enzymes, they are important nutritional attributes of forages. Sources of protein absorbed from forages are from two major sources: protein synthesized by rumen microorganisms and protein that escapes rumen degradation (Broderick, 1994). Although the concentration of protein (estimated by CP) is important, many nutritionists may also be interested in the amount of forage protein that passes undegraded from the rumen (undegraded intake protein, UIP) and is digested in the small intestine. Additionally, protein can be too closely associated with cell wall fibers and rendered nondigestible. Acid detergent insoluble CP (ADICP) estimates the undigestible (typically lignified and heat damaged) CP. In addition to heat damaged and undegraded protein being a negative factor, excessive degradation of CP in the rumen is also a negative quality factor if the rumen microbes do not fully utilize the ammonia nitrogen (N) for microbial protein. This excess ammonia N is absorbed through the rumen wall, and much of the ammonia is converted into urea via an energy-dependent process, which is then excreted in the urine. High rumen degradable protein can be a problem with very leafy immature forages, and these highly digestible proteins can lead to bloat in ruminants.

Ruminally effective fiber

The provision of ruminally effective fiber with a high level of digestibility is a major attribute provided by forage crops in ruminant rations, especially those with high grain additions. In addition to high fiber (NDF) being a problem for forages, as it limits energy and intake, low fiber is also a problem, as effective NDF is a valuable component of forage crops (Mertens, 1994; Mertens, 2010).

Energy and intake are generally inversely related to fiber concentration (ADF and NDF) in the hay, particularly energy available per unit time in the rumen. Thus, as the percentage of ADF or NDF goes up, digestible energy and intake go down. As a result, dairy managers frequently demand low-NDF or low-ADF hays. However, reduction of fiber to very low levels can create problems in rumen function because dietary fiber stimulates rumination, chewing, and saliva production; the latter helps to stabilize rumen pH. High-producing ruminants can suffer physical problems with rumen health when 'effective fiber' is too low in their diet. Thus, the fiber in forage crops provides positive physical and chemical attributes to ruminant rations. It is clear that both the concentration of the NDF and the rates of digestion of the fiber fraction (estimated by NDFd) are important attributes of forage quality.

Ash and minerals

Ash is an estimate of total mineral content in a forage, which could originate from normal mineral uptake by the plant, for example, phosphorus (P), potassium (K), sulfur (S), calcium (Ca), magnesium (Mg). Ash can also result from excessive salt accumulation or contamination with soil. In general, as ash increases, the level of digestible energy declines, because minerals do not contain energy. Thus, ash is considered to be a negative factor in predictions of energy for ruminants, and lower ash forages should generally contain higher energy.

However, forages provide several essential minerals contained in the ash fraction. Mineral ions such as Ca, P, and K in forage may be important nutritionally, but it is also clear that may be easily supplied as a supplement to most livestock if deficient.

Some minerals may be negatives for animal nutrition. High K concentration is a negative attribute for dairy animals just before and after calving (often termed the 'close-up' or 'transition' period), as excessive K contributes to an increased incidence of milk fever (postparturient hypocalcemia). Additionally, excessive concentrations of micronutrients (such as selenium [Se] or molybdenum [Mo]) can be toxic when present in high amounts in the diet. Conversely, forages can provide necessary micronutrients that otherwise might be limiting in diets. Nutritionists are often interested in the balance of mineral nutrients in forages (DCAD, see text box).

Other quality factors

There are visual, textural, and olfactory attributes of forage quality that are not easily analyzed in laboratories. The presence of noxious weeds, foreign objects in hay or silage, dirt, secondary plant compounds, aromas or odor, dust, and molds, all may affect animals' performance. Insects (e.g., blister beetle) can be important antinutritional or toxic factors in hay. Each year, many animals are sickened or die from poisonous weeds, excess nitrate (from weeds), botulism (from dead animals), or excess micronutrient concentrations in hay (Puschner *et al.*, 2006). These are all attributes under the umbrella of 'forage quality.'

There are also physical aspects that affect quality (e.g., grind, fiber length, and moisture). Particle size affects the ability of rumen microbes to break down cellulose and hemicellulose in the rumen (Mertens, 2010). Olfactory factors (e.g., odor, dustiness, and chemical attractants that encourage uptake) can influence intake. Contaminants (e.g., toxic weeds, dirt, molds, and toxic insects) can affect palatability, intake, and thus overall quality. Several subjective factors (e.g., visual inspection, touch, and smell) may assist in predicting animal acceptance, but palatability may be less important in total mixed rations (TMRs), because other feeds and additives impact voluntary intake by ruminants.

It should be clear from the above discussions that forage quality is a complex trait that includes a range of factors. These factors are, in turn, influenced by agronomic and environmental factors.

What Influences Forage Quality in Crop Plants?

Forage quality is a function of both species (grass, legume, etc.) and variety within species as well as various management practices (Rotz and Muck, 1994; Ball *et al.*, 2001). The major agronomic factors that affect quality are species (e.g., legumes vs. grasses, warm season vs. cool-season crops), cutting frequency (plant maturity at harvest or grazing), weed and pest management, baling and conditioning effects, and seasonal or weather patterns (Buxton and Fales, 1994; Ball *et al.*, 2001; Putnam *et al.*, 2008a,b). Less significant but still important are the effects of variety, time of day of harvest, soil type, fertility, and irrigation. These factors typically affect quality via two fundamental mechanisms: the leaf:stem ratio and effects on cell structure. Agronomic and environmental factors have a strong influence on total yield and there is normally an inverse relationship between yield and forage quality.

Plant Maturity at Harvest

It is a nearly universal axiom of forage production that as a plant grows and develops, forage quality declines. Immature herbage growth is nearly always higher in quality than more mature forages (Marble, 1974). Therefore, the stage at which the plant is harvested is usually the most critical factor determining forage quality in nearly all forage crops. The exceptions to this rule are seed-producing forage crops, such as corn or sorghum, grain legumes, and small grains that translocate nutrients (protein, starch, and oils) to seeds, but even in those plants, immature vegetative growth is higher in quality than late vegetative growth.

Plant morphology

The change in forage quality due to plant maturity is the result of several powerful mechanisms. First, immature plants tend to be much higher in leaf percentage (**Figures 10** and **11**). Leaf percentage declines as the plant grows, as a percentage of the total plant biomass. In alfalfa, this is primarily due to the increase in stem weight that occurs during growth. In most grasses, tillering and reproductive stages also produce multiple flowering culms that are lower in quality than the leafy immature crop.

The decline in forage quality in alfalfa and many grasses is also due to a reduction in the quality of the stems with advancing maturity. In alfalfa, this is approximately a 0.5 percentage point decline in digestibility (IVDDM) per day, which increases dramatically in NDF and ADF, whereas the quality of leaves declines only very slightly over time, especially in legumes (**Figure 10**).

Additionally, there are changes that take place on the cellular basis. Cell solubles are reduced with plant maturity. These are sugars and soluble proteins that are essentially 100% digestible and decline with maturity. Secondly, the stem fraction develops much more secondary wall (increased lignification and lignin–cellulose complexes), reducing the digestibility of the cell wall fraction as the plant matures.

The NDF fraction reflects cellulose, hemicellulose, and lignin, whereas the ADF fraction largely measures cellulose and lignin (**Figure 11**). As a plant matures, secondary cell wall development leads not only to a higher concentration of NDF but also to fiber that typically becomes more poorly digested in ruminants.

Factors and principles that influence alfalfa quality:

Primary mechanisms
- Plant maturity at harvest
- Leaf percentage
- Mixture with weeds
- Environmental effects

Agronomic factors
- Cutting schedules
- Harvest management
- Rain damage
- Time of day for harvest
- Variety
- Irrigation and soil factors
- Pest interactions

For these reasons, cutting schedule is, overwhelmingly, the most powerful method under a grower's control to manipulate forage quality for herbaceous forages, as both maturity and leaf percentage and even weed intrusion are impacted. In alfalfa, growers have generally gravitated toward early- to late-bud harvests to attain high forage quality, but at great expense of yield and persistence (**Table 3**).

If yield, stand persistence, and weeds were not important, the earliest cutting dates would typically provide the highest

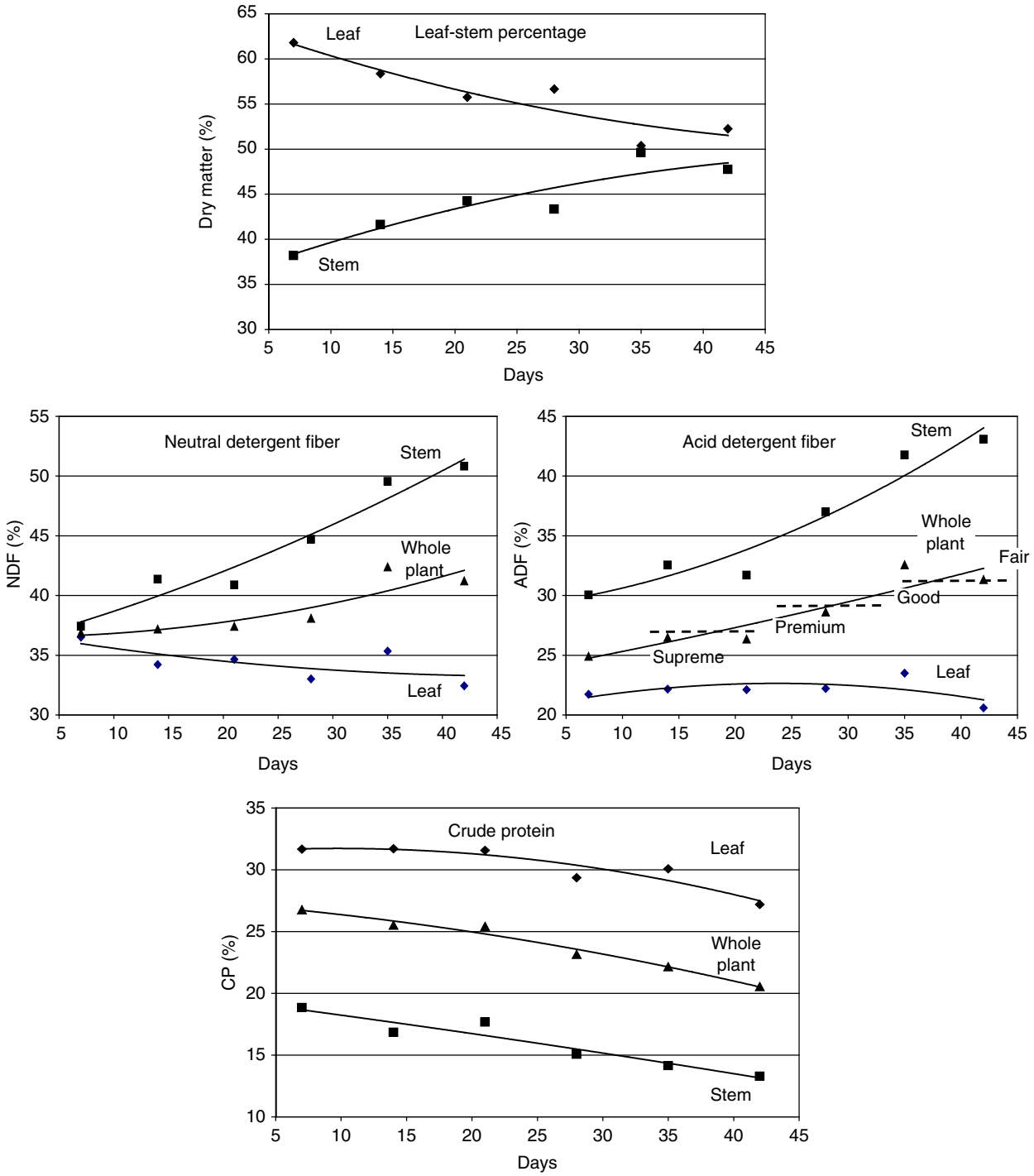


Figure 10 Plant maturity effects on alfalfa dry matter percentage, acid detergent fiber, neutral detergent fiber, and crude protein concentrations of the first growth period, Yolo Co., CA. 'Supreme,' 'Premium,' 'Good,' and 'Fair' are market guidelines as per USDA-Market News. Reproduced from Ackerly, T.L., 2001. Characterizing and predicting the yield/quality tradeoff in alfalfa. MS Thesis. University of California.

quality forage, but this would rarely provide optimum economic returns. The vigorous cutting schedules commonly practiced to attain high quality may ultimately work against high-quality production because stands may thin and weeds may invade (Table 3). Although forage quality is dramatically improved by short cutting schedules (e.g., 21-day intervals), yield is also dramatically reduced, as is stand life, allowing for increases in weed infestation (Table 4). The optimum profitability point as determined by cutting schedule is almost never the point where maximum quality is obtained, nor at the point where maximum yield is obtained (Marble, 1974; Orloff and Putnam, 2010). Clearly, a more integrated

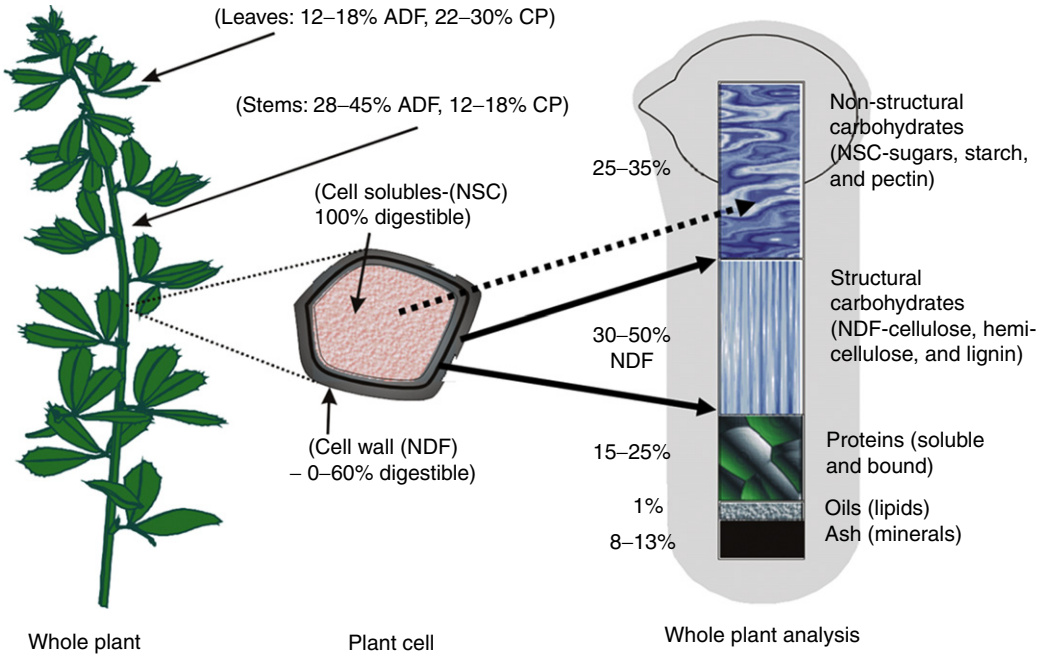


Figure 11 Forage quality (for example in alfalfa) is influenced by both morphological factors (e.g., leaf/stem ratio) and cellular factors (development of the fibrous cell wall and cell-soluble content). Important laboratory measurements for forages include NDF and ADF (structural carbohydrates), crude protein, and ash, as well as *in vitro* NDF digestibility or total DM digestibility. Nonstructural carbohydrates are typically measured indirectly as nonfiber carbohydrates by subtraction from NDF, protein, ash, and lipid. Lipids do not vary much in herbaceous forages and are generally not measured.

Table 4 Effect of maturity at harvest and harvest interval on alfalfa yield, quality, leaf percentage, weeds, and stand life (data from Davis, CA)

Maturity at harvest	*Harvest interval (days)*	*Yield (tons per acre)*	*Acid detergent fiber*	*Crude protein*	*Leaf*	*Weeds*	*Stand percentage*[a]
			%				
Pre-bud	21	7.5	26.3	29.1	58	48	29
Mid-bud	25	8.8	29.5	25.2	56	54	38
10% bloom	29	9.9	32.2	21.3	53	8	45
50% bloom	33	11.4	32.7	18.0	50	0	56
100% bloom	37	11.6	35.5	16.9	47	0	50

[a]Percentage of alfalfa stand after three harvest years.

Source: Data from Marble, V.L., 1974. How cutting schedules and varieties affect yield, quality, and stand life. In: Proceedings, 4th California Alfalfa Symposium. 4–5 December 1974. Davis, CA: University of California, Davis. Available at: http://alfalfa.ucdavis.edu (accessed 14.01.14).

approach balancing yield, quality, persistence, and economics is required.

The process of drying, raking, handling, baling, and storage of forages has long been known to have large effects on forage quality (Rotz and Muck, 1994). For leguminous forages like alfalfa, the leaves dry much faster than stems, and hay is often baled at a point where leaves are too dry for handling. Leaf shatter during haymaking is a significant hazard during harvest and can reduce forage quality by reducing leaf:stem ratio. Any method, irrespective of whether it is mechanical-intensive conditioning, chemical conditioning, wider swath width, or skillful raking that speeds the drying process of stems, may improve forage quality. Grasses tend to be far less sensitive to leaf loss during haymaking than are legumes.

Environmental Services of Forage Crop Systems

> Our goal is permanency in agriculture – an agriculture that is stable and secure
>
> –GRASS – The Yearbook of Agriculture, 1948, USDA

More than any other crop group, forages provide a range of important environmental services that largely escape notice by the general public. The diversity of legumes, grasses, and forb forages support wildlife habitat, build soil quality, stabilize soils from erosion, purify the air and prevent dust pollution, prevent degradation of water quality, suppress weeds, recycle nutrients, provide crop rotation benefits, and assist in mitigation of environmental problems, such as nitrate pollution and greenhouse gas accumulation (Barnes and

Nelson, 2003; Wedin and Russelle, 2007; Karlen *et al.*, 2007; Keeney and Sanderson, 2007; Franzluebbers, 2013; Putnam *et al.*, 2001). Legumes like alfalfa provide a profound service by producing high nitrogen-containing protein with nearly zero fossil fuel-requiring N fertilizers, unlike corn, rice, wheat, and grain crops that use huge quantities of N fertilizers.

However, there are environmental risks and impacts of forage crops that must be considered. Manures are a risk to grazing lands, pasture, and CAFOs, and nitrate contamination of groundwater and air quality problems have been associated with many animal production areas. Forages themselves may provide risks to the environment through crowding out native species (vigorous pasture grasses), or from pesticide runoff (alfalfa).

However, on balance, there are clearly many more environmental services from forages than negatives (Putnam, 2010). Forages have numerous ecological attributes to support robust and sustainable agroecosystems, irrespective of whether they occur as managed forage systems, naturalized grasslands, or native prairies. Perennial grasses and legumes are particularly important to landscape health and sustainability, in addition to providing significant quantities of human food. These services fall into several categories.

Soil Erosion Control

Soils formed under vast grasslands, such as the Central Great Plains of the United States, are very rich, due primarily to the grass ecosystem that builds organic matter over many millennia (Barnes and Nelson, 2003). But in the short run as well, grasses and legumes help to build soil quality due to the many rhizosphere biological interactions (micro- and macroorganisms) and their ability to firmly hold soil in place. The dense forage canopy and extensive rooting patterns prevent both water and wind erosion, and rooting channels provide habitat for invertebrates and create stable aggregates and biopores, furthering plant growth. This landscape provides protection from sheet and rill erosion in agricultural landscapes (**Figure 12**). The value of forage crops to prevent soil erosion, long promoted by the US Soil Conservation Service (now Natural Resources Conservation Service), is a well-established environmental service of forages. Many environmentalists and agronomists have promoted the incorporation of forage legumes and grasses into row crop rotations for their soil building and conservation properties.

Water-Use Efficiency, Water Quality, and Mitigating Water Pollution

Perennial forage crops are highly beneficial for water quality and are highly water-use efficient. Perennial forages grow rapidly after rainfall or irrigation events and capture utilizable water in the root zone due to extensive and deep rooting patterns. Unlike annual crops, which must utilize water during stand establishment to achieve a full canopy, forages begin growing quickly. Dense plant, surface residue, and rhizosphere create stable surface soil aggregates, assisting water infiltration and percolation (Karlen *et al.*, 2007). The extensive root system, fully canopy, combined with the fact that 100% of the above-ground dry matter is harvested, make forage crops one of the most water-use efficient crop species (Putnam, 2012).

Further, water with suspended solids is purified in grassy or leguminous forage stands, benefitting both surface water and groundwater. 'Grassed waterways' are commonly recommended for erodible areas in row crop production systems, but pastures and hay fields themselves serve as natural filtering buffers to improve water quality (Karlen *et al.*, 2007).

Nitrate pollution of groundwater is a frequent concern of agricultural communities. Forage crops, particularly productive grasses and alfalfa, are excellent at absorbing nitrates from

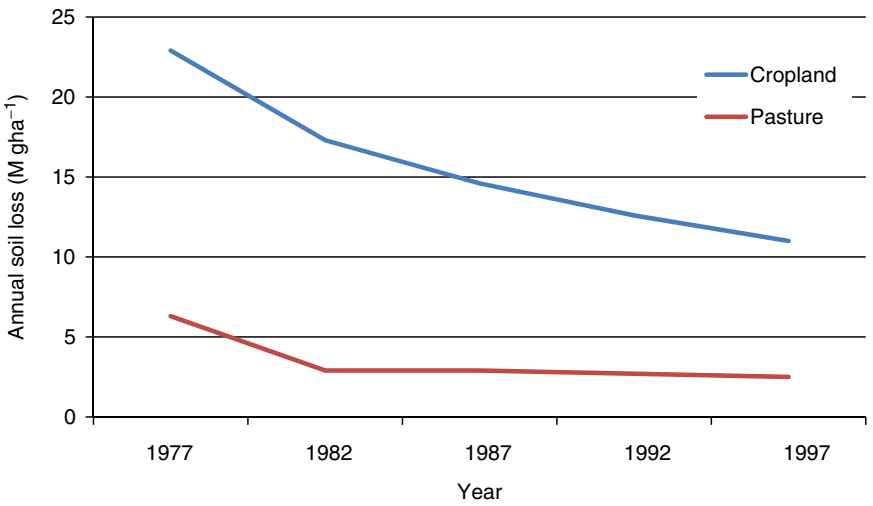


Figure 12 Effects of row crops versus pasture on annual soil erosion losses in Iowa. Although no-till techniques have reduced row crop effects on erosion in recent years, pastureland provides permanent protection for soils. Data from USDA-NRCS, 2007 National Resources Inventory (USDA, 2009).

municipal wastes and from manure sources (Wedin and Russelle, 2007). In the case of alfalfa, N uptake may range from 300 kg ha^{-1} to 900 kg ha^{-1}, depending on yield and protein content of the forage.

Air Quality, Dust Prevention, and Greenhouse Gasses

Productive forage crops generate oxygen and absorb CO_2 from the atmosphere. Additionally, forage canopies protect soils from wind erosion, due to the perennial nature of forages and their vigorous rooting patterns. Protection of erodible soils by forages in windy regions has been widely promoted. Depending on the degree of N fertilizers used, moisture regime, and the animal management system, forage systems can either have positive impacts on greenhouse gas production or have negative impacts (Keeney and Sanderson, 2007). The clearing of grassland sod has been widely recognized as releasing large stores of CO_2 as well as N_2O. Thus, tilled cropping has resulted in carbon losses in plowed prairies, resulting in losses in organic matter concentration of 50–70% (Lal *et al.*, 1998). Whalen *et al.* (2003) found that continuous wheat resulted in 30–39% carbon losses compared with native grassland after just 5 years.

Nutrient Cycling

Deep-rooted forages, such as alfalfa, tend to cycle nutrients from depth, in comparison with row crops (Wedin and Russelle, 2007). Cycling of nutrients under perennial forages are often characterized by a high proportion of nutrients in the organic form compared with annual grain crops. This makes nutrients less susceptible to leaching through the soil (nitrate loss) or dissolved fractions in surface runoff or volatile losses to the atmosphere through denitrification. Soil microbial biomass and N mineralization can be significantly greater under forages than row crops, which improves both nutrient cycling and soil tilth (Arshad *et al.*, 2004).

Wildlife Habitat and Biodiversity

Forage crops are the primary producers at the beginning of a food chain that supports a wide diversity of insects, invertebrates, lizards, mammals, and birds. Alfalfa, which is very high in nutrient value, can support up to 1000 species of insects, most of which do not negatively affect its growth. Grasslands are important providers of wildlife habitat and open spaces worldwide (Franzluebbers, 2013). Migratory waterfowl, raptors, songbirds, and wading birds often prefer forages to even natural landscapes due to the diversity of insects and prey, cover, and stability (Putnam *et al.*, 2001). Endangered or species of concern, such as the Swainson's Hawk, long-billed curlew and, white faced ibis, have been found to prefer alfalfa fields over other landscapes (Hartman and Kyle, 2010). Larger wildlife, such as elk, deer, fox, coyote, snakes, utilize forage fields extensively. Of the >600 species that are listed in the California wildlife database, >28% utilize alfalfa for feeding, cover, or reproduction (Putnam *et al.*, 2001).

The future of forage crops will likely depend both on their important role as a food-producing agroecosystems and the provision of ecosystem services.

See also: Agroforestry: Fodder Trees. Beef Cattle. Biosecurity and Equine Infectious Diseases. Dairy Animals. Soil: Conservation Practices. Soil: Nutrient Cycling

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From Foraging to Agriculture

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Glossary

Adjustment equilibrium Food supply balance achieved between small bands of hunter-gatherers and food available in a given ecological setting.

Annual round of activities Seasonal migration practices of hunter-gatherer bands as they search for food throughout their territories.

Competitive Foraging Strategies Systematic study and analysis how nonhuman primates and contemporary human hunting-gathering bands search for, identify, and forage for food.

Geophagia The practice of consuming clay as a food.

Incipient planting Condition where wild species are removed from bush lands, and either seeded or transplanted adjacent to human settlements for ready access as food or for other utilitarian purposes.

Toxic analogs Describes the condition where a species is safe to consume in one environmental niche but poisonous in another.

Introduction

In the Beginning

The domestication of plants and development of agriculture are relatively recent activities in the vast time span of hominid and human evolution. Scholars interested in these topics have posed and debated a variety of questions for more than a century: how did earliest hominid groups and subsequent human hunting-gathering bands determine what was safe to eat; procure their food resources; and satisfy their basic physiological/health requirements? In subsequent millennia, what factors facilitated the decision for earliest human settlement, stimulated incipient planting, and the development of agriculture? During the long, evolved passage from hunting-gathering livelihoods to settled agriculture, how and why were certain plants selected and ultimately domesticated?

A basic consideration in understanding agriculture and plant domestication is separating conscious from unconscious decisions: human settlement and the development of agriculture were conscious choices whereas initial plant domestication processes were not. In essence, individuals and early hunter-gatherer bands decided to cultivate; they did not decide to domesticate crops because it was the basic process of selecting and gathering wild plants that initiated the steps toward domestication. Plant eco-niches were modified through time as hominids and early humans foraged and selected their respective food and nonfood items from vast arrays of plant assemblages. Domestication has been a long-standing, continuous, unconscious process that predates human settlement and agriculture, as visualized in the following schematic (Figure 1).

Consensus suggests that human-like hominids developed initially in the warm tropical savannah regions of what is now east Africa perhaps 2.3 million years ago (Clark, 1980; Strait *et al.*, 1997). Much speculation has surrounded the presumed primary food patterns of these early hominids: were they vegetarians, meat-eaters, or omnivores? The answer, however, is seen on inspection of jaw and teeth structures of both ancient hominids and modern human descendants: both groups exhibit characteristic molars for seed grinding and shortened canines, a dental pattern that reflects a mixed diet of both plant and animal foods (Le Gros Clark, 1955; Jolly, 1970; Isaac, 1971; Walker, 1981; Teaford and Ungar, 2000; Rodman, 2002; Ungar and Teaford, 2002; Unger *et al.*, 2006).

Long after the initial stages of plant domestication humans settled and subsequently planted and tended crops. What has been called agricultural revolution occurred at different times globally at widely separated geographical locations. Earliest evidence for settled agriculture stems from East Asia in a geographical zone encompassed today by southwestern China and northwestern Vietnam and Laos during what is called the Hoabinhian Period, dated to c. 15 000 BCE (Gorman, 1969, 1971; Solheim, 1972). Dates for settlement and agriculture in the so-called Fertile Crescent of the Middle East are somewhat later, attributed to c. 11–8000 BCE (Zohary and Hopf, 2000), whereas settlement and plant domestication in different parts of the New World, specifically in Mexico and the highland Andes region, date to 6000 BCE and 4000 BCE, respectively (Bellwood, 2005). Because early human-like hominids

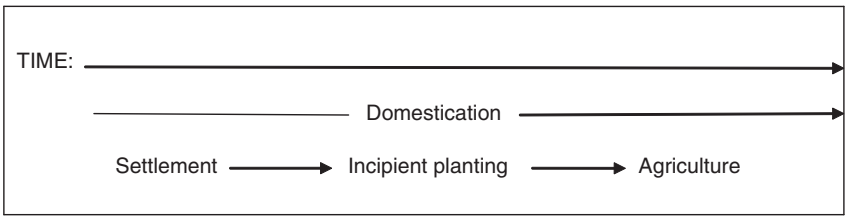


Figure 1 Settlement-agriculture-domestication schematic.

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evolved more than 2 million years ago, for the vast majority of time they hunted, foraged, and scavenged for food.

Ethnographic studies of modern twentieth and twenty-first centuries hunter-gatherer societies offer complementary insights on the early human quest for food. Such groups throughout antiquity into the twenty-first century are defined uniformly by their lack of agriculture and domesticated plants or animals (save the dog) and by food patterns based solely on plant and animal bush products that are highly diverse and varied (Heinz and Maguire, 1974; Lee, 1979). Such hunting-gathering groups in the twenty-first century exist in narrowly defined regions of Asia, Africa, the Americas, and Oceania where small bands usually numbering less than 40 individuals follow their traditional lifestyles through what is called the annual round of activity, a repetitive migration pattern through different ecological zones where the hunter-gatherer bands follow wild game and gather plant products (Anderson, 2004). Such groups eke their livelihood through a mix of gender-specific activities where adult males primarily hunt, while adult women and girls primarily gather plants and plant products, although exceptions are known where women participate in hunting activities and adult males sometimes participate in gathering plants/plant products. Although these small groups commonly are known as hunter-gatherers, in reality female gathering activities commonly provide the vast bulk of food resources for the band, a behavior that suggests more realistic terms such as collector-predator or gatherer-hunter societies should be applied (Dornstreich, 1973; Hiatt, 1970; Teleki, 1975; Garber, 1987; Domínguez-Rodrigo, 2002).

Scavenging, Hunting/Gathering, Fire, and Cooking

Studies of free-ranging primates (baboons) confirm that when meat, animal products, and insects are available for consumption, these items are preferred over available plant foods (Hamilton *et al.*, 1978; Hamilton and Busse, 1978). In contrast, studies of contemporary human hunting-gathering bands suggest that earliest hominid societies would have formed food patterns that contained reasonably balanced quantities of wild plants and animal products (Lee, 1979; Lee and DeVore, 1968). This dichotomy – meat versus plant-based patterns – poses an enigma because the majority of wild plants growing in any ecological niche potentially are toxic to humans (Leopold and Ardrey, 1972a, 1972b). Foraging through the bush to collect plant food resources, whether berries/fruits, leaves, nuts/seeds, or tubers, would not have been simply making selections from wild food offerings. The African savannah where humans evolved would have represented an environment where most ancient (as well as recent humans) had to resolve a basic issue: how to identify consumables safe to eat so not to be poisoned by bush plants.

One key to solving the safe versus toxic plant problem was advanced in the early 1970s. The argument posed was that the ability to make and maintain fire led to cooking and cooking, in turn, rendered a significant suite of available plants and plant products safe to consume (Leopold and Ardrey, 1972a, 1972b). Cooking plant foods would have improved the survivability of these early consumers because enzyme inhibitors in legumes and cereals would be denatured; physiological irritants such as saponins as well as lathyrogens, irritant oils, and cyanogenic compounds reduced or neutralized; some allergens would have been deactivated; and compounds that interfered with hominid hormonal systems, goiter-producing compounds, and vitamin and amino acid antagonists also would have been reduced (Leopold and Ardrey, 1972a, 1972b). Cooking also would have improved digestibility of plants, the bioavailability of nutrients, and caloric value of cooked foods would have been increased compared to raw foods (Wrangham and Carmody, 2010; Carmody *et al.*, 2011).

Yet early hominids and human hunter-gatherer populations lived without benefit of fire and cooked foods for most of their existence. Earliest archeological evidence for the ability of hominids to make, maintain, and use fire is highly variable by global geographical region: dated to 300–400 000 BP in Europe (Roebroeks and Villa, 2011); 790 000 BP in the Middle East (Goren-Inbar *et al.*, 2004; and c. 1 000 000 BP in Northern Cape Province, South Africa (Berna *et al.*, 2012).

Food Safety

For the vast majority of time early hominids and humans existed they did so without the benefit of regular cooking fires. Throughout this lengthy time period hunting-gathering groups had to determine what was safe to eat. One consideration could have been to focus on wild plant products that were sweet and to reject bitter items. Still, some sweet plant products (berries, leaves, roots) can be toxic, and some bitter plants/plant parts can be safe to consume.

Regarding meat and animal products earliest hominids and humans would have been scavengers and only rarely would have killed large game (Shipman, 1983). They would have consumed smaller animals, scavenged carrion, and eaten the digestive stomach contents of animals previously killed by predators. Scavenging from kills made by larger savannah predators, hunting smaller game, gleaning berries and fruits, nuts, and pods, and digging for and washing/stripping tubers would have presented options that were either safe or toxic to consume. Identifying what was safe to consume in a specific environmental niche remained the first problem that had to be solved, one that has continued into historic times as well. If food safety was learned only through basic trial and error, then untold numbers of hunting-gathering band members would have died periodically because of toxic plant poisoning.

In solving this problem early hominids might have observed what birds or mammals ate and followed such patterns? Eating carrion from fresh or older kills made by carnivorous predators also could have been an early hominid food pattern. (Although Jewish, Christian, and Muslim religious texts decry and condemn the consumption of carrion, the baTlokwa ba Moshaweng of southeastern Botswana have no taboos against the practice and regularly practiced carrion consumption (Grivetti, 1976). Some minority societies in Europe regularly have feasted on carrion (Petrovic, 1939).) William Hamilton and his research team studied free-ranging baboons in the Okavango region of northern Botswana and reported that members of the troop ate widely across the available plant spectrum, consumed large quantities of ripe and unripe fruits, dug for tubers, and stripped and ate a broad range of grass

seeds (Hamilton *et al.*, 1978). These baboons, however, regularly vomited as they foraged for food. Further, they ate large quantities of clay throughout the day (Hamilton, personal communication, 1990). Such a pattern of eating clay along with wild bush plants could have been an unconscious mechanism that protected these hominid consumers. Given that the practice (geophagia) can lessen the absorption and physiological effects of certain categories of plant toxins (Halstead, 1968). Further, contemporary studies document that if consumers vomit after eating, this result can lead to future rejection of the offending products (Garb and Stunkard, 1974; Stockhorst *et al.*, 2006). Perhaps through such methods and through basic trial and error, the hominid consumers could have learned and ultimately differentiated between 'safe' and 'toxic.'

Determination of food safety might also have come about through potential 'selective filters' consciously or unconsciously that led earliest hominids and early humans to initially identify and repeat consumption of safe foods. Although dogs were domesticated c. 30 000 BP canines have served more recent hunter-gatherers to determine which bush plants are safe to consume. The Gwembe Tonga of southern Africa, a contemporary agro-pastoral-hunting-gathering society, allow their children to forage in bush lands without adult supervision where they search for and experiment with different plants as potential foods. When a questionable species is encountered, presumed edible portions initially are fed to their companion dogs. The children observe the canine's behavior and after a reasonable period of time – if the dogs do not vomit and survive – then the adventurous children may taste and eat the new plant (Scudder, 1971).

Might human 'tasters' also have been used in early antiquity to test the safety of new plants or suspicious items? Could they have been adults captured from rival bands; perhaps women beyond childbearing years; aged men who had lost their hunting acuity; or perhaps the sick or the infirm? (The third century Egyptian-Greek writer Athenaeus addressed the issue of the ancients using elderly women as food tasters (Athenaeus, IV:172:A) and regular reports document that Southeast Asian immigrants to the US have been poisoned after incautious foraging and consuming what they believed to be species safe to eat (Fischer, n.d.).) Although such suggestions pose moral and ethical considerations when examined through contemporary twenty-first century prisms, would such cultural niceties have characterized earliest hunting-gathering groups?

Learning the safe plant foods in one niche, however, would not necessarily extend safety into other ecological zones, as the botanical assemblages might contain items that only appeared similar to safe items. Identical species that grow in two different environmental niches can pose problems: plants safe to eat in one ecological zone, but poisonous in another niche, are called 'toxic analogs.' Toxic analogs look nearly identical to species already accepted as safe foods and illness and/or death from such plants has remained a perpetual problem facing hunting-gathering groups in antiquity and sometimes even modern societies today (Gadd *et al.*, 1962; Scudder, 1971; Beug, 2005).

Ultimately hunting-gathering bands would have expanded their territorial ranges leaving the warm, moist tropical regions of eastern Africa to explore and exploit more temperate and colder climes and ultimately extended the early human geographical range into global subarctic and arctic zones. In addition, consider massive human movements such as the peopling of the Americas, crossing the Bering Sea land bridge, and how hunting-gathering bands worked their way southward toward the equator – eating along the way. Recent evidence suggests that the people of the Americas occurred in multiple pulses from Asia and possibly from Europe (Bradley and Stanford, 2004; Fagundes *et al.*, 2008). Moving from north to south through what is now Alaska to what is now southern Chile, many dozens of ecological zones would have been negotiated and food safety issues solved. From twenty-first century vantage points we may only speculate how safety was learned and transmitted throughout the millennia.

Nutritional Balance and Competitive Foraging Strategies

As the food safety issue was solved, there remained issues of dietary adequacy and overall nutritional balance. If ancient hunter-gatherers subsisted on a diet that was deficient in energy, protein, or essential vitamins or minerals, the group would languish; individuals would become weak or ill; and either would have succumbed directly to dietary imbalance or easily predated (Speth and Spielmann, 1983; Speth, 1987). Countering this 'survival of the fittest' view is one suggested since the 1920s that humans (infants) instinctively know what to eat and how to balance their food intake patterns and diet (Davis, 1928, 1939). By extension some have speculated that early humans might have exhibited an inborn mechanism that assured dietary balance. Most nutritionists today, however, reject this view because careful examination of the 'self-selection' research conducted in the 1920–30s does not support this contention (Story and Brown, 1987). Early hominid and human consumers could not have determined or known what constituted a physiologically or nutritionally balanced diet: there is no 'felt need' for protein or for specific vitamins or mineral. The problem would have been solved, therefore, through natural selection: good food intake patterns would have evolved through trial and error; those hominids and early humans with sound patterns survived and reproduced; those who made poor food intake choices did not. Contemporary hunter-gatherer bands in the Kalahari Desert of southern Africa, for example, have continued to exhibit basic good health and overall sound nutrition without the aid of twentieth or twenty-first century theories (Truswell and Hansen, 1968; Truswell, 1977).

Competitive foraging strategy analysis has been used by behaviorists (ethologists) to investigate and categorize the food patterns, band movements, and interanimal activities. Among free-ranging primate troops, males and females with highest status (identified as Alphas) enter prospective plant zones to forage for food; troop members with lower status remain along the periphery and wait until the Alphas have finished eating before entering the zones. During their time in the food zones, the Alphas will have stripped and gleaned most of the edible foods leaving behind less favored items. Those lowest in troop social status (identified as Omegas) remain along the periphery for longest periods of time and

invade the food resource areas only after the Alphas have eaten and moved on to other localities. Time is a great enemy to the Omegas because lingering along the periphery presents greater risk through predation. In addition, the Omegas who eat last from the residual food resources experience reduced food selection opportunities and potential dietary imbalance. Poor diets through time lead to malnutrition: the Omegas then become weak, eventually ill, and are easily predated. The well-fed Alphas continue their lives, mate with the best females and reproduce, and the band survives. This natural selection process could result in sustained and potentially repeated food patterns by the Alphas who if their food intake patterns were balanced nutritionally, the pattern could continue into the next generation. In contrast, the Omegas gradually would vanish as the strong survived (Pyke *et al*., 1977; Hladik, 1981).

Just being an Alpha, however, does not assure that the knowledge of what is safe and not safe to consume is transmitted to other troop members or to subsequent generations because food sharing among most nonhuman primates has not been observed. William Hamilton's team of primate researchers working in the Okavango region of northern Botswana never recorded instances where adult male or female baboons picked, dug, or striped plants and then shared the food items with other adults, juveniles, or infants. (Hamilton personal communications, 1985–90). Sanford Harcourt working among gorillas in Rwanda, never recorded that these great apes offered or shared food with adults or juveniles (Harcourt, personal communication, 2013). One general explanation for this 'personalized egocentric' behavior has to do with limited brain development and intelligence, which sets early hominids apart from early humans. Still, food-sharing behavior among other nonhuman primates has been reported, specifically by chimpanzees, douc monkeys, and gibbons (Kavanagh, 1972).

Could it be that food safety and ultimately dietary balance was transmitted to infants through observation and mimicking what their mothers had consumed, or perhaps infants nuzzling adult females to obtain scents of foods just eaten? However, given that free-ranging primates and early humans ate broadly and widely across the spectrum of available plant and animal items, it seems likely that dietary and nutritional balance came about through natural selection and survival-of-the-fittest processes – provided they were not poisoned.

Food Security

Through the millennia hunting-gathering bands ultimately solved these food safety and nutritional balance problems. Having enough to eat, however, during wet and dry seasons within the tropics and during colder/warmer periods when bands ranged outside the tropics, remained still another problem. So long as band size remained small (c. 30–40 individuals), 'adjustment equilibriums' would have evolved where foraging/hunting did not outstrip the available food resources in specific occupation regions.

Food storage, however, would require a formidable conscious decision, given the ease of hunting-gathering through well-traveled ecological zones familiar to the band. Amassing a large quantity of gathered foods would make little sense to hunter-gatherers conditioned to a pattern of hunting-gathering their food needs on a regular basis. Yet, what if through trial and error some groups discovered that left over grain could be fermented to produce a mind-altering beverage? The possibility then could be that some band members might make conscious decisions to gather grain in excess, develop pits for storage, and convert a portion into beer (Katz and Voigt, 1987).

Plant Selection and Incipient Cultivation

Study of contemporary hunter-gatherer societies during the past 150 years has revealed that they exhibit wide knowledge of plant availability and uses for esthetic decorative items, clothing, cooking devices, cosmetics, dye, fiber, food, medicine, poisons, toys, weapons, and other utilitarian needs. Some plants merely would have been gathered; others dug up, harvested, or berries, nuts, seeds, or tubers collected and some of these could have been planted adjacent to hunting-gathering encampments. Such could be the case where shamans gathered and transplanted medicinal and/or ritual species to have more easy access. The present author observed this practice when working among the baTlokwa ba Moshaweng in the eastern Kalahari Desert of modern Botswana – where medicinal species had been planted adjacent to homesteads of traditional healers that had continued to flourish long after the sites had been abandoned. Such limited planting without tending or cultivation is not agriculture, *per se*. The present author also observed that the baTlokwa also regularly dug up more than 50 wild bush species and transplanted them in their settlement compounds: only five of these species, however, served as food and the vast majority provided social/cultural needs for esthetics (attractive blooms), dye, fiber, medicine, and magical/protective charms (Grivetti, 1976).

Human Settlement and Development of Agriculture

Settlement and the subsequent development of agriculture radically changed forever human societies. Agriculture in the strict sense cannot predate human settlement. Planted gardens/fields need to be watered, tended, and protected lest mature plants be stripped by wild animals or competing rival human groups. Questions where and why settlement initially occurred, as well as how and why incipient planting and agriculture developed, have been debated by anthropologists, botanists, geographers, and others for more than a century (Ucko and Dimbleby, 1969; Isaac, 1970; Gepts, 2004; Grivetti, 2004).

Settlement also reflects individual or collective decisions whether or not to continue hunting and gathering, whether or not to remain mobile during portions of the year, or to take the drastic economic step and become sedentary. It is reasonable that early settlers could do so only in the midst of wild plant food abundance, where the initial 'settlement' might be perceived as a central node where band members not only could initiate the process of growing plants for food and other needs, but also hunt and gather in different directions (perhaps up and down slope if settled in a highland region) which would allow selections from within a highly diversified range of plant resources. Such clan-based decisions to become

sedentary also would require stable and reliable water resources, perhaps adjacent to lakes or rivers. Other potential areas for settlement could have been near oceanic shores where clan members could take advantage of intertidal organisms, hunt marine mammals, and fish, and augment their diets by gathering plants (Braidwood, 1960; Sauer, 1969; Sauer, 1972).

Initial settlements, however, need not have been stable or have led to incipient planting. Within bands of hunter-gatherers, there could have been individual and/or collective decisions to settle based on specific nonfood needs: perhaps illness/infirmity of key band members could have led to temporary year around or seasonal settlements where the annual round of activities would have been abandoned until the group decided to move on as before. Small groups within larger bands of hunter-gatherers might have elected to stay at a localized camp, but for such a group to flourish both genders would be represented, especially women of childbearing age. Such early settlements would require joint decisions how to protect against predator animals and/or against potential raiders from competitive bands.

As decisions to settle were made a suite of potential problems unrelated to incipient planting and ultimately to agriculture would have occurred. Earliest settlements would experience increased populations and a complementary rise in population density and a corresponding higher risk for illness and disease caused by more frequent human-to-human contact, coupled with probable contamination of water resources (Heizer, 1978). Intensive gathering would have continued in lands adjacent to these early settlements, and as locally available food resources became in short supply the adjustment equilibrium would change dramatically requiring further and further treks into the bush to obtain wild food resources.

There then could come a time when it became obvious to certain settled band members that seeds or roots of preferred species could be planted near the settlements to stabilize the food supply and meet other utilitarian needs whether for dye, fiber, medicine, perhaps religious uses. Such incipient planting activities would reduce the need for longer treks into the bush for game and wild plants. The process of selecting utilitarian plants to grow already would have been in place, and as culling practices altered gene pools and the species grown became distinct from their wild progenitors, the process of plant domestication would be achieved (Helbaek, 1959; Ucko and Dimbleby, 1969; Isaac, 1970; Cowan and Watson, 1992; Gepts, 2004).

Earliest Agriculture: Theories and Constructs

Some have suggested that the transition from hunting-gathering livelihoods to settlement, to incipient cultivation, and to agriculture were lengthy processes. These processes while lengthy could have been facilitated by observational behaviors that ultimately resulted in cultivation.

Predisposing Factors

The argument has been advanced that hunter-gatherers must be predisposed to perceive the potential value of incipient cultivation. Predisposed in this context would be similar to the case where Alexander Fleming recognized the importance and implications of the contamination of his agar-plated laboratory dishes and the 'ring of inhibition' that ultimately led to the recognition and isolation of penicillin – because he was 'predisposed' to consider why the 'ring of inhibition' was present (Macfarlane, 1984). Two predisposing factors have been advanced as processes that could have led early hunter-gatherers to perceive that certain wild plants might be grown near their campsites. At the core of both is the notion that before incipient cultivation and formal agriculture could be implemented, wild plants with potential food or other utilitarian uses first had to be brought into a proximal relationship with hunter-gatherer encampments.

Animals as seed concentrators

Through digestion and excretory processes wild animals and subsequently domesticated animals serve as selective filters as they graze through the plant kingdom. The berries, fruits, and seeds consumed ultimately fit two categories: items totally digested, and those where the partially digested seeds remain viable in animal feces. Although not tempting from twenty-first century perspectives, the feces of many wild herbivores – and domesticated mammals as well – may be harvested for human food through 'fecal gleaning,' where animal droppings are examined for undigested seeds that could also serve as human food. The baTlokwa ba Moshaweng of the eastern Kalahari Desert feed fruits of *Sclerocarya kaffra* to their goats; the goats digest the soft outer pulp, while the kernels pass out with the feces. These 'goat-gut treated' nuts subsequently are collected, washed, dried, and consumed by women as special dietary treats during pregnancy (Grivetti, 1976).

Goats from the baTlokwa family herds are let out from their pens in the morning to forage widely within adjacent bush lands then are re-penned at night. During the dry season dung accumulates in the goat *kraals* and so long as the goats remained penned, any seeds that might be viable cannot sprout or grow because of repetitive hoof actions. With the arrival of seasonal rains the goat *kraal* floors become sloppy; coats of the goats are washed; and the animals removed and penned in newly constructed *kraals*. The seed-rich nitrogenous ground inside the abandoned *kraals* then burst forth with new growth and so-called 'goat-*kraal* garden' are created. Young girls then are sent to inspect the previously abandoned goat *kraals* and report whether or not useful plants are present. If so, these areas are re-fenced with acacia branches and the enclosures treated, collectively, as family properties for harvesting (Grivetti, 1976; Grivetti, 1980).

The goats in this baTlokwa system acted as 'selective filters' and brought a spectrum of plants into proximal relationships with humans. Given that goats may be among the earliest animals to be domesticated, and that animal domestication preceded agriculture (Reed, 1959), might it have been that animals serving as seed concentrators contributed to incipient cultivation and eventually to the development of agriculture?

Humans as seed concentrators

The thesis proposed by Edgar Anderson known as the 'garbage dump hypothesis' also casts light on potential incipient cultivation, earliest agriculture and plant domestication.

Hunter-gatherer bands establish temporary camps at well-defined locations during their annual round of activities that are revisited during subsequent periods. Such groups keep their camps relatively clean of garbage and human excreta so their 'garbage dumps' are located along the periphery of these temporary camps. After hunting-gathering groups have returned to an earlier encampment, one of the initial activities is to inspect the peripheral 'garbage dump' for possible utilitarian uses. Growing from such sites are seeds that germinated from discarded food and human excreta. Anderson suggested that if certain individuals in the hunting bands were predisposed to and perceived the utilitarian value of such garbage dumps, it would not be a difficult leap forward to the idea of transplanting favorite plant species – and incipient cultivation would result (Anderson, 1952; Hughes *et al.*, 2007).

Purposeful Constructs

Some scholars have argued that the development of agriculture was driven by specific human need-based decisions, considerations sometimes called economic or purposeful views or constructs.

Sudden insight

Some fiction writers have suggested that stone-age persons – men or women – suddenly developed the brilliant idea: let us go out and start raising beans or grains – for whatever purpose. The thesis advanced suggests that some individuals became tired of their nomadic existence and perpetual roaming in the quest for game and wild plants. This thesis, in one form or another, has appeared in popular literature (cf. Michener, 1965). Sudden insight – also called the 'good idea' concept – commonly is articulated like this:

> I'm tired of walking long distances and spending most waking hours looking for food; let us settle and not follow the herds of wild game; after we settle we can plant wild foods near our encampment and when the plants grow we will have all the food we need.

Could be that individuals just decided to settle because they were tired? Or perhaps some groups settled because band leaders (Alphas) were injured and unable to travel with the remainder of the band? Regardless of motivation early bands would have done so in the midst of food plenty among plant species already known and consumed.

Hunger and necessity

The oft spoken adage 'necessity is the mother of invention' sometimes has been applied to understanding settlement and the development of agriculture. Some have argued that agriculture came about because of the need to incessant hunger or to offset famine. The argument goes that continued hunger drove early hunter-gatherers to develop their stable food supply through agriculture (Cohen, 1977).

Hunger and famine, however, need not lead to planting and agriculture because there is not enough time for the solution to solve the need. Evidence from recent centuries demonstrates that individuals and families either cope with famine – or die. Further, hunger strike survival rates reveal that most adult individuals – if already well-fed, in good health and with access to water – can exist without food only for 40–60 days (Collins, 1986; Rodriguez *et al.*, 1993). During periods of extended food deprivation individuals become lethargic and have little energy for cultivation and agricultural pursuits (Richards, 1932; Keys, 1950; Matalas and Grivetti, 2007).

Environmental desiccation

Some scholars have argued that during periods of major climatic change and drought, environmental desiccation drove humans and animals into riverine environments. such as valleys of the Nile, Tigris-Euphrates, Indus, and Yangtze (Childe, 1936, 1951). It is argued that once inside these well-watered river zones, humans and animals competed for space, food, and water needs, and the development of agriculture and domestication of plants were the results of these interactions brought about by proximity (Braidwood, 1960).

River valleys could offer safe-havens for hunting-gathering bands searching during drought for stable water supplies. But river valleys flood periodically and without the skills to manage water, annual flooding would be a constant challenge to early hunter-gatherers and/or early settlers if attempting to cultivate. Still, living in population-dense river valleys would have forced people together with animals and plants; herds then would have been culled and the botanical array extensively harvested and selected for specific traits. Perhaps some plants and animals were easier than others to work with, to transplant, to tame, or to manage? Evidence from ancient Egyptian tomb art depicts historical attempts to tame and perhaps domesticate ibex and hyena. But attempts with these animals were not successful and were abandoned. Thus, mere proximity to specific plants and/or animals may or may not have led to the development of agriculture or to animal domestication (Darby *et al.*, 1977).

Population pressure/density

One popular thesis holds that the need for humans to eat and to maintain a stable food supply ultimately led to domestication and agriculture. In this instance the 'necessity' was pressure for land or space. Proponents of this theory claim that the prime mover was population density, where increased population pressure on a given landscape area offering edible wild plants, ultimately forced humans to settle and raise crops. The explanation offered considers there were simply too many people around settlement campfires, too many mouths to feed, so population pressure/density and the need to feed more individuals ultimately led to agriculture (Cohen, 1977).

Degenerate hunters

At the heart of the degenerate hunter thesis – sometimes called the 'poor shot' or 'beer-brewing thesis' – is the view that the best hunters in early hunter-gatherer groups ultimately became discouraged with the poor hunting skills of others in the band. The argument follows that hunting bands split: excellent hunters went in one direction, whereas those with poor hunting skills remained behind and settled in locations with abundant wild cereals. The thesis holds that through a long process some band members learned to ferment quantities of excess wild grain into beer. Because each band would be composed of both excellent and poor hunters, it could have come about that the best hunters ultimately became

discouraged in having to share meat with those band units unable to 'do their fair share.' Proponents of the degenerate hunter thesis argue that the best hunters made decisions with far-reaching implications:

> You no longer will hunt; you and your women remain in camp and gather wild grains; we will continue as before and hunt; we will supply you with meat – you will provide us with beer.

And the theory contends that from this dichotomy the degenerate hunters tended and protected stands of wild barley and wheat and from these harvesting/culling actions grains agriculture and domestication evolved (Katz and Voigt, 1987).

This thesis suggests, too, that agriculture ultimately develop because early humans initially sought plants for their mind-altering, drug-inducing capabilities. Plants containing seeds that could be sprouted and fermented would have been favored over others and used for production of alcoholic beverages. Proponents suggest that it was the discovery of alcoholic stupor and desire to experience repeated intoxication that was the impetus for cereal agriculture and ultimately – settlements, villages, towns, and technological advances made by settled peoples – whereas the best hunters continued in their annual rounds of activities, did not domesticate, develop agriculture, or achieve technological benefits.

Contemporary studies of hunting-gathering groups, however, provide insights on processes whereby individuals with disparate hunting skills remain associated with the same bands. The !Kung Bushmen of the northwestern Kalahari Desert practice two such behaviors that keep the best hunters from 'hiving-off,' taking women and leaving less gifted hunters to their 'agricultural' fate. One such mechanism is that !Kung hunting arrows carry specific markings that identify their owners; before leaving camp, the men share arrows in a manner that the quivers of the best hunters contain arrows belonging to others who may be 'poor shots.' When an elite hunter kills a large beast he is required to share half the meat with the owner of the arrow used to kill the animal, a process that assures that meat is shared among the various band members and not just within the immediate family unit of the best hunter. The second behavior occurs when one of the best hunters kills an animal: other hunters subsequently deprecate his skills and heap scorn on him, saying 'lucky shot' and other derisive comments. Arrow trading and such comments serve the function of reducing egotism among the best hunters – so the 'good shots' do not become self-centered and decide to leave (Marshall, 1957; Lee and DeVore, 1968; Lee, 1969; Lee, 1979).

Unconscious Constructs

Still other scholars reject such economic or purposeful factors and hold that the development of agriculture had no 'prime motivations.'

Intimate knowledge

This thesis holds that during the process of managing everyday life humans unconsciously alter their environmental setting. Early humans readily utilized both plants and animals whether for food or other purposes. In doing so humans gained an intimate knowledge of the local flora and fauna for different purposes whether for dye, fiber, food, medicine, mind altering drugs, toxins for arrow poisons, and perhaps religious uses. In gathering these species and ultimately practicing incipient planting adjacent to campsites, the environmental setting and gene pools unconsciously were altered and the process leading to domestication was accelerated (Anderson, 1952; Sauer, 1969; Sauer, 1972).

Mutual domestication

The theory holds that human gathering of wild plants never would have been random because examples gathered would have been selected for a range of needs and impulses, of which use as human food was merely one. Massive and long-term culling of stands of wild plant species ultimately produced a genetic shift away from the wild progenitor. It has been argued that both plants and humans produced evolutionary changes in both directions: that human physiology changed as domestication of carbohydrate-rich plant foods advanced and plants changed and became codependent on humans and in some instances such as maize, required human involvement and supervision for propagation (Rindos, 1984).

Agriculture-Domestication Enigma Revisited

Scholars have examined and debated preconditions and the various agriculture and plant domestication theories for many decades. Within these debates four basic issues for consideration have remained.

Why Settle?

Before the development of agriculture, all people lived as hunter-gatherers. Hunter-gatherer are not settled and move in well-defined annual routes during their annual round of activities, and move through broad territorial ranges in search of game and plant foods. Agriculture, in contrast, requires a settled lifestyle, a social-economic pattern divorced and unrelated to the previous lifestyle where hunter-gatherers migrated in search of food.

Carl Sauer argued that agriculture developed among 'sophisticated fishing societies,' groups of hunter-gatherers already settled along the shores of highland lakes, or perhaps along coastal strips where they fished, hunted, and collected plants (Sauer, 1969, 1972). Solomon Katz suggested that settlement and first agriculture evolved, instead, from 'gatherer groups' left behind by better hunters where the prime motivation for settlement was the preparation of intoxicating beverages (Katz and Voigt, 1987). Both arguments place earliest settlements in zones of wild plant abundance and diversity. The Katz thesis placed earliest settlers in the midst of food plenty where they subsequently adopted a sedentary lifestyle. The Sauer thesis considered that the bands already were settled but continued to hunt and gather up and down slope to obtain plants for utilitarian purposes. But with ample supplies of fish and/or other animals for hunting, coupled with and an already rich plant food base, why would such groups start to grow plants given the available species diversity?

Why Settle in the Midst of Plenty?

Nikolai Vavilov the Soviet botanist and plant geneticist developed a widely considered thesis that has served as one of the foundation stones for the discussion of early agriculture and plant domestication. Vavilov argued that geographical locations that exhibited the highest hybrid diversity were the earliest locations for agriculture: most hybrids – most ancient agriculture and domestication. What became known as Vavilov's 'Centers of Diversity' were distributed geographically within Africa, the Americas, Asia, and Europe (Vavilov, 1949). The Vavilov center concept continues to present students of agricultural origins with a basic problem: why would hunter-gather societies settle and cultivate food plants in the midst of geographical zones of wild food plenty?

Jack Harlan traveled to southeastern Turkey/northwestern Syria – and conducted a simple experiment. This was the earliest geographical location where Vavilov argued that barley/wheat had been domesticated and cultivated based on highest frequencies of hybrids. Harlan took a primitive flint tool and started harvesting wild wheat. In a very short time he had obtained enough wild grain that could have fed a family of hungry hunters-gatherers for several weeks: with such conditions and ease of collection, why would settlements and agriculture develop (Harlan, 1967)?

Harlan concluded there would be no pressure to settle or ultimately develop agriculture: and offered a counter proposal, one he called 'The Noncenter Thesis.' He suggested that settlement and earliest agriculture would have taken place along the peripheries of the Vavilov 'Centers,' in geographical areas that provided the impetus for initial incipient planting and ultimately the development of a stable food supply (Harlan, 1971).

The 'Center' versus 'Noncenter' debate continues: those who support Vavilov must provide solutions to the question why hunter-gatherers would develop agriculture in the midst of such wild food abundance. Those who support Harlan must answer why agriculture would develop at the periphery of the 'centers' where the archeological evidence remains controversial.

Why Domesticate Toxic Plants?

A third controversial supposition suggests that in some geographical areas earliest cultivation and domestication was not for food but was driven by utilitarian needs for plants that could be processed for their toxins and used to kill fish or other game. Such an example of a toxic plant that ultimately can serve as a human food resource is manioc or cassava (*Manihot esculenta*).

Manioc was domesticated and initially cultivated in tropical South America in the Amazon basin perhaps 10 000 BP (Olsen and Schaal, 1999). Manioc roots contain significant quantities of cyanide, must be processed, and the poison eliminated before the starchy residue is suitable for human consumption. How would it be possible to recognize that a poisonous plant could serve as a potential food resource without first developing the technology to render it safe for human consumption? The only logical conclusion to be drawn is that manioc initially was selected, cultivated, and ultimately domesticated for its toxic properties before recognition that after processing it could serve as a food resource.

More than 50 years ago the botanist Edgar Anderson proposed that food was not the primary rationale behind plant selection and ultimate domestication. He suggested that plants were domesticated and cultivated because of their esthetics, beauty, color, and other nonnutritional reasons (Anderson, 1952). Through the ensuing decades Anderson's thesis has not found fertile ground among many agricultural scientists, especially those who believed and echoed the viewpoint that food was the primary driving reason/force behind domestication and the development of agriculture. But consider Anderson's thesis, especially in light of the domestication of manioc, and how by stripping away the concept that food was the rationale for early agriculture and domestication, how this toxic food ultimately became a dietary staple, through a process that might be called 'the-child-who-did-not-die' thesis (Susan Birch, an undergraduate student at the University of California, Davis, may have been the first to coin the 'child-who-did-not-die-thesis' when she suggested that manioc initially had not been domesticated for food, but as a fish toxin; the processed mash would have been discarded and not perceived suitable as human food – until accidental consumption of the processed mash by a child – who did not die. Simple and parsimonious!):

> In the central Amazon region an early cultivator pounded and pressed cassava/manioc to extract fluids used to kill fish; doing so the starchy pulp was discarded. An unsupervised child wandered by, reached out and stuck a handful of still damp cyanide-extracted mash into its mouth. The adult watched horrified but was too slow to respond. The child smiled, survived, and the adult made the association that cassava mash was not poisonous; the adult tasted the mash and found it bland but pleasing.

This 'child-who-did-not-die' thesis also could apply to other human foods, for example, acorns and cycads that initially are toxic and require extensive processing before human consumption.

Adverse Dietary Impact

Once agriculture and domestication occurred, the dietary diversification of items that formed human food patterns decreased. Reduction in dietary diversity and a focus on carbohydrate-rich grains and tubers produced radical changes and impacts on the overall composition of human diet that ultimately resulted in major physiological changes. Accompanying the development of agriculture and plant domestication human stature decreased and human cranial capacity declined. These reductions seen in the archeological record were caused in part by higher intakes of cultivated plant foods and lower meat consumption. Is it not curious that Mesolithic European hunters c. 20 000 BCE were taller and had larger brains than their c. 10 000 BCE settled Neolithic European plant-raising counterparts? The same patterns are seen when analyzing skeletons buried at sites before and after maize domestication in the New World (Newman, 1975; Cohen and Armelagos, 1984; Larsen, 1995).

All studies of contemporary, traditional hunting and gathering societies reveal high dietary diversities. In some

instances more than 300 different animals and plants regularly are consumed annually (Grivetti, 1976). Further, studies conducted in Botswana by Barbara Metz compared food patterns of hunter-gatherers, pastoralists, and agriculturists that occupied the same general geographical territory and ecological niche in northwestern Botswana. The !Kung hunter-gatherers included in her studies exhibited better overall nutrition and health status than either the Herero cattle pastoralists or the baTawana agriculturists who occupied the same niche, whereas the health-nutritional status of Herero pastoralists was superior to that exhibited the settled baTawana farmers whose diet was based primarily on sorghum augmented with plant relishes (Metz *et al.*, 1971).

It is axiomatic among nutritionists that the best practices to assure quality diet is to expand dietary diversity – not reduce the number of foods consumed. But with the development of agriculture and animal husbandry, and with subsequent domestication of animals and plants, human dietary diversity decreased sharply, a factor that presents an interesting counterpoint to the principles on which dietary security in the twenty-first century are based.

Agriculture, Domestication, and Future Food Security

Regardless of debates why early humans settled, developed agriculture, and ultimately domesticated plants, agriculture stabilized human food supply and expanded food production not possible merely through hunting-gathering activities. Given the broad diversity of potential plants that could be domesticated, researchers have debated why humans focused on specific categories of plants, whether food or nonfood items, and if for food, were the choices dictated primarily for caloric energy or for protein content (Lechler, 1944; Dart, 1963; Gaulin and Konner, 1977; Isaac and Crader, 1981; Peters and O'Brien, 1981; Stahl, 1984; Eaton and Konner, 1985).

After human settlement and the development of agriculture there followed a general reduction in the variety and numbers of plant foods consumed. Today in the twenty-first century the number of known plant species is c. 400 000 (Botanic Gardens Conservation International, n.d.). Of this number, however, only a small minority contribute 90% of all carbohydrate calories consumed globally, among them: barley, cassava/manioc, maize, millet, potato, rice, rye, sorghum, sugarcane, sweet potato, taro, wheat, and yam. This pattern of reduced food diversity exhibited by advanced agricultural and urban societies in the twenty-first century differs sharply from food intake approaches followed by hunting-gathering societies who because of remote antiquity have eaten broadly across the spectrum of both plant and animal kingdoms.

Agriculture as practiced today by traditional societies in the Americas, Asia, Africa, and Oceania is represented by fields that appear 'jumbled,' where many types and varieties of plants are grown within the same plots. Throughout traditional fields in Mexico and Central America maize, beans and squash are planted together. Maize extracts nitrogen from the earth, whereas beans being nitrogen-fixing, replenish soil fertility. The maize stalks serve as 'beanpoles,' and the broad leaves of the interspersed squash plants shade the earth and reduce evaporation. Such a sustainable agricultural pattern does not lend itself to mechanical harvesting. In Africa traditional household gardens and small cultivated fields may contain 20 or more different plant species, including both domesticated and wild plants that represent both food and nonfood uses. Such convoluted, mixed gardens and fields appear in sharp contrast to the vast fields of grain or other plants grown under near monoculture conditions in more economically developed regions of the world. These large primarily single-crop fields lend themselves to mechanical harvesting, whereas the 'messy' traditional fields do not. Because both approaches to agriculture are practiced globally, a question may be posed: which pattern presents a more secure food base for current and future human consumers?

What if an unusual plant virus, a mold, rust, or smut, attacked the botanical spectrum of cereals cultivated today in 2013 and caused a 20%, 50%, 75% reduction of cereal yields for just one year? What would be the worldwide economic and social impact? What economic, political, military, and moral-ethical problems would follow such a collapse of the global grain distribution system? What decisions to alleviate local, regional, and national food shortages would be taken by responsible leaders of government, industry, and academia? Could the economic and human chaos sure to follow under such a condition be averted? What would be the impacts if such a disaster were to occur in 2020; within the next 20 years; perhaps during the year 2050?

More than 50 years ago John Christopher wrote a chilling novel, entitled *No Blade of Grass*. His thesis set within the classic doomsday genre of the Cold War was published during an era of press scenarios of a global population crisis and Malthusian future, raising doubts on the abilities of poverty-stricken countries to feed and maintain their expanding citizens through the so-called Green Revolution and beyond. The central thesis of Christopher's novel was that a virus suddenly appeared that attacked rice and eliminated the dietary staple of Asia. In Christopher's fictional account 200 million Chinese suffered famine and starved, followed by the collapse of rice-consuming nations in southeast and south Asia. And as scientists rushed to halt the spread of the rice-specific virus and to restabilize world food supplies, the virus mutated and infected all wild and domesticated grasses: barley, maize, millet, oats, rye, sorghum, wheat, and even sugarcane. Although the dietary-food catastrophe initially was limited essentially to Asia, the loss of domesticated cereals progressed quickly to Africa, then the Americas and Europe (Christopher, 1956).

We in the twenty-first century should not smile smugly and reject the basic premise on which Christopher's novel was based – an attack on the global food supply by a fungus, virus, or other organism – because such an event would produce unthinkable consequences. One measure of the importance and potential impact that such a disaster would have on human food resources is to examine what actually happened in the late 1960s and early 1970s when many American farmers lost their entire maize crop because of blight (Cordain, 1999).

But what were the ripple effects from the loss of the maize crop in this more localized agricultural catastrophe? Consider how maize – then and now – continues to be interwoven

through the international food and grain markets whether in the 1970s or in 2013, or 2050: as a source of human food, cooking oil; petrol; sweeteners; chicken and hog feed; and nonedible commercial products even dusting powder used to keep paper cups from sticking together.

What lessons should be learned from this maize near catastrophe? One lesson is how potentially precarious global food markets are in a complicated, technical world. As agriculture has moved toward fewer and fewer varieties under cultivation agricultural practices of the last century have tended more toward monoculture in order to facilitate mechanical harvesting, with a parallel loss of genetic diversity in the types of domesticated products grown. As a result, has the human agricultural food supply become more secure or less secure because of changes in cultivation systems during the past 10 000 years?

Do modern humans have greater food security than their ancient or contemporary hunter-gatherer societies? Will the global food supply be more (or less) secure in 2050 and beyond as a result of plant domestication and current agricultural practices? Finally, let us ponder the questions posed at the onset of this essay regarding the early human quest for food, how food safety issues were solved, and the rationales behind human settlement, plant domestication, and development of agriculture: do modern humans (*Homo sapiens urbanensis)* have greater food security because of agriculture and domestication – or might our species actually be less secure today because of modern, more technical approaches to agriculture?

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The Origin of Agriculture – By Steve Gagné.

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Genebanks: Past, Present, and Optimistic Future

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Glossary

Accession A distinct, uniquely identifiable biological sample representing a variety, breeding line, or population maintained in storage for conservation and use.
Cryopreservation A technique of preservation of cells or tissue at the temperature of liquid nitrogen.
Genotype The genetic constitution of an individual organism.
Germplasm The genetic material that forms the physical basis of heredity and that is transmitted from one generation to the next by germ cells.
Phenotype The external appearance of an organism that results from the interaction of its genetic composition (genotype) with the environment.
Phytosanitary Relating to plant health and the control of pests and diseases.
Polyploid The presence of multiple sets of chromosomes beyond the usual two, in some cases rendering organisms sterile.
Regeneration Growing out of seeds of an accession to obtain a fresh sample with high viability and a sufficient quantity for conservation and use.
Somaclonal variation Changes observed in plants as a result of genotypic variation caused by growth in tissue culture.
Subculture The excision and transfer of a plant part from an aged culture medium to a fresh culture medium for renewal and strengthening.

Origins of *Ex Situ* Conservation

Plant genetic resources (PGR) provide the food and fabric of our livelihoods, determining the security or insecurity of 7 billion human lives. Evidently our ancestors showed a great interest in plants and a talent for nurturing and domesticating those that showed valuable attributes. The generations of farmers that followed them have developed and dispersed a vast diversity of domesticated crop varieties, which have adapted to local climates, conditions, and tastes. Scientists avoid answering questions such as "How many varieties of crop are there?" Suffice it to say that there are a few hundred crop species and a few million crop varieties.

Farming communities selected and conserved the plant diversity that they found useful, distributing it to the wider community and passing it down through the generations, as they still do. Such practices took on a more ambitious scope during the expansion of successful civilizations, such as the Romans in Europe, the Harappans in Asia, or Inca in Latin America, resulting in the wide dissemination of certain staple crops. An early protoscientific interest in crop diversity was expressed by the Ancient Egyptians, who organized collecting missions to acquire new plants (Plucknett *et al.*, 1987). Gatherings of plants for practical uses were organized into the first *ex situ* collections in botanical gardens associated with early medical institutions, monasteries, and royal palaces. These collections would have served to demonstrate the use of plants and to allow their study. The conservation of crop diversity remained solely in the hands of farmers and growers until the twentieth century.

By the end of the nineteenth century, scientists were taking a closer interest in agriculture. The term 'landrace' was coined for a locally adapted variety (Zeven, 1998). A few decades later, the pioneer collector and geneticist, Nicolai I. Vavilov opened up the study of crop genetic resources by describing the global patterns of crop diversity according to eight 'centers of origin' (Vavilov, 1949). Scientific breeding took off in the 1940s, and to support it large *ex situ* crop collections were brought together and formally managed in the USA, the Soviet Union, and Europe (Plucknett *et al.*, 1987). These collections provided breeders with an essential resource for crop improvement and vastly facilitated the international exchange of materials. The modern varieties that resulted from these efforts defied expectations for agricultural production and provided the basis for what is now known as the Green Revolution. Mexico, as a frequently cited example, previously imported half the wheat it consumed. In the two decades after the adoption of semidwarf wheat varieties, yields increased eightfold, bringing a new wealth to the country and paving the way for the economic development that followed.

The success of scientific breeding programs led to the intensification of agriculture and the spread of modern varieties.

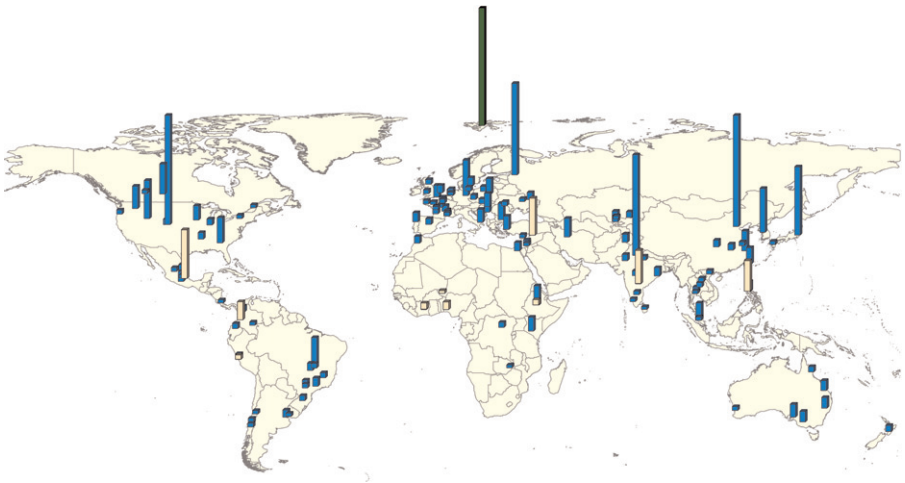


Figure 1 Geographic distribution of genebanks with holdings of more than 10 000 accessions (national and regional genebanks in blue, CGIAR centers in beige, and the Svalbard Global Seed Vault in green). Reproduced with permission from FAO, 2010. The Second Report on the State of the World's Plant Genetic Resources for Food and Agriculture. Rome, Italy: Food and Agriculture Organization of the United Nations.

As the adoption of modern varieties increased, growing concern for disappearing traditional landraces and the genetic diversity that they represented spurred further collection and conservation of crop genetic resources (Frankel and Bennett, 1970). The International Board for Plant Genetic Resources (IBPGR), now known as Bioversity International, was set up to coordinate this collecting effort from 1974. The major international breeding and research programs were also now organized in a public-funded consortium known as the Consultative Group on International Agricultural Research (CGIAR). The importance of ensuring crop diversity continues to be made publicly available was reaffirmed in 1994, when the collections associated with the CGIAR became formalized as international collections held for the public good under the auspices of the Food and Agriculture Organization (FAO) of the United Nations.

The expansion of *ex situ* collections, both in size and number, continued in the 1980s and 1990s. FAO reports that 7.4 million accessions are presently held in 1750 genebanks (**Figure 1**; FAO, 2010), apparently representing 70% of the genetic diversity of 200–300 crops (SBSTTA, 2010). These genebanks range from large public collections with global or regional coverage to national collections maintained by formal sector agricultural research institutions or universities to collections of local heirloom cultivars held by nongovernmental organizations. Private sector seed companies both large and small also maintain collections but these are not included in these figures as data on holdings are not generally made public. **Table 1** outlines the *ex situ* conservation of the 20 most represented crops in genebanks. In addition, some 2500 botanic gardens conserve 80 000 plant species, including many of economic importance (FAO, 2010). The Millennium Seed Bank (MSB) of the Royal Botanic Gardens, Kew, is the largest *ex situ* collection of wild plant diversity and conserves more than 10% of the world's flora. Most nations of the world now boast a new and powerful resource for future agricultural development in the form of genebanks.

How to Keep Plants in Storage Alive

Seeds of most major crop species are orthodox (e.g., sorghum, rice) and may be stored in dried form at low temperature for several decades and potentially up to several thousand years. Seeds of some species from some plant families or ecological origins, although it is hard to predict which, exhibit relatively short shelf life (Hay *et al.*, 2012; Nagel and Börner, 2009; Probert *et al.*, 2009; Walters *et al.*, 2005) and are intermediate in storage behavior (e.g., lettuce, barley). Some species (e.g., cacao, coffee) produce seed that are recalcitrant. They do not survive drying or storage at all. Finally, there are species that are propagated vegetatively through roots, tubers, and suckers. Species with recalcitrant seed and vegetatively propagated species and crops must be conserved using other methods, in field genebanks or in tissue culture.

The objectives of a genebank usually focus on maintaining the viability and genetic integrity of the stored samples at the best possible levels for the longest possible time. Genebank procedures have been researched and described extensively and will not be covered in detail here. The international community has also agreed standards for genebank procedures for seed crops to guide operations and help ensure quality (FAO/IPGRI, 1994). A revised version of these standards is now published and separate standards are available for non-orthodox seeds and clonally propagated plants (see FAO guidelines from the FAO website given in the Relevant Websites section). Bioversity International has published comprehensive technical guidelines and handbooks for genebanks (see Relevant Websites section for the website address). The Royal Botanic Gardens, Kew, provides online access to a Seed Information Database at see address in the Relevant Websites section and Smith *et al.* (2003) have compiled an invaluable resource, covering scientific research and practice in all areas of seed conservation from collection to use.

A specific understanding of the biology of the crop, together with an intimate awareness of the origin of the accessions in

Table 1 Twenty crops most numerically represented in *ex situ* conservation

Top 20 food crops held in ex situ *conservation*	*Total accessions worldwide*	*Coverage*	*Countries holding the largest collections, international and national genebanks*
Wheat	856 168	More than 200 collections exist. Landraces and modern cultivars are relatively well represented. Genetic stocks are more likely to be found in research institutes. Collecting of wild relatives is needed.	CIMMYT, USA, China, India, ICARDA
Rice	773 948	More than 175 collections with large collections in Asia. Landraces, modern cultivars and genetic stocks are well represented. Wild relatives are represented mainly in 2 collections.	IRRI, India, China, Japan, Republic of Korea, USA
Barley	466 531	More than 75 institutes conserve barley. A large part of the crop diversity is represented *ex situ*. Collections are made up predominantly of landraces, also breeding materials, modern cultivars, genetic stocks, and wild relatives.	Canada, USA, Brazil, ICARDA, Japan, Germany
Maize	327 932	Existing collections hold wide diversity but landraces from the Amazon, parts of Central America and Southeast Asia are inadequately conserved. Hybrids, certain inbred lines, and wild relatives also need better coverage. Some high-altitude varieties are very difficult to regenerate in the right conditions and perhaps better conserved *in situ*.	CIMMYT, Portugal, USA, China, Mexico, Russia
Beans	261 963	Several bean species are cultivated and represented in *ex situ* conservation. Some 70 wild species are included in genebank collections. Detailed gap analyses have been done by CIAT to identify priority species for collecting.	CIAT, USA, Brazil, Mexico, Germany, China
Sorghum	235 688	Some 30 institutes conserve sorghum. There are gaps in coverage of diversity from W Africa, Central America, Central Asia, and Sudan.	ICRISAT, USA, China, India, Ethiopia, Brazil
Soybean	229 944	Important collections exist in China, including traditional varieties that are no longer found in farmers' fields. One of the major crops that are not included in the International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA).	China, USA, Republic of Korea, World Vegetable Center, Brazil, Japan
Oats	130 653	Oats are conserved in a few very large collections and many smaller collections. Important collections of threatened wild species exist in the center of diversity in the Mediterranean.	Canada, USA, Russia, Germany, Kenya, Australia
Groundnut	128 435	Diversity from centers of origin is well represented in genebanks. More materials from other areas and wild relatives need to be collected. Some of the wild species are conserved in field genebanks. One of the major crops that are not included in the ITPGRFA.	ICRISAT, India, USA, Argentina, China
Cotton	104 780	Cotton is the best-represented fiber crop in *ex situ* conservation. Some 45 wild species are conserved among eight major collections but several areas of the genepool are underrepresented and under threat in the wild. One of the major crops that are not included in the ITPGRFA.	Uzbekistan, USA, India, China, Russia, France
Chickpea	98 313	Nearly 50 institutes conserve collections mainly of chickpea landraces. There are some wild species in *ex situ* conservation. Gaps exist in coverage from Central Asia and Ethiopia. More wild species need to be collected. Some are perennial and will need to be conserved in field genebanks.	ICRISAT, India, ICARDA, Australia, USA, Iran
Potato	98 285	Diversity is quite well represented, mostly in 30 key institutes. The widest diversity is held in collections in Latin America from where the potato originates. Collections include wild species but more diversity remains to be collected. *In situ* conservation is particularly important. The crop is conserved as seeds, tissue culture, or as plants in the field.	France, Russia, CIP, Germany, USA, Japan
Pea	94 001	There are 16 major collections comprising mainly cultivated forms, with some highly diverse wild relatives. Representation of wild species needs to be improved.	Australia, Russia, ICARDA, Germany, USA, Italy
Medicago	91 922	Medicago is a genus of temperate forages, which includes cultivated alfalfa and numerous wild species. It is one of the best-represented taxa in forage collections. The Rhizobia bacterial strains that are associated with legume crops and provide their nitrogen-fixing properties are also held in *ex situ* conservation. More collecting is needed, especially in rangelands that are rapidly disappearing.	Australia, Uzbekistan, ICARDA, USA, Morocco

(*Continued*)

Table 1 Continued

Top 20 food crops held in ex situ *conservation*	*Total accessions worldwide*	*Coverage*	*Countries holding the largest collections, international and national genebanks*
Tomato	83 720	Collections include modern cultivars, landraces, genetic stocks, and a small but very important number of accessions of wild species.	World Vegetable Center, USA, Philippines, Germany, Russia, Japan
Trifolium	74 158	Predominantly wild species are conserved with some cultivars of a few cultivated species. The Rhizobia bacterial strains that are associated with legume crops and provide their nitrogen-fixing properties are also held in *ex situ* conservation. More collecting is needed, especially in rangelands that are rapidly disappearing.	Australia, New Zealand, ICARDA, Great Britain, Spain, USA, ILRI
Rubber	73 656	Malaysia holds by far the largest collection with nearly 60 000 accessions. One of the major crops that are not included in the ITPGRFA.	Malaysia, Indonesia, Côte D'Ivoire, Liberia, Brazil, Vietnam
Capsicum peppers	73 518	More than 30 species of *Capsicum* are conserved, several of which have commercial value. One of the major crops that are not included in the ITPGRFA.	World Vegetable Center, USA, Mexico, India, Brazil, Japan
Prunus	69 497	Prunus includes cherry, plum, peach, and almond as well as other fruit and timber tree species. The seeds are difficult to conserve so generally whole trees are conserved in the field, including wild species, local varieties, and modern cultivars. One of the major crops that are not included in the ITPGRFA.	Russia, USA, Italy, Hungary, Turkey
Pearl Millet	65 447	ICRISAT's collection holds a third of global pearl millet accessions. The collection is made up mostly of landraces. Relatively few wild species, improved varieties, and breeding materials are held in collections. More collecting is needed.	ICRISAT, Brazil, India, France, Canada

Note: Vegetative propagated crops are conserved in relatively small collections and are underrepresented in this table.
Source: Adapted with permission from FAO, 2010. The Second Report on the State of the World's Plant Genetic Resources for Food and Agriculture. Rome, Italy: Food and Agriculture Organization of the United Nations and Crop Conservation Strategies. Available at: www.croptrust.org

the collection, contribute to determining the appropriate size and structure of a collection, the way the accessions are managed, regenerated, and made available, as well the acquisition of new germplasm. The methods used to sample and collect germplasm from farmers' fields or other sites have a profound impact on its subsequent long-term conservation and use (Rao *et al.*, 2006). The state and stage of development of the plant material is critical to its long-term storage. Guidelines and standards for collecting are provided by Guarino *et al.* (1995a), and also in updated form at the Crop Genebank Knowledge Base (see address in the Relevant Websites section).

Seed Genebanks

Approximately 90% of accessions in *ex situ* collections are held as seed (Rao *et al.*, 2006). Seed genebanks follow common procedures to process and conserve seeds as illustrated in **Figure 2**.

Drying

To introduce a seed accession into a collection, first the sample is cleaned and processed for storage. Moisture content is the most important factor that influences the longevity of orthodox seed in storage and should range between 3 and 7% (Rao *et al.*, 2006). The drying of the fresh seed sample before conservation is thus one of the most essential steps in the conservation process.

Seed Storage

In an active genebank, accessions are regularly accessed and used. Every transaction, whether it is removing a subset of seeds for a trial or planting seeds out to refresh the stock, has the potential to change the genetic composition of the original seed sample. For this reason, genebanks normally keep a sample of the original dried seed undisturbed in hermetically sealed containers in long-term storage conditions (at −18 °C). Another sample in medium-term storage (at 5 °C) is used as the active source of material for distribution, research, or planting. A description of this arrangement is described by Sackville Hamilton *et al.* (2003a).

Germination Testing and Regeneration

The predicted seed longevity in storage governs the frequency at which the samples are monitored. Monitoring involves removing a small subsample of seeds to test their germination. In an optimal situation, samples are monitored at regular intervals and regenerated to produce fresh seed when the viability or numbers of seeds in the sample drop below an acceptable level for storage or use. Sackville Hamilton and Chorlton (1997) have authored a decision guide to help determine the timing and effective procedure for regeneration. Standards currently advise that at least 85% of the seed sample should be viable for cultivated accessions and somewhat less for accessions of wild species (FAO/IPGRI, 1994). The process of regeneration demands individual procedures for each crop.

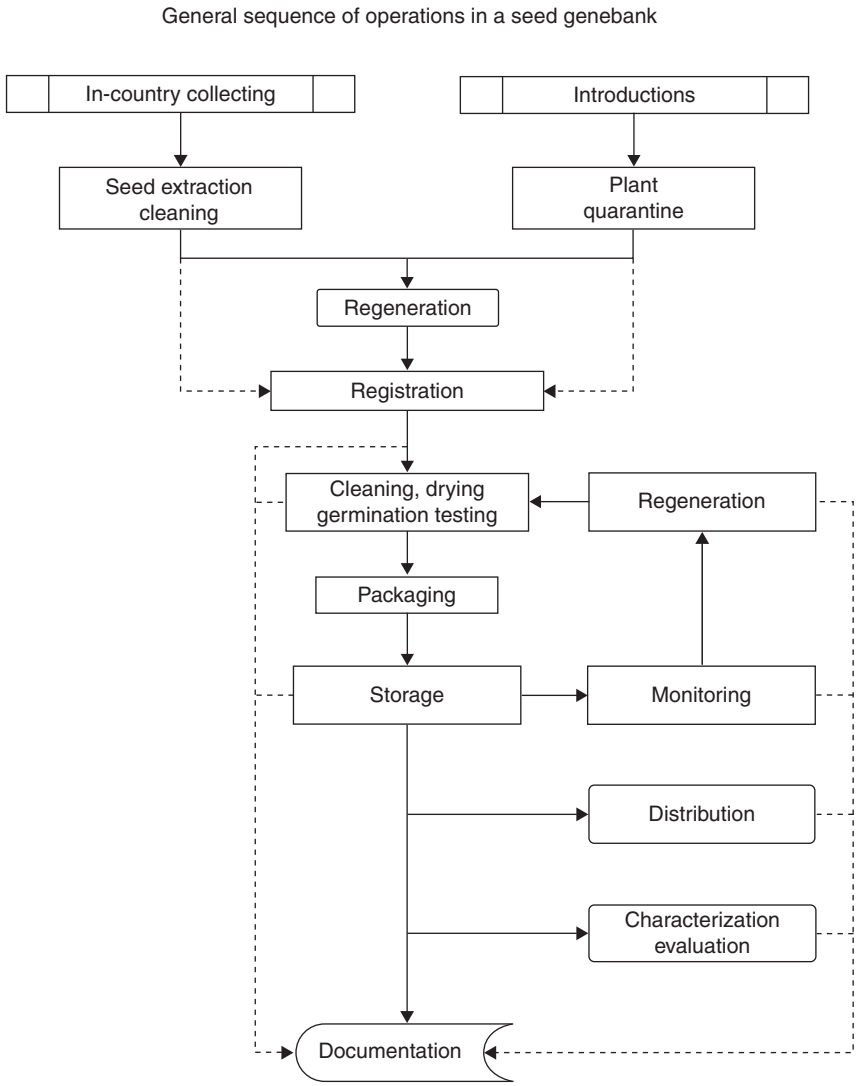


Figure 2 General sequence of operations in a seed genebank. Reproduced with permission from Rao, N.K., Hanson, J., Dulloo, M.E., *et al.*, 2006. Manual of seed handling in genebanks. Handbook for Genebanks No.8. Rome, Italy: Bioversity International, 147 pp.

These have been documented in guidelines (Dulloo *et al.*, 2008). Self-pollinating species are relatively straightforward to regenerate but for species that outcross, some form of controlled pollination is usually necessary to prevent one accession mixing with another. Regeneration is generally minimized as much as possible, especially for outcrossing species, as it heightens the risk of changes in genetic composition of an accession through unintentional selection, gene flow, and genetic drift (Chebotar *et al.*, 2003; Parzies *et al.*, 2000).

Difficult-to-Conserve Species

Many temperate and tropical fruit crops and most root and tuber crops are propagated vegetatively or produce seed that is recalcitrant to drying and cold storage. Collections of these species depend on the conservation of the entire plant in the field or of plantlets in tissue culture, and involve an entirely different procedure to the conservation of seeds (**Figure 3**).

Field collections take up large amounts of space, are expensive to maintain, and suffer regular and inevitable losses of accessions to pests, diseases, and adverse weather. On the positive side, accessions are readily observable and relatively easy to study and evaluate. As an alternative or more usually as a complement to field collections, shoot cultures may be maintained on a growth-retarding medium in test tubes in the laboratory. Tissue culture became viable as a conservation technique in the 1980s and has since been routinely adopted in international genebanks and in some national genebanks. Its use is most convenient for the short-term production of clean planting material but some institutes are successfully implementing protocols for tissue culture for medium-term conservation.

Operations in tissue culture genebanks revolve around maintaining the health of the accession sample and extending the duration of the interval between subcultures (Benson *et al.*, 2011; Reed *et al.*, 2004a). The sterility of media and equipment and the daily monitoring of cultures are of



Figure 3 Tissue culture of cassava at International Centre for Tropical Agriculture (CIAT) (photo credit Global Crop Diversity Trust).

critical importance, as is the timely subculturing of plantlets before they have outgrown the test tube or exhausted the medium. Reducing temperature and light intensity helps to slow the growth of cultures but few laboratories are able to extend the subculture period of the major part of their collections beyond 12 months. Certain genotypes and wild species require much more frequent subculturing. Conservation standards for recalcitrant seed and vegetatively propagated species are under preparation (see FAO draft guidelines from their website given in the Relevant Websites section).

Tissue cultures are continually growing and they do not need regeneration in the same way as seeds. However, the periodic rejuvenation of tissue cultures in the field has been considered a necessity to identify somaclonal variants, which can appear because of the stresses of tissue culture (Jain *et al.*, 1998; Withers, 1993). Experience with longer-term tissue culture or cryopreserved collections suggests that tissue culture does not produce significantly more somaclonal variation than field conditions (Reed *et al.*, 2004a; Keller *et al.*, 2008). However, the tissue cultures of some crops age with repeated subculture and become vulnerable to endophytic bacteria (Keller *et al.*, 2011), eventually requiring renewal.

Cryopreservation

The most secure method of long-term conservation for both seeds and tissue culture is cryopreservation whereby plant materials are stored in liquid nitrogen and chilled to a temperature of −196 °C. At this temperature, cellular and metabolic processes are slowed to a virtual standstill. Germplasm in liquid nitrogen is generally believed to be storable for an indefinite period without the loss of viability (Engelmann, 1997), although recent empirical studies on seeds have detected some deterioration in cryopreservation depending on the conditions in which they were previously stored (Walters *et al.*, 2004). For large collections of some crops, cryopreservation presents the only feasible conservation alternative to field conservation (e.g., coconut, coffee, garlic) (**Box 1**).

Germplasm Health

All genebanks are concerned with the health of accessions, particularly collections of whole plants or tissue cultures where contamination and infection occurs and spreads easily. The importance of avoiding the distribution of diseased materials, particularly across international boundaries, cannot be overemphasized. Crop-specific guidelines have been published on the safe movement of germplasm (see Bioversity International website given in the Relevant Websites section). Phytosanitary controls exist in most countries to reduce the risk of spreading specific crop pests and diseases. The use of diagnostic tools to detect pathogens has evolved rapidly with the introduction of molecular techniques, and accessions in active collections are usually submitted to health tests upon arrival into and dissemination from the collection. In cases of very high risk, such as the virus-prone banana, electron microscopy is used to detect any unknown virus particles or mycoplasma. Developing methods of cleaning diseased materials is also, by nature, an active area of research, which exploits various therapies involving temperature or chemical applications.

Characterizing and Documenting Accessions

Data are required in genebanks at multiple levels to manage samples, and to identify and classify accessions, and to help the user make informed decisions. Each sample is accessed into the collection with passport data to document its origins. Its accurate identification and classification is dependent on characterizing the principal morphological attributes of the living plant. Generic and crop-specific descriptors are available to help standardize the data gathered during characterization (see Bioversity International website given in the Relevant Websites section). The genebank user, however, is generally seeking information on the attributes relating to the use of the accession, such as its yield, pest and disease-resistance, and consumer qualities. These characteristics are not covered in standard descriptors but can be gathered through specific replicated and often multilocational evaluation trials.

Safety Duplication

An important responsibility for any genebank is to ensure that all unique accessions are held in an alternative location as a security measure in the event of a catastrophe or accidental loss. Civil war, natural disasters, fires, and diseases can claim unique collections of crop diversity in minutes. National and international genebanks in Afghanistan, Egypt, Iraq, and Syria have been recently looted or damaged during periods of unrest. In the past year alone, fire and floods destroyed major genebanks in the Philippines and Thailand.

Duplicated accessions may be treated as 'black box'; they remain effectively unopened and untouched unless requested by the donor. The Svalbard Global Seed Vault provides a new level of safety duplication for seed genebanks. This facility is described in the photograph given in **Figure 4**.

Box 1 Cryobanking

Research on the cryopreservation of plant genetic resources over the past 20 years has established protocols for approximately 200 crop species. Protocols are not only highly crop specific and sometimes genotype specific but their successful application is heavily influenced by the culture, skills, and experience of the practicing technicians and laboratory (Reed *et al*., 2004b). Several international and national genebanks are now refining protocols specifically for cryobanking the crop collections under their management. More than one protocol may be required to cryopreserve all the genotypes in a single crop species (Panis, 2009).

Currently used cryopreservation techniques include the dormant bud method, controlled freezing, vitrification, encapsulation, and droplet methods (Keller *et al*., 2011). Research and refinement of protocols focus on improving the rates of postthaw regeneration of cryopreserved plant material by examining variables such as explant size, dehydration conditions, cryoprotection, and speed of temperature reduction (Keller *et al*., 2011). Research is also aimed at developing tools to help genebank managers determine which protocols are best suited to which genotypes.

A few genebanks are cryopreserving accessions as a routine operation or maintaining sizeable cryobanks. The largest cryobank collections of vegetatively propagated crops comprise the collection of apple and vegetatively propagated crops (3750 accessions) at the National Center for Genetic Resources Preservation of the US Department of Agriculture; cassava, the potato, garlic, and mint collections (1300 accessions) at the Leibniz Institute of Plant Genetics and Crop Plant Research in Germany; the global banana collection (880 accessions) managed by Bioversity International; and the cassava core collection (640 accessions) at the International Center for Tropical Agriculture (CIAT), Colombia. A significant number of accessions have been cryopreserved of collections, including European Elm managed in a collaboration between French and German research institutes; potato at the International Center for Potato (CIP) in Peru; hops and potato at the Crop Research Institute in the Czech Republic; and mulberry and garlic in national genebanks in Japan and South Korea, respectively.

Cryopreservation is presented as a cost-effective long-term alternative to other forms of conservation (Dulloo *et al*., 2009; Koo *et al*., 2004; Li and Pritchard, 2009). Cryopreservation is also an effective method to eliminate viruses (Keller *et al*., 2011; Wang *et al*., 2008). However, cryobanking in the plant world has proven slow to take off. There are substantial startup and recurring costs to train and sustain the highly skilled staff, develop and refine protocols, ensure continuous liquid nitrogen supply, and prepare source materials in sufficient quantities. Furthermore, the rate at which cryopreservation currently takes place can severely limit the number of accessions that can be cryopreserved. The target tissue is pared down to a minimum size in order to limit the effects of the damage and subsequent oxidation of the tissue. The technique demands surgical skill. Several hundred samples of a single accession must be cryopreserved to guarantee successful regeneration (Dussert *et al*., 2003). Presently, a fully skilled technician may be able to cryopreserve between 50 and 100 accessions per year. Cryobanks of vegetatively propagated crops, therefore, are not accessible for general routine use and cannot entirely replace active tissue culture or field collections. The chief importance of cryobanking is to provide a secure form of long-term conservation. Closer collaboration between practicing institutes is advocated by several practitioners to make better use of cryopreservation (Keller *et al*., 2011; Lerman *et al*., 2009). In the animal world, a coalition of institutes is cryopreserving threatened amphibian species in the *Amphibian Ark* (Lerman *et al*., 2009).

Cryopreservation of dormant buds and seeds is considerably less costly than that of excised tissues. USDA maintains a collection of more than 35 000 cryopreserved seed samples. For seed crops, cryobanking presents not only a unique opportunity for improving the long-term security of the collection but also a means to reduce the need for costly germination testing and regeneration. Li and Pritchard (2009) highlight the fact that approximately 26% of species with apparently orthodox seed do not store well at −20 °C under conventional seed genebank conditions (Probert *et al*., 2009). Cryopreservation may be a more effective form of long-term conservation for these species.

Maintaining Standards

Although a rich resource of crop-specific and generic guidelines and standards exist, individual genebanks will invariably need to modify their procedures according to the precise complement of crops being conserved, the use and objectives of the genebank, available expertise, and the conditions under which they are functioning. Compliance with standards depends on adequate resources. In all cases, the development of an operation manual is essential for every *ex situ* collection and is the basis for achieving any kind of quality standard for the genebank. Sharing standards is also important in moving toward closer collaboration and sharing responsibilities between genebanks (Sackville Hamilton *et al*., 2003b).

Brief Glimpses into Genebanks

The Svalbard Global Seed Vault (**Figure 4**) is not a conventional genebank. It is a security bank for duplicates of seed samples from genebanks worldwide. Built into the permafrost of an ice-covered mountain within the Norwegian Arctic Circle, the vault will keep seeds frozen even with a loss of power.

The door of the vault opens only three times a year, during which time deposits are made by genebanks who wish to safety duplicate their accessions in 'black box.' This means that only the depositor is able to request access to the seeds that they send. Even the Svalbard genebank manager asks for permission from the depositor to access the deposits should a bag or crate require repairs. This arrangement is sealed with a Standard Depositors' Agreement.

The International Coconut Genebank (**Figure 5**) managed by Center National de Recherche Agronomique in Côte D'Ivoire conserves 99 accessions of coconut, each comprising at least 100 palms and covering more than 1000 ha. Collecting pollen, pollinating flowers, and harvesting the seednuts from the 20 m-tall trees is a major part of the annual workplan. The germplasm maintained here is provided to coconut breeders around the world. It is a valuable resource, yet it is at risk. Not far away in neighboring Ghana, a coconut

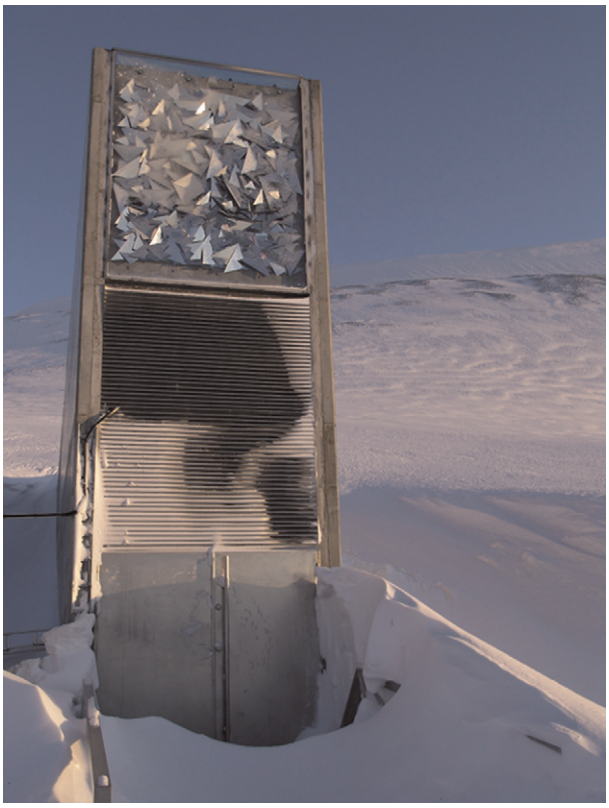


Figure 4 Svalbard Global Seed Vault (photo credit Global Crop Diversity Trust).



Figure 5 International Coconut Genebank in Côte D'Ivoire (photo credit Global Crop Diversity Trust).



Figure 6 Maize accessions at CIMMYT (photo credit Global Crop Diversity Trust).

disease called Lethal Yellowing is destroying plantations. It is essential that this unique collection be adequately safety duplicated.

The International Maize and Wheat Improvement Center (CIMMYT) in Mexico (Figure 6) specializes in the conservation of wheat and maize. The two collections together comprise more than 170 000 accessions originating from more than 100 countries. Both collections date back several decades and include the original materials used in the Green Revolution. The maize collection includes a number of highly endangered wild maize, or teosinte, subspecies.

Wild bananas produce seeds, but most cultivated forms have lost them. The most common way to conserve bananas is as whole plants in the field. It is possible to distribute banana germplasm from field genebanks as plant suckers, but the germplasm is quite likely to harbor pests and disease no matter what cleaning measures are in place. Bioversity International conserves and provides a wide range of banana diversity as clean tissue cultures from its collection held in the Katholieke Universiteit of Leuven, Belgium.

In the Solomon Islands, an archipelago of small, isolated islands, the available infrastructure does not favor conserving such a vital crop as banana in a centralized genebank. A nonprofit organization, The Kastom Garden Association works with local farmers to conserve banana in a network of community genebanks. Dorothy Tamasia (Figure 7) is one of these farmers. She conserves a small but diverse collection in a plot near her village on the island of Makira.

Complementarity Between *In Situ* and *Ex Situ* Conservation

Typically *ex situ* conservation is considered to be static in evolutionary terms in comparison with *in situ* conservation (Bretting and Duvick, 1997). Indeed, it is an important objective of a genebank to maintain genetic stability so that users



Figure 7 Dorothy Tamasia, Solomon Islands (J. Daniells).

may be assured of the trueness-to-type of the material they are requesting. Both *ex situ* and *in situ* conservation share the same objective to enhance or promote the value of individual varieties or accessions in order to assure their conservation. The target audiences are different, however. Genebanks are generally targeting researchers and breeders at a national or international level. *In situ* conservation efforts are generally managed at a local or experimental scale, targeting farmers, traders, processors, or local communities. *In situ* conservation cannot be easily designed to support wide scale availability of germplasm or to provide long-term security (Engels and Visser, 2003a; Fowler and Hodgkin, 2004; Jarvis *et al.*, 2000, 2004; Visser and Engels, 2003a).

The *ex situ* conservation of some crops, however, remains technically challenging and expensive. For most vegetatively propagated species and crop wild relatives, the conservation of the entire genepool depends heavily on conservation by farmers and managers of natural landscapes or protected areas (Fowler and Hodgkin, 2004). *In situ* conservation initiatives are gaining momentum in numerous countries, although up until now they are focused on inventorying and prioritizing *in situ* sites (FAO, 2010). The coverage of crop diversity and the potential effectiveness of *in situ* conservation in safeguarding diversity over the long term under present-day climate and conditions remain largely unknowable at present.

Genebank Use and Impact

Role of Genebanks

Genebanks provide a broad range of diversity for use, including modern cultivars, obsolete cultivars, breeding lines, traditional varieties, and wild relatives. Conventionally, they feed directly into breeding programs, providing the raw materials from which new modern varieties are developed. Breeders may keep their own working collections of the materials that they are currently using, but only genebanks have the capacity to store a wide range of diversity in long-term conservation. Genebanks also contribute to research that leads to the development of new varieties. In a survey of four major (non-PGR specialist) crop science journals, 191 out of 859 (22%) articles published in a single year involved the access and use of more than 36 000 samples of 112 species. Eighty percent of these articles sourced their materials from genebanks in 27 countries and seven CGIAR centers (Dudnik *et al.*, 2001).

There are uses for genebank material apart from breeding and research. Genebanks may play a role in disseminating materials directly to farmers. For clonal crops, genebanks provide disease-cleaned tissue cultures, which can contribute dramatically to increasing yields. A potato cultivar, Achirana INTA from Argentina was distributed by International Center for Potato (CIP) as a pathogen-free variety to China where it was released as CIP-24 (Thiele *et al.*, 2008). Surveyed users of the global banana collection, managed by Bioversity International, state the most important reason for using the genebank is the reliable, virus-free status of the germplasm (Garming *et al.*, 2010).

Genebanks also provide backup sources of seed in the event of a disaster. Seeds were provided from genebanks to redevelop agriculture after civil war in Angola and Rwanda, and after widespread damage caused by adverse farming policies in Cambodia. Genebanks were called upon to restore planting material and seed after Hurricane Mitch in Central America.

Promoting Use

The active use of a genebank depends on the availability of the material conserved within it. Fowler and Hodgkin (2004) distinguish the concepts of 'access,' a measure of the legal attainability of germplasm, from 'availability,' which relates to whether the material can be identified and obtained in a usable form. The availability of an accession is influenced by multiple factors, which extend back to the moment when it is first collected. It touches upon the nature and quality of the material, the quantity and form in which it can be provided, and most particularly the information associated with it to identify it and indicate its potential value and application. Much of the work of an active and well-resourced genebank is dedicated to making material available through maintaining viability, health-testing and disease-cleaning, structuring the

collection, and most directly through evaluating accessions and improving accession-level information to promote use.

Several important mechanisms have been developed in recent years to promote the use of diversity and genebank collections.

- Core collections include a minimum number of well-documented and identified accessions as a means to showcase or represent genetic diversity (van Hintum *et al.*, 2000) and to provide an entry point into the wider collection. If an initial search of the core collection produces something of interest, the user may search the particular branch of diversity that is of interest in more depth. Some large collections reduce their core sets even further into minicores (1% of the entire collection) or trait-specific subsets (Upadhyaya *et al.*, 2008).
- Focused identification of germplasm narrows the search for certain adaptive traits by identifying accessions originating from specific environmental or climatic conditions that are associated with those traits (Street *et al.*, 2008). The approach has helped identify barley and wheat accessions with resistance to certain fungal pathogens and Russian wheat aphid (El Bouhssini *et al.*, 2011; Endresen *et al.*, 2011).
- Evaluation, base broadening, and prebreeding are all activities that create attractive products for further research and breeding. The level of involvement of genebanks in these activities is controversial, especially for major crops such as rice, which have well-developed programs for crop improvement. For many less well-resourced crops, the genebank may be the best place, if not the only, facility for carrying out these activities. In all cases, strong feedback loops between genebanks, breeders, and users are essential.
- Significant investment has been made in developing or revising databases. The quality of data is also receiving increasing attention. van Hintum *et al.* 2011 have devised a passport data completeness index, which has been tested on data from European collections, as an aid to help raise data quality standards.
  - EURISCO (see Relevant Websites section) provides a catalog of more than one million accessions representing approximately half the number of accessions held in 318 genebanks in 42 countries in Europe.
  - Germplasm Resources Information Network (GRIN; see address in Relevant Websites) provides access to more than 500 000 accessions held in National Plant Germplasm System of the US Department of Agriculture. A comprehensive revision of this software, GRIN-Global, has recently been made freely available for general use by genebanks.
  - International Crop Information System (ICIS; see address in Relevant Websites section) provides pedigree information for wheat, rice, and maize collections.
  - GeneSys (see Relevant Websites section for address) brings together GRIN, EURISCO, and CGIAR center accession data, representing some 2.4 million accessions in one web portal.

Good quality data can strongly influence use. As a result of enabling search engines, such as Google, to index the data in GRIN, requests have increased by more than 80% in a period of 4 years. There is a correlation between web page hits and number of requests for germplasm from the genebanks (Bretting, 2012, personal communication).

International Distribution and Politics

Several economists have illustrated the importance of access to materials from numerous countries for the improvement of crops (Johnson *et al.*, 2003). Most genebanks provide germplasm to local users but few disseminate germplasm internationally (FAO, 2010). The CGIAR centers and a few major genebanks – national genebanks in Australia, Brazil, Canada, China, Germany, Netherlands, Russia, USA, as well as the Nordic Genebank, the Tropical Agricultural Research and Higher Education Center (CATIE), and the World Vegetable Center – are the source of the vast majority of international distributions. In the 12-year period up to 2010, the genebanks of the CGIAR centers plus the World Vegetable Center distributed more than 1 million samples of accessions, of which 77% were landraces and wild species (FAO, 2010).

The CGIAR breeding programs may disseminate more than twice the number of samples as the genebanks. In a 6-year period, CIMMYT alone distributed 1.2 million samples to over 100 countries through its international nursery system (Fowler *et al.*, 2001). However, genebanks disseminate a broad range of landraces and crop wild relatives, fulfilling a unique role in support of breeding and research (**Table 2**). Their role is not comparable to that of breeding programs, which at any one time disseminate large quantities of just a few improved

Table 2 Percentage of accessions of different types of crop resources distributed by the International Agriculture Research Centers to different users from 1996 to 2006

Type	*Within/between IARCS*	*NARS developing countries*	*NARS developed countries*	*Private sector*	*Others*	*Total number of accessions*	*Percentage of the total*
Landraces	57.9	48.5	45.0	51.7	65.7	194 546	51
Wild species	29.2	19.0	40.5	7.1	19.1	104 982	27
Breeding lines	8.5	23.1	5.4	36.0	6.5	56 804	15
Advanced cultivars	3.5	8.0	9.1	5.1	8.6	24 172	6
Others	0.9	1.4	0.1	0.1	0.1	3 767	1

Source: Reproduced with permission from FAO, 2010. The Second Report on the State of the World's Plant Genetic Resources for Food and Agriculture. Rome, Italy: Food and Agriculture Organization of the United Nations.

varieties from breeding programs to national agriculture programs and farmers.

Germplasm distributions have been influenced by a changing political climate (Halewood *et al.*, 2012). International distributions were adversely affected by the adoption of the Convention on Biological Diversity (CBD) in 1992, which established national sovereignty over PGR and determined that if one country wanted to request resources from another, a process of attaining prior consent and agreement would need to take place in each case (Engels and Visser, 2003a; Tansey, 2008; Visser *et al.*, 2000). The International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA) came into force in 2004 to ensure that the major staple crops would remain easily available through a multilateral system (MLS) of access and benefit sharing (FAO, 2001). The MLS is embodied in a Standard Material Transfer Agreement (SMTA), which lays down standard terms and conditions for general use to ensure access to germplasm and sharing of any benefits derived from its use. The mechanisms for access and benefit sharing are still very much on trial. Although many countries are establishing national laws and mechanisms for accommodating the CBD, the ITPGRFA and now the Nagoya Protocol on Access and Benefit Sharing, which was adopted under the CBD in 2010, the full effects of these policy changes on international exchange of germplasm are yet to be seen. However, the movement of germplasm between more than 50 countries under SMTA, as part of a project funded by the Global Crop Diversity Trust to support national genebanks, provides tentative evidence of resurgence in international germplasm exchange.

Economic Impact

Numerous studies have assessed the impact of PGR in crop improvement and found high rates of return on investment particularly for major staple crops, wheat, rice, maize, and potatoes (Evenson, 2001; Evenson and Gollin, 2003; Renkow and Byerlee, 2010). The improvement programs of CGIAR centers for 10 crops made an average 25–33% annual contribution to crop yield increases across all geographical regions between 1965 and 1998 (Renkow and Byerlee, 2010). These contributions are of continuing or increasing importance, and in economic terms are worth billions of dollars (Evenson and Gollin, 2003).

According to Smale and Hanson (2010), only two studies have evaluated the specific contributions of genebanks to these impacts. There are multiple factors contributing to the lack of data on the value and impact of genebanks and their roles. Tracing the pedigree of improved varieties and the contributions and sources of ancestral materials is fraught with difficulty. Fowler and Hodgkin (2004) cite the Sonalika wheat cultivar, widely planted in the 1960s, with a pedigree which when printed out extends over 6 m. Few pedigrees are that well-documented. Breeders' logbooks and records of ancestral materials are of varying comprehensiveness and may include prebred materials, the origins of which are undocumented. Also many different factors, other than PGR, contribute to improved yields and economic benefits. The magical contribution of a winning trait from a specific variety is a relatively rare occurrence. The value of any one variety or gene is hard to disentangle and unlikely to be great (Smale and Hanson, 2010). Consequently economists have dwelled on the easier task of calculating the cost of maintaining crop diversity in genebanks and the marginal cost of adding accessions to collections, arguing that if the costs are low the benefits will always be higher (Smale and Hanson, 2010).

Table 3 Numbers of accessions screened at the IRRI genebank for resistance to specific pest and disease

Pest/disease	*No. of accessions screened in genebank*	*Resistance discovered (%)*
Brown planthopper biotype 1	44 335	15.4
Brown planthopper biotype 2	10 053	1.9
Brown planthopper biotype 3	13 021	1.8
Green leafhopper	50 137	2.8
Rice whorl maggot	22 949	3.0
White-backed planthopper	52 042	1.7
Zigzag leafhopper	2 756	10.1
Rice leaffolder	8 115	0.6
Yellow stem borer	15 656	3.8
Striped stem borer	6 881	<0.02
Blast	36 634	26.2
Sheath blight	23 088	9.3
Bacterial blight	49 752	11.1
Rice rugged stunt virus	13 759	2.4
Rice tungro disease	15 795	3.5

Source: Reproduced from Jackson, M.T., 1995. Protecting the heritage of rice biodiversity. Geo Journal 35, 267–274.

Genebanks are particularly useful, and their impact is likely to be great, when new problems occur and the necessary traits are not present in adapted germplasm in breeders' working collections. At times like these, breeders turn to the genebank to search for new genetic sources of traits. More than 11 000 accessions of landraces and primitive wheats have been screened in ICARDA genebank for resistance to the recent outbreaks of Ug99 strain of stem rust in wheat. Useful genes can be extremely rare, necessitating exhaustive searches to find them. **Table 3** provides numbers of rice accessions screened from the International Rice Research Institute (IRRI) genebank to locate resistance to major pests and diseases.

Theoretical models provide support for the argument that it is economically efficient to keep landraces unused in genebanks because of the potential pay-offs of finding specific traits in certain conditions over the long term (Gollin *et al.*, 2000).

Genebanks of the Twenty-First Century

Genebanks as Museums

Genebanks are sometimes ineffective at addressing the needs of breeders and farmers and function more like museums or, worse, morgues (Weidong *et al.*, 2000; Marshall, 1989). All genebanks have difficulty sustaining the necessary levels of expertise and trained staff to take care of or use the collections. In a project, coordinated by the Global Crop Diversity Trust, to

regenerate and safety duplicate threatened accessions held in national genebanks, 85 000 accessions were identified by 77 countries as requiring urgent regeneration. Slightly more than half of the institutes involved found that more than 10% of the accessions that they intended to regenerate were no longer viable and in half of these cases the loss in viability concerned 25% or more of the collection. A larger number were unable to produce sufficient quantities of seed for safety duplication. More than 65 000 accessions were regenerated but less than half of these have been safety duplicated and made available.

Where genebanks are resourced adequately, various factors contribute to lack of use. The appropriate management and ultimate availability of a crop collection is underpinned by a sound knowledge of the taxonomy of the crop and of how genetic diversity is distributed within the genepool (Jaradat *et al.*, 2004; Parzies *et al.*, 2000; van Treuren and van Hintum, 2001; van Treuren *et al.*, 2005). However, even for a major crop such as wheat, there are 14 taxonomic classification systems in use around the world and no undisputable way to identify botanical varieties (Pinheiro de Carvalho *et al.*, 2012). Issues of taxonomic identification of accessions are exacerbated by the inadequacy of passport data, mislabeling, changes in naming conventions, and changes in the genetic integrity of the sample during the course of genebank operations. Although the taxonomy of numerous crops remains a sticking point, stricter genebank procedure and standards have addressed other issues apparently with some success. A study of accessions in the lettuce collection held at the Center for Genetic Resources (CGN) showed that cultivars dating from before 1900 had more than 40% probability of being nonauthentic to their labeled identity, those released between 1960 and 1990 had a 10% rate of nonauthenticity, whereas those released in the past 20 years are all labeled correctly (van de Wouw *et al.*, 2011).

Large parts of any collection, no matter how well managed, will remain unused until its value is appreciated either through study or the rise of new pests, disease, or other needs. At any one time, only a small proportion of the available germplasm of a crop will have value (Sackville Hamilton *et al.*, 2003b). Robinson notes that the maize cob that contributed to the development of quality protein maize languished in a genebank for 30 years before its specific attributes were called upon.

There are also strong reasons for supposing that the use of genebanks will change dramatically in the future. Gollin *et al.* (2000) demonstrated that cost and time lags incurred when searching for pest and disease traits in unimproved wheat germplasm deter breeders from using unknown materials in genebanks. They predict that landraces and wild relatives will remain unused until molecular data reduce search time and costs. In a similar vein, McCouch *et al.* (2012) report, "Only a small fraction of the naturally occurring genetic diversity available in the world's germplasm repositories has been explored to date, but this is expected to change with the advent of affordable, high-throughput genotyping and sequencing technology."

This is already becoming a reality. Under the RiceSNP Consortium (see Relevant Websites section), several thousand accessions of rice from the IRRI genebank are being genotyped using high-density single nucleotide polymorphism (SNP) arrays, and 10 000 accessions are the subject of multiplex resequencing strategies (McCouch *et al.*, 2012). A significant part of the maize and wheat collections at CIMMYT are also being genotyped under a Mexican Government–funded project called Seeds of Discovery. The results will help determine the genetic diversity within and between accessions and provide the levels of detail needed to identify duplicates with confidence. Furthermore, linking genotype to detailed information on the phenotype of a critical number of accessions will enable any number of accessions to be screened for sought-after phenotypic characteristics or traits by using just their genotype data – a possibility that will make screening genebanks much quicker and more effective.

Such genotyping efforts are possible for all crops, although cross-pollinating species and polyploid crops pose challenges. However, the demands of managing and transcribing the vast quantities of data produced are on a scale of magnitude far beyond what any genebank has experienced to date. McCouch *et al.* (2012) continue, "While the power and cost of the new technologies have reached a level where we can begin to contemplate routine whole-genome genotyping or sequencing of entire collections, there is an urgent need to develop strategies and protocols for managing both sequenced germplasm and sequencing information in a rational and productive way."

Sustaining and Securing the CGIAR Collections

Long-term sustainable funding in the early years of the establishment of the CGIAR was critical to its contribution to the Green Revolution (Byerlee and Dubin, 2010). Since then, areas of research have vastly broadened within the CGIAR, whereas the focus of funding has become more restricted. In the 1990s, genebanks were experiencing diminishing support and funding (Clark *et al.*, 1997). The difficulties of keeping up with operating standards and backlogs of regeneration were becoming evident (FAO, 1998).

By the end of the last century, the CGIAR center genebanks were in crisis and emergency funding was sought by the CGIAR System-wide Genetic Resources Program to renew equipment, upgrade cold rooms, and clear the backlogs in regeneration, health-testing, and other routine operations, which had built up over years of inadequate funding. In response to the evident difficulty of attracting sustainable funding for routine genebank operations, the CGIAR together with the FAO established an endowment fund with the aim of financing the routine operations of priority crop collections from the annual income of the invested fund. The fund and disbursements are managed by an independent organization called the Global Crop Diversity Trust, which was established in 2004. The principles and criteria behind the use of the fund are described in a Fund Disbursement Strategy (see Relevant Websites section). Currently, grants are provided to 20 major crop collections to help support their routine management in perpetuity.

The hugely varying approaches to conservation operations is illustrated in a survey of expenditures on PGRFA conservation conducted by Virchow (1999) in 39 countries, which indicate that per accession costs range from US$1 to US$1293. If a genebank undertakes only the minimum activity required to keep seeds in a cold room or freezer, the costs of operation

may be kept as low as US$1 per accession. However, the collection will not remain viable for more than a few years. The operation costs of a number of international seed genebanks have been studied in some detail (Hawtin *et al.*, 2011; Koo *et al.*, 2004, Pardey *et al.*, 2001). The reproductive biology of the crop is the major determinant of the scale of the costs, varying widely between outcrossing and self-pollinated species and between seed and vegetatively propagated crops (Horna *et al.*, 2010). Health-testing, disease-cleaning, information management and characterization are also highly variable and costly. The most recent costing establishes per accession operation costs (not including capital costs) at US$3/accession for wheat compared with US$33/accession for tropical forages with an overall average of US$12/accession for seed accessions (Hawtin *et al.*, 2011). Clonal crops are substantially more expensive to conserve and distribute because of the labor-intensive nature of field and *in vitro* conservation and the average per accession cost is at least 10 times higher than that for seed crops.

The scale of the cost of conserving 7.4 million accessions worldwide to minimum acceptable standards raises the question of what actually needs to be conserved as a global priority. Fewer than 2.25 million accessions are actually believed to be distinct accessions (FAO, 2010). Part of the duplication of conservation efforts occurs because of the need for breeding and research institutes in different countries to have ready access to popular varieties (Hodgkin *et al.*, 1991; van Treuren *et al.*, 2010). However, unplanned and unnecessary duplications account for a significant proportion of recent increases in accession numbers.

This growing historical load borne by present-day genebanks and the need to rationalize collections has been a regular discussion point over the past decade (Engels and Visser, 2003b). Rationalization becomes all the more important when considering that the coverage of numerous crops needs to be improved (FAO, 2010), especially of crop wild relatives, which contain considerable amounts of untapped genetic diversity.

Some efforts at rationalizing collections have been made. CGN in the Netherlands is one of the few institutes that have expressed clear priorities: 80% of its core budget is dedicated to eight out of 20 crop collections based on user demand, representativeness, and availability of the germplasm elsewhere (Visser and Engels, 2003b). A European integrated genebank system (AEGIS) with minimum duplication is also being established (ECPGR, 2009). Other regions have also set up centralized facilities, which allow national programs to relinquish certain conservation roles. The Nordic Genebank represents Scandinavian countries, the Southern African Development Community Plant Genetic Resources Center conserves materials on behalf of South African countries, and the Center for Pacific Crops and Trees (CePaCT) conserves vegetatively propagated crops for the Pacific community.

Processes of rationalizing accessions are not straightforward and are potentially more costly than the savings made, especially for seed collections. In many cases, molecular markers are not powerful enough to be used for distinguishing accessions and eliminating duplicates (McCouch *et al.*, 2012), although they have been successfully used for some clonal crops (Motilal *et al.*, 2011). Rationalizing operations or limiting the availability of less-requested accessions may be more useful ways of cutting costs (Sackville Hamilton *et al.*, 2003b). The genotyping of a wider range of crops will present a tremendous opportunity to develop a more rationalized global system of genebanks.

A Final Word on the Future

Many genebank accessions are no longer available in the farmers' fields from where they were collected (Guarino, 1995b; Dulloo *et al.*, 2010; van de Wouw *et al.*, 2010). According to country reports to the FAO, genetic erosion in cereals appears to be the most severe (FAO, 2010). Pinheiro de Carvalho *et al.*, (2012) reviewed a number of studies that show massive loss of cereal landraces in European countries. According to bioclimatic modeling, genetic erosion from populations of wild relatives is projected to increase, causing the potential extinction of 16–22% of species such as peanut, potato, and cowpea (Jarvis *et al.*, 2008). Major shifts in crop climates are also predicted to occur, potentially causing major losses of crop diversity from existing cooler climates and the urgent need for crop diversity adapted to heat and drought (Burke *et al.*, 2009).

Conflicting results have been published on the trend in levels of genetic diversity within modern varieties, but recent findings suggest that, overall, the genetic base has broadened (van de Wouw *et al.*, 2010). The number of landraces in the pedigrees of Spring bread wheat varieties in developing countries increased from 24 in 1966 to 60 in 1997 (Smale *et al.*, 2002), and more than 2000 new varieties of wheat have been released in the developing world at an increasing rate over time since the 1960s (Dixon *et al.*, 2006). Genetic erosion is occurring in traditional varieties *in situ*, but the potentially dangerous trend toward diminishing genetic diversity in improved varieties, which started in the 1960s and 1970s, appears to have been reversed thanks to the establishment and use of genebanks, especially those of the CGIAR centers (van de Wouw *et al.*, 2010).

The value and use of particular crops or varieties change with time, markets, needs, and capacity of the users to exploit them (Fowler and Hodgkin, 2004). We have no way of accurately predicting what the future will demand and what crop diversity will be needed. *Ex situ* collections remain the best and most cost-efficient way to study, store, document, share, pass on, and make available the widest possible crop diversity to the widest possible audience of users, researchers, and breeders.

See also: Agricultural Policy: A Global View. Intellectual Property in Agriculture. From Foraging to Agriculture. Biodiversity: Conserving Biodiversity in Agroecosystems. Heterosis in Plants. Breeding: Plants, Modern. Domestication of Plants. Forage Crops. Tree Fruits and Nuts. Genomics: Plant Genetic Improvement. Green Revolution: Past, Present, and Future. International and Regional Institutions and Instruments for Agricultural Policy, Research, and Development. Pathogen-Tested Planting Material. Quarantine and Biosecurity. Regulatory Conventions and Institutions that Govern Global Agricultural Trade. Root and Tuber Crops

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United States Department of Agriculture.

Genomics of Food Animals

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Glossary

Contig It is a continuous region of the genome covered by overlapping sequence reads (a sequence contig) or BAC clone inserts (a BAC contig).

Expression quantitative trait locus (eQTL) A polymorphic allele that differentially affects the level of expression of a gene.

Linkage disequilibrium (LD) A nonrandom association of nearby alleles in a population; arises from preexisting allele configurations that are not yet randomized by recombination.

Library A collection of recombinant deoxyribonucleic acid (DNA) clones (e.g., a BAC library) or DNA fragments used in mapping and/or sequencing.

N50 The size of the smallest contig or scaffold such that 50% of the genome is covered by it and all larger contigs or scaffolds.

Orthologous genes (orthologs) A pair of genes from two species are orthologous if they derive from a single gene present in their last common ancestor; usually this means that they are the most homologous of all possible interspecies pairs (contrast to paralogous).

Paralogous genes (paralogs) A pair of genes from two species are paralogous if they evolved from two different genes both of which existed in the last common ancestor genome (contrast to orthologous).

Shotgun sequencing The process of accumulating manyfold coverage of random sequence reads from a target DNA, followed by computational reassembly of its complete sequence based on read overlaps.

Single nucleotide polymorphism (SNP) Single base changes for which both alleles segregate within a given population.

Sequence-tagged site (STS) Any unique sequence within the genome (usually small). These are often used to generate polymerase chain reaction fragments, hybridization probes, or to identify SNPs within the STS for use in linkage mapping.

Introduction

Genomics is a term first popularized by the journal of the same name, where it was described as being "born from a marriage of molecular and cell biology with classical genetics" and "fostered by computational science" by McKusick and Ruddle (1987), who also laid the foundation of genomics in the two complementary functions of mapping and sequencing of genomes. Little did they know at the time that genomics would be the prototype for a variety of related subdisciplines also given the suffix 'omics' to connote that one is addressing the complete genome and/or all of its components, rather than one gene or a small gene family.

Similar to all aspects of genetics, genomics explores the connection between genotype and phenotype, and the genomics of food animals primarily addresses economic traits related to agricultural productivity. Most of these are inherently polygenic traits influenced by alleles (polymorphisms) at numerous quantitative trait loci (QTL). Although a major focus of food animal genomics is to use genomic data to improve breeding, genomics is not simply a tool or a technology. It is a fundamental discipline that is essential to understand almost all aspects of animal biology. At the same time, progress in genomics is very much technology dependent, and few other aspects of biology have seen their tools evolve so rapidly. Most of these new techniques were first applied to either human biology or 'model' species (e.g., *Drosophila melanogaster* and *Caenorhabditis elegans*). As a result, food animal genomics often involves applying similar approaches to those already pioneered in medical/human genomics, and, despite the different practical uses to which they are put (meat, milk, eggs, and wool), genomic technologies used for almost all food animal species are similar. Thus, no attempt will be made here to address each aspect for every species of interest – only selected individual examples will be given.

Genome Maps

Linkage Maps

Linkage mapping goes back to early stages of classical genetics, including the study of several domestic species. The fundamental principle is that the closer two marker alleles are on a chromosome, the more likely they are to cosegregate during meiosis, i.e., to violate Mendel's second law of independent segregation. However, the paucity of useful monogenic marker polymorphisms (and the difficulty in generating mapping families with multiple polymorphisms) prevented these maps from being of much use in breeding. All this changed with the ability to directly genotype deoxyribonucleic acid (DNA) polymorphisms – changes in DNA sequence (Dodgson *et al.*, 1997). Today, the most commonly used DNA marker is the single nucleotide polymorphism (SNP). The genomes of virtually any two members of any breed (unless highly inbred) typically differ by ~3 million SNPs. Thus, in the extreme case where the genomes of parents and offspring in a segregating family are fully sequenced, an average SNP marker spacing of ~0.001 cM (~1000 bp) theoretically could be obtained. Linkage map resolution no longer depends on marker density but only on the density of meiotic recombinants (i.e., number of informative meioses, which is a function of family size).

Linkage mapping in domestic animals today is most commonly done using SNP arrays. The technology underlying these arrays changes rapidly and depends on manufacturer. In brief, arrays that genotype 50 000 to 600 000 SNPs currently are available for many food animal species (Illumina and Affymetrix being the most common providers). It should be kept in mind that only a subset of the SNPs on the array will be polymorphic in any population of interest. Depending on the objective and the amount of linkage disequilibrium (LD) (a nonrandom association of nearby alleles within a population), smaller and/or custom SNP arrays may be used, for example, to trace genetic relatedness in a closed family where LD remains high. For example, LD has been shown to be higher in white egg layers versus meat-type chickens (Muir *et al.*, 2008) and in thoroughbreds versus other horses (McCue *et al.*, 2012). Custom panels might include only those SNPs that previously have been shown to be informative for a particular population and/or trait of interest. The cost of whole genome sequencing (WGS) (rapidly approaching US$1000 per animal) is nearing that of high density SNP genotyping (~US $300 per animal). However, in many applications, there is little extra value in going from ~300 000 genotyped SNPs to the ~3 million SNPs likely to be revealed by WGS. Occasional applications still exist in which microsatellite markers (Dodgson *et al.*, 1997) are of value. Although microsatellites are much less dense and more cumbersome to genotype than SNPs, they are more polymorphic on a per marker basis, so, for example, a small microsatellite panel may be used to rapidly determine genetic identity or parentage.

There are three major applications of linkage mapping. One is to aid in assembly of genome sequence data, to be discussed later. The second is to locate genetic polymorphisms that affect a phenotype of interest (sometimes referred to as positional cloning, although cloning is no longer required, or QTL mapping). Thus, the goal of linkage mapping is to find the 'disease gene' or the 'QTL gene.' Both of these terms are misnomers, as the same gene exists in both sick and normal or fast- and slow-growing individuals – it is rather their alleles that differ. Note that in many cases, the only identifying characteristic of the trait in question is its phenotype and thus the only way one can find the causal allele in the genome is to observe phenotypic cosegregation with markers. There are two basic approaches. Classic linkage or identity by descent mapping, which involves generating families segregating for the phenotypic traits of interest and genotyping the family as deeply and broadly as possible (Andersson and Georges, 2004; Philip *et al.*, 2011). Association or identity by state analysis, on the other hand, involves comparison of animals that vary in phenotype for correlated allele genotypes at markers that are then presumed to be in LD with the causal allele(s). Association analysis attempts to detect the residual linkage of the causal (or mutant) allele(s) for the phenotype to nearby flanking marker alleles that existed on the chromosome in which the mutation first occurred, despite the historical recombination since the mutation first occurred in the population ancestors. Originally, this was limited to a small number of 'candidate' alleles chosen in genes that seemed likely to be involved (Linville *et al.*, 2001). The advent of dense SNP arrays allows for genome-wide association studies, in which one assumes that at least some of the thousands of SNPs tested will remain in LD with the trait-causing allele (Risch, 2000; Weller and Ron, 2011). Genome-wide association analysis now can also be done using high throughput sequencing (Huang *et al.*, 2010).

The third application uses linkage map markers as surrogates for the trait phenotype or the causal genotype for diagnostic or predictive purposes. In agriculture, this primarily involves using marker information to inform selection decisions during breeding, i.e., marker-assisted selection. Here again, the advent of genome sequences and dense SNP arrays allows for globalizing this approach into genome-wide marker-assisted selection ('genomic selection'; Meuwissen *et al.*, 2001; Goddard *et al.*, 2010). In theory, all the causal alleles (i.e., all of the heritable variation) should be in LD with some of the array SNPs, so once the relationship of the trait to SNP genotype is worked out (by 'training' the model on one or a few generations of phenotyped and genotyped animals), SNP array data could replace the need to measure phenotypes for selection decisions (at least until allele fixation and recombination break down that relationship).

Radiation Hybrid Maps

Linkage mapping aligns markers by the likelihood of cosegregation in the face of meiotic recombination breaks, whereas radiation hybrid (RH) mapping uses the likelihood of cosegregation of genes/markers (into hybrid somatic cell lines) following radiation-induced chromosome fragmentation (**Table 1**). The details (McCarthy, 1996) will not be considered here other than to note that almost any unique gene or sequence element (called a sequence-tagged site (STS)) can be placed on the RH map, and RH maps measure marker distance

Table 1 Types of genome maps

Map type	*Measurement unit*	*Marker binning method*	*Typical resolution in DNA Mb*	*Resolution ultimately limited by*[a]
Linkage	centiMorgan (cM)	Meiotic cosegregation	0.5–5	Mapping population size
Radiation hybrid	centiRay (cR)	Cosegregation upon radiation breakage	0.1–1	Radiation intensity
Cytogenetic	Band location or FLpter	Fluorescence *in situ* hybridization	1	Chromosome spread method
Bacterial artificial chromosome (BAC) contig (a physical map)	kb	Localization to common BAC insert	0.1	BAC insert size

[a]Assuming unlimited marker density.

in centiRays, rather than in centiMorgan (cM) (in both cases, one unit equals 1% probability of breakage). The main advantage of RH mapping is that the required panels are all obtained by cell culture techniques with no need to generate families or populations. However, this means that RH maps are of no use in trait mapping and primarily are employed to aid in assembling either other maps or DNA sequence assemblies. RH maps have been generated for many mammalian species (Lewin *et al.*, 2009) and for chicken (Morisson *et al.*, 2007).

Cytogenetic Maps

Cytogenetic maps place markers (usually genes or large segments of genes) in their locations directly on chromosomes, either with reference to nearby stained 'bands' on the chromosome arms (e.g., 5q11.2 for band 11.2 on the q (long) arm of chromosome 5) or by FLpter value representing the fractional length from the p (short arm) terminus. Today, the most common approach to generating cytogenetic maps involves fluorescence *in situ* hybridization (FISH) (**Figure 1**). Although cytogenetic mapping is labor intensive for whole genome analysis (Cheung *et al.*, 2001), it provides a rapid assay for specific genome aberrations, like major deletions or translocations. Furthermore, it is the only approach to definitively map chromosome structures such as centromeres and telomeres and large tandem-repeated blocks such as ribosomal ribonucleic acid (RNA)-encoding regions (rDNA). Generally, FISH provides relatively low resolution (~1 Mb) but high contiguity (i.e., any two markers on the same chromosome will be detected as such, whereas this may not be possible with linkage or RH mapping when markers are far apart). The resolution of FISH can be improved by employing pachytene-stage meiotic chromosomes rather than mitotic chromosomes or in other ways (Heiskanen *et al.*, 1996). Cytogenetic maps are also very useful for comparative genomics, i.e., identifying genome changes that distinguish two or more evolutionarily related genomes (e.g., Zhang *et al.*, 2011).

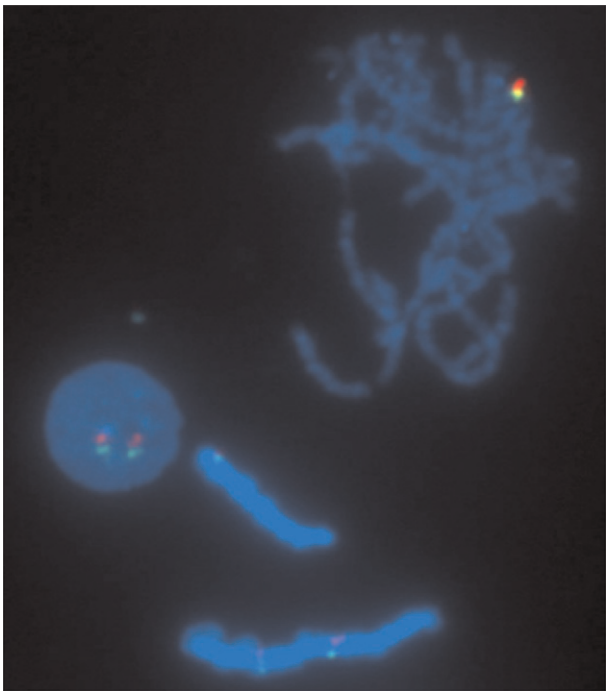


Figure 1 Multicolor fluorescence *in situ* hybridization (FISH). Hybridization of two labeled turkey bacterial artificial chromosome (BAC) clones (110H19, green; 94E20, red) to DNA (blue) of turkey pachytene chromosomes (upper right), an interphase nucleus (left center), and three sperm (bottom center). The two BACs are adjacent in the turkey genome. As the two homologous chromosomes are synapsed at pachytene, only single hybridization signals are found. Methods are as described in Zhang, Zhang, O'Hare, *et al.* (2011). Jiang, Delany and Dodgson, unpublished.

Physical Genome Maps

Although some consider RH and cytogenetic maps to be physical maps, herein this is restricted to maps in which marker separation is a direct measure of DNA length (**Table 1**). The ultimate physical map, then, is the DNA sequence itself, but physical maps also include restriction maps and clone-based contig maps. Recombinant DNA clone-based maps have the advantage that, as part of their generation, the complete genome is divided into clone inserts that then can be used for further molecular analyses. Originally, such maps were believed to be an essential precursor to genome sequencing, but this is no longer the case. The most common form is the bacterial artificial chromosome (BAC) contig map. 'Contig' indicates a continuous segment of the genome that is completely covered by an overlapping collection of cloned inserts (e.g., a BAC contig) or overlapping DNA sequence reads (sequence contig). Most food animal BAC libraries in use were constructed and are available at BACPAC Resources (http://bacpac.chori.org/). Typical BAC libraries have average inserts of 130–180 kb (the larger, the better) and in total span the genome in question ~12 times over (12×coverage). Despite this high redundancy, some sequences cannot be cloned and therefore inevitably result in physical map gaps. The most common approach to assembling BAC contigs is the 'fingerprint' method in which many thousands of BACs are individually digested with one or more restriction enzymes to generate ~50–100 fragments per BAC, and those fragment sizes are measured by gel or capillary electrophoresis (Meyers *et al.*, 2004). The FPC computer program is commonly used to assemble the data into a BAC contig map (Soderlund *et al.*, 2000). The basic principle is that the more the two BAC inserts overlap, the greater the length of common restriction fragments they share. Long repetitive regions and regions of unusually low or unusually high frequency of restriction sites can be problematic for contig building. BAC fingerprint maps have been constructed for many food animal genomes (Wallis *et al.*, 2004; Ng *et al.*, 2005; Humphray *et al.*, 2007; Snelling *et al.*, 2007; Xu *et al.*, 2007; Palti *et al.*, 2009; Zhang *et al.*, 2011). Fingerprint-based BAC contig maps can be augmented by hybridization (**Figure 2**) of unique sequences designed using linkage or RH map markers, comparative maps (see Section Genome Evolution), and from BAC end sequences (BES) (the two ends can be sequenced at high throughput without the need to sequence the full insert). BES are also used to align sequence contigs to the physical map (**Figure 2**). In this way the BAC contig map forms a platform on which the DNA sequence assembly is built (Lewin *et al.*, 2009; Nelson and

Soderlund, 2009). Note that BACs are also used for FISH mapping (Figure 1) to integrate cytogenetic and physical maps, and BES can act as STS probes for RH maps and harbor polymorphisms that can be used to integrate the linkage map as well (Figure 2). Thus, the ideal situation is an interlocking grid of mapping and sequence data that can correct errors or close gaps present in any one assembly.

Reference Genome Assemblies

Methods and Principles

The reference genome sequence assembly and its accuracy are critical to nearly all aspects of modern genomics.

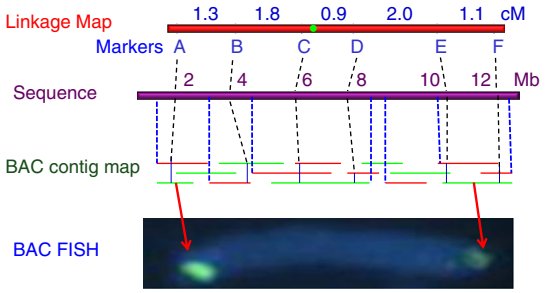


Figure 2 Integration of genome maps and sequence assembly. The linkage map (red) at the top contains six polymorphic sequenced markers ((a)–(f), e.g., single nucleotide polymorphisms (SNPs) within a sequence tagged site) whose intermarker distance is shown in centi Morgan (cM). These markers can be placed uniquely within the DNA sequence assembly (purple line, sequence coordinates shown in Mb from the left end), as shown by connecting black dashed lines. The linkage map can thus be used to align the sequence (Figure 3 for more detail). Linkage markers also can be used as hybridization probes (additional connecting black dashed lines) for alignment with the physical/bacterial artificial chromosome (BAC) contig map (BAC inserts depicted as overlapping narrow red and green lines). The sequence assembly can be aligned using the BAC contig map with BAC end sequences (connecting blue dashed lines) or additional hybridization experiments. The BAC contig map can be aligned with the cytogenetic map using BACs as fluorescence *in situ* hybridization (FISH) probes (red arrows, Figure 1). Similarly, the sequence, linkage, and physical maps can be integrated with radiation hybrid maps using common marker probes (not shown for purposes of clarity).

Sequencing methods (Table 2) change rapidly and space precludes a full description of each. Sanger sequencing is done using one template (usually a recombinant DNA plasmid) in one reaction run on one capillary gel. Typical Sanger reads are highly accurate at least up to 500–800 bases, their maximum length, but certain types of sequence (high GC content and/or inverted repeats) are problematic. Current 'next generation sequencing' (NGS) techniques have much higher throughput, mainly because they employ polymerase chain reaction (PCR) rather than cloning to amplify the signal (sequencing libraries are created directly from genomic DNA), and they are 'multiparallel,' that is, thousands of reactions are run and monitored simultaneously (Shendure and Ji, 2008). Roche/454 has the lowest NGS throughput, but it generates read lengths almost comparable to Sanger sequencing, whereas the others currently give reads in the 35–100 base range. Newer NGS approaches include methods that employ neither PCR nor cloning but sequence single DNA molecules. Nanopore sequencing is just becoming generally available, but offers exciting prospects for the future (Schneider and Dekker, 2012). Most NGS methods have higher error rates per read than Sanger method, but they compensate by higher throughput such that their 'consensus' sequence (average compilation of all reads) may be of comparable accuracy (Metzker, 2010; Glenn, 2011; www.molecularecologist.com/next-gen-fieldguide/).

Given this brief overview, it is important to understand a few general principles of sequence assembly. By itself, the size of vertebrate genomes (haploid size, 1–3 Gb) is no longer a major obstacle. The critical problem is that they contain large numbers of repetitive sequences of varying sizes (1 to $>10\,000$ bp), varying numbers (2 to >1 million copies), and varying locations (Treangen and Salzberg, 2011). Currently, all proven methods (including Sanger) generate read lengths that are shorter than at least some repeats. If long repeats are identical in sequence, or very nearly so, no internal sequence read from one copy can be distinguished from one from a different copy elsewhere in the genome, thus confounding the assembly process. Fortunately, most repeats derive from transposable elements that are no longer active but have replicated during the evolutionary history of the genome, and they have had enough time to diverge in sequence such that the assembler can distinguish them. The longer and more

Table 2 Genome sequencing technologies[a]

Technology or manufacturer	*Type of DNA template sequenced*	*Single read or multiparallel*	*Typical read length (bp)*[a]
Sanger (e.g., ABI 3730)	Recombinant DNA or PCR fragment	Single read	~650
Roche/454	PCR-amplified fragment library	Multiparallel	400–650
Illumina/Solexa	PCR-amplified fragment library	Multiparallel	100–150
Life Tech/ABI SOLiD	PCR-amplified fragment library	Multiparallel	35–75
Life Tech Ion Torrent	PCR-amplified fragment library	Multiparallel	200
Helicos	Single DNA molecules	Multiparallel	35
Pacific Biosciences	Single DNA molecules	Multiparallel	>1000
Complete Genomics[b]	PCR and *Phi*29 amplified library	Multiparallel	35
Oxford Nanopore	Single DNA molecules	Multiparallel	~10 000

[a]Major current commercial providers are listed. Different manufacturers provide multiple instruments with differing specifications. Current estimated typical read lengths are based on manufacturer web sites or the 2012 NGS Field Guide, http://www.molecularecologist.com/next-gen-fieldguide/ (Glenn, 2011).

[b]Complete Genomics provides a sequencing service but does not sell instruments (Drmanac *et al.*, 2010).

accurate any sequence read is, the higher the chance that it can tell one repeat from another and be properly aligned. Repetitive elements are not evenly spread across the genome; they tend to cluster around centromeres and sometimes near telomeres and on the Y- or W-sex chromosomes. The denser the repeats are, the more difficult it is to assemble such regions. This is why centromeres are often left as arbitrary gaps in the assemblies. Similarly, the clusters of rDNA made up of long tandem, near-identical repeats are never fully assembled in the sequence, they are just estimated in size. A related problem is posed by segmental duplications. These are blocks (often large) of DNA repeated a small number of times, most likely due to errors in replication or recombination. They tend to have high sequence identity that confounds the assembly process. Moreover, they are polymorphic in existing populations, so the sequenced 'reference' animal's genome may differ from that of any other animal of interest. A common situation is that reference sequence assemblies will 'over-collapse' segmental duplications (especially those that are nearby one another). For example, earlier versions of the chicken genome sequence included only a single interferon alpha (*IFNA3*) gene, whereas the current (Gallus_gallus-4.0) version, based on ordered sequencing (see below) of the chicken Z-chromosome by Bellott *et al.* (2010), contains the previously known number of ten linked copies (Sick *et al.*, 1996).

Almost all food animal reference genomes (**Table 3**) are based on sequencing a single, individual animal. These animals are diploid, of course, and at best only partially inbred, so their genomes retain allelic diversity in some locations (certain aquaculture species can avoid this problem, *see* Davidson *et al.*, 2010). When the sequence assembly program sees two different sequences that are, for example, 99% similar, it may interpret these as a segmental duplication and build two copies of that sequence into the reference, when in fact these represent two alleles of the same single copy sequence (Kelley and Salzberg, 2010). For example, even though a substantially inbred animal was used for the chicken genome sequence (International Chicken Genome Sequencing Consortium, 2004), 17 Mb of erroneous duplicated sequences were present in earlier versions (removed in the Gallus_gallus-4.0 assembly). All food animal genomes are considered 'draft' sequences denoting their incomplete and occasionally inaccurate nature, but the quality of draft sequences spans a wide range. Even though the human genome has been intensively studied and is considered a 'finished' sequence, it still contains some gaps and errors and is continually being updated (Church *et al.*, 2011).

Table 3 Example food animal reference genome sequence assemblies[a]

Species	*Assembly*[b]	*Method*[c]	*Sequenced bases (Gb)*[d]	*Scaffold number*	*Scaffold N50 (Mb)*	*Contig number*	*Contig N50 (kb)*
Cow[e]	Btau_4.6.1 October 2011	Shotgun Sanger	2.983	13 387	2.60	81 416	83.7
Cow[e]	Bos_taurus_UMD_3.1 November 2009	Shotgun Sanger	2.670	6 510	6.38	75 771	97.0
Horse	Broad/equCab2 September 2007	Shotgun Sanger	2.475	9 688	46.8	55 317	112
Sheep	Ovis_aries_1.0 February 2010	Shotgun Roche	2.860	1 331	34.1	2.35 million	0.685
Pig	Sscrofa9.2 November 2009	Shotgun and ordered Sanger	2.262	3 135	1.11	100 198	54.4
Chicken[f]	Gallus_gallus-4.0 November 2011	Shotgun Sanger	1.047	16 847	12.9	27 027	280
Turkey	Turkey_2.01 December 2009	Shotgun Roche Illumina	1.062	24 484	0.858	152 639	12.5
Atlantic cod	GadMor_May2010 May 2010	Shotgun Roche	0.824	427 427	0.393	554 869	2.31
Atlantic salmon	ASM23337v1 October 2011	Shotgun Sanger Illumina	2.435	NA[g]	NA[g]	555 960	9.34
Nile tilapia	OreNil1.1 January 2011	Shotgun Illumina	0.928	5 909	2.77	77 754	29.5

[a]Statistics from NCBI Assembly, http://www.ncbi.nlm.nih.gov/assembly, accessed June 28, 2012.
[b]Assembly names are from the UCSC browser (http://genome.ucsc.edu), where available, or NCBI Assembly.
[c]Predominant method used, although supplemented by alternative approaches. For example, the chicken Z chromosome has been sequenced by ordered sequencing (Bellott *et al.*, 2010).
[d]These assemblies are 90–95% complete; multiply sequenced bases by 1.05 to 1.1 for haploid genome sizes.
[e]There are two comparable cow assemblies using much the same data but different assemblers.
[f]The bird that was sequenced was a red junglefowl, the nearest wild progenitor of chickens.
[g]The Atlantic salmon contigs are yet to be joined into scaffolds.

Reference genome sequences are assembled as various combinations of two basic approaches (Table 3): the ordered or 'BAC by BAC' approach versus the whole genome approach first proposed by Venter *et al.* (1996). The ordered approach requires that one first assemble a high quality BAC contig physical map. One then sequences the fewest possible BACs that together most fully cover the genome, one at a time. The advantage of the ordered approach is that assembling the sequence of the 100–200 kb insert in a single BAC is much easier and more accurate because the computer, on average, deals with approximately 0.01% of the number of repeats in the total genome. The disadvantage, especially in today's world of NGS, is that the cost and effort required to generate the BAC map far exceeds that required for bulk sequencing. Examples of ordered genome sequences include maize (Schnable *et al.*, 2009), the chicken Z-chromosome (Bellott *et al.*, 2010), and partially that of swine (Groenen *et al.*, 2012). In the first two instances, ordered sequencing was chosen due to a very high density of repetitive elements. For the swine genome, the decision was driven, in part, by the preexisting availability of a very high quality BAC contig physical map (Humphray *et al.*, 2007).

Most genomes today are sequenced either solely by shotgun methods or with a hybrid approach (Green, 2001), primarily with shotgun reads but with the added use of BAC contig maps to assist in assembly and alignment to chromosomes. A limited number of BACs are often sequenced one at a time as a reference to judge assembly accuracy. The key tool for accurate shotgun assembly is the 'mate pair' or 'end pair' (Figure 3). Most animal genomes are collections of tens of thousands (or more) sequence contigs (Table 3) that typically range in size from approximately 1 kb to 1 Mb. These pieces of the linear genome jigsaw puzzle are aligned into 'scaffolds' with mate pairs, sequences from opposite ends of fragments whose approximate size is known. Typically, a genome sequencing project will include libraries of mate pair fragments of different sizes, for example, 3 kb, 10 kb, and 50 kb. Assembly programs align the two mate pair reads (with appropriate orientation) assuming that they are the distance apart indicated by the fragment library size. For example, if there were two 500 bp mate pair sequences from a 3 kb fragment, the assembler assumes that there is a 2 kb gap between the two. Obviously, the accuracy of the estimated gap size depends on how narrow is the library fragment size distribution. For Sanger sequencing, the libraries are recombinant clone libraries, whereas the various NGS sequencers each have methods to obtain end-pair reads from size-selected DNAs. The sequence assembler uses mate pair sequences (usually requiring at least two to prevent 'false joins') to align adjacent sequence contigs and estimate the gap size. Collections of sequence contigs are called scaffolds (Figure 3). Gaps remaining between scaffolds not spanned by mate pairs are likely to be larger (and/or problematic due to repetitive sequence). Generally, there will be thousands of scaffolds in a draft genome. (The numbers and average sizes of contigs and scaffolds are usually dominated by a preponderance of small fragments, for example, unplaced 'singletons' that overlap nothing else. Thus, the preferred measure of assembly quality is the N50, which is the smallest contig or scaffold such that 50% of the genome is covered by it and all larger contigs or scaffolds, Table 3.) In any good quality-assembled genome, many scaffolds will be large enough to contain multiple physical map, RH map, or linkage map markers. Those maps can then be used to align scaffold order and identify the appropriate chromosome from which they are derived (Figure 3). This results in 'superscaffolds' that often are melded into a full chromosome-sized 'pseudomolecule,' with numerous gaps connected by Ns (unknown bases), usually including a large, poorly estimated gap at the centromere.

Table 3 indicates the current status of several food animal genomes. Many of these were generated primarily, if not solely,

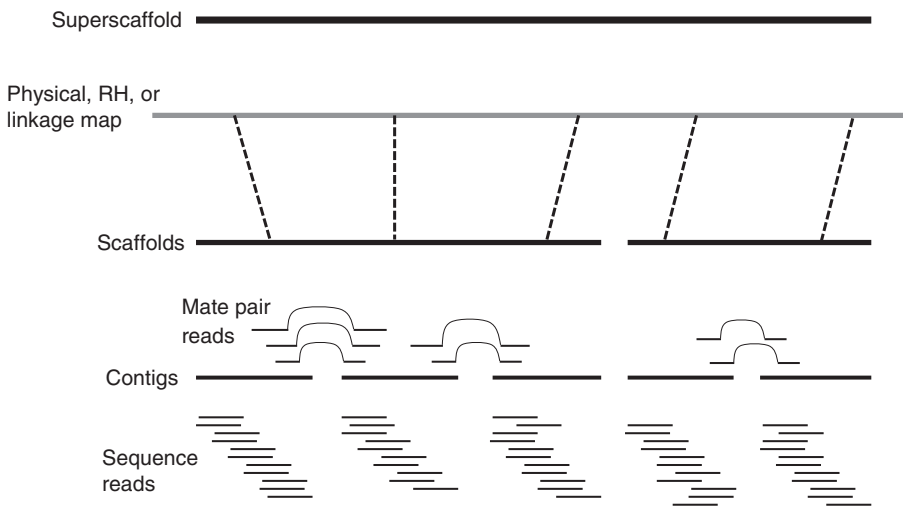


Figure 3 Sequence assembly from shotgun sequence reads. Overlapping sequence reads at the bottom are assembled into sequence contigs. Mate pair reads with one end in each of two contigs and an estimated total size are used to align adjacent contigs and estimate gap size. Contigs joined by mate pairs form scaffolds (in this example, mate pairs join the first three contigs into one scaffold and the last two into another scaffold). Dashed lines indicate sequence segments that can also be located on a physical map (bacterial artificial chromosome (BAC) end sequences or hybridization probes), a radiation hybrid (RH) map (sequence-tagged site (STS) markers), or a linkage map (polymorphic markers, e.g., single nucleotide polymorphism (SNP)). These are used to orient and align scaffolds into superscaffolds (top line).

with Sanger sequencing, although all have been, or will be, supplemented with additional NGS reads. The turkey genome (Dalloul *et al.*, 2010) likely set the stage for the future in that it was solely assembled from NGS reads but with the adjunct of dense BAC contig and linkage maps to aid in alignment. There often is a considerable time gap between the initial 'release' (**Table 3**) of a genome sequence and its annotation and availability on genome browsers (described next).

Genome Annotation

By itself, the reference genome sequence is of limited utility to much of the user community, with its ultimate value depending on proper annotation (Yandell and Ence, 2012). In its widest sense, annotation means linking the DNA sequence to all the information available on genes, messenger RNAs (mRNAs), proteins, etc. This ideal is never realized, but because much of that information is linked via a gene name, the first, and most critical, step is locating and appropriately naming all of the genes (encoding both proteins and noncoding RNAs (ncRNAs)). Once the genome is sequenced, there are two methods to find the genes – both of these are, at least initially, done by a computer (see Yandell and Ence, 2012), although they can be improved by subsequent manual curation. The first is evidence based – this primarily uses cDNA (complementary DNA, that is, DNA copied from a mRNA) clone sequences (often called expressed sequence tags (ESTs)) and other transcriptomic or proteomic (see below) data, as well as homology to known genes in other species. At least for mammalian food animal species, comparisons to the very well annotated human and mouse genomes are especially powerful. (However, keep in mind that those aspects of animal physiology most relevant to agricultural utility may tend to be among the least likely to have direct counterparts in humans or mice, e.g., wool production in sheep.) The second general method to identify genes involves *ab initio* annotation. In this case the program searches for open reading frames, likely initiation and stop codons, splice junctions, and other sequence-based characteristics to predict the existence of genes for which no experimental evidence is available. Some of these programs (e.g., Genscan) are first 'trained' on a set of strongly supported, evidence-based genes. *Ab initio* annotation is more successful at predicting protein-coding genes than ncRNA genes (the latter are predicted on the basis of characteristic secondary structures). Transposable elements can be annotated on the basis of their repetition in the genome, relatedness to transposons in other species, and their characteristic end structures (Jurka *et al.*, 2005). Annotating regulatory sequences (such as transcription factor-binding sites) is more problematic, but accuracy can be improved if one can employ a cluster of evolutionarily related genomes and use purifying selection among the identification criteria (e.g., Stark *et al.*, 2007). The human ENCODE project (The ENCODE Project Consortium, 2012) has made extensive and detailed observations at specific sequence regions to understand what characteristics are of critical importance, and such data have improved annotation substantially, especially for regulatory sequences.

Most food animal species genomes reliably can be expected to contain 20–30 000 protein-coding genes, as do those of most vertebrates (there may be more in species such as salmonids that have gone through a recent genome duplication, Davidson *et al.*, 2010). As more mRNA sequence data accumulate (see Section Transcriptomics) from more and more tissues, it should be possible to find some evidence to support virtually all functional genes. (Even now, one tends to distrust *ab initio* predictions for which there is no supporting RNA or homology evidence.) However, an important problem for annotation is that what might naïvely be described using a single gene name, in fact, encodes many different transcripts due to alternative transcription start sites (TSS), transcription termination sites (TTS), and splicing patterns. Many, and probably most, genes exhibit some of these alternatives, the functional significance of which remains to be worked out in most instances. Alternative TTS and TSS are nearly ubiquitous, but many of these do not alter the encoded protein sequence, whereas alternative splicing often does. The various possible transcripts for a given locus may be described as different 'gene models.' It is nearly impossible for *ab initio* methods to accurately annotate a set of transcripts. Even with high throughput RNA sequence data, it can be challenging to estimate which of several possible combinations of TSS, TTS, and exons are employed by the cell without detailed gene by gene molecular analysis.

Genome Browsers

The interface for most of the user community with reference sequences is provided by a genome browser. There are three major browsers: University of California at Santa Cruz (UCSC) Genome Bioinformatics (www.genome.ucsc.edu), Ensembl (www.ensembl.org), and the National Center for Biotechnology Information (NCBI) Map Viewer (http://www.ncbi.nlm.nih.gov/genome), each of which has its own unique characteristics and options. There are also a variety of species-specific genome browsers (e.g., BovineGenome.org) that often contain additional information of interest. (See http://www.animalgenome.org/ for updated lists of relevant links for food animal genomics.) One begins by finding the genome browser gateway and choosing the species and the sequence build of interest. (Note that sequence coordinates change from one build to another as do the available annotation tracks, see the paragraph below.)

The browsers all employ the same reference sequence information as a series of linear sequences, usually chromosome-specific 'pseudomolecules,' but sometimes just a list of scaffolds that are yet to be aligned to chromosomes (or both). The presence or relative intensity of any characteristic (exons, %GC, depth of transcription, homology with other sequences, etc.) that can be mapped on the sequence can be displayed as a 'track' on the genome. The user controls the tracks displayed (**Figure 4**), their format and order, and can also submit their own data for either private or public access as additional tracks. Each build of a genome will have its own available track annotations, not all of which may be available on another build. It is not possible here to begin to summarize the various options and datasets available; however help and tutorials are provided at each site. The most common use of browsers is probably to view genes, gene models, repetitive elements, transcription data, and homology/conservation evidence (**Figure 4**).

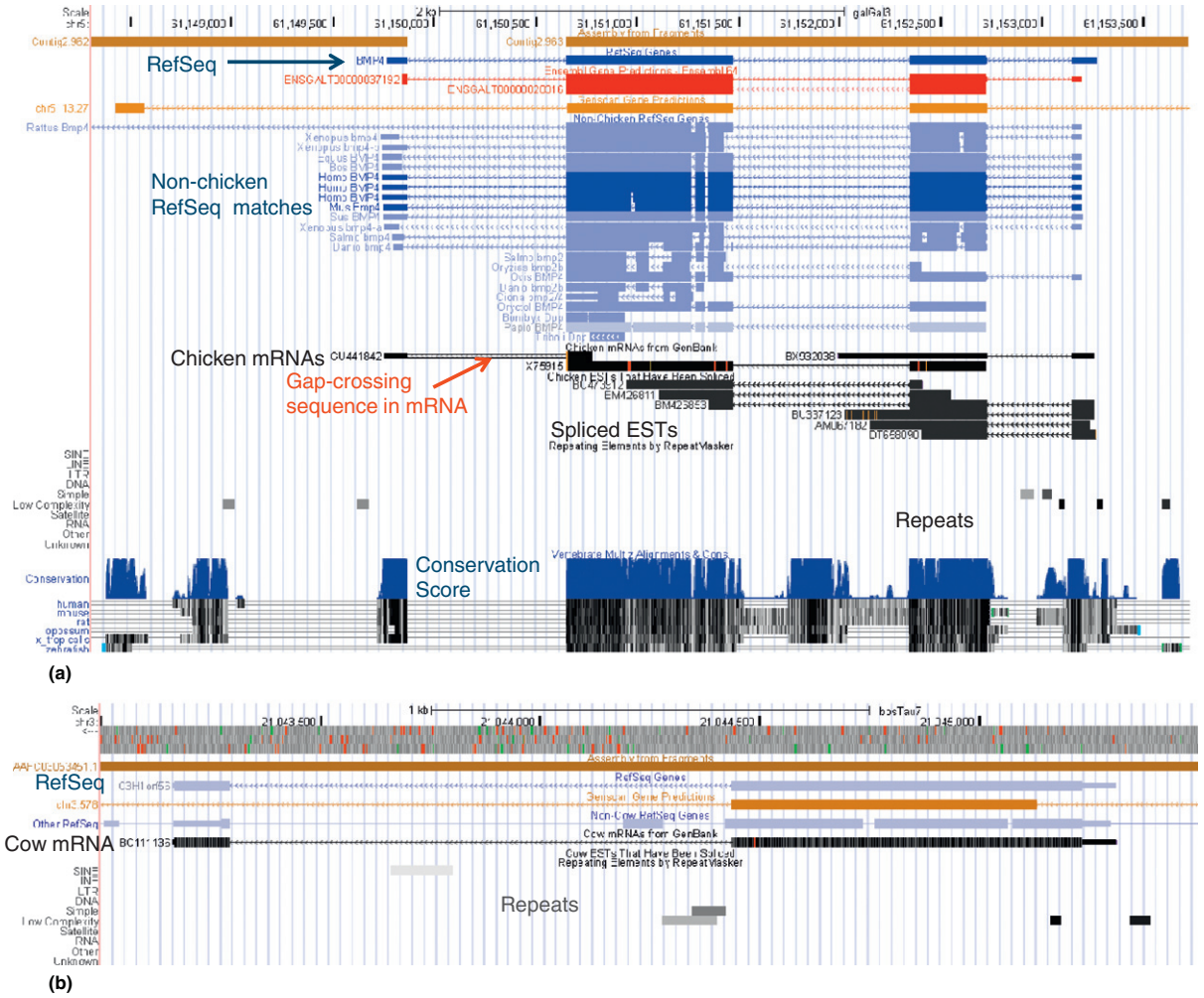


Figure 4 Example uses of UCSC genome browser. (a) The chicken *BMP4* gene from the (May 2006) Gallus_gallus-2.1 assembly. *BMP4* is transcribed right to left. Thick brown lines below sequence coordinates depict the two sequence contigs in this region. Below it, top to bottom, are the RefSeq gene model (blue arrow), two different Ensembl gene models (dark red), the *ab initio* Genscan model (light brown, note incorrect exons at both ends), homology to nonchicken RefSeq genes (various shades of blue), and sequence mapping to 'chicken mRNAs' and to spliced expressed sequence tags (ESTs) (black). Exons are shown as boxes with coding regions thicker than untranslated regions (UTRs); introns are depicted as narrow lines with arrowheads in the direction of transcription. Chicken mRNAs are cDNA clone sequences entered into Genbank as full length, but often (as shown here) they are not. ESTs are single pass partial cDNA sequences – spliced ESTs are more reliable, so only those are shown here. This gene has an exon that crosses the gap region whose sequence can be inferred from the sequence of the mRNA marked with a red arrow. (The gap is estimated to be 790 bp in the assembly but actually is 129 bp.) At the bottom are shown various repeat sequences (gray blocks, only a few simple or low complexity repeats are found) and a blue 'wiggle' plot depicting the (multispecies) Multiz evolutionary conservation score of the chicken sequence (usually highest near exons) with homology to individual genomes below this as mostly gray tracks. This view was generated with track settings: Base Position – full, Assembly – pack, RefSeq Genes – pack, Other RefSeq – pack, Ensembl Genes – pack, Genscan Genes – pack, Chicken mRNAs – pack, Spliced ESTs – pack, Conservation – pack, and RepeatMasker – full. All other tracks were set to hide. The UCSC Genome Browser Gateway at http://genome.ucsc.edu was accessed on 29 June 2012 (Kent *et al.*, 2002). (b) The cow *C3H1orf56* gene from the Btau_4.6.1 assembly is transcribed right to left. This is the cow ortholog of an anonymous human gene named *H1orf56* to indicate open reading frame 56 on human chromosome 1. The ortholog is on cow chromosome 3, so the name is changed to *C3H1orf56* to indicate both its chromosome in cattle and in human. At this magnification level, the Base Position (gray) tracks at the top show all three reading frames, here set to show the negative (right to left) strand. Green and red tick marks indicate methionine and stop codons, respectively. The bottom frame is used (no stops) for exon 1 and the top frame is used for exon 2 by *C3H1orf56*. This region is covered by a single contig (long brown bar at top), below which are shown the cow RefSeq gene (light blue), the Genscan prediction (light brown, highly inaccurate), homology to noncow RefSeq genes (light blue, dense version, so all of these are compacted into one line), the single cow mRNA in Genbank (black) and repetitive elements detected by RepeatMasker. (Ensembl gene predictions are not currently available.) Exons are depicted as boxes, thicker for coding regions, and introns as lines with arrowheads depicting transcription direction. This view was generated with track settings: Base Position and RepeatMasker set to full; Assembly, RefSeq Genes, Genscan Genes, Cow mRNAs, Spliced ESTs (there are none) all set to pack; and other RefSeq set to dense. All other tracks were set to hide. The UCSC Genome Browser Gateway at http://genome.ucsc.edu was accessed on 29 June 2012. Kent, W.J., Sugnet, C.W., Furey, T.S., *et al.*, 2002. The human genome browser at UCSC. Genome Research 12, 996–1006.

The browser offers a variety of gene model outcomes (depending on the tracks displayed, Figure 4). The most reliable are the RefSeq genes that have been manually annotated by NCBI, but the RefSeq set is conservative (i.e., low false positive and high false negative rate). Ensembl gene predictions (and UCSC, where available) detect most (but not all) genes in a vertebrate genome and provide more possible models per coding locus but with more false positives. Each gene predictor may fail to specifically name a gene of interest, giving it instead an anonymous LOCxxxxxx (or ENSxxxxxxxxxxxx) name, even when it may be easy to deduce the proper name by manual curation. For the great majority of food animal genes, the species nomenclature defers to the human gene nomenclature, so the name of the nearest homologue in human is also the name in, for example, cow (see an exception in Figure 4(b)). If there is a single copy of the gene in both species (called 1:1 orthologs), then the proper name is obvious. When there are 5 copies of closely related genes in human and 8 in cow, things can get tricky (e.g., the current human assembly annotates *NOS1*, *NOS2*, and *NOS3* genes, the bovine genome only *NOS2* and *NOS3*, and the chicken only *NOS2*, although it contains currently unannotated *NOS* sequences, probably *NOS1* and *NOS3*). Usually, the most homologous (most similar in sequence) pair of genes between the two species are considered orthologs and other possible pairs are paralogs (see Glossary for the strict definition). The orthologous gene pair members should have the same name. Another way to identify orthologous pairs employs conserved gene order. Vertebrate genomes, especially those of amniotes (mammals and birds), tend to have reasonably long segments in which genes are aligned in the same order and direction. For example, assume there are two related human gene family members, B1 and B2, and cow gene X exhibits similar sequence homology to both B1 and B2. If gene order in human is A – B1 – C on one chromosome with M – B2 – N on another, and cow gene X is between cow M and N, then it is likely to be the cow B2 gene.

Genome browsers are only as good as the underlying sequence assembly and annotation. The problem of assemblers 'overcollapsing' repeated sequences and segmental duplications already has been discussed. As shown in Figure 4, gene models (Ensembl, Genscan, etc.) should always be treated with caution. Automated gene predictors will often try to place missing exons in whatever sequence exists rather than in a gap between contigs where they really should be. (The correct exon sometimes can be determined from mRNA or EST sequences corresponding to the gene in question, Figure 4(a).) For those species with good EST collections (true for many food animals), the ESTs (or RNA-seq data, see Section Transcriptomics) are often the most reliable predictors of the true gene models. In addition, gene predictors may fail where homology between the gene and its orthologs in other species is low, especially, but not solely, in 5′ and 3′ untranslated regions (UTRs). Genes that are large and/or have limited transcriptional evidence may be split into two or more gene models; conversely, programs sometimes merge two adjacent genes (transcribed in the same direction) into one long gene model. Gene prediction programs are very poor at accurately annotating 5′UTRs and especially 3′UTRs, in part because of the diversity of alternative TSS and TTS discussed previously.

Resequencing Genomes

Mutant Analysis

The availability of a reference genome sequence enables rapid 'resequencing' of any animal genome using NGS. Resequencing is much easier than *de novo* sequencing because one only has to align all the reads with the preassembled reference (using one of several programs designed for the purpose such as BLAST, Altschul *et al.*, 1990). Indeed, some resequencing methods only work by mapping to a reference; they cannot do *de novo* assembly. The goal is to ascertain where and how the genome being resequenced differs from the reference. These differences typically will include millions of SNP polymorphisms, 100 000 or more small indels and possibly hundreds of differences in segmental duplications (also called copy number variations), or rare large-scale rearrangements. Furthermore, even if resequencing is 99.99% accurate, there would be 300 000 errors in a mammalian-sized genome, plus any errors remaining in the reference sequence itself (NGS manufacturers report 99.99% accuracy in consensus high coverage reads, but coverage levels across the genome are variable and some regions are more error prone.) How do we find needles in this haystack?

First consider a situation in which a trait of interest is due to a single mutation at one site in the genome and the comparison is made between the mutant genome sequence and a reference genome or that of a nonmutant relative. The first choice is between whole genome sequencing (WGS) and 'exome' sequencing. Exome sequencing uses an array of synthetic oligonucleotides (see Section Transcriptomics) to hybridize to and enrich the target genome DNA for only those sequences in exons. (Similarly, if your mutation of interest is already mapped to a segment of the genome, you can enrich for just that region, Charlier *et al.*, 2008; Robb and Delany, 2012.) Exons make up less than 2% of a typical mammalian genome, so if exome enrichment were perfect, coverage would increase by ~50-fold. Increased NGS coverage translates to increased accuracy; important when searching for a single causal mutation in a potentially large background of errors and polymorphisms. Despite the significant challenges posed by background diversity and errors, exome sequencing is now being widely applied in medical genetics (Gonzaga-Jauregui *et al.*, 2012). Obviously, if the causal mutation lies outside of an exon, exome sequencing will not work. WGS can be used, but filters must be applied to narrow the search. As an example, Roach *et al.* (2010) used WGS (Complete Genomics) of a quartet (both parents and two children) in which both children suffered from the same two rare inherited diseases. By focusing only on coding regions within the 22% of the genome inherited identically by both children and assuming that the causal alleles must be rare (i.e., ruling out all variants already within the large and rapidly growing human SNP database), the authors were able to narrow candidate disease-causing mutations to four genes, two of which were confirmed by other studies.

Diversity Analysis and Signatures of Selection

Resequencing is more commonly used in food animals to sample existing genetic diversity within breeds, commercial

lines, or the domesticated species as a whole. First, this provides data for the design of high-density SNP arrays previously discussed (Matukumalli *et al.*, 2009; Ramos *et al.*, 2009; Groenen *et al.*, 2011; Liu *et al.*, 2011; McCue *et al.*, 2012). As noted above, NGS costs are now approaching a level at which WGS and high-density SNP genotyping applications are merging. For example, both WGS and high-density SNP typing allow one to estimate worldwide breed diversity and the history of domestication and selection that led to their current state (Muir *et al.*, 2008; Bovine HapMap Consortium, 2009; Kijas *et al.*, 2009; Kijas *et al.*, 2012; McCue *et al.*, 2012). Such studies also document genomic features related to recombination rate and its inverse, LD (International Chicken Polymorphism Map Consortium, 2004; Groenen *et al.*, 2009; Megens *et al.*, 2009). For example, Auton *et al.* (2012) recently generated a fine-scale recombination map for chimpanzee by sequencing only 10 animals. Of particular interest for food animals is the search for selective sweeps, regions of unusually high LD due to intense selection during domestication or later breeding for an allele that has a major effect on a desirable trait (Bovine HapMap Consortium, 2009; Rubin *et al.*, 2010; Moradi *et al.*, 2012) which again can be done either by resequencing or high density SNP genotyping. Note that in detecting a selective sweep, one identifies a common distribution at many linked SNPs within a segment of the genome on the order of 10–100 kb or larger. Thus, such an analysis is much more robust than identifying a single point mutation and can more easily tolerate the background error rate of NGS.

Comparative Genomics

Genome Evolution

Comparative genomics refers to the alignment of genes and sequences between species either to draw inferences as to how their genomes evolved or to compare and contrast genetic mechanisms. Comparative genomics is especially important in food animal species because it provides connections to aspects of genetics and physiology that sometimes are better studied in humans (e.g., medical genetics) or 'model' species such as mouse and zebrafish. The previously described development of DNA-based markers allowed for alignment of genome maps across multiple species (O'Brien *et al.*, 1988; Nadeau, 1989) at much greater resolution than did previous linkage and cytogenetic maps. Because exon sequences of most genes are evolutionarily conserved, gene-based maps could be aligned between species whose last common ancestor lived hundreds of millions of years ago. For example, long segments of bird and mammalian gene alignments have been conserved for >300 million years of separate evolution (Burt *et al.*, 1999; Suchyta *et al.*, 2001), despite the fact that avian genomes are only approximately a third the size of those of mammals. The clear implication is that introns and intergenic sequences can expand or contract greatly (most often through insertion and removal of transposable elements) over evolutionary time, whereas the chromosomal order of genes remains largely preserved. This is the basis for the use of conserved gene order to infer orthologous gene pairs as described above, and it probably reflects the fact that large chromosome rearrangements can severely reduce reproductive fitness. The most common rearrangements that have occurred during evolutionary history seem to be inversions within a single chromosome rather than translocations between two different chromosomes (e.g., Zhang *et al.*, 2011).

Sequence Evolution

The advent of whole genome reference assemblies allows for full sequence alignment of genomes between species along individual chromosomes. Obviously, such alignments are much more fine grained than chromosome or gene order-based alignments (**Figure 5**). The questions addressed differ depending on the pair (or group) of genomes chosen. For example, aligning the recently diverged human and chimpanzee genomes (Chimpanzee Sequencing and Analysis Consortium, 2005) will generate high (>90%) levels of homology across almost the entire genome. The focus then is on the relatively rare differences between the two and what differences in human and chimp biology they might explain. However, aligning the widely divergent human and chicken genomes (International Chicken Genome Sequencing Consortium, 2004) gives only short, discontinuous blocks of similarity (bottom of **Figure 4(a)**) separated by long regions with no more than random homology. In this case, one examines what is similar between the two genomes and what that might tell us. Indeed, a primary rationale for National Institutes of Health financial support for sequencing the chicken genome was that one could clearly detect sequences under long-term evolutionary selection because the background similarity between neutrally evolving sequences is nonexistent. The outcome was that approximately 2.5% of the human genome (~7% of chicken) appears to have been under selective pressure over their 300 million years of separate evolution (International Chicken Genome Sequencing Consortium, 2004). Because only approximately half of this encodes proteins, a major question remains as to what the function of the rest might be (Lindblad-Toh *et al.*, 2011; The ENCODE Project Consortium, 2012). Alignment of related genome sequences provides a powerful tool for detecting and annotating sequences that are of functional importance, especially in nonprotein coding regions (Stark *et al.*, 2007; Lindblad-Toh *et al.*, 2011; Lowe *et al.*, 2011). As many more vertebrate genomes are expected to be sequenced in the next few years (Genome 10K Community of Scientists, 2009), the power of comparative sequence analysis to explore the biology of food animals should grow rapidly.

Transcriptomics

Microarrays and RNA-seq

Full genome reference sequences lead to predictions of ~20 000 genes (potentially 100,000 or more transcripts). Having this in hand allows for global measurements of RNA (usually mRNA) expression, the domain of transcriptomics. Originally, these analyses employed microarrays typically containing 10 000 to 1 million elements. Each element contains a unique DNA hybridization probe (usually 25–50

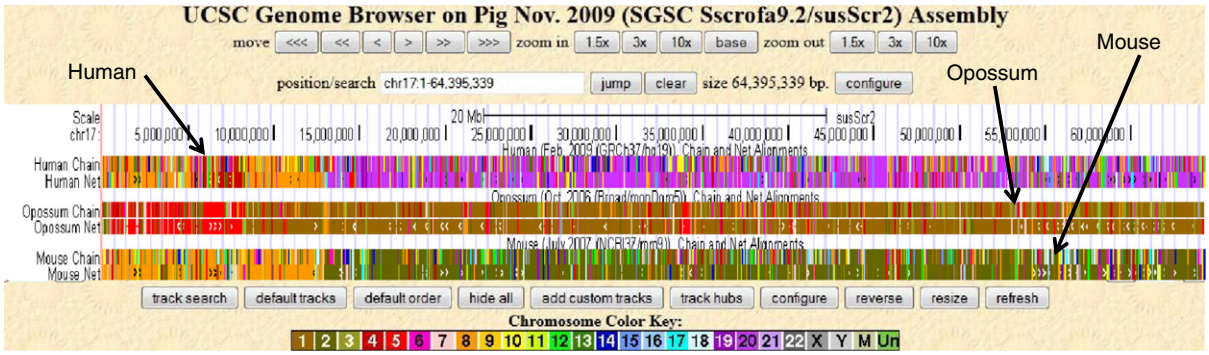


Figure 5 Comparative maps. The full length (64 395 339 bp) of swine chromosome 17 (SSC17) is shown with paired tracks matched to the human, opossum (*Monodelphis domestica*), and mouse genome sequences. (The two tracks, Chain and Net, use different parameters for the alignment with the Chain version being somewhat more finely grained.) Using the color key at the bottom, it can be seen that SSC17 consists primarily of two blocks of homology to the human genome, the first homologous to HSA8 and the second to HSA20, with the junction between the two at approximately 13 Mb. The same two blocks are observed by comparison to the mouse genome with the first block being homologous to MMU8 and the second to MMU2. Two major homology blocks are also observed by comparison of SSC17 to the genome of the more distantly related marsupial, *M. domestica*, but the breakpoint is different, close to 8.2 Mb. Note that there are frequent small blocks where the region of greatest homology differs from these overall trends. These are unlikely to be due to chromosomal rearrangements (translocations) that occurred during mammalian evolution and are more likely due to transposition (e.g., transposable element movements) or fortuitous matches to paralogous rather than orthologous members of multigene families. This view was generated with track settings: Base Position – full, Human Chain/Net – squish, Mouse Chain/Net – dense, and Opossum Chain/Net – dense. All other tracks were set to hide. The UCSC Genome Browser Gateway at http://genome.ucsc.edu was accessed on 29 June 2012. Kent, W.J., Sugnet, C.W., Furey, T.S., *et al.*, 2002. The human genome browser at UCSC. Genome Research 12, 996–1006.

nucleotides) designed using the predicted exons. Although there are technological differences between the available platforms, it is generally found that they generate similar relative gene expression profiles (Chen *et al.*, 2007; Li *et al.*, 2009). Transcriptomics involves the isolation of mRNA from multiple cells, tissues, and/or individuals, typically after different treatment regimens (e.g., pathogen infection, drug treatment, and diet) and/or at different developmental times. The mRNA sequences are converted to cDNA (or cRNA), then labeled, and finally hybridized to arrays, followed by washing and label quantification. In some cases, experiments simultaneously hybridize two differently labeled probes, providing an internal control (e.g., posttreatment vs. pretreatment). Alternatively, the Affymetrix platform averages the intensity ratio of multiple experimental probes per gene to that of control probes that contain a designed mismatch to the target sequence.

Decreased NGS costs have led to sequence-based transcriptomics technology, called RNA-seq (Wang *et al.*, 2009), in which high throughput short sequence reads are made from cDNA copied from (fragmented) mRNA (or other types of RNA). The measure of gene expression is digital (the number of times one obtains a give unique sequence) rather than analog (fluorescence intensity on a microarray). RNA-seq reads are often mapped to a reference genome and expressed in reads per kb per million mapped reads or an equivalent measure. Although RNA-seq remains a bit more expensive than microarrays, it offers the advantage that the expression of any unique sequence in the reference genome can be measured (not just what is probed on an array), and sequence reads have single base resolution, so two alleles (or two repeats) that differ by a single base in a mapped read can potentially be distinguished (Malone and Oliver, 2011). Microarray data usually give a single averaged measurement per gene per sample, whereas RNA-seq data are often used to detect differential expression of exons within a gene (due to alternative TSS, TTS, and splice sites) and can directly be mapped to predicted splice junctions and/or poly (A) termini (e.g., Pickrell *et al.*, 2010). Both techniques generate a list of hundreds to thousands of genes (or exons) with a measure of their expression (or differential expression relative to a control) for each experimental sample.

The question of how to treat these huge datasets is nontrivial. What is a significant change in gene expression? At first, an arbitrary criterion, such as a twofold or greater difference, was often employed. Of course, the proper way to address statistical significance is to repeat the experiment many times and determine confidence intervals, but this is often too costly for microarray and RNA-seq analyses. RNA-seq gives an integral number of observations of any given read that can be directly translated to a *p*-value, and more sophisticated methods of handling microarray data also have been developed. As with so many aspects of genomics, one must also correct for the multiple hypothesis testing problem in some fashion (Cheng and Pounds, 2007). Beyond simple significance, are questions of sorting and interpreting the results. Typically, one is dealing with a two-dimensional matrix in which one dimension is the number of genes under study and the other dimension is the number of expression measurements for each gene (time points, dosages, diets, etc.). A common approach to dealing with the data matrix is hierarchical clustering (Eisen *et al.*, 1998) which basically aligns each gene in a linear order such that its expression profile differs least from its nearest neighbors in a local cluster. A dendrogram can be drawn that, like an evolutionary phylogeny, connects the clusters (clades) with the distance

along the dendrogram connecting any pair of genes being proportional to their difference in expression pattern. Other approaches such as k-means clustering and self-organizing maps (Sherlock, 2000) are available that can group the genes into a predetermined number of clusters. These methods are of particular value for imputing the function of otherwise unknown genes, because one expects that the unknown will cluster with known genes of similar function.

Another mechanism by which any list of genes can be connected to functional information is via Gene Ontology (GO) annotation. GO is a 'controlled vocabulary of terms for describing gene product characteristics and gene product annotation data' (http://www.geneontology.org/). Genes are described in terms of the biological processes in which they participate, the cellular components in which the encoded protein is found, and its molecular function. These overarching categories are subdivided into more narrow and specific terms in a hierarchical fashion. Genes of known function (at least partially known in some species) have been annotated within the appropriate categories or term associations. For example, histone H5, an avian variant of the histone H1 type, is associated with chromosome condensation and nucleosome assembly under biological process; with Golgi apparatus, nuclear chromatin, and nucleosome under cellular component; and with DNA binding under molecular function. Bovine beta casein is associated with regulation of blood pressure under biological process; extracellular region under cellular component; and antioxidant activity, metalloendopeptidase inhibitor activity, protein binding, and transporter activity under molecular function. GO analysis of a list of genes (such as would be obtained from a microarray study) counts the number of genes in the list that fall into each of the GO term associations. Statistical analysis determines if the gene list was 'enriched' for that category, i.e., exhibited significantly more genes with that association than the random expectation. Thus, if a list of genes that were upregulated in cattle placed on a high-fat diet was analyzed, enrichment for terms such as adipose tissue development, fat cell accumulation, fat cell differentiation, white fat cell proliferation, etc. might have been found. The connection between diet and GO term would be obvious in this case, but interesting and unexpected connections do arise that can generate hypotheses for further testing. Another popular approach is to do pathway (or network) analysis of a microarray or RNA-seq gene list. As with GO analysis, the gene list will be searched for enrichment (vs. random expectation) for genes known to function in a particular metabolic or physiological pathway (or a previously determined network of interacting genes, see below). A popular site for pathway analysis is the Kyoto Encyclopedia of Genes and Genomes (http://www.genome.jp/kegg/).

Others may disagree, but this author's opinion is that, to date, transcriptomic studies in food animals have failed to generate novel or transformative biological insights in proportion to the effort and cost expended. In part, this is due to the incomplete annotation of animal genomes. Automated annotation of the reference genome is used to design probes for microarrays and to analyze the data produced by either arrays or RNA-seq. If a substantial number of genes or exons are inaccurately annotated or are given anonymous gene designations, the power of any downstream analysis of transcriptome data will be reduced. A larger problem is our very incomplete understanding of function and relation to phenotype for most genes. For example, sequence homology might suggest that a certain gene encodes a protein kinase that functions in cell–cell signaling. At least in model species, some of the proteins that this kinase phosphorylates might be known, but this fails to provide a full understanding of how polymorphic variations in the gene sequence translate into complex phenotypes. This is especially true for the phenotypes that are of particular relevance to agriculture (e.g., feed conversion efficiency, egg production, and susceptibility to pathogens). Finally, there is the fundamental question of how well mRNA levels reflect ultimate gene function. For example, von Merling *et al.* (2003) found that correlation of mRNA levels (coexpression) was a rather poor predictor of proteins that interacted with one another or functioned in a common pathway. One assumes that most mRNAs exert their effect through the proteins they encode, and global mRNA–protein level correlations (r^2) have generally been found to be approximately 40% at best (de Souza Abreu *et al.*, 2009; Maier *et al.*, 2009; Vogel *et al.*, 2010; Schwanhäusser *et al.*, 2011). This would seem to set an upper limit on the extent to which mRNA level measurements could explain cellular, let alone organismal, phenotypes.

eQTLs

The level of mRNA expression for a given gene in a given condition is a quantitative trait in the same sense that egg production or backfat thickness might be, and in any segregating population, it should be possible to map the genetic polymorphisms that influence each gene's expression, an approach sometimes called 'genetical genomics' (Jansen and Nap, 2001; Rockman and Kruglyak, 2006). Brem *et al.* (2002) identified these so-called expression QTLs (eQTLs) in yeast and showed that they could map in *cis* (close to the gene whose expression they controlled) or in *trans* (distant from the gene in question). The former might include sequence polymorphisms in a gene that influence mRNA processing (e.g., in a splice donor site), stability (e.g., a nonsense mutation leading to nonsense-mediated decay), or synthesis (e.g., in a promoter). Polymorphisms in the genes that encode transcription factors (TFs) or other regulatory proteins can lead to *trans*-eQTL (the TF-encoding gene is distant from the gene whose expression is measured, **Figure 6**). *trans* eQTL are more likely to be pleiotropic, leading to altered expression levels of multiple downstream genes. A number of eQTL studies have been performed in food animal species (Steibel *et al.*, 2011), but these can be challenging, especially for outbred species with modest family sizes (Haley and de Koning, 2006; Kadarmideen *et al.*, 2006). Among the biggest challenges is accurately assessing statistical significance. For example, if a segregating population is genotyped at 50 000 SNP and the expression of 10 000 genes are measured, 500 million possible SNP-gene associations are examined, a massive multiple hypothesis testing problem. As with so many aspects of genomics, one can be confident of getting results, but it may be hard to know what those results mean.

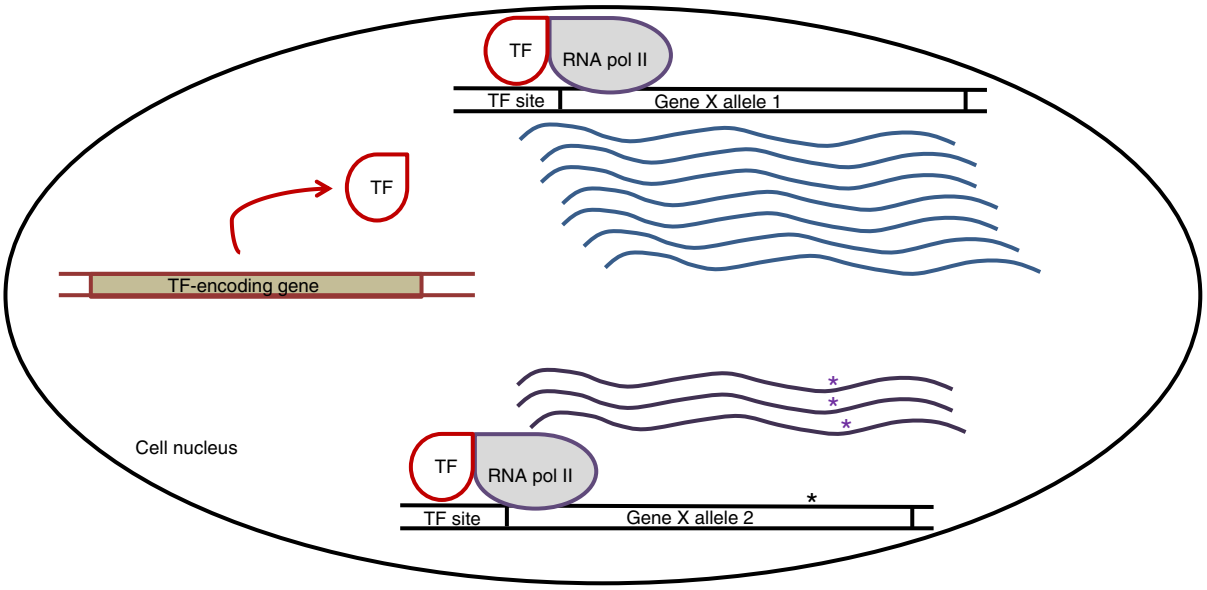


Figure 6 Expression quantitative trait loci (eQTLs) and allele-specific expression (ASE). Genetic polymorphisms that influence the level of mRNA expression of gene X (eQTL) could exist within one or both alleles of gene X itself (for example, in an enhancer, promoter, coding sequence, or UTR) in which case this would be a *cis*-eQTL, or they could exist within a regulatory gene, like the transcription factor (TF)-encoding gene shown here (only one of the two TF alleles is shown) in which case they would lead to a *trans*-eQTL (distant from gene X in the linkage map). ASE for gene X is observed when one of the two alleles expresses significantly more mRNA than the other (here allele 1 expresses more than allele 2). To observe this, there must be a polymorphism in the mRNA sequence (e.g., asterisk in allele 2). Note: this need not be the polymorphism that causes the ASE effect. The causal ASE polymorphism may be in an exon, an intron, or a flanking sequence of gene X, but it must be in *cis*, i.e., mapping in or near gene X itself, because both alleles 1 and 2 are exposed to exactly the same *trans*-acting environment.

Allele-Specific Expression

Another transcriptomic approach involves allele-specific expression (ASE) (Pastinen and Hudson, 2004; Pastinen, 2010). In ASE, the relative expression is measured of the two copies of any unique gene in a diploid cell (**Figure 6**). This requires a sequence polymorphism within the gene's mRNA that distinguishes one allele from the other (i.e., a coding SNP (cSNP)). ASE can easily be measured using reasonably deep RNA-seq data, but other, more directed approaches also are available. Because food animals are outbred, any individual's genome contains abundant cSNPs. However, F1 progeny from a designed wide cross often are examined to maximize cSNP frequency and distinguish between maternal and paternal alleles. (Generally, expression is also measured in the parents to compare with the F1, and parental genomes may be sequenced to identify the polymorphic cSNPs in advance.)

The goal of ASE is to detect sequence changes that influence the level of gene expression, but, in contrast to eQTL, ASE in the F1 is only sensitive to *cis*-acting polymorphisms. The two different alleles coexist in the same nucleus and therefore are in the same environment of *trans*-acting factors (*trans*-effects can be distinguished by comparison of the F1 allele ratios to average parental values). ASE requires neither segregating families nor linkage analysis. Although it might be expected that maternal and paternal alleles express themselves equally for most genes, and indeed this is usually the average outcome, large numbers of genes exhibit ASE in most, if not all, individuals (Pastinen and Hudson, 2004). Some of this ASE will be due to epigenetic effects such as imprinting (parental sex-specific allele programming, discussed under the Section Epigenetics below). However, sequence polymorphisms within the gene whose expression exhibits ASE are most often involved. Generally, it is not the cSNP used to detect ASE that causes the ASE effect. The former must be present within the gene's exons, whereas the latter could be anywhere in the nearby vicinity of the gene (example *cis*-acting mechanisms are given above). As with other transcriptomics, the output of ASE will be a list of gene identity numbers (associated with ASE level and, hopefully, significance values) that requires downstream analysis. One approach to narrowing that list is to specifically identify significant changes in ASE due to some treatment, for example, infection (Maceachern *et al.*, 2011). Such changes may be due to the treatment somehow differentially modifying the response of the two alleles (e.g., a virus produces a TF that binds better to one allele than the other), but it also could be a generic effect that raises a previously insignificant ASE ratio to a statistically significant difference (or vice versa).

Proteomics

Protein Expression Levels

One aspect of proteomics involves the global measurement of protein levels within a given cell or tissue type or in response to a specific treatment. This is fully analogous to transcriptomics in concept, but the task is complicated by the myriad posttranslational modifications of proteins and by the fact that

proteins occupy various cellular compartments with differing biochemical properties. Most current large proteome surveys rely on mass spectrometry (MS) (Yates *et al.*, 2009) as the primary detection tool. Typically, fractionation steps (e.g., differential centrifugation, gel electrophoresis, and column chromatography) are performed on cell extracts, along with specific proteolysis into peptide fragments that are then resolved by MS (most often tandem MS/MS, two MS runs with a further fragmentation in between). MS very accurately measures the charge/mass ratio of any peptide and therefore its amino acid composition. Tandem MS/MS results can determine peptide amino acid sequences. The main contribution of genomics to the process is that, based on the annotated reference sequence, the peptides and their mass spectra can be predicted for any protein in the genome and matched to the MS/MS output. Of course, this is complicated by posttranslational modification (as well as RNA-editing), but these factors can be taken into account, where predictable. This approach has been used to analyze the proteome of whole organs of food animals (e.g., McCarthy *et al.*, 2006) and their response to treatments (e.g., Thanthrige-Don *et al.*, 2009). Owing to variable yields during the fractionation steps, these methods sometimes do not provide good estimates of the relative amounts of the various proteins detected in the starting tissue. However, this problem can be obviated by other techniques, for example, differential heavy isotope labeling and comparing peaks of labeled to unlabeled peptide fragments (Brewis and Brennan, 2010). The eventual output of these methods will be lists of proteins with associated expression levels that can be analyzed further using clustering, GO, and pathway analysis as described in the Section Transcriptomics.

Protein–protein Interactions

The sole function of most mRNAs presumably is to template protein synthesis, whereas proteins have an enormous variety of molecular functions and cellular locations, making the domain of proteomics much broader than transcriptomics. Only one additional aspect will be discussed here, that of protein–protein interactions (PPIs). Usually this refers to physical interactions, i.e., direct contact (stable or transient) between the protein partners. However, proteins also interact functionally, for example, as part of a common pathway such that altering one of the proteins affects the function/role of the other. Several methods have been used to detect PPIs (**Table 4**). Among the most powerful is yeast two hybrid (Y2H) analysis originated by Fields and Song (1989) with a number of variations subsequently developed. Y2H provides a genetic method to detect a physical PPI (**Figure 7**). It takes advantage of the fact that most transcriptional activators exhibit a domain structure consisting of, at least, a DNA-binding (DB) domain and a transcriptional activation (TA) domain in which the two domains are encoded by non-overlapping sequences. Y2H employs recombinant DNA methods to fuse the DB domain sequence to any protein of interest (or a portion thereof), often called the bait. Likewise the TA domain is fused to another protein, the prey. The DB-bait and TA-prey hybrid constructs are transformed into a yeast strain with one or more reporter genes (selectable markers and/or color markers like *lacZ*) driven by promoters that require DB-TA transactivation to function. Only if bait and prey protein domains interact will the reporter(s) function and a PPI be scored (**Figure 7**). Rather than using a single bait or prey protein, clone libraries can be generated that contain large, even genome-wide collections of proteins, each individually fused to DB or TA. The libraries can be cross-screened to generate large 'interactomes' of PPIs for a given species (Simonis *et al.*, 2009; Venkatesan *et al.*, 2009). Protein complementation assays work similarly, except the PPI directly generates a functional reporter protein rather than a transcriptional activator that drives reporter genes.

Affinity purification/mass spectrometry (AP/MS) PPI methods are purely biochemical (Rigaut *et al.*, 1999). Recombinant proteins are generated in which a bait protein is fused with sequences (usually two in tandem) that encode binding to different affinity columns. Extracts of cells expressing the fusion are passed over the columns. All proteins (prey) bound to the affinity-purified bait are identified by MS. AP/MS requires that the PPIs in question be stable to cell lysis and passage on the columns, under whatever (mild) conditions are used. An advantage of AP/MS is that all components of multiprotein

Table 4 High throughput protein–protein interaction (PPI) methods[a]

Technology	*Brief summary*	*Advantages*	*Disadvantages*
Yeast two hybrid (Y2H)	Fusion proteins bind to transactivate reporters	High throughput, need not use full-length proteins	PPI must occur in a yeast nucleus in the correct orientation
Protein complementation assay	Fusion proteins bind to form an active reporter protein	Similar to Y2H	PPI must occur in the correct cell location in the correct orientation
Mass spectrometry of affinity-tagged complex (AP/MS)	Affinity tag purification of protein complexes followed by MS	Physiological, one bait can pull down a large complex	Interactions must be stable to purification, affinity tags could interfere with PPI
Synthetic lethality	Two mutant proteins together are lethal, but not individually	Physiological, can detect genetic versus physical PPI	Works best in model genetic species, need mutant collection
Coexpression	Proteins (or mRNAs) show common expression under multiple conditions	Fast, lots of existing data	Coexpression likely to correlate poorly with other PPI

[a]See von Merling *et al.* (2003).

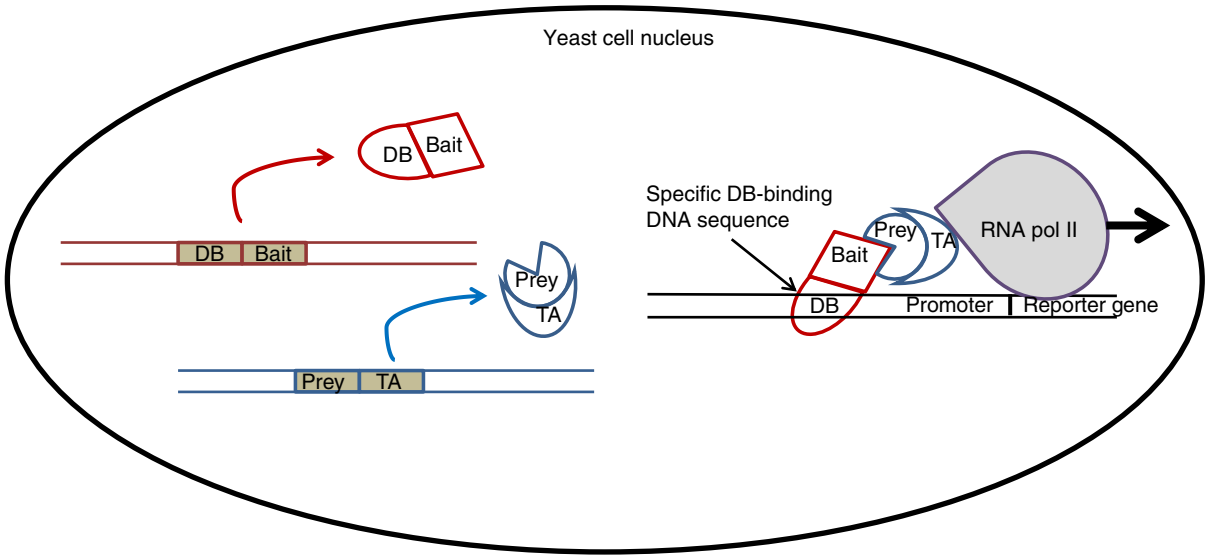


Figure 7 Yeast two hybrid (Y2H) system. Two fusion protein-encoding DNA constructs are made and introduced into the cell (left); one encodes the DNA-binding (DB) domain of a transcription factor (TF) (e.g., *GAL4*) fused to one or more 'bait' proteins of interest, whereas the other encodes the TF-transactivation domain (TA) fused to one or more 'prey' proteins. If (and, hopefully, only if) the bait and prey domains bind to one another, the two fusion or hybrid proteins couple to generate a functional complex that both binds to the specific TF DB site and transactivates RNA polymerase II. A reporter gene (right, usually multiple independent reporters are used) is constructed with the appropriate binding site such that it only functions when activated by a DB-bait–prey-TA complex.

assemblies containing the bait fusion can be identified, not just those in direct contact with the bait.

A purely genetic PPI method involves synthetic lethality (or synthetic interaction) between genes encoding two proteins. Synthetic lethality occurs when mutation of genes A and B together confers lethality (or a significant growth reduction) under a certain condition (e.g., elevated temperature), whereas mutants in A or B alone do not. Synthetic interactions do not necessarily require contact between the A and B proteins. For example, A and B might encode redundant functions (e.g., enzymes catalyzing the same reaction) or generate insignificant loss of fitness when only one is mutant, whereas mutation of both lowers fitness below a critical threshold. Synthetic lethality has been most effectively applied in model genetic organisms such as yeast (Tong *et al.*, 2001).

Venkatesan *et al.* (2009) calculated that the human interactome consists of 74 000–200 000 PPI, although this involved a number of assumptions and is likely an underestimate. All the methods mentioned have large false negative rates, and typically only a small fraction of PPIs are positive for all of multiple independent screening methods (Simonis *et al.*, 2009). Although such methods have been powerful in generating large PPI networks that can be used similarly to pathway analysis, they currently fail to fully capture organismal complexity or to provide much predictive value, at least for food animal species.

Epigenetics

Overview

Epigenetic phenomena are heritable changes that do not involve changes to the genome sequence (see Bird, 2007, and Bonasio *et al.*, 2010, for alternative definitions). Several epigenetic phenomena have been known for decades, such as position effect variegation (the same gene sequence is active in one chromosome location, but not in another) and X-inactivation (one of two equivalent X chromosomes in female mammals is almost totally inactive). Another example is that of imprinting, in which males and females specifically restrict the expression of certain genes they transmit to their offspring. Even though the imprinted gene sequence may be identical, only the paternal or only the maternal allele is expressed (regardless of sex of the offspring). The imprints on these genes are then erased and replaced with the appropriate sex-specific imprints in the offspring's germline. Imprinting probably impacts a few hundred genes that tend to be clustered in the genome of mammals and is thought to have evolved due to differing interests between male and female parents in offspring survival. (Obviously, both parents have an interest in maximizing progeny survival, but the female, especially among placental mammals, has a concurrent interest in her own survival in the face of demands on maternal resources by the fetus or newborn.) A good example is found at the insulin-like growth factor 2 locus at which an imprinting control region (ICR) is present in the genome between the *IGF2* gene and its enhancer. On the maternally derived chromosome, the ICR binds a protein (CCCTC-binding factor (CTCF)) that blocks or insulates *IGF2* from any enhancer effect. On the paternal chromosome, ICR DNA is highly methylated, CTCF does not bind, and the enhancer activates full expression of *IGF2* (Bell and Felsenfeld, 2000; Hark *et al.*, 2000). Over the past 10–20 years, it has become clear that imprinting and several other epigenetic phenomena result from an interlocking pattern of DNA methylation, altered chromatin proteins, and RNA interference.

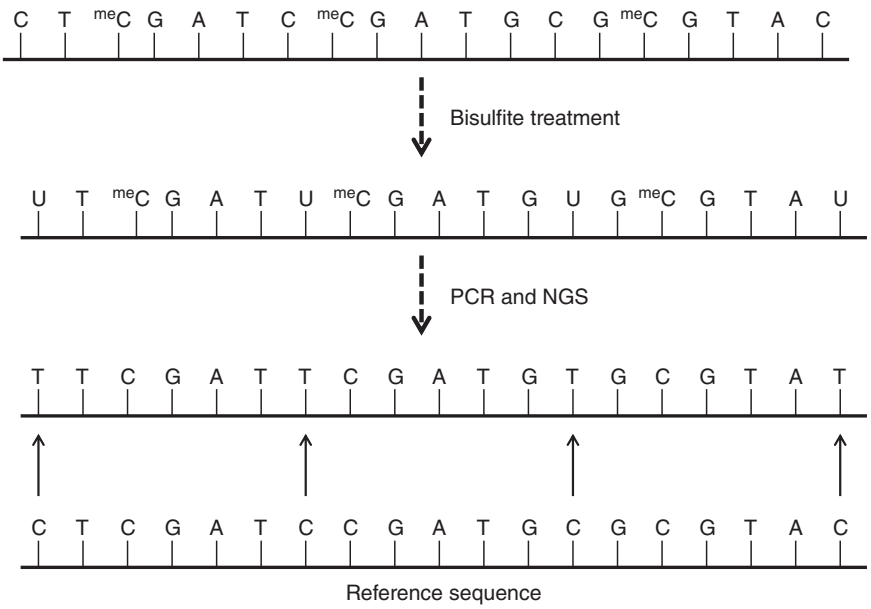


Figure 8 Methyl-sequence Genome-wide methylation analysis is done by treating DNA with bisulfite, which converts cytosine bases to uracil but has no effect on 5meC (upper dashed arrow). Subsequent polymerase chain reaction (PCR) and next generation sequencing (NGS) analysis converts sites with uracil to sites with thymine (lower dashed arrow). Comparison of the methyl-seq read with the reference sequence shows that unmethylated Cs have become Ts (upward arrows), whereas methylated C bases remain C. This will be true to the extent of the methylation (a C that originally was 50% methylated will end up 50% C and 50% T).

DNA Methylation

DNA methylation is found in most eukaryotes as 5-methyl cytosine (5meC), often at the dinucleotide sequence CpG (Zemach *et al.*, 2010). Methylation at CpG sites near individual gene promoters (often in clusters called CpG islands) has long been known to correlate inversely with nearby transcriptional activity, but recent studies provide a genome-wide perspective. The technique used (methyl-seq; **Figure 8**) involves bisulfite treatment of genomic DNA, which converts cytosine bases, but not 5meC, to uracil that subsequent PCR amplification converts to thymine in the sequence. When bisulfite-treated DNA is subjected to NGS, the extent to which a C in the reference sequence is protected from conversion to T is a measure of its methylation level. Although only limited methyl-seq studies have been done in food animals, vertebrates in general exhibit high levels of CpG methylation across the body of most genes (TSS to TTS), with a notable decrease in methylation close to the TSS, the magnitude of the decrease being correlated with gene expression level (Lister *et al.*, 2009; Zemach *et al.*, 2010). Interestingly, at least in humans, methylation at sites other than CpG (CHH or CHG, H=A, T or C) seems to be confined mostly, but not solely, to stem cells (Lister *et al.*, 2009; Varley *et al.*, 2013). Beyond these genome-wide correlations, the details of how DNA methylation regulates individual genes vary. The above example of ICR methylation activating the *IGF2* gene (simultaneously repressing the nearby *H19* gene) by blocking insulator function demonstrates one of many possible mechanisms of action. Vertebrate genomes also tend to highly methylate repetitive element sequences and heterochromatin regions (condensed blocks of chromatin often found, among other locations, in regions of tandem repeats near centromeres; Grewal and Elgin, 2007). This helps to repress transposable element activity that would otherwise be mutagenic. DNA methylation state is maintained by a system of multiple DNA methyltransferases (DNMT) and demethylases (Zemach *et al.*, 2010) and is heritable (even across generations of vertebrate animals, Natt *et al.*, 2012), in part, because after DNA replication, daughter duplexes retain methyl groups on one strand which induce maintenance DNMTs to methylate the newly synthesized strand (Bonasio *et al.*, 2010).

Chromatin and Chromatin Immunoprecipitation (ChIP)

DNA methylation does not alter gene sequence but obviously does involve covalent DNA modification. Other epigenetic chromatin marks are noncovalent. Chief among these are variations in histone proteins that make up nucleosomes (the primary protein component of chromatin), sometimes called 'the histone code' (Gardner *et al.*, 2011). Histones can be modified posttranslationally (e.g., methylation, acetylation, phosphorylation, etc.) with methylation of lysine 9 on histone H3 (H3K9) being particularly important in heterochromatin formation. Alternatively, variants can replace the common H1, H2A, H2B, H3, and H4 histones (e.g., histones H2A.Z, H3.3, and H5; Talbert and Henikoff, 2010). Other heterochromatin-specific proteins (e.g., HP1; Grewal and Elgin, 2007) bind and contribute to heterochromatin spread and maintenance. Although the association of these proteins with DNA is noncovalent, their localization can be heritable because they

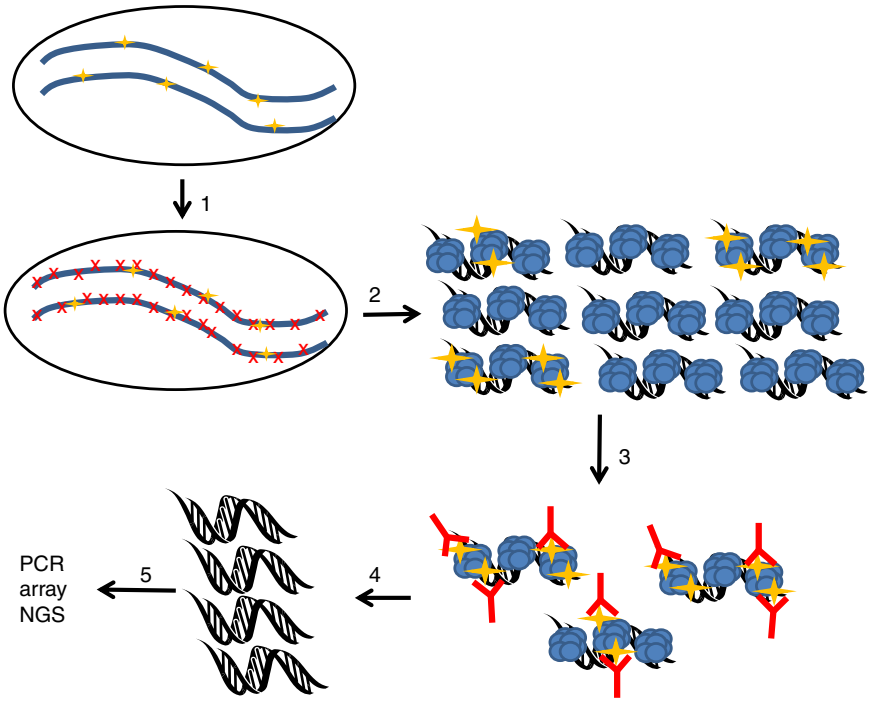


Figure 9 Chromatin immunoprecipitation (ChIP). *In vivo* chromatin (thick blue line) is shown in the cell nucleus (top left) with a localized histone modification (yellow stars), for example, H3K9 acetylation. In step 1, the cell is treated with formaldehyde to cross-link chromatin proteins to DNA (red Xs, not shown in later images). In step 2, the cell is lysed and chromatin fragmented by sonication. In step 3, a specific antibody (red) recognizing the modified histone (e.g., H3K9-OAc) is used to immunoprecipitate only those chromatin fragments containing the modification. In step 4, cross-links are reversed and the DNA is deproteinized. In step 5, enrichment of DNA fragments is assayed by gene-specific PCR, microarray (ChIP-chip), or NGS sequencing (ChIP-seq). (As a control, the same process would be done using preimmune serum or no antibody in step 3.)

remain associated with both daughter duplexes after DNA replication, and they can catalyze the local spread of the heterochromatic state (Bonasio *et al.*, 2010). Furthermore, the presence of these marks can recruit DNMTs that then proceed to methylate heterochromatin DNA. The primary method used to map these epigenetic protein marks is via ChIP (**Figure 9**). Following cross-linking of bound proteins to DNA *in vivo*, chromatin is fragmented and precipitated using an antibody recognizing the protein or modified histone of interest. Cross-linking is reversed and the enrichment of protein-bound DNA sequences is measured using PCR gene-specific assays or with microarrays (ChIP-chip) or NGS (ChIP-seq). Intensive global ChIP analyses have been performed, especially in human and model organism species (Gerstein *et al.*, 2010; The mod-ENCODE Consortium, 2010).

RNA Interference

A third major epigenetic system involves small RNAs of two types: microRNAs, miRNA, and small interfering RNAs, siRNAs, components of the endogenous RNA interference (RNAi) system. RNAi has been widely used for experimental manipulation of the expression of specific genes (Dorsett and Tuschl, 2004; Chang *et al.*, 2006), but the focus here will be on natural RNAi. miRNAs are ~23 nucleotide RNAs that function in most eukaryotic species as an internal gene regulatory network (Grimson *et al.*, 2008; Bartel, 2009). They are generated by the processing of larger initial transcripts in a multistep manner, and they function as part of a ribonucleoprotein RNA-induced silencing complex (RISC). The RISC binds to the target mRNA and can block its translation and/or degrade it to induce 'posttranscriptional gene silencing' (PTGS). miRNAs form imperfect matches to their target sequences which are found most often in mRNA 3′UTRs. miRNAs are identified by both genome annotation and deep sequencing of small RNA fractions (e.g., Burnside *et al.*, 2008). Although surveys are incomplete (lineage-specific miRNAs can be hard to distinguish by automated annotation), it is likely that most vertebrate genomes encode several hundred miRNAs. Currently, miRBase (www.mirbase.org) includes 791 mature chicken miRNAs, 360 for horse, 755 for cattle, 306 for swine, and 103 for sheep. All these are sure to be underestimates because the better annotated human and mouse genomes encode 2042 and 1281 mature miRNAs, respectively. A single miRNA can target 100 or more mRNAs, and any mRNA can contain multiple miRNA target sites. Indeed, it is clear that mRNA 3′UTR sequences have evolved to appropriately match (or avoid matching) the developmental profile of miRNA expression (Farh *et al.*, 2005). However, the effect of any single miRNA on a specific mRNA target is rarely 'all or none,' but usually modulatory in nature. Thus, miRNA and mRNA generate a complex, evolutionarily flexible, and highly redundant interlocking network of post-transcriptional gene regulation, perhaps one explanation for the only modest correlation of mRNA and protein levels discussed in the Section

Transcriptomics. Studies of the influence of miRNAs on food animal phenotypes (e.g., Trakooljul *et al.*, 2012) are still in their infancy.

The other major component of RNAi machinery involves siRNAs (Grewal and Elgin, 2007). (There are also piRNAs that seem to function during meiosis and will not be discussed further, Castel and Martienssen, 2013.) siRNAs are generated by digestion of double stranded RNA (dsRNA) by *Dicer* ribonucleases. The dsRNA can either be exogenous (e.g., dsRNA generated during the replication of RNA viruses) or endogenous (e.g., from bidirectional transcription of DNA, especially repeats). Like miRNAs, siRNAs can bind to RISCs and generate PTGS, but they also can block transcription of the target sequence (transcriptional gene silencing (TGS)). In doing so, siRNAs bind to an RNA-induced transcriptional silencing (RITS) complex that localizes to target chromatin sites in the nucleus. siRNAs also differ from miRNAs in that they generally are fully complementary (or nearly so) to their target RNAs. Thus, miRNAs work in *trans*, i.e., they target sequences different than their own, whereas siRNAs work in *cis*, targeting the same loci from which they are transcribed (and any like it). TGS works by a complex process in which the RITS localizes to the target repetitive sequence. Directly or indirectly, the RITS complex recruits H3K9 methyltransferase activity, HP1 binding, and other factors required for the assembly and spread of the heterochromatic state (Grewal and Elgin, 2007). Note that for this mechanism to function, TGS must be 'leaky,' i.e., there needs to be at least a low level of transcription of the heterochromatic repeats to generate the initiating siRNAs and provide the nascent transcripts with which they pair.

In summary, siRNAs, chromatin protein modification, and DNA methylation form a self-reinforcing regulatory system that allows eukaryotes to tolerate the pot`ential danger to the genome posed by transposable elements and repetitive sequences in general. Heterochromatic regions also perform essential structural roles such as the generation and maintenance of chromosome centromeres and telomeres in most species. Specific RNAs are also known to play key roles in other epigenetic phenomena such as imprinting and X-inactivation. Certain eukaryotes have been able to dispense with RNAi or DNA methylation (Grimson *et al.*, 2008; Zemach *et al.*, 2010), but all food animal species are likely to possess the full arsenal (e.g., Giles *et al.*, 2010), even though currently there is very little understanding of their role in agriculturally important traits.

Impact of Food Animal Genomics

Genomic technologies and the insights they provide will continue to advance at a remarkable pace. Just as it seems likely that many readers of this article will, at some point, have their own personal genomes sequenced, so will those of the core breeding stock of the relevant species, and just as human genomics has begun to impact most aspects of medical science, genomics will affect nearly all aspects of animal science. In addition to facilitating transcriptomics, proteomics, and epigenetics, as discussed above, genomics has already elucidated the causal alleles for numerous important monogenic traits (Andersson and Georges, 2004), several of which relate to coat or plumage color, with others influencing traits like muscle development and sensitivity to disease. In one case (Eriksson *et al.*, 2008), the 'yellow skin' allele was not only of commercial importance but also proved that both red and grey junglefowl contributed to the origin of the domestic chicken, resolving a long-standing controversy. Alleles that contribute to epigenetic determination of muscle mass have also been pinpointed (Van Laere *et al.*, 2003; Freking *et al.*, 2002; Smit *et al.*, 2003). Linkage mapping and association analysis are generating many more candidate causal alleles for a wide variety of polygenic QTL traits (Animal QTL database, http://www.animalgenome.org/cgi-bin/QTLdb/index). A major challenge for farm animal species is to develop cost-effective methods which can confirm the correctness of the candidate QTL alleles (as opposed to other alleles in LD with the candidate). Another major impact has been the remarkably rapid acceptance of genomic selection into commercial breeding strategies, especially for dairy cattle (Wiggans *et al.*, 2009) and, to some extent, in poultry (Wolc *et al.*, 2011). This is likely to continue, although the cost-effectiveness of genomic selection will depend on the population structure of the relevant commercial stocks as well as the traits of most interest.

If any message is to be derived from this article, it should be that the connection is extremely complex between the genome sequence and the traits sought to be maximized in the species of interest. Although genomic selection strategies ignore this connection and simply train algorithms on the assumption that a correlation exists, it seems likely that improved progress can be made with an understanding of the biological mechanisms involved. Among other things, a more detailed understanding of the genotype–phenotype connection might allow for rapid advances using genetic engineering, a technology not considered in this article. Although consumer and political resistance to genetically engineered animals remains significant, opposition to genetically modified crops seems to be weakening and may further decline as population growth increases the need for food in the face of limited natural resources. It would take a more prescient author than this one to accurately estimate all the ways through which genomics will impact the future of animal science, but it seems certain that it will.

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See also: Advances in Animal Biotechnology. Breeding: Animals. Cloning Animals by Somatic Cell Nuclear Transplantation. Domestication of Animals. Genomics: Plant Genetic Improvement. Transgenic Methodologies – Plants

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Genomics: Plant Genetic Improvement

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Glossary

Allelic diversity Refers to the differences in deoxyribonucleic acid (DNA) between specific genes when they are in different individuals within the population of a species.

Homoeologous Refers to gene or chromosome regions that are genetically similar but not identical, particularly in polyploid species.

Quantitative trait loci (QTL) These are regions of the genome (Loci) that are associated with variation in phenotype (Quantitative Trait) of individuals in a genetic mapping population.

Retrotransposable elements These are elements in the genomes of many life-forms that can amplify themselves and move to different parts of the genome.

Translation The context in which this is used is to describe the process of transferring knowledge from research projects to application in industry.

Introduction and Key Concepts

The integration of biotechnology concepts and technologies are now accepted as part of an overall strategy in plant breeding that needs to consider water conservation, soil fertility, resistance of domesticated plants and animals to pests and diseases, and the production of quality grain from resilient, productive, and adapted varieties. Solutions involve innovation and improved management of resources, best practises, so that scale of effort is proportionate to need and opportunity. Complementing this is the need to capture biotechnological breakthroughs that can radically change the phenotypes of domesticated plants and animals for maximum performance in specified environments. Speedy delivery of new genotypes for planting is crucial and marker-assisted selection applications provide more informative diagnostic probes for identifying favorable combinations of alleles and genome segments in new germplasm. The multidisciplinary approaches that now characterize crop improvement enable a holistic systems approach to the study of expression and regulation of genes (and gene networks) at various levels of the plant (i.e., organism, tissue, organ, and cellular level) and developmental stages, in order to identify key cues in the plant environment, which influence the final phenotype of the plant.

Initiatives to generate reference genome sequences for rice, barley, and maize have provided the basis for an increasing number of structural/functional studies cataloging and characterizing major genes underlying important agronomic traits. Completion of the reference sequence in rice heralded the beginning of a new era (the postgenome era) in which a suit of complementary 'omics' disciplines (i.e., transcriptomics, proteomics, and metabolomics) can now exploit and leverage the knowledge of the full genome sequence to discern at greater resolution than ever before, the complex regulatory mechanisms determining expression and function. For wheat, the genome sequence representation in relation to high-resolution genetic maps is still in progress and will be based on a chromosome-by-chromosome analysis (Feuillet *et al.*, 2012).

As crop researchers transition into the 'postgenome' era, the expanded knowledge base conferred by having sequenced reference genomes will facilitate improved efficiency for delivering crop genetic gains by way of more targeted research that is better equipped to accurately identify, evaluate, and quantify: (1) the genetic potential held in crop genomes (and or subspecies/population) which is currently underutilized, in as yet uncharacterized gene(s) and/or unidentified alleles, that confer to plants the ability to thrive in rapidly changing environmental conditions caused by climate change (and the emerging biotic and abiotic stresses accompany these changes), and (2) the relative level of plasticity of particular crop genomes to evolve and thrive in response to changing environmental stresses, and the extent to which favorable heritable mutations and/or epigenetic changes may influence this adaptive evolution.

Parallel and ongoing research for the advancement of genomics platforms, sequencing technologies, and molecular marker development will continue to be essential in providing the molecular tools to capture and introgress existing and evolving allelic diversity for new cultivar development. Wide crossing and genetic transformation programs are currently the main sources of new genetic variation. In the case of an emerging threat to wheat in the form of the stem rust Ug99, for example, a basic strategy is to build a combination of genes into a new source of resistant phenotypes which may include unknown additive genes to achieve long-term resistance (Singh *et al.*, 2006). This process can be accelerated by new insight into the molecular basis for disease resistance. Similarly, increased efficiencies in photosynthesis and water use, as well as the incorporation of nutritional attributes, also require more fundamental changes to the genomes of mainstream cereals in order to provide grain for future generations. An important variable in dealing with a polyploid crop such as wheat is that it shows homoeologous gene silencing (Mochida *et al.*, 2003; Zhang *et al.*, 2008; Bottley and Koebner, 2008). Bottley and Koebner (2008) identified homoeolog nonexpression for 15 single-copy genes across a panel of 16 wheat varieties and found that for the expression profiles of eight genes only two varieties shared the same pattern of silencing. Homoeologous gene silencing can be

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tissue specific and is most likely a significant factor in generating phenotypic variation.

Plant breeding in the postgenome sequencing era is developing capacity to utilize the very large databases of molecular markers linked to key agronomic traits. Genome wide association studies (GWAS) in rice, maize, and barley have provided high-density single nucleotide polymorphisms (SNPs) coverage of genome regions controlling components of yield. For wheat, the high-density SNP technology is also in place (**Figure 1**; Cavanagh *et al.*, 2013). The genome sequences available for cereals and the parallel functional (mutation and transformation) studies in rice and Arabidopsis have provided examples of successful 'walking' to a gene of interest. The challenge for plant genetic improvement resides in combining genetic gain and improvement in management practises for increasing yield, with the targeting of food crops to particular food products. Changing environments in soil fertility and climate need to be considered as classical G×E (genotype by environment) interactions, but in the context of changes in field and trait-management variables. Although historically improvements have been achieved through plant breeding based on crosses between parents that show attributes of interest, more recent developments have, as noted above, considered targeted introductions of genes through transformation technologies.

When crosses are made between two individuals, the genetic differences between the two individuals, which can be defined at the level of DNA sequences, will segregate among the progeny of the cross. Differences between individuals at the DNA level are called polymorphisms and can be assayed as molecular markers using a range of standard molecular technologies. The pattern of segregation of molecular markers relative to each other, among individual progeny, reflects their distribution along the long linear strand of DNA that makes up a chromosome so that molecular markers on different chromosomes will segregate at random from each other among the individual progeny from a cross. Molecular markers on the same chromosome will show nonrandom segregation from each other and this apparent linkage between the markers will depend on how far apart the molecular markers are from each other in the chromosome. When molecular markers are far apart, the meiotic process of recombination has a greater probability of separating the molecular markers than when they are very close together (=closely linked) and thus the % recombination provides a measure of genetic distance. This distance is measured in units called centiMorgans (cM). When phenotypic characteristics are determined for each of the segregating lines derived from a cross, the variation in the traits measured can be statistically associated with a polymorphism in the molecular marker (=allele) between the parents used in the cross and as these associations generally account for proportions of variation in the phenotype, these associations are referred to as quantitative trait loci (QTL).

The high-resolution genetic maps shown **Figure 1** derive from crosses between wheat lines Westonia × Kauz (far left panel) and a multiparent cross called MAGIC (middle panel, based on Cavanagh *et al.*, 2013) and were produced by assaying many SNPs using the 9000 SNP array made available by Illumina (Cavanagh *et al.*, 2013). The genetic maps for chromosome 7A are shown as an example (for a published example for chromosome 2D of wheat, see Jia *et al.*, 2013). The genetic map on the far right is a composite map and summarizes the broad output from a literature focused on mapping QTLs for phenotypes that are important in agriculture (green lines on the far right of **Figure 1**). QTLs usually occupy a region of the genetic map rather than a single point because of the variation inherent in measuring a phenotypic trait.

Molecular markers that are shared between the many crosses analyzed in the literature provide the basis for linking the maps to each other and, importantly, to link the QTL that have been mapped over an extensive period of time and in different environments, to the contemporary high-resolution molecular genetic maps. The DNA sequences of the molecular markers also provide a direct link to the reference genome sequences that are being determined and allow the location, or projection, of QTL on to the DNA sequence for analyzing the genes that underpin the QTL. The lines joining the maps indicate the shared location for a molecular marker and **Figure 1** shows a generally good alignment between the maps although the detailed alignments of some regions indicate a reversal in the order of molecular markers in one map relate to the other. These reversals in order may indicate genuine differences at the DNA level between wheat varieties due to an altered distribution of repetitive DNA sequences, or regions of the genetic map that require re-examination to check for errors. The maps illustrated are displayed using the software called CMap.

The releases of contemporary varieties now generally describe the integration of molecular markers (the outputs from genomics) into the selection technologies utilized for both the selection of parents as well as the selection of progeny from crosses to carry forward in the breeding scheme (Lee *et al.*, 2011; Miedaner and Korzun, 2012). Although the use of molecular markers provides faster results, it is critical that the linkage between the molecular marker and the trait of interest is reliable. In the postgenome sequence era the availability of molecular markers tends to be no longer limiting and this has turned the focus on improving the accuracy of assessing the phenotypes that are important for success of the breeding program (Miedaner and Korzun, 2012).

The Basic Technologies

Genome sequencing of cereals is now maturing as the bacterial artificial chromosome-based sequence assemblies for rice, maize and barley (International Barley Genome Sequencing Consortium, IBGSC, 2012) are being utilized to display phenotypic traits important to the industry on the genome DNA sequence (**Figure 1**). For hexaploid wheat (Brenchley *et al.*, 2012) and the A genome (Ling *et al.*, 2013) and D genome (Jia *et al.*, 2013) diploid genome donors, the whole genome sequencing technology has provided an important step in assigning genome sequences to molecular genetic maps and traits of agronomic significance (Feuillet *et al.*, 2012). The physical/sequence map for barley, for example, comprises 4.98 Gb with 79 379 transcript clusters identified using alignments with cDNA and RNA-seq data, and homology to genes in other plants (Middleton *et al.*, 2012). Based on RNA-seq data, at least half of the genes classified in barley show for alternative splicing (IBGSC, 2012), a process that can be a significant variable in establishing the final phenotype.

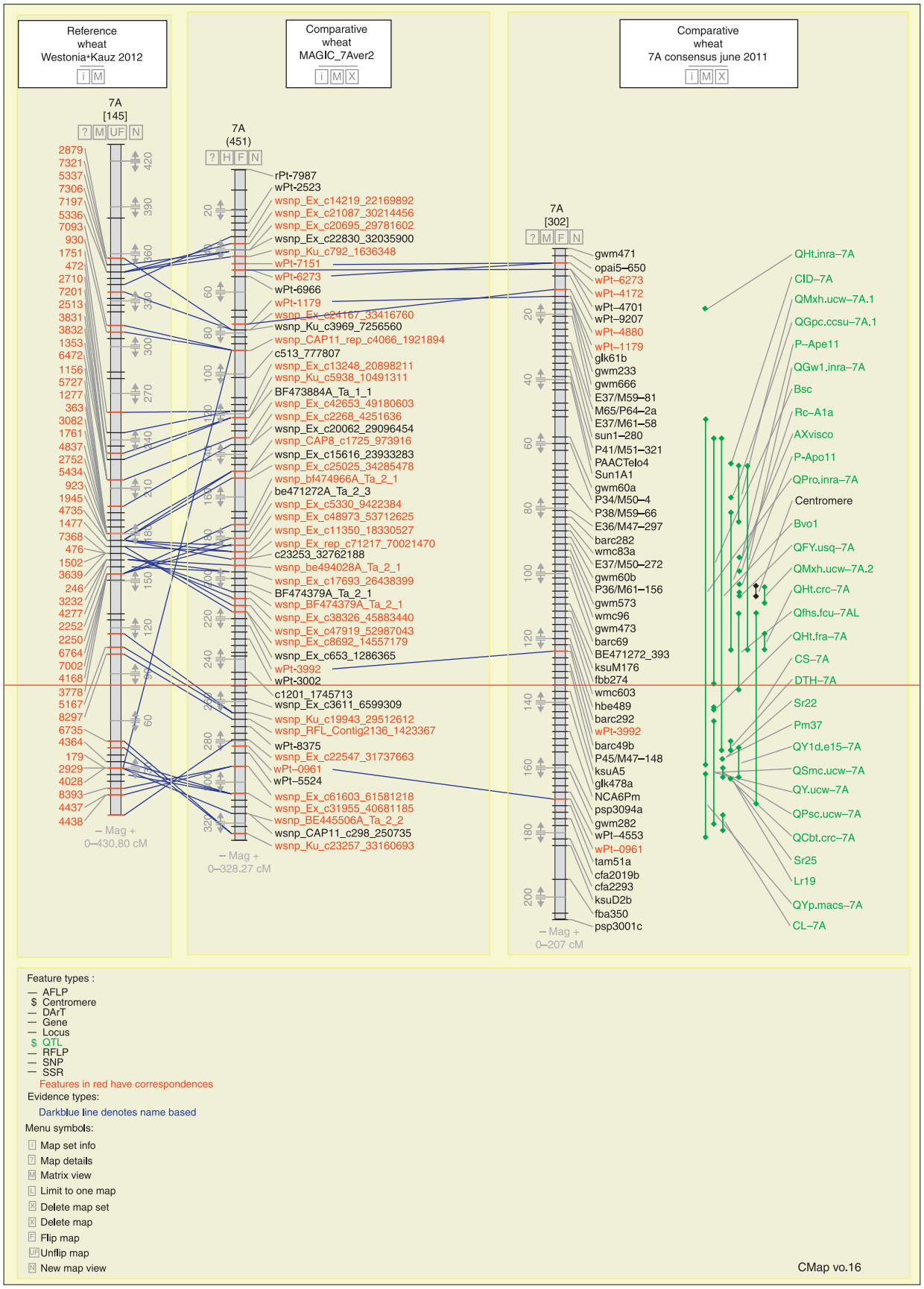


Figure 1 Comparative map of chromosome 7A.

The retrotransposable element/repetitive sequence content of cereal genomes is generally estimated to represent over 80% of the total DNA sequence. Advances in barley are representative of what is happening in the scientific area and have provided the mapping of SNPs using genome sequencing (IBGSC, 2012). Surveys of wild and cultivated barleys by comparative genome hybridization arrays (Muñoz-Amatriaín *et al.*, 2010) indicate that a significant proportion (15%) of the barley genome is affected by copy number variation (CNV) in DNA sequences. The telomeric regions of chromosomes were enriched for CNVs and this distribution correlated with an enrichment of genes in these regions and may thus contribute to the phenotypic diversity of barleys (Muñoz-Amatriaín *et al.*, 2010). These variable regions of the genome can now be assigned to the conditionally dispensable regions of the genome discussed in Appels *et al.* (2013).

The transfer of basic findings from barley genome studies into industry is based on the utilization of molecular data to predict phenotypes so that speed and efficiency is increased in breeding programs as well as reducing costs (Waugh *et al.*, 2010; Comadran *et al.*, 2011; Okagaki *et al.*, 2012; Blake *et al.*, 2012; Berger *et al.*, 2012). Tools such as The Hordeum Toolbox (THT) provide a good model for integrating extensive phenotypic and genotypic data sets for further downstream analyses (Szűcs *et al.*, 2009; Blake *et al.*, 2012; Matthews *et al.*, 2012) as well as the sharing of data between breeding programs. The analysis of a complex trait such as resistance to fusarium head blight (FHB), for example, requires the integration of a broad range of variables including the identification of resistance haplotypes in wild germplasms and QTL for FHB resistance in molecular marker genetic maps (Huang *et al.*, 2013). The studies can provide novel alleles for FHB resistance. The broad integration of technologies, particularly through the increased use of GWAS (Berger *et al.*, 2013; Cuesta-Marco *et al.*, 2010), expands the database of molecular information linked to phenotype and THT provides a valuable model for the integration of data and adoption by industry.

Rice also provides a well-developed model for the translation of genome-based research to breeding outcomes. GWAS have been carried on a very large scale in rice by Susan McCouch and colleagues (summarized in Appels *et al.*, 2012) using 413 diverse rice varieties and a 1 M oligonucleotide genotyping array, estimated to assay SNPs every 0.4–0.5 kb of genomic DNA. The study identified associations consistent with many previously reported QTLs as well as new candidate chromosome regions and genes contributing to agronomically important phenotypes (Zhao *et al.*, 2011).

Better utilization of wild relatives of rice to improve all aspects of yield in cultivated rice is a clear output from the studies to define the *Oryza* sp. genome (Kovach and McCouch, 2008). The wild relatives of rice carry sources of genes and alleles that have been lost through the domestication process to produce cultivated rice. Targeting wild relatives (based on GWAS-based identification of chromosome regions controlling agronomic traits) for crossing to cultivated rice opens the possibility for transgressive segregation to enhance specific features in rice cultivated in particular environments (Kovach and McCouch, 2008) and this is now carried out in developing new germplasm for breeding programs.

The Phenotype and Environment

A phenotype of central importance in crop breeding is yield stability, both in terms of total yield (underpinned by grain number and size) and consistency of quality attributes specific to end use and classification for processing. This is particularly important as climate change introduces conditions not previously experienced. Wheat grain yield has many components including whole plant attributes for optimal establishment and maturity/height features that in turn confer adaptive traits better enabling the plant to be suited to the environment in which it is grown. The supply of sugars to immature pollen in the developing head, and thereafter maturing grain during grain fill, has been identified as a critical plant metabolic phase determining grain yield and size, a result which has been consistently reported in studies on tomato (Ruan, 2012), cereals (Dolferus *et al.*, 2013), and tobacco/Arabidopsis (Le Roy *et al.*, 2013). Abiotic stresses (particularly water deficiency and frost) affect the developing spike and maturing grain due to the downregulation of key carbohydrate mobilization and cleavage genes (cell wall invertases and fructosyl transferases and exohydrolases). Tolerance at the genetic level requires expression of these genes under stress conditions to be maintained so that the developing pollen and grain receive sufficient energy supplies for development to reach completion unimpeded (Ruan, 2012; Barrero *et al.* 2011; Dolferus *et al.*, 2013; Moghaddam and Van den Ende, 2012).

The major genes underpinning tolerance to a number of biotic stress factors includes genes belonging to the NBS-LRR class of proteins which have conserved features relating to signal transduction involved at the host–pathogen interface. Genome-level sequencing in wheat, for example, has demonstrated that the tan spot resistance *Tsn1* gene encodes a NBS-LRR protein (Lu *et al.*, 2011) consistent with gene structures found in other resistance genes (e.g., *Rpg5* in barley, Brueggeman *et al.*, 2008). In contrast, the leaf rust *Lr34* gene (Krattinger *et al.*, 2009) has been identified as belonging to the ABC transporter class of gene, postulated to be involved in secreting a currently undefined molecule to inhibit the growth of fungal hypha penetrating the leaf tissue. The stripe rust resistance *Yr36* gene encodes a protein with a novel architecture resulting from domain reshuffling involving a kinase and a putative lipid binding domain (Fu *et al.*, 2009). The stem rust resistance *Sr2* gene in wheat has not been definitively identified but a cluster of germin-like protein coding genes is located at the *Sr2* resistance locus and these have characterized as being analogous to the germin-like cluster of genes encoding blast resistance in rice (Breen and Bellgard, 2010).

Although components of yield can be readily defined, variation in the measured phenotype remains a significant factor in breeding programs. Breeding design must be sufficiently flexible to allow changes in crossing decisions to be made when instances of negative interactions between genotypes and environments arise. Designing trials and activities in a systematic way allows optimization of information to identify the genotypic basis of phenotypic differences in germplasm and the selection of lines for use in the crosses. The process by which these activities are structured requires the identification of parents for crosses, allocation into a design, data collection, and then the analysis of data from derived progeny. The science of trial

design and the optimization of crossing/mating information is extensive (Kempton, 1982; Singh and Hinkelmann, 1998; Smith *et al.*, 2006; Williams *et al.*, 2011) and can be simulated using tools such as QU-Gene.

Important to information collection is the concept that the breeding process involves the generation of genetic variation, followed by the selection of elite germplasm, and the characterization of elite lines for desired traits. This process has the potential for errors to be transferred into consecutive stages of the breeding process. Developing trial designs such as 'chained trial design' that minimize type-II errors (false-positives and true-negatives) are becoming important considerations for breeding. The chained designs cover multiple testing of a plot (or grain sample) by incorporating within and between replication in each step tests to allow variance estimates. The statistical methods utilized are based on mixed-model restricted likelihood (REML).

With increasing amounts and complexity of information being generated from breeding operations, breeders need to collate this information into a format for decision making. Decision-making methodologies have been well researched (Dams *et al.*, 1977; Csáki, 1985; Saaty, 2005) but less often applied to plant breeding (Timmermann, 2006). The concept of a data matrix formed by taking germplasm lines and matching each line with the results for the plant breeder to interpret is widely used. Decision matrices use a weighing or prioritizing process that allows the combining of multiple results into scores to enable data reduction and easier decision making. Statistical approaches which calculate estimated breeding values (EBVs) for a trait associated with each line are designed to reduce environmental and/or extraneous factors and thus greatly enhance the decision matrix process. Diepeveen (2011) demonstrated this process for grain quality traits in a wheat breeding program.

The incorporation of marker/genomic information into the decision matrix process distorts the decision matrix because inputs of this type comprise data points that are highly correlated with each other when they are genetically closely linked to each other (see **Figure 1** and the associated box). The incorporation of correlated data structures within a multivariate REML analyses is one tool that can be applied for data reduction of genomic information and the subsequent estimation of EBVs for decision making (Kempton and Fox, 1997).

Comparative Genomics and Phenomics

A major effort to capture plant phenotype descriptions in a standardized way is being undertaken through efforts such as the Plant Ontology project in Gramene (Ni *et al.*, 2009) and Crop Ontology (Srestha *et al.*, 2012), based on the premise that essential features of traits can be identified across a wide range of species. For example, the Zadok scale is widely used to describe stages in plant development and it has been incorporated into the Biologische Bundesanstalt Bundessortenamt and Chemical industry (BBCH) scale (Meier, 2001). The BBCH scale provides the basis for describing equivalent stages in a range of cereals which can then be linked through a website such as Gramene (Ni *et al.*, 2009). A particular advantage for cross-referencing phenotypes of diverse but related species is that advances made in well-characterized species can be more easily applied to complex species such as wheat, thus facilitating meaningful comparisons.

Plant phenotypes including aspects of maturity such as earliness per se, vernalization responses (Vrn), photoperiod response (Ppd) and height phenotypes (Rht genes), efficient plant establishment based on root growth, early vigor in vegetative growth, cold tolerance in some environments, tillering and leaf expansion constitute important features of the overall plant that have been especially well characterized at the gene-level through comparative genomics and phenomics (Feuillet *et al.*, 2012). Abiotic stress tolerance in breeding is generally environment-specific and can range from being simple to complex at a genetic level. The study of boron and aluminum tolerance (Feuillet *et al.*, 2012; Delhaize *et al.*, 2012), and water stress (preceding in the Section The Phenotype and Environment) in crops such as wheat have benefited from analyses of these traits in a range of related plant species.

Barrero *et al.* (2011) provided a detailed analysis of the potential value gained from utilizing comparative genomics as a selection tool in the preliminary stages of the candidate gene identification pipeline, in which gene structure and function information accumulated on well-studied species (particularly rice) can be transferred to complex polyploid species such as wheat. Using the grain weight QTL called QTgw.ipk-7D QTL as an example, this trait mapped to the most telomeric bin (7DS4-0.61-1.00) in the physical map of wheat chromosome arm 7DS. Barrero *et al.* (2011) estimated that a total of 173 annotated wheat EST loci were located in the wheat chromosome bin 7DS4-0.61-1.00. These wheat ESTs were then assigned positions on the rice genome and those ESTs uniquely mapping to rice chromosome 6, which is the syntenic region to wheat chromosome 7DS, were identified for further analysis. This process identified 23 wheat ESTs aligned to rice chromosome 6 from position 369 919 to 25 106 896 bp. To further narrow this 25 Mbp region, Barrero *et al.* (2011) screened the rice genome for overlapping grain weight QTLs and identified a rice qrGW-6 QTL flanked by the G200 and C235 molecular markers that were located at 50.1 and 53.5 cM on the rice chromosome 6, respectively. The genetic markers overlapping this region from the Rice Genome Annotation database resulted in 11 rice genetic markers that mapped specifically to rice chromosome 6 from 6 978 639 to 9 153 520 bp. In this way it was possible for Barrero *et al.* (2011) to reduce a 25 Mbp region for analysis down to a 2.1 Mbp region, in order to search for possible grain weight candidate genes. These candidates include genes in a diverse class of E3 ubiquitin ligases involved in protein degradation. The *GW2* gene for grain weight is in this class of proteins. Also included in this region was an E2FE transcription factor which negatively regulates cell division.

Changing Agendas to Meet New Challenges and Conclusions

Future trends in plant genetic improvement will tend to focus on utilizing molecular biological techniques to consolidate pyramiding gene networks for new purposes/end-products, combined with yield gains. Although new phenotypes such as

bioethanol production from specialized pastures and biofactories for speciality products will continue to emerge, the basic concepts for tackling the new challenges will tend to follow the approaches outlined in this article. Transformation technologies have significant contributions to make in defining the functions of gene networks and providing a potential basis for new varieties when suitable government legislation/policy can be developed. The genetic engineering of crop plants to produce biofactories in controlled environments is more likely to receive increasing attention in the future for producing high-value molecules such as vaccines (Huang *et al.*, 2010; Phoolcharoen *et al.*, 2011).

The genomic resources of grain crops can now contribute to refining molecular marker development and mapping strategies for increasing the efficiency of both the breeding processes and the utilization of diverse germplasm resources. Harnessing the genetic potential of novel allelic combinations in diverse germplasm resources will require breakthroughs in disrupting linkage blocks and/or altering recombination rates along the length of the chromosome (Yousafzai *et al.*, 2010; Saintenac *et al.*, 2011; Higgins *et al.*, 2012).

The main aim of researchers in the 'postgenome era' is to exploit data from crop genome sequences, using complimentary 'omics' tools, to continue delivering genetic gains at a rate that meets increasing global demand for grain commodities and provides yield stability to withstand climate change stresses. The success in obtaining reference genome sequences for broad acre crops is providing new high throughput technologies for assaying variation in combinations of genes that was not previously possible. In particular, it is providing the basis for improved understanding of mechanisms regulating the epigenome (postreplication modification of the genome sequence and its folded structure) which holds promise for delivering crop genetic gains via strategically targeting new adaptive alleles.

See also: Analyses of Total Phenolics, Total Flavonoids, and Total Antioxidant Activities in Foods and Dietary Supplements. Biotechnology: Herbicide-Resistant Crops. Breeding: Plants, Modern. Climate Change: Cropping System Changes and Adaptations. Determining Functional Properties and Sources of Recently Identified Bioactive Food Components: Oligosaccharides, Glycolipids, Glycoproteins, and Peptides. Emerging Plant Diseases. Food Chain: Farm to Market. Food Security: Yield Gap. Heterosis in Plants. Organic Agricultural Production: Plants. Plant Abiotic Stress: Temperature Extremes. Plant Abiotic Stress: Water. Plant Biotic Stress: Weeds. Plant Disease and Resistance. Plant Virus Control by Post-Transcriptional Gene Silencing. Precision Agriculture: Irrigation

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Global Agriculture: Industrial Feedstocks for Energy and Materials

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Glossary

Anaerobic digestion The biochemical conversion or fermentation of organic materials, such as biomass, by mixed bacterial communities under anaerobic (without free oxygen) conditions. The process is typically used to produce a methane-containing biogas. Anaerobic digestion also occurs naturally in solid waste landfills.

Biochar Charcoal or black carbon produced by the pyrolysis or other thermochemical processing of biomass.

Biochemical conversion Conversion by biological and chemical processing, typically through microbial systems but also involving the use of enzymes or chemical pretreatment.

Biofuel A fuel product made from a biomass feedstock.

Biomass Living material. In the context of energy and materials, biomass is nonfossil material of biogenic origin.

Biomaterial A material synthesized or produced from biological resources or biomass.

Biorefinery A processing facility, similar in function to a petroleum refinery, used to refine or upgrade biomass feedstocks to higher value fuels, materials, and other products.

Gasification The thermochemical conversion of a biomass feedstock or other organic material by heating and reaction at elevated temperatures through partial oxidation using a controlled amount of oxygen, steam, or other oxidant. Gasification is used principally to produce fuel or synthesis gases containing carbon monoxide and hydrogen along with other species.

Lifecycle analysis An accounting technique used for evaluating and comparing the environmental and other impacts of a product, process, or system from the start to end of its useful life.

Pyrolysis The thermochemical heating of a biomass feedstock or other organic material in the absence of free oxygen. The process typically produces liquid, gaseous, and solid (char) products.

Thermochemical conversion Conversion by thermal and chemical processing such as by combustion, gasification, or pyrolysis.

Introduction

Technological innovations and the complex composition of biomass offer immense opportunities for new materials and products from agriculture. Many of these opportunities also come with immense challenges. Biomass can be used to produce a wide variety of biofuels to replace petroleum and natural gas, for example, but large-scale production is at present a vigorously contested global issue with many uncertainties as to net environmental, social, and economic benefits despite the promise of increased renewable energy supplies and enhanced national and global energy security. Less heavily debated is the production of new pharmaceuticals, nutritional products, specialty chemicals, and biomaterials, but these also are subject to concerns over the lifecycle implications of feedstock production and product manufacturing. Together with new tools and techniques for crop improvement, genetic modification, and biomass conversion, agriculture has the capacity to add significant new economic and development value. Agriculture, as a primary land use sector, also has the option to transform into new ways that have little to do with food or biomass production, including land conversion to support wind and solar energy deployment that may be only partially compatible with more conventional agricultural production but which may offer greater profit to the land owner. With the overall sustainability of the current agricultural system still an open question, the expansion, intensification, or redirection of agriculture toward new markets will require careful analysis and management.

Although agriculture has long provided many products in addition to food, it has the productive capacity to supply much larger quantities of industrial feedstock for other markets, in many cases in direct competition with food production. European, US, and other national or regional policies to encourage biofuel production have been heavily criticized for this reason and for their potential to increase greenhouse gas emissions rather than reducing them as intended. Increased demand for biomass, whether food crop or otherwise but especially for food crops like corn (maize) and soybeans for industrial products, is also criticized for increasing food and feed prices with particular impact on the world's poor. This food versus fuel debate is characterized by large uncertainties that lead to difficulties in the design of effective policies for the broader use of products from agriculture. As the development of agriculture has had significant global impact due to land conversion, transitions in agriculture to take advantage of new technologies and new markets for energy, chemicals, materials, and other nontraditional products require an improved understanding of global consequences and a larger systems perspective beyond what has been applied to date. The success of agricultural and industrial research in producing new conversion methods and new products from biomass has created enormous economic and environmental potential, as well as a greater imperative for better information and strategies in managing land resources and the global agricultural enterprise.

Resources and Feedstocks

Photosynthetic Pathways, Efficiencies, and Global Biomass Production

Biomass is living material, and in the context of energy and materials from agriculture and other sources, biomass is

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interpreted to mean nonfossil material of biogenic origin. Biomass includes purpose-grown organisms and crops as industrial feedstocks, crop, and processing residues from agricultural, industrial, and commercial operations, and biogenic fractions of municipal solid wastes and wastewaters among other sources. Agriculture is increasing its production of purpose-grown crops for energy and materials including trees and shrubs, grasses and other herbaceous materials, algae, and other aquatic and terrestrial species. Primary agricultural residues include cereal straws and stovers, animal manures, orchard and vineyard prunings, forest slash from timber operations, forest stand improvement thinnings (such as small trees and brush removed to reduce wildfire intensity), and green waste from yard- and landscape maintenance. Secondary residues arise from food processing, lumber production, and other industrial operations. Black-liquor is a lignin-containing secondary residue from pulp and paper production, but is most commonly burned in recovery boilers at the mill in order to regenerate pulping chemicals and generate steam and power. Tertiary residues are associated with end-of-use materials such as wastepaper, food scraps and other biogenic fractions of municipal solid wastes, biosolids from waste water treatment, and waste fats, oils, and greases (FOG) although advances in reuse, recycling, and product recovery are expanding the perception of these as resources rather than wastes and altering their overall economic value and utility in society. Large amounts of biomass reside in waste landfills that are now being considered for materials mining to reclaim energy and product value. Distinct in arising from different economic objectives, residues and purpose-grown crops nonetheless share many similarities in composition, use, and lifecycle impacts.

The total global resource potential in biomass from agriculture and other activities has been variously estimated. The principal photosynthetic pathway produces carbohydrate biomass from carbon dioxide and water (Calvin, 1976). The process is endothermic and requires energy in the form of light (photons, ν) as well as water as a source of electrons for the overall reduction of CO_2 to carbohydrate:

$$nCO_2 + nH_2O + \nu = (CH_2O)_n + nO_2 \qquad [1]$$

where n indicates the mean polymer chain length of the carbohydrate. The photosynthetic efficiency dictates the number of photons needed per mole of carbohydrate. Anoxygenic photosynthesis also occurs that does not result in oxygen as a product and does not use water as an electron donor (see reaction [2] below) (Sato-Takabe *et al.*, 2012; Buchanan, 1992; Cohen *et al.*, 1975).

An estimated 0.02% of the 175 PW (PW = Petawatt = 10^{15} W) of incoming solar radiation to the Earth (Hubbert, 1971) is used to produce approximately 70×10^{12} kg (70 Gt (Gt = Gigaton = 10^9 metric tons = 10^{12} kg)) of biomass each year through oxygenic photosynthesis (based on an average dry matter heating value of approximately 16 MJ kg^{-1}) (Jenkins *et al.*, 1998). More detailed analyses of biomass production by type of ecosystem yield global estimates in the range of 170–220 Gt year^{-1} (Klass, 1998; Hall *et al.*, 1993). Total plant biomass currently accumulated in all global ecosystems is estimated at approximately 10^{15} kg (1000 Gt) dry matter, or approximately 10 times annual production (Hall *et al.*, 1993; Salisbury and Ross, 1992).

Biomass is also produced through processes other than oxygenic photosynthesis. Hyperthermophilic bacteria, such as those associated with hydrothermal vents at the deep ocean floor, use chemosynthetic pathways for energy and biomass production and are utilized in symbiotic relationships by other organisms (e.g., tube worms) for survival in these extreme environments (Kato *et al.*, 2010). Overall, sulfide chemosynthesis produces elemental sulfur and water in converting carbon dioxide and hydrogen sulfide:

$$nCO_2 + 2nH_2S = (CH_2O)_n + nH_2O + 2nS \qquad [2]$$

Oxygen gas is not released by this mechanism. Sulfur metabolizing bacteria that utilize chemosynthetic pathways are now being investigated for their use in hydrogen sulfide removal from biogas produced during anaerobic digestion of manure and other feedstocks (Ho *et al.*, 2013; Camarillo *et al.*, 2013). Sulfur removal is required for the successful application of most postcombustion catalysts for NO_x emission reductions from engines burning biogas for power generation (Camarillo *et al.*, 2013; Liu and Gao, 2011).

Biomass provides approximately 15% of world energy needs, but in developing countries constitutes a much higher fraction of energy supply: 35% overall, and in excess of 80% in many rural areas (Hall *et al.*, 1993; Bain *et al.*, 1998). Globally, agriculture produces approximately 5 Gt year^{-1} of crop residues of which perhaps less than half may be sustainably available for energy and industrial purposes although larger fractions may be used in developing countries (Jenkins, 1995). Resource-focused studies of global bioenergy potentials range widely, differing by at least an order of magnitude depending on the assumptions made regarding land availability and crop yields (Berndes *et al.*, 2003). Considerations of lifecycle environmental effects, particularly greenhouse gas emissions, also influence global potentials (Searchinger *et al.*, 2008; Fargione *et al.*, 2008).

Plants utilize three principal pathways in assimilating atmospheric carbon dioxide and synthesizing carbohydrate structures and other compounds through photosynthesis. The biological or dry matter yield is dependent in part on the pathway used. Light energy is absorbed in two pigment systems called photosystem I (PS-I) and photosystem II (PS-II). In both the systems, absorption of light by chlorophyll and accessory pigments leads to the emission and transport of electrons against an adverse voltage gradient. As noted above (refer to reaction [1]), in oxygenic photosynthesis the electrons are derived from the photolysis of water mediated by a manganese-containing enzyme in PS-II (Salisbury and Ross, 1992; Marschner, 1986). Electrons are transferred from PS-II through what is called the Z-scheme to PS-I, storing energy in the carriers adenosine triphosphate (ATP) and the reduced form of nicotinamide adenine dinucleotide phosphate (NADPH) for later use in CO_2 reduction and carbohydrate synthesis. Mineral nutrients are directly involved in electron transport, and in other processes of the plant. The mineral or ash concentration and composition are often quite important in the subsequent use of the biomass, and can influence the design of the production and utilization system.

The light reactions store energy in NADPH and ATP. In the so-called C3 plants, CO_2 and water react with ribulose-1,5-diphosphate to produce 3-phosphoglyceric acid as part of the Calvin–Benson cycle. The glyceric acid is subsequently converted using NADPH and ATP into 3-phosphoglyceraldehyde and then into hexose phosphate and ribulose-5-phosphate. The latter reacts with ATP to regenerate ribulose-1,5-diphosphate, whereas hexose is used in the synthesis of the primary storage products, sucrose and starch. The C3 pathway takes its name from the 3-carbon intermediates produced during the cycle. C3 plants include the cereals barley, oats, rice, and wheat, alfalfa (lucerne), cotton, *Eucalyptus*, sunflower, soybeans, sugar beets, potatoes, tobacco, *Chlorella*, and others. Gymnosperms (with a few possible exceptions), bryophytes, and algae are C3 organisms, as are most trees and shrubs.

Along the C4 pathway, CO_2 combines with phosphoenolpyruvate (PEP) via a PEP-carboxylase catalyzed reaction to form oxaloacetate, which is reduced to malic-acid (malate) or aspartic-acid (aspartate), 4-carbon intermediates giving the pathway its name. These are translocated from the mesophyll cells where the primary CO_2 fixation occurs to the bundle sheath cells from which CO_2 is released for subsequent fixation through reactions of the Calvin–Benson cycle as in C3 plants. Decarboxylation of the acids regenerates PEP. C4 plants are usually of tropical origin and have higher photosynthesis rates and higher biological yields (dry matter production) compared with C3 plants. C4 plants include sugarcane, sorghum, maize, and Bermuda grass. *Euphorbia* species considered for direct hydrocarbon production are mostly C3, but a few have evolved to use the C4 pathway.

The third primary pathway is that of crassulacean acid metabolism (CAM) used by many succulents. The CAM pathway also fixes CO_2 via PEP carboxylase, but in the CAM species the stomata are open at night rather than during the day in order to reduce water loss. Malate is stored in the vacuoles during the night and then released during the day when the stomata are closed. CAM plants have lower growth rates than the C4 species but have high water use efficiency due to their adaptation to low-water environments, including semiarid and saltmarsh regions, and epiphytic sites, such as those used by orchids.

For photosynthetic organisms, biological yield (total biomass) is a function of the net production by photosynthesis and consumption by respiration, the latter including photorespiration in C3 plants. Respiration provides energy through the oxidation of organic compounds in generating substrates for the synthesis of other plant products in essentially the reverse of reaction [1] above. Maximum theoretical photosynthetic efficiencies can be derived based on a minimum requirement of eight photons of photosynthetically active radiation (PAR, light of 400–700 nm wavelength) per molecule of CO_2 used to produce glucose, the minimum ν in reaction [1] (Klass, 1998; Hall *et al.*, 1993; Loomis and Williams, 1963). Approximately 43% of the energy in sunlight at the ground level is contained within the PAR band, and of this a maximum of approximately 80% is actively absorbed during photosynthesis. Only approximately 28% of this energy is stored in glucose. In C4 plants respiration consumes somewhere between 25% and 40% of the energy in glucose. The maximum net efficiency of photosynthesis based on incident sunlight is therefore 6–7%. Photorespiration in C3 plants generally leads to efficiencies of approximately 3%, lower than the C4 plants. Photosynthetic efficiencies can be translated to biomass yields using site-specific insolation data and the energy content of the biomass (heating value). At maximum efficiency, theoretical yields can exceed 400 metric tons of dry matter per hectare per year. Agricultural yields are generally far below this due to nonoptimal crop conditions, limited inputs, and losses to diseases and pests. In practice, yields are also lower because not all biomass is or can be harvested. Genetic modifications and other crop improvements are widely investigated to increase productivity and yields.

Efficiencies for agricultural crops typically are of the order of 1%, although tropical crops, such as sugarcane and high-yielding grasses, can produce at 2–3% efficiency with dry matter yields of 50–100 Mg ha^{-1} $year^{-1}$. Intensive production of green algae can approach 5% efficiency, similar to the best efficiencies with C4 crops under research conditions. A maize (corn) crop grown in Davis, California achieved 5.6% photosynthetic efficiency under optimized conditions where only light was limiting (Loomis and Williams, 1963). Seasonal efficiency for many C3 crops when given sufficient water and nutrients is closer to 2% (Monteith, 1977). Natural forest efficiencies trend lower. The production of purpose-grown industrial and energy crops seeks to produce biomass at relatively high photosynthetic efficiency. Owing to the costs of inputs, an optimal production system based on maximum profit may not operate at maximum yield; however, yields are nevertheless of high relative importance to the overall economic feasibility.

Biomass can be used for remediation of environmental contamination (phytoremediation), and the use of biomass as fuel in the substitution of fossil resources can help mitigate greenhouse gas and global climate change impacts, but its production and use requires careful lifecycle assessment to ensure net environmental benefits. As noted earlier in the Section Introduction, many policies and incentives for the production of biofuels are highly controversial.

Biomass production has significant utility in serving to store solar energy. Hybrid renewable energy systems using biomass can take advantage of this attribute in helping to stabilize electricity grids supplied with high levels of intermittent solar and wind power generation.

Biomass is a distributed resource, and its use to supply large quantities of energy and materials requires relatively large amounts of land. The overall conversion efficiency from solar energy to final energy product is low due to the inherently low efficiency of photosynthesis. The overall electrical efficiency, for example, using biomass produced at 2% photosynthetic efficiency as feedstock for power plants operating at 25% average thermal efficiency is 0.5%. Solar photovoltaic systems, including inversion of DC to AC power for grid interconnection, currently generate at efficiencies of 6–12% (with peak research efficiencies well above this), but suffer from the intermittency of sunlight. The higher efficiency of direct solar energy conversion coupled with declining manufacturing costs generates competition between the agricultural and energy sectors for land resources, a subject of additional controversy and developing policy.

Improvements in biomass-fueled power systems will increase conversion efficiencies, but the overall solar conversion efficiencies for biomass are likely to remain below 1% for power. To meet the current (2013–14) world primary energy demands of approximately 600 EJ (EIA, 2013a) would require approximately 600 million hectares of land (1 TJ of energy in biomass per hectare per year) for crops continuously producing at 2% photosynthetic efficiency (approximately 6 kg per square meter or 60 Mg ha^{-1} $year^{-1}$ dry matter). This is approximately 40% of the world's cultivated land area, and 15% of forest lands. It is only approximately 30% of the area of degraded tropical lands, and half the area of these lands considered suitable for reforestation (Hall *et al.*, 1993). Abandoned agricultural land is estimated to range globally from 385 to 470 million hectares (Campbell *et al.*, 2008). The actual land requirement to meet the world energy demand would be much greater than this because of the differences in conversion efficiencies between the current energy resources and biomass to satisfy the same end uses, and because not all land would be kept in continuous production and the overall photosynthetic efficiency would not likely reach 2%. This estimate does not include aquatic or marine species such as algae that might also contribute. More considered estimates of the contributions from bioenergy range from 50 to 240 EJ $year^{-1}$ and closer to 10% of the global energy demand (Berndes *et al.*, 2003). Meeting the world energy demand from biomass is neither necessary nor desirable, but the potential scale for industrial feedstock production is large, even for relatively small shares of the energy market alone and highly significant in terms of land use impacts, both direct and indirect.

Types of Biomass

Agricultural residues

Agricultural residues are coproducts of the principal commodity production system. These include primary vegetation as well as animal manures composed of digested feeds. Corn stover, for example, which is a residue of grain production, is now receiving considerable attention as an energy resource in addition to its potential use in new materials. Increasing economic value of residue biomass can lead to changes in the overall crop production system, such as attention to improving yields of residues as well as the primary crop. Increased fertilization may be needed to replace nutrients exported with the residue biomass when harvested. Alternatively, the farming system may adapt to the application of recycled ash or other nutrients returned from the biomass utilization system. Changes in residue management can also lead to addition or loss of soil carbon, adjustment of fertilizer composition to reduce the uptake of chlorides and other constituents that can be detrimental to downstream conversion, modified tillage strategies to protect against soil erosion when residue cover is reduced or to take advantage of decreased amounts of residue needing to be incorporated into the soil, changes in irrigation practices to manage soil and crop moisture for biomass harvesting, modified chemical applications due to changes in weed, pest, and disease pressure from residue removal, and changes in the harvesting system design and operation to integrate primary crop and residue collection.

Controversy over indirect land-use change effects and food versus fuel impacts associated with purpose-grown crops for biofuels shifted focus onto agricultural residues as seemingly benign sources of feedstock. However, residue use also needs to be carefully evaluated for more global sustainability effects. Harvesting of corn stover in the midwestern US for biofuels, for example, may result in losses of soil carbon that increase the net greenhouse gas emissions above the levels for petroleum-based fuels (Murphy, 2013). Purpose-grown crops such as mixtures of native grassland perennials may prove superior in overall environmental performance (Tilman *et al.*, 2006; Murphy, 2013). Broad generalizations relating to the relative impacts of agricultural residues and industrial crops should be carefully inspected.

Other changes to the production system may occur when modifications are desired in the properties of the biomass. One example is the delayed harvesting of cereal straws to take advantage of natural precipitation in the leaching of alkali metals and chlorine to improve the combustion or gasification properties for biomass power generation and to reduce the export of nutrients from the field when harvesting residues. Residue harvesting reduces air pollution when substituted for traditional open burning disposal practices with some crops, and also removes nonvolatile nutrients such as phosphorous (P) and potassium (K) (Jenkins *et al.*, 1992). Leaching by precipitation readily removes soluble potassium and a number of other constituents and returns them to the field before harvesting, although in-field decomposition of the residue and dry matter loss may reduce the overall economic value (Bakker and Jenkins, 2003).

Residue yields from selected crops are listed in **Table 1**. The estimated production rates for animal manures are also shown. When not measured directly, residue yields are frequently estimated from primary crop yields using the harvest index, the ratio of crop yield to total above ground biomass, typically determined from test plots (Huehn, 1993). Harvested yields are typically lower than listed due to losses in collection and handling, adding to the uncertainty associated with resource supply.

Forest residues and stand improvement biomass

Forest residues include tree tops and branches from timber harvesting operations referred to as forest slash (due to the practice of removing them from the commercially valuable bole of the tree). Biomass can also be collected in the form of forest thinnings of two forms: (1) lower quality stock that is often unsuitable for traditional markets and which contributes to poor forest health or (2) as increased production from more intensively managed regrowth forests. In many temperate forests, the mean annual growth far exceeds the mean annual harvest, and the overall stand quality can be diminished. Understory brush and dense stands of trees can contribute to high fuel loadings in forests with increased danger of catastrophic wildfire, higher incidence of crown fires and greater damage and mortality among mature trees, and high costs of fire suppression if practiced. Many forests of the western United States are now particularly at risk of catastrophic fire due to high fuel loads resulting from more than a century of fire suppression (Jenkins, 2005).

Table 1 Agricultural residue yields and manure production rates

Crop residue	*Yield (Mg ha^{-1} year^{-1})*
Almonds	2.2
Apples	3.7
Apricots	3.4
Artichokes	3.8
Asparagus	4.9
Avocados	2.5
Barley	2.5
Beans	1.9
Cherries	0.7
Citrus	1.7
Corn (maize)	9.0
Cotton	2.9
Cucumbers	3.8
Dates	1.7
Figs	3.7
Grapes	3.4
Lettuce	2.2
Melon/squash	2.7
Oats	2.3
Peaches	3.4
Pears	3.8
Plums	2.5
Potatoes	2.7
Prunes	1.7
Rice	6.7
Safflower	1.9
Sorghum (grain and milo)	5.0
Sugar beets	4.6
Tomatoes	2.9
Walnuts	1.7
Wheat	3.7

Livestock manures	*Production (kg dry matter per animal per day)*
Beef cattle	4.1
Dairy cattle	5.9
Chickens (layers)	0.04
Chickens (broilers)	0.02
Turkeys	0.1
Swine	0.5

Source: Adapted from Knutson, J., Miller, G.E., 1982. Agricultural residues in California, factors affecting utilization. UC Cooperative Extension Leaflet No. 21303. Berkeley, CA: University of California.

Industrial and energy crops

Terrestrial (land-based) purpose-grown industrial and energy crops are typically classified as woody or herbaceous although not all industrial crop types are readily classified in this way. Jatropha, for example, includes approximately 170 species of succulent plants, shrubs, and trees. The more common species of this plant considered for biofuel purposes is the drought-resistant shrub *Jatropha curcas* that produces an oil-bearing seed useful for biodiesel production among other uses. The plant also contains toxic compounds including phorbol esters and other terpenoid compounds, but even these also have some beneficial uses (Devappa *et al.*, 2011; Wang *et al.*, 2013a). The phorbol esters demonstrate insect deterrent and cytotoxic antitumor and antimicrobial properties (Devappa *et al.*, 2011). Woody crops are predominantly plantation trees, frequently grown in short-rotation intervals of from 1 to 20 years between harvests. Cultural practices for these crops have been well established for roundwood and papermaking, and have been more recently extended to the production of fuel wood. Herbaceous crops include annual and perennial grasses and other nonwood plants. Production practices for these crops are in most cases similar to other agricultural crops, although in both woody and herbaceous crop production, the end use for the biomass can influence the management and cultural inputs and practices employed to optimize the production system. A number of more commonly considered industrial and energy crops are listed in **Table 2** but many more have been investigated for specific material recovery or energy purposes.

Just as they are for current agriculture, water availability and water costs are key constraints in industrial biomass production. Water requirements vary considerably but are typically in the range of 300–1000 kg per kg of dry matter produced. Arid or semiarid regions of the world are not anticipated to produce substantial quantities of biomass for energy markets even where water is commonly imported for agriculture. The exception may be in the production of algae due to the high availability of solar radiation and the potential for the use of brackishwater, waste water, or seawater (Renuka *et al.*, 2013). Lands in these areas might be used in the production of feedstocks for higher value industrial and consumer products.

Biomass production can play an integral role in managing salts and remediating other undesirable impacts of irrigated agriculture in arid or semiarid regions and in reclaiming lands degraded by unsustainable agricultural practices. Integrated farm drainage management (IFDM) systems have been evaluated in California and other irrigated agricultural regions to reclaim salt-affected soils and to reduce the environmental impacts of agriculture in these areas (Lin *et al.*, 2002). IFDM systems employ sequential reuse of water through a cascade of increasingly salt-tolerant crops with the objective of continuously reducing water volume and increasing salt concentration for ultimate recovery or removal. Fresh irrigation water applied to high-value vegetable crops, for example, results in drainage water that can be applied to more salt-tolerant agricultural crops such as cotton or barley. Biomass crops, such as *Eucalyptus* or Jose tall wheat grass (*Agropyron elongatum*) are suitable for irrigation with the secondary drainage water from these, with tertiary drainage from the biomass crops applied to halophytes, and solar evaporators or other salt separation and purification systems used for final treatment and salt removal. The biomass crops transpire large amounts of water and act as biopumps to lower groundwater tables and reduce salt accumulation in the root zone, and also help in removing toxic elements, such as selenium, that is taken up and accumulated in the plant biomass. Crop harvesting removes undesirable materials from the field for downstream recovery, utilization, or disposal. Biomass yields under these conditions are substantially less than the best yields obtained for the same species under optimal conditions. Where other agronomic or environmental purposes are involved, yield is not necessarily the primary consideration for these systems although still an important consideration for economic performance. Biomass crops can in

Table 2 Selected industrial and energy feedstock crops

Woody species – biomass/fiber/pulp
Alder (*Alnus* spp.)
Australian pine (*Casuarina*)
Birch (*Onopordum nervosum*)
Black locust (*Robinia pseudoacacia*)
Eucalyptus (*Eucalyptus* spp.)
Lucaena (*Lucaena leucocephala*)
Poplar (*Populus* spp.)
Willow (*Salix* spp.)

Herbaceous species – biomass/fiber/energy grain
Alfalfa (*Medicago sativa*)
Corn/Maize (*Zea mays*)
Flax (*Linum usitatissimum*)
Hemp (*Cannabis sativa*)
Jose tall wheatgrass (*Agropyrum elongata*)
Kenaf (*Hibiscus cannabinus*)
Miscanthus (*Miscanthus* spp.)
Napier grass/Bana grass (*Pennisetum purpureum*)
Spanish thistle or Cardoon (*Cynara cardunculus*)
Spring barley (*Hordeum vulgare*)
Switchgrass (*Panicum virgatum* L.)
Triticale (*Triticosecale*)
Winter rye (*Secale cereale*)
Winter wheat (*Triticum aestivum*)

Herbaceous species – sugar/starch/biomass
Buffalo gourd (*Curcurbita foetidissima*)
Cassava (*Manihot esculenta*)
Jerusalem artichoke (*Helianthus tuberosus*)
Sugar/energy cane (*Saccharum* spp.)
Sugar/fodder beet (*Beta vulgaris*)
Sweet sorghum (*Sorghum bicolor*)

Wetland species – biomass/fiber
Cattail (*Typha* sp.)
Cordgrass (*Spartina* spp.)
Giant reed (*Arundo* spp.)
Giant reed (*Phragmites* spp.)
Reed canary grass (*Phalaris arundinacea*)

Seed/oilseed/terpenes
Amaranth (*Amaranthus* spp.)
Castor (*Ricinus communis*)
Crambe (*Crambe abyssinica*)
Euphorbia (*Euphorbia* spp.)
Jojoba (*Simmondsia chinensis*)
Linseed (*Linum usitatissimum*)
Oilseed rape (*Brassica* spp.)
Safflower (*Carthamus tinctorius*)
Soybean (*Glycine max*)
Sunflower (*Helianthus annuus* L.)
Jatropha (*Jatropha curcas*)

Aquatic species – biomass/lipids
Brown algae (*Sargassum* spp.)
Giant kelp (*Macrocystis pyrifera*)
Microalgae (*Botryoccus braunii*)
Red algae (*Gracilaria tikvahiae*)
Unicellular algae (*Chlorella and Scenedesmus*)
Water hyacinth (*Eichhornia crassipes*)

general be used for the restoration of abandoned or degraded agricultural lands (Campbell *et al.*, 2008), and economic and environmental reasons are frequently proposed for planting in marginal areas.

Short-rotation woody crops grown for energy or other purposes are typically grown in plantations with stand densities ranging up to 10 000 trees per hectare depending on the size of the tree desired at harvest, harvesting technique employed, and end use intended for the biomass (Smith *et al.*, 1997). More than 100 million hectares are in industrial tree plantations (Hall *et al.*, 1993), most in longer rotations for roundwood and pulp production. Production site selection depends on soil properties, water availability, slope, climate, and distance from market. As with agricultural crops, high yields are associated with better soil types, although trees can generally take advantage of higher groundwater tables (Siren *et al.*, 1987). Soil preparation commonly involves land clearing to remove the existing vegetation and eliminate weeds, soil amelioration to adjust pH and improve tilth, drainage, and nutrient concentrations, and leveling and in some cases mulching. The plant bed is prepared in a manner similar to agricultural crops, although tillage is typically deeper than for cereals. Following soil preparation, cuttings, slips, or seedlings are planted either manually or by machine or by machine-assist to manual planting (Golob, 1987). Soil moisture management following planting is critical as deeper tillage increases drying rates, potentially leading to inadequate water availability without rain or irrigation. Cultivation, chemical application, or mulching (including plastic sheet mulching) to control weeds, and in some cases pruning to improve shoot vigor, are typically required following planting for proper stand establishment. Some crop species, such as *Salix* (willow), are highly susceptible to common herbicides. Biological weed control is sometimes practiced, usually by planting weed-competitive crops such as *Trifolium*, although these can also compete for nutrients and water with the primary crop until good canopy cover is achieved. Fencing to control grazing by animals may also be needed. Irrigation and fertilization can be accomplished in the same manner as for agricultural crops. Drip irrigation systems can be combined with chemigation (injection of nutrients and other chemicals into the irrigation system for distribution to the plants). Frost protection is not commonly practiced, but frost damage is a concern in many locales. Where frosts are frequent, more tolerant species or varieties are selected. Fire suppression may be needed in dry areas, and varietal or species selection is important in reducing damage from insects and diseases. Plantation design can include set-aside areas harboring native predators of pests, and division of the plantation into blocks of different clones or species to make the overall plantation less susceptible. Owing to the lower frequency of planting and other operations in tree plantations, soil erosion rates are generally lower compared

with agricultural crops. Seedling survival rates in well-managed plantations are typically approximately 85%. Coppice (resprouting) crops are harvested in 3–10 year cycles, with up to six cycles before replanting. Mean annual dry matter increments in practice are 10–20 Mg ha^{-1} $year^{-1}$, generally declining at higher latitudes for reasons of climate and insolation. Crop improvements may extend these yields to 15–30 Mg ha^{-1} $year^{-1}$ or higher.

Production of herbaceous crops in many respects bears greater resemblance to conventional forage and other agricultural crops, although many of the same considerations apply to the production system design as do for short-rotation woody crops (Smith *et al.*, 1997; Gosse, 1996). Regional mixed cultivation of perennial and annual species, as opposed to large-scale monoculture, is seen in many cases to be of benefit both in terms of environmental and economic performance (Tilman *et al.*, 2006). Depending on the location, the regional mix might include legumes and warm and cool season grasses. Total dry matter yields for herbaceous species under good management are typically in the range of 10–30 Mg ha^{-1} $year^{-1}$. Sugarcane, a C4 species, is one of the most productive crops, with world average yields of approximately 35 Mg ha^{-1} $year^{-1}$ (Hall *et al.*, 1993) with fresh wet-weight yields including sugar above 250 Mg ha^{-1} $year^{-1}$ although few countries exceed 100 Mg ha^{-1} $year^{-1}$ fresh-weight (Duke, 1983). Where proposed as energy or industrial crops, particular attention must be given to the composition of the plant. Herbaceous species, especially grasses, generally contain more ash than woody species, and the ash is higher in alkali metals and silica. The latter, for example, combine at high temperatures in thermochemical systems to form slags and deposits that increase maintenance costs. Leaching with water can remove most of the alkali, and delayed harvest to take advantage of rain-washing can improve the combustion properties in the same manner as noted earlier for residues (Jenkins *et al.*, 1998; Huisman, 1999). Chlorine, primarily supplied in potassium fertilizer (e.g., as muriate of potash or KCl) or present as chloride in irrigation water, facilitates alkali volatilization and fouling at high temperatures, accelerates corrosion of metals, and contributes to acid gas (principally HCl) and toxic emissions such as dioxins and furans from combustion systems (Jenkins *et al.*, 2011). Sulfur, although typically present in plant biomass at low concentrations, also contributes to fouling and air pollutant emissions. Restricting chlorine from fertilizers in energy crop production is generally advantageous, as is proper management of sulfur. These concerns are reduced for crops grown as feedstock for direct chemical extraction, fermentation, or manufactured fiber products, where oil, sugar, starch, or structural carbohydrates are of more importance, unless ligneous residues of the fermentation are to be burned as fuel as is commonly considered for cellulosic biorefineries. However, in all cases the composition of the feedstock needs to be considered in terms of the requirements of the manufacturing or conversion process and any accompanying waste disposal. Consideration also needs to be given to the introduction of exotic species that may grow well initially but lack biological disease and pest controls in new environments and are, therefore, more susceptible to later damage or that may prove adaptive and invasive to the detriment of native species or other crops.

Except for phytoplankton, aquatic species tend to demonstrate higher yields than terrestrial crops (Klass, 1998). Aquatic species include both unicellular (e.g., *Chlorella*, *Scenedesmus*) and macroscopic multicellular (e.g., *Macrocystis*, *Gracilaria*, *Sargassum*) algae (seaweeds), and a number of water and salt marsh plants such as cordgrass (*Spartina* spp.), reed (*Arundo*, *Phragmites*), bulrush (*Scirpus*), and water hyacinth (*Eichhornia*). Dry matter yields range between 5 and 75 Mg ha^{-1} $year^{-1}$. Water hyacinth is considered a nuisance plant in many inland waterways and is difficult to control, but is hardy and disease resistant. Many of the aquatic species are currently produced under much more intensive conditions, and generally for more valuable products than energy and fuels, for example, *Spirulina* for food protein or for antihistamine peptides used in the prevention of atherosclerosis (Spolaore *et al.*, 2006; Vo and Kim, 2013), although benefits of its use as a supplement for animal feeds are still in question (Holman and Malau-Aduli, 2013).

Algae and cyanobacteria represent a significant fraction (20–30%) of global photosynthetic productivity and are widely investigated for their energy and industrial product potential (Waterbury *et al.*, 1979; Spolaore *et al.*, 2006; Pisciotta *et al.*, 2010). High lipid concentrations in some strains of algae (up to 50% in *Nannochloropsis* and 60% in *Botryococcus braunii* (Scott *et al.*, 2010)) have encouraged research and commercial development into the production of biodiesel fuel from algal extracts and fermentation of algae for alcohol, biogas, and other products using algal production in open natural systems, ponds and raceways, as well as in highly engineered bioreactor systems (Sheehan *et al.*, 1998; Cheng *et al.*, 2013). Petroleum resources that supply current motor fuels and other energy demands predominantly originate from algal and zooplankton biomass deposited during periods of global warming approximately 90 and 150 Ma ago (Campbell, 1988). Interest in algae is also driven by perceived high productivities and the potential for carbon uptake and sequestration in mitigating carbon dioxide emissions from power plants. Single-day maximum productivities obtained in research trials are up to 50 g of dry matter per square meter per day, which if sustained throughout the year would equate to 183 Mg ha^{-1} $year^{-1}$, well above yields from the best producing C4 species. Commercial yields are unlikely to exceed approximately 80 metric tons dry matter per hectare per year (Scott *et al.*, 2010) although more optimistic estimates are frequently made. Sea-based floating membrane bioreactors have also been proposed to enable large-scale off-shore farming of algal biomass using municipal wastewaters as nutrient sources (Howell, 2009; Harris *et al.*, 2013).

Structure, Composition, and Properties of Biomass

Biomass is a chemically rich feedstock that can be used in its native form, converted into intermediate chemicals and materials for further downstream processing to final products, or converted directly to the final product. Composition varies by the type of feedstock, location of production, and by a number of other cultural attributes, but can be generally classified into organic and inorganic constituents all of which can be important in the conversion to energy, materials, and fuels. These

constituents can be further divided into a number of components and properties subject to international standards of analysis (Figure 1).

Fresh or crude biomass contains water as moisture and dry matter, the latter comprises organic constituents that are volatile under heating (volatile solids) and an inorganic fraction represented as ash. Moisture content influences the entire production chain due to its importance in determining the harvesting conditions, transportation modes and costs, conversion technology type and performance. For the processes involving thermal transformations (e.g., combustion), the organic fraction is typically classified into volatile matter (not to be confused with volatile solids) and fixed carbon, but combined these two fractions comprise most of the structural components of biomass (principally hemicellulose, cellulose, and lignin but also pectin and other cell wall polymers) and extractives (e.g., lipids in algae or oilseeds, sugars, starches, and terpenes and also many other compounds including some of the inorganic constituents). The ash consists typically of salts and other minerals, metals, and adventitious material, that is, materials not inherent in the biomass but added instead through handling and processing, such as soil accumulated during harvesting. Organic materials may also be adventitious, and alterations in the organic composition and structure can occur through degradation or decomposition of the feedstock during handling, storage, and processing. More fundamentally, the biomass can be characterized by its elemental composition that will contain essentially every natural element but more practically is limited to a smaller number of major elements with a large number of minor and trace elements at concentrations of significance, some of which will be important to industrial processing or energy conversion (e.g., lead, mercury, and other heavy metals). The design of any industrial system requires a careful analysis of the chemical and physical properties of the intended feedstock to evaluate influences on process operations and product quality.

The structure of biomass varies depending on the species and the tissue type. Microstructures of some higher plants (woods and grasses) are shown in Figures 2–4. The term 'wood' more specifically refers to the secondary xylem tissue arising from cell division in the vascular cambium (Hon and Shiraishi, 2001), but bark and other tissues are also generally included when referring to feedstock materials even though compositions can be widely different. Ash content, for example, is frequently higher in bark than in wood. Its distribution also varies in herbaceous species such as rice (Summers *et al.*, 2003). Woods are classified as softwoods and hardwoods. Tracheid and parenchyma cells are the principal types in softwoods, with tracheids in some comprising 90% of the wood volume. Hardwoods are more complex. Principal cell types in hardwoods are fibers, vessels, and parenchyma. Herbaceous species such as the grasses have tubular or solid stems (culm) divided into node and internode regions, the latter typically surrounded by leaf sheaths originating from the nodes. Algae constitute a highly diverse group of eukaryotic organisms that can be unicellular or multicellular and differ in fine structure compared with terrestrial green plants (Bouck, 1965). They range in size from microalgae under 5 μm (e.g., *Scenedesmus*) to the macroscopic giant kelp (*Macrocystis pyrifera*) exceeding 50 m in length. They also vary substantially in lipid, carbohydrate, nucleic acid, and protein composition (Sheehan *et al.*, 1998). Fresh-weight moisture is more than 65% and more commonly more than 85%; dry weight ash contents can exceed 30%; protein concentrations can approach

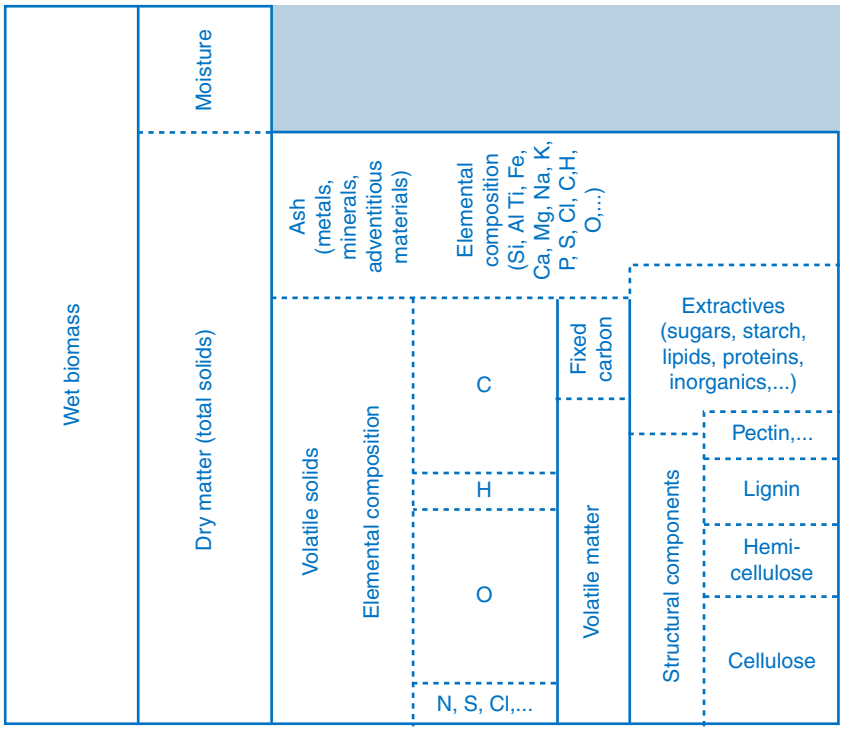


Figure 1 Biomass composition (dashed lines indicate variable concentrations).

half the dry weight; and lipid concentrations range up to 60% dry weight (Butler, 1931; Renaud *et al.*, 1999; Sheehan *et al.*, 1998). Cell wall components include cellulose, hemicelluloses, lignin, pectins, arabinogalactan proteins, extensin, carrageenan, agar, and in diatoms sculpted silica composites (Blumreisinger *et al.*, 1983; Abo-shady *et al.*, 1993; Domozych, 2011; Domozych *et al.*, 2012). The so-called blue-green algae (prokaryotic cyanobacteria) are now classified with the bacteria. Chitin (polymeric *N*-acetylglucosamine, also found in the exoskeletons of arthropods) rather than cellulose is the primary structural component of the cell wall among the true fungi (Blumenthal and Roseman, 1957; Sikkema and Lovett, 1984).

The dominant structural compounds making up the plant biomass are cellulose (six-carbon or C6 polymers) and hemicellulose (predominantly C5 polymers but including C6 species) produced via condensation polymerization of the monosaccharides (Chum and Baizer, 1985; Schultz and Taylor, 1989; Sudo *et al.*, 1989; Lynd, 1990; Wyman and Hinman, 1990; Hon and Shiraishi, 2001). The other primary structural components are lignins, aromatic polymers of variable structure derived in one proposed pathway from coniferyl, sinapyl, and *p*-coumaryl alcohols. The alcohols arise through the shikimic acid pathway, and are polymerized into lignin via free-radical reactions (Salisbury and Ross, 1992). Organic compounds in biomass also include proteins, triglycerides (fats and oils), terpenes (including isoprenes), waxes, cutin, suberin, phenolics, phytoalexins (antimicrobial compounds produced by the plant), flavonoids, betalains, alkaloids, and other secondary compounds as well as sugars and starch. Plants accumulate inorganic materials (ash), sometimes in concentrations exceeding those of the hemicellulose or lignin. The composition of wood can depend on the applied forces during growth ('reaction' wood). Compression wood typically has highly lignified tracheid walls, in contrast to tension wood with lower lignin concentrations.

Cellulose is a linear crystalline polysaccharide of β-D-glucopyranose units linked with (1–4) glycosidic bonds. Cellulose serves as a framework substance, making up 40–50% of wood. In the cell wall, cellulose exists in the form of thin threads or microfibrils, each 2–5 nm wide in wood, but up to 30 nm wide in algae (*Valonia*). The polymer is formed from repeating units of cellobiose, a disaccharide of β-linked glucose moieties (**Figure 5**). The structure of cellulose renders it highly insoluble and resistant to biochemical degradation. The α-linked disaccharide of glucose forms starch (**Figure 6**). Starch is an amorphous material, and as such is more readily degraded by biochemical means than is cellulose and hence the relative ease of fermenting starch to ethanol whereas cellulose requires substantial pretreatment to deconstruct it before fermentation.

Hemicelluloses are matrix substances laid down between cellulose microfibrils. They are polysaccharides of variable

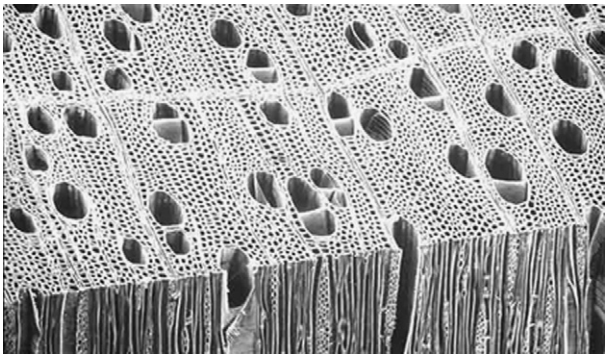


Figure 3 Scanning electron micrograph of birch hardwood showing a more complex structure compared with softwoods. Large holes are vessel elements. Reproduced from Society of Wood Science and Technology, 2013. Structure of Wood. Available at: http://www.swst.org/edu/teach/teach1/structure1.pdf (accessed 11.11.13).

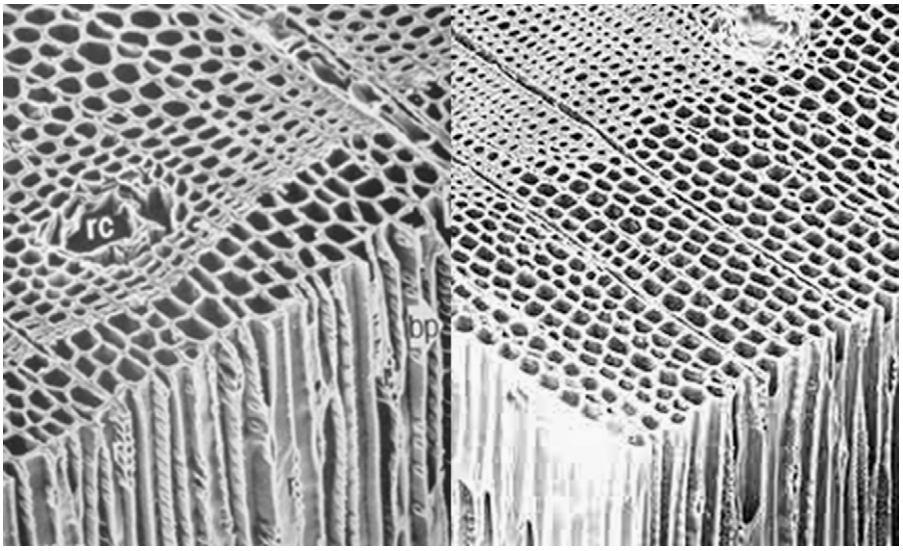


Figure 2 Scanning electron micrographs of softwood showing longitudinal tracheids, horizontal rays, and other structures. Left: spruce wood (rc, a resin canal; bp, a bordered pit). Right: pine wood. Reproduced from Society of Wood Science and Technology, 2013. Structure of Wood. Available at: http://www.swst.org/edu/teach/teach1/structure1.pdf (accessed 11.11.13).

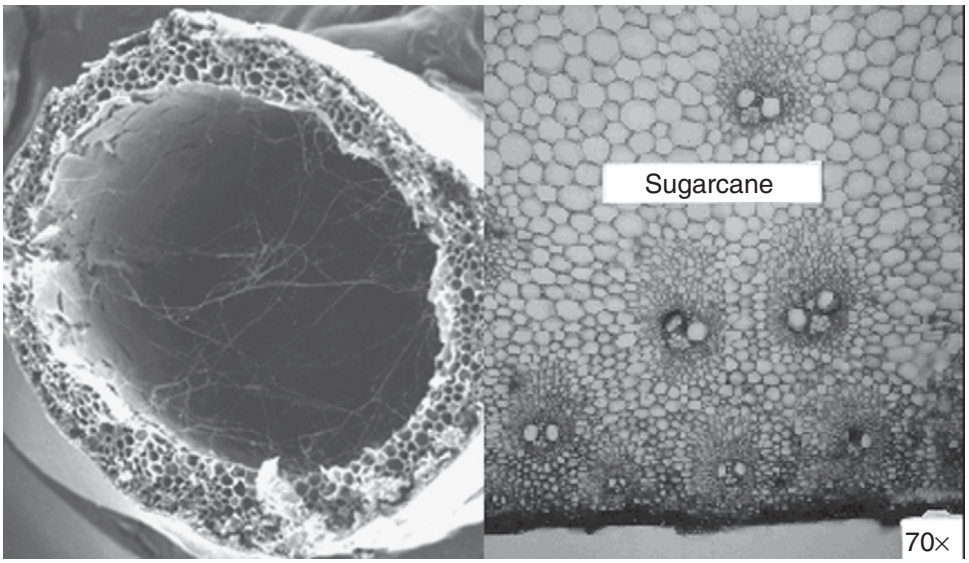


Figure 4 Scanning electron micrographs of a wheat straw stem (left) showing hollow tubular structure of vascular bundles in culm, and sugarcane (right) showing solid stem with distributed vascular bundles. Left: Reproduced from Malhotra, V., 2013. Bio-Composites from Agricultural Raw Materials. Available at: http://www.physics.siu.edu/malhotra/vivek/biocomposites.htm (accessed 11.11.13). Right: Reproduced from NTNU, 2013. Monocotyledons. Norwegian University of Science and Technology – Trondheim. Available at: http://www.chemeng.ntnu.no/research/paper/Online-articles/Nonwoods/Nonwood.html (accessed 11.11.13).

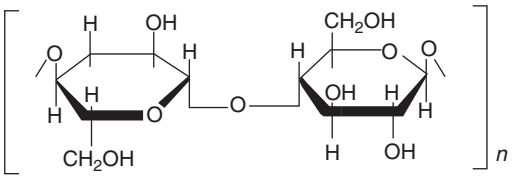


Figure 5 The β-linked glucose units forming cellobiose, the repeating unit of cellulose. Reproduced from Salisbury, F.B., Ross, C. W., 1992. Plant Physiology. Belmont, CA: Wadsworth Publishing Co.

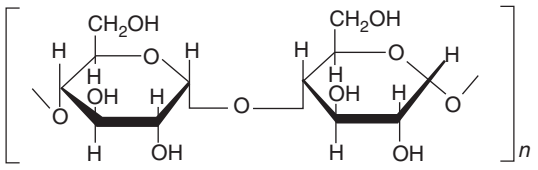


Figure 6 The α-linked glucose units making up starch. Reproduced from Salisbury, F.B., Ross, C.W., 1992. Plant Physiology. Belmont, CA: Wadsworth Publishing Co.

composition containing both five- (including xylose and arabinose) and six-carbon (including galactose, glucose, and mannose) monosaccharide units. Like starch, hemicelluloses are mostly amorphous, making them more readily hydrolysable than cellulose. Hemicelluloses constitute 20–30% of wood, generally with higher concentrations in hardwoods than softwoods. Hemicelluloses also constitute 20–30% of dry matter in most other biomass. Partial structures for the primary forms of hemicellulose in hardwood and softwood are shown in Figure 7.

Lignin is the encrusting substance ('glue') solidifying the cell wall. Lignin is an irregular polymer of phenylpropane units and the structure varies among different plants. Lignin is thought to occur through the enzymatic dehydrogenation of phenylpropanes followed by radical coupling (Hon and Shiraishi, 2001). Softwood lignin is composed principally of guaiacyl units stemming from the precursor *trans*-coniferyl alcohol (Figure 8). Hardwood lignin is composed mostly of guaiacyl and syringyl units derived from *trans*-coniferyl and *trans*-sinapyl alcohols. Grass lignin contains *p*-hydroxyphenyl units deriving from *trans*-*p*-coumaryl alcohol. Almost all plants contain all three guaiacyl, syringyl, and *p*-hydroxyphenyl units in lignin. A partial structure of softwood lignin is shown in Figure 9.

Partial compositions of selected biomass materials are listed in Table 3. The four materials – Monterey pine (*Pinus radiata*, a softwood), eastern cottonwood (*Populus deltoides*, a hardwood), sugarcane bagasse (from *Saccharum* spp.), and wheat straw (from *Triticum aestivum* var. *Thunderbird*) – were analyzed as reference materials for the purposes of providing reference characterizations of industrial and energy feedstocks (NIST, 2003).

Plants producing large amounts of free sugars, such as sugarcane and sweet sorghum, are attractive as feedstocks for ethanol fermentation, as are starch crops such as maize (corn) and other grains. Current attention is focused on the fermentation of the cellulosic components because of the perceived economic and energetic advantages for large-scale liquid fuel production. Cellulose and hemicellulose are not fermentable by conventional means, as more aggressive pretreatment and hydrolysis must precede the fermentation step. Lignins are not yet generally considered fermentable, and thermochemical means are usually proposed for their conversion to fuels. Typically, 60–80% of the biomass feedstock mass is ultimately fermentable based on cellulose and hemicellulose (holocellulose) concentrations.

Oil crops such as rape and canola, soybean, sunflower, safflower, algae, and others have been widely investigated for

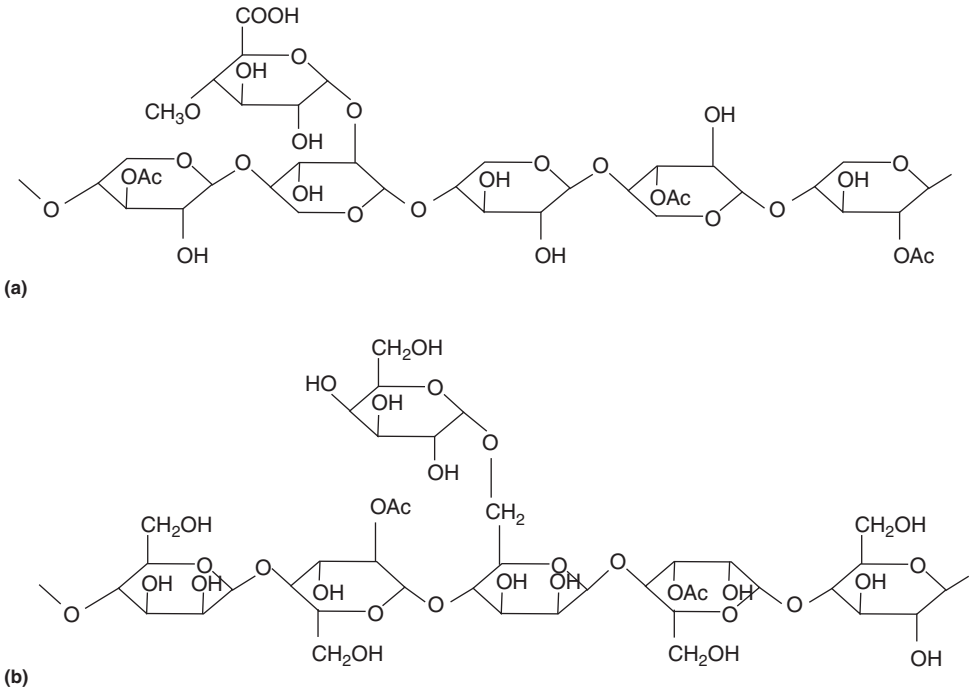


Figure 7 Partial structures of the principal hemicelluloses in wood (Hon and Shiraishi, 2001): (a) *O*-acetyl-4-*O*-methylglucuronoxylan from hardwood; (b) O-acetyl-galactoglucomannan from softwood. Ac = acetyl group.

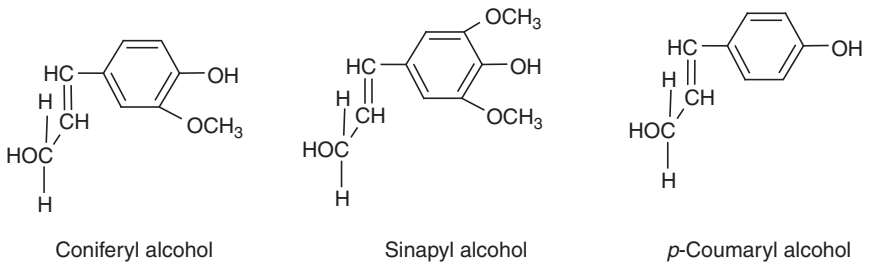


Figure 8 Phenolic subunits of lignin. Reproduced from Salisbury, F.B., Ross, C.W., 1992. Plant Physiology. Belmont, CA: Wadsworth Publishing Co.

their potential in producing diesel fuel substitutes (commonly referred to as 'biodiesel'). Although raw plant oils are not generally satisfactory as fuels for diesel-type (compression-ignited) engines, methyl and ethyl esters formed by reacting the oil with an alcohol (methanol or ethanol) have lower viscosity and improved injection and combustion properties making them suitable for engine use (Peterson *et al.*, 1992). Other crops, such as *Euphorbia*, have been investigated for direct production of hydrocarbons (Nishimura *et al.*, 1977; Nemethy *et al.*, 1981).

Roughly half of the plant organic matter is carbon, the rest being made up of 5–7% hydrogen, 30–50% oxygen, along with nitrogen, sulfur, chlorine, and other elements (Jenkins and Ebeling, 1985; Jenkins *et al.*, 1998). The ash or inorganic fraction of biomass may account for more than 30% of the dry mass in some cases (e.g., animal manures and other waste materials, some algae). Temperate region woods typically have ash contents below 1%, whereas some tropical woods contain up to 5% ash (Chum and Baizer, 1985). Leaves and young tissues contain more ash than mature wood. Cereal grain straws, hulls (husks), and other agricultural biomass have ash contents ranging up to approximately 25% of the dry mass. The amount of ash in a biomass material, and the composition of the ash are important for the selection of the conversion technology. As noted earlier in the Section Types of Biomass, alkali metals (especially the macronutrient potassium) in the ash of many agricultural residues can cause slagging and boiler fouling and corrosion in the case of direct firing as a result of high temperature reactions with silica and other minerals. Chlorine is important in corrosion and as a facilitator in the alkali reactions leading to deposition in boilers. Biochemical methods avoid this problem because of the lower temperatures involved although corrosion can still be of concern. Other methods, such as supercritical water oxidation, in which the oxidation is carried out at a relatively low temperature but high pressure, may suffer less from ash reactions although salts can be an issue, but such processes are not yet commercial. In certain circumstances, fouling is reduced by the extraction of the offending elements before introducing the fuel to the boiler. Such is the case of sugarcane

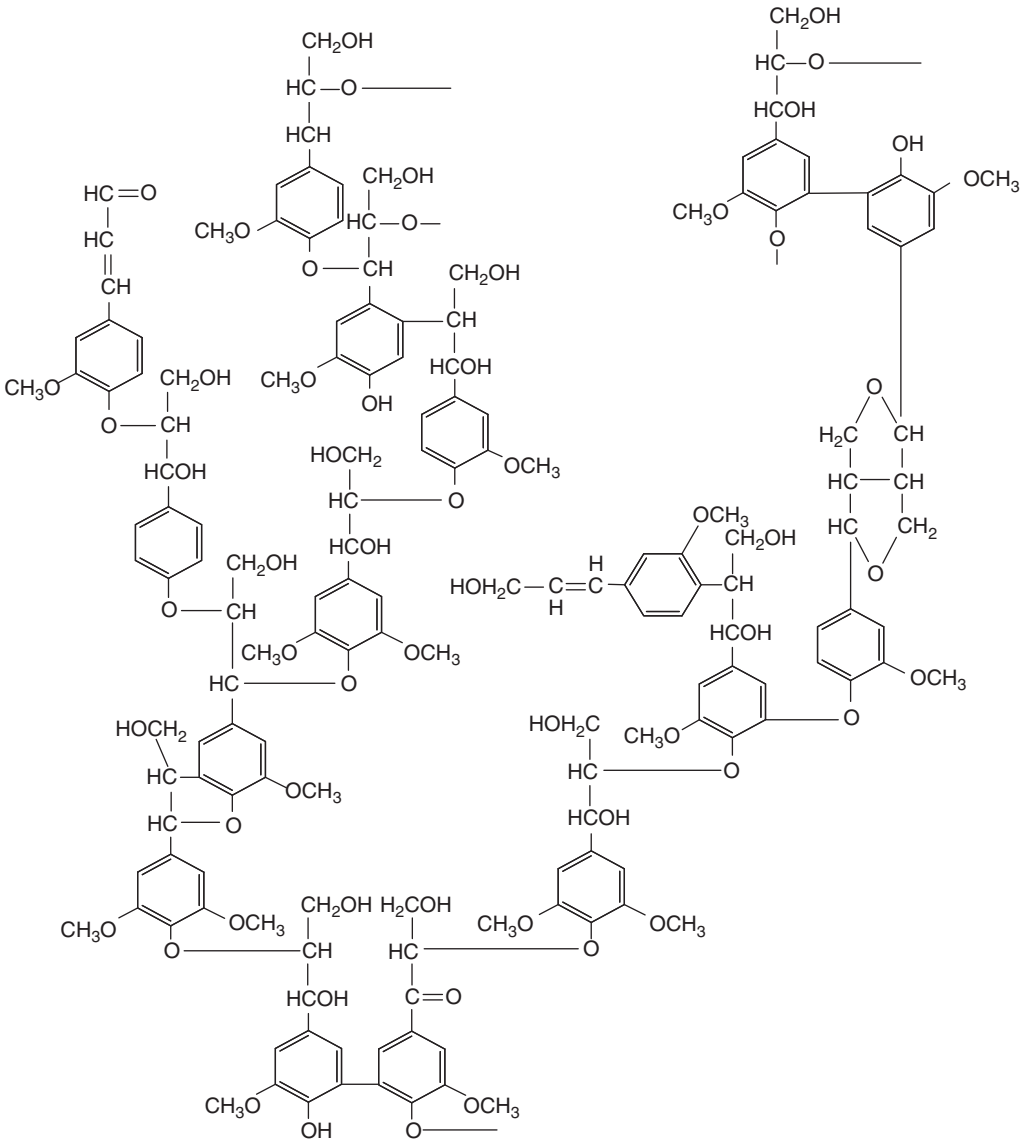


Figure 9 Partial lignin structure of softwood. Reproduced from Salisbury, F.B., Ross, C.W., 1992. Plant Physiology. Belmont, CA: Wadsworth Publishing Co.

Table 3 Partial compositions (%) of biomass materials (NIST, 2003)

Biomass constituent	*Populus deltoides (rm #8492)*	*Pinus radiata (rm #8493)*	*Sugarcane bagasse (rm #8491)*	*Wheat straw (rm #8494)*
Ash	1.0	0.3	4.0	10.3
95% ethanol extractives	2.4	2.7	4.4	13.0
Acid soluble lignin	2.4	0.7	2.0	2.3
Acid insoluble lignin	23.9	25.9	22.3	15.9
Total lignin	26.2	26.6	24.2	18.0
Glucuronic acid	3.7	2.6	1.3	2.1
Arabinan	0.7	1.5	1.8	2.5
Xylan	13.9	6.2	21.5	21.7
Mannan	2.0	10.9	0.4	0.3
Galactan	0.6	2.4	0.6	0.8
Glucan	43.2	42.9	40.2	37.6

Each value is mean from round-robin testing of approximately 20 laboratories.

bagasse, commonly used as a fuel in the sugar industry, but which has passed through the sugar extraction step and had most of the alkali leached in the process. Direct firing of cane trash, currently under investigation for increasing the power generation from the cane industry, does not extract these elements, and may suffer from deposition common to straws and other high ash, high alkali biomass fuels.

The energy content or heating value (heat of combustion) of biomass can be partially correlated with ash concentration. Woods with less than 1% ash typically have heating values near 20 MJ kg^{-1}. Each 1% increase in ash translates roughly into a decrease of 0.2 MJ kg^{-1} (Jenkins, 1989) because ash does not contribute substantially to the overall heat released by combustion, although elements in the ash may be catalytic to thermal decomposition. Heating values can also be correlated to carbon concentration, with each 1% increase in carbon elevating the heating value by approximately 0.39 MJ kg^{-1}, a result identical to that found by Shafizadeh (1981) for woods and wood pyrolysis products. The heating value relates to the amount of oxygen required for complete combustion, with 14 022 J released for each gram of oxygen consumed (Shafizadeh, 1981). Cellulose has a smaller heating value (17.53 MJ kg^{-1}) than lignin (26.7 MJ kg^{-1}) because of its higher degree of oxidation. Other compounds, such as hydrocarbons, with lower degrees of oxidation or containing no oxygen tend to raise the heating value of the biomass.

Proximate and elemental compositions and heating values for selected biomass are listed in **Table 4**. The heating value shown in the table is the constant volume higher heating value that is one of four that can be defined based on whether the test is carried out at constant pressure or constant volume and whether water produced from the hydrogen in the biomass is in the vapor or liquid phase at the end of the test (Jenkins, 1989). Wheat straw and sugarcane bagasse listed in **Table 4** are not the same samples listed in **Table 3** and hence have different compositions. The proximate analysis yields ash content and the fraction referred to as volatile matter (**Figure 1**) evolved during a short heating at 950 °C in a nonoxidizing atmosphere representing pyrolysis. The difference between the total dry matter and the sum of ash and volatile matter is fixed carbon (essentially charcoal). The ultimate analysis yields elemental concentrations of carbon, hydrogen, nitrogen, and sulfur, with oxygen usually determined by difference. Although not part of the standard for ultimate analysis, chlorine is also sometimes analyzed due to its importance in many conversion systems. The Jose tall wheat grass listed in the table was grown as a phytoremediation crop under saline conditions, and has a high Cl content.

Logistical Supply Chains

The use of biomass for industrial products and energy typically requires a supply chain of multiple operations to deliver biomass feedstock or biomass-derived intermediates from the site of production to the conversion facility and then the finished product into final demand (**Figure 10**). For food processing facilities, lumber mills, wastewater treatment plants, dairies, and other animal operations, the supply chain may be relatively simple due to the generation of the feedstock on-site.

For crop and forest residues and energy crops, supply operations upstream of the conversion facility will typically include collection or harvesting, packaging and processing such as baling, pelleting or grinding, loading and unloading onto transport vehicles, transportation on roads, rail, river or marine routes, and in most cases storage, possibly at one or more intermediate sites (depots) in addition to the primary site of conversion. Densification of the bulk biomass may be preferred for the purposes of achieving high transportation payloads on trucks and other vehicles but contributes to the cost of processing. Whether the cost can be justified depends in part on transport distance and other factors associated with the handling and use of the feedstock and the cost of transport otherwise. Conversion into pyrolysis oils, sugars, and other intermediate products at depots or other satellite facilities may also be considered for logistical purposes to reduce the total costs of feedstock transportation to larger central facilities for final processing and production.

Drying to reduce moisture content may be needed, especially for feedstocks intended for many types of thermochemical conversion facilities. For some facilities, for example, biochemical conversion facilities using fermentation systems, the moisture in feedstock may be an important contribution toward meeting the overall process water demands and may enhance conversion but adds to transportation costs and increases the risk of spoilage during handling.

The costs associated with feedstock supply, conversion, and the distribution of finished products influence the optimal size of a conversion facility (Jenkins, 1997). Economies of scale typically exist for capital and operating costs so that as the production capacity or size increases, these costs typically do not increase in the same proportion and the cost per unit of product output decreases. However, as the size of the facility increases, the feedstock demand increases as well, and for distributed feedstocks such as crop and forest residues and purpose-grown crops, this means the supply region will generally increase unless crop productivity and yields can be increased to compensate for the added supply needs. Transportation costs, therefore, increase, but not generally in direct proportion to the facility size. These competing effects lead to a system size at which either total cost of production is minimized (**Figure 11**) or profit is maximized depending on the objective function. For example, economies of scale in the capital and operating costs of facilities to generate electricity (power plants) from biomass coupled with increasing costs of feedstock acquisition yield a minimum in the levelized (amortized) cost of energy from the plant (**Figure 11**). The scaling in capital and operating cost may take a functional form such as

$$\frac{C}{C_o} = \left(\frac{M}{M_o}\right)^s \quad [3]$$

where C is the cost; M is the facility size or capacity; the subscript denotes a reference facility of known cost and size; and s is the scaling factor that specifies how cost varies with size. The optimum size is sensitive to the scaling relationship and the value of s. The two cases of **Figure 11** were derived for s is constant for all sizes and s is variable and increasing with size to account for increasing risk as the facility size becomes very

Table 4 Proximate and elemental compositions and heating values of selected biomass materials (Jenkins *et al.*, 1998), Composition of selected biomass materials (Jenkins *et al.*, 1998)

Type	*Alfalfa straw*	*Rice straw*	*Wheat straw*	*Miscanthus*	*Switch grass*	*Jose tall wheat grass*	*Hybrid poplar*	*Willow*	*Water hyacinth*	*Nonrecyclable waste paper*	*Sugarcane bagasse*	*Municipal digester sludge (class B biosolids)*
Typical harvest moisture (% wet basis)												
	14	14	10	14	14	10	45	45	85	6	50	75
Proximate composition (% dry matter)												
Ash	4.88	18.67	14.48	4.90	6.53	12.34	1.6	0.95	22.40	8.21	3.61	37.91
Organic fraction	95.12	81.33	85.52	95.10	93.47	87.66	98.40	99.05	77.60	91.79	96.39	62.09
Volatiles	76.48	65.47	69.94	78.20	77.03	72.18	86.14	85.23		82.50	84.51	53.68
Fixed carbon	18.64	15.86	15.58	16.90	16.44	15.48	12.26	13.82		9.29	11.88	8.41
Higher heating value (MJ kg^{-1})												
Moisture free (dry)	18.16	15.09	16.33	18.05	18.90	17.86	18.93	19.38	16.02	21.52	18.50	15.38
Moisture and ash free	19.09	18.55	19.09	18.98	20.22	20.38	19.24	19.56	20.64	23.44	19.19	24.77
Wet	15.62	12.97	14.69	15.52	16.26	16.08	10.41	10.66	2.40	20.22	9.25	3.85
Structural composition (% dry matter)[a]												
Cellulose	29	34	40	45			41	49	16		36	
Hemicellulose	12	28	29	30			33	28	56		30	
Lignin		9	14	21			26	22	6		19	
Ultimate elemental composition (% moisture and ash free)												
Carbon	48.40	47.02	48.08	53.31	50.69	52.86	51.65	49.56	52.96	53.66	49.99	58.29
Hydrogen	6.15	6.39	6.08	4.63	6.08	5.05	5.99	5.95	6.82	7.60	5.86	7.18
Oxygen (by difference)	43.05	44.77	43.99	41.59	42.57	39.59	41.75	44.11	37.16	38.18	43.94	24.17
Nitrogen	1.19	1.07	1.19	0.21	0.60	2.00	0.60	0.35	2.53	0.38	0.15	9.08
Sulfur	0.19	0.22	0.28	0.11	0.06	0.37	0.02	0.03	0.53	0.22	0.08	1.72
Chlorine	1.17	0.71	0.71	0.21	0.10	2.21		0.01		0.04		0.16
Ash analysis (% ash)												
SiO_2	7.04	74.67	54.64	70.60	66.53	46.71	1.17	8.08		19.44	41.87	47.11
Al_2O_3	1.12	1.04	5.73	1.10	6.98	3.09	0.41	1.39		63.97	22.25	17.9
TiO_2	0.05	0.09	0.23	0.06	0.34	0.09	0.21	0.06		3.81	3.87	1.22
Fe_2O_3	0.41	0.85	6.16	1.00	3.56	1.00	0.76	0.84		0.42	20.90	5.64
CaO	21.37	3.01	5.02	7.50	7.14	4.59	59.16	45.62		8.37	3.50	8.65
MgO	5.83	1.75	2.45	2.50	3.17	2.03	5.76	1.16		1.68	1.45	2.98
Na_2O	11.2	0.96	2.16	0.17	1.03	8.60	0.31	2.47		0.83	0.26	1.33
K_2O	22.9	12.3	14.09	12.80	7.00	15.68	26.76	13.2		0.23	2.59	1.32
P_2O_5	6.32	1.41	2.43	2.00	2.80	2.70	0.20	10.04		0.10	1.13	14.65
SO_3	4.27	1.24	3.03	1.70	2.00	2.05	5.26	1.15		1.14	0.90	1.38
Cl						13.43						0.01
CO_2						0.05						0.21

[a]Structural data representative only and not necessarily from same sample used for elemental analysis and heating value.

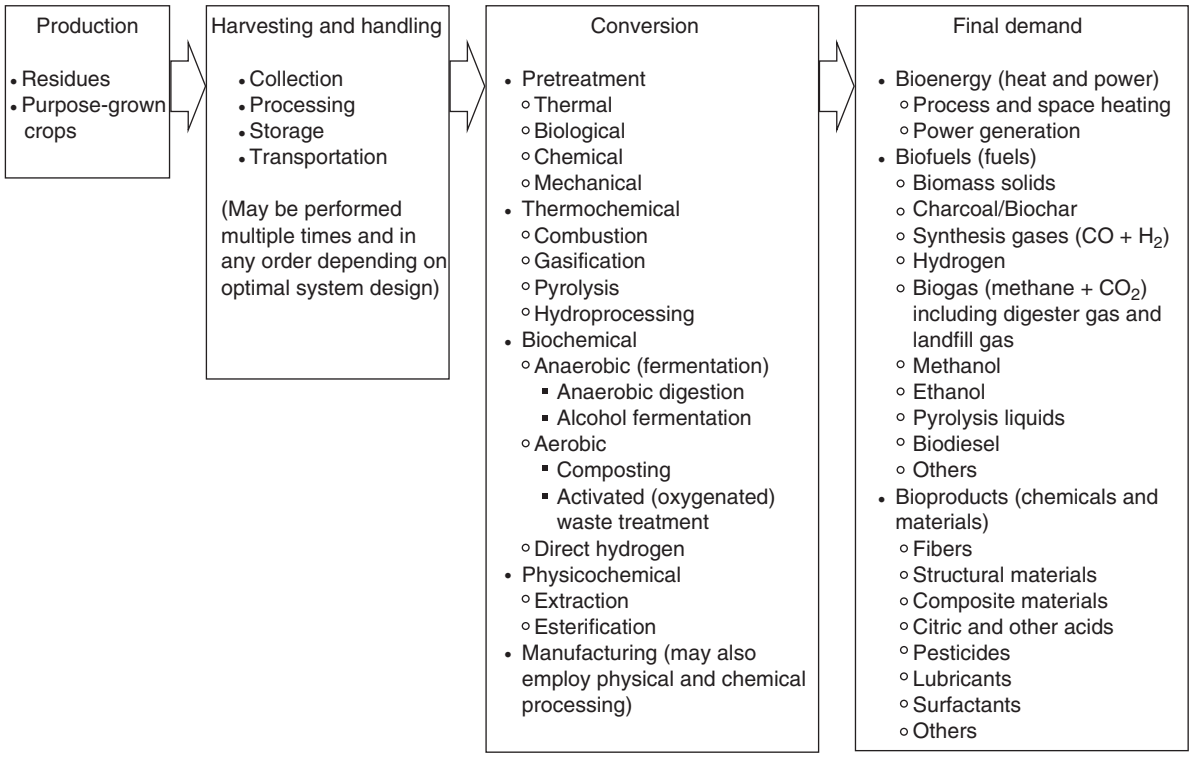


Figure 10 Supply-chain processes for biomass to energy and products.

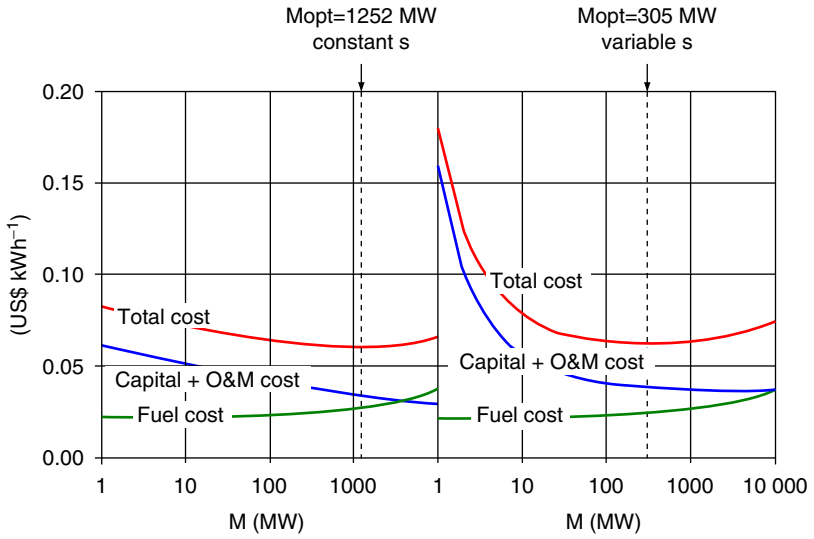


Figure 11 Economy of scale and capacity optimization in biomass conversion (Jenkins, 1997).

large. The cost–size dependence for regionally distributed feedstock typically follows a different relationship, contributing an increasing cost per unit of production as the facility scale increases (Figure 11) (Jenkins, 1997). The estimated cost of power generation is plotted in Figure 11 against the facility size on a logarithmic scale, which masks to some degree the broad range around the optimum in which cost does not vary substantially, a characteristic of larger size facilities. The optimal sizes in both examples are quite large for biomass power generators and few facilities approach these sizes in practice. To some extent, this is due to regulations that also affect facility siting and permitting. In California and the US, for example, new facilities must undergo a siting review when the size exceeds 50 or 80 MW electrical capacity and this adds to the cost of facility development (Jenkins, 1997).

Consideration of the feedstock properties and availability, the regional product markets, and the costs and prices associated with production and sales are important to the size,

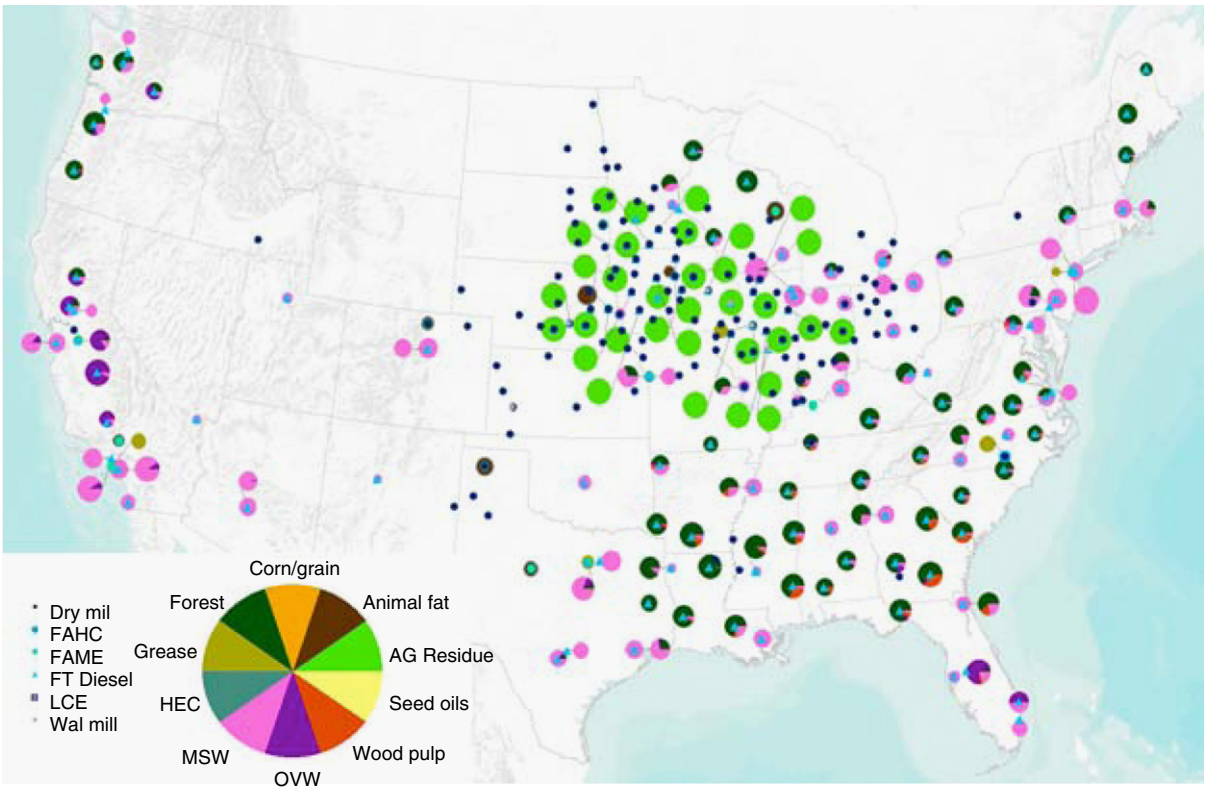


Figure 12 Optimized potential biorefinery locations in the US identified through geospatial modeling of biomass resources, supply infrastructure, and fuel demand (Parker, 2011).

type, and location of conversion or production facilities. Geospatial modeling using resource location data to give the spatial distribution of feedstock coupled with technoeconomic models of conversion facilities and distribution models of finished product have been used, for example, to project policy outcomes for biorefinery development in the US and to speculate on the optimized structure of the future industry (**Figure 12**) (Parker *et al.*, 2010; Tittmann *et al.*, 2010; Parker, 2011).

Chemicals and Materials from Biomass

Products from biomass originate both from direct use or extraction of materials from the parent tissues and via conversion of the biomass to alternate forms. In related bioprocessing, the biomass can serve as a substrate by which the cellular mechanisms are used by another organism to express the desired product, for example, the transient expression of a protein through the process of agroinfiltration (Joh and Vander-Gheynst, 2006).

The potential to produce a much larger range of chemicals, materials, and other products from biomass has been widely recognized, including direct replacement of products now synthesized from petroleum, natural gas, and other nonrenewable resources (Johnson, 2007). Biobased plastics, lubricants, solvents, surfactants, composites, and other products are increasing in market shares as technology improves, new markets are developed, and demand increases for more sustainable or 'green' products (BIOCHEM, 2010). Global production of bioplastics is projected to increase five-fold by 2016 to close to 6 million metric tons compared with the production in 2011, although in this case demand for biodegradable plastics does not appear to be the major driver of growth as only 13% of the total is anticipated to be in polymers of this type (European Bioplastics, 2013). Biobased polyethylene terephthalate (PET) is likely to make up the largest fraction (greater than 40%) of the total. Other drivers, such as displacement of petroleum and reduced greenhouse gas emissions, plus economic and market factors account for the increasing demand of biologically derived materials. For example, in the making of riboflavin (vitamin B2), single-step instead of six-step processing, increased productivity, and reduction in cost are quoted as the main forces in the adoption of a biobased process (Johnson, 2007). Similar rationale exists for the production of antibiotics and acrylamide monomers (Johnson, 2007; Scott *et al.*, 2007). Improved processes and efficiencies in the manufacturing of biobased intermediates and final products are the subject of substantial research, such as the use of biomass-derived furans in the catalytic production of *p*-xylene that is, in turn, used to make terephthalic acid, a monomer for PET (polyester) plastics (Williams *et al.*, 2012), or the conversion of biomass-derived carbohydrates to chemical feedstocks, such as alkenes and aromatics, that are now principally produced from petroleum (Arceo *et al.*, 2009; Arceo *et al.*, 2010).

Agriculture and forestry have long supplied materials other than food and feed for construction, pulp and paper, textiles,

medicine, cosmetics, soaps, and other uses, and the production of materials such as plastics from biomass is not new, although many new and novel chemicals are now becoming available. Crude plastics were historically made from natural proteins, such as those from blood, egg, and milk. Goodyear's vulcanization of natural rubber beginning in 1838 provided a pathway to thermoset materials (Richardson, 2010). Shellac was produced by dissolving the natural resin secreted by the lac bug in ethanol (Patel *et al.*, 2013). The conversion of cellulose to nitrocellulose by the addition of nitric acid was discovered in 1846 and used for the preparation of guncotton, and nitrocellulose modified by camphor as a plasticizer was being used by 1889 for photographic film by Eastman Kodak (Michel, 2006; PHS, 2013a). Nitrocellulose is now applied in such diverse uses as membranes for protein immobilization and analysis and solid-rocket motors. The compound (as celluloid) was also famously used in the attempted replacement of natural ivory for billiard balls but the balls had a tendency to explode on impact. Cellulose acetate, the acetate ester of cellulose, was first prepared in 1865 and is still widely used for plastic films and other applications (PHS, 2013b). Viscose, a polymer of wood pulp, was patented in 1892 and the process for making cellophane, a viscose plastic film produced by dissolving cellulose in alkali and carbon disulfide was established by 1913 (PHS, 2013c). Despite the pollution issues associated with disulfide in the manufacturing process, cellophane is biodegradable and has remained in continuous production since the 1930s especially for food packaging (Rojo *et al.*, 2010; PHS, 2013c). Rayon fiber used in textiles is made through a similar process.

Comprehensive studies have examined candidate materials from sugars, synthesis gases (syngas), and lignin, all derived from biomass (Werpy and Petersen, 2004; Holladay *et al.*, 2007). The study by Werpy and Petersen (2004) identified an initial set of 300 possible building-block chemicals from sugars and syngas in integrated biorefineries. Such biorefineries conceptually involve various processing operations within the same production facility (**Figure 13**) for the manufacturing of multiple value-added products, similar to but potentially more complex than modern petroleum refineries that produce a variety of commodity chemicals and fuels (Johnson, 2007). Screening criteria for the chemical selection included feedstock cost, estimated processing costs, market information, and compatibility with current and projected future refining operations. From this initial set, a foundational suite of chemicals was selected based on more strategic criteria (direct product replacement, novel products, and building-block intermediates) and the value chains associated with processing to products for final demand (**Figure 14**). The resulting network of product interactions has been widely referenced in relation to potential biorefinery design and opportunities for products from biomass. The final suite includes compounds with carbon numbers (number of carbon atoms in the molecule) ranging from C1 to C6 (**Table 5**). These compounds have multiple functionality for further downstream conversion and could be produced from both lignocellulose and starch in making sugars or syngas as intermediate chemical platforms, some of the principal platforms under development for energy and products from biomass. The study by Holladay *et al.* (2007) later identified other products from lignin using the criteria based on technical difficulty in production, market potential, market risk, building-block utility, and whether the product could be made as a single compound or would be present in a mixture with other compounds (**Table 5**).

As illustrated in **Figure 14**, a wide spectrum of products can be produced from biomass to serve multiple markets in what is loosely classified a biobased economy. These products can range from higher value, generally lower production and sales volume chemicals such as pharmaceuticals, food additives, and cosmetics, to lower value, higher volume chemicals and materials such as biobased plastics and composites, chemical feedstocks, fuels, and environmental products such as biochar or black carbon now being investigated for its agronomic

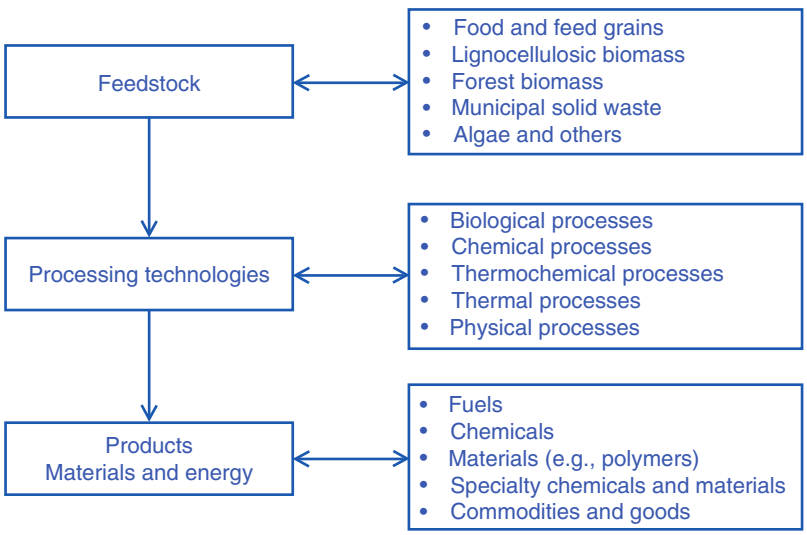


Figure 13 Basic integrated biorefinery concept. Adapted from Johnson, F.X., 2007. Industrial Biotechnology and Biomass Utilization, Prospects and Challenges for the Developing World. Vienna: Stockholm Environment Institute and United Nations Industrial Development Organization.

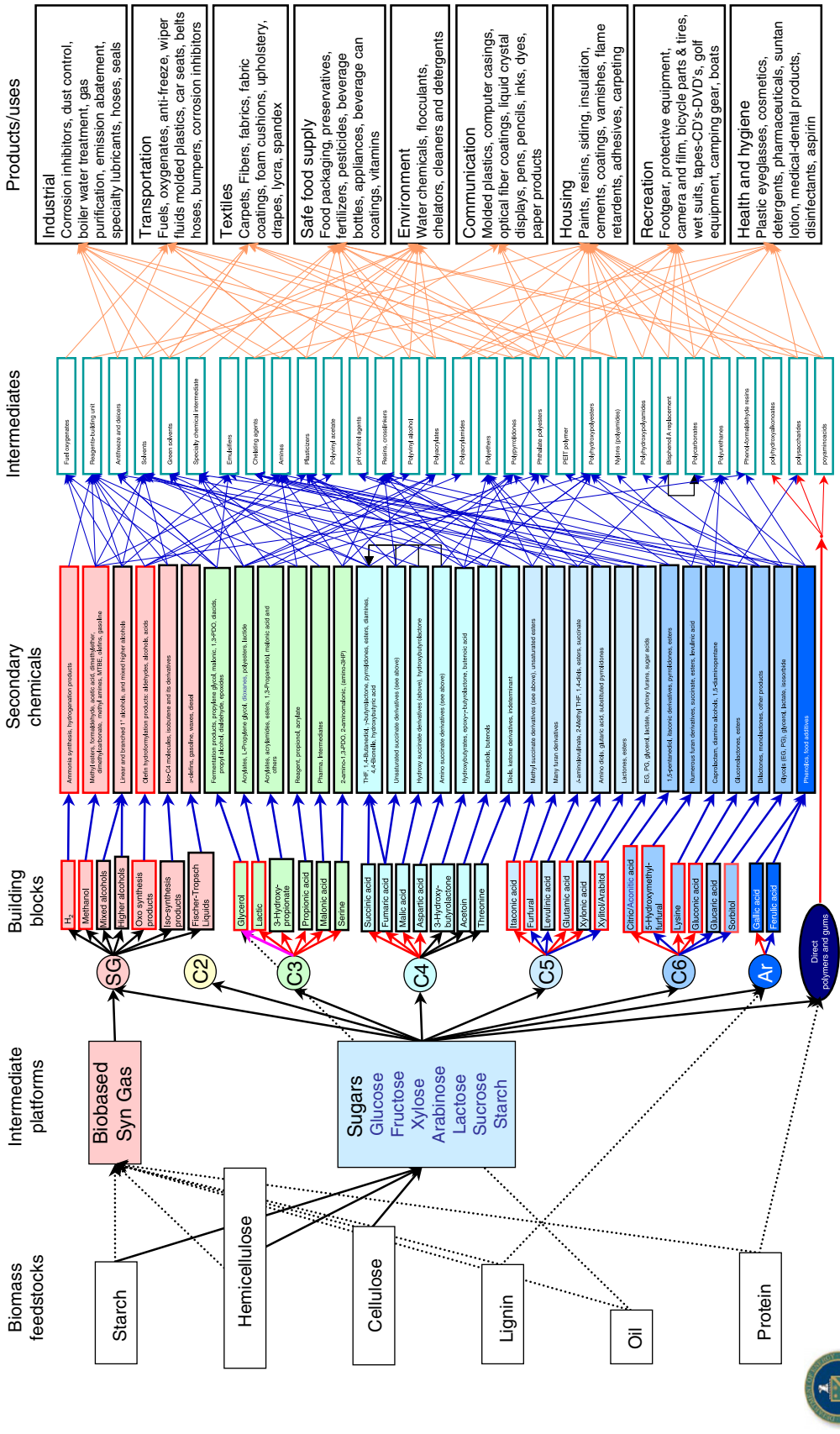


Figure 14 Chemical platforms for biobased products from biomass feedstocks (Werpy and Petersen, 2004).

Table 5 Building-block chemicals and products from sugars, syngas, and lignin (Werpy and Petersen, 2004; Holladay *et al.*, 2007)

Source	*Chemical*
Sugars/ syngas	C1: Carbon monoxide (CO) and hydrogen (H_2) (syngas) C3: Glycerol, 3 hydroxypropionic acid, lactic acid, malonic acid, propionic acid, and serine C4: Acetoin, aspartic-acid, fumaric acid, 3-hydroxbutyrolactone, malic-acid, succinic acid, and threonine C5: Arbinitol, furfural, glutamic acid, itaconic acid, levulinic acid, proline, xylitol, and xylonic acid C6: Aconitic acid, citric acid, 2,5 furan dicarboxylic acid, glucaric acid, lysine, levoglucosan, and sorbitol
Lignin	Process heat and power, syngas, methanol, dimethyl ether (DME), ethanol, mixed alcohols, hydrocarbons (Fischer–Tropsch liquids), C1 – C7 hydrocarbon or oxygenates, alkylates (benzene, toluene, xylene, and higher), cyclohexane, styrenes, biphenyls, phenol, substituted phenols, catchols, cresols resorcinols, eugenol, syringols, coniferols, guaiacols, vanillin, vanilic acid, DMSO, aromatic acids, aliphatic acids, syringaldhyde and aldehydes, quinones, cyclohexanol/al, beta-keto-adipate, carbon fiber, polyelectrolites, polymer alloys, fillers, polymer extenders, substituted lignins (carbonylated, ethoxylated, carboxylated, epoxidized, and esterified), thermoset resins, composites, formaldehyde-free adhesives and binders, wood preservatives, nutraceuticals and drugs, and mixed aromatic polyols

utility in soils and as a means to sequester carbon (BIOCHEM, 2010; Keiluweit *et al.*, 2010; Woolf *et al.*, 2010).

Biobased plastics (bioplastics) constitute the class of manufactured plastics that are either entirely or partially composed of biologically derived materials, that is, biomass. Plastics certified as compostable frequently contain a high proportion of biobased materials but not all biobased polymers are biodegradable (BIOCHEM, 2010). Current bioplastics include the bulk materials polylactic acid (PLA), polyamides (nylon), polyhydroxyalkanoates, polybutyleneterephthalate and PET and polyethylene from among a larger number of thermoplastics, and polyurethane from among the thermosetting materials. These are typically prepared from sugars and starches or from processing residues (e.g., lignin). PLA is principally made from plant sugars polymerized through a process of fermentation. Corn is a major source. Biobased succinic acid, a precursor to various bioplastics, can be produced from glucose and sucrose sugars and is a replacement for petroleum-based adipic acid (Chimirri *et al.*, 2010; Liang *et al.*, 2013).

Composite materials are standard products of the wood industry (e.g., particleboard) but a wider variety of biomass feedstocks are now being investigated for their application in this market, including woody and herbaceous biomass such as *Eucalyptus*, Athel (*Tamarix* aphylla), and Jose tall wheatgrass (*A.* elongatum) used also in phytoremediation of salt-affected soils (Pan *et al.*, 2007; Zheng *et al.*, 2006, 2007a). Particleboards made from saline wood generally had equal or better mechanical qualities compared with boards made from more conventional nonsaline wood materials (Zheng *et al.*, 2006, 2007a).

Nanomaterials from biomass are also being investigated for a wide variety of applications. Low-cost carbon fiber production has been the subject of much interest especially in the wake of recent legislation to increase vehicle fuel economy standards in the US that add motivation to finding new lightweight materials with good strength and from sustainable sources. Toward this purpose, lignin has been investigated for its use in producing carbon fiber but is required to be of high purity with a narrow molecular weight distribution, and greater research is needed in the refining of this potential feedstock (Baker and Rials, 2013). Carbon nanofibers, nanotubes, graphenes, and other materials have also been investigated for use in energy storage devices, particularly ultra- and supercapacitors. Carbon nanosheets for use in high energy density supercapacitors have been made from hemp bast fibers, yielding a maximum energy density of 12 Wh kg^{-1} and 8–10 Wh kg^{-1} after charge times of less than 6 s, comparable to or greater than the conventional activated carbons (Wang *et al.*, 2013b). The multilayered structure of the feedstock biomass in this case provides a unique starting morphology for producing the carbon sheets.

Biobased lubricants and solvents are similarly classified as being comprised entirely or in part from biomass. Biobased lubricants predate petroleum-based compounds and are either vegetable oil-based or manufactured from modified oils including synthetic esters made from mineral oil-based products (BIOCHEM, 2010). Finished products can be biodegradable with improved environmental properties and lower toxicity allowing use in more sensitive environments. Canola and a number of other vegetable oils have been investigated as feedstocks in the production of more environmentally benign motor oils for engines (Johnson *et al.*, 2002). Solvents are used in many different applications, such as additives in paints, degreasing agents, pharmaceutical extractions, stripping agents, and cleaners. A key property of some biobased solvents is their low emission of volatile organic compounds that are both direct health hazards and contribute to reduced air quality, for example, in reactions with oxides of nitrogen or NO_x in the formation of tropospheric ozone, a breathing hazard and regulated air pollutant (U.S. EPA, 2013). The fatty acid methyl ester of soy oil made from soybeans, in addition to its use as biodiesel, is also a biosolvent, as are lactate esters, limonene, and other citrus terpenes. Although limonene (as D-, L-, and DL-limonene), for example, is listed as a generally recognized as safe synthetic flavoring substance by the US Food and Drug Administration (CFR, 2006), and high-purity products may generally prove of low allergenic properties, oxidized products (such as obtained by exposing to air for prolonged periods) have been shown to produce sensitivity in animals (Karlberg *et al.*, 1991) and safety properties need to be carefully considered in application.

Plant oils are also used in the production of surfactants – chemicals that lower the surface tension of liquids to allow better mixing. By definition, biosurfactants have at least one of the hydrophobic or hydrophilic groups associated with the surfactant molecule from a biobased source and so can also be either entirely or partially derived from biomass.

Feedstocks include palm oil, sorbitol, sucrose, glucose, and animal fats such as tallow. Surfactants are common ingredients in detergents but are used in a wide range of other products including agricultural chemicals, textiles, paints, and lubricants (BIOCHEM, 2010), and nonionic surfactants have been employed in the enzymatic hydrolysis of biomass as pretreatment for fermentation and biofuel production (Zheng *et al.*, 2007b).

Biochar or black carbon from biomass has received much attention in recent years for its perceived utility in maintaining soil carbon stocks and soil fertility. Although carbon produced from biomass in various stages of activation has long served for water treatment and environmental remediation, the discovery of the *terra preta do índio* soils in the Amazon stimulated new research related to understanding the properties of carbons for soil applications including chars produced in conjunction with energy conversion, especially biomass pyrolysis but also thermal gasification. The potential new market in biocarbons is fortuitous also for thermochemical energy conversion systems where char coproducts have in the past posed a disposal problem given the limited capacity of the activated carbon markets. The terra preta soils, which originate from pre-Columbian times and accumulated charcoal, bone, and manure as part of kitchen middens from food preparation and other activities, have been shown to have lower greenhouse gas emissions (as CO_2) per unit of carbon in the soil compared with similar soils with low or no black carbon (Liang *et al.*, 2010). In a study of black carbon from 12 different biomass feedstocks including hardwoods, softwoods, algal digestate, walnut shell, and turkey litter, char surface area, an important measure of sorptive properties, increased with charring temperature whereas chemical functionality could be separated into wood and nonwood feedstock groups (Mukome *et al.*, 2013). The presence of carbonate and chloride salts increased the basicity of chars from nonwood feedstock. Agronomic properties and impacts can be related to feedstock composition (Mukome *et al.*, 2013). Biochar applications to soils may also reduce the overall lifecycle greenhouse gas emissions for bioenergy systems (Gaunt and Lehmann, 2008).

Energy and materials from biomass frequently compete for common resources, hence in addition to lifecycle environmental concerns, debate also arises over the highest and the best use of biomass. Policies favoring one use over another can introduce economic distortions, as in the food-versus-fuel debate where both sectors may receive government incentives or subsidies but without substantial coordination aimed at improving the overall sustainability. Given the limited supplies of biomass, the potential to extract multiple products through integrated biorefining (cascading the biomass use) has been suggested as a way to maximize the value of the resource (Keegan *et al.*, 2013). Such practice already exists in both the forestry and agriculture sectors, for example, in pulp and paper manufacturing and sugar milling in which high-value materials are extracted before processing residues (e.g., lignin from wood or bagasse from sugarcane) are utilized for energy conversion. As energy values increase, however, economic distinctions tend to disappear in many cases, shifting focus onto other performance metrics as indicators of social good. Greenhouse gas emissions may be reduced through the production of biomaterials, many of which can sequester renewable carbon over long periods of time in addition to displacing fossil emissions from petroleum or other nonrenewable resources. Significant opportunities exist to improve material flows through the society to meet both material and energy needs. Just as integrated technologies may improve the economic benefits for energy and materials from biomass, policies that address system-level resource management effects may realize a greater social benefit. Uncertainties remain in the assessment of net benefits for both materials and energy conversion from agricultural feedstocks and distinct needs exist for improved information.

Energy from Biomass

The potential for biomass to supply much larger amounts of useful energy has stimulated substantial research and development into systems to convert biomass into the principal forms of heat, electricity, and solid, liquid, and gaseous fuels (Bungay, 1981; Hall and Overend, 1987; Kitani and Hall, 1989; Klass, 1998; Brown, 2003). Although substantial debate continues over the sustainability of large-scale bioenergy development, so do advances continue across a wide range of conversion technologies and systems to improve the overall efficiencies and fuel yields, fuel properties, lifecycle costs, and environmental performance.

Three principal routes exist for converting biomass to energy: (1) thermochemical, (2) biochemical, and (3) physicochemical. In practice, combinations of two or more of these routes may be used in the generation of the final product or products. Chemical or biological catalysts are employed in many cases. Thermochemical conversion includes combustion, thermal gasification, and pyrolysis along with a number of variants involving microwave, plasma arc, supercritical fluid, hydrothermal, and other processing techniques (Brown, 2011). Products include heat, fuel gases, liquids, and solids. Thermochemical techniques tend to be of high rate and relatively nonselective for individual biomass components in that the chemically complex biomass is substantially degraded into simple compounds (e.g., CO, CO_2, H_2, and H_2O), which may later be reassembled into more complex compounds through either chemical or biological processing (Chum and Baizer, 1985). Biochemical conversion includes fermentation to produce alcohols (ethanol being perhaps the best known), fuel gases (such as methane by anaerobic digestion), acids, and other chemicals (Klass, 1998). Among the physicochemical methods are alkaline and acid processes, esterification, mechanical milling, steam and ammonia freeze explosion and other explosive decompression processes, and pressing and extrusion, many times in combination with a biochemical or thermochemical reaction process. One major process under this category is vegetable oil extraction and esterification to manufacture biodiesel as a substitute for engine fuel. Biochemical and physicochemical processes in general are intended to be more selective for biomass components and higher value products, although thermochemical routes can also be used, as in the indirect production of methanol via thermal gasification (Hos and Groeneveld, 1987). There are other means of producing useful energy from biomass, such as biophotolysis for the production of hydrogen by plants

(Bungay, 1981), and other direct hydrogen routes (Cortright *et al.*, 2002), but these are not yet demonstrated on a commercial scale. Ethanol is already produced on a large scale as a biofuel, mostly for light-duty automotive use including as an oxygenate blendstock for motor gasoline as well as in higher concentrations for flexible fuel (FlexFuel) and neat (100%) fuel vehicles. Hydrocarbon liquids from biomass are of particular interest due to their similarity to current gasoline, diesel, and aviation fuels and their fungibility in existing fuel transportation and distribution systems such as pipelines. These and other so-called drop-in biofuels avoid the need for new infrastructure or the use of more expensive truck transport for large-scale application.

Thermochemical routes generally involve the heating and thermal decomposition of feedstock biomass to compounds that can either be directly used or reacted to produce other and potentially more valuable chemicals and fuels. Gasification and pyrolysis are thermochemical approaches that involve thermolysis of the feedstock to intermediate gases (e.g., CO and H_2 as synthesis gas or syngas) and liquids (e.g., biocrude) that can be burned directly, chemically synthesized into drop-in liquid fuels along with a wide variety of other fuels including methane, hydrogen, methanol, and dimethylether, or fermented biochemically to alcohols. These thermal processes can also produce biochar (see the discussion on materials from biomass above). Torrefaction is a light pyrolysis that typically is carried out as a pretreatment at temperatures between approximately 200 and 300 °C to produce a carbonized feedstock or biochar with improved grindability, densification, and other handling characteristics. Biochar production can add coproduct value to gasification, pyrolysis, and other thermochemical conversion processes although there remain many uncertainties regarding its value for these purposes. Intermediates such as biocrude produced through pyrolysis and lipids extracted from algae or oil seeds (vegetable oils) can be hydrotreated through the addition of hydrogen for upgrading to renewable diesels and other hydrocarbons. Combustion of the feedstock generates heat which can then be used in the generation of electricity or process steam and hot water, and is historically the largest energy use of biomass.

Biochemical routes, predominantly fermentation, rely principally on microbes (yeasts, bacteria, or fungi) for the conversion to useful fuels and chemicals. In most instances, hydrolysis of structural polymers (starch, hemicellulose, and cellulose, see above) through enzymatic or chemical means, possibly in combination with thermal or mechanical pretreatment, is necessary to generate the sugars or other simpler compounds upon which the microbes feed. Starch and sugar fermentation by yeast is well known and has long been used in making beverage alcohol (ethanol) and is currently used in producing most of the world's fuel alcohol from corn (maize) and sugarcane. The use of lignocellulosic biomass is less well developed and the subject of much research directed at improving hydrolysis, particularly enzymatic hydrolysis, of both the hemicellulose and cellulose fractions and simultaneous cofermentation of the resulting five and six-carbon sugars for which recombinant organisms have also been developed to work in association with or in place of yeast. Lignin is mostly recalcitrant to biological conversion and is often considered for use as boiler fuel in making process heat or steam (such as that used in distilling the alcohol) and electricity for the biorefinery but higher economic value may reside in fuel products if effective conversion techniques can be developed, for example, gasification to syngas for subsequent catalytic conversion to substitute natural gas or liquid fuels. Anaerobic digestion is another type of fermentation that typically uses mixed populations of bacteria to digest biomass to make biogas, a multicomponent gas consisting mostly of methane (CH_4, the major component of natural gas) and CO_2 with other more minor species including hydrogen sulfide (H_2S). Sulfide removal is typically needed before the use of biogas in engines especially those employing catalytic aftertreatment of combustion products for control of oxides of nitrogen (NO_x) and other air pollutants. Anaerobic digestion is commonly used in waste water treatment facilities and is becoming more common for managing animal wastes in concentrated animal feeding operations such as dairies and hog and poultry farms. Biogas is used as engine and boiler fuel, sometimes in combined heat and power (CHP) operations, such as for cheese making at the dairy. Biogas can be upgraded to pipeline quality methane to complement natural gas or for use as vehicle fuel as compressed natural gas (CNG) or liquefied natural gas (LNG), and can serve as chemical feedstock. Biogas has also been used in microturbines and for fuel cells for distributed power applications. Landfill gas is a biogas that is produced by the anaerobic decomposition of organics in solid waste landfills and is recovered for electricity generation and other energy purposes and to reduce hazardous migration of the gas into nearby structures.

Physicochemical processes are used in the making of biodiesel, a product of the catalyzed reaction between an oil, such as the vegetable oil, and an alcohol, such as methanol or ethanol, all of which can be produced from biomass. In the conventional biodiesel process, triacylglycerides that make up vegetable oils and other FOG are converted by transesterification into long-chain esters and coproduct glycerol. The esters (biodiesel) have lower viscosity than the original vegetable oil and have better injection and spray properties for use in diesel engines. Biodiesel can also be produced using enzymatic techniques. Coproduct markets for glycerol exist in soaps, cosmetics, and many other products but the potentially large production of fuel could saturate these markets so that additional uses are being investigated, including production of other fuels.

Industrial facilities to produce fuels and chemicals from biomass are typically classified as biorefineries. Integrated biorefineries can include multiple processing operations in making a suite of products from the same production facility, similar to modern petroleum refineries (**Figure 15**). Biofuels are often classified as first generation, second generation, and beyond, the terms intended to convey the development status and to some extent the perceived sustainability of the production systems although there are not always clear distinctions. First-generation biofuels include ethanol from starch and sugar as well as biodiesel, both mostly from food crops, but may also include biogas, syngas, and pyrolytic biooil. Second-generation biofuels include ethanol, hydrocarbons, and other fuels produced from lignocellulosic and algal feedstocks. Later generations are associated with more advanced

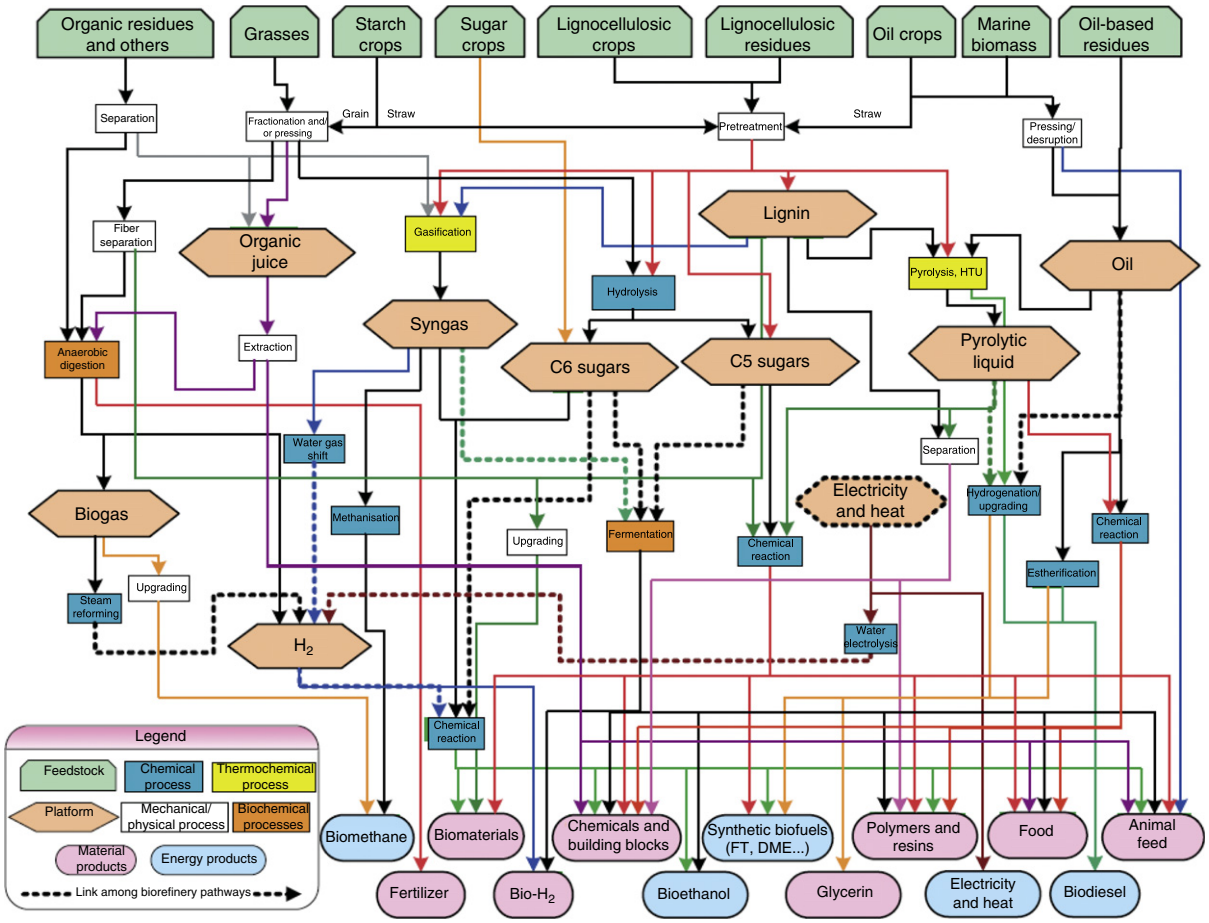


Figure 15 Partial classification system for biorefining options (Cherubini *et al.*, 2009).

production and processing and improved lifecycle performance. Third-generation biofuels are based on feedstocks modified to improve processing, such as reduced lignin or increased oil content. Fourth-generation technologies involve both improved feedstocks and improved processing and conversion techniques, including genetically modified microorganisms, that result in net negative carbon impacts as an outcome of the biofuel production system (Lu *et al.*, 2011).

The conversion strategies are integrally coupled to the properties of the biomass. Moisture has often been used as a discriminating parameter in the selection between thermochemical and biochemical processes, although by itself this is not usually sufficient. In many cases, the properties of the biomass necessary for engineering design have not been properly characterized before commercial implementation of a technology. Operation of combustion-type power-generating stations intended to burn certain types of agricultural residues (in particular cereal straws and other herbaceous biomass) has been hindered by fouling of boiler heat transfer surfaces from the inorganic compounds in the biomass (Turnbull, 1991; Wiltsee, 2000; Jenkins *et al.*, 1998, 2011), a phenomenon that was largely overlooked in the design phase of many facilities, but is well known for coal (Baxter, 1992). Effective biomass energy development demands a continuing program in resource and technology development.

Thermochemical Conversion

Combustion

Historically, and still so today, the most widely applied energy conversion method for biomass is combustion. The chemical energy of the fuel is converted into heat energy. Heat can be used directly and also transformed by heat engines of all sorts into mechanical and electrical energy. Theoretically, biomass could be directly converted into electricity by magnetohydrodynamic power generation in the same way coal might be, but the technology is still mostly speculative (Rosa, 1961; Mikheev *et al.*, 2006). Burning of wood and agricultural materials in open fires and simple stoves for cooking and space heating is common around the world and a vital source of heat, although less desirable than advanced conversion techniques from the perspective of atmospheric pollution and undue health impacts from incomplete combustion (Jenkins *et al.*, 2011). Electricity generation using biomass fuels has received considerable attention in recent years, although sugarcane bagasse has long been used as fuel for electricity generation at sugar mills and is now an integral component of biofuel production from sugarcane with surplus power exported for distribution. Wood also has been widely used for cogeneration of heat and electricity in sawmills, with heat and steam generation being the primary function for kiln drying of lumber.

A large independent power-generation industry in the US developed in response to incentives provided directly and indirectly by federal legislation, with approximately 10 GW_e of electrical-generating capacity from biomass currently operating in the United States alone (EIA, 2013b). CHP facilities using wood, straw, and municipal solid wastes are operating in Europe and elsewhere for electricity generation and district heating (COGEN Europe, 2011). Additional incentives exist in the form of renewable portfolio standards (RPS) such as that in California that now calls for a third of retail electricity sales to come from renewable resources by the year 2020. Total installed capacity in biomass power generation around the world is approaching 50 000 MW_e including large-scale solid fuel combustion as well as small-scale digester and landfill gas applications (IEA, 2007). In many regions of the world, Asia being an exception, biomass utilization is below the sustainable resource capacity and potential exists to increase uses for fuels, heat, and power (Parikka, 2004).

Viewed simply, the complete combustion of biomass in air transforms the organic fraction into carbon dioxide and water:

$$C_xH_yO_z + n_1H_2O + n_2(1+e)(O_2 + 3.76N_2) = n_3CO_2 + n_4H_2O + n_5N_2 + n_6O_2 \quad [4]$$

where the stoichiometric coefficients n depend on the concentrations of carbon, hydrogen, and oxygen in the original feedstock (here expressed on a moisture-free, ash-free basis), and on the amount of excess oxygen, e, added to the reaction. Feedstock moisture is accounted for in the reaction by the coefficient n_1, and air is approximated in the normal engineering fashion as consisting of 21% by volume oxygen and 79% equivalent nitrogen.

A more sophisticated global combustion reaction for biomass that better accounts for the range of species present is represented by the mass balance of eqn [5] in which the mass coefficients $m_{r,i}$ designate the masses of the reactant species and $m_{p,j}$ designate the product species. In this case, the biomass is divided into three fractions: an organic phase, a moisture phase, and an ash phase. The feedstock elemental mass fractions described by the coefficients γ_i arise from the analysis of the dry feedstock for C, H, O, N, S, and Cl. Moisture in biomass is represented by a separate water fraction (free and bound moisture). The oxidation medium, air, for example, is considered to consist of O_2, CO_2, H_2O, and N_2, all in the gas phase. The reaction is represented as resulting in eleven main gas phase products and a residual mass containing ash and unreacted portions of the other element masses from the biomass. The residual can consist of solids such as particulate matter, carbon in ash as charcoal or carbonates, and chlorides and sulfates in furnace deposits. Equation [5] is reasonably general in that it can equally be used to describe the combustion of other fuels such as (bio)methane, biodiesel, Fischer–Tropsch liquids, and other hydrocarbons, biooils from pyrolysis, and many others:

$$m_{r,1}\left(\sum_i \gamma_i \middle| C,H,O,N,S,Cl,ash\right) + m_{r,2}H_2O(l) + \ldots + m_{r,3}O_2 + m_{r,4}CO_2 + m_{r,5}H_2O(g) + m_{r,6}N_2 = \ldots = m_{p,1}CH_4 + m_{p,2}CO + m_{p,3}CO_2 + m_{p,4}H_2 + m_{p,5}H_2O + m_{p,6}HCl + \ldots \quad \ldots + m_{p,7}N_2 + m_{p,8}NO + m_{p,9}NO_2 + m_{p,10}O_2 + m_{p,11}SO_2 + m_{residual} \quad [5]$$

In addition to the product composition, eqn [5] allows for the estimation of other properties of the reaction, such as the flame temperature under different burning conditions, an important parameter for estimating heat transfer, efficiency, and thermal performance.

Equation [5] also specifies the oxidant-to-fuel ratio, or in the case of air as the source of oxygen, the air–fuel ratio, along with the equivalence ratios often used to specify combustion conditions. The air–fuel ratio, AF, defines the mass of air added relative to the mass of feedstock, expressed on either a wet or dry basis. The stoichiometric value, AF_s, defines the special case in which only the amount of air theoretically needed to completely burn the feedstock is added to the reaction. The air–fuel ratio, the fuel–air equivalence ratio, ϕ, the air–fuel equivalence ratio or air-factor, λ, and the excess air, e, are all related as follows:

$$\phi = \frac{AF_s}{AF} \quad \lambda = \frac{1}{\phi} \quad e = \lambda - 1 \quad [6]$$

The combustion regimes are defined by the value of ϕ with $\phi = 1$ ($e = 0$) being the stoichiometric combustion, $\phi > 1$ the fuel-rich regime (insufficient air), and $\phi < 1$ the fuel-lean regime (excess air). The equivalence ratio is particularly important in characterizing the potential air pollutant emissions from a combustion system. For fuel-rich conditions, concentrations increase for products of incomplete combustion such as hydrocarbons, CO, and particulate matter. NO_x emissions may peak under slightly fuel-lean conditions due to high flame temperatures and reaction of nitrogen and oxygen in air (the so-called thermal NO_x). NO_x is also produced from nitrogen in the feedstock (fuel NO_x). Other pollutant species are also produced in varying amounts under all three combustion regimes but are not specifically included in eqn [5].

Fuel moisture is a limiting factor in biomass combustion. The autothermal limit for most biomass fuels is approximately 65% moisture content wet basis (mass of water per mass of moist fuel). Above this point, insufficient heat is liberated by combustion to satisfy the energy needs for evaporation and product heating. Practically, most combustors require a supplemental fuel, such as natural gas, when burning biomass in excess of 55% moisture wet basis. In the US, Federal Energy Regulatory Commission regulations developed after the enactment of the Public Utilities Regulatory Policies Act in 1978 permit up to 25% of the power plant energy input to come from natural gas or other fossil fuel (depending on air permits) for qualifying biomass cogenerators. Many independent power producers and biomass facilities employ cofiring for startup and flame stabilization.

The most common type of biomass-fueled power plant today utilizes the conventional Rankine or steam cycle, as illustrated in **Figure 16**. The fuel is burned in a boiler, which consists of a furnace and one or more heat exchangers to make superheated steam. Typical medium efficiency units utilize steam temperatures and pressures of approximately 500 °C and 6 MPa. The steam is expanded through one or more turbines that drive an electrical generator. The steam from the turbine exhaust is condensed, and the water recirculated to the boiler through the feedwater pumps. Combustion products exit the combustor, are cleaned, and vented to the atmosphere.

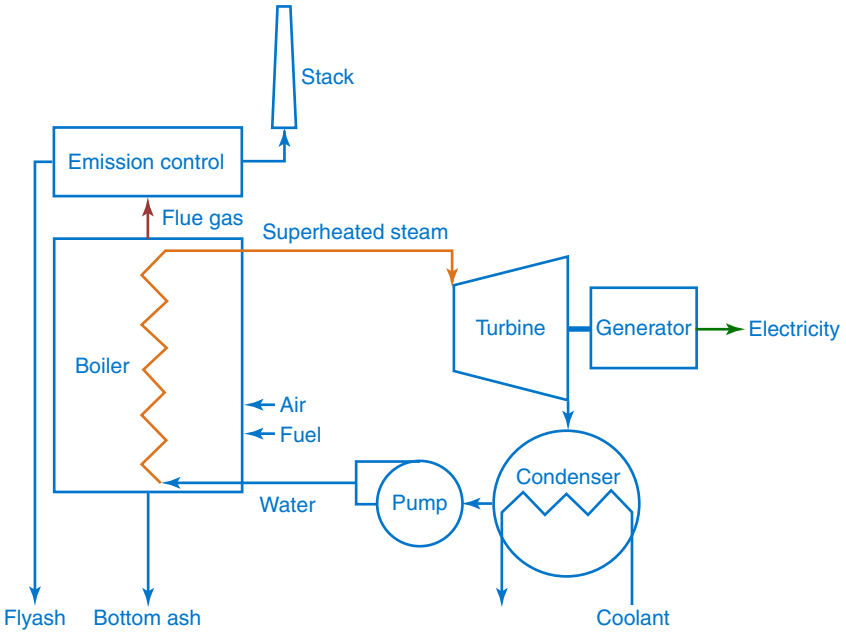


Figure 16 Schematic of a Rankine or steam cycle power plant.

Typical cleaning devices include wet or dry scrubbers for sulfur and chloride control, cyclones or other inertial separation devices, baghouses (filters) or electrostatic precipitators for particulate matter removal, and selective catalytic or selective noncatalytic reduction of NO_x. Low CO and hydrocarbon emissions are maintained primarily by proper control of air–fuel ratio in the furnace and boiler.

Ash fouling on the superheaters, the heat exchangers used to increase steam temperature above its saturation temperature and that are commonly located in the hottest parts of the furnace, has been a severe problem in many biomass-fueled boilers. Pretreatment of the feedstock to remove much of the alkali and chloride before firing to the boiler has proved beneficial in reducing fouling (Jenkins *et al.*, 1998, 2011). Coproduct bottom and fly ash can be used for industrial materials or land applied as fertilizers, potentially from the same fields that produced the feedstock. Ash from municipal solid waste incinerators, which commonly employ additional control of chlorides, mercury, and other hazardous products, may require hazardous waste disposal.

Individual power plants using biomass fuels in the manner described here typically range up to approximately 50 MW electrical capacity, which in the US is sufficient to supply the needs of from 25 000 to 50 000 people. Larger sizes are possible, and size selection is accomplished through an analysis of fuel resource availability, plant economy, and local regulations as described earlier under feedstock logistics. The distributed nature of biomass fuels and the limited economy of scale associated with plants of this type have kept the size of individual facilities relatively small in comparison with coal, petroleum, or nuclear-fueled power-generating stations. The largest biomass-fueled power station is a 240 MWe unit in Finland that operates at 545 °C and 16.5 MPa and produces process steam and hot water for district heating, but this unit can also accept peat and coal as fuel (Alholmens Kraft, 2013). A larger project in the UK (750 MWe) based on replacing coal with biomass was recently abandoned for financial and feedstock supply reasons, the latter based on uncertainties about local supplies from the region (Ross, 2013). Conversion of coal-fired facilities to biomass continues to be considered, however, in order to help meet the standards for reduced greenhouse gas emissions.

The efficiencies of biomass power plants are generally lower than comparable fossil-fueled units because of higher fuel moisture content, lower steam temperatures and pressures (due to the need to control fouling at higher combustion gas temperatures), and to some extent the smaller sizes, with a proportionately higher parasitic power demand for pumps, fans, and other electrical devices associated with the power plant itself. Large fossil-fueled units normally incur approximately 3% parasitic demand but with biomass plants the demand is more commonly approximately 10%. Currently, biomass power plant efficiencies are in the range of 17–28%, compared with good single-cycle fossil-fueled units ranging up to 40% overall efficiency. Gas and distillate (diesel) fired combined cycle power plants have efficiencies ranging more than 50% overall. Biomass integrated combined cycles are projected to exceed 35% electrical efficiency. Cofiring of biomass at 10–15% of energy input in higher capacity, higher efficiency fossil (e.g., coal) stations can also lead to a higher efficiency in biomass conversion. Increasing the power generation efficiency is a major goal for advanced biomass designs (Jenkins *et al.*, 2011).

Gasification and pyrolysis

On heating, biomass fuels will decompose into a number of gaseous and condensable species, leaving behind a solid carbonaceous residue known as char. This is an early stage of combustion, and the luminous flame seen when burning wood and other biomass is a result of the oxidation of volatile

compounds emitted during pyrolysis and gasification of the feedstock and thermal radiation from soot particles from the flame giving a characteristic yellow color.

When the fuel–air equivalence ratio, ϕ, of eqn [6] is substantially greater than unity (fuel-rich), the fuel will be only partially oxidized due to the insufficient oxygen, and the reaction products will consist not only of carbon dioxide and water, but of large amounts of carbon monoxide and hydrogen in addition to variable amounts of gaseous hydrocarbons and condensable compounds (tars and oils), along with char and ash. Other oxidants, including steam, can also be used instead of air, in which case the reaction product suite will differ. Reaction conditions can be varied to maximize the production of fuel gases, fuel liquids, or char (as for charcoal), depending on the intended energy market or markets. The term gasification is applied to processes that are optimized for fuel gas production (principally CO, H_2, and light hydrocarbons). Under heating alone without the addition of an oxidant the feedstock will pyrolyze. Pyrolysis reactors are typically designed to maximize the production of liquids through fast rather than slow heating although increasing interest in biochar or black carbon is now shifting the preferred product mix. Catalysts are sometimes employed to promote various reactions, especially the cracking of high molecular weight hydrocarbons produced during gasification and also in chemical catalytic synthesis of liquid hydrocarbons and other products in making transportation biofuels.

Gasification technology was developed more than 200 years ago (Kaupp and Goss, 1984), and lately has been improved primarily for the purposes of providing solid fuels (biomass, coal, and coke) access to some of the same commercial markets as natural gas and petroleum. Gasifiers have long been used to convert solid fuels into fuel gases for operating internal combustion engines, both spark ignited (gasoline) and compression ignited (diesels). They can also be used for external combustion devices, such as boilers and Stirling engines. The most common types are the direct gasifiers, where the partial oxidation of the feedstock in the fuel bed provides the heat for pyrolysis and gasification reactions, which are mostly endothermic. Indirect gasifiers and pyrolysis reactors use external heat transfer to provide the heat necessary to pyrolyze the fuel. The heat may be produced by the combustion of some of the original biomass fuel, or by the combustion of output fuel gases, liquids, or char. Allothermal reactors have been developed to supply heat by internal but separate burning of the char phase following gasification of the feedstock, mostly in dual reactor systems (Wilk and Hofbauer, 2013). Gasifiers may have less difficulty with ash slagging because of the lower operating temperatures compared with combustors, although slagging, fouling, and bed agglomeration remain problems with some fuels (e.g., straw).

When direct gasifiers are supplied with air to react the feedstock, the fuel gases will contain large amounts of nitrogen and the heating value or energy content of the gas will be low (3–6 MJ m^{-3}) in comparison to natural gas (compare methane at 36.1 MJ m^{-3}) and other more conventional fuels. Nonsupercharged engines operating on such gas will be derated in power output relative to their operation on gasoline or diesel (Jenkins and Goss, 1988). In the case of diesel engines, the gas cannot be used alone, and pilot amounts of diesel fuel are injected to provide proper ignition and timing. For spark-ignited engines, the engine power output is about half that of the same engine on gasoline, because the air capacity of the engine (the amount of air drawn into the engine cylinder during the intake stroke) is reduced by the large volume occupied by the fuel gas, and so not as much fuel can be burned during each cycle (Jenkins and Goss, 1988). Supercharging the engine can overcome this in part. For dual-fuel diesel engines, the gas can generally supply up to 70% of the total fuel energy without encountering severe knock, which results from the long ignition delay associated with the producer gas, the same property which gives the gas excellent octane rating (Chancellor, 1980; Ogunlowo *et al.*, 1981). The same properties of producer gas which lead to late ignition and knock in a diesel engine make it quite knock resistant in a spark-ignited engine, so compression ratios well above 10 can be used. With proper design of the cylinder head at increased compression ratio, the engine efficiency can be improved over gasoline, offsetting some of the derating due to reduced air capacity.

If the gasification reactor uses enriched or pure oxygen, the fuel gas, or syngas, produced is of higher quality. The cost of producing the oxygen is high, however, and such systems are generally proposed for larger scales or for producing higher value commodities, such as chemicals and liquid fuels. Methanol, a liquid alcohol fuel, CH_3OH, is produced by the catalytic reaction

$$CO + 2H_2 = CH_3OH \qquad [7]$$

This reaction is favored by low temperature (400 °C) but by high pressure (30–38 MPa). Zinc oxide and chromic oxide are the common catalysts. With copper as the catalyst, the reaction temperature and pressure can be reduced (260 °C, 5 MPa), but copper is sensitive to sulfur poisoning and requires good gas scrubbing (Probstein and Hicks, 1982). Fischer–Tropsch reactions can be utilized to produce a spectrum of chemicals including alcohols and aliphatic hydrocarbons. Temperature and pressure requirements are reduced, and greater selectivity can be obtained by the choice of catalyst.

Liquids, such as gasolines, can be produced via indirect routes involving the gasification or pyrolysis of the solid biomass to produce reactive intermediates that can be catalytically upgraded (Kuester *et al.*, 1985; Prasad and Kuester, 1988; Kuester, 1991; Brown, 2011). Liquids produced directly by pyrolysis are usually corrosive, suffer from oxidative instability, and cannot be directly used as engine fuels. Many products are also carcinogenic. Refining of some sort is generally necessary to produce marketable compounds. Despite this, fast pyrolysis reactors employing biomass and other fuels are in commercial startup to produce biooils (Ensyn Corp, 2014). Liquid fuels can also be produced by direct thermochemical routes, such as by hydrogenation in a solvent with a catalyst present (Elliott *et al.*, 1991; Bridgwater and Bridge, 1991).

One of the principal technical hurdles, especially at the small scale, in applying gasifiers for applications other than direct burning of the raw gas is gas cleaning and purification. Removal of particulate matter and tars from the gas is critical in downstream power generation and fuel synthesis. Tars comprise a class of heavy organic materials that are particularly difficult to remove or treat. Systems are available to produce acceptable gas quality, but generally rely on some

combination of wet and dry scrubbing and filtering and add expense to the conversion system. Small-scale gasifiers used for remote power generation have often been deployed without adequate handling procedures for tar separated from the gas. Gas cleaning and tar handling remain critical engineering challenges for a wider adoption of the technology at all scales.

Advanced power generation options from biomass include the use of a biomass gasifier to produce fuel gas for a gas turbine in an integrated gasification combined cycle system (**Figure 17**; Meerman *et al.*, 2013). The efficiency of these systems could be considerably higher than the conventional Rankine cycle power generation systems. Major engineering challenges include hot gas cleaning to provide a gas of adequate quality to avoid fouling the turbine, and the development of reliable high pressure reactors or compressors and fuel feeding systems. The use of a gasifier is thought to be an advantage over a direct combustor because heat loss in the gas cleaning system is of less concern, most of the fuel energy being in the form of chemical energy in the product gas. Other advantages for gasifiers over combustors include the ability to operate at lower temperatures, and lower gas volumes per unit of feedstock converted, which assists in the removal of sulfur and nitrogen compounds to reduce pollutant emissions. Systems of this type are currently under development and several large-scale demonstration projects have been completed, but the technology has not yet been deployed commercially for

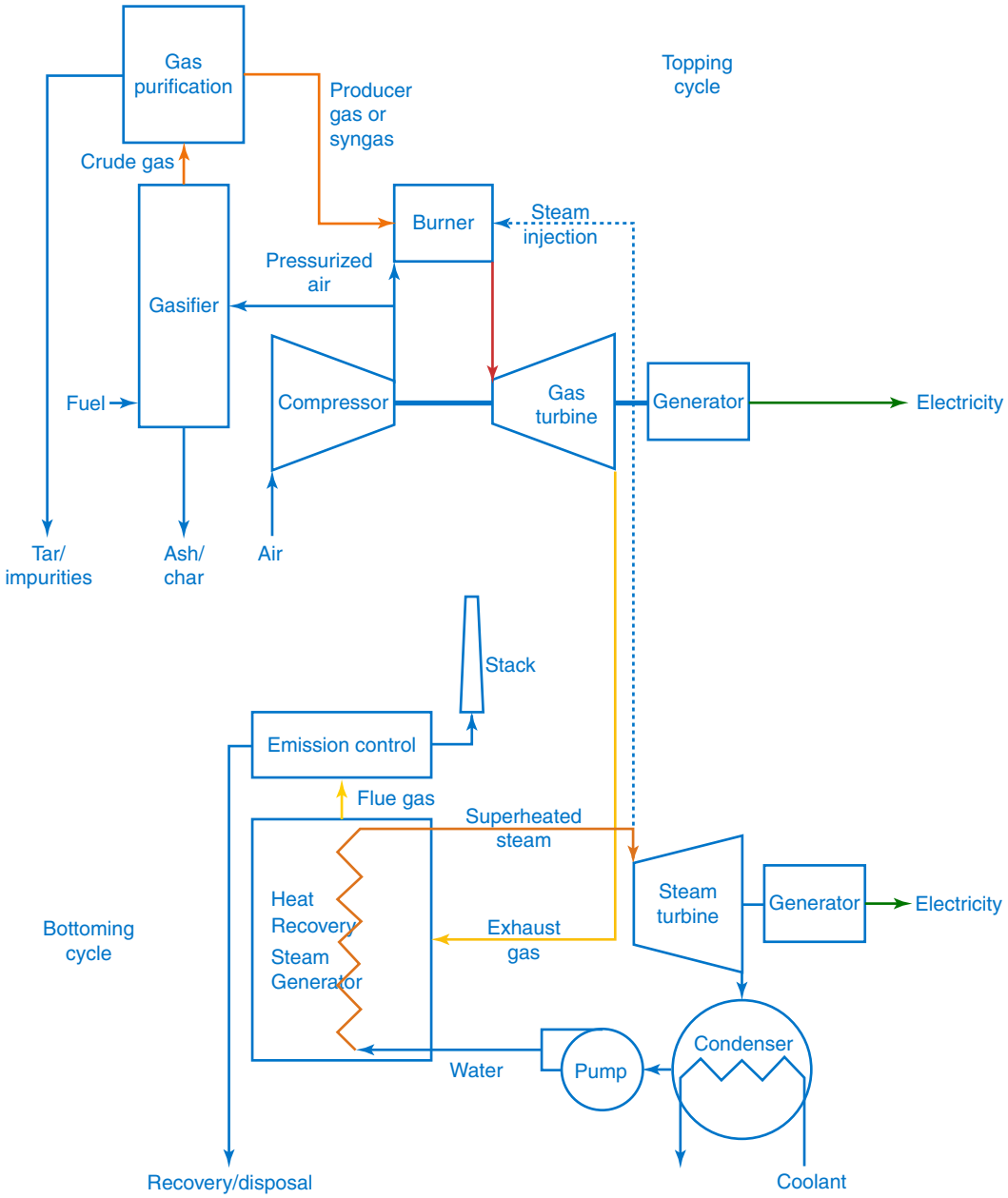


Figure 17 Integrated gasification combined cycle advanced power generation concept. Pressurized air gasification shown. A steam-injected gas turbine option is also shown (IG/STIG).

biomass although it has for coal at larger scales (Stahl and Neergaard, 1998). **Figure 17** also illustrates the possible use of steam injection for reducing thermal NO_x emissions and enhancing the power output of the gas turbine. The high heat capacity of the steam in comparison to the combustion products leads to a power increase, and the addition of steam reduces the flame temperature, which is beneficial for reducing thermal NO_x formation (Weston, 1992). Many other thermochemical conversion options are under development (Brown, 2011).

Biochemical Conversion

Biochemical conversion relies primarily on the abilities of microorganisms to convert biomass components into useful liquids and gases. Yeast fermentation is the principal means of producing ethanol. Biogas is a product of bacterial fermentation in anaerobic digestion, although bacteria are also used in alcohol fermentation. Fermentation is a widely used industrial process and an active area of biotechnology research and development.

Fermentation

Ethanol (C_2H_6O) is widely produced by fermentation and is the predominant liquid fuel derived by biochemical means from biomass. In the United States, ethanol is currently used as a oxygenate blending agent in gasoline to help reduce air pollutant emissions from vehicles as well as a major fuel product in the form of E85, an ethanol–gasoline blend containing nominally 85% ethanol and 15% gasoline although actual blends may range as low as 70% ethanol. In Brazil, ethanol is used both as a pure or 'neat' (100% ethanol) fuel, and as a blending agent with gasoline at 20% concentration (E20). The primary feedstock for ethanol production in the United States is corn (maize) grain as a source of readily fermentable starch but sorghum and other agricultural feedstocks are used as well. In Brazil it is sugarcane as a source of sugar. The yeast *Saccharomyces cerevisiae* has been the most widely used organism for ethanol fermentation (Sen, 1989). The fermentation process involves the necessary pretreatment of the feedstock to produce a fermentable substrate (sugar), fermentation, and product separation.

Corn biorefineries producing ethanol are of two types: wet mills and dry mills. Wet mills extract multiple products from the grain including oil, fiber, gluten, and starch, with the starch fraction used for fermentation. Dry mills (**Figure 18**) use the entire corn kernel for fermentation. The grain is not directly fermentable, but requires milling, hydration and gelatinization, and enzymatic or acid hydrolysis of the starch to fermentable sugars before the actual fermentation. Theoretical yields from glucose ($C_6H_{12}O_6$) are 51% ethanol and 49% carbon dioxide (mass basis). The overall reaction for the fermentation of glucose to ethanol is

$$C_6H_{12}O_6 = 2C_2H_6O + 2CO_2 \quad [8]$$

The theoretical yields from starch and sucrose are somewhat higher. Actual yields from fermentation are lower due to production of the microbial cell biomass and incomplete conversion of the substrate.

Ethanol concentrations reach approximately 10% in the fermentation beer before separation; higher concentrations inhibit the microbial activity. The ethanol is typically separated by steam distillation to 95% concentration, the azeotropic point at which water and ethanol evaporate to yield the same concentration in the vapor as in the liquid and no further separation by distillation is possible. The distilled product is dehydrated using solvents or other desiccants to produce anhydrous ethanol. A high protein stillage is produced and is used as animal feed (distillers grains). Beverage grade alcohol includes removal of fusel oils during distillation. For fuel grade alcohol, this step is usually eliminated.

Cellulosic feedstocks are more difficult to hydrolyze into monosaccharides for fermentation, thereby incurring more costly pretreatment. Current methods under development for cellulosic biomass hydrolysis and fermentation essentially fall into four categories: (1) concentrated acid hydrolysis (**Figure 19**), (2) dilute acid hydrolysis, (3) enzymatic hydrolysis (**Figure 20**), and (4) thermochemical conversion (gasification and pyrolysis) followed by fermentation of synthesis gases, a process that attempts to circumvent problems associated with hydrolysis (Skidmore *et al.*, 2013). Concentrated acid processes have long been used to produce ethanol from cellulosic materials, but for economic and environmental reasons in modern applications require substantial recovery and recycling of the acid, adding expense. Enzymatic hydrolysis is widely investigated in an effort to improve yields and reduce costs. Enzymatic processes developed following research during World War II to control deterioration of military clothing and equipment. This research identified the fungal organism *Trichoderma viride*, later renamed *Trichoderma reesei*, important to the development of cellulose enzymes (cellulase) for decrystallization and hydrolysis of cellulose. Genetically modified and recombinant organisms have been developed to enhance both the hydrolysis and fermentation of cellulosic materials (Luli *et al.*, 2008; Singh, 2010). The cost of enzyme production remains high, however, and major research investigations continue to explore means of reducing the cost. Alternative techniques are under development to produce sugar aldonates as the reactive intermediates rather than sugars to replace the pretreatment, cellulase production, and enzymatic hydrolysis processes with a single biological step (Fan *et al.*, 2012).

Cellulose hydrolysis yields hexoses, primarily glucose, fructose, mannose, and galactose. Hemicellulose hydrolysis yields mostly pentoses, principally xylose and arabinose. Lignin is currently unfermentable in any commercial application. The sugars are fermented to ethanol whereas lignin is mostly considered as boiler fuel (e.g., in steam production for distillation and power generation) or for conversion to other products, such as aryl ethers (Salanitro, 1995; Sergeev and Hartwig, 2011; Parthasarathi *et al.*, 2011). Sequestering of lignin has also been proposed to reduce net greenhouse gas emissions from biochemical conversion (Murphy, 2013).

Energy balances associated with fermentation of lignocellulosic materials are thought to be improved relative to those for corn grain, although commercial data are not yet substantially available. For lignocellulosic feedstocks, overall ethanol yields are likely to be in the range of 300 l Mg^{-1} of dry feedstock compared with 400 l Mg^{-1} for corn grain. The ideal

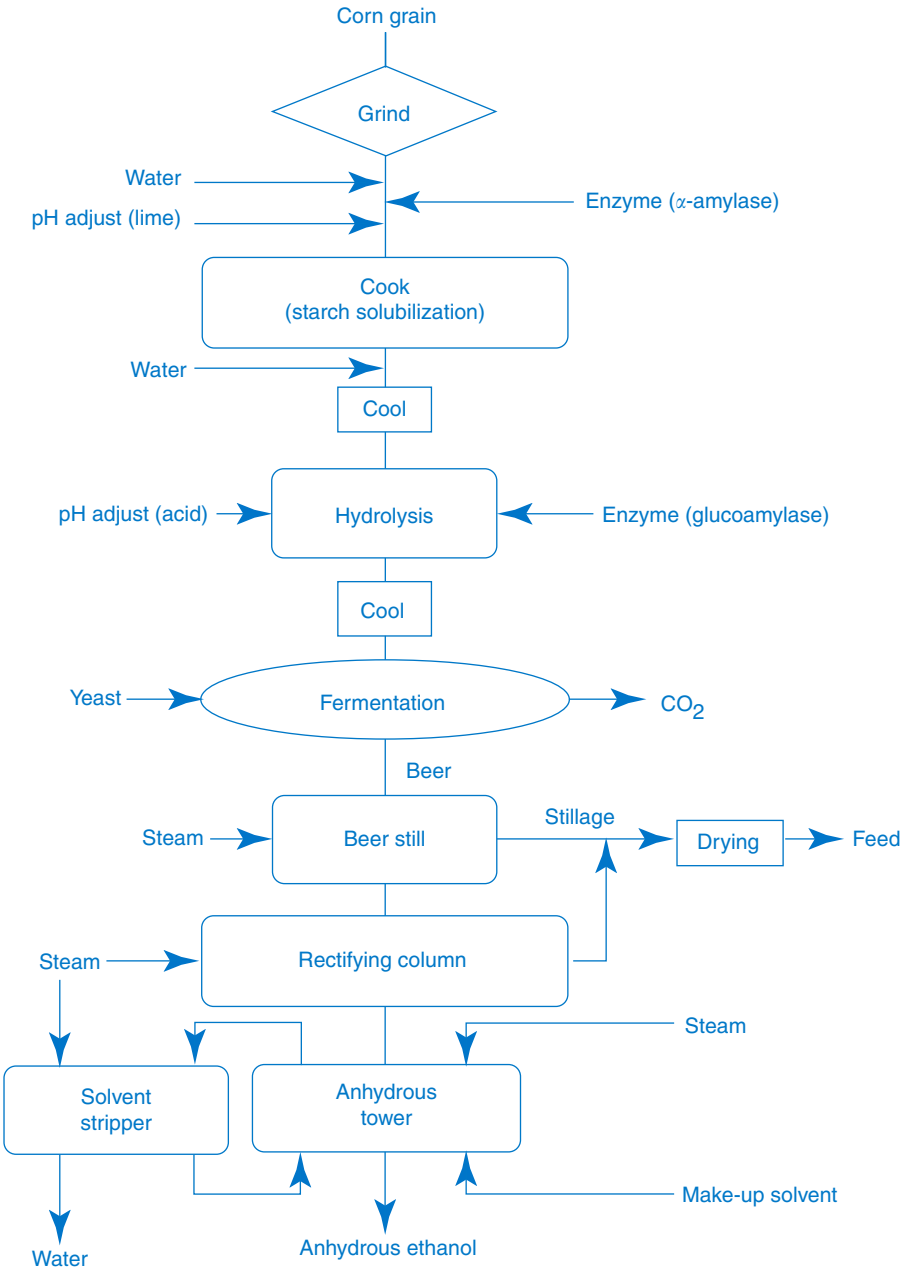


Figure 18 Process for the production of anhydrous ethanol from corn.

energy recovery assuming complete conversion into ethanol for cellulose fermentation is approximately 97% of the feedstock energy. The overall reaction of cellulose to glucose is

$$(C_6H_{10}O_5)_n + nH_2O = n(C_6H_{12}O_6) \quad [9]$$

with glucose fermented to ethanol as in reaction [8]. The fractional energy yield for cellulose to ethanol is shown in Table 6. Actual energy yields are substantially lower. At 300 l Mg^{-1} the energy yield from feedstock is 40%. This does not include the supplemental energy involved in feedstock production, handling, and conversion.

As an improvement over the separate hydrolysis and fermentation (SHF) of the cellulosic biomass, simultaneous saccharification and fermentation (SSF) processes are perceived to have certain advantages in avoiding end-point inhibition in the fermentation stage and the possibility of reducing the fermentation time. The cost of ethanol from SSF processes may, therefore, be reduced relative to SHF. In SSF, a mixed culture of organisms is used, typically *Brettanomyces claussenii* and *S. cerevisiae*, with *B. clausenii* being active early and the more robust *S. cerevisiae* continuing to completion. More recent developments employ simultaneous saccharification and cofermentation of multiple sugars, or combined enzyme production, saccharification, and fermentation

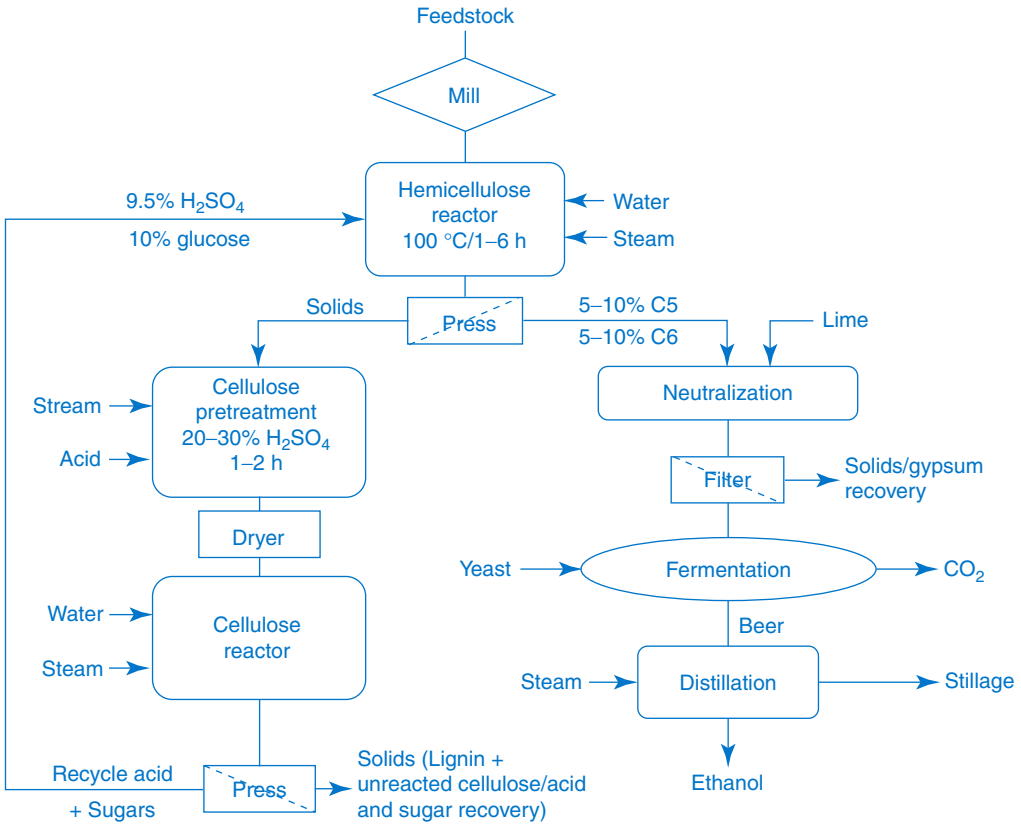


Figure 19 Process for fermenting cellulosic feedstocks using concentrated acid hydrolysis with acid recycle. Adapted from Barrier, J.W., Moore, M.R., Broder, J.D., 1986. Integrated Production of Ethanol and Coproducts from Agricultural Biomass. Muscle Shoals, AL: Tennessee Valley Authority.

processing in consolidated bioprocessing (Olson *et al.*, 2012).

Gasification systems coupled with a bioconversion stage are proposed to take advantage of the capability of anaerobic organisms, such as *Clostridium ljungdahlii* to ferment syngas to ethanol. These systems potentially would operate at a higher rate than the hydrolytic fermentation systems (Skidmore *et al.*, 2013).

Thirty-five percent of the weight of ethanol is due to oxygen. In the United States, ethanol is used as an oxygen source in gasolines where it assists in controlling CO emissions from engines. At present, ethanol can be blended up to 10% by volume. Fuel oxygen promotes CO oxidation to CO_2, and the ethanol in the gasoline tends to create a leaning effect in most spark-ignited engines, causing them to operate at higher effective air–fuel ratios with lower CO emission rates (OTA, 1990). Ethanol has a high octane rating, as does methanol, and engines using neat or blended fuels can be designed for higher compression ratios and higher efficiencies. Therefore, even though ethanol has a heating value which is 60% that of gasoline (**Table 7**), the effective fuel consumption on a properly configured engine should only be increased by approximately 25% relative to gasoline. Stable blends of ethanol with gasoline require anhydrous ethanol to avoid phase separation, an issue in ethanol transportation and distribution.

The use of ethanol as blending stock for gasoline in California has also been controversial due to the higher vapor pressures when blended compared with gasoline alone, although the vapor pressure of neat ethanol is less than gasoline. The higher blend vapor pressure can result in higher evaporative losses of reactive hydrocarbons, although improved automotive fuel systems have reduced this concern in late model vehicles and blending ratios have shifted from 5.7% to 10%. The hydrocarbons react with NO_x in the atmosphere to produce ozone, a lung irritant and undesirable tropospheric pollutant. The level of ethanol blending is also a point of contention between oil refiners and ethanol producers due to rules under the US federal renewable fuel standard (RFS), a part of the Energy Independence and Security Act of 2007 (U.S. Congress, 2007; Podkul, 2013). A 10% blend ratio limits the total amount of ethanol that can be used in motor fuel (the so-called blend wall), and changes in gasoline demand could result in refiner demands that are lower than called for under the RFS, making financing difficult for new biorefining capacity additions. Vehicle warranties, other than for E85-capable vehicles, mostly cover only up to 10% ethanol, adding to the blend-wall constraints. Further constraints to the growth of a corn ethanol industry in the United States and elsewhere arise in California from estimates of lifecycle carbon intensities (net greenhouse gas emissions) under the low-carbon fuel standard (LCFS) that requires fuel suppliers to reduce intensity by 10% (CARB, 2012). Where coal is used for process energy in biorefineries producing fuel ethanol, estimated carbon intensities exceed those of the reference gasoline from petroleum.

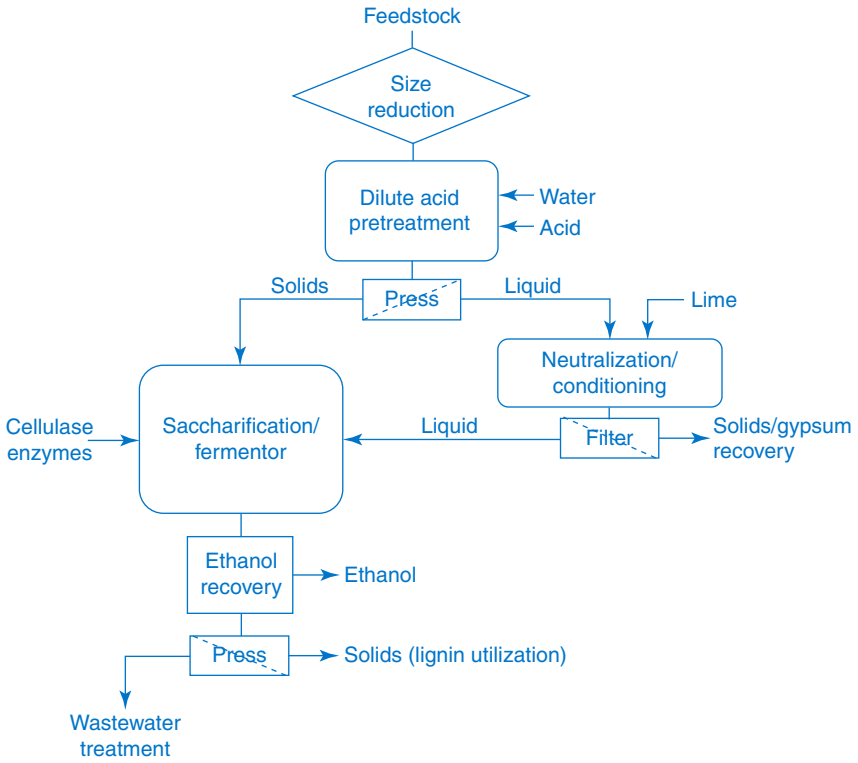


Figure 20 Process for fermenting cellulosic feedstocks using enzymatic hydrolysis. Adapted from McMillan, J.D., 2004. Biotechnology routes to biomass conversion. DOE/NASULGC Biomass and Solar Energy Workshops, August 3–4. Golden, CO: National Renewable Energy Laboratory.

Table 6 Ideal fractional energy yields in the conversion of cellulose into ethanol (actual yields lower)

Compound	*Molecular weight (kg kmol^{-1})*	*Higher heating value (MJ kg^{-1})*	*Molar energy (MJ)*	*Fractional energy yield*
Cellulose	162	17.53	2840	1.000
Glucose	180	15.67	2820	0.993
Ethanol[a]	46	29.78	2740	0.965

[a]2 mol of ethanol produced per mole cellulose reacted.

Although concerns such as these will likely be resolved over the longer term, the role of policy is evident in influencing system design and industrial capacity.

Anaerobic digestion

Fermentation by anaerobic bacteria is used to produce biogas, a gaseous fuel consisting of 50–80% by volume methane, 15–45% carbon dioxide, and 5% water, with small concentrations of H_2S and other species (Krich *et al.*, 2005). The technology is extensively employed in municipal waste water treatment. Often the biogas is burned in engines to generate power, with engine waste heat used to heat the digester for improved performance. The same biological processes are active in waste landfills, where gas recovery has become an integral part of landfill design, both as a means to control gas migration and as a means of energy recovery. Other products can also be produced through anaerobic digestion including carboxylic acids, ketones, and alcohols (Thanakoses *et al.*, 2003).

Table 7 Properties of ethanol and gasoline

Property	*Ethanol*	*Unleaded regular gasoline*
Specific gravity (15 °C)	0.79	0.78
Lower heating value (MJ kg^{-1})	26.9	44.0
Lower heating value (MJ L^{-1})	21.2	34.3
Octane number ((R + M)/2)[a]	98	88
Stoichiometric air–fuel ratio	9.0	14.7
Lower heating value of stoichiometric air–fuel mixture (MJ kg^{-1})	2.7	2.8
Enthalpy of vaporization (kJ kg^{-1} at 15 °C)	840	335
Reid vapor pressure (kPa)[b]	16	55–103

[a]Average of research (R) and motor (M) octane test methods (pump value).
[b]Reid vapor pressure of 10% ethanol in gasoline is 3–7 kPa higher than gasoline alone.

The overall reaction for anaerobic digestion of the organic portion of the feedstock (represented as $C_xH_yO_z$) to biogas is

$$C_xH_yO_z + \left(x - \frac{y}{4} - \frac{z}{2}\right)H_2O = \left(\frac{x}{2} - \frac{y}{8} + \frac{z}{4}\right)CO_2 + \left(\frac{x}{2} + \frac{y}{8} - \frac{z}{4}\right)CH_4 \quad (10)$$

The actual concentration of CO_2 is typically reduced due to its solubility in water.

The digestion of the feedstock is commonly described as occurring in three stages although the cooperative mechanisms among the organisms involved has been emphasized (McInerney and Bryant, 1981; Hills and Roberts, 1982; Parkin and Owen, 1986). After loading feedstock to the digester vessel, much of the organic material is solubilized by bacterial metabolism or chemical hydrolysis. Acid-forming bacteria utilize the soluble compounds and produce low molecular weight organic acids, principally acetic acid, that are used by methanogenic (methane-forming) bacteria for the final conversion to biogas. In a properly operating digester, these processes take place simultaneously within the digester contents, although in some recent designs the hydrolysis and methanogenic processes have been largely separated (Zhang and Zhang, 1999). Acid-forming bacteria are generally more robust than the methanogens, and can overwhelm the system with acids, causing a decrease in pH and unfavorable conditions for the methanogens. A properly functioning digester will have a pH in the range of 7–8. The health of the digester is controlled by proper management of nutrient loading, retention time, temperature, and, in dilute slurry digesters, mixing.

Digesters most often operate with dilute slurries. Bioreactor designs include covered lagoons commonly used in dairy and other agricultural operations, batch digesters, plug-flow digesters, completely stirred tank reactors, upflow anaerobic sludge blanket systems, anaerobic sequencing batch reactor systems, anaerobic-phased solids systems, and in landfills enhanced bioreactors employing leachate recycle. Plug-flow reactors utilizing higher solids concentrations are also used. High solids or dry-fermentation digesters have been developed to reduce some of the problems associated with handling dilute slurries in tank reactors (Jewell, 1982). These high solids digesters are similar in nature to landfills, but implemented at smaller scales and with greater automation.

Digesters can operate on almost all biomass feedstocks, although with differing conversion rates and efficiencies. They are well suited for wet or moist feedstocks that would require drying for thermal conversion systems. Nitrogen availability is limiting in most cases, particularly when woods or herbaceous materials are used alone. Animal manures and mixtures of manures with agricultural residues, such as straw, give better performance due to improved carbon-to-nitrogen (C/N) ratios, which are recommended to be in the range of 25–30 overall (Hills and Roberts, 1981). The biogas produced typically has a heating value of 22–24 MJ m^{-3} with yields of 50–400 l per kg dry solids depending on feedstock and digester conditions, including temperature, inoculation levels, and hydraulic retention time. Design operating conditions include the psychrophilic (ambient temperature or below), mesophilic (30–40 °C), and thermophilic temperature regimes (50–60 °C) with conversion rates generally increasing with temperature although heating requirements also increase. Hyperthermophiles that can withstand even higher temperatures have not yet been employed in commercial systems. Energy conversion efficiencies for anaerobic digesters are relatively low if based on the yield of the gas alone. Typical energy efficiencies of biogas are 20–50%, and up to approximately 20% for electricity. The stabilized sludge remaining after digestion can be used as fertilizer, unless contaminated with heavy metals or other toxic materials from the input feed. Nutrient management is an important issue in many agricultural systems and digesters can be used to advantage, especially in mineralizing nitrogen before land application or discharge of effluent.

Biogas is a reasonably versatile fuel and can be burned directly for heating the digester (to improve performance), to heat water, or for cooking and lighting purposes. The gas can also be used as fuel for engines, turbines, and boilers, including cogeneration, and more recently in fuel cells (Krich *et al.*, 2005; Lo Faro *et al.*, 2013). As noted earlier, NO_x emissions from engines are currently a key issue for small digester-power systems. H_2S can be scrubbed from the gas to reduce corrosion and SO_2 emissions, although in small-scale applications such as individual dairy operations, the cost of more effective removal systems is a concern. Siloxanes typically present in landfill gas may need scrubbing (usually on charcoal) for some applications, turbines in particular and also in fuel cells and reciprocating engines. Biogas has been used as transportation fuel, including low pressure applications with large flexible bags on the roof of the vehicle serving as the fuel tank (Stout, 1990), but is now more widely considered for CNG or LNG applications. CO_2 stripping followed by gas compression is mostly required for these purposes. CO_2 stripping has also been used to produce pipeline quality gas for blending into natural gas distribution systems and to produce transportation fuels. Small-scale digesters have been promoted in many areas to improve sanitation as well as to supply fuel gas. The process is also considered in the design of integrated biorefineries (Thomsen *et al.*, 2013).

Physicochemical Conversion

Biodiesel has recently emerged as a commercial renewable alternative to petroleum-derived diesel. Biodiesel can be produced from virgin plant and algal oils and also from waste oils such as cooking oils and greases, the latter incurring lower procurement costs and hence lower cost of production. In the United States, the RFS mandates increasing the amounts of biodiesel although the amount required is a fairly small share of the total biofuel under the standard (U.S. Congress, 2007). Recent reversals in European Union (EU) policies due to sustainability concerns have reduced mandated biofuel volumes with impacts on the existing biodiesel producers and suppliers. Although potentially resource and policy constrained, the current production of biodiesel represents one of the predominant physicochemical conversion techniques.

Unlike petroleum-based diesel fuels, which are primarily straight or branched chain hydrocarbons, vegetable oils are primarily mixtures of triacylglycerols composed of fatty acids esterified to the three –OH positions on glycerol (Goering

et al., 1982; Robbelen *et al.*, 1989). Although crude or refined vegetable oils can be used as fuel for compression-ignited (diesel) engines, such use is not recommended except on an emergency basis for short periods of time (Peterson, 1989). Engine damage arising from fuel polymerization and ring sticking, along with lubricating oil contamination, is likely to occur after prolonged operation. Vegetable oils have heating values similar to diesel fuel (approximately 90% of ASTM No. 2 diesel), but the viscosity is one to two orders of magnitude higher. The high viscosity causes irregular spray patterns from fuel injectors inside the engine cylinders, which in turn leads to injector coking (carbonization of the fuel on the injector nozzles) and deposits on cylinder walls and pistons. Vegetable oils also have higher cloud point and pour point temperatures, which makes them inferior to diesel fuels for cold weather operation. However, they have higher flash point temperatures, and are therefore somewhat safer, and are less toxic than diesel fuels and mostly biodegradable. Stable blends of diesel fuel with vegetable oils can be made to improve the fuel properties, but modification of the oil is preferred for general engine application.

The reaction of a triglyceride, such as a vegetable oil, with an alcohol in the presence of a catalyst such as sodium hydroxide, produces upon separation a fatty acid ester and glycerol. The ester is an improved diesel fuel substitute over the original oil and the basis for current biodiesel manufacturing. When methanol is used, the result is a fatty acid methyl ester. Fatty acid ethyl esters, produced from oil and ethanol, have also emerged as diesel fuel replacements, with some possible advantages over the methyl esters in reduced smoke opacity and lower injector coking. The esters have viscosities that are only 2–3 times that of diesel fuel, which leads to reduced injector coking and decreased deposit formation compared with the original vegetable oil. The esters have improved cetane numbers relative to the original oils, and in some cases relative to diesel fuel. This makes them useful as blending stocks for diesel. Although esters reduce smoke emissions compared with diesel fuel, NO_x emissions are about the same or higher, as are acrolein emissions. Aromatic aldehyde emissions depend on the aromaticity of the fuel such that blends of biodiesel with regular diesel tend to have higher emissions than pure biodiesel fuel (B100) (Qi *et al.*, 2013; Cahill and Okamoto, 2012).

Fuel specification standards for biodiesel have been developed in Europe (Mittelbach *et al.*, 1992) and the US including standards (ASTM D6751, 2012) for 100% biodiesel fuel (B100) as blending stock for distillate fuels. Owing to its typically low sulfur content, biodiesel can be blended with petroleum diesel that otherwise does not meet newer low-sulfur fuel standards. B20, a 20% biodiesel blend, can be used in some unmodified diesel engines. The use of B100 may require modifications to the fuel supply system if the engine has not been warranted for it.

The Challenge of Sustainability

The production of industrial feedstocks by agriculture involves land and other resources that provide many different agronomic and ecosystem services. As the scale of production capacity for fuels and other commodity chemicals has increased, so has the debate around the wisdom of converting forest lands and prime or marginal agricultural lands to purposes other than traditional food, feed, and fiber production, especially food for a growing global population. Policies intended to improve sustainability in one sector, such as energy security, have often been contested for their narrow focus and lack of analysis and consideration of larger system issues, such as net global greenhouse gas emissions or net energy benefits (Searchinger, 2008; Pimentel, 1991). The reversal in EU policies regarding biofuels was motivated largely by reconsideration of sustainability impacts associated with resourcing large supplies of biodiesel and other fuels from palm oil and other crops where global environmental, social, and economic impacts had not been systematically evaluated (Turner *et al.*, 2008).

Challenges to US federal policies relating to biofuels developed following the first oil shock of 1973–74 when the US initiated policy supporting alternative fuels. Debate initially centered on net energy yields associated with producing ethanol from corn with suggestions that the amount of energy embodied in fossil fuels and other inputs to grow corn and manufacture ethanol exceeded the energy in the ethanol, thus negating any intended energy benefits (Pimentel, 1991). Criticisms were largely addressed through improvements in conversion technologies (Shapouri *et al.*, 2002; Farrell *et al.*, 2006), but other questions of sustainability continue to arise. In addition to a more recent debate over the net greenhouse gas emissions from industrial feedstock production, the effects on food prices have been called into question (the food-versus-fuel debate) with concerns over food security, especially for the poor. The Brazilian program to produce ethanol from sugarcane, widely viewed as a successful national response to improve domestic energy security, also generates concerns over environmental sustainability although the net greenhouse gas impacts are mostly regarded as lower than for corn (Smeets *et al.*, 2008).

The global energy markets are large and can easily absorb large quantities of feedstock biomass. Estimates for the United States suggest that only approximately a third or less of transportation fuel could be supplied from biomass (Perlack and Stokes, 2011; Parker *et al.*, 2011). Increasing biofuel demand potentially leads to direct land-use changes (dLUCs) as well as indirect land-use changes (iLUCs) through market-mediated effects (Searchinger *et al.*, 2008) unless yield intensification on the same land base is able to compensate, a goal of crop research but not so far achieved. iLUC can cause substantial emissions of carbon to the atmosphere from clearing of standing biomass and depletion of carbon stocks in the soil in response to crop shifting elsewhere in the world (Fargione *et al.*, 2008; Searchinger *et al.*, 2008). The amount of carbon released, like many other issues in agricultural sustainability, is highly uncertain and estimates vary widely. Inclusion of iLUC effects in environmental lifecycle assessments can result in higher attributed greenhouse gas emissions for some biofuels in comparison with petroleum-derived gasoline or diesel fuels. Policies to encourage biofuels based solely on direct substitution effects therefore may fail to achieve the intended outcomes for total greenhouse gas emission reductions. In California, the development of a LCFS to limit the

carbon intensity of transport fuels and electricity so as to reduce carbon emissions has been particularly contentious (CARB, 2012). Other standards, such as the US renewable fuel standard (U.S. Congress, 2007), also require set levels of lifecycle greenhouse gas emission reductions to qualify for a renewable identification number for the fuel, a key objective for market access and financial success in meeting fuel blending obligations (U.S. Congress, 2005; 2007). Sustainability considerations for biofuels also apply to issues of environmental justice and other social implications in addition to environmental and economic effects (RSB, 2010).

Bioenergy production has been viewed as a way to provide additional economic opportunities for farms and rural areas, improve the environment, enhance energy security, and help to stabilize fuel prices. Substitution of biofuels for gasoline and other petroleum products can result in direct reductions in greenhouse gas emissions and other benefits, but can also lead to changes in the type of air pollutants that are emitted, affect water demand and quality, alter land use, and increase or destabilize other commodity prices. Demand for wood and other biomass feedstocks for traditional uses in cooking, heating, and charcoal making has contributed to deforestation in many regions of the world in addition to causing adverse health effects from exposure to smoke (Jenkins *et al.*, 2011). Concerns have long been expressed over harvesting of agricultural residues for energy and other industrial uses due to possible agronomic impacts associated with nutrient depletion, changes to soil organic matter and carbon, and soil erosion (Jenkins *et al.*, 1981). Similar criticisms arise in the large-scale production of chemicals and materials from agriculture. In adopting new uses for crops and resources, careful consideration must be given to the lifecycle impacts and sustainability of the entire production system and feedstock supply chain.

Economic sustainability is a primary factor in motivating investment financing for industrial feedstock production, where environmental and social sustainability factors are satisfied. The costs of producing energy and other products from biomass are heavily influenced by feedstock acquisition costs as well as by the costs of conversion. For comparison, costs to generate electricity in the existing biomass-fueled power plants are approximately US$0.06–0.08 kWh^{-1} (US$17–22 per GJ), sometimes higher, at an average fuel cost of US$30 per metric ton, principally as wood residue (Jenkins, 2005). Cost projections for purpose-grown crops range substantially higher, typically beyond $50 per metric ton dry weight and often more than $100 per metric ton (Parker *et al.*, 2011).

Exclusive of harvesting and downstream processing and conversion operations, production costs for agricultural and other biomass residues are typically allocated to the primary crop production system and not always separately accounted. Byproduct or waste biomass may be available at no cost, or in some cases disposal fees (tipping fees) can be applied to cover the costs of handling, an advantage to systems receiving municipal solid wastes. In contrast, industrial and energy crops assume full allocation of production costs. These costs are quite variable depending on the species, production site, level of management, and resulting yield. Total average delivered costs, including harvesting and transportation (85 km), for *Eucalyptus* plantations in northeast Brazil producing at 12.5 Mg ha^{-1} $year^{-1}$ have been estimated at US$2.50–3.40 per GJ, or approximately US$52–67 per metric ton dry matter (CPI inflation adjusted 2013 US dollars) (Hall *et al.*, 1993). Of the total, 40% is associated with stand establishment including nursery production, land, planting, and administration, and another 10% is associated with plantation maintenance including management, cultivation, and research. Half the delivered cost is in the production of the biomass. Under Canadian conditions, the total delivered cost including harvesting, chipping, and transportation for a typical 5 year rotation, 4 rotation cycle forestry crop with a yield of 12 Mg ha^{-1} $year^{-1}$, was similarly estimated at US$58 per metric ton (CPI adjusted 2013 US dollars), of which 40% was allocated to the production system including land, nursery, planting, and tending (Golob, 1987).

Other energy and chemical feedstock costs influence decisions to produce industrial feedstocks from agriculture. Natural gas prices in the US in the period 1999–2001, for example, fluctuated between US$2 and US$15 per GJ. Owing to the development of hydraulic fracturing (fracking) techniques and expansion of natural gas reserves, prices are now in the vicinity of US$3 per GJ and anticipated to remain below US$4 per GJ through 2020, increasing to US$8 per GJ by 2040 (EIA, 2013c). Although policies such as California's RPS require increasing supplies of electricity from renewable sources, resource neutrality within the policy provides no specific advantage for biomass over other renewable resources and principal capacity additions have been in wind and solar (EIA, 2013d). Policy stability is also important in motivating financing for biorefineries and other industrial applications. Reversals such as that of the EU over biofuels (colloquially referred to as the 'biofuels disaster') and possible adjustments in the renewable fuel obligations under the RFS in the US create significant uncertainties associated with security of investments in facilities with decades-long economic lifetimes. Research along with genetic and cultural improvements are projected to reduce biomass production costs, but biomass production levels will also be influenced by direct and indirect environmental and socioeconomic consequences external to the direct costs of production (Hanegraaf *et al.*, 1998).

Sustainable large-scale production of industrial feedstocks will require a broad systems view and well-designed standards and best practices. International standards for certifying sustainable production of biofuels are currently in development with early versions in use (RSB, 2010). The principles on which these are based – attention to law, stakeholder participation, climate change mitigation, human, labor and land rights, rural and social development, food security, waste management, resource conservation and environmental protection – apply equally well to agricultural production systems for biobased products as they do for bioenergy, a point reinforced by the recent name change of one of the principle cooperative initiatives in international standardization to broaden from biofuels to biomaterials and biomass production, more generally (RSB, 2013). Local standards may in some cases exceed international standards but will need close coordination to avoid conflicts with international agreements and rules such as those of the World Trade Organization. The complex issues now being researched and addressed in

sustainable industrial feedstock production should provide new perspectives on the improved sustainability of agriculture overall.

See also: Agroforestry: Practices and Systems. Air: Greenhouse Gases from Agriculture. Climate Change: Agricultural Mitigation. Computer Modeling: Applications to Environment and Food Security. Economics of Natural Resources and Environment in Agriculture. Global Food Supply Chains. International and Regional Institutions and Instruments for Agricultural Policy, Research, and Development. International Trade. Land Use, Land Cover, and Food-Energy-Environment Trade-Off: Key Issues and Insights for Millennium Development Goals. Markets and Prices. Natural Capital, Ecological Infrastructure, and Ecosystem Services in Agroecosystems. Soil: Carbon Sequestration in Agricultural Systems

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http://www.eia.gov/
U.S. Energy Information Administration.
http://www.epa.gov/
U.S. Environmental Protection Agency.
http://www.nist.gov/index.html
U.S. National Institute for Standards and Technology.
http://www.nrel.gov/
U.S. National Renewable Energy Laboratory.
http://www.nsf.gov/
U.S. National Science Foundation.

Global Food Supply Chains

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Glossary

Customer order decoupling point (CODP) A CODP is an inventory point in the company's value chain where products are linked to specific customer orders. After the CODP raw materials, half-fabricates, or end-products are processed and delivered to start fulfilment of customer orders.

Food logistics management Concerns the planning, implementation, and control of the supply, storage, and distribution of food products and related information from the point-of-origin to the point-of-consumption in order to meet customer requirements.

Food quality standards Concerns requirements on integrated sets of food quality and safety attributes, designed by retailers, large food industries, or other supply chain stakeholders (e.g., NGOs), to which supply chain parties have to comply to achieve a 'license to operate and deliver.'

Logistics network A network of interdependent organisations who jointly manage the flow of materials and information from suppliers to end users.

Supply chain A supply chain consists of all parties, from primary producers to final consumers, involved in fulfilling customer demands.

Traceability The ability to determine the on-going location of products and to trace products back to their origin and used production methods.

Virtualization Virtualization in a supply chain context is the digital representation of physical or imaginary products and resources, which allows for the decoupling of physical flows and information aspects of supply chain operations.

Introduction

Since the 1980s, management literature stresses the need for collaboration among successive actors in the (global) supply chain, from primary producers to final consumers, to better satisfy consumer demand at lower costs (Lambert *et al.*, 1998; van der Vorst, 2000). This new way of managing the business within each link and the relationships with other members of the supply chain has been named supply chain management (SCM). A driving force behind SCM is the recognition that suboptimization occurs if each organization in a supply chain attempts to optimize its own results rather than to coordinate its goals and activities with other organizations to optimize the results of the chain (Cooper *et al.*, 1997). This holds true especially in food supply chains because of shelf-life constraints of food products and increased consumer attention for safe and environment/animal-friendly production methods (van der Vorst *et al.*, 2005).

The increased interest in SCM has been spurred by intensified global competition, demographic and market developments (such as product proliferation and shorter product life cycles) combined with developments in information and communication technology (ICT) that enable more efficient execution of processes and more frequent exchange of huge amounts of information for coordination purposes and to provide transparency of production and distribution processes for the food supply chain's stakeholders. These stakeholders, in Western markets as well as in emerging economies, have become more demanding and place new demands on attributes of food such as safety, quality (guarantees), diversity, and associated information (Jacxsens *et al.*, 2010). **Table 1** depicts some of the main developments in demand and supply in (global) food supply chains.

These developments put dynamic requirements on the performance of the food system initiating a reorientation of companies in agriculture and food industry on their roles, activities, and strategies (van der Vorst *et al.*, 2005). Demand and supply are no longer restricted to nations or regions but have become international processes. An increasing concentration has been seen in agribusiness sectors, an enormous increase in cross-border flows of livestock and food products, and the creation of international forms of cooperation. The food industry has become an interconnected system with a large variety of complex relationships, reflected in the market place by the formation of (virtual) food supply chains via alliances, horizontal and vertical cooperation. The latter encompass the development and implementation of enhanced quality, logistics, and information systems. To satisfy the increasing demands of consumers, governments, business partners, Non Governmental Organisations (NGOs) and to obtain the 'license to produce and deliver,' companies continuously have to work on innovations in products, processes, and forms of cooperation in food supply chains.

This article focuses on the concepts and main developments in logistics, quality management, and transparency in food supply chains. An overview of these developments will be given and the impact on the design and management of the food supply chain network (FSCN) will be discussed. Practical examples will be presented in boxes to exemplify and clarify theoretical concepts.

Global Supply Chain Management and Logistics (Parts of this Section are Based on van der Vorst *et al.* (2005))

Food Supply Chain Management

The term 'SCM' is relatively new. It first appeared in logistics literature in 1982 as an inventory management approach with

Table 1 Overview of generic developments at the demand and supply side

Demand side	*Supply side*
• Higher quality, safety, and convenience products	• International geographical transitions
• More value-added products (ready to eat)	• Bigger firms (concentration) and specialization
• Increasing product variety	• Outsourcing; focus on core competences
• Shorter product life cycle	• More cooperation in (dynamic) supply chain networks
• Healthy and ecological	• Focus on added value and sustainability
• More powerful well-informed customers	• Branding strategy, search for consumer contact
• Bigger retail firms (concentration)	• Search for new distribution channels
• 24×7 Retail services	• More use of new technologies
• Battle between private and brand label	• New entrants in the network
• New types of stores; market differentiation	

Source: Adapted from van der Vorst, J.G.A.J., Da Silva, C., Trienekens, J.H., 2007. Agro-industrial supply chain management: Concepts and applications. FAO Agricultural Management, Marketing and Finance, Occasional Paper 17, 56 p. Rome: FAO.

an emphasis on the supply of raw materials (Oliver and Webber, 1982). Logistics managers in retail, grocery, and other high inventory industries began to see that a significant competitive advantage could be derived through the management of materials through inbound and outbound channels. Purchasing literature states that SCM evolved from an upgrade of the purchasing function to an integral part of the corporate planning process. Since its introduction in the retail industry, the supply chain concept has spread to other industries such as computers and copiers.

Around 1990, academics first described SCM from a theoretical standpoint to clarify how it differed from more traditional approaches to managing the flow of materials and the associated flow of information (Cooper and Ellram, 1993). SCM can be defined as follows (based on van der Vorst, 2000):

SCM is the integrated planning, coordination, and control of all business processes and activities in the supply chain to deliver superior consumer value at less cost to the supply chain as a whole while satisfying the variable requirements of other stakeholders in the supply chain (e.g., government and NGOs).

The ultimate aim of a supply chain is to deliver value for customers. Value is first of all the amount consumers are willing to pay for what a company provides and it is measured by total revenue. The concept 'value-added activity' originates from Porter's 'value chain' framework and characterizes the value created by an activity in relation to the cost of executing it (Porter, 1985). Currently, the value concept is more expanded. Here values associated with the so-called 'Triple Bottom Line' or 'Triple P': People, Planet, and Profit (FAO, 2012) are dealt with. So next to the financial performance, the social and environmental performances are also incorporated (Baldwin, 2009). These latter two lead to (qualitative) attributes that are generally spoken associated with the product itself (biologically produced), the companies producing it (social policy), and the raw materials (genetically modified organisms?) and resources (child labor?) used.

Figure 1 depicts a generic supply chain at the organization level within the context of a complete supply chain network. Each firm is positioned in a network layer and belongs to at least one supply chain: that is, it usually has multiple (varying) suppliers and customers at the same time and over time. Other actors in the network influence the performance of the chain. Therefore, the analysis of a supply chain should preferably take place or be evaluated within the context of the complex network of food chains, in other words a FSCN.

In promoting and building a strong supply chain, organizations need to understand the way competition is changing. Competitiveness currently depends on being able to join supply chains, and effective participation in, and control of, global food chains. To be competitive, coordination and sharing of information need to be undertaken between network partners. The result of the supply chain is measurable via the acceptance of the end product by the consumer. Nowadays, as discussed, this acceptance is a combination of availability, price, quality and food safety and other quality attributes. The highest added value for all participants can only be achieved when these aspects are optimized at the chain or network level. This is especially true for realizing a high quality and safe product. Food safety and high quality products are not the sole responsibility of an individual organization, but of the entire food chain. As the different actors in the supply chain each have their own role in ensuring the quality and safety of the end product, their activities should be closely coordinated. This should and can be facilitated by efficient logistics systems and exchanging information between chain/network participants. Note that FSCN have a number of specific characteristics that impact the design and management of these systems, depicted in **Table 2**.

The authors look at the operational processes that make use of inventory, transportation, facilities, and information. The traditional view on logistics management in a supply chain is the cycle view. A cycle view of the supply chain clearly defines the business processes and activities involved and the owners of each process (hence roles and responsibilities). Furthermore, because of the inventory being held between the cycles, the main processes are decoupled to a certain extent. This implies that each process can function independently and is not hindered by 'problems' in other processes. This opposes the just-in-time philosophy, which states, among other things, that the decoupling of activities by inventories should be eliminated as it hinders supply chain visibility and supports the suboptimization of the supply chain.

Owing to increasing consumer demand variability and uncertainty resulting in an increased demand for capacity–flexibility

(and thus reduction of inventories), the push/pull view on supply chains has gained more interest (Figure 2). This view focuses on the extent to which customer orders penetrate or may penetrate the logistic system. The customer order decoupling point (CODP) – also called order penetration point (Olhager, 2003) – separates the part of the organization whose management decisions are governed by customer orders (pull process) from the part of the organization where production plans are made based on forecasted demand of consumers or forecasted orders from partners downstream in the chain (push process). Downstream of the CODP the material flow is directly controlled by customer orders and the focus is on customer responsiveness (lead time and flexibility). Upstream toward suppliers, the material flow is controlled by forecasting and planning, and the focus is on efficiency (usually employing large batch sizes) and taking into account inherent properties of material flows and production capacities and resources. It must be determined where the decoupling point should be for each product–market combination or product group in the company. Therefore, a company can have multiple CODPs at different locations and even a single product can have more than one, as it can serve multiple product–market combinations.

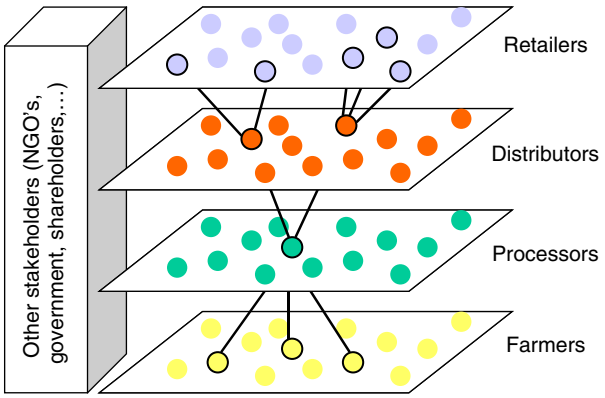


Figure 1 Schematic diagram of a supply chain from the perspective of the processor (bold flows) within the total supply chain network. Adapted from Lazzarini, S.G., Chaddad, F.R., Cook, M.L., 2001. Integrating supply chain and network analyses, the study of netchains. Journal on Chain and Network Science 1, 7–22.

The CODP and postponement concepts result in logistics structures in which a consolidation point is used to perform product differentiation to customer demands; the supply part toward the consolidation point is efficiency oriented and the distribution part aims for responsiveness. Hoekstra and Romme (1992) distinguish five possible positions of a decoupling point (DP). When these positions are translated to the example of the fresh produce sector (flowers, vegetables, fruits, etc.), four chain designs come to the front (see Figure 3). In the first two designs all products are delivered to the customers from local or regional stock – no customization activities are performed. In design 3, products are customized (that is value-adding activities to make the product customer specific are performed) at the auction, trader or hub and successively delivered to the market outlets. Finally, in design 4

Table 2 Overview of main characteristics of food supply chains and their impact on management of these chains

SC stage	*Product and process characteristics*	*Impact on management*
Overall	• Shelf-life constraints for raw materials, intermediates, and finished products and changes in product quality level while progressing the supply chain (decay) • Recycling of materials required	• Timing constraints • Information requirements • Return flows
Growers/ producers	• Long production throughput times (producing new or additional products takes a lot of time) • Seasonality in production • Variability of quality and quantity of supply	• Responsiveness • Flexibility in process and planning
Food industry	• High volume and low variety (although the variety is increasing) production systems • Highly sophisticated capital-intensive machinery focusing on capacity utilization • Variable process yield in quantity and quality due to biological variations, seasonality, random factors connected with weather, pests, other biological hazards • A possible necessity to wait for the results of quality tests (quarantine) • Alternative installations, alternative recipes, product-dependent cleaning and processing times, carryover of raw materials between successive product lots, etc. • Storage buffer capacity is restricted, when material, intermediates or finished products can only be kept in special tanks or containers • Necessity to value all parts because of complementarity of agricultural inputs (e.g., beef cannot be produced without the coproduct hides) • Necessity for lot traceability of work in process due to quality and environmental requirements and product responsibility	• Importance of production planning and scheduling focusing on high capacity utilization • Flexibility of recipes • Timing constraints, information and communication technology-possibility to confine products • Flexible production planning that can handle this complexity • Need for configurations that facilitate tracking and tracing
Auctions/ wholesalers/ retailers	• Variability of quality and quantity of supply of farm-based inputs • Seasonal supply of products requires global (year-round) sourcing • Requirements for conditioned transportation and storage means	• Pricing issues • Timing constraints • Need for conditioning • Preinformation on quality status of products

Source: Adapted from van der Vorst, J.G.A.J., Beulens, A.J.M., van Beek, P., 2005. Innovations in logistics and ICT in food supply chain networks. In: Jongen, W.M.F., Meulenberg, M.T.G. (Eds.), Innovation in Agri-Food Systems. Wageningen: Wageningen Academic Publishers, pp. 245–192 (Chapter 10, ISBN 9076998655).

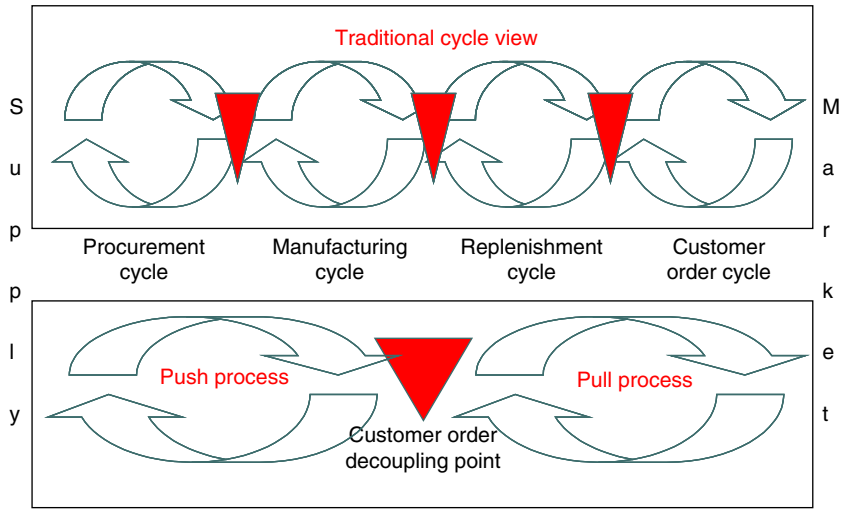


Figure 2 Views on supply chain processes (note that a reversed triangle stands for an inventory). Based on Chopra, S., Meindl, P., 2001. Supply Chain Management. New Jersey: Prentice Hall.

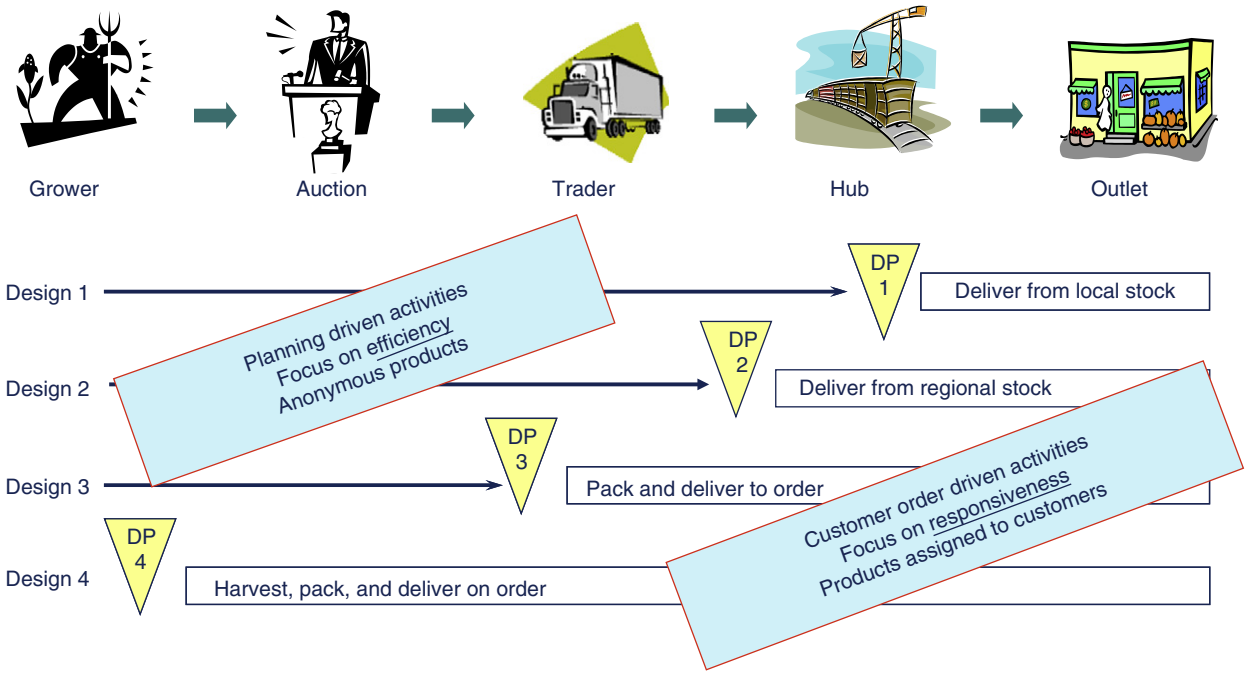


Figure 3 Four network designs with different decoupling points (reversed triangle refers to inventory that acts as a decoupling point). Reproduced from van der Vorst, J.G.A.J., Duineveld, M., Scheer, F.P., 2006. Logistics orchestration in the ornamental plant supply chain network: Towards responsive and differentiated demand driven networks. FloriLog-regie Position Paper, 46 pp. Zoetermeer: Transforum Agro & Groen.

the grower has a direct relationship with the final customer and harvest, packs and delivers its products (via traders or transporters) to customer outlets. The auction is bypassed in this network design.

There are many factors exerting an upstream or downstream influence on the position of the CODP. It is a balancing process between (Olhager, 2003):

1. Market-related factors, such as the delivery lead time requirements set by the market, product demand uncertainty, product range, and product customization requirements;
2. Product-related factors, such as possibilities for modular product design and product customization opportunities; and
3. Production- and distribution-related factors, such as the production and distribution lead time and the flexibility of the production and delivery process.

All these factors indicate to what extent it is possible or reasonable to harvest or pack products to order; for example, the more unpredictable the demand, the more responsive the supply chain should be; and if long delivery lead times are

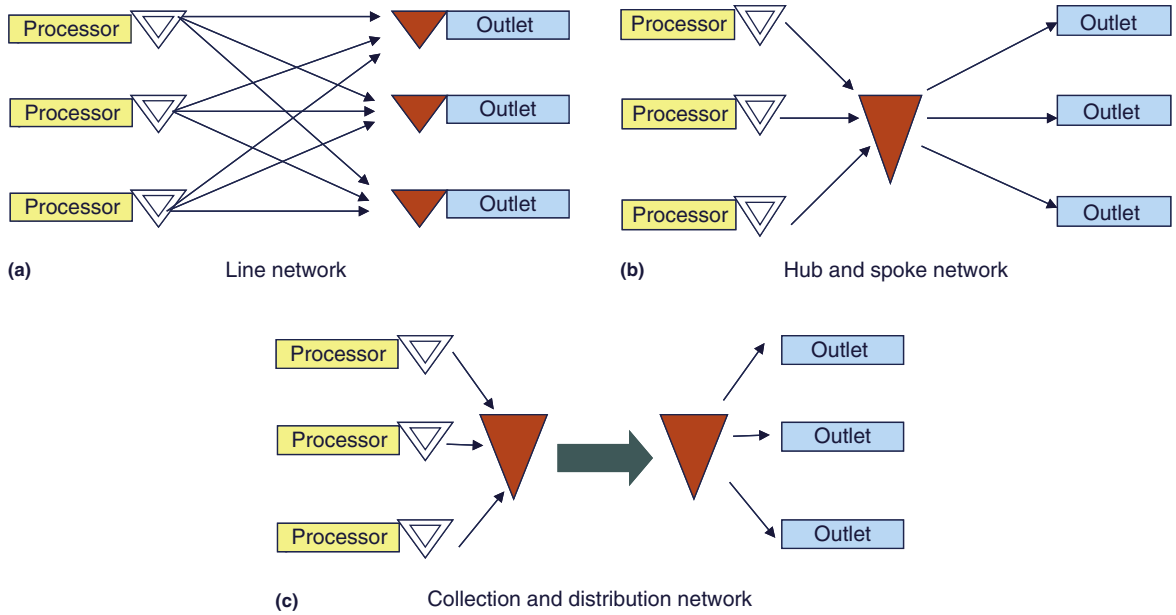


Figure 4 Overview of the three main network designs (reverse triangle = stock point).

accepted by customers, the more efficient the supply chain can be organized.

The last decade, the general trend is to shift the CODP upstream the supply chain (toward suppliers) in order to increase the responsiveness to variable market demand and limit the amount of nonvalue-adding activities. Information is then required to increase the speed of information exchange as to realize acceptable lead times. A good example is the fabrication of cars; nowadays cars are assembled only after the customer order has been received requiring very flexible manufacturing systems. However, if short lead times are requested and distances are large it is evident that one needs a stock point close to the market.

Logistics Network Design

A lot of research has been conducted on the design of distribution networks (including inventory location) and the added value of consolidation practices. Key decisions are where to store goods, where to (re)pack goods, and how to transport goods to customers.

Consolidated distribution is required when the volume of the goods to be distributed is smaller than the transport unit size (combining less than truck loads) or when the total traveling distance can be reduced by recombining full truck loads. Consolidation is often needed when, for example, the delivery frequency is increased with a resulting decrease in delivery batch size. There are three types of consolidated transportation (Ghiani *et al.*, 2004):

- Temporal consolidation, this means that goods from trucks that have different departing times are consolidated into other transport units (shifting with schedules in time);
- Facility consolidation, this means that goods that have different destinations are now transported together in a transport unit for (part of) the route; and
- Product consolidation, this means that goods with different characteristics (e.g., chilled, frozen or potted plants and vegetables) are transported together in one transport unit.

The result of consolidation should be a reduced total number of transport unit kilometers (and thus environmental pollution) by either a reduced transport distance (by optimal route planning) or reduced number of freights movements (by more full transport unit loads). Consolidated distribution is therefore a specific network design of sources (departing points), routes and sinks (destinations).

In general, one can state that there are three basic distribution network designs (see Figure 4):

- Line network, where each distributor has its own transport network to outlets.
- Hub and spoke network, where each distributor delivers the goods to a central hub where goods are exchanged aiming for specific network destinations.
- Collection and distribution network, especially suited for international networks, where each distributor delivers the goods to a central collection hub; goods are consolidated in time, regional destination, and product type; and successively transported to a distribution hub, where goods are resorted (added with products from other sources) and distributed to specific locations.

Note that inventory management is one of the design variables in the distribution network. In Figure 3(a) a number of inventory points are presented; however, these could just as well be cross-dock facilities where consolidation activities are performed and no inventory is kept.

As can be seen from Figure 4(a) hub may perform a consolidation or concentration function to combine many small separate flows into larger flows or split a larger flow into separate smaller flows for different destinations. Thus, hubs are intermediate points along the paths followed by

Box 1 Consolidation of distribution

In 2012 in the Netherlands, four producers of fast moving consumer goods (namely HJ Heinz, FrieslandCampina, Hero Benelux, and SCA Hygiene Products) started a collaboration to consolidate the distribution of their goods flows to (the same) retail distribution centers. They jointly selected a logistics service provider (Nabuurs) who established a new joint distribution center that stores products from all four producers. Distribution now takes place from three locations with a total surface of 63 000 m^2 (90 000 pallet locations). With this process they have changed from a line network, in which each partner delivered the retailers independently, to a hub and spoke network, in which all products are delivered to and from a central warehouse. Research is taken place to assess the possibility of setting up a joint distribution center in the international market as well, from which the products would be distributed to the international clients. This would then further transform their network into a collection and distribution network. The same research activities (and transition processes) are taken place in the flower trade network (see www.davinc3i.com).

origin–destination flows. Groothedde (2005) provides an excellent literature review on hub network design.

It is clear that the network complexity greatly influences the opportunities for improved logistics network designs and roles of logistics orchestrators. The next section will discuss the ins and outs of logistics orchestration concepts (**Box 1**).

Logistics Orchestration

'Orchestrate,' by Webster dictionary definitions, refers to 'the act of arranging or combining so as to achieve a desired or maximum effect.' Orchestration, translated to global food supply chains, means coordination of these chains so as to achieve maximum customer value. Owing to the high complexity and multitude of actors and stakeholders in global food supply chains, logistics orchestration is in many cases performed by third party logistics service providers (LSP).

Logistics outsourcing means an organization uses an LSP to carry out an activity, which is originally performed in-house (Bolumole, 2001). The role of LSPs has changed since the emergence of the SCM concept. SCM asserts that organizations along the supply chain need to reconfigure their operations by internal and external cooperation in order to accommodate changing customer requirements. To achieve seamless supply chain operations, organizations are looking for solutions from LSPs (van der Vorst *et al.*, 2006).

There are different ways to distinguish LSPs, for example, according to their degree of customization (Delfmann *et al.*, 2002), or by ability of general problem solving and customer adaptation (Hertz and Afredsson, 2003). On the basis of these researches, three main types of LSPs (Hsiao *et al.*, 2010) can be distinguished:

1. Standard LSPs (second party logistics): The companies who provide standard and traditional services, such as transportation and warehouse-based (Long, 2003). The service fulfilled for the customers are standardized, resulting in highly interchangeable services among this type of LSPs. These companies are highly specialized in their field and do not take over coordination or administrative functions for their customers. Standard LSPs plan, implement, and control their own logistics system according to their requirements and considerations.
2. Integrated LSPs (third party logistics; 3PL): These companies provide value-adding services and also provide at least two standard services without becoming the owner of the goods. In other words, they combine selected standard services to bundles of logistics services according to their customers' wishes. The operational coordination and arrangement of these services bundles are provided by the LSP, whereas the disposition lies in the responsibility of the buying company (Delfmann *et al.*, 2002). For example, transportation combined with value-adding activities such as assembly, repacking and quality control activities. These bundles are offered undifferentiated for all potential customers and thus cannot be regarded as customized services.
3. Logistics network orchestrator (fourth party logistics; 4PL): The term 4PL was first coined and registered by Accenture Consulting Company as a trademark in 1996. Accenture defined that "A 4PL provider is a supply chain integrator that assembles and manages the resources, capabilities, and technology of its own organization with those of complementary service providers to deliver a comprehensive supply chain solution." (Hertz and Afredsson, 2003). A network orchestrator is a nonasset-based service provider, which means that it has no trucks or warehouses of its own, who outsources logistics activities to standard or integrated LSPs. It is a company who provides supply chain planning activities and designs logistics services and logistics systems according to the preferences of their clients. Overall, a network orchestrator takes over coordinative and administrative responsibility for their customers, and takes over responsibility for the effectiveness and efficiency of the logistics system of its customer (Delfmann *et al.*, 2002).

Koppius and Eric (2005; 274) state that "A network orchestrator has an overview of the resources and capabilities of the network members on one hand and the demands of the end-customer on the other hand. The network orchestrator is responsible for configuring the network such that customers and network member preferences are satisfied." A network orchestrator assembles and manages the resources, capabilities, and technology of its own organization, clients, with those of complementary service providers. Collaborators together carefully plan how capacity should be created throughout the system, and decide jointly where and in what quantities inventories of various types should exist (Stadtler, 2005). Moreover, they must also decide in advance what actions will be taken when various unplanned events occur. Thus strategic and tactical plans must be created collaboratively to achieve the maximum system effectiveness. These plans describe how the supply chain will respond to variations and uncertainty (Muckstadt *et al.*, 2001). Activities that are executed by a 4PL are all related to the obtaining of the right information, and translate this into activities. Examples of activities executed by a 4PL are: market search, logistic network management, transport sourcing, optimization, administration, carrier contract negotiation, order handling and invoice management, production,

warehousing and distribution, returns management, and analyzing and reporting of key performance indicators (performance management).

Several researches are done about the reasons for the increasing use of 3PLs in the supply chain. Shanahan (2004) surveys in his article '3PL Roles Continue to Grow,' the growing role of logistic providers as integral part in the global supply chain and the arguments behind this. According to Bolumole and Wilding, the main reasons why organizations decide to make use of 3PLs are:

- To deal with a more complex supply chain;
- Increasing focus on core business processes;
- Reduction of distribution costs;
- Avoiding extra (inefficient) investments;
- To get access to more centralized distribution systems, what many companies do not have;
- Getting access to wider and existing markets (globalization);
- Improving service level;
- Assessing present and future market prospects for products and services; and
- To keep up-to-date with technological advancements (Box 2).

Quality Management and Standards in Global Food Supply Chains

The previous section considered logistics processes in global food supply chains. Quality is a key attribute of food products in production as well as in logistics and distribution processes.

Quality management systems enable companies to assure quality and safety of their products and to serve various market segments with the requested quality preferences. Quality management systems encompass elements such as product design, process management, supplier quality management, customer involvement, information exchange, strategic planning, training, and employee involvement. Although most quality management systems include procedures for purchasing, sales and distribution processes, the focus so far is on quality management within firms or from a single firm's perspective.

Gradually, however, attention for intercompany management relationships and chain management has increased in the last decades. Referring to the previous section, a quality management system involving horizontal and vertical dimensions of a chain can provide the means to deal with the complexities related to specific quality characteristics of food products. In this regard, it has been noted that actors in global food supply chains increasingly link their firm level quality management systems. The driving force is the awareness that each actor in a chain can enhance its performance and product quality through aligning its goals and activities with other actors, thus optimizing the results of the whole chain.

In the past decades, many firms have adopted private quality standards to which suppliers have to comply. For example, large retailers have developed initiatives to commit their suppliers globally to strict food safety and environmental regulations and to a high standard with regard to labor conditions. These quality and safety standards require extensive documentation of products and production processes combined with third-party certification and auditing, and strict gathering, storing, processing, and transferring of quality-related information between firms in the chain (Trienekens and Zuurbier, 2008).

In this section, first the typical aspects of quality management in food supply chains are considered, using the pork supply chain as an illustrative example. In Section Tracking and Tracing, public and private standards in global food supply chains will be discussed.

Box 2 Case example: Nike Inc. (Harps, 2004)

Nike is an example of a company, which has possession over the commercial as well as the logistic orchestration. Nike designs sport accessories for all kind of sports and ships products to 143 global destinations. Nike's logistics operations are complex, involving three product lines – footwear, apparel, and equipment – and four regions, managing orders through the company's logistics service provider network. Setting up the network of providers is a collaborative process between the regions and Nike's corporate logistics group. Nike works with two global ocean consolidators, five ocean carriers, four airfreight forwarders, and one courier. The two consolidators (APL Logistics and Maersk Logistics) are responsible for physically handling the cargo from the factory, receiving the freight, loading the containers, communicating to destinations in planning shipment deliveries, collecting documents from the factory, and forwarding them to the destination regions. Nike has chosen to manage its logistics providers in-house rather than outsourcing management to a lead (or fourth-party) logistics provider. The main reason to do so is the complicated supply chain network process, the in-house expertise on supply chain management and the need to stay in constant contact with their customers regarding need dates and freight movement.

Quality Control in Supply Chains – Example of the Pork Chain (Parts of this Section are Based on Trienekens and Wognum (2013))

A food supply chain delivers products to consumers who are at the downstream end of the supply chain. These consumers have differentiated demands with respect to the attributes of the products they consume. In general, intrinsic and extrinsic product attributes are distinguished. Intrinsic attributes can be measured on the product itself and are typical search and experience attributes. Classes of intrinsic characteristics are sensory characteristics such as tenderness of meat or color of fruits, health characteristics such as safety of the product and convenience characteristics such as type of packaging. Extrinsic product characteristics are linked to the production process and, in general, cannot be measured (by consumers) on the product itself. Typical classes of extrinsic attributes of food products relate to animal welfare in various stages of an animal food chain, ecological aspects like waste management, and origin and authenticity of the products.

In Table 3 the example of the pork supply chain is given.

As the aim of food supply chains is to support the end-customer/consumers with superior value, an interesting

Table 3 Intrinsic and extrinsic pork product attributes and indicators

Intrinsic		*Extrinsic*	
Sensory	Tenderness	Animal welfare	Farm production system
	Color		Transportation
	Marbling		Slaughter
Health	Safety (zoonosis)	Ecological food print	Farm manure and waste management
	Food additives		Transportation
	Antibiotics		Slaughter products (high and low value)
	Residues		
Convenience	Packaging	Origin and authenticity	Production location
	Shelf-life		Community impact
	Preparation characteristics		Farm production system
			Processing system

Table 4 Product and production attributes of interest at different pork chain links

Actor	*Attributes valued*
Feed producer	Value added feed mixtures and conversion rate
Breeder	Growth rate, feed conversion, muscle structure, and carcass characteristics
Farmer (farrowing and fattening)	Growth rate, feed conversion, slaughter weight, meat percentage, and muscle structure
Slaughterhouse	Water holding capacity (WHC), intramuscular fat, pH, and tenderness
Processing	WHC and intramuscular fat
Retail	Color, shelf-life, freshness, tenderness, juiciness, and marbling,
Consumer	Taste, tenderness, color, juiciness, marbling, and convenience

question from a food SCM perspective is, whether all stages in the food supply chain are directed at the achievement of the product attributes that are requested by the consumers the supply chain aims at.

In the pork example chain considered, a feed producer is mainly interested in selling feed mixtures with high added value. A breeder will focus more on pig genetics for achieving high growth rate and optimal feed conversion. A farrowing farmer is interested in sow performance and mother behavior. A finishing farmer is also interested in pig characteristics like growth rate, feed conversion, and specific characteristics like meat percentage and muscle structure, because these are the characteristics that he is paid for by the slaughterhouse. However, although the payment system of slaughterhouses is based on these carcass characteristics, the payment of further downstream stages in the supply chain is largely based on process qualifications like weight, size, fat layer, and meat quality characteristics such as juiciness, marbling, and Ph value. Alternatively, for retailers attributes like color and shelf-life are of interest, whereas for consumers these and other attributes like taste and tenderness are of importance. Table 4 shows some of the major attributes as valued by various pork chain partners.

Chain actors can also influence quality attributes of the products they produce in various ways. For example, in the pork meat chain the choice of genotype at the farmer stage will impact on the final meat quality achieved (e.g., Duroc delivers more tender meat and Large White less); at the transportation and slaughterhouse stages limitation of stress at the animal (e.g., by adequate resting time after transportation and CO_2 stunning before slaughter) will impact the final meat quality, as accelerated chilling after slaughter may have. Further, specific diets may influence meat quality, where additives like vitamin E and magnesium may lead to better color and water holding capacity (WHC), respectively. In general, one could say that tuning of production processes throughout the chain to end-customer demands may lead to more differentiated food products that better match with differentiated markets.

A major reason that attributes as valued in the various stages of the supply chain are not aligned is that processes from farm until the slaughterhouse are not directed at end markets, mainly because the payment system of slaughterhouses to farmers does not well relate to final market value. When, for example, the meat percentage is high, fat content will be lower. This means again that tenderness and juiciness (WHC) of the best valued carcasses is lower. The situation is somewhat different for supply chains directed at more differentiated and high-demanding consumer markets. In this type of supply chains, there is a tendency to align processes in the first stages of the chain more with consumer demands. In particular in niche chains like Iberian pigs, Mallorca Black, or Parma pork production in Europe a lot of attention is given to special feed and special meat-processing techniques to achieve the product that the consumer values. Such supply chains can be characterized by a clear vision on the markets they want to serve and the chain-wide approach that is necessary to best serve those markets.

In the last decade, however, globalization of meat distribution networks and large concentration through mergers and acquisition of slaughterhouses and meat processors brought about changes in the organization of the mainstream meat supply chains as well. The large players in these supply chains

are better able to meet differentiated market demand, as they increasingly cover diverse production systems at their input side (e.g., use of different genotypes, free range, etc.) that deliver meat with differentiated quality attributes and at the same time are able to reach more diverse markets globally. For example, fat pork bellies are highly valued in some Asian markets and much less in Western markets.

In the following section, translation of extrinsic quality attributes throughout the pork chain is dealt with. Table 4 mentions three classes of extrinsic attributes of pork products, namely animal welfare, ecological foot print, and origin and authenticity.

Animal welfare

Different stages in the pork supply chain can pay attention to animal welfare. Different levels of animal welfare have been defined which specify, for example, living space for pigs on the farm, feeding regimes through feeding systems where animals can choose themselves when to go for feed or innovative feeding systems that can recognize which pigs already received (sufficient) feed, housing for the pigs, like possibilities to stay outdoor, straw beds instead of slats, and group housing. During transportation small nonmixed groups may have a positive effect on animal welfare. At the slaughter stage, resting time before slaughter, nonuse of electric prods, and ways of stunning (electrical or CO_2) have an impact on animal welfare.

Ecological footprint

Current research indicates that pork supply chains negatively impact the environment. For example, global warming potential of pork ranges from 2.9 to 5.6 kg CO_2e per kilogram carcass weight, depending on the differences in production systems and management (Nguyen *et al.*, 2012). In pig farming, feed production has the most impact on global warming potential. As the largest part of the production cost of a pig is covered by the feed the animal consumes, conversion rate of feed is of ecological interest to the farmer. Manure surplus is the second major contributor to the ecological load of pig farms (Nguyen *et al.*, 2012). Transport is not a major contributor to the negative impact of pork production on the environment (Hermansen and Kristensen, 2011), at least when restricted to regional transportation. Cooled international transportation does have a larger impact. At the slaughterhouse stage, the main impact is from fossil energy use and waste.

Origin and authenticity

In the European Union, authenticity and origin of food are in many cases related to systems known as protected designation of origin (PDO), protected geographical indication (PGI), and traditional specialty guaranteed (TSG) (European Commission (EC), 2006a,b). PDOs are agrarian products or foodstuffs, which are produced, processed, and prepared (almost) exclusively in a given geographical area. The product's characteristics are also the result of the geographical conditions. To obtain a PGI designation at least one of the stages of production, processing, or preparation must be linked to the specified region (European Commission (EC), 2006b). In contrast to PDOs and PGIs, TSGs do not need any specific connection to a geographical area. They are characterized by special attributes of ingredients or processing stages and they must have a traditional background, which means that they must have existed on the market for at least 25 years.

Box 3 Iberian cured ham

Iberian cured ham has four denominations of origin: Dehesa de Extremadura, Guijuelo, Jamon de Huelva, and Valle de los Pedroches. Most Iberian pigs come from the Southwestern regions of Spain, in the 'dehesa' (meadows and woods). Apart from Iberian, there are two other Spanish PDOs in cured ham, Jamon de Teruel and Trevelez. There are two breed designations: 'Iberico puro' from sow and boar of pure Iberian breed with genealogic documentation, and 'Iberico' from pure Iberian sows. Feeding practices in the finishing period (Iberian pigs grow up to 160 kg) are also grouped into four designations: 'Bellota' (finished on a diet of acorn, grasses, etc. in the 'dehesas'); Recebo (finished on partly the same diet as the 'Bellota' animals but with additional concentrates); and Cebo (mostly fed with feed concentrates and sometimes additional acorn and grasses). Bellota and Recebo live a large part of the year in open areas with abundant acorns or fenced meadows. The fabrication of the hams is according to traditional procedures. (Trienekens *et al.*, 2009)

Box 3 depicts an example of a PDO product. In Iberian cured ham production, besides a focus on origin and authenticity, free range keeping of animals is considered to have a positive impact on animal welfare (see Box 3).

The next section will go into food quality and safety standards that are the basis for many quality management systems throughout (global) food supply chains.

Global Food Quality and Safety Standards

Public regulations

On a global level, in particular, the Food and Agricultural Organization (FAO), the World Health Organization (WHO), both United Nations organizations, and the World Trade Organization (WTO) deal with food safety issues. In 1962, as a result of the Food Standards Program, the Codex Alimentarius was established by the WHO and FAO to act as an umbrella organization for policymaking regarding food on a global level. The aim of the Codex is to protect public health and to support balanced trade relationships in food. For this purpose, standards are developed. Codex Alimentarius food standard issues range from specific raw and processed materials characteristics to food hygiene, pesticides residues, contaminants, and labeling, to analysis and sampling methods. Since the establishment of the WTO in 1995, Codex standards are used in trade disputes. Most countries around the world are members of the Codex, covering 98% of the world population. The Codex Alimentarius has great relevance to the international food trade. With respect to the increasing global market, in particular, the advantages of having universally uniform food standards for the protection of consumers are self-evident. It is not surprising, therefore, that the Agreement on the Application of Sanitary and Phytosanitary Measures (SPS) and the Agreement on Technical Barriers to Trade (TBT) both encourage the international harmonization of food standards.

According to the SPS agreement, WTO members are obliged to apply only those measures for food safety and quality that are based on scientific principles and do not constitute a disguised restriction on international trade. Article 2.2 of the SPS Agreement states: "Members shall ensure that any sanitary and phytosanitary measure is applied only to the extent necessary to protect human, animal or plant life or health, is based on scientific principles and is not maintained without sufficient scientific evidence."

On national and international levels also much legislation on quality and safety of food has been established. For example, the EU has developed a wide range of legislative demands with regard to food safety. The EU Directive 93/43 on the hygiene of foodstuffs states that food business operators shall identify any step in their activities critically to ensure food safety and to ensure that adequate procedures are identified, implemented, maintained, and reviewed on the basis of HACCP. The General Food Law of the EU, implemented in January 2005, states the primary liability of food (and animal feed) companies in the event of unsafe products. This implies the implementation of monitoring systems at company level. With information from these systems it should be possible to determine the source of safety or quality problems, and it must be possible to find out where other items with the same problem are located in the supply chain. With regard to traceability, as of 1 January 2005, companies are obliged to keep registration of raw materials supplies and customer deliveries on a transaction basis.

In the USA the FDA Food Safety Modernization Act (FSMA) of 21 December 2010 aims to ensure that the US food supply is safe by shifting the focus of federal regulators from responding to contamination to preventing it.

FDA has a legislative mandate to require comprehensive, prevention-based controls across the food supply. The legislation transforms FDA's approach to food safety, which requires food facilities to evaluate the hazards in their operations, implement and monitor effective measures to prevent contamination, and have a plan in place to take any corrective actions that are necessary. The legislation provides significant enhancements to FDA's ability to achieve greater oversight of the food products coming into the US from other countries.

Private standards

Baseline for private standards

The three most important generic standards for quality assurance in the food sector are good agricultural practices (GAPs), hazard Analysis of critical control points (HACCPs) and International Organization for Standardization (ISO).

GAP systems include a set of guidelines for agricultural practices aiming at assuring minimum standards for production and storage. Important topics are pest management (optimal use of pesticides), manure handling at animal farms, maintenance of water quality, worker and field sanitation, guidelines for postharvest handling and transportation, among others. In the last decades, increasing attention has been given to managerial aspects like documentation, complaint and recall procedures, labeling, etc. HACCP is a systematic approach to the identification, evaluation, and control of those steps in food manufacturing that are critical to product safety. Currently, HACCP principles are the basis of most food quality and safety assurance systems (Codex Alimentarius, EU and US food legislation). HACCP identifies risks in the production processes that can lead to unsafe products, and designs measurements to reduce these risks to acceptable levels. HACCP aims at prevention of hazards instead of end-of-pipe inspection. It is basically designed for application in all links of the food chain, ranging from growing, harvesting, processing, distribution, and retail to preparing food for consumption (Box 4).

Box 4 HACCP

HACCP involves seven principles:

- Analyze hazards (biological, chemical, or physical);
- Identify critical control points (these are points in a food's production at which the potential hazard can be controlled or eliminated);
- Establish preventive measures with critical limits for each control point;
- Establish procedures to monitor the critical control points;
- Establish corrective actions to be taken when monitoring shows that a critical limit has not been met;
- Establish procedures to verify that the system is working properly; and
- Establish effective recordkeeping to document the HACCP system.

Preconditions for HACCP implementation are: sanitary design principles (e.g., linear product flow), GMP, and safety programs should be present; written specifications for all ingredients, products, and packaging materials should be present; sanitary design principles and maintenance schedules should be present; personal hygiene requirements, documented procedures to assure segregation and proper use of nonfood chemicals should be in place; traceability and recall procedures should be in place, etc.

Although GAP and HACCP pay attention to both technological and management issues, ISO focuses on management. The most used of all ISO standards is the ISO 9000 series for quality. These standards are independent of any specific industry. In the 2000 version (ISO 9001:2000) the objectives are: achievement of customer satisfaction by meeting customer requirements, continuous improvement of the system and prevention of nonconformity. In 2005, the ISO 22 000 standard, specifically aiming at managing safety in the food chain, has been published. It is a specific standard for food processors setting out safety management procedures. The standard applies to organizations ranging from feed producers, primary producers through food manufacturers, transport and storage operators and subcontractors to retail and food service outlets. The standard extends the ISO 9001:2000 quality management system standard, which is widely implemented in all sectors but does not specifically address food safety.

Private food safety and quality standards

Since the 1990s many private food quality and safety standards have been developed.

Standards can be set up to specify quality attributes of a product, including origin and authenticity, and production and processing methods. Increasingly, they include sustainability and ethical specifications relating to environmental impact, animal welfare concerns, and worker conditions.

Table 5 Quality standards in global food supply chains

System	*Based on*	*Origin*	*Aim/set up of the system*
British retail consortium standard (BRC)	HACCP and ISO	British retailers	Requires an operational quality system and an HACCP plan that includes environmental issues, product, process, and staff. Aims at processing/distribution stage of the chain
International Food Standard	HACCP, ISO, and BRC	German, French, and Swiss retailers	Aims to ensure food safety and the quality level of retailer-branded food products. Aims at processing/distribution stage of the chain
Safe Quality Food	HACCP and ISO	Australian retailers	Addresses not only food safety and quality, but also other issues such as animal welfare, environmental impact, ethical production, organic production, and religious preparation requirements. Aims at all stages of the chain
International Standard Organization (ISO 22 000)	HACCP	ISO	Management standard for any organization in the food chain, including feed producers and service providers
Retailer produce good agricultural practices (Global-GAP)	HACCP	European and US retailers	Global-GAP supports the use of HACCP and members are obligated to comply with national and international legislation. Primary producers have to show commitment to issues such as reduction of environmental damage, pesticide use, and efficient use of natural resources, health and safety for employees and traceability efforts

Abbreviations: HACCP, hazard analysis of critical control points; ISO, International Organization for Standardization.

The aim of standards is to:

- Ensure product quality attributes as well as origin and production methods used;
- Improve supplier standards and consistency and avoid product failure;
- Eliminate multiple audit of food suppliers and manufacturers through certification of their processes;
- Reduce transaction costs; and
- Serve as strategic tools for market penetration and competitive advantage of food supply chains.

Table 5 describes examples of globally applied standards. Being largely based on HACCP and ISO hygiene and food safety regulations, these systems are similar in many respects.

Besides the quality assurance standards that focus on quality and safety of food, standards that pay major attention to extrinsic characteristics, like sustainable 'Utz' coffee or Chiquita's 'Rainforest alliance' bananas are now increasingly observed. Moreover, in Europe there is an increasing number of PDO that are labeled as such to create extra value added. Although until recently these specific product and processing attributes were aimed for niche markets in Western countries, some of the extrinsic product attributes, such as animal welfare or sustainability attributes, are now swiftly integrated in basic retail and industry standards as indicated above. However, the design of new niche market-directed standards seems to be an ongoing process. Table 6 depicts typical extrinsic food product characteristics that might, given the developments depicted in the table, increasingly be included in quality assurance standards.

In general, three levels of quality standards can be distinguished. The base level comprises public regulations and standard baseline standards such as HACCP that are legally required in most Western countries. The second level consists of private standards that are widely applied by retailers and industry across the world and that, although not legally required, have become compulsory for food producers to get access to these particular buyers. However, above these private 'compulsory' systems layer, another layer of standards with even more specific demands has evolved. Well-known examples are Tesco's 'Nature's Choice,' which puts a number of environmental demands on top of Global-GAP demands, PDO labels, and fair-trade labels. In this perspective, it is expected that proliferation of standards will continue, only on a different level as was the case so far. Figure 5 depicts this three-layer model for quality system standards.

The Global Character of Food Safety and Quality Standards

In industrialized countries, most companies in the food chain comply with basic standards on food safety and quality. For developing countries and emerging economy producers the situation is more difficult.

Table 7 depicts the major trends, bottlenecks, and opportunities related to food quality and safety in Western Organisation for Economic Cooperation and Development (OECD) economies, emerging economies, and in developing countries.

Table 7 shows that the OECD countries especially focus on consumer-related topics with regard to quality management. Consumers increasingly are aware of safety and quality problems and companies should increasingly focus on consumers for the execution of food quality and safety management, for

Table 6 Extrinsic product attributes that might be included in production standards

Extrinsic attributes	*Consumer and governmental demands*	*Developments*
Process technology	• Animal welfare	• Increasing legislation on animal welfare
	• Nature of production system (e.g., traditional and organic)	• Increasing consumer interest in regional and 'natural' production
	• Feeding regime	• Strict legislation regarding animal feed content
	• Transportation distances	
	Input materials (fertilizers, pesticides, etc.)	Risk-based inspections of products (e.g., products from countries considered high-risk countries are inspected more often)
	Biotechnology	Consumer reluctance in EU (e.g., against gene technology)
Impact on environment, people, and society	Environment	• Attention of leading retailers (e.g., Tesco, UK) for environmental aspects in labeling
	Manure disposal	
	Deforestation	• Attention of global food companies for sustainability issues (e.g., Rain Forest Alliance label at Chiquita bananas)
	Pollution	
	Packaging	
	Food miles	• Strict legislation against manure disposal
	Global warming	
	Working conditions	• (International) legislation against child labor
	Child labor	• Corporate Social responsibility (CSR) policy at many multinational companies
	Contracts	
	Education, housing legal rights	
	Community	CSR policy at many multinational companies
	Educational support	
	Economic development	
	Healthcare	
Supply and demand	Fair trade	Increasing consumer attention for fair-trade products
	Procurement	• Stricter legislation of Western countries against unethical practices
	Favoritism	
	Bribery	• CSR policy at many multinational companies

example, through traceability systems covering the whole chain. Communication about food safety and quality in the chain can be further improved, for example, dissemination of R&D knowledge. Currently, food chains have to comply with many private and public demands on quality and safety, which may result in multiple audits, although harmonization efforts have been successful at the level of the private 'compulsory' systems (see Figure 5). In this regard the Global Food Safety Initiative, initiated by a number of global retailers, has put a lot of effort in harmonization of these systems. However, companies are also involved in developing innovative products, such as organic products, and packaging materials, complying with new standards.

Emerging economies are focusing on developing new markets, both national and international. Several of these countries (Brazil, China, and India) have considerable home markets, but due to the unequal income division, requirements on these markets differ heavily, which results in the development of separate supply chains including different quality requirements for national and international markets. In fact, this group of countries is in the middle of a process of awareness and adoption of quality and safety regulations both for government as for the business. The design of organizational and governmental structures for ensuring food safety and quality has priority. In this regard, food safety policies are greatly influenced by the requirements of international trade. A major challenge is that food control is not adequately done, there are very few activities involving preventive inspection, little attention is paid to education of these standards and the sanction system is weakly developed.

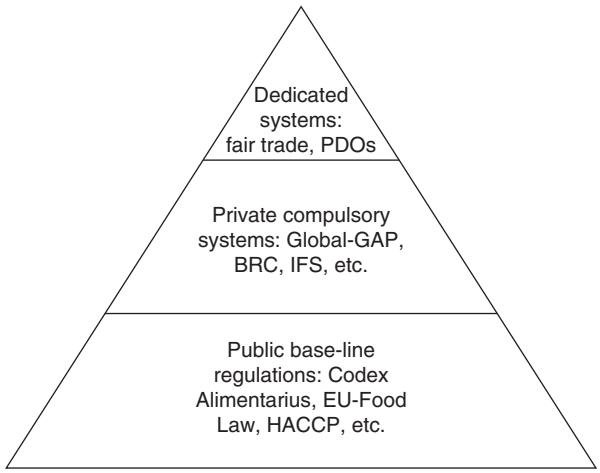


Figure 5 The three-layer model of quality standards. Reproduced from Trienekens, J.H., Zuurbier, P.J.P., 2008. Quality and safety standards in the food industry, developments and challenges. International Journal for Production Economics 113 (1), 107–122.

Developing countries are in a phase of discovering quality and safety of food as important conditions of international food trade and in many cases have to start from scratch or build on Western standards (Box 5).

Table 7 Trends, bottlenecks, and opportunities in international food chain development in different countries and regions

	Trends	*Bottlenecks*	*Opportunities*
Organisation for Economic Cooperation and Development (OECD) economies	• High consumer awareness regarding food safety and quality • Innovative materials/ products • Niche market development	• Limited communication on food safety and quality attributes • Limited knowledge of consumers on food safety and quality • Low dissemination of research and development knowledge on food safety and quality • Many private quality labels and public quality regulations	• Traceability to gain consumer confidence • Knowledge and experience dissemination • Chain-wide monitoring to ensure safety and quality of food • Possibilities for self-regulation for food companies
Emerging economies	• Focus on international markets (beef, soy, orange, coffee, pork, etc.) • Increasing local markets (e.g., Brazil, Russia, and China)	• Uneven income distribution • Lack of coordination (horizontal and vertical) • Lack of infrastructure (cold chain and roads/ports)	• Design of two coordinated subsystems on agrifood: (a) high quality for modern market segments and (b) average (but safe) quality for local market • Standards (PP) harmonization within countries and among countries • Coordination to improve inspections and enforcement
Developing countries	• Development of codes and standards • (Slowly) improving infrastructure/distribution • Producer collaboration	• No laboratories to analyze samples • No investments in transport and storage • Lack of legal framework and enforcement • Lack of market information • Lack of skilled/educated people	• Asia and Middle-East as new markets with less strict quality assurance standards • Improving feed and feeding system • Public/private network development • Cheap labor costs

Box 5 EU-regulation-based quality standard in Uganda and Kenya

The quality standard for fish in Uganda is based on EU directive 91/493/EEC and on Codex Alimentarius. The standard covers the following fields: microbiology levels, pesticide residues, heavy metals, effluents, Good Manufacturing Practices (processing stage), and HACCP (processing stage). For its export of fruit and vegetables, Kenya complies as much as possible to the UK's Food Safety Act of 1990.

Moreover, SPS and TBT often constitute barriers for export from developing countries to industrialized countries and producers at most times lack awareness and adequate information about specific demands of (the variety of) western standards. Important issues often deal about what, which, and how quality regulations and systems should be adapted. Moreover, the building of facilities to improve quality regulations and the building of governmental structures for ensuring quality and safety of products are key points of attention. Investments in (cooled) transportation and storage are necessary to effectively participate in international trade. The governments must encourage financial institutions to avail credit to farmers and play a facilitating role by providing market information, education, and the establishment of standards. Further, there is an opportunity for governments of these countries to work together in order to adopt a common stance and generate consensus with regard to trade negotiations in the WTO.

A big challenge for many developing country producers is the high costs of implementing and maintaining standards. In the last decade, however, initiatives from large industries (such as Unilever and Nestle) for collective certification of farmers have been observed.

Standards as organizational arrangements in global supply chains

Relationships between actors in global food supply chains are often hindered by uncertain supply markets and weak monitoring and enforcement regimes, although high investments are often necessary. Therefore, these relationships have to be safeguarded by the right organizational arrangements (governance mechanisms). In general, a distinction can be made between formal and informal governance mechanisms. Formal governance mechanisms include vertical coordination and (formal) contracts (Williamson, 1985, 1999). Informal governance mechanisms include informal agreements, trust, commitment, and reputation.

Quality and safety assurance standards, in many cases supported by third party certification organizations, are a formal governance mechanism through which coordination and control of quality attributes and safety of food products are assured. These standards are in most cases also included in bilateral (formal) contracts between parties in global food supply chains. However, as even specified arrangements do not

always guarantee compliance to standards and integrity of the information exchanged, informal governance mechanisms such as trust and commitment based on long-term relationships play an important role in compliance with customer demands and safeguarding information exchange in the supply chain. In this respect, trust often replaces more integrated governance mechanisms to safeguard against opportunistic behavior (Gulati, 1998). This article will not go further into governance arrangements in global food supply chains, as its focus is on operations. For further reading, refer to Williamson, 1999; Gulati, 1998; Gereffi *et al.*, 2005; Kaplinsky, 2000; Ruben *et al.*, 2007.

Box 6 StarBucks' Coffee and Farmer Equity practices

The Starbucks' Coffee and Farmer Equity (CAFÉ) Practices Program includes a broad set of social, economic, environmental, and quality guidelines developed by Starbucks in collaboration with Conservation International. The program started in 2001, as a response to pressure placed on Starbucks during the late 1990s by NGOs. The CAFÉ practices standard promotes coffee production practices that protect biodiversity, maintain healthy ecosystems, and support economic and social development in coffee production. To support the quality guidelines, Starbucks offers technical support via farmer support centers. Compliance with the standard is verified by a range of third-party verification organizations.

Transparency in Food Supply Chains

Transparency of information is an essential issue in food supply chains for logistics management and to guarantee food quality and provenance to all users of food and food products. More specifically:

1. Consumers require more and more information about the origin of products and the way the product is produced.
2. A reliable exchange of quality and health data throughout the chain provides actors with an instrument to better plan their production and sales processes and better match the right quality to the right market.
3. Availability of operational quality and safety data across the chain supports adequate risk management.
4. The increasing complexity of logistics flows caused by product differentiation, market segmentation, and internationalization, demands insight into production and stock data throughout the food chain, so that companies can make better forecasts and more effectively plan logistics and distribution processes.
5. On the basis of experience gained during the recent crises in the global food sector, traceability has shown to be a key capability for companies to find the origin of problems and recall hazardous products quickly.

Transparency Demands

As described in Section Global Supply Chain Management and Logistics, besides sensory, health and convenience (intrinsic) product attributes, consumers increasingly put demands on process (extrinsic) attributes. These extrinsic demands pose a number of information exchange challenges to actors in the food supply chain as people and organizations must be informed with integrity about these attributes.

For the government the main incentives to support food supply chain transparency include protection of public health through timely withdrawal of unsafe products, to prevent fraud regarding food product authenticity, and to control livestock diseases (such as classical swine fever).

The industry motivation regarding transparency is fourfold: first, companies need to comply with differentiating demands from consumers as well as legislative demands as described in the previous section. Second, when incidents occur companies are required and want to be able to quickly recall products from markets or links downstream the supply chain to limit the impact of the incident and minimize costs. Third, by improving information exchange through integrated information systems, optimization of business processes will be much easier as product and process attributes can be coupled with process performance. Fourth, an important way for food companies to add value is by paying attention to and labeling products according to distinguishing intrinsic and extrinsic food product attributes, such as those listed in the previous section. In the last decade, many companies in the food sector have been stimulated to implement corporate social responsibility strategies in which special attention is paid to ethical aspects of production and procurement. For example, supermarkets increasingly sell ethical responsible products, such as chocolate, with cacao produced according to fair-trade principles (Box 6).

By implementing transparent and integrated information systems supporting transparency aims, organizations can improve their image as they can propagate that products satisfy specific quality (intrinsic and extrinsic) demands. As referred to earlier, other motivations are logistical optimization, quality assurance, and process optimization.

Tracking and Tracing

The required ability to trace products back to their origin and production methods and to track the ongoing location of products has forced companies worldwide to implement coordinated information systems along the food supply chain.

The basic idea of tracking and tracing is the possibility to determine where a certain item is located and to trace the history of that item (**Figure 6**, van der Vorst, 2006):

- Tracking of items: the determination of the ongoing location of items during their way through the supply chain.
- Tracing aims at defining the composition of an item and the treatments that item has received during the various stages of the product life cycle. Chain upstream (backward) tracing aims at determining the history of items and is used to determine the source of a problem of a defective item. Chain downstream (forward) tracing aims at the determination of the location of items that were produced using, for example, a contaminated batch of raw materials.

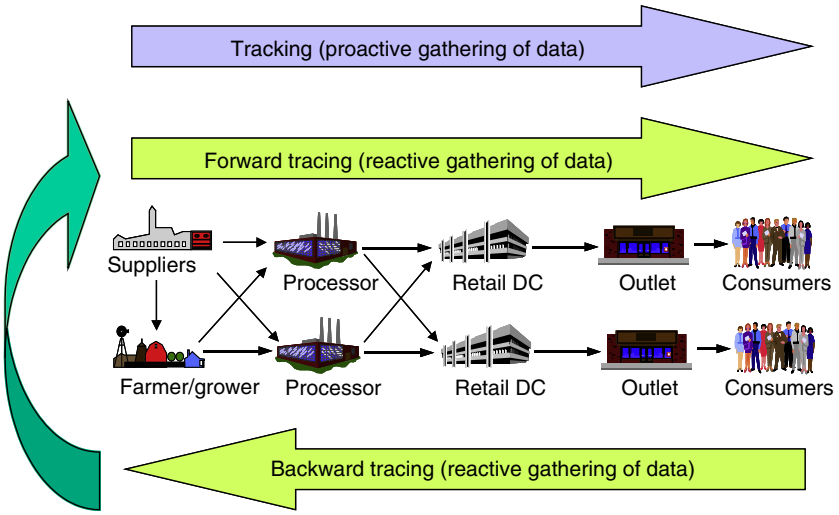


Figure 6 Tracking and tracing. Reproduced from van der Vorst, J.G.A.J., Beulens, A.J.M., van Beek, P., 2005. Innovations in logistics and ICT in food supply chain networks. In: Jongen, W.M.F., Meulenberg, M.T.G. (Eds.), Innovation in Agri-Food Systems. Wageningen: Wageningen Academic Publishers, pp. 245–292. (Chapter 10, ISBN 9076998655).

Tracking and tracing in food supply chains is a challenging issue. There are many sector-specific characteristics that complicate tracking and tracing, such as the following:

- The sector is characterized by high flow complexities. Food supply chains often combine continuous product flows (bulk, traced in volumes/weight) and discrete product flows (countable, traced in units). For tracking and tracing these mixed flows lots of bulk products downstream have to be linked with packaged products upstream.
- The lots of food product have to be clearly separated in order to prevent contamination. In particular for the continuous flows in food supply chains this is not easy to implement.
- Many food supply chains consist of alternating diverging and converging processes and byproducts. There are many composite products consisting of many components, including ingredients and packaging. All these components have to be tracked and traced. Food supply chains result also in a lot of waste and byproducts, which have to be tracked and traced as well.
- The product flows in different food supply chains are highly interdependent, for example, byproducts of one end product are input of other food products.
- Food products are natural products with a high perishability (in particular fresh food). There are also high demands from consumers and society, including food safety legislation, and quality standards. As a consequence traceability information must include additional information such as best-before-dates, country of origin of the ingredients, and certificates for quality, phytosanitary/veterinary, and ecological inspections.
- Food supply chains have a complex network structure where small and medium enterprises (farms and parts of the processing industry) trade with huge multinationals in the input and retail sector. Many food supply chains are also very international, among others to ensure a year-round-supply of seasonable products. As a consequence, supply has to be collected from many small producers all over the world that all have to be tracked and traced properly.

To enable tracking and tracing, detailed registration of process, resource, and product characteristics, such as origin and history of products, quality variation, etc., is essential for the food industry. Product information concerns the composition and sensory aspects of the products, as well as residue information (e.g., pesticides and hormones). Process information to be exchanged includes the origin of the product (and its components in the case of a composite product); the history of the product (where the products has been on its trajectory through the food supply chain and who has dealt with it), storage time and quality decay, quality variation within and between different product lots and resources used and waste.

A large actuality gap between the occurrence of events and recording of data is often a problem when systems have to be used more or less in real time, like in the case of product recalls. In many cases, it has been a (sometimes too) big challenge to timely and adequately link a food incident to data recorded earlier in time.

Virtualization of Food Supply Chains

Traceability systems focus on the information to track the location of certain items and to trace the history of that item. Building on these systems and utilizing new internet and sensor technologies, food supply chains can increasingly be virtualized, which implies that not only the location of items ('whereabouts') can be tracked and traced, but also the dynamic properties including quality conditions.

Virtual supply chains combine the perspectives of virtual organizations and virtual things (Verdouw *et al.*, 2012). Virtual organizations are dynamic organizational structures that temporally bring together resources of different organizations to better respond to business opportunities (Davidsow and

Malone, 1992; Goldman *et al.*, 1995; Venkatraman and Henderson, 1998). The virtual things perspective is related to the Internet of Things (IoT), which provides a vision of a world where physical objects are connected real-time to the internet. Virtual supply chains combine these two perspectives and can be defined as dynamic organizational structures that temporally bring together resources of different organizations based on the virtualization of the physical logistic objects such as containers, shipments, products, trucks, and vessels. The virtualization of physical objects allows for the decoupling of the physical and information aspects of logistics operations (Clarke, 1998). The actors responsible for planning, orchestration, and coordination are not necessarily also the ones handling and observing these physical objects and they can be at totally different locations. As a consequence, virtualization enables the decentralization or decoupling of physical flows from (centralized) planning, orchestration, and coordination taking place in other locations and by other partners.

Information systems can enable these virtual logistic networks with flexible chain-encompassing tracking and tracing systems and decision support based on that information. These systems effectively virtualize the logistics flows from farm to fork, support a timely and error-free exchange of logistics information, and provide functionality for intelligent analysis and reporting of exchanged data to enable early warning and advanced forecasting. Three critical features of these systems are distinguished (Verdouw *et al.*, 2013): real-time virtualization, logistics connectivity. and logistics intelligence (**Figure 7**).

Real-time virtualization

The interaction between real/physical and digital/virtual objects as apparent in the (IoT) is an essential concept of virtual logistic networks. In the IoT, physical entities have digital counterparts and virtual representations; things become context aware and they can sense, communicate, interact, exchange data, information, and knowledge (Guillemin and Friess, 2009). In other words, each physical object is accompanied by a rich, globally accessible virtual object that contains both current and historical information on that object's physical properties, origin, ownership, and sensory context (Welbourne *et al.*, 2009). Geographically dispersed physical objects have to be tied to and continuously update a virtual representation of the object, i.e., (lots of) products and logistic resources such as containers. The virtual objects must 'adequately' represent the identity, place, and (dynamic) properties of the (physical) objects of interest; they must be 'reliable' for different purposes of usage; they must be timely available and the security and privacy must be unquestionable.

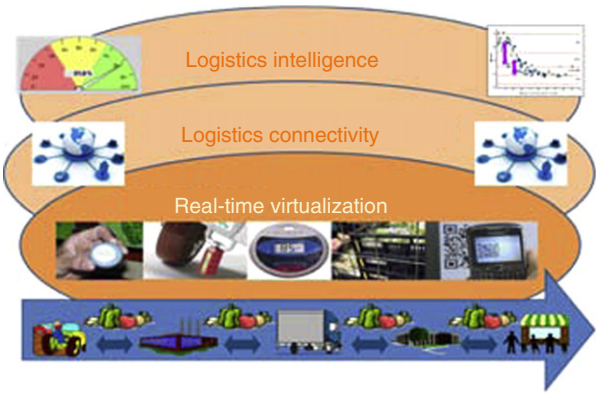


Figure 7 Virtualization of food supply chains.

A complicating factor in the food and agribusiness is that the properties of agrifood products are highly dynamic because they are living products. Furthermore, virtual objects must provide multiple views for different users, having distinct purposes of usage. Visualization plays an important role to create views that are experienced by human users as reality. Promising enabling technologies include advanced visioning technologies (including high-speed/low-cost solutions, 3D, and internal features such as ripeness), the mixture of real and virtual objects in augmented reality (including mobile applications), and in particular the combination of both the technologies.

Logistics connectivity

The internet acts as a storage and communication infrastructure that holds a virtual representation of things linking relevant information with the object (Uckelmann *et al.*, 2011). As such, virtual objects serve as central hubs of object information that combine and continuously update data from a wide range of sources. Logistics connectivity is of vital importance to enable timely, reliable, secure, and flexible data communication. This in particular requires (1) solid infrastructures to communicate information of objects while safeguarding property, access and usage rights and (2) standards for a seamless identification and exchange of product/logistics data. An important underlying challenge in virtual networks is to find solutions to support rapid configuration and the combination of federated and centralized solutions.

Logistics intelligence

The usage of dynamic virtualization data for intelligent decision support is an important future challenge. The shared information needs to be appropriate for planning, coordination, orchestration, and control of the logistics network. Therefore, information systems must support the intelligent analysis and reporting of exchanged data. These functionalities enable early warning in case of disruptions or unexpected deviations (e.g., in lead time, temperature, etc.) and advanced forecasting about consequences of detected changes by the time the product reaches destination.

Information Technologies Enabling Transparency of Food Supply Chains

The information intensiveness is very high in food supply chains. A lot of information must be continuously captured, edited, and communicated throughout the food supply chain to ensure the transparency needed for the tracking and tracing of food products from farm to forks as well as for the virtualization of planning and control. Automating these information-processing activities in information systems is of vital importance to make the resulting complex, frequent and interenterprise information flows manageable.

Information systems make it possible to share supply chain information in an efficient, timely, secure, and reliable way. The main enabling technologies are discussed below.

Automatic identification and data capture

Automatic identification and data capture (AIDC) is concerned with technologies that automatically identify objects, collect data about them and enter that data directly into computer systems. In the food sector, important AIDC technologies are barcoding, radio frequency identification (RFID), and in the future biometrics as well (e.g., deoxyribonucleic acid (DNA) technology). Pork and veal supply chains, for example, use RFID tags in ear labels to identify the animal throughout the supply chain until the processing stage. In recent years, the application of RFID in animal supply chains was extended to automatic identification (through readers) at feeding stations, enabling the adaptation of feeding and medicine use (mixed with the feed) to the individual animal, automatic weighing and selection of animals, temperature measurement to identify sickness of the animal, etc. RFID is also increasingly used in vegetables and fruit and in processing companies to identify lots of products. This enables adequate management of production and distribution processes and traceability and recall management. The use of DNA technology will be increasingly viewed as a promising solution to check provenance of food products.

Quality monitoring technologies

The monitoring of quality parameters is an essential issue in food supply chains that deal with fresh products. It is an important basis for quality-controlled logistics, that is, advanced logistics decision making taking real-time information on product quality behavior into account (van der Vorst *et al.*, 2011). Important enabling technologies are fixed sensors, advanced barcodes, data loggers, time–temperature Indicators, RFID-enabled sensors, and wireless sensor networks.

Enterprise information systems

Like in other industries, data captured in enterprise information systems are used for the planning and evaluation of production. These information systems support the processing of information at different levels ranging from (technical) operational to strategic. Here it is worth referring to examples such as warehouse management systems, specifically designed for the food industry for quality-controlled storage and distribution processes; laboratory information management systems, for quality and safety control of certain product lots or (groups of) animals; and the more generic enterprise resource planning (ERP) systems for integrated planning purposes. The applicability of ERP in the food sector is often considered to be limited, in particular in fresh food supply chains. Many ERP systems lack food-specific functionalities and the rigid planning and scheduling systems of traditional ERP systems may cause problems in the highly dynamic food sector. However, this situation is changing. The ERP industry has acknowledged the lack of flexibility and in the previous decade it has worked hard to transform ERP into web-based systems that are componentized based on service-oriented architecture. Furthermore, many sector-specific ERP solutions have emerged, also in the food sector.

Information integration

The previous technologies support the basic registration of data that are needed for tracking and tracing and supply chain virtualization. These data have to be shared within the supply chain via integrated information systems in order to create transparency. There can be defined four levels of integration (Wolfert *et al.*, 2010):

- Physical integration: technical infrastructure to enable communication between hardware components.
- Data integration: alignment of data definitions in order to be able to share data.
- Application integration: alignment of software systems so that one system online can use data generated by another one.
- Process integration: alignment of tasks by coordination mechanisms.

A rapid, error-free and efficient information transfer is only possible when information systems in the chain 'speak the same language.' This can be realized by basing information standards on business processes. These standards are fixed agreements on the size, contents, and meaning of the information (messages and coding) that is exchanged and the way in which these have to be communicated technically (via internet of labels). The most important information standards for the different integration level are (Wolfert *et al.*, 2010) the following:

- Standardization of the physical communication infrastructure makes it technically possible to connect products, hardware, machines, devices, and their operating systems. In general, standardization at this level is very mature, although new technologies are emerging, requiring new standards (e.g., RFID).
- Standardization for data exchange focuses on the format of messages and data definitions. The eXtended Markup Language (XML) has succeeded Electronic Data Interchange technology as the leading basis for data exchange standards.
- Application integration is mainly supported by standards for web services, that is, autonomous, reusable software components that are based on XML message technology that can be described, published, and invoked over the internet.
- Standards and reference process models that support design of integrated intra- and interenterprise business processes (Verdouw, 2010).

Many of the standards needed in food supply chains are not sector specific, in particular the technical standards, identification standards, and generic message standards. GS1, the international association that develops and implements standards for use in logistical systems (unique coding of product entities, transportation entities, etc.), is one common and standardized infrastructure to facilitate the efficient and effective exchange of data in the supply chain. Food-specific standards are mainly related to semantics for data exchange and process integration.

Supply Chain Information Systems

Supply chain information systems are software systems that support the rapid, error-free, efficient, and safe information exchange between supply chain participants, including systems

for tracking and tracing and supply chain planning. In collaborative supply chain environments, where there is close collaboration between horizontally and vertically linked companies in the food chain a joint infrastructure consisting of networks, coding standards, and integrated or coupled databases is established. Large companies, for instance slaughterhouses in meat supply chains, design their own systems to communicate with suppliers and for analysis purposes. Furthermore, increasingly small producers start collaborating through integrated information exchange, supported by third party service (software) providers. Integrated or coordinated databases at various network partners serve as the backbone of these integrated supply chain systems. The goal of these systems is the exchange of (quality performance and safety) data to enable transparency in the chain and to optimize processes throughout the chain.

However, in food supply chains that lack a dominating company, the adoption of centralized systems advances only with difficulty. Important limiting factors are a lack of intraenterprise interoperability and organizational factors such as unclear business models and a lack of trust in the privacy of data. Furthermore, the technology is complex. In particular, SMEs miss the competences and mass needed for implementation. As a consequence, the emphasis in this theme is shifting toward distributed software applications based on web services that support a rapid, reliable, secure, and flexible data communication.

In this section, it has been shown how information exchange in food supply chains is supported by information systems and information technology and that increasingly flexible systems are needed to be able to meet the broad range of information required by various chain actors and consumers (groups) and governments worldwide. However, although information systems and technology can enable and support information exchange and transparency in food chains, they can never guarantee the integrity of information and transparency that is wished for. Therefore, the authors state that trusted information exchange and transparency always imply a good match with supporting organizational arrangements (e.g., contracts and trust) and compliance with quality and safety standards.

Disclaimer

The contents of this article are for a large part based on previous publications of the authors.

See also: Consumer-Oriented New Product Development. Critical Tracking Events Approach to Food Traceability. Food Chain: Farm to Market. Food Labeling. Food Law. Food Marketing. Policy Frameworks for International Agricultural and Rural Development. Simulation Modeling: Applications in Cropping Systems

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Relevant Websites

www.codexalimentarius.org
Codex Alimentarius.
www.conservation.org
Conservation International.
www.fao.org
FAO.
www.fda.gov
FDA.
www.GS1.com
GS1.
www.ISO.org
International Organization for Standardization.
http://www.merriam-webster.com
Merriam-Webster Dictionary.

Government Agricultural Policy, United States

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Glossary

Crop-revenue insurance Deficiency payments have been largely replaced by crop-revenue insurance, which guarantees farmers fixed total revenues for their crops (based on acreage and average historical yield) regardless of fluctuations in price or yield.

Deficiency payment In US agricultural policy, the expected deficiency payment for a particular crop, c, is $E(d_{ct}) = \left[P_{ct}^{T} - \text{Max}\left(P_{ct}^{S}, E(P_{ct})\right)\right](1-\omega_{ct})L_{ct}Y_{ct}$, where P_{ct}^{T} is the target price; P_{ct}^{S}, the support price; $E(P_{ct})$, the expected average price received by farmers; ω_{ct} the percentage of land base required to be idled; L_{ct} the land base in period t; and Y_{ct}, the program yield per unit of the land base.

Nominal rate of assistance (NRA) The NRA measures market distortions imposed by governments that create a gap between the current domestic price of a product and the price that would exist under free markets. Under the 'small-country' assumption, this rate is computed as the percentage by which government policies have raised gross returns to farmers above what they would have been had the government not intervened (or the percentage by which government policies have lowered gross returns, if NRA <0). It, therefore, includes the effect of not only output-price-distorting policy instruments but also measures that alter the cost of farm inputs.

Relative rate of assistance (RRA) The RRA is defined in percentage terms as

$$\text{RRA} = 100 \times [(100 + \text{NRAag}^{t})/(100 + \text{NRAnon} - \text{ag}^{t}) - 1]$$

where NRAag^{t} and NRAnon-ag^{t} are the percentage NRAs for the tradable parts of the agricultural and nonagricultural sectors, respectively. If both of these sectors are equally assisted, the RRA is zero. This measure is useful in providing an internationally comparable indication of the extent to which a country's sectoral policy regime has an anti- (or pro-) agricultural bias. The RRA recognizes that farmers are affected not just by prices of their own products and inputs but also by the incentives faced by nonagricultural producers bidding for the same mobile resources.

Trade-reduction index (TRI) TRI measures the extent to which import protection or export taxation reduces the volume of trade. The TRI is defined as the percentage uniform trade tax which, if applied equally to all agricultural tradables, would generate the same reduction in trade volume as the actual intrasectoral structure of distortions to domestic prices of such tradable goods.

Welfare-reduction index (WRI) The percentage uniform trade tax which, if applied equally to all agricultural tradables, would generate the same reduction in national economic welfare as the actual intrasectoral structure of distortions to domestic prices of these tradable goods. The WRI recognizes that the welfare cost of a price distortion imposed by a government is related to the square of the price wedge and thus is positive, regardless of whether the government's policy favors or hurts producers in a particular sector.

Introduction

Agricultural policy in the United States is a complex and evolving web of governmental interventions in output markets, input markets, trade, public-good investments, renewable and exhaustible natural resources, regulation of externalities, education, and the marketing and distribution of food products. For the US federal government, these interventions have resulted in enormous budgetary costs, huge surpluses of farm products, major disputes with other countries, distorted international markets, and special benefits to interest groups that are often highly concentrated. These same programs, however, have contributed to an agricultural sector whose productivity over much of the last century has been spectacular.

Early US Agricultural Policies

In the second half of the nineteenth century, the US federal government began to design and implement programs to increase growth in the agricultural sector. From 1850 to the early 1900s, important institutions aimed at lowering transaction costs in the private sector began to emerge. For example, the Morrill Act of 1862 offered federal land grants to states so they could establish free, public institutions of higher education. Even at the outset, agricultural science research was a crucial component of these institutions. The US Department of Agriculture (USDA) was also created in 1862. It focused initially on collecting and disseminating research and designing regulations. In 1887, the Hatch Act created the Agricultural Experiment Station system by providing annual agricultural research grants to each state. In 1914, the Smith-Lever Act set up the nationwide Cooperative Extension Service, whose purpose was to provide new agricultural technologies and knowledge directly to farmers through a network of agents in each county of each state. The Cooperative Extension Service proved effective, partly because it served as the conduit for farmers to communicate back to the USDA and to the land-grant universities information about obstacles that needed to be researched.

These early federal policies can be generally characterized as long-run institutional developments: the government was supplying public goods whose associated benefits and costs

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were widely dispersed. In the next phase, beginning in the 1930s, the US agricultural policies focused on controlling supplies of commodities in order to increase market prices and net farm income. The agricultural industry was highly competitive, and competition gave individual producers incentive to adopt new technologies that would augment productivity and market supply. However, the inelastic aggregate demand for agricultural commodities meant that a large increase in supply would result in unacceptable price declines. Over time, this combination of low-demand elasticity and a high rate of innovation exerted downward pressure on agricultural and food prices. Not surprisingly, income and wealth in the agricultural sector often declined. Moreover, as agriculture is based on natural resources, it is vulnerable to productivity changes due to climate fluctuation, pest infestation, and other environmental factors. Thus, in addition to declining prices, farmers are often exposed to price instability.

In sum, the declining rate of profitability and return on agricultural assets over time generated economic incentives to reallocate resources away from agriculture. However, agricultural capital (both physical and human) are specialized, so that there are barriers to reallocating them to other sectors. As a result, owners of agricultural assets and skills have been left with little flexibility to respond to worsening terms of trade. This dynamic led historically to what was termed the 'agricultural problem' of decreasing prices, low income, and rural poverty (Schultz, 1964; Cochrane, 1958).

The tendency for pockets of rural poverty to persist in US agricultural regions led the government to develop policies aimed at raising farm income and supporting the value of agricultural assets. Thus, price and income support have become major features of agricultural policy since the 1930s. The instability of agricultural supply, which has affected both the well-being of farmers and the availability of food to consumers, also spurred the establishment of policies designed to stabilize supply of agricultural commodities. The vulnerability of agricultural crops to climatic and environmental conditions also motivated the introduction of governmental programs that extended beyond price and income supports.

Another major factor that has driven governmental agricultural policy is the desire to ensure affordable food. Once most of the agricultural land base of the United States had been settled, the most effective way to increase agricultural food supply (and, in turn, reduce prices) was to improve technology. This effort led the public sector (both federal and state) to continuously support agricultural research. However, farm groups (and their representatives) recognized that increased supply tended to reduce prices. As a result, additional policies aimed at supporting agricultural income implicitly became part of the compensation to farmers for enabling increased supply through publicly funded research (de Gorter *et al.*, 1992). The political bargaining between agricultural and urban groups led to coalitions that generated cooperative solutions aimed at sustaining farmers' welfare and expanding food demand through governmental food-assistance policies (such as food stamps and food aid to developing countries).

Naturally, the extent to which agriculture has been supported has depended on budgetary constraints and political–economic considerations (Rausser and Goodhue, 2002). The pressure to reduce support for agriculture may increase in periods in which the public feels growing concern about budget deficits and in which the political strength of agricultural lobbies is declining. The need to control costs and to respond effectively to natural variability thus caused the design of US agricultural policies to evolve over time.

Farm to Food Legislation

During the past 30 years, each successive 'farm bill' (the legislation that sets forth US agricultural policy) has reflected the public discourse of the day. For example, the Food Security Act of 1985 focused on loan programs, target prices, deficiency payments (the expected deficiency payment for a particular crop, c, is

$$E(d_{ct}) = \left[P_{ct}^{T} - \mathrm{Max}\left(P_{ct}^{S}, E(P_{ct})\right)\right](1-\omega_{ct})L_{ct}Y_{ct}$$

where P_{ct}^{T} is the target price; P_{ct}^{S}, the support price; $E(P_{ct})$, the expected average price received by farmers; ω_{ct} the percentage of land base required to be idled; L_{ct} the land base in period t; and Y_{ct}, the program yield per unit of the land base), acreage reduction, and public grain-stock reserves. The export provisions of the 1985 Act included food-aid and cargo preferences. Conservation provisions created 'sodbuster,' 'swampbuster,' and conservation reserve programs (CRPs), with the stated intent of removing highly erodible land and wetlands from production – and thus, indirectly, managing supply response (Rausser, 1992). The 1985 Act also authorized three alternative market-promotion programs and continued food-stamp programs. After the bill was passed, export subsidies from both the European Union and United States created a prisoners' dilemma global competition, with the net effect of decreasing world food-commodity prices as well as their volatility (Reagan, 1987).

By the end of the 1990s, it had become increasingly clear that any incremental improvement to the economic well-being of the US agricultural sector depended more on access to overseas markets than on domestic market demand. Accordingly, the flavor of public discourse resulted in a 1990 Farm Bill that particularly aimed to enhance exports. For the first time, this legislation included planning-flexibility provisions that promoted economic freedom by increasing farmers' ability to shift their resources in response to world market conditions. During this period (which coincided with the ongoing Uruguay Round negotiations), clear empirical evidence emerged that coupled-subsidy policies ultimately depressed market prices (Rausser, 1995).

In the political–economic process that shaped the 1996 Farm Bill (the Federal Agriculture Improvement and Reform Act), after the Uruguay Round had concluded, various commodity organizations and agribusiness interests coalesced in the hope of eliciting a more market-oriented agricultural policy. Partly as a result of these groups' influence, target-price deficiency payments were replaced by fixed 'production-flexibility contract payments' that would be paid during the ensuing 7 years, and both the crop-basis and the acreage-reduction programs were eliminated. For the first time, farmers participating in US government programs were allowed to make their own planning decisions free of government

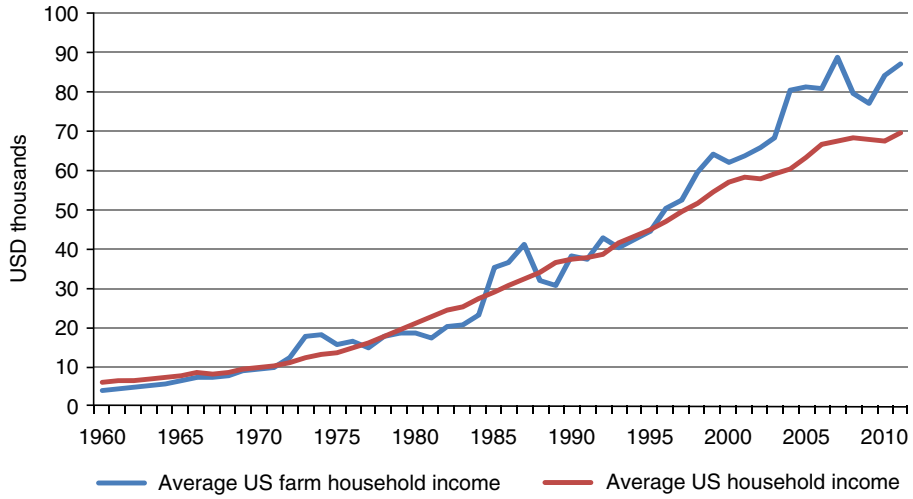


Figure 1 Mean US farm household income and mean US household income, 1960–2011. Reproduced from United States Department of Agriculture Economic Research Service, 2013. Farm Household Income and Characteristics. Available at: http://www.ers.usda.gov/data-products/farm-household-income-and-characteristics.aspx#.UhJrEpK1FAI (accessed 20.05.13).

regulations (with minor restrictions). Meanwhile, many in the economics profession hoped that these 7-year payments would allow the US government to gradually terminate commodity-market subsidization.

Unfortunately, political–economic forces squelched this hope. The 2002 Farm Security and Rural Investment Act budgeted almost US$40 billion over a 6-year period for commodity programs and almost another US$10 billion for conservation. Accentuating the movement from legislation focused on agriculture to legislation focused on food consumption, more than 50% of the allocations made in the 2002 Act (US$149.6 billion) was directed to food stamps and other nutrition-title programs.

This trend accelerated with the passage of the 2008 Food, Conservation, and Energy Act. The Act renamed the federal 'food-assistance' programs the Supplemental Nutrition Assistance Program (SNAP). SNAP's nutrition subsidies accounted for more than 75% of the outlays for authorized programs under the Act, and the budget authority more than 5 years for this Act totaled US$284 billion. By the second half of 2012, 47.7 million Americans (more than 15% of the population) received benefits from SNAP. During the last survey (2010), average net monthly household income for recipients was US $336. Children included 49% of the recipients' households, and 20% included nonelderly disabled individuals (USDA, Center for Nutrition Policy and Promotion, 2011). Thus, farm-bill legislation had gradually become 'food-bill' legislation.

Nutrition legislation, such as SNAP, has provoked intense debate between congressional conservatives and liberals – so much so that it is not clear whether SNAP will survive in its current form. As budgetary concerns increase, some members of the Congress are trying to reduce SNAP funding by tens of billions of dollars (Nixon, 2013). Others have proposed to separate SNAP from the farm bill completely (Weisman and Nixon, 2013). Still other critics of SNAP assert that the assistance provided is not doing enough to enhance health and nutrition. Public concern about obesity may lend force to such criticisms (Guthrie *et al.*, 2007).

As the explicit purpose of US support to agriculture has changed from subsidizing farmers to subsidizing food programs, a simultaneous shift has occurred away from deficiency-payment policies toward crop revenue insurance programs. Deficiency payments provided farmers with insurance in the event of low prices but failed to protect them against variability in yields. To help farmers hedge against the risk of falling prices as well as variable yields, crop revenue insurance programs guarantee that farmers will receive minimum total revenues (based on acreage and historical average yields). As a result, crop revenue insurance has quickly become the most expensive agricultural subsidy in the United States, costing taxpayers nearly a trillion dollars over the past decade. Crop revenue insurance programs in the United States have a sizable subsidy component because without the subsidy, participation would be low. It is important to note that these policies tend to reduce agricultural efficiency (Goodwin and Smith, 2013).

Another factor in the development of US agriculture and agricultural policy is a continuous trend toward increasing automation, capital intensity, and size of agricultural operations. Partly as a result of this trend, the wealth gap between farmers and the rest of the population has continued to shrink; in fact, both the income and the wealth of agricultural households have recently exceeded those of US households generally (**Figures 1–3**).

The changing profile of American farms has weakened the rationale for supporting farmers financially (Gardner, 1992). The relative wealth of agricultural and nonagricultural households is largely sourced with steadily increasing land values (**Figure 4**). However, governmental support for agriculture continues unabated.

Empirical Consequences of Market-Distorting Policies

The two main types of policy that distort agricultural markets are controls on quantity (output quotas) and controls on price (price targets that result in deficiency payments). In general,

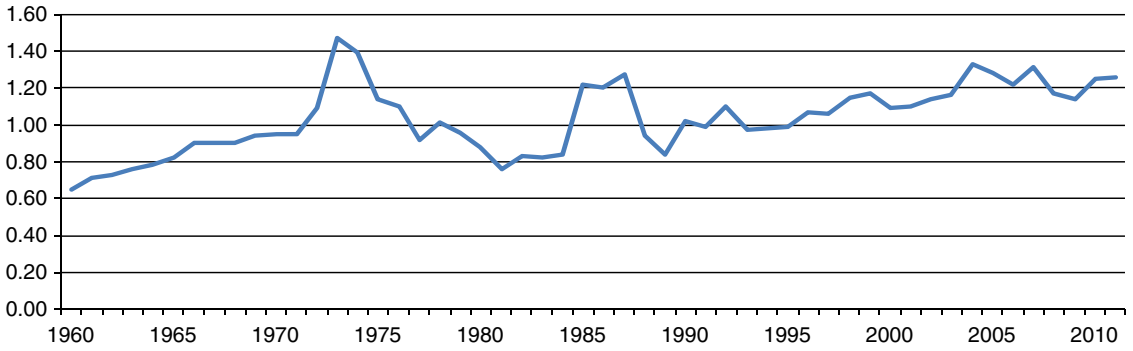


Figure 2 Ratio of mean US farm household income to mean US household income, 1960–2011. Reproduced from United States Department of Agriculture Economic Research Service, 2013. Farm Household Income and Characteristics. Available at: http://www.ers.usda.gov/data-products/farm-household-income-and-characteristics.aspx#.UhJrEpK1FAI (accessed 20.05.13).

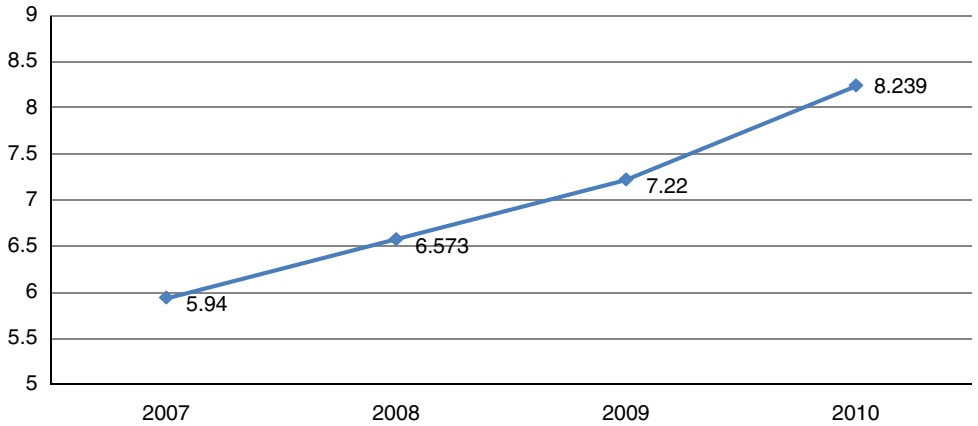


Figure 3 Ratio of median US farm household wealth to median US household wealth, 2007–11. Reproduced from Gottschalk, A., Vornovytskyy, M., Smith, A., 2011. Household Wealth in the United States: 2000 to 2011. Washington, DC: United States Census Bureau. Available at: http://www.census.gov/people/wealth/files/Wealth%20Highlights%202011.pdf (accessed 20.05.13) and Ahearn, M.C., 2012. Financial Position of Farm Operator Households. In: Agricultural Outlook Forum 2012, 126270. Washington, DC: United States Department of Agriculture.

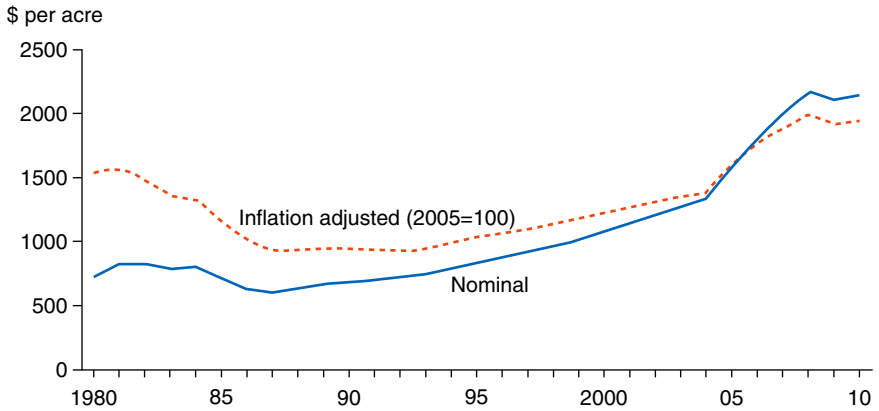


Figure 4 Average US farm real-estate values, 1980–2010. USDA National Agricultural Statistics Service (http://www.nass.usda.gov/).

setting a fixed output quota benefits producers but harms consumers, because it triggers higher prices relative to the decreased supply, given the inelasticity of demand. In contrast, setting a price control (i.e., instituting price support) benefits both producers and consumers but hurts taxpayers, because they must pay the difference between consumers' and producers' prices in the form of deficiency payments (Alston and James, 2002).

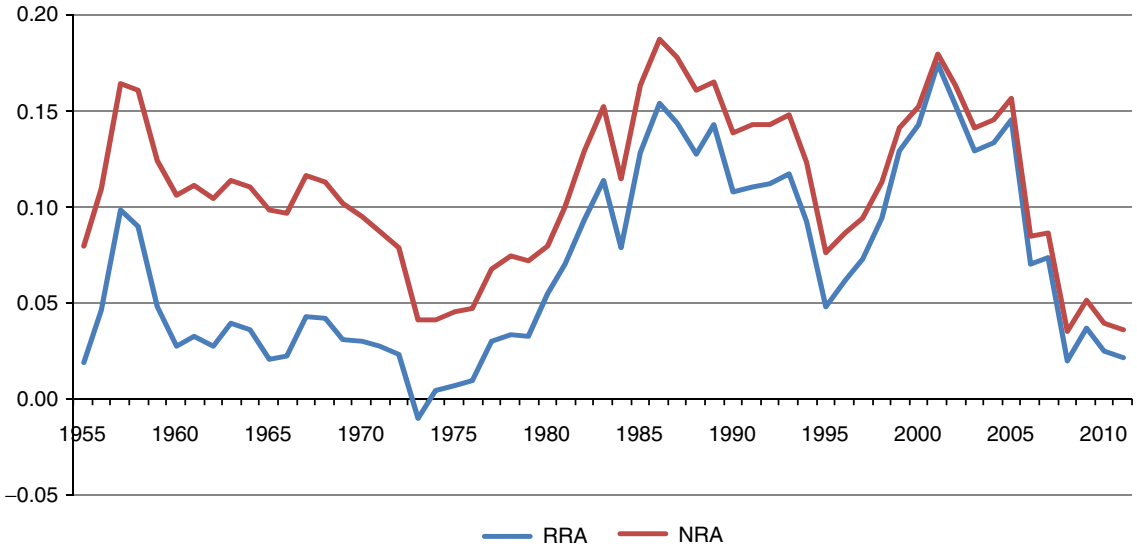


Figure 5 US RRAs and NRAs, 1955–2011. Reproduced from Anderson, K., Nelgen, S., 2013. Updated National and Global Estimates of Distortions to Agricultural Incentives, 1955–2011. Washington, DC: World Bank. Available at: www.worldbank.org/agdistortions (accessed 30.09.13).

The high levels of distortions to agriculture that result from government intervention have been recognized for decades. Recently, however, new and comprehensive data aggregated and synthesized by the World Bank (most recently by Anderson and Nelgen, 2013) have made it possible to analyze selected key metrics that quantify the impact of US agricultural policies. These statistics account for 77% of global output of the 30 most valuable agricultural products and represent 85% of global exports (Anderson *et al.*, 2013). The Nominal Rate of Assistance (NRA) reported by the bank approximates the governmental distortions that result in a gap between the current market prices and the prices that would exist in the counterfactual world of no governmental intervention (note that an NRA can be less than 0 if high export tariffs and farm taxes create a political environment in which the agricultural sector is stifled). The United States, of course, has had only positive NRAs in the last half-century (**Figure 5**).

Another, arguably more expressive, metric is the relative rate of assistance (RRA). It is calculated as follows:

$$\text{RRA} = 100 \times [(100 + \text{NRAag})/(100 + \text{NRAnon-ag}) - 1]$$

As it measures the percentage of a country's agricultural distortion relative to its nonagricultural market distortion, the RRA provides insight into a country's bias toward its farm sector (i.e., when RRA > 0, indicating that a country favors agricultural productivity) or against its farm sector (i.e., when RRA < 0, indicating that a country fails to stimulate agricultural productivity). As **Figure 5** suggests, when agricultural commodity prices were high in the United States (e.g., 1973, 2006, and 2009), RRAs were low. In contrast, during periods of low agricultural commodity prices (e.g., 1983–90), RRAs were high. Note that although agricultural prices have risen during the new millennium, rates of assistance have naturally fallen.

Traditionally, NRA and RRA levels increase with a country's per capita income; high-income countries have a positive agricultural bias and developing countries have a negative bias. However, in the last few decades, developing countries have shown a significant increase in their RRAs, so that the RRAs of both developed and developing countries are converging toward zero (**Figure 6**). This trend implies that less-distorting policy programs are generally being instituted.

The other two metrics that are important for understanding economic distortion caused by the government intervention are the welfare-reduction index (WRI; **Figure 7**) and the trade-reduction index (TRI; **Figure 8**). The WRI measures the welfare cost to consumers of these price distortions. As the WRI is related to the square of the deadweight loss wedge, it is always positive, whether the policy hurts or helps the agricultural sector. During periods of low commodity prices, when government subsidization has been substantial, high rates of welfare loss are evident. In recent years, however, increased openness of agricultural trade and the introduction of biofuels have led the welfare loss to decline.

Similarly, the TRI measures the percent change in trade volume caused by governmental policies, such as export tariffs and import caps (it could also be interpreted as the taxation amount that, if applied to all tradable agricultural products, would produce the same effect on trade). The 1980s, for example, was a period of high distortion and trade reduction (presumably, the government's goal at the time was to protect international prices of grain from further deterioration). In contrast, the new millennium has seen increased trade openness.

It is important to remember that the agricultural sector has unique subtleties, because the firm that owns the land is often not the same as the firm that operates the land. Landowners benefit the most from a system of price supports and output controls, as long as the output (or quota) certificates are issued to them, not to tenants. If the output certificates were issued to tenants, landowners would lose out, as the tenants, not owners, would receive any deficiency payments.

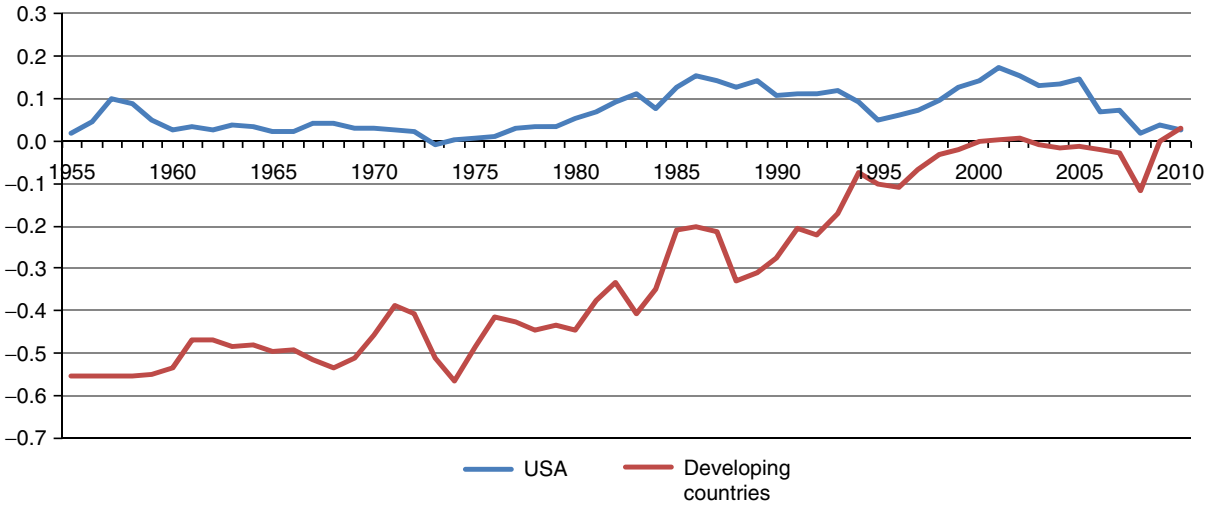


Figure 6 RRAs in the United States and developing countries, 1955–2011. Reproduced from the World Bank, 2013. Database for Distortions to Agricultural Incentives. Available at: http://go.worldbank.org/YAO39F35E0 (accessed 22.08.13).

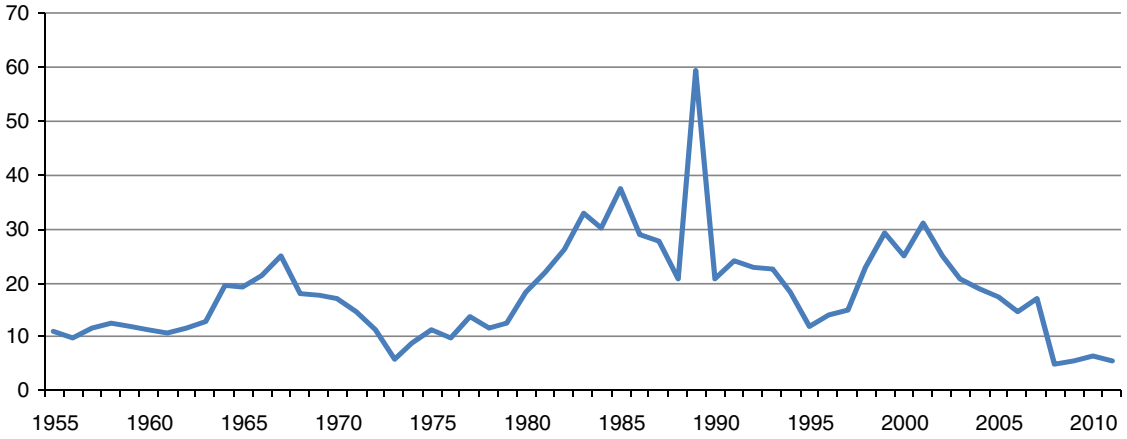


Figure 7 US WRI, 1955–2011. The WRI is related to the square of the deadweight loss wedge, so it is always positive, whether policies hurt or help the agricultural sector. Reproduced from Anderson, K., Nelgen, S., 2013. Updated National and Global Estimates of Distortions to Agricultural Incentives, 1955–2011. Washington, DC: World Bank. Available at: www.worldbank.org/agdistortions (accessed 30.09.13).

Even without output controls, landowners still benefit under price controls (price support). However, they would be adversely affected by acreage control or land set-asides. In contrast, tenants of agricultural land would be worse off under the dual price support–output control system than under no regulation, unless output certificates were issued to them rather than to landowners. Meanwhile, owner-operators of agricultural land who hire labor benefit under output controls because of their overwhelming land share compared with labor share. However prospective farmers trying to enter the industry, who often possess neither land nor capital, would be discouraged by both price support and output controls, as such measures would make agricultural land more expensive and thus create barriers to entry (Floyd, 1965). Price support or output controls favor preexisting farmers who captured the initial land rents that resulted from historical governmental intervention.

Unintended Consequences of US Agricultural Policies

Over the years, US agricultural policy interventions have resulted in significant unintended consequences. These consequences include periods in which the government has held large stores of agricultural commodities, variable input resources have been overallocated, and world food-commodity prices have been depressed. To relieve the pressures of excess supply, the US government has attempted to expand demand via programs such as foreign food aid, domestic food-stamps, export subsidies, and the USDA's Foreign Agricultural Service's export enhancements. The voluntary nature of these programs has allowed participants to gain access to governmental subsidies as long as they honor crop-acreage-base restrictions, acreage-idling programs, and conservation measures.

One of the most significant unintended consequences of US policy has been to create and exacerbate booms and busts

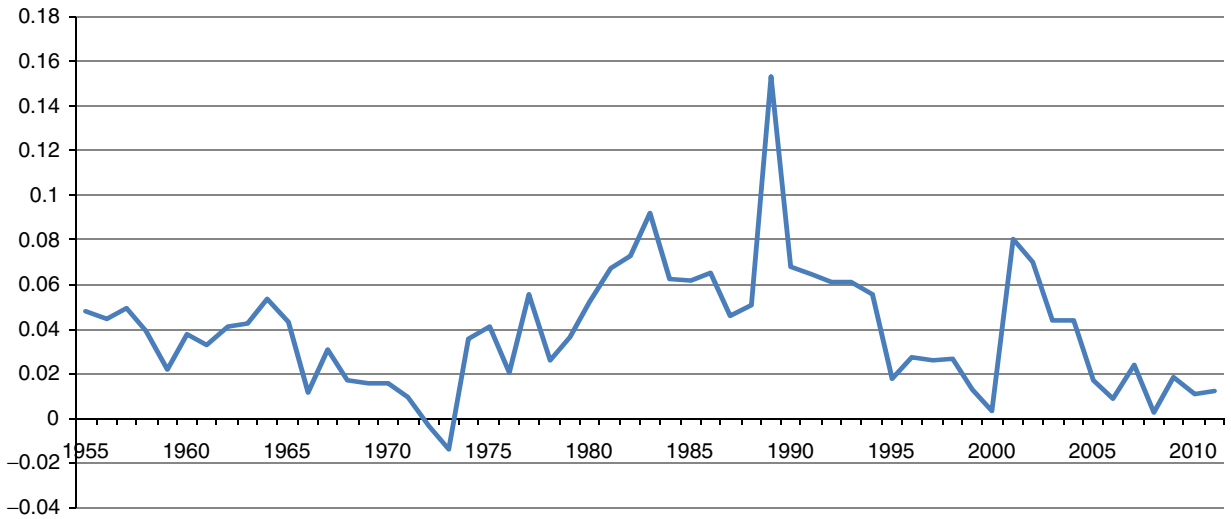


Figure 8 US TRI, 1955–2011. Reproduced from Anderson, K., Nelgen, S., 2013. Updated National and Global Estimates of Distortions to Agricultural Incentives, 1955–2011. Washington, DC: World Bank. Available at: www.worldbank.org/agdistortions (accessed 30.09.13).

in domestic and global commodity markets. Such commodity booms and subsequent busts are clearly exemplified in the early 1970s and again in 2008. Following shocks to either demand or supply (or both), market structures themselves tend to be the sources of these booms and busts. For example, in the 1970s, a huge outward shift in commodity export demand caused a spike in commodity prices. Similarly, in 2008, sharply increased demand for grains resulting from a huge increase in US biofuel production drove grain prices upward quickly.

Another major factor in commodity price fluctuation is stockholding. Both the 1970s and the 2008 price boom were directly preceded by the lowest levels in years of inventories of corn, wheat, and rice. These very low inventories help to explain the high volatility of commodity prices in the 1970s and in 2008: no stockpile could be drawn from to increase supply when needed. One early attempt to solve this problem failed: in the early 1970s, the US government started to print more money in the hope of inflating away the high real price of energy (Carter *et al.*, 2011). This increase in the supply of money simply drove prices higher, showcasing how macroeconomic linkages can cause price spikes in commodities across the board.

The varied effects of US monetary and fiscal policies, in combination with US agricultural policies, resulted in greater volatility of food-grain and livestock prices, with booms in the 1970s and busts in the 1980s. Booms can result from the 'overshooting' phenomenon, which was traced to the flex-versus-fixed-price dichotomy of Okum and Dornbusch (Rausser *et al.*, 1986). In particular, the disequilibrium in money markets caused disequilibrium in commodity-storage markets and exchange-rate markets. Economists recognized that both of these phenomena helped explain the price spikes that had taken place throughout the 1970s. In contrast, during the 1980s, the disequilibrium in money markets and exchange-rate markets ran in the opposite direction, forcing volatility on the downside for a number of food-commodity markets. Had it not been for government market-subsidy programs, the agricultural financial crisis of the mid-1980s would have been even more dramatic (Rausser *et al.*, 1986; Foster and Rausser, 1991).

The intricacies of cross-commodity linkages also can often conceal forces that drive price booms and busts. For example, high-energy costs during the 1970s and in 2008 more than doubled the cost of many fertilizers used as agricultural inputs, so that booms in agricultural commodity prices were inevitable (Carter *et al.*, 2011). Historically, short-term policy responses to supply shortages have exacerbated such problems and caused even larger price spikes. In one instance, after the former Soviet Republic bought 30 million metric tons of grain from the US in 1972, a domestic shortage of grains and soybeans occurred. To decrease demand sufficiently to mitigate the shortage, the federal government created an export embargo on soybeans in 1973. Although this measure worked in the short term, farmers were forced to sell at such low market prices that they had little incentive to increase soybean production. The resulting impacts helped Brazil displace the United States as the largest producer of soybeans (Carter *et al.*, 2011).

Other Forms of Intervention

Public Investment in Research and Development

Publicly funded research and development (R&D) has been a crucial component of the federal government's expenditures benefiting US agriculture as the Morrill Act secured land grants for public research institutions. The steady increase in public R&D (**Figure 9**) contributed to the sustained increases in agricultural productivity that occurred in the second half of the twentieth century.

In the United States, the complementarity between public-good R&D and commodity-based subsidization largely account for the huge productivity increases in food-commodity production (Rausser, 1992; de Gorter *et al.*, 1992). The federal

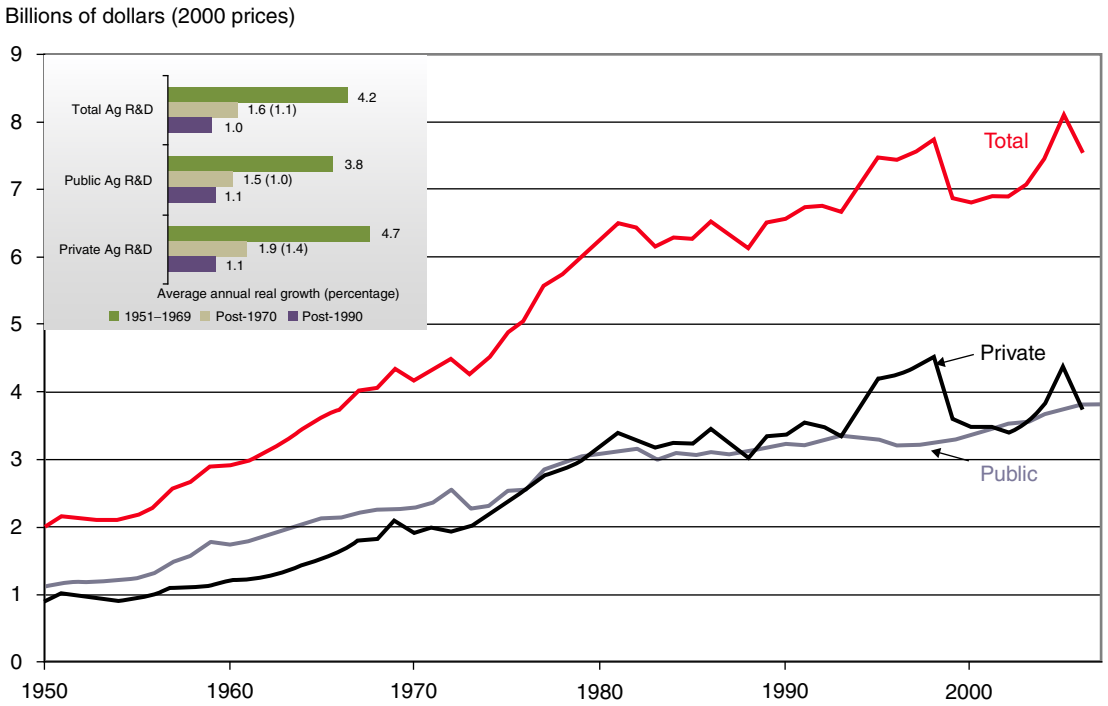


Figure 9 US agricultural R&D expenditures, 1950–2007. Reproduced from Pardey, P.G., Alston, J.M., 2012. Global and US trends in agricultural R&D in a global food security setting. In: Improving Agricultural Knowledge and Innovation Systems: OECD Conference Proceedings, pp. 19–40. Paris and Washington, DC: Organisation for Economic Co-Operation and Development.

and state support of land-grant universities and public-good R&D, along with the support of cooperative extension, has been instrumental in expanding supply response to both market- and governmental-based incentives. This joint complementarity between public-good R&D and commodity subsidization has been theoretically demonstrated on numerous occasions (Innes and Rausser, 1989; Foster and Rausser, 1993; Rausser and Foster, 1990). Keeping everything else constant, the complementarity of these two policies has reduced the price volatility that would otherwise have occurred and depressed market price levels, especially when price supports were abandoned and replaced by target prices and deficiency payments (the expected deficiency payment for a particular crop, c, is

$$E(d_{ct}) = \left[P_{ct}^{T} - \mathrm{Max}\left(P_{ct}^{S}, E(P_{ct})\right)\right](1-\omega_{ct})L_{ct}Y_{ct}$$

where P_{ct}^{T} is the target price; P_{ct}^{S}, the support price; $E(P_{ct})$, the expected average price received by farmers; ω_{ct}, the percentage of land base required to be idled; L_{ct}, the land base in period t; and Y_{ct}, the program yield per unit of the land base). In the final analysis, the combination of research and subsidization policies is largely responsible for the relatively low ratio of food expenditure to income in the United States versus that of many other countries.

Environmental Intervention

As concern for environmental amenities has increased, environmental conservation has become an increasingly important element of agricultural policy in the United States. The expansion of agriculture to environmentally sensitive areas and the damage to ecosystems and water sources caused by agricultural activities have spurred legislation designed to mitigate such effects. One type of legislation, for example, has restricted agricultural activities in environmentally sensitive areas. Such land-use restriction has been introduced not only to lessen environmental hazards but also, as previously noted, as a means to control agricultural supply.

Historically, nonvoluntary regulation has been the method of choice in industrial settings when it comes to environmental policy. However, in the agribusiness sector, the United States has heavily favored conservation policies called 'payment for environmental services' (PES) programs. These PES programs adopt a voluntary approach to environmental conservation in sectors where firms do not explicitly reap the benefits of conservation themselves and have no incentive to conserve without some external motivation. Originally, such agricultural conservation programs came in the form of payments to farmers for letting arable land lie fallow after the Great Depression, in order to maintain adequate soil quality and avoid another Dust Bowl.

Fifty years later, the institution of the CRP by the Food Security Act of 1985 marked a turning point for conservation efforts. The CRP constituted an effort to protect wildlife and to improve water and air quality as well as to mitigate soil erosion. Although the PES programs began by diverting land from agricultural uses, many CRP programs applied to working lands. In 1985, cross-compliance requirements were introduced requiring that both land-diversion and working-land measures be undertaken in order for a farmer to be eligible for income-support programs (Claassen *et al.*, 2008). A decade later, another environmental policy, the Environmental

Quality Incentive Program, was introduced. It subsidizes investments in animal-waste management that meet environmental objectives. Government-support programs continue to reflect concern for the environment, and environmental support programs are looked upon favorably by the World Trade Organization.

Biofuel Policies

The 2008 farm bill, for the first time, included incentives for energy production and explicitly connected the agricultural and energy industries at their nexus: biofuels. Although the biofuel provisions were a minimal budgetary line-item in the 2008 bill, they should be viewed in the context of the renewable-energy legislation that was enacted at the same time, which also promoted biofuels. From the standpoint of US agricultural interests, the most obvious motivation for instituting these biofuel policies was that they would allow agricultural producers to receive advantageous prices for corn, oilseeds, and perhaps even wheat. Biofuel policies also held out hope that taxpayers would be relieved of the burdensome commodity subsidies (deficiency payments) paid to agricultural producers. In fact, the legislation worked exactly as expected. Increased demand for corn and other biofuel inputs raised prices and lowered deficiency payments. It also caused US ethanol production to increase sevenfold (Rausser and de Gorter, 2013).

The federal government supported the introduction of biofuels by mandating that a minimum percentage of fuel used for transport be biofuel. This mandate connected agriculture more closely to energy, with the result that another set of forces began to influence food-grain price volatility. A 2007–08 commodity price boom correlated closely with a boom in crude-oil prices. Though the energy-policy arena had been saturated with biofuel mandates since 2006, only tax credits for ethanol fuel blenders explicitly linked corn prices to ethanol prices (Rausser and de Gorter, 2013). Thus, in order to gain a comprehensive picture of food-grain commodity volatility and pricing, one must look not only at agricultural and macroeconomic policy but also at environmental and energy policies (the interdependency of agricultural and environmental policies and the need to coordinate policy design were recognized early by Lichtenberg and Zilberman, 1986). The potent effect of the 'ag-energy' legislation becomes clear when corn prices before and after the legislation's adoption in 2008 are compared. In 2005–06, the lower bound on corn price was US$1.75 per bushel. In 2009–10, the lower bound did not drop below US$3.21 per bushel. In just 4 years, the price of corn increased to more than 80%.

Food Quality and Ecological Farming

Concerns about both nutrition and the environment have been on the rise in recent years in the United States. These concerns have brought new participants into the debates about agriculture, especially people interested in organic farming and other ecological practices. Originally, US organic certification was voluntary: farmers who wanted to certify their products as organic could apply to industry associations and, if they met certain requirements, receive certification. More recently, however, organic certification has become a strictly regulated, government-supported process. More than 50 certification agencies and a USDA organization called the National Organic Program now oversee the multibillion-dollar organic farming industry.

One of the big questions regarding the future of organic farming is whether it will include genetically modified (GMO) crops. Traditional supporters of organic farming have been very public about their opposition to GMO crops (Freedman, 2013). However, some scientists have argued that a symbiosis between organic agriculture and plant genetics will be able to meet future nutritional demands and also address environmental concerns (Ronald and Adamchak, 2010; Bennett and Jennings, 2013). Nonetheless, a vocal contingent of the organic-food and sustainable-farming movement seeks to reduce public support for agricultural commodities and restore traditional agriculture because this contingent is concerned about the long-term effects of genetic monocultures (a spokesperson for this movement is Michael Pollan, author of the bestsellers The Omnivore's Dilemma and In Defense of Food). However, critics of this movement assert that such proposals will make food more expensive, to the disadvantage of low-income consumers. For this reason alone, they argue, supporting efficient, high-yield farming remains vital. Still other food-policy experts maintain that these debates rest on the false premise that industrial and organic farming are mutually exclusive alternatives. They maintain that both types of agriculture have established their own markets and that this pluralistic approach to agriculture can satisfy diverse needs.

Policy Making and the Changing Political–Economic Landscape

In the current century, the US – and the world – has shifted from chronic excess supply caused by growing farm productivity to chronic excess demand and rising real food prices. The reasons for the shift include increasing demand for food as income grows (especially in Asia and other developing regions) and increased consumption of meat. Raising meat animals for human consumption entails producing significant amounts of grain, introducing biofuel, and slowing growth in agricultural productivity (Zilberman *et al.*, 2013). Changing political conditions have also led to increased demand for nonfood uses of agricultural crops. In particular, as it was suggested, rising energy prices and increased public concern about climate change, environmental sustainability, and energy security have increased opportunities to produce fuel from agricultural crops (Zilberman *et al.*, 2013).

As energy uses constitute a new source of demand for agricultural commodities and have much higher price elasticity than does food demand, demand for biofuel crops can elicit increased supply without generating significant price erosion. Corn-based biofuel was first introduced in the United States as a food additive, but corn-ethanol production drastically increased when fossil-based fuel prices almost doubled, between 2004 and 2007. Biofuels and the rising food prices associated with them even contributed to accumulation of

wealth in the farm sector: prices for agricultural land continued to grow even when other real estate prices were on decline, accentuating the shift of relative resource allocation toward the farm sector relative to the rest of the economy (Figures 1–3).

Since 2007, however, public concern about the impact of corn-ethanol production on food prices has led to the imposition of limits on the amount of corn-ethanol mandated (Rajagopal *et al.*, 2007). Furthermore, the demand for corn ethanol has been constrained by the 'blend wall' (the limit on the proportion of ethanol that can be used by gasoline engines). The US government has, therefore, mandated that a second generation of biofuels be developed, preferably from nonfood products that compete only minimally for land and other resources with agricultural food production.

Despite attempts within the federal government to mitigate harmful effects of biofuels on world food prices, the agricultural sector's political muscle has been sufficiently strong to secure continued support for traditional or agricultural commodities program. Agriculture continues to become more capital intensive and uses a diminishing share of labor, so that farms are becoming fewer in number but larger in size. This transformation makes it possible for these fewer but larger entities to become a more cohesive and politically effective group. Furthermore, the introduction of biofuels has motivated some of the major multinational oil companies to join the agricultural policy debate. Some of these companies may oppose mandates for second-generation biofuels that could reduce oil prices.

Although a movement to reduce unconditional transfer of income to the agricultural sector has recently gained traction, the net effect of this trend is debatable, as public resources are increasingly being invested instead in crop-insurance programs. However, as the average household income grows and interest in environmental issues expands, environmental groups exert greater influence on agricultural policies. Some environmentalists support biofuel policies, as do biofuel producers, automakers, many fuel transporters, the energy-security community, and certain growers' associations. Even some environmental groups that opposed tax credits and tariffs now seek to retain mandates. However, other groups are coalescing in opposition to mandates, tax credits, and subsidies. As ethanol policies support food-grain markets through higher prices, groups such as livestock, dairy, and poultry producers are beginning to form organized opposition to continued support for ethanol producers. So are food processors that no longer enjoy the low market prices that traditional agricultural policies supported (one example of these new interest groups is BalancedFoodandFuel.org, whose members include various meat, livestock, poultry, and dairy producer associations (Hahn, 2008)).

In summary, the landscape of organized interest groups that seek to influence the US agricultural policy continues to change at an increasingly rapid pace. The 'iron triangle' that once shaped governmental intervention in commodity markets has expanded into an 'iron maze' of organized environmental, energy, consumer, and agricultural interest groups. To complicate matters, at least three executive-branch agencies (the Department of Energy, the USDA, and the Environmental Protection Agency) also play significant roles. What remains to be to be seen is whether such changes can lead to less distorting and expensive policies.

See also: Biodiversity: Conserving Biodiversity in Agroecosystems. Changing Structure and Organization of US Agriculture. Farm Management. Human Nutrition: Malnutrition and Diet. International and Regional Institutions and Instruments for Agricultural Policy, Research, and Development

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Green Revolution: Past, Present, and Future

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Glossary

Biotechnology Use of genomic-based technologies that include identifying the genetic code of important genes, the following of traits by tracking DNA sequences flanking the gene(s) controlling the trait, and the molecular transfer of genes known as genetic engineering.

Genetic resources The array of inherited traits present among various accessions of the organism. Selection and breeding of new varieties depend on the available genetic variation represented among the available genetic resources.

Germplasm The collection of various genotypes available for breeding programs.

Immunodeficiencies Immune system compromises due to the lack of various factors, including Vitamin A.

No-till cropping system Direct seeding into undisturbed or minimally disturbed soil seed beds, thus reducing environmental degradation of soils and saving time and cost of tillage.

Population monster A term used by Norman Borlaug to indicate that the human population is increasing so fast that maintaining sufficient food is nearly impossible.

Semidwarfness Crop plants with shorter stature compared to common varieties. Generally, the reduction in height of perhaps 30% leads to a shorter and stronger stem that can hold more grain and not fall over due to the weight.

Stem rust A fungal disease that can cause serious losses of yield in certain small grains. The organism can mutate and become virulent on new varieties, such as the new strain called Ug99.

Father of the Green Revolution

If the word 'Green' is entered in Google, the term 'Green Revolution' does not appear in the list of sites – at least not in the first 30 pages of Google listings. Terms such as Green Building and Leadership in Energy and Environmental Design scorecards, the Green Party, Energy and the Environment, Sustainable Living, Green Chemistry, Green Colleges, Green Hotels, Greenpeace, and even the Green Bay Packers appear without a mention of the Green Revolution. Many people have heard of the Green Revolution, but few have heard the name of the 'Father of the Green Revolution,' Norman E. Borlaug. This is in contrast to what one would expect because he was one among the five people to receive the Nobel Peace Prize (Borlaug, 1970), the National Medal of Freedom, and the Congressional Gold Medal. The other four were Martin Luther King, Mother Teresa, Nelson Mandela, and Elie Weisel. From the time when Borlaug was awarded the Congressional Gold Medal in 2007, two others have received this trifecta of awards, namely, Mohamed Yunis and Aung San Suu Kyi. Norman Borlaug died at the age of 95 in 2009 and had lived an active life up to the time of his death, contributing to a more food-secure world (Vietmeyer, 2008, 2009, 2010, 2011; Phillips, 2009). Although most developed countries had sustained food surpluses by 1950–2000, developing countries were and still are under the threat of starvation.

Why do so few people know about Norman Borlaug? One would think that receiving more important awards than other famous people would make his name a household one. It has been stated that Borlaug saved the lives of more people (approximately 1 billion) than anyone else who has ever lived through his wheat improvement efforts and his persistence in convincing other countries to use the new seed, especially India and Pakistan (Borlaug, 2007). Borlaug's name is recognizable by many residents of South Asia, with his efforts being taught in their school history classes.

Defining the Green Revolution

So, what is the Green Revolution? The term was coined in 1968 by the U.S. Agency for International Development Administrator William Gaud and encompasses many aspects, but essentially involves the breeding of high-yielding crops that positively respond to fertilizers and irrigation. The crops that led the Green Revolution were wheat and rice. Henry Beachell bred rice at the International Rice Research Institute (IRRI) in the Philippines in ways that were similar to those by Borlaug when he bred wheat at the Center for the Improvement of Maize and Wheat (Spanish acronym 'CIMMYT') in Mexico. A key feature was to shorten and strengthen the stems (straw) such that the plant could bear more grain without falling over; it is difficult to realize the gain in yield when the heads of grain are on the ground. This shortening of the stem was the result of bringing in genes for 'semidwarfness' that allowed the plant to make good use of fertilizer and water in producing higher recoverable yields. Borlaug also bred for resistance to wheat diseases such as the devastating stem rust. This disease was a serious problem but was largely overcome by the discovery of resistance genes and breeding them into the new varieties. However, in 1998 a new strain of stem rust was detected and reported in Uganda (known as Ug99). Borlaug sounded the alarm because he knew that 80–90% of the world's wheat varieties are susceptible to this strain, and the pathogen was spreading to other countries. A huge effort was mounted to develop resistant varieties, largely funded by the Bill & Melinda Gates Foundation. Several varieties are now available for Africa with a reasonable degree of resistance to Ug99. This virulent strain is yet to reach the United States; however, various major wind currents will probably bring it there before too long. The Green Revolution technology has been extended to many other developing-country crops, including sorghum, millet, maize, cassava, and beans.

Borlaug developed a strategy whereby he utilized two locations for breeding. One was near sea level at Ciudad Obregon in northern Mexico and the other was near his home base of CIMMYT at nearly 2000 m elevation. The purpose for having nurseries in two distinct locations was to obtain two generations per year, thus presumably allowing greater progress in making crosses and selecting for yield. What he did not know was that many of the selections that were impressive at both locations would respond well in diverse environments around the world, specifically in locations with very different lengths of the day. This trait was called 'photoperiod insensitivity.' These selected varieties yielded well in Mexico as well as in faraway places such as India and Pakistan. In fact, the Borlaug varieties responded so well that Mexico soon did not have to import wheat to feed the population – and the same came true for India.

Food Production versus Human Population

Before the Green Revolution-varieties were developed, the world had almost lost hope that anything could stave off the starvation and death of millions of people due to production of food crops not keeping up with the increase in population. In fact, Paul Ehrlich (1968) had published a book called the 'Population Bomb' in which he indicated that the battle to feed the world had been lost. This was probably a reasonable prediction; few people, if any, would have predicted that technology would provide the food needed to keep so many people alive. Remember, for example, that rice still feeds half the world. Keeping up the yield of rice and wheat is essential in providing sufficient food even today. The world population is now more than 7 billion people, reflecting a rate of adding 1 billion people to this planet every 14 years. Clearly, there is a major challenge ahead for agriculture to produce sufficient food in order to meet this 'population monster' (Borlaug's term). Even in his Nobel Peace Prize speech, Borlaug stated that there must be a push for increased food production for population control to be successful. One of the criticisms of the Green Revolution is that increased amount of food led to overpopulation worldwide. Some people subscribe to the Malthusian theory that population growth will increase to an extent where food production cannot cope with and widespread deaths will inevitably occur (Malthus, 1798) (**Figure 1**).

The population of the world increased from 1 billion to 2 billion from 1804 to 1927 (123 years). The last increase of 1 billion people occurred in just 14 years. The current population of over 7 billion will increase to approximately 9 billion by 2050. One way to buy some time in order to balance the relationship of population growth and food production is to have population control. The length of time to double the human population depends on the rate of population growth. As can be ascertained in **Figure 2**, a reduction from a 4.0% rate of population increase to a 1% rate changes the years required to double the population from 18 to 70 (Conway, 2012).

China currently has the highest population of any country (1.3 billion); however, the rate of population growth has been slowed by the one-child policy enacted in 1979. India (1.2 billion in 2011) will probably surpass China in population during the next two to three decades.

Malnutrition

Why did Borlaug receive the 1970 Nobel Peace Prize? The Nobel committee was most likely trying to make the same

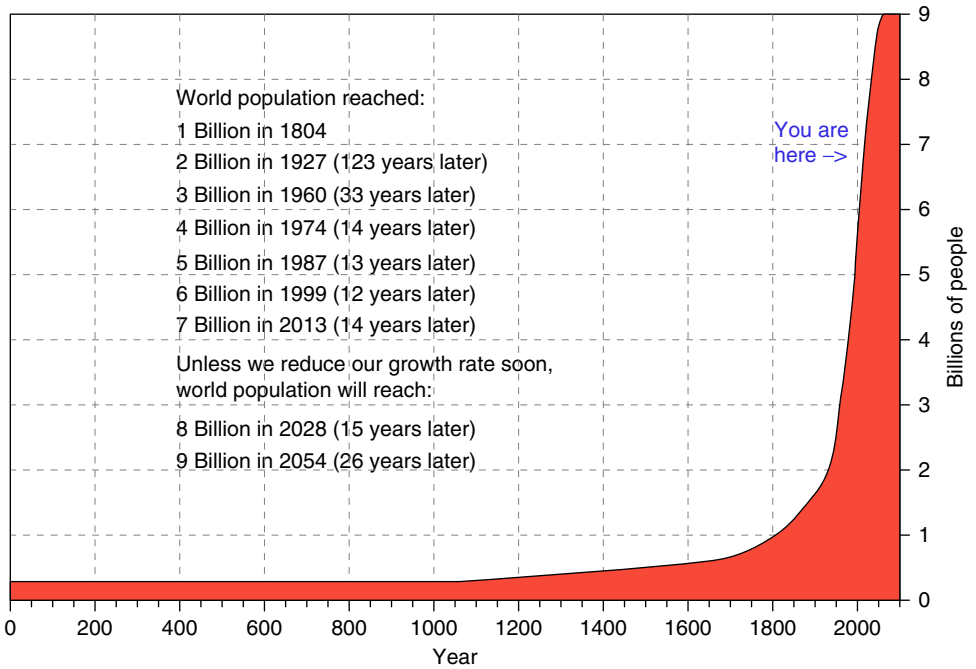


Figure 1 Past and future human population numbers. Reproduced from United Nations, Population Prospects; The 1998 Revision (United Nations Population Division, Department of Economics and Social Affairs).

Rate of population increase	Years required to double population
0.01%	6930
0.1%	693
0.5%	139
1.0%	70
1.5%	47
2.0%	35
2.5%	28
2.8%	25
3.0%	23
3.5%	20
4.0%	18

Figure 2 Years required to doubling population relative to rate of population increase.

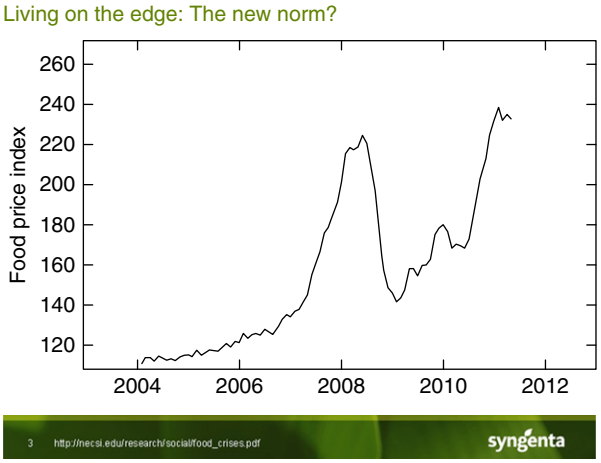


Figure 3 Food price spikes (2004–11). The FAO defines the Food Price Index as a measure of the monthly change in international prices of a basket of food commodities. It consists of the average of five commodity group price indices (representing 55 quotations), weighted with the average export shares of each of the groups for 2002–04.

point that Borlaug had always believed, that "You could not have peace on empty stomachs and human misery." Borlaug also believed that "Food is a moral right." One of the problems of malnourishment is that, if a child does not die due to starvation, he or she is still affected for the rest of the life due to poor early-brain development. Stunting in children is common when food is in short supply; this is not something that is readily corrected by providing sufficient food later in life. A country with malnutrition has a populace that is less productive. We have known for many years that diet is linked to immunodeficiencies. Malnutrition increases the occurrence of intestinal infections and diarrhea. The gut in healthy people has thousands of microorganisms (more microbes than cells in the whole body); malnutrition alters this microbial community and affects the transport of nutrients and the occurrence of inflammation (Icue and Powrie, 2012).

The link between nutrition and agriculture is now being recognized more than ever before. The World Health Assembly recently set a goal of reducing the number of stunted children by 40% by 2025 (Swaminathan, 2012). Hunger, therefore, is not just a matter of insufficient food. Deficiencies in the diet of zinc, iron, iodine, vitamin A, and vitamin B12, for example, all lead to malnutrition. This condition has been called 'hidden hunger.' Many believe that not being chronically hungry is a fundamental human right. It is recognized that intervention programs need to be available for the first 1000 days of life, from pregnancy to 2 years of age. Having new food-crop varieties genetically enriched in these important micronutrients is an efficient way to intervene. The Green Revolution also indirectly assisted in providing better nutrition, especially in Asia via increased income that allowed people to have a more diversified diet, including the consumption of meat, vegetable oils, fruits, and vegetables.

Importance of a Reliable Food Supply

Food security has become a major issue. As the price of food staples went up during 2008 due to shortages in storehouse levels of grain, there were food riots in at least 30 countries. Grain warehouses often needed to be guarded because of people stealing bags of grain. Figure 3 shows the spike in prices in 2008 and 2011. Figure 4 shows when food riots occurred in various countries; the striking coexistence of price with food riots.

Because of the importance of food production, Borlaug asked the Nobel Prize Committee to fund a Nobel Prize in Agriculture. After reviewing the 'last will and testament' of Alfred Nobel, the committee along with their legal counsel decided that such a Nobel Prize in Agriculture was not within the realm of the will. Undaunted, Borlaug and others established in 1986 the World Food Prize (considered by many as the Nobel Prize in Agriculture). This annual award provides US $250 000 to the winner(s). The World Food Prize Foundation also sponsors the Global Youth Institute to expose high school students from the US and abroad to opportunities in meeting world food needs. This youth institute was also Borlaug's dream. Although he had only one Ph.D. graduate student, he trained hundreds of young people from around the world. These students, who he called 'Hunger Fighters,' carried the technology and the philosophies back to their home countries. Borlaug believed in advanced technology, including biotechnology, to maximize yields. He also believed in the education of young people. Yet another unique feature of Borlaug's approach was to address political barriers to food production by telling his story and seeking government help in utilizing new technologies.

India was facing mass famine in the 1960s. Fortunately, Borlaug was invited to India by the Minister of Agriculture M.S. Swaminathan. Together with the Ford Foundation and the Indian government, wheat seed was imported from CIMMYT and first grown in the Punjab area. The results were dramatic and India augmented its program on plant breeding, irrigation, and agrochemicals. Based on these successes, India soon started using the new so-called 'Miracle Rice' labeled IR8, developed at IRRI, which had been established in 1960 in Los Banos, Philippines, by the Ford and Rockefeller Foundations along with the Philippine government. Peter Jennings, Sterling Wortman, Akira Tanaka, and Hank Beachell developed IR8 by

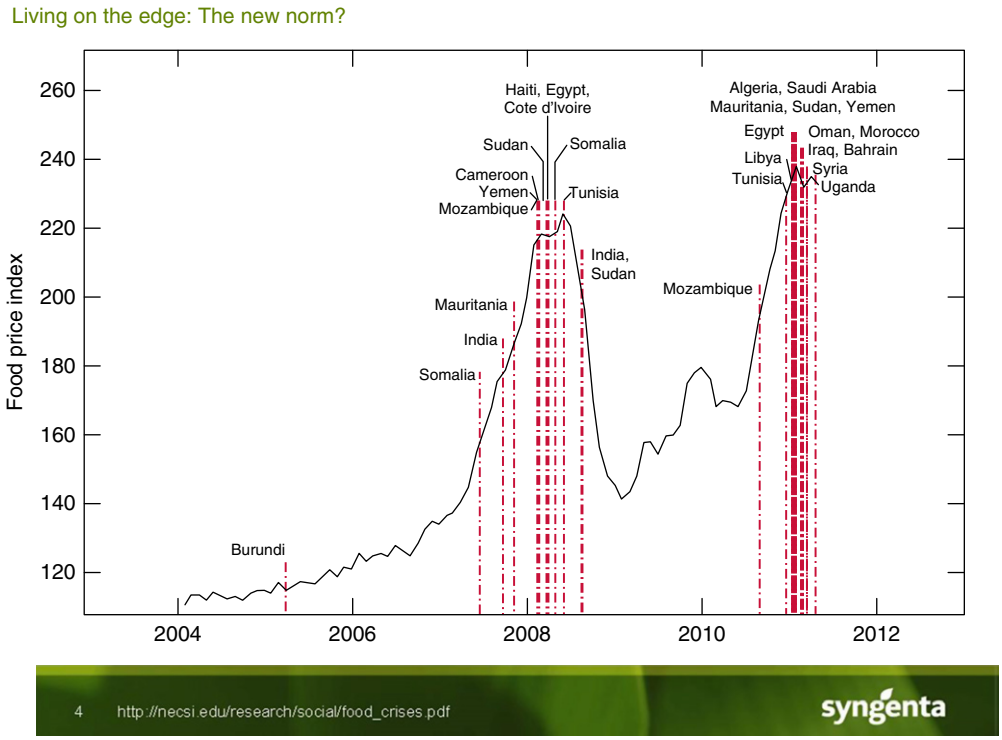


Figure 4 Food riots correlated with changes in the food price (2004–11) shown in Figure 3.

crossing a tall variety from Indonesia (Peta) with a short Chinese variety called Dee-geo-woo-gen. The high yield of what became known as IR8 was first recognized by IRRI scientist S.K. De Datta. The yield of this rice was ten times that of traditional rice. The Philippines also switched to IR8 and became a rice exporter. IR8 was released in 1966, which was the time that Borlaug's wheats reached India (Dar, 2012)

The 1970 Nobel Peace Prize to Borlaug signaled the importance of what was happening in agriculture. The new varieties were being rapidly adopted by farmers. Approximately 75% of the rice in Asia, half the wheat planted in Africa and more than half in Latin America and Asia, and 70% of the corn worldwide were new varieties. Some reports estimate that 40% of the farmers in the developing world were using the new varieties by the 1990s. The production of wheat in Pakistan, for example, increased from 4.6 million tons to 8.4 million tons from 1965 to 1970, almost doubling in 5 years. India's production went from 12.3 million tons to 20 million (Lobb, 2003). Countries other than Pakistan, India, Mexico, and the Philippines also benefited from the Green Revolution, namely, Afghanistan, Sri Lanka, China, Indonesia, Iran, Kenya, Malaysia, Morocco, Thailand, Tunisia, and Turkey. By the year 2000, more than 60% of the rice in developing countries had been generated by the research institutes.

Green Revolution in Africa

The Green Revolution largely missed Africa. Several reasons have been given for this situation; these include the infertile soils of Africa, uncertain rainfall, the lack of agricultural technology, the need for quality seeds, limited investment in irrigation, poor roads, immature markets and high transportation costs, the requirement for more information and know-how, and probably corruption and lack of political will among the countries. Clearly, improvements in any of these areas would have a positive impact. Kenneth Quinn, former Ambassador to Cambodia, has noted that the growing of miracle rice IR8 followed the development of roads that reduced the cost of moving fertilizers and other inputs to the farms and enhanced the ability to move the rice to markets. Several government agencies, nonprofit organizations, universities, and agricultural companies have now seized the opportunity to help in Africa. The countries of Africa are finally realizing the importance of putting more of their GDP toward agricultural goals. Malawi is a good example where the government developed a highly successful Agricultural Input Subsidy Program to assist smallholder farmers to obtain nitrogen fertilizer and maize seeds. A new African rice called NERICA (New Rice for Africa), derived from an African species of rice, has the potential to provide substantial yield increases. The food crisis in several African countries is being addressed through a program called Sasakawa-Global 2000. Norman Borlaug and former President Jimmy Carter were involved in the development of this program.

Poor infrastructure of a country contributes to its demise in terms of getting inputs to the farm and products to the market. In Africa, the larger markets are often many hours away (Figure 5).

Is the Green Revolution a Myth?

With all the positive aspects of the Green Revolution, why are some saying that its success is a myth and not sustainable?

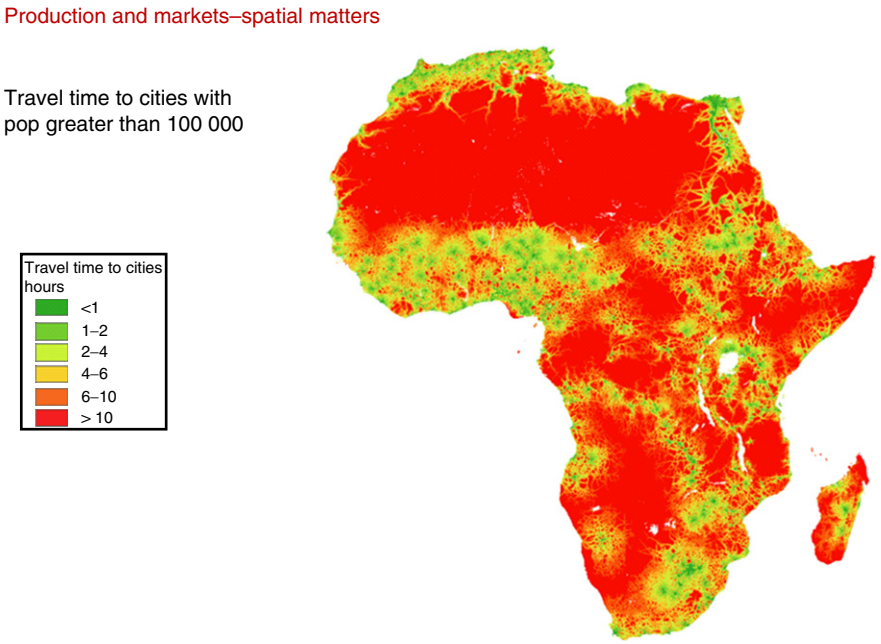


Figure 5 Time (travel) to move product from farm to market in Africa. Reproduced from Harvest Choice/Joint Research center of the European Commission. Available at: http://harvestchoice.org/topics/market-access (accessed 24.01.14).

They argue that the high yields are achieved at the expense of the environment due to the use of synthetic fertilizers, the exhaustion of water supplies, and the build-up of salt due to irrigation. They also argue that adoption of the new varieties leads to a monoculture more susceptible to new stresses such as diseases and insects, and decreases the level of biodiversity across the agricultural landscape. Borlaug countered that the Green Revolution allowed farmers to produce more grain on the same amount of land, and thus he viewed the high-yielding varieties as environmentally friendly. In 1930, one farmer fed 10 people; today one farmer feeds 155 people. The amount of income spent on food in the US was 25% in 1930 compared to 10% today. The world's grain production in 1950 was 692 million tons. By the 1990s, the world's farmers were producing 1.9 billion tons on approximately the same amount of land. If it were not for improved agricultural technology, 1.8 billion more hectares of land would have been needed. Future Green Revolutions must address these issues (IFPRI, 2003).

Other Issues

Increasing interest in eating meat in developing countries will place additional strains on the food production system. Obtaining our food needs from meat is highly inefficient because it takes so much more grain and water to produce meat. Approximately 35% of the world grain harvest is used to produce meat. The water required to produce rice is approximately $1600\,l\,kg^{-1}$ rice, whereas beef requires $12\,000\,l\,kg^{-1}$ beef. Although much of the world's peoples are vegetarian and healthy, several studies show that meat provides nutrients not available in plant sources. The increasing use of meat in diets, such as in China, will put more pressure on increasing the yield of maize, which recently surpassed rice in the amount produced, according to the U.S. Grains Council.

Water-use efficiency in crops is a trait under study by many researchers. All aspects of food production, and even biofuels, require much water. Seventy percent of the fresh water in the world is used by agriculture. The competition for water will intensify in the future as it becomes more of a scarce commodity. This issue is now receiving international attention.

Although the yield of maize has progressed well over the years with the advent of various new technologies such as hybrids and biotechnology (Figure 6), the yields of wheat and rice have plateaued. This is another cause for concern.

So, if the rate of increase in yields of maize via plant breeding and biotechnology is doing so well, why are people concerned? The concern stems from the lack of sufficient progress in the breeding of staples such as rice and wheat. For rice, the yield gains have decreased from 3.1% per year in the 1980s to only 0.8% in the 2000s. Similarly for wheat, the yield gains have decreased from 2.9% in the 1980s to only 0.4% in the 2000s (Figure 7). Approximately 50% of the yield gains generally are from improved genetics of the crop and approximately 50% from better management such as irrigation, fertilizers, pesticides, and planting protocols. The increase in food production via breeding offers good potential. In countries such as India, Pakistan, Nepal, and Bangladesh, approximately 80% of the area is rain-fed, which makes the maize quite vulnerable to abiotic stress such as drought. Extreme heat at flowering time can dramatically reduce yield. New technologies such as genetic engineering should help. For example, changing the photosynthetic system is a goal of several research programs. Maize is what is called a C4 species

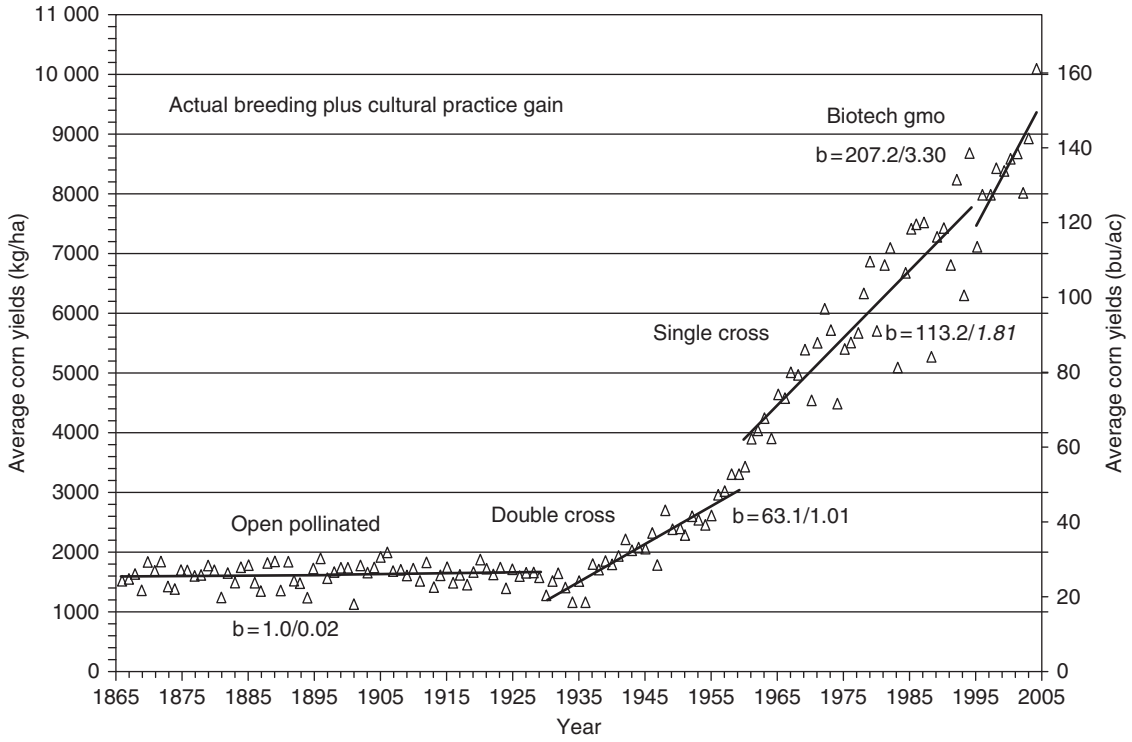


Figure 6 The maize yield-improvement graph from the time of open-pollinated varieties to the new biotech varieties.

that has benefits in situations such as drought, high temperatures, and nitrogen limitations. C4 plants such as maize also have an advantage over C3 plants such as rice and wheat in atmospheres with CO_2 limitations and high temperatures, theoretically giving C4 plants a mechanism to deal with climate change. C4 photosynthesis has evolved several times and, thus it seems reasonable that a C3 plant might be changed into a C4 plant via selection, mutagenesis, or genetic engineering.

Preservation of Biodiversity

The genetic resources existing around the world that will be used to create the next breakthrough in crop yields must be protected. In recent years, countries have begun to realize the value of the rich genetic materials that they possess. This has created considerable tension among countries and led to extensive examination of policies to govern the availability of such materials to others. This in turn has led to several treaties, protocols, and conservation methods to protect/share genetic resources. The International Rice Research Institute has a massive collection of rice accessions numbering over 100 000 types, all freely available to the public. CIMMYT has large collections of maize and wheat, also freely available. The Consultative Group on International Agricultural Research (CGIAR) and Bioversity International play a major role in germplasm collections, including the Fort Collins, Colorado, National Center for Genetic Resources Preservation. This is a long-term storage facility. "The mission of the National Center for Genetic Resources Preservation is to acquire, evaluate, preserve, and provide a national collection of genetic resources to secure the biological diversity that underpins a sustainable US agricultural economy through diligent stewardship, research, and communication." A recent development is the establishment of the Svalbard Global Seed Vault (affectionately known as the 'Doomsday Vault') in the frozen mountainside of Norway where a large cavern that is naturally cool contains much of the world's genetic variations of crops. In all, an estimated 1750 germplasm collections are said to exist with 7.4 million accessions.

Some believe that biodiversity was sacrificed when the Green Revolution was applied to new areas of marginal land. Others believe that genetic engineering will be a powerful tool in achieving biodiversity and meeting the huge demand for food by 2050. In 2012, biotech crops were grown on 170 million hectares by 17.3 million farmers. Developing countries now grow slightly over 50% of the total biotech crop. Genetically engineered cotton with insect resistance encompasses 80–90% of the crop. The top ten countries in growing biotech crops are the US, Brazil, Argentina, Canada, India, China, Paraguay, South Africa, Pakistan, and Uruguay (James, 2011).

Nutritional Changes in Food Supply

One tends to think that our food and feed crops are very good from a nutritional standpoint. However, the reality is that they can be improved, including through traditional breeding. For example, maize is deficient in the amino acids lysine and tryptophan, and beans are deficient in the amino acid

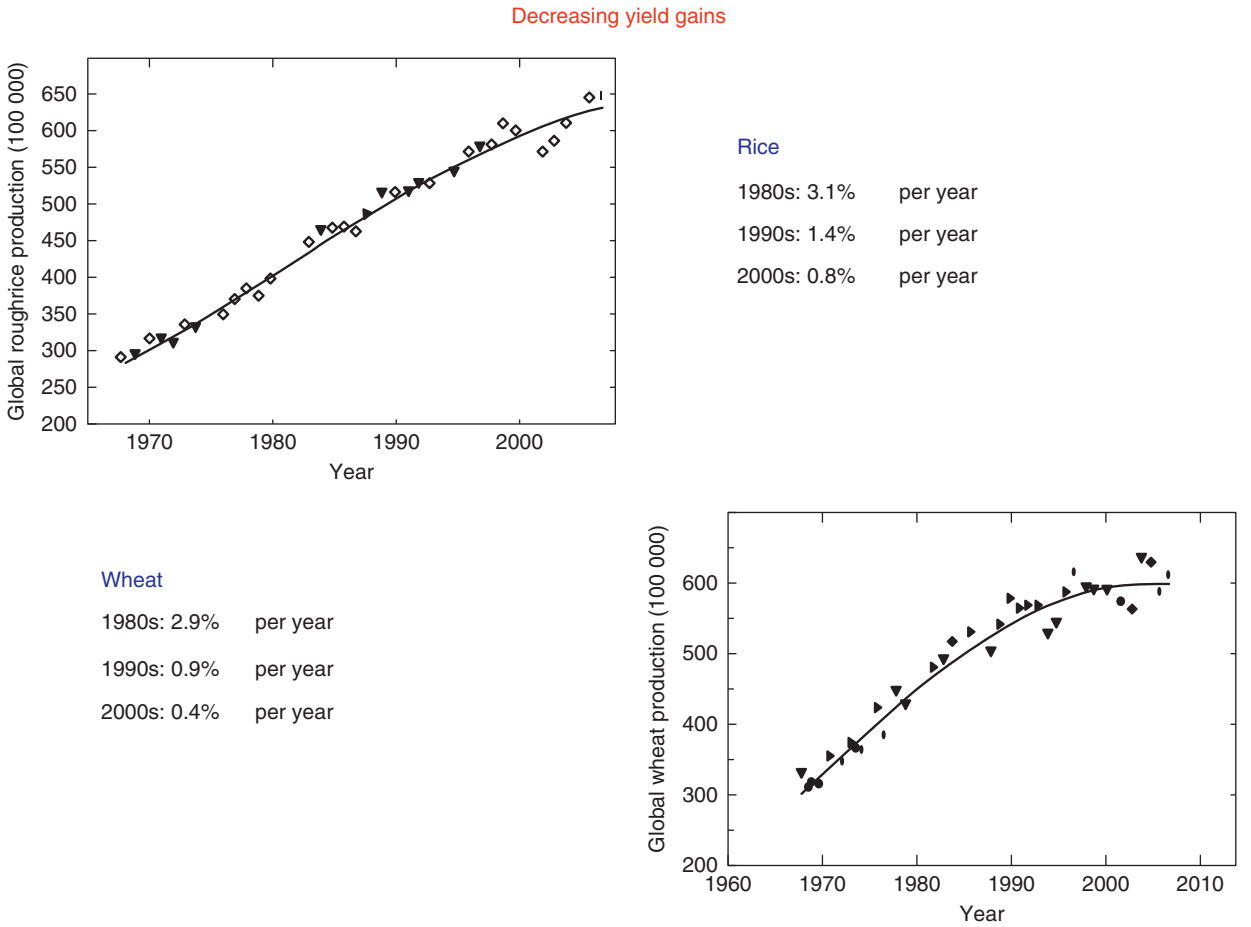


Figure 7 Yield curves for rice and wheat over three decades. Courtesy: Lewis Ziska, USDA.

methionine. A diet of maize and beans provides a relatively balanced diet. A type of maize called QPM or Quality Protein Maize has been developed mainly via a CIMMYT breeding program. Use of this variety of maize can alleviate a major protein deficiency in humans, called kwashiorkor. QPM maize is grown on approximately 9 million acres.

Micronutrients such as iron, zinc, iodine, and provitamin A are often deficient in crop plants. Varieties enriched in these micronutrients are being developed, especially under a program called Harvest Plus. Such varieties, bred to be adapted to various environmental and geographic regions, are under development. It is expected that rice enriched in provitamin A (or β-carotene), called Golden Rice, will be available soon. Our bodies need β-carotene in the diet in order to be converted to Vitamin A. Golden rice should solve a serious problem; approximately 500 000 children go blind every year due to Vitamin A deficiency. Many die because a deficiency in Vitamin A affects the immune system, making the individual more susceptible to diseases such as measles. There are considerable background data on the value of Vitamin A supplementation. Alfred Sommers of Johns Hopkins University provided 15 000 children with two doses of Vitamin A per year and found that it cut childhood morbidity and mortality by one-third. The World Bank and the Copenhagen Consensus indicate that supplementation with Vitamin A is one of the most effective health interventions in the world. Soon this could be achieved through genetically modified rice.

Role of Poverty

Poverty is often cited as one of the most important factors in malnutrition. Today 1.3 billion people live on less than US $1.00 per day, and 162 million people live on less than US $0.50 per day. This lack of money precludes many people, especially in the developing world from buying fruits and vegetables or even other grains that could provide a nutritionally balanced diet. The Green Revolution and current breeding and genetic engineering all can increase the income of farmers around the world. Many of these farmers are smallholder farmers and try to eke out an income from marginal lands. More income means that a more balanced diet can be available. It also means that both boys and girls can go to school and wear school uniforms not previously available to them because of the cost. Some of the recent agricultural programs are targeted toward the so-called 'Islands of Poverty' with the expectation that the funds will have an impact on hunger in these areas. Research indicates that rural poverty decreases by 1.83% for every 1% increase in agricultural growth.

Role of Women in Agriculture

Another targeted group is women – because women do much of the farming in the developing world while men are off to the cities to earn an income. Women are making more and more of the farming decisions. They grow a variety of crops and maintain some livestock and have to deal with many biotic (such as diseases) and abiotic stresses (such as drought), while also caring for children and other family members. These women are often malnourished or ill themselves. "Half of all farmers in the developing world are women. Many women work 6 h more a day than men on tasks like cooking, cleaning, and caring for children, which limits the time they have to farm. Women in the developing world are five times less likely than men to own land and their farms are usually smaller and less fertile."

The United Nations has set out several Millennium Development Goals to be achieved in the future, and these all have a direct bearing on the food security issue. The goals can be briefly stated as: (1) End poverty and hunger; (2) Achieve universal education; (3)Promote gender equality; (4) Reduce child mortality rates; (5) Improve maternal health; (6) Combat HIV/AIDS; (7) Ensure environmental sustainability; and (8) Develop a global partnership for development. All of these goals have direct implications relative to the Green Revolution and our attempt to reduce the 126 000 people dying every day due to malnutrition and poverty. Some of the targets of Goal #1, for example, are to "halve, between 1990 and 2015, the proportion of people whose income is less than $1 a day" and "halve, between 1990 and 2015, the proportion of people who suffer from hunger."

Paying Forward

Funding from the US has played a major role in maintaining a relatively plentiful supply of food. Some wonder whether the investment in international agriculture is cost effective for the developed world. Several hundred studies, according to Pardey *et al.* (2012) and Pardey and Alston (2011), show that the rates of return on American R&D investments are 40–60% per year with a benefit-cost ratio of at least 20:1. Investments in agricultural research take a long time to pay off – perhaps as long as 50 years. Even the development of a single new variety usually takes approximately 10 years. The International Food Policy Research Institute nicely sums up the "conditions under which the Green Revolution and similar yield-enhancing technologies are likely to have equitable benefits among farmers. These conditions include: (1) a scale-neutral technology package that can be profitably adopted on farms of all sizes; (2) an equitable distribution of land with secure ownership or tenancy rights; (3) efficient input, credit, and product markets so that farms of all sizes have access to modern farm inputs and information and are able to receive similar prices for their products; and (4) policies that do not discriminate against small farms and landless laborers (for instance, no subsidies on mechanization and no scale biases in agricultural research and extension). These conditions are not easy to meet. Typically, governments must make a concerted effort to ensure that small farmers have fair access to land, knowledge, and modern inputs."

Some argue that the Green Revolution of the 1960s was not the first green revolution. Sinclair and Sinclair (2010) suggest that the Sumarians developed what might be considered the basis of modern agriculture requiring math and written language along with markets. Water from the rivers (e.g., Euphrates) carried nitrogen to the crops and, over the years, nitrogen drove higher food production. This aspect of crop production was fostered via the ability to manufacture synthetic nitrogen by the Haber–Bosch process. Crop rotations were recognized as a good management tool, sometimes doubling yields. Therefore, one might consider that there were several green revolutions preceding the one in the 1960s and beyond. The wheat and rice Green Revolution is recognized as being unique, however, in that it allowed the saving of perhaps a billion people on the brink of starvation (Borlaug, 2009).

Support of Research and Development

Funding of agricultural research and development (R&D), both public and private, has decreased over the years. The success of the Green Revolution may have resulted in a complacent attitude among funding agencies. Given the recognition of the need for food and the cost of research and development, most people now view this reduction in funding as a huge mistake. Several agencies, NGOs, and private sector firms are now reversing this trend. Private funding plays an important role in taking the new developments to the farmer. However, many of the breakthroughs in research happen in the public sector. An investment in the public sector is essential to create the breakthroughs in helping the world meet the food demands of the future.

Biotechnology

Many believe that biotechnology, along with other technologies, will contribute significantly to food production in the future (Borlaug, 2007). Commercial biotech products started reaching the market in 1996, and this technology has been adopted more rapidly than any previous agricultural technology. New biotech crop varieties are being developed and tested that provide a more nutritious grain and meet certain industrial needs including biofuels. The so-called stacked varieties carry genes providing benefits in more than one aspect or make the product more durable in terms of disease or insect resistance. In some cases biotech products have saved an industry, such as papaya in Hawaii susceptible to the deadly papaya ring spot virus.

Biotechnology does not only encompass genetic engineering. Many efficient methodologies are emerging using DNA genetic markers that allow regions of the genome, if not the entire genome, to be followed in crosses. These markers also serve as a 'tag' for a particular trait that is often otherwise difficult to score. For example, submergence-tolerant rice is an exciting new development. Whereas normal rice dies after being submerged for 3 or 4 days, the gene 'submergence 1'

allows good yields even when the crop is submerged for 2 weeks or more. DNA regions around that gene can be followed in crosses, reducing the time to introduce the trait into new genetic backgrounds to 2.5 generations rather than 6 by traditional breeding. Now that the gene is cloned, the trait could be introduced by genetic engineering to prevent yield losses due to flooding.

Private companies often invest approximately $40 million to bring a new biotech variety to the market. This private sector investment has allowed new biotech products to come to the market. They also invest heavily in patents to recover the cost of development. Some people are concerned that the intellectual property protection provides too much corporate control. The USDA indicates that the company, the grower, and the consumer all benefit from products of biotechnology. Pollen flow creates situations where crosses may occur between the biotech variety and a wild but related species or nonbiotech varieties. However, there are ways to prevent these possibilities. A long-range concern deals with any environmental effects of biotech crops. Although many scenarios can be considered, no negative effects are clearly evident (National Academy of Sciences, 2002). The regulatory rules are taken very seriously; the rare breaking of a rule creates considerable concern, even if the effect is not a problem. These concerns and others have detracted from the use of biotech products in some countries, especially European countries.

The seventh annual PG Economics report on crop biotechnology impacts states that "Over the 15 year period covered in the report, crop biotechnology has consistently provided important economic and production gains, improved incomes and reduced risk for farmers around the world that have grown GM crops. The environment in user countries is benefiting from farmers using more benign herbicides or replacing insecticide use with insect resistant GM crops. The reduction in pesticide spraying and the switch to no-till cropping systems is also resulting in reduced greenhouse gas emissions. The majority of these benefits are found in developing countries" (Brooks and Barefoot, 2013).

M.S. Swaminathan (2011) has stated that "The bottom line for any biotechnology regulatory policy should be the safety of the environment, the well-being of farming families, the ecological and economic sustainability of farming systems, the health and nutrition security of consumers, safeguarding of home and external trade, and the biosecurity of our nation."

The Green Revolution of Today and the Future

The future of the Green Revolution revolves around technology that will increase food production but not at the expense of the environment. This concept is manifested in the term 'Evergreen Revolution' coined by M.S. Swaminathan, a compatriot of Borlaug, the first World Food Prize laureate (1986), and a major contributor to the Green Revolution in India. A reduction in the use of pesticides, judicious use of fertilizer, no-till (direct seed) planting, and efficient use of water are all part of having a productive and sustainable agriculture. In his speech at the 2011 World Food Prize event, Swaminathan stated that "During the next 25 years, the most important breakthrough we need is environmentally friendly and climate resilient farming techniques, which can increase productivity without adverse ecological side effects. This is what I have been referring to as the 'evergreen revolution.' We have to produce more food and agricultural commodities while per-capita arable land and irrigation-water availability diminish due to expanding biotic and abiotic stresses. To meet this challenge, we will have to harness all the tools of science, including recombinant DNA technology. By blending frontier technologies with traditional wisdom and ecological prudence, we can develop eco-technologies which can help us to achieve sustainable food security through the ever-green revolution pathway."

Sir Gordon Conway (1997) has called for a 'Doubly Green Revolution' where agriculture is highly productive, stable, resilient, equitable, and sustainable. He points out the value of the CGIAR (Consultative Group for International Agricultural Research), which was founded in 1971 and operates under the World Bank. There are now 15 CGIAR centers focusing on food crops, livestock, aquatic resources, water, forestry, and policy. More than 50% of the world's agricultural land planted with important food crops is derived from CGIAR research. Without these contributions, the world food production in developing countries would be approximately 8% lower. The CGIAR centers has also trained thousands of workers in the application of the information flowing from the research who return to their countries better prepared to enhance agricultural production. The centers also interact with the national research system and provide germplasm and information. This has been a powerful approach.

See also: Biotechnology Crop Adoption: Potential and Challenges of Genetically Improved Crops. Biotechnology: Herbicide-Resistant Crops. Breeding: Plants, Modern. Food Security: Yield Gap. Genebanks: Past, Present, and Optimistic Future. Genomics: Plant Genetic Improvement. Plant Disease and Resistance. Policy Frameworks for International Agricultural and Rural Development

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The Consultative Group of International Agricultural Research.
http://www.un.org/popin
United Nations Population Information Network.

H

Heterosis in Plants

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Glossary

Additive It is the quantitative measure of traits or gene expression in a hybrid at the mid-parent value of the parents.
Complementation It is the combination of alleles in a hybrid that produce a normal phenotype from parental lines that are true breeding for a mutant phenotype.
Double-cross hybrid It is an early method of producing hybrid seed by crossing two inbred lines in order to generate hybrids and then using the two hybrids to produce abundant amounts of seeds. In tetraploids, this method is used for producing progressive heterosis.
Inbreeding It is the result of a crossing scheme by which an increasing number of genes become homozygous.
Inbreeding depression It is the reverse of heterosis, in which there is a decline in vigor with an increase of homozygous alleles with respect to the starting hybrid.
Nonadditive It is a quantitative measure of traits or gene expression in a hybrid that is not at the mid-parent value.
Polyploidy The multiple copies of the complete set of chromosomes beyond the diploid level.
Progressive heterosis In polyploids, the further increase in heterosis beyond the single-cross hybrid level that occurs in double-cross hybrids is defined as progressive heterosis.
Single-cross hybrid The progeny of a cross between two inbred lines.
Tetraploid An individual or line that contains four copies of the basic number of chromosomes of a species.

Heterosis is the phenomenon in which hybrids typically exhibit greater biomass, fertility, and other characteristics superior to the better of the two parents. The effects in the hybrids appear to involve a greater number of cells in individual plants (East, 1936), but there are also reports that cell size is altered in hybrids at least in some tissues (Greaves *et al.*, 2012). The developmental program is not perceptively changed but various aspects of the whole ensemble of traits do not necessarily correlate with each other (Flint-Garcia *et al.*, 2009), suggesting independent control. In hybrids between wide phylogenetic distances, hybrids can exhibit rather spectacular growth (Gravatt, 1914; Karpechenko, 1927).

The phenomenon of hybrid vigor has been used unwittingly in various civilizations in order to produce superior crops (Chen, 2010) but came under scientific investigation with the study of Darwin on inbreeding and outcrossing (Darwin, 1876). Darwin investigated various species that were self-pollinating or outcrossing and studied the consequences of inbreeding. He found an overall generalization that the species which typically were self-pollinating showed lesser effects of inbreeding than species that usually were outcrossing.

Genetic thought about heterosis began in the early 1900s following the rediscovery of Mendel's Laws (Bruce, 1910; Shull, 1908; Jones, 1917). In this case, inbred lines of maize were crossed together and the hybrids were found to exhibit excellent growth characteristics compared with both parents. This realization led to the development of inbred lines and eventually to the widespread use of hybrid maize following the suggestion by D. F. Jones of the double-cross hybrid method of producing seed for planting by farmers. Subsequent development of the use of cytoplasmic male sterility for the production of hybrid seed in various species (for review of early work: Duvick, 1959) expedited the production of hybrid materials. With the continual improvement of inbred lines, single-cross hybrids in maize are now used for hybrid seed production.

Potential Genetic Explanations

Despite the widespread use of hybrid vigor for commercial production in many plant species, the genetic and molecular basis of the phenomenon has been stubbornly resistant to an understanding. An early explanation was that different sets of slightly deleterious alleles were present in different inbred lines and when crossed together, the complementation of both sets from the two parents was responsible for hybrid vigor (Jones, 1917; Charlesworth and Willis, 2009). This undoubtedly occurs, but it is not yet clear whether the cumulative complementation across loci is the responsible mechanism. Another idea is that different alleles or genes interact in

the hybrid state to trigger the superior growth of the hybrid (Shull, 1908).

A variant of the complementation hypothesis was formulated from the finding in maize that different inbred lines have slightly different gene repertoires (Fu and Dooner, 2002). This presence–absence variation is manifested by the observation that genes present in one inbred are missing in others and vice versa. Hybrids would have a greater number of genes and would complement any detrimental effects of gene absence in the respective parents. The gene absences are more likely restricted to those that are nonvital or without effect on development. It is not known whether the classes of genes that can be deleted without major effects would nevertheless play a role in heterosis in hybrids between vigorous inbreds.

One set of observations that bear on this issue is that early in the study of heterosis it was realized that improvement of inbred lines did not diminish the observable level of heterosis (East, 1936). If the inbred lines were improved, it might be argued on the complementation model that the magnitude of heterosis would decline. But this is not observed (East, 1936). Duvick conducted a very thorough examination of this issue (Duvick, 1999). He used inbred lines developed at Pioneer Hi-Bred over decades and tested their yield when crossed to a common parent and of the inbred themselves. When yield was plotted by year, there was a progressive improvement in inbreds and hybrids. However, the contribution of heterosis to the yield was resistant to change and was of similar magnitude. In this extensive experiment, the purging of detrimental traits did not seem to impact heterosis.

How Many Genes Are Involved?

Typically, the phenomenon of heterosis appears to be affected by multiple genes. Inbreeding experiments have produced estimates in the order of dozens that are responsible (Sprague, 1983), but such estimates are fraught with many difficulties in their determination. In terms of the total gene repertoire (Schnable *et al.*, 2009) in maize, the number is quite small. Indeed, different combinations of inbred lines produce different levels of heterosis (e.g., see Flint-Garcia *et al.*, 2009) and sets of inbreds can be grouped together for 'combining ability,' which would be consistent with a small fraction of genes being involved. The recognition of individual genes involved with heterosis has been difficult perhaps because of the small contribution that each gene makes to the full spectrum of hybrid vigor.

In contrast, there have been numerous reports of single-gene heterosis. Convergence of mutant alleles of *erecta* and *angustifolia* in Arabidopsis and then examination of hybrids led to superior performance of the heterozygotes (Redei, 1962). Single genes in maize have been suggested to produce a heterotic effect (Dollinger, 1985). In tomato, this issue has been examined rigorously with single genes producing greater biomass for yield of the SINGLE FLOWER TRUSS locus (Krieger *et al.*, 2010). Also in tomato, the transfer of small genomic regions from wild tomato into the domesticated variety and then testing for heterosis in heterozygotes revealed that small portions of the genome were effective, leading to the suggestion that single-gene allelic differences were responsible (Semel *et al.*, 2006).

It should be noted that the multigenic view and the single-gene effects are not mutually exclusive. The single-gene effects might operate in such a manner that the allelic differences are sufficiently great that their impact can be found in experimental comparisons. In other circumstances, it might be the case that the allelic differences are more subtle and therefore the contribution of each gene to the total effect is much less.

Gene Expression in Hybrids and Inbreds

Numerous studies have examined gene expression in inbreds and hybrids. A variety of findings have emerged from these studies (Andorf *et al.*, 2010; Chen *et al.*, 2008, 2010; Frisch *et al.*, 2010; Groszmann *et al.*, 2011; He *et al.*, 2010; Paschold *et al.*, 2010; Hoecker *et al.*, 2008; Huang *et al.*, 2006; Meyer *et al.*, 2007; Ni *et al.*, 2009; Pea *et al.*, 2008; Shen *et al.*, 2012; Stupar *et al.*, 2008; Stupar and Springer, 2006; Sun *et al.*, 2004; Swanson-Wagner *et al.*, 2006; Thieman *et al.*, 2010; Uzarowska *et al.*, 2007; Wang *et al.*, 2006; Wei *et al.*, 2009; Zhang *et al.*, 2008; Zhuang and Adams, 2007). Many genes are additive in the hybrids being at the mid-parent value. Others deviate toward the value of one parent or the other and some expressions lie outside the parental values. The proportion of genes that exhibit these various behaviors is variable among experiments and may differ depending on the experimental methods, tissues, species, or developmental stage examined. There are reports that the numbers of genes that exhibit non-additive (deviating from the mid-parent value) expression are greater in more heterotic hybrids of various species (Li *et al.*, 2009, 2011; Riddle *et al.*, 2010). The basis of this observation is unknown and might reflect different mixtures of cell types in hybrids or true changes in gene expression associated with differing magnitudes of heterosis. Others suggested that potential mechanisms involve metabolic networks (Fievet *et al.*, 2010; Lisec *et al.*, 2011), protein quality control (Goff, 2011), control of cell number (Guo *et al.*, 2010), and altered circadian rhythms (Ni *et al.*, 2009).

Heterosis in Polyploids

The behavior of heterosis in polyploids has been discussed much less than the behavior in presumed diploids and has sometimes been dismissed in discussions of mechanism. However, given that all plants have a history of repeated polyploidization and then evolutionary return to a more diploid state (Jiao *et al.*, 2011), it would seem that these considerations are important. Indeed, heterosis is more likely to have played a role in this cycle of polyploidization and diploidization.

The first issue of note involving heterosis in polyploids is that there is evidence of a genomic dosage effect on the magnitude. This realization was first made by East (1936), involving tobacco polyploids in which different doses of the distinct genomes contributing to the polyploid were present. Although the results from these experiments were straightforward, they did involve genomes that originated from

different species. It is unknown how this parameter might affect the results and thus how this information might be incorporated into developing hypotheses about heterosis.

To examine this question within a single species, Yao *et al.* (2013) produced triploid maize that were derivatives of two different inbred lines and also two types of triploid hybrids (ABB and BAA). The matched diploids were also studied. The reciprocal hybrids at the diploid level were very similar to each other as is usually the case. However, at the triploid level, the two types of triploid hybrids exhibited heterotic effects that were quite distinct from each other using better parent heterosis. However, when a weighted average was produced and mid-parent heterosis was examined, the two types of triploid hybrids produced a very similar result. These two types of analysis indicate that genomic dosage plays a role in heterosis and the effects are proportional to the change in dosage, i.e., the weighted averages become basically equivalent. These results suggest that heterosis is affected by dosage-sensitive genetic factors similarly to many quantitative traits (Tanksley, 1993; Liu *et al.*, 2003; Lee *et al.*, 1996). They also indicate that complementation of detrimental recessive alleles from the different parents is unlikely to be the sole contributor to heterosis.

Progressive Heterosis

Another aspect of heterosis of note is the phenomenon of progressive heterosis (Bingham *et al.*, 1994; Groose *et al.*, 1989). This phenomenon was first defined in alfalfa, an autotetraploid. The finding was that single-cross hybrids between inbred lines would produce a certain level of hybrid vigor, but when two single-cross hybrids were mated, the progeny with now more potential alleles present at each locus exhibited even greater heterosis. In other words, by maximizing the allelic diversity, there was an increase in the magnitude of heterosis. Although this phenomenon has been most thoroughly studied in alfalfa, related results have been found in maize and potato (Levings *et al.*, 1967; Mok and Peloquin, 1975; Randolph, 1942; Sockness and Dudley, 1989a,b; Chase, 1980; Riddle and Birchler, 2008). It is also likely that the fact that heterosis can be observed in hexaploid wheat (Briggle, 1963) and octoploid triticale (Goral *et al.*, 2005), when different varieties are crossed together, reflects a similar phenomenon.

The genetic basis of progressive heterosis has not been explored in depth. The hypothesis that heterosis results from complementation would require that any four inbred lines would have different slightly deleterious mutations so that in the single-cross hybrids some of them would be complemented in any combination of inbreds. However, it would also require that for the double-cross hybrid, there must be still different sets of recessives that are homozygous in the two single-cross hybrids so that they would be complemented in the double cross to provide a further boost via complementation. But at the same time, the double-cross hybrid could not return any loci to the homozygous state to the point of canceling the added gain from complementation because complementation would be eliminated for these loci. The genetic parameter that correlates with progressive heterosis is the maximization of allelic diversity. There is no theoretical or experimental exploration of the basis of this relationship.

Inbreeding Depression

A third aspect of heterosis in polyploids of note is that inbreeding curves between matched diploids and tetraploids are much more similar than predicted by the mechanisms of homozygosis at the two ploidy levels (Alexander and Sonnemaker, 1961; Busbice and Wilsie, 1966; Rice and Dudley, 1974). For example, at the diploid level, a heterozygote (A/B) when selfed will produce half of the next generation as homozygous and the other half as heterozygous for that locus. At each subsequent generation, the amount of heterozygosity will decline by one half. In contrast, for a heterozygous tetraploid (A/A/B/B), the homozygosis will depend on the location of a gene on the chromosome, but for genes near the centromere, a self-pollination will produce one in 36 homozygotes for the two respective alleles for a total of one in eighteen homozygous progeny. There is, however, one half of the progeny that remains heterozygous (A/A/B/B). The other classes of progeny have different numbers of alleles present (A/B/B/B or A/A/A/B). Certainly, these conditions described above apply to individual loci without regard to how interactions occur across the genome, which would no doubt complicate how inbreeding operates in practice.

Another consideration that might slow the inbreeding in a tetraploid is that pollen from a tetraploid can be heterozygous and potentially exhibit a heterotic effect on growth. This situation might favor fertilization by heterozygous pollen grains that can outcompete any homozygous pollen. In diploids, all pollen grains are haploid and heterozygosity will not occur. There has been no concerted study of how this fact of polyploidy biology might affect inbreeding, but it would be expected to slow inbreeding rather than accelerate it.

The above considerations suggest that the homozygosis of recessive mutations would proceed at a vastly different rate in matched diploids and tetraploids. However, when matched diploid and tetraploid hybrids are produced and then carried through a regime of continued self-pollination over generations, the decline in vigor between the two ploidy levels is similar. This finding was first thoroughly characterized in alfalfa (Busbice and Wilsie, 1966), but related findings have been made in maize (Rice and Dudley, 1974). These data would suggest that the decline in vigor is at least not solely due to the homozygosis of recessive alleles. Busbice and Wilsie (1966) suggested that a shift in the allelic numbers might contribute to a similar inbreeding curve. This interpretation is consistent with the genomic dosage effects impacting heterosis noted above. The shift in allelic numbers in a tetraploid might not produce an exactly equal inbreeding curve to the diploid, but it is unlikely that any experiment has been sufficiently large to distinguish what is certain to be a subtle difference.

Conclusion

Given the central role that heterosis plays in crop production, continued investigation of the genetic and molecular basis of heterosis is clearly justified. As further data become available, the possible explanations and models to explain hybrid vigor will become constrained as the scientific community

asymptotically approaches a consensus. An elucidation of the underlying basis of heterosis might provide the ability to manipulate and maximize it for crop production.

See also: Breeding: Plants, Modern

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Human Nutrition: Malnutrition and Diet

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Glossary

Food security Availability and access to food.
Indispensible amino acids Amino acids whose carbon skeletons cannot be synthesized from simpler molecules in animals, and therefore must be provided in the diet.
Macronutrients Fats, carbohydrates, and proteins; components of the diet that provide calories.
Micronutrients Vitamins and minerals, compounds needed in the diet in small amounts to aid metabolism. Micronutrients do not provide calories, but are involved in metabolic pathways.
Protein quality Ability to provide the nitrogen and amino acid requirements for growth, maintenance, and repair.
Recommended Dietary Allowances (RDA) The amount of essential nutrients needed to provide nutrients needs of most individuals in the population.

Principles of Human Nutrition

Humans are mammals and start life by drinking their mother's milk. Breast milk of humans is high in fat (50% of calories) and carbohydrate and low in protein. Human breast milk composition is considered closest to marsupials, species that carry their young around to allow for regular infant feeding. Best practices for infant feeding supports that mothers have easy access to their infants as young babies will feed up to 12 times per day.

Calories and protein needs are highest per pound body weight for infants and children. Babies triple their body weight in the first year, which requires regular feeding of breast milk or high-quality infant formula. Failure to thrive in infants is linked to infrequent feeding or dilution of infant formula to lower costs. Nutrient content of breast milk is maintained in women on inadequate diets, although milk volume may decrease. Often in a famine, the breastfed infant or toddler is the best nourished in the population.

When resources are scarce, nutritional priority should go to pregnant and lactating women, infants, and children. During growth and development, calorie and protein needs are high and nutrient insults are much more serious than for adults.

Generally, the diet expands during the weaning stage. Usual recommendations are to include foods high in iron as breast milk is particularly low in iron. Interestingly, the bioavailability of iron in breast milk is very high so breastfed babies tend not be iron deficient. Mainstays of the local diet are then introduced to the child. In most cultures, these are high-starch foods, such as rice, cassava, potatoes, corn meal, or bread. Fruits and vegetables are also introduced into the diet and provide the needed vitamins and minerals. As breast milk consumption decreases, good-quality protein sources also are needed in the diet. Animal proteins, such as cow's milk, meat, fish, and eggs are highest in protein quality. Other protein sources include legumes, nuts, and grains.

Macronutrients

Unlike vitamins and minerals, fats, carbohydrates, and proteins, the macronutrients, can substitute for each other to meet the body's energy demands (Otten *et al.*, 2006). In diet planning, protein is considered first as it is the most important macronutrient. On average, approximately 15% of the total calories in the diet should come from protein.

Protein is the major structural component of all cells in the body and functions as enzymes, hormones, and other important molecules. Proteins are also important as a source of calories and low-calorie diets are necessarily high in protein. The Recommended Dietary Allowance (RDA) for both men and women is 0.80 g of good quality protein per kg body weight per day and is based on careful analyses of available nitrogen balance studies. Data were insufficient to set a tolerable upper intake level for protein or amino acids.

The Acceptable Macronutrient Distribution Range (AMDR) for protein is 5–20% of total calories for children 1–3 years of age, 10–30% of total calories for children 4–18 years of age, and 10–35% of total calories for adults older than 18 years of age (Otten *et al.*, 2006).

Both protein and nonprotein energy (from carbohydrates and fats) must be available to prevent protein-energy malnutrition (PEM). If amino acids are not present in the right balance, the body's ability to use protein will be affected. Protein deficiency affects all organs and is particularly concerning during growth and development. The risk of adverse effects from excess protein intake from food appears very low. The data are conflicting on the potential for high-protein diets to produce gastrointestinal effects, change nitrogen balance, alter mineral absorption, or affect chronic diseases such as osteoporosis or renal stones.

Carbohydrates

Carbohydrates – the sugars, starches, and fibers found in fruits, vegetables, grains, and milk products – are an important part of a healthy diet. Sugars and starches supply energy to the body in the form of glucose, which is the primary energy source for the brain, central nervous system, and red blood cells. Fibers, unlike sugars and starches, do not supply glucose to the body. They promote healthy laxation and decrease the

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risk of certain chronic diseases such as coronary heart disease (CHD), obesity, and colon cancer (Slavin, 2008).

The nomenclature for carbohydrates is somewhat confusing. Sugars can be one sugar unit (monosaccharides) such as glucose, fructose, and galactose; and they can be two sugar units linked together (disaccharides) such as sucrose, lactose, and maltose. A further distinction is sometimes made between intrinsic and extrinsic sugars. The term intrinsic sugar means those sugars that are naturally occurring within a food, whereas extrinsic sugars are those that are added to foods. The US Department of Agriculture (USDA) has defined added sugars as sugars and syrups that are added to foods during processing or preparation, and also includes sugars and syrups added at the table. There is no difference in the molecular structure of sugar molecules, whether they are naturally occurring in the food or added to the food (Hess *et al.*, 2012).

Starches are many glucose units linked together (polysaccharide). Although most starch can be broken down by human enzymes into glucose for absorption, some starch does not undergo digestion in the small intestine and is called resistant starch, which is found in plant foods such as legumes, pasta, and refrigerated cooked potatoes. Fibers, like starches, are polysaccharides made up mostly of glucose units (in the case of cellulose) or other combinations of monosaccharides. However, the monosaccharides in fibers are bonded to each other differently than they are in starches, and human enzymes cannot break the bonds in the fibers. Thus, fibers are not absorbed from the small intestine and pass relatively intact into the large intestine, as does resistant starch.

Recommendations for the Intake of Sugars and Starches

The Institute of Medicine (IOM) report Dietary Reference Intakes for Energy, Carbohydrate, Fiber, Fat, Fatty Acids, Cholesterol, Protein, and Amino Acids (IOM, 2005) established an RDA for carbohydrate of 130 g day^{-1} for adults and children. This value is based on the amount of carbohydrate (sugars and starches) required to provide the brain with an adequate supply of glucose. Glucose is the only energy source for red blood cells and the preferred energy source for the brain, central nervous system, placenta, and fetus. When muscle cells operate anaerobically (without oxygen), they rely 100% on glucose. If glucose is not provided in the diet and the body's storage form of glucose (glycogen) is depleted, the body will break down protein in the muscles to maintain glucose blood levels and supply glucose to the brain (IOM, 2005).

The IOM also set an AMDR for carbohydrate of 45–65% of total calories. At the low end of this range it is very difficult to meet the recommendations for fiber intake, and at the high end of the range overconsumption of carbohydrates may result in high blood triglyceride values. A comparison of the RDA to the AMDR shows that the recommended range of carbohydrate intake is higher than the RDA. For example, if an individual with a caloric intake of 2000 kcal day^{-1} were to consume 55% of calories as carbohydrate (the mid-range of the AMDR) that would mean that 1100 kcal would be from carbohydrate. This equates to 275 g carbohydrate (1 g carbohydrate = 4 kcal), well above the RDA of 130 g day^{-1}. In summary, the primary beneficial physiological effect of sugars and starches, and the basis for setting an RDA for carbohydrate, is the contribution of glucose as an energy source for the brain. However, the amount of glucose needed by the brain is lower than the AMDR for carbohydrate (45–65% of total calories).

Recommendations for the Intake of Fiber

Fibers are different from sugars and starches in that they are not digested and absorbed in the small intestine and converted to glucose. Humans do not have the necessary enzymes to break down fibers into their constituent parts so that they can be absorbed into the body. Therefore, fibers pass from the small intestine into the large intestine relatively intact. There they can be fermented by the colonic microflora to gases such as hydrogen and carbon dioxide and to short-chain fatty acids. Although fibers are not converted to glucose as are sugars and starches, some of these short-chain fatty acids are absorbed and can be used for energy in the body. However, determining the amount of calories supplied by fiber is complex because it depends on such factors as the fermentability of the fiber, the individual's colonic microflora, how long fiber stays in the colon, etc. The IOM has set an Adequate Intake (AI) value for fiber of 14 g of fiber per 1000 kcal. This AI is based on the totality of the evidence for fiber decreasing the risk of chronic disease and other health-related conditions, but the actual numbers for the AI were derived from the data supporting a decreased risk for the development of CHD. The major food sources of fiber are fruits, vegetables (particularly legumes), and grains. Milk does not contain fiber although certain milk-containing products may.

Major Food Sources of Carbohydrates (Fruits, Vegetables, Grains, and Milk Products)

Because the RDA for carbohydrate is relatively easy to meet, and carbohydrates (sugars and starches) supply calories, it is important to choose food sources of carbohydrates carefully to maximize nutrient value per calorie. Also, because fiber has known health benefits (e.g., promoting a healthy laxation and decreasing the risk of CHD and obesity) it is advisable to select high-fiber foods where possible. For example, fruits provide sugars, usually at a relatively low calorie cost, and they are important sources of fiber and at least eight additional nutrients. Some vegetables are high in starch and some are very low in both starch and sugar, but they all are important sources of fiber. They also are important source of nutrients, including vitamins A, E, and folate and potassium, and, in general, do not supply many calories. Whole grains are high in fiber and starch, but most of the fiber is removed when grains are refined. Milk and milk products contain the sugar lactose and generally do not contain fiber.

Fat

Fats in food provide a major source of energy for the body. Humans store energy as fat.

During malnutrition, the body will burn fat for energy. But metabolically it takes carbohydrate to burn fat. This is often referred to as 'fat burns in the flame of carbohydrate.' In starvation, there are no carbohydrate stores left in the body. The body cannot burn fat for energy without carbohydrate so the body starts breaking down body protein to make carbohydrate. As starvation continues, the body adapts to other pathways to burn fat which yield ketone bodies.

Dietary fat is either saturated or unsaturated. Total fat intake is generally 20–35% of energy for adults; higher levels are recommended for growing children. The main fat sources are butter, margarine, vegetable oils, whole milk, meat, and baked products. Breast milk supplies 50% of calories as fat. Thus, usual feeding practices for children are to maintain higher intakes of fat for children. Usual recommendations are to transition to whole cow's milk from breast milk during the weaning process, generally after age 1 year.

Two unsaturated fatty acids, linoleic and α-linolenic are essential and thus must be obtained from foods. Only small amounts of these essential fatty acids are needed, therefore, inadequate intakes are not practical nutritional problems.

Proteins

Different sources of protein vary widely in their chemical composition as well as in their nutritional value. The quality of a protein is an expression of its ability to provide the nitrogen and amino acid requirements for growth, maintenance, and repair. Protein quality is determined by two factors, digestibility and amino acid profile.

Whole wheat flour is low in lysine and navy beans are low in methionine. Thus, the concept of complementing proteins is to encourage consumption of vegetarian foods low in one amino acid with vegetarian foods low in another – examples being beans and rice, a peanut butter sandwich, or hummus on crackers.

Recommendations for the Intake of Amino Acids

Dispensable, indispensable, and conditionally indispensable amino acids are needed in the human diet. The nine indispensable amino acids are those whose carbon skeletons cannot be synthesized from simpler molecules in animals, and therefore must be provided in the diet. The indispensable amino acids are histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophan, and valine. Dispensable amino acids are alanine, aspartic acid, asparagine, glutamic acid, and serine. Conditionally, indispensable amino acids include arginine, cysteine, glutamine, glycine, proline, and tyrosine.

Major Food Sources of Proteins

Proteins found in animal sources such as meat, poultry, fish, eggs, and milk provide all nine indispensable amino acids and are referred to as 'complete proteins.' Proteins found in plants, legumes, grains, nuts, seeds, and vegetables tend to be deficient in one or more of the indispensable amino acids and are called 'incomplete proteins.' Isolated proteins from dairy products (casein/whey), soy, and other products can also be added to foods or taken as dietary supplements. Isolated amino acids are also sold as dietary supplements, but intakes tend to be low. Data are limited on the adverse effects of high amounts of amino acids from dietary supplements and therefore caution is recommended in consuming any single amino acid at levels significantly above those found naturally in foods.

For men and women, protein provides approximately 15% of total calories. As calorie intake decreases, it is essential to increase the percentage of calories from protein to consume the RDA for protein. Thus, the wide range of 10–35% of total calories coming from protein for adults is based on the large range of calories consumed depending on physical activity and body size.

Any animal protein, such as eggs, meat, fish, and milk are high-quality proteins and are 'complete,' meaning they supply all the nine essential amino acids needed to build body protein (Otten *et al.*, 2006). Plant proteins, from grains, legumes, nuts, seeds, and vegetables are 'incomplete' as they do not have adequate amounts of all essential amino acids. Generally, grains are low in the amino acid lysine, whereas legumes are low in the amino acid methionine. Because foods are eaten in combination, it is not difficult to build complete proteins. Many traditional eating patterns, such as beans and rice, beans and corn tortillas, or a peanut butter sandwich combine legumes and grains and provide complete protein.

Both protein and nonprotein energy (from carbohydrates and fats) must be available to prevent PEM. If amino acids are not present in the right balance, the body's ability to use protein will be affected. Protein deficiency affects all organs in the body.

Protein quality of a food depends on the amino acid composition and digestibility of the protein. If the content of a single indispensible amino acid in the diet is less than the individual's requirement, then this deficiency will limit utilization of other amino acids and prevent normal rates of protein synthesis. There is no perfect way to measure protein quality; however chemical score and protein efficiency ratio (PER) are both used to rank protein quality.

Chemical score is determined in comparison to egg protein, which is considered the reference protein and given a score of 100. The amino acid patterns in all protein sources are measured and the amino acid in the test protein with the lowest level is called the limiting amino acid of the protein. The value of the percentage is the chemical score (**Table 1**). In this system, fish has a chemical score of 71, whereas lentils have a chemical score of 31.

PER requires monitoring the growth of laboratory animals. PER is defined by dividing the weight gained by the animal by the weight of protein consumed. The conditions for gathering PER data are standardized. With this system, animal products are the highest quality proteins, whereas plant products are not complete and are of lower quality (**Table 1**).

Dietary reference intakes for total protein vary by life stage group. Values are based on grams of protein needed per kilogram of body weight. Values are highest in infancy (1.52), decrease during childhood from 1.2 to 0.85, and then remain at 0.8 after age 19. Values increase during pregnancy (1.1) and lactation (1.3).

Table 1 Measures of protein quality (Source: National Research Council, 1974)

Protein	*Chemical score*	*Protein efficiency ratio*
Egg	100	3.92
Fish	71	3.55
Beef	69	2.30
Sunflower seed	61	2.10
Casein	58	2.86
Oats	57	2.19
Rice	56	2.18
Peanuts	55	1.65
Soybeans	47	2.32
Wheat	43	1.53
Lima beans	41	1.53
Maize (corn)	41	1.12
Lentils	31	0.93

Both protein and nonprotein energy must be available to prevent PEM. Worldwide PEM is common in both children and adults and is associated with deaths of approximately 6 million children each year (FAO, 2010). In developed countries, PEM is seen mostly in hospitals in patients with chronic disease and in the elderly. Protein deficiency affects all parts of the body, especially the immune system, so malnourished people are more susceptible to all diseases and infections. Gut mucosal systems and permeability are particularly affected, so refeeding programs are often unsuccessful because the body can no longer digest and absorb foodstuffs.

The AMDR for protein in adults is 10–35% of total calories. Because protein requirements are set with body weight, low-calorie diets must contain a higher percentage of protein to supply the RDA for protein.

After protein needs are met, diets must also supply the remaining essential nutrients, fats, carbohydrates, fiber, vitamins, minerals, and fluids. When adequate amounts of a variety of foods are consumed, it is generally not difficult to obtain the essential nutrients. Some exceptions include iron and zinc, which may be low in plant sources and the iron and zinc that is in the foods is not bioavailable. Additionally, calcium may be a problem nutrient, especially during growth and development. Thus if children do not have access to dairy products, other sources of calcium will need to be consumed. Soups made with meat or fish with bones may be the source of the necessary calcium. Some dark green vegetables and seeds also provide calcium to the diet.

Micronutrients

Vitamins

There are 13 essential vitamins, 4 fat soluble and 9 water soluble. Fat-soluble vitamins include vitamins A, D, K, and E. Because of the importance of these vitamins to health and past low intakes, vitamin A and D are added to milk in the US to ensure that children get adequate intakes. Past feeding programs have given cod liver oil to children to make sure they have adequate levels of vitamin D to prevent rickets, the deficiency disease associated with low intakes of vitamin D.

Vitamin A deficiency causes xerophthalmia, which is estimated to affect 3–10 million children (mostly in developing countries) annually. Of those affected 250 000–300 000 go blind every year. Xerophthalmia is an irreversible drying of the conjunctiva and cornea. Efforts to deliver vitamin A to susceptible populations are difficult as preformed vitamin A occurs mostly in animal products. Golden rice, a genetically modified rice with high levels of vitamin A shows great promise, but to date has had limited acceptance (Chassy, 2010).

Vitamin K is involved in blood coagulation and infants in the US and Canada receive routine injections at birth to prevent bleeding diseases. Vitamin K deficiencies are rare and limited to individuals with malabsorption syndromes. Vitamin E functions as an antioxidant in the body. Deficiency is rare except with fat malabsorption syndromes or PEM.

The water-soluble vitamins include vitamin C, thiamin, riboflavin, niacin, vitamin B_6, vitamin B_{12}, pantothenic acid, biotin, and folic acid. Fruits and vegetables are typically concentrated in water-soluble fibers, especially vitamin C and folic acid. B_{12} is found only in animal products, whereas vitamin B_6 is also associated with foods high in protein. Niacin can be made from the amino acid tryptophan, hence diets deficient in protein and niacin are associated with pellagra, the deficiency disease of niacin.

Minerals

There are 20 minerals that are essential to the humans. Calcium and iron are most likely to be deficient in humans. Calcium plays a role in bone health and is most important during childhood. Foods rich in calcium include milk, yogurt, cheese, kale, and broccoli. Calcium may be poorly absorbed from foods that are rich in oxalic acid or phytic acid, such as kale. Calcium intake may drop significantly during weaning if no dairy products are available to the weaned child.

Iron-deficiency anemia is the most common nutritional deficiency in the world. Functional indicators of iron deficiency include reduced physical work capacity, impaired cognitive function, and adverse effects for both the mother and the fetus (premature delivery, low birth weight, and increased perinatal infant mortality). Approximately half of the iron from meat, poultry, and fish is heme iron, which is highly bioavailable. The rest is nonheme iron which is less readily absorbed in the digestive tract. All vegetable foods, grains, vegetables, legumes contain nonheme iron.

Water

A safe, abundant water source is also essential to good health. The body is well adapted to balance water needs if electrolytes such as sodium and potassium are also available in the food supply, typically in fruits and vegetables. Fluid problems generally develop because of contaminated water supply or diarrhea; these problems are usually most serious in infants, children, and the elderly.

Growth and Development – When Are Nutrient Needs Highest?

Energy is required to sustain the body's various functions including respiration, circulation, metabolism, physical work, and protein synthesis. Nutrient needs are highest for infants and young children, although these needs are on a body weight basis. Calorie needs are also greatest during growth and development, so increased daily calorie needs during pregnancy average 300 kcal day^{-1}, whereas increased daily calorie needs during lactation average 500 kcal. Children and adolescents need higher calories during growth spurts. Energy needs are also based on lean muscle weight, so adolescent males in a growth spurt generally need the highest amount of calories in a family.

Calorie needs are also affected by energy expenditure. Hard physical labor will require many more calories than the calories needed for basal metabolism. Inactivity, the usual state in most developed countries, is generally linked to obesity because food is readily available, yet so few calories need to be expended during the usual day's activities.

Malnutrition Is Most Likely in Children and the Elderly

Food security refers to the availability of and access to food. Other issues in food security include access, utilization, stability, and the contribution of vulnerability of individuals (Pinstrup-Andersen, 2009). According to the Food and Agriculture Organization of the United Nations (FAO) food security exists when all people, at all times, have physical, social, and economic access to sufficient, safe, and nutritious food that meets their dietary needs and food preferences for an active and healthy life. The 2010 FAO report 'The State of Food Insecurity in the World' estimated that globally 925 million people are undernourished. The FAO defined undernourishment as when caloric intake is below the minimum dietary energy requirement (Broca, 2002).

One of the challenges in discussing food insecurity is the lack of a standardized measure which works in all settings and cultures. Barrett (2010) suggests that the difficulty in measurement is because food insecurity is a multidimensional concept that encompasses aspects of availability, access, and utilization. Studies quoted in the literature use a variety of tools including the USDA Household Food Security Scale, the Radimer/Cornell Hunger and Food Insecurity Instrument, and the Household Food Insecurity Access Scale (Ivers and Cullen, 2011).

Food security requires nutritional adequacy. Any individual that has micronutrient deficiency is food insecure. In a US study, food insecurity was associated with reduced micronutrient intake among women of childbearing age (Rose and Oliveira, 1997). Problem nutrients included calcium, iron, vitamin E, magnesium, and zinc. Nutrient deficiencies can be made worse by other medical conditions. Human immunodeficiency virus infections increase resting metabolic expenditure and impair absorption and utilization of nutrients (Katona and Katona-Apte, 2008).

Severe acute malnutrition (SAM) is a consequence of sudden food shortage and is associated with loss of a person's body fat and wasting of their skeletal muscle (Picot *et al.*, 2012). Many of the affected are already undernourished and susceptible to disease. Infants and young children are most susceptible as their nutrient needs are highest and they depend on others to provide food and nourishment. SAM is associated with high levels of morbidity and mortality.

Picot *et al.* (2012) evaluated the effectiveness of interventions to treat infants and children aged <5 years who have SAM. A total of 8954 records were screened and 74 articles (describing 68 studies) met the inclusion criteria and were included. Generally, evidence was lacking or inconclusive. No dietary treatment was found to offer significant benefits, although individual studies assessed zinc and potassium. Additionally, no dietary treatment for the diarrhea seen with acute malnutrition showed any significant difference on recovery.

No doubt the best strategy is to prevent malnutrition, as dietary treatment is difficult and often not successful.

Overfed, but Undernourished – the New Malnutrition

In many developed countries, the new malnutrition is obese children who are food insecure. Often in these situations, children have access to poor quality foods that are too low in protein and micronutrients to promote adequate growth and development. In the US, 21% of children live in a food-insecure household (Nord *et al.*, 2007), which means that children in the household live without the financial means to access enough food for active, healthy living.

Eisenmann *et al.* (2011) reviewed studies on the relationship between obesity and food insecurity. Although it is generally accepted there is a relationship, the majority of studies studies with larger sample sizes found no relationship between body weight and food insecurity. Smaller studies in rural Malaysia found that 58% of food-insecure women were overweight compared with 38% of those who were food secure (Shariff and Khor, 2005). It is suspected that the lack of accepted measures for food security may hinder research in this field.

Conclusion

Adequate nutrition is needed to support growth and development and it is a basic human right to have adequate food and water. Yet many in the world lack access to safe food and water. This situation may be acute or chronic. The most immediate need is access to pure water to maintain hydration. Most previously well-nourished adults can live for 2 months without food as long as water is available. Water must be consumed within 2 days to maintain hydration status.

If this situation is chronic, then malnutrition is much more serious and often deadly. Malnutrition is typically linked with disease and outcomes may be poor even when food becomes available. These are the challenges of refeeding programs; success is often elusive. Malnourished individuals are often immunocompromised and are unable to digest and absorb the nutrients they need.

Malnutrition is of greatest concern in infants and children as their nutrient needs are highest and they are less able to

source and ingest foods. All children need access to nutrient-rich diets and these include high-quality protein, essential fatty acids, vitamins, and minerals. Many foods can provide these nutrients and local customs and tastes must be considered. Food that is not eaten provides no nutrient value.

See also: Determining Functional Properties and Sources of Recently Identified Bioactive Food Components: Oligosaccharides, Glycolipids, Glycoproteins, and Peptides. Vitamins and Food-Derived Biofactors

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ENCYCLOPEDIA OF AGRICULTURE AND FOOD SYSTEMS

VOLUME 4

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VOLUME 4

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GUIDE TO USING THE ENCYCLOPEDIA

Structure of the Encyclopedia

The material in the encyclopedia is arranged as a series of articles in alphabetical order.

There are four features to help you easily find the topic you're interested in: an alphabetical contents list, cross-references to other relevant articles within each article, and a full subject index.

1 Alphabetical Contents List

The alphabetical contents list, which appears at the front of each volume, lists the entries in the order that they appear in the encyclopedia. It includes both the volume number and the page number of each entry.

2 Cross-References

Most of the entries in the encyclopedia have been cross-referenced. The cross-references, which appear at the end of an entry as a See also list, serve four different functions:

i. To draw the reader's attention to related material in other entries.
ii. To indicate material that broadens and extends the scope of the article.
iii. To indicate material that covers a topic in more depth.
iv. To direct readers to other articles by the same author(s).

Example

The following list of cross-references appears at the end of the entry Critical Tracking Events Approach to Food Traceability.

> *See also*: Agribusiness Organization and Management. Food Chain: Farm to Market. Food Labeling. Food Law. Food Packaging. Food Security: Development Strategies. Food Security: Food Defense and Biosecurity. Food Security, Market Processes, and the Role of Government Policy. Food Security: Postharvest Losses. Global Food Supply Chains. Government Agricultural Policy, United States. Regulatory Conventions and Institutions that Govern Global Agricultural Trade

3 Index

The index includes page numbers for quick reference to the information you're looking for. The index entries differentiate between references to a whole entry, a part of an entry, and a table or figure.

4 Contributors

At the start of each volume there is list of the authors who contributed to that volume.

SUBJECT CLASSIFICATION

Agriculture and People

Agribusiness Organization and Management
Agricultural Cooperatives
Agricultural Ethics and Social Justice
Agricultural Finance
Agricultural Labor: Demand for Labor
Agricultural Labor: Gender Issues
Agricultural Labor: Labor Market Operation
Agricultural Labor: Supply of Labor
Agricultural Law
Agricultural Policy: A Global View
Analyses of Total Phenolics, Total Flavonoids, and Total Antioxidant Activities in Foods and Dietary Supplements
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Consumer-Oriented New Product Development
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Food Chain: Farm to Market
Food Labeling
Food Law
Food Marketing
Food Security, Market Processes, and the Role of Government Policy
Food Security: Development Strategies
Food Security: Food Defense and Biosecurity
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PREFACE

Food is absolutely necessary for human existence, yet for most in wealthy nations it is largely taken for granted because of its abundance. Sufficient food is a concern, however, for about 1 billion of the earth's inhabitants today who often go to bed hungry. Food security in a broad sense is becoming a worry of the future for those who understand the limitations of our earth's ecosystems. Malthusian prophecies have so far been wrong, but there is growing concern that we are rapidly reaching the point where feeding the world's growing and richer population will be at the cost to our environment that is unacceptable. In the next few decades we face the challenge of growing more food, with less water, with less fertilizer on less land – because of the growth of urban areas on prime agriculture land. We also face the largely unknown consequences that global warming will have on agricultural production. During the last century agricultural scientists were able to bring cutting-edge science into traditional agricultural practices and increase food production sufficiently to prevent global food shortages. The hope that new scientific discoveries will provide the means to keep ahead of world food demand is complicated by a growing public discomfort with biotechnology being applied to food production.

The concept of services being provided by the ecosystems of the earth is a fairly recent attempt to understand and place value on functions of natural lands that have historically been assumed to have few limits. In the past, if more food was needed, new lands were converted from forests or steppe lands into farm land and new water systems developed to provide the water needed for agriculture. When human populations were low our activities were largely buffered by the abundance of forest and steppe, but too late, we are beginning to understand that these provisioning services of our ecosystems are being overused and are no longer buffered by the abundance of wild lands and waters. We are rapidly losing our planet's biodiversity, irreplaceable ground water is being unsustainably consumed, and major river systems are being overused and polluted. Our oceans, the last place on the planet that still support our hunter and gathering traditions may not be able to sustain these activities into the future. And, food production and processing activities contribute to the greenhouse gas emissions that are rapidly warming our planet. Agriculture is the single greatest user of the earth's land and water resources. In the concept of ecosystem services, provisioning or providing food for all organisms is one of the services provided by ecosystems. Human population growth has and will continue to overtax the ecosystems we inhabit. The ultimate outcome of this major diversion of nature's resources into provisioning the human species is unknown, but it is critically important for us to understand what we must do to sustain our planet.

The breakthrough discovery about 10 000 years ago that plants and animals could be bred to provide a more abundant and secure food source was the foundation upon which all other human activities were able to flourish. Activities other than finding food now became possible and our diverse cultures were able to develop because of agriculture. Until fairly recently, however, the majority of the population of most nations was still directly involved in producing food. Mechanization of agriculture and continued improvements in genetics, fertilizers, and pesticides made food production very efficient in developed nations. In the United States, the leading nation in value of agricultural exports, less than 2% of the workforce is currently employed in producing food. The United States, however, is alone among the most populous nations of the world in having such a small population employed as farmers. In countries such as China, India, Indonesia, and Nigeria the majority of people are rural and involved in agriculture either directly or indirectly. But, as food production becomes more efficient in these countries, and as wages increase in other sectors, a major shift is occurring from rural to urban occupations. This revolution is potentially as important in affecting our cultures and community structures as was the development of agriculture. Many nations are currently experiencing a very rapid transition from rural to urban living with all of the social and logistic problems associated with such rapid structural changes. While this transition in our social and cultural structures is a broad subject, it does have significant impacts on agriculture and our food systems. To mention just a few, agriculture labor, food transport, food safety, and access to healthy food.

There is genuine concern among agricultural scientists that human populations and changing diets are outpacing our ability to meet the increasing food needs of the planet. In the first iteration by Academic Press in 1994 of the *Encyclopedia of Agricultural Science*, Noble Prize Winner Normal Borlaug wrote in its forward:

> Had the world's 1990 food production been distributed evenly, it would have provided an adequate diet (2350 calories, principally from grains) for 6.2 billion people – nearly one billion more than the actual population. However, had the people in Third World countries attempted to obtain 30% of their calories from animal products – as in the United States, Canada, or European Economic Community countries – a world population of only 2.5 billion people could have been sustained – less than half of the present world population.

The issue raised by Dr. Borlaug is probably the most important challenge we face. Human behavior and the food choices of consumers will determine the outcome of the race between food supply and population. Population control has been advocated for decades, and in some cases has become part of national policy, but the world's population continues to grow. Science breakthroughs cannot solve our food security and environmental quality challenges if consumers reject food that is not traditionally produced. Likewise, if meat products and other inefficiently produced food continue to be in high demand by consumers, there will be increased pressure on our food production systems. As supplies become short, prices rise. While this may be good for farmers, high food prices and food shortages will probably undermine our efforts to preserve the

world's remaining arable land as natural lands. We must change human behavior to solve the problems we face.

Food choices, nutrition, diets, food cultures, water and air quality, GMOs, global warming, food security, and similar topics are daily in the news throughout the world. We are all concerned about these issues, yet with all of the information easily available in the popular media about food there seems to be too little informed discussion on these various topics. In planning the *Encyclopedia of Agriculture and Food Systems* the editorial committee chose to organize the topics primarily by issues, rather than to focus on a traditional topic approach. We organized the issues that would be discussed in the chapters around the broad topics of Agriculture and People, Agriculture and the Environment, Agricultural Products, Plant Health Management, Animal Health Management, and Agriculture and Science. The issues raised in this preface are the ones that we felt needed to be addressed in this encyclopedia.

The associate editors joined me in the development of topics for the encyclopedia and were responsible for working with the authors – they deserve particular recognition. I was fortunate to be joined by a very distinguished group of colleagues who, I hope, are still friends. They spent much more time and effort in bringing this project to completion than any of us anticipated. I want to thank our authors who while overly committed and overworked, fulfilled their commitments to contribute to this work. I have been impressed with the quality of their contributions. The editorial staff of Elsevier have had the professionalism and patience to work with scientists who do not work under the same time and budget constraints that the staff work. I want to particularly thank Kristi Gomez, Donna de Weerd-Wilson, and Simon Holt who, each in succession, oversaw this effort, and I especially thank the project managers, who worked directly with me, and the associate editors, Kate Miklaszewka-Gorczyca, Will Bowden-Green, and Sam Mahfoudh.

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Industrialized Farming and Its Relationship to Community Well-Being

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Glossary

Community social fabric Refers to social organization, the features of a community that reflects its stability and quality of social life. Impacts on community social fabric are seen in social indicators such as population change; social disruption indicators; educational attainments and schooling quality; changes in social class structure; health status; and changes in local governance.

Family farm A farm operation where the farm household owns and controls the majority of farm production factors, land, labor, capital, technology, and management.

Industrial farm A nonhousehold-based farm production unit, with absentee ownership and control over production factors.

Marketing contracts The mechanism used by farm operators to reduce their exposure to market price swings; these contracts stipulate a commodity price or pricing mechanism for delivered goods and are used mainly for crop and dairy commodities.

Organizational changes in farming An increase in the relative proportion of hired to family labor, greater use of incorporation as a form of legal organization, and the movement toward a more integrated industry from farm to grocery, whose 'hallmark' is 'contract production and vertical integration.'

Organizational measures of industrialized farming Vertical integration of corporations into farming; contract farming arrangements; absentee ownership of production factors; dependency on hired labor; operation by farm managers, as opposed to material operation by family members; and legal status as a corporation.

Production contracts Mechanisms that involve cost-sharing arrangements and payment for farm operators' services usually for livestock production except for dairying.

Socioeconomic well-being Refers to standard measures of economic performance (employment, income, and business activity) and to a broader range of socioeconomic indicators used by sociologists to tap material conditions of families and populations (family poverty rates and income inequality).

The industrialization of farming The transformation whereby farms have become larger-scale, declined in number, and integrated more directly into production and marketing relationships with processors through vertical or contractual integration.

Vertical integration Operation of farms by firms that also operate in at least one other stage of the food chain, such as input supply, processing, and marketing.

Introduction

Public concern about the consequences of nonfamily owned and operated, industrialized farms for communities dates back to the 1920s (Boles and Rupnow, 1979). (Boles and Rupnow (1979, p. 471) state that public concern about corporate influence in farming began in the 1920–30 period when concern about large, publicly held corporations centered on fears about the effect of mechanization, foreclosure of farm land mortgages held by corporations, and corporate monopoly of land.) The first published research on the topic appeared in the 1930s. Since then, government and academic researchers have produced numerous studies showing the potential for adverse impacts on community life. The bulk of evidence indicates that public concern about the detrimental community impacts of industrialized farming is warranted. This article summarizes results from more than five decades of research that has investigated the relationship between nonfamily industrialized farming and community well-being. The purposes of this article are: To document the types of studies that have been conducted on the topic; to delineate their results as to whether adverse consequences were found; and to document the aspects of community life that may be jeopardized by industrialized farming. This article is grounded in Lobao's (1990) longstanding research on farm change and its impacts on communities and families (Barlett *et al.*, 1999; Belyea and Lobao, 1990; Kenney *et al.*, 1989; Lasley *et al.*,1995; Lobao (Reif), 1987; Lobao, 1990; Lobao (Reif) and Jones, 1987; Lobao and Meyer, 1995a,b, Meyer and Lobao, 1997; Lobao and Schulman, 1991; Lobao *et al.*, 1993; Lobao and Thomas,

1992, 1988) as well as her research on the broader topic of community development. (Lobao, 1993a,b,c, 1996, 1998; Lobao and Rulli, 1996; Lobao *et al.*, 1999). She updated this research in 2000 (Lobao, 2000), which was further updated in 2006 (Stofferahn, 2006), and which was updated and published in 2008 (Lobao and Stofferahn, 2008). This article further updates the research on the topic, and it is based on a systematic article of 56 studies on the topic of industrialized farming and community well-being.

The industrialization of farming refers to the transformation whereby farms have become larger-scale, declined in number, and integrated more directly into production and marketing relationships with processors through vertical or contractual integration (Drabenstott and Smith, 1996, p. 4). In the past two decades, farms in the farming-dependent Heartland states (The states forming the nation's farm heartland extend from the Mississippi River to the Rocky Mountains and from Texas to Canada. These states are Colorado, Iowa, Kansas, Minnesota, Missouri Montana, Nebraska, New Mexico, North Dakota, Oklahoma, South Dakota, and Wyoming (Barkema and Drabenstott, 1996, p. 1). More than two-thirds of the nation's farm-dependent counties are located in these states.) declined by roughly one-fourth, whereas average acreage grew by one-fourth to approximately 750 acres (Barkema and Drabenstott,1996, p. 62). As the number of farms declines, production becomes concentrated on larger farms. Nationally, small farms (defined here as those having annual gross sales of less than US$50 000) made up nearly three-quarters of the nation's farms in 1995 but they produced only approximately 8% of sales, whereas the top 2% of farms (those with sales of over a half million dollars annually) accounted for 44% of all sales (Sommer *et al.*, 1998, p. 10). Half of the nation's agricultural sales are produced by 3% of farms (Sommer *et al.*, 1998, p. 8).

Accompanying the growth of scale of operations are organizational changes in farming. These include an increase in the relative proportion of hired to family labor and greater use of incorporation as a form of legal organization. (In 1995, more than 98% of the nation's 2.07 million farms were classified as family operations. A total of 91% were sole proprietorships and 5% were partnerships. Only 3% of all farms were incorporated, and of these, 86% were considered family-held corporations by United States Department of Agriculture (USDA) as they had 10 or less stockholders (Sommer *et al.*, 1998, p. iv). Another organizational shift is the movement toward a more integrated industry from farm to grocery, whose 'hallmark' is "contract production and vertical integration that is linking farmers, food processors, seed companies, and other agribusiness" (Barkema and Drabenstott, 1996, p. 64). Vertical integration refers to operation of farms by firms that also operate in at least one other stage of the food chain – such as input, supply, processing, and marketing. In addition to their direct involvement in farm production, agribusiness firms contract with farmers for goods and services. Two types of contracting arrangements should be distinguished. Marketing contracts are used by independent operators to reduce their exposure to market price swings; these contracts stipulate a commodity price or pricing mechanism for delivered goods and are used mainly for crop and dairy commodities. Production contracts involve cost-sharing arrangements or payment for operators' services usually for livestock production except for dairying. On farms using production contracts, the largest share of farm sales accrues to the contractor (an agribusiness processor and/or producer), with the operator generally receiving a fixed fee for services (Sommer *et al.*, 1998, pp. 16–17). Production contracts extend agribusiness firms into direct farm production using the vehicle of the local farmer. To sociologists, production contract farms are an integral component of the agribusiness chain in which agribusiness firms, depending on corporate strategy, may enter farming through direct operation of their own units or through employing local farmers to participate in production homework. Sociologists are concerned with contract farming because of the risks it poses to agrarian social structure, communities, and families. (Sociologists are concerned with contract farming insofar that: it alters agrarian social structure by creating a segment of farmers who are the structural equivalent of factory production homeworkers; it extends the influence of industrialized farming in a community; and it erodes formally independent operators' autonomy in direct production, farm decision-making, and control over assets. Sociologists also are concerned with the general well-being of contractees (operators) and their families given their asymmetrical relationship in bargaining power with agribusiness firms.)

In classifying farms as 'industrialized' or 'family,' social scientists distinguish between the construct (an ideal-type concept) and its actual measurement (variables used to define the concept in practice). Different classifications of farms have been developed over the years because the structure of agriculture is continually changing. The term 'farm structure' or 'agricultural structure' refers to a broad set of characteristics that describe US farms, as well as the distribution of farm production resources and returns to those engaged in farm production activities (Sommer *et al.*, 1998, p. 6). Sommer *et al.* (1998, p. 6) provide a useful overview of the criteria used to classify farms. For sociologists, family farming is identified by whether the family unit owns a majority of capital resources, such as land, machinery, buildings, makes the majority of managerial decisions, and provides the bulk of labor (Goss *et al.*, 1980). Social scientists often use farm scale as a proxy measure to classify farms, because it is simple, clear, and often correlated with organizational characteristics of units. A recent USDA article classifies 'commercial farms' as those with US $50 000 or more in gross sales and 'small farms' as those with gross sales of less than US$250 000 (Sommer *et al.*, 1998, p. 69). Family farms (organized as sole proprietorships, partnerships, or family corporations) with gross sales of more than US$25 000 are classified as 'large-family farms,' whereas 'nonfamily farms' are any farms organized as nonfamily corporations, cooperatives, and farms operated by hired managers (Sommer *et al.*, 1998, p. 72). 'Family' farms and 'industrialized' farms are constructs at opposite ends of the farm continuum. To sociologists, the construct 'family farm,' is that where the farm household owns and controls the majority of farm production factors, land, labor, capital, technology, and management. At the other end of the farm continuum, the construct, 'industrial farm,' refers to a nonhousehold-based production unit, with absentee ownership and control over production factors. As with nonfarm firms, industrialized farms have a division of labor among owners, managers, and

labor with different groups of people assigned to different positions in the production process. Industrial farms "...are owned by one group of people, managed on a daily basis by another person or group, and worked by yet another group" (Browne *et al.*, 1992, p. 30). Between these 'ideal-type' descriptions of family and industrialized farms are other arrangements in organizing farming, such as part-owner farming (a form of family farming where the operator both owns and rents the land). Again, these are 'ideal-type' constructs, whose specific definition and measurement must depend upon the time period and public context.

When social scientists refer to 'industrialized' farms, they invariably are referring to both scale and organizational characteristics of the farm unit. (Social scientists measure industrialized farming by both scale and organizational variables. Scale is usually measured by sales and sometimes by acreage and real estate and for livestock operations, animal inventory. The actual dollar value for scale indicators used by analysts to indicate a 'large-scale' farm will obviously vary by the time period of study. In addition, what is considered a 'large-scale farm' also varies by regional context and commodity. Organizational measures of industrialized farming include vertical integration of corporations into farming; production contract farming arrangements; absentee ownership of production factors; dependency on hired labor; operation by farm managers, as opposed to material operation by family members; and legal status as a corporation (family or nonfamily) or syndicate.) In general, but not always, scale will coincide with organization. That is, large-scale farms (relative to smaller farms) are more dependent on hired labor and managers and more likely to have absentee owners, to be incorporated, and to be vertically integrated with agribusiness. For example, in 1995, mean gross sales of corporate farms were US$576 925 as compared with US$54 287 for sole proprietorship farms and US$218 795 for farms organized as partnerships (Sommer *et al.*, 1998, p. 15). Farms with production or marketing contracts also tend to be larger. In 1995, farms with marketing contracts (approximately 11% of all farms) had mean gross sales of US$242 888; whereas farms with production contracts (2.3% of all farms) had mean gross sales of US$617 858 (Sommer *et al.*, 1998, p. 12). For the purposes of this article, the umbrella term 'industrialized farm' is used to refer to both scale and operating characteristics of industrialized farms. Where it is useful and feasible to do so, a distinction is made between between scale and operating characteristics.

This article is organized into four sections. First, the article discusses the history of government and academic concern about the risks of industrialized farming for community well-being, from the 1930s to the present. Second, the article summarizes the findings from Lobao's research and that of her colleagues. Third, the article findings from five decades of social science research. It is divided into several subsections discussing, respectively, research issues involved in analyzing industrialized farming and community impacts, focusing on indicators of industrialized farming and types of consequences that a summary evaluation must consider; the various research designs used to assess the consequences of industrialized farming; and a summary of the results of past studies as to whether detrimental impacts were found. Eventually, the article ends with summary and conclusion.

It should be noted that public concern about industrialized farms extends beyond the well-being of states and their communities. Rather, public as well as academic concern extends to national food system issues, such as agribusiness concentration, consumer health, food safety, and sustainability of the national ecosystem. The immediate effects of industrialized farms, however, are on the day-to-day lives of people residing in the places where these farms are located. It is also at this level that social scientists have conducted a great deal of research over a long period of time. For these reasons, this article deals with the consequences of industrialized farming for well-being at the community level.

History of Public, Government, and Academic Concern with the Consequences of Industrialized Farming

More than a half century of research centers on the potential detrimental social consequences of industrialized farming. Since 1930s, the government and academic researchers have investigated the extent to which large-scale, industrialized farms adversely affect the communities in which they are located. One of the first series of studies was conducted by a sociologist, Tetreau (1938, 1940), who found that large-scale, hired labor-dependent farms were associated with poor social and economic well-being in rural Arizona communities.

In the early 1940s, the USDA sponsored a research project on the effects of industrialized farming using a matched-pair of two California communities, Arvin where large, absentee-owned, nonfamily operated farms were more numerous, and Dinuba, where locally owned, family operated farms were more numerous. The article on this project was prepared by Walter Goldschmidt, a USDA anthropologist. The purpose of the study was to assess the consequences of a California law with a provision placing acreage limitations on large farms located in California's Central Valley, so as to support family-size farms in the region. Goldschmidt (1978a, p. 458) notes that "The comparative study of Arvin and Dinuba was designed to determine the social consequences that might be anticipated for rural communities if the established law was applied or rescinded."

In this article, Goldschmidt (1978a) systematically documented is the relationship between large-scale farming and its adverse consequences for a variety of community quality of life indicators. Goldschmidt (1978a) observed that, relative to the family farming community, Arvin's population had a small middle class and high proportion of hired workers. Family incomes were lower and poverty was higher. There were poorer quality schools and public services, fewer churches, civic organizations, and retail establishments. Arvin's residents also had less local control over public decisions, or 'lack of democratic decision-making,' as the local government was prone to influence by outside agribusiness interests. By contrast, family farming Dinuba had a larger middle class, better socioeconomic conditions, high community stability, and civic participation. Goldschmidt's review was eventually published as Congressional Testimony (1968) and as a book (1978a). Goldschmidt's conclusion that large-scale industrialized farms create a variety of social problems for communities has been confirmed by a number of subsequent studies. One criticism

of Goldschmidt's (1978a) research was published by agricultural economists Hayes and Olmstead (1984). They did not challenge Goldschmidt's (1978a) conclusion that large-scale, industrialized farms have adverse community impacts. Rather they argued that Arvin and Dinuba were not as closely matched research sites in the 1930s as Goldschmidt had intended. Nearly four decades after Goldschmidt's study, the state of California, through its Small Farm Viability Project (1977, pp. 229–230), affirmed Goldschmidt's conclusions by revisiting Arvin and Dinuba. They concluded that: "The disparity in local economic activity, civic participation, and quality of life between Arvin and Dinuba...remains today. In fact, the disparity is greater. The economic and social gaps have widened. There can be little doubt about the relative effects of farm size and farm ownership on the communities of Arvin and Dinuba."

As the US agricultural structure has evolved toward larger and fewer farms, government and academic researchers have continued to investigate the extent to which large-scale, nonfamily owned and operated industrialized farms adversely affect communities. Congress has conducted inquiries, such as that by the Senate Subcommittee on Monopoly dealing with Corporate Secrecy and Agribusiness, in which rural sociologists and agricultural economists provided testimony in 1973 about the dangers to communities posed by increasing corporate control of agriculture (Boles and Rupnow, 1979, pp. 468–469). The Office of Technology Assessment (OTA), concerned that the relative growth of large-scale industrialized farms might have adverse impacts on communities, commissioned a series of research papers on the topic. The OTA research came as a request from Congress and was published first as a review (OTA, 1986) and later as a book (Swanson, 1988). Federal and state funding has been directed to at least two Agricultural Experiment Station projects that assess the community consequences of large-scale, nonfamily farms: Project S-148 'Changing Structure of Agriculture: Causes, Consequences, and Policy Implications' (1982–86); and Project S-198 'Socioeconomic Dimensions of Technological Change, Natural Resource Use, and Agricultural Structure' (1986–90). The later project resulted in a monograph on the consequences of industrialized farming for communities (Lobao, 1990) among other publications.

In the 1990s, public concern with industrialized farming has centered particularly on large integrated livestock producer/processor enterprises. Recent studies supported by the NCRCRD (1999), the University of Missouri Agricultural Experiment Station (Seipel *et al.*, 1998, 1999) and Duke University Medical School (Schiffman, 1998) have documented a variety of adverse impacts of these enterprises on communities, households, and individuals.

In summary, there has been more than 50 years of public, academic, and government concern that large-scale, industrialized farms jeopardizes community well-being. This concern has resulted in numerous studies, in government-sponsored reviews, and in congressional hearings. In the 1990s, public concern with industrialized farming has increased due to the problems posed by large-scale animal confinement operations. Social scientists have responded to this increased public concern by initiating a number of recent projects, leading to a new generation of literature on the community consequences of industrialized farming.

Research by Lobao and Colleagues

The most recent, comprehensive sociological study on the effects of industrialized and family farming on communities was conducted by Lobao (1990). This study examined relationships across more than 3000 US counties. The study used both farm scale and organization to measure farm structure; examined direct and indirect consequences of farming patterns; and examined long-term and immediate relationships for two time periods, 1970–80. To measure community outcomes, the study focused mainly on socioeconomic well-being indicators (median family income, poverty, and income inequality between families measured by the Gini coefficient. The Gini coefficient is used by the federal government to document income inequality in the US and is the measure used most frequently in recent studies of economic development across spatial units such as counties (Lobao *et al.*, 1999)) but also included of community social disruption (births-to-teenagers) and health status (infant mortality). The study examined the effects of three different community farm structures: 'smaller family farming' (small, part-time family farms); 'larger family farming' (moderate-size, capital-intensive, family operated units using little hired labor), and industrialized farming (large-scale, hired-labor-dependent farms).

The community farming structures were constructed based on the research by Wimberley (1987). Each of the measures of farm structure was a composite of scale and organizational indicators, created through a statistical technique called factor analysis. Multivariate statistical methods, regression, and discriminant analysis, were used to analyze the effects of the three farm structures net of other community conditions, including nonfarm industrial employment, establishment size of local businesses, human capital, and demographic characteristics of the population (educational attainments, ethnicity), unemployment, social welfare payments, unionization, and spatial factors, such as region of the country.

The findings were the following. There was consistent support that moderate-sized family owned and operated farms benefit communities. Counties where these types of farms (i.e., larger family farming) predominated had better socioeconomic well-being (lower family poverty, higher median family income, lower unemployment, and lower infant mortality). The beneficial effects of this family farming were found across the US, for two time points, 1970 and 1980. Moreover, this type of farming continued to result in beneficial effects over time. Counties where larger family farming was greater in 1970 continued to have better socioeconomic well-being over time. This study indicates that the 'high road' to community development is a farming system based on moderate-sized family operations. Such farming not only increases aggregate well-being, as indicated by income levels, but it also sustains a larger middle class, as indicated by lower income inequality and poverty, and thus allows more families to benefit from the income produced.

Where industrialized farming was greater, however, there were mixed effects on community well-being, either detrimental or no statistically significant impacts. For example, industrialized farming had no relationship with family poverty or median family income at either of the two single time points (1970 and 1980). Industrialized farming, however, was

related to higher income inequality at both time points, and also to lower family income, higher poverty, and higher income inequality across time, over the decade from 1970 to 1980 (i.e., counties with greater industrialized farming in 1970 experienced relative declines in socioeconomic well-being over the decade). The finding that industrialized farms are associated with high income inequality indicates that this farming segments social class structure by polarizing families into richer and poorer income groups. Income polarization is related to other social problems, such a crime and other breakdowns in the social fabric of the community. The study also found that where very small farms predominated, well-being was poorer. This indicates that researchers should distinguish between small and moderate family operated units in assessing consequences for well-being. Smaller family farming tends to predominate more in the South.

As would be expected in a postindustrial society, nonfarm manufacturing and service employment were stronger predictors of community well-being than farming. It is important to note, however, that the study found that farming, nonfarm industry, and other local characteristics were interrelated, mutually sustaining a population in a locale. (That farming has a smaller impact on community well-being than does nonfarm industry is expected even for communities highly dependent on farming. Farming is interrelated with local nonfarm industry and other sectors, forming a community livelihood strategy which sustains a population in a locale. Communities where larger family farming predominated had a much higher wage, durable manufacturing employment, and greater employment in local schools and retail industries. Communities where industrialized farming predominated had greater employment in lower wage manufacturing such as food processing, less employment in education, health, and retail services, a higher minority population, and provided relatively higher per capita benefits to welfare recipients.) Good quality farms and high quality local employment were interrelated, with 'larger family farming' associated with greater employment in high wage manufacturing and other beneficial sectors. The study offered consistent support that when farming is an economic development strategy of choice, moderate-sized family farms are best for communities.

This research on farming systems and community and regional well-being has been elaborated in other reviews (Kenney *et al.*, 1989; Lobao, 1987, 1993c, 1996, 1998; Lobao and Jones, 1987; Lobao and Schulman, 1991; Lobao *et al.*, 1993; Lobao and Thomas, 1992).

One of the most recent sociological analyses on industrialized farming and inequality is that conducted by one of Lobao's students (Crowley, 1999). The methodology used in the study is similar to that followed in Lobao (1990), but the indicators of farm structure differ. She analyzed the effects of farm concentration using several indicators (concentration of land, value of land and buildings, and the value of equipment and machinery, indicators measured by the Gini coefficient), and data for all (1053) counties in the North Central US (Illinois, Indiana, Iowa, Kansas, Michigan, Minnesota, Missouri, Nebraska, Ohio, North Dakota, South Dakota, and Wisconsin). She analyzed consequences of these dimensions of farm-sector concentration for local levels of family poverty and family income inequality net of other community characteristics. In counties where farm-sector concentration was higher (i.e., a few large farms held a disproportionate share of local property in land and real estate), there was significantly higher poverty among families and significantly greater income polarization between families. Moreover, where farm concentration was higher, residents had lower education.

In the 2004 study, Crowley and Roscigno documented how concentration of agricultural resources shapes rural community stratification through the political economic process. In addition to measures of farm sector resource concentration, measured by the Gini coefficient, and labor endowment (percentage of county work force employed in core, extractive, competitive, and state sectors), they included measures of political process (proportion of votes in presidential election for Democratic Party, average household payment rates, average per farm county level spending on agricultural assistance), and worker power attributes (percentage of manufacturing employees that are unionized, proportion of population that are a minority, percentage of population, aged 25+ years with a high school diploma, and proportion of labor force unemployed). Using data for all (1053) counties in the North Central US, it was found that dimensions of farm sector concentration shape both poverty and inequality. Furthermore, they found that farm sector concentration is explained by political economic processes, and these processes mediate the negative effects of land concentration on economic well-being. In particular, they found that relative to large-scale farms, capital concentration promotes government spending that benefits large farms, whereas it blocks government or labor-market programs that assists farmers whose farms it consumes and farm workers it exploits. These attempts are evident by the increased funding for agricultural research which benefits large farms, decreased redistribution efforts through transfer payments to benefit small farms and workers, decreased political consciousness through lower levels of Democratic Party support, and reduced labor power through lower unionization rates and education and higher unemployment and minority representation.

To provide a balanced assessment of the consequences of industrialized farming, it is useful to review the past findings of other investigators, using different methodologies, for different time periods, and from different disciplines. In the Section Review of Past Research on Industrialized Farming and Well-Being, the types of studies conducted on the relationship between industrialized farming and community well-being and their conclusions are discussed. On balance, the social science evidence accumulated from these and other studies supports public, academic, and government concern about the potential risks of industrialized farming. Recent research indicates that the public's welfare is at risk in at least four major areas. Industrialized farming (1) has a detrimental impact on certain aspects of socioeconomic well-being; (2) disrupts the social fabric of communities; (3) poses environmental threats where livestock production is concentrated; and (4) is likely to create a new pattern of 'haves and have nots' in terms of agricultural production, whereby some communities gain large, industrialized farms (and attendant social problems), and others lose their farming base as production becomes concentrated elsewhere in the state and regional economy. (Drabenstott and Smith, 1996, p. 4)

Review of Past Research on Industrialized Farming and Well-Being

Over the past half century, numerous studies, spanning different time periods and regions of the county have tended to find that large-scale industrial farming has detrimental community impacts. This does not mean that every study has produced these results, but rather that empirical evidence accumulated over the years shows a repeated trend that large-scale industrialized farms have adverse impacts on a number of different indicators of community well-being and that this trend is sufficiently established in the social sciences, to the point that almost all sociological studies begin with the working hypothesis (research expectation) that large-scale industrial farms will have adverse community effects. The extent to which past research supports this hypothesis is discussed in the Section Research Issues Involved in Analyzing Industrialized Farming and Its Community Impacts. It should be stressed that no single study can provide a definitive answer as to whether large-scale industrialized farming will or will not adversely affect public well-being in any particular region or state. This is due both to the complexity of the research question and to the lack of existing data required to fully analyze it. At best, a single study can assess the extent to which certain indicators of industrialized farming have adverse affects on certain indicators of community well-being in certain places and time periods. Therefore, the most comprehensive answer to the question of whether industrialized farming adversely affects public well-being comes not from a single study but from assessing the conclusions of decades of past research.

Research Issues Involved in Analyzing Industrialized Farming and Its Community Impacts

To adequately assess the consequences of large- scale industrial farming, the following issues about indicators of industrialized farming and types of consequences must be considered.

Industrialized farming should be analyzed using scale as well as indicators of farm organization. Scale is usually measured by sales or sometimes acreage. As a measure of industrialized farming, scale is limited for several reasons: Family owned and operated farms may be large scale owing to technology; scale alone does not capture organizational features of industrialized farming, such as absentee ownership and nonfamily control over production, that are thought to put communities at risk. Organizational measures of industrialized farming include: Vertical integration of corporations into farming; contract farming arrangements; absentee ownership of production factors; dependency on hired labor; operation by farm managers, as opposed to material operation by family members; and legal status as a corporation. With regard to legal status, family and nonfamily-held corporations should be distinguished. (It should also be recognized that farms may be incorporated because of family farmers' interests in estate planning, greater assurance of business continuity, limited liability, and income tax advantages.)

To adequately assess consequences for community well-being, the full array of outcomes should be considered. Research points to three major sets of consequences of industrialized farming in a community: impacts on socioeconomic well-being, community social fabric, and environment.

Socioeconomic well-being refers to standard measures of economic performance (essentially employment, income, and business activity) and to a broader range of socioeconomic indicators used by sociologists to tap material conditions of families and populations (family poverty rates and income inequality).

Community social fabric refers to social organization – the features of a community that reflects its stability and quality of social life. Impacts on community social fabric are seen in social indicators such as population change; social disruption indicators (crime rates, births-to-teenagers, social-psychological stress, community conflict, and interference with enjoyment of property); educational attainment and schooling quality; changes in social class structure (decline of local middle class and in-migration of low-wage workers); health status, such as mortality rates; civic participation (e.g., declines in church attendance, voluntary organizational membership, and voting); and changes in local governance, such as loss of local control over community decision-making, and resource/fiscal pressures on local government, such as those due to increased need for social services and diversion of public funds to subsidize agribusiness development.

Environmental indicators include quality of water, soil, and air, energy usage, and environmentally related health conditions.

Industrialized farming has both direct and indirect consequences for community well-being. Both sets of consequences should be considered. Industrialized farms directly influence community well-being: Through the quantity of jobs produced and the earnings' quality of those jobs; by the extent to which these farms purchase inputs and sell outputs locally; by affecting the quality of local environmental conditions; and by affecting local decision-making about economic development and other public-interest areas relevant to community quality of life.

First-order, indirect effects on local economic performance and general socioeconomic conditions occur because the quantity and quality of jobs plus purchases affect total community employment, earnings, and income (e.g., economic multiplier effects), the local poverty rate, and income inequality. First-order, indirect effects on local social fabric occur because the quantity of jobs created by industrial farms affects total community population size; the quantity and quality of jobs affect social class composition, such as a when an increase in hired farm workers reduces the proportion of the local middle class; local control over community decision-making may erode or become conflictual, as the interests of industrialized farmers and absentee owners are detached from those of local residents.

Second-order, indirect effects on local social fabric work through first-order effects cited above. Population size and social class composition are related to indicators of community social disruption, such as crime, family instability, the high school dropout rate, and conflict resulting in civil suits; local demand for schooling, public assistance, health, and other social services; and the property tax base (Boles and Rupnow, 1979; Freudenburg and Jones, 1991; Murdock *et al.*, 1988;

NCRCRD, 1999 (Rapid increases in population size and poorer social class composition tend to be related to the indicators of social disruption noted and also place increased demands on local schooling and other social services. Population decline reduces local demand for services and the property tax base.). Decline of local control over community decision-making creates problems associated with poor governance, such as the potential for diversion of public resources toward financial incentives supporting the interests of agribusiness developers over the community at large; and the loss of public and private revenues to support local schools, community services, and infrastructure, which contributes to a downward spiral of community social and economic conditions.

The direct and indirect paths by which industrialized farming may affect community well-being are delineated in various studies, including Boles and Rupnow (1979), Lasley *et al.* (1995), Lobao (1990), MacCannell (1988), and the NCRCRD (1999).

Differences in impacts for diverse social groups within the community must be considered. Changes in farming affect social groups differently, depending upon their age, class position, and residents' proximity to industrialized farms. The elderly and poor are affected by rising costs of housing and services whenever large corporations migrate to a rural community (Summers *et al.*, 1976). Within communities with large confined animal-feeding operations (CAFOs), residents who live closer to the operation review inability to enjoy their properties and physical and psychological problems associated with odor (Schiffman *et al.*, 1998; Wing and Wolf, 1999; Reisner *et al.*, 2004; Constance and Tunistra, 2005). Property closer to CAFOs has been found to fail to appreciate in value relative to places further away (Seipel *et al.*, 1998). Income generated by industrialized farming (relative to family farming and over time) also appears less likely to filter down to families of different social classes. As noted, Lobao (1990) and Crowley (1999) observed that income inequality was higher in communities where industrialized farming was greater.

There are long-term as well as short-term consequences of industrialized farming for communities and for regional development within a state. Industrialized farming puts a community on a path of development whose consequences are not fully manifest in the short term of 1 or 2 years. Lobao (1990) observed that some impacts were manifest a decade later. As noted earlier, counties with greater industrialized farming in 1970 had a significantly poorer well-being a decade later: These counties had a lower median family income, higher family poverty rates, and higher income inequality relative to other counties and net of past county conditions. For the heartland states, economists at the Federal Reserve Board of Kansas City (Drabenstott and Smith, 1996, p. 4) indicate that differences in communities will widen over time. According to these economists, industrialized agriculture will have two effects on rural communities. Industrial agriculture production and processing will cluster in some communities resulting in an increase in jobs and income. The economic links between industrial agriculture and communities, however, will be different than they were under commodity production because more production inputs are purchased from nonlocal sources, and more of the profits go to nonlocal owners of the firm.

Types of Studies Conducted on the Effects of Industrialized Farming: Research Designs and Methodology

Analysts have used primarily four different types of research designs to assess whether industrialized farms have detrimental impacts on communities. Each design has inherent strengths and limitations in being able to comprehensively analyze industrialized farming and its many potential impacts. (The author has outlined the strengths and limitations that are intrinsic to each research design. An individual study will vary as to how the analysts have exploited the strengths or overcome the limitations of the design.)

Case-study designs provide indepth analysis of the consequences of industrialized farming in a single or multicommunity site. Usually, a comparative case-study design is implemented whereby a community or communities characterized by industrialized farming are contrasted with a community or communities with a different farming pattern (usually moderate-sized, family owned and operated farms). A comparative case-study design allows communities to be matched on similar background characteristics, such as location near cities and dependency on farming as an economic base, which helps to 'control' (or exclude) extraneous factors that influence the relationship between farming type and community well-being.

Macrosocial accounting designs involve statistical analysis of secondary or precollected data from government and other sources, such as the Census of Agriculture and Census of Population, to document relationships found in regional social structure (MacCannell, 1988). Community units, such as counties and townships, and states are the research focus. To assess the consequences of industrialized farming, analysts usually compare its effects relative to other farming (usually smaller or moderate-sized family farm units) and over time, while controlling for other, nonfarm factors known to affect community well-being. Multivariate statistical techniques, such as regression procedures and discriminant analysis, are used so that the effects of farm structure are assessed net of other community conditions.

Regional economic impact models use linear programming methods to estimate impacts on employment and income for regions, states, and smaller units such as counties and cities. These studies focus on the integration of business enterprises in markets and use programs, such as variants of input–output analysis, to model the backward and forward linkages with enterprises in other industries and to estimate resulting local impacts. The costs and benefits of varying different firm-level practices can be estimated.

Survey-design studies use samples of populations from any number of communities. These studies use interviews or questionnaires to document how industrialized farming affects residents or a particular social group exposed to industrialized farming as compared with those who are not (such as those residing in family farming communities). In contrast to macrosocial accounting and economic impact models which are based usually on secondary or precollected data, the researchers using a survey design collect primary data directly from individuals or families. Multivariate statistical procedures such as regression are used to assess the consequences of farm variables net of other community and individual characteristics.

Conclusions of Studies Examining Industrialized Farming and Community Well-Being

As noted, to assess the consequences of industrialized farming, it is useful to examine the body of past work conducted by researchers from various social science disciplines, over time, and using different methodologies. This analysis is built upon a metaanalysis by Lobao (1990), who examined research from 1930 to 1988. A metaanalysis is a quantitative assessment across individual studies that allows for comparison and integration of empirical findings (Cooper, 1989). Metaanalyses are useful for drawing systematic conclusions when many empirical studies by different researchers exist that examine the same research question. To develop the pool of empirical studies used in the analysis, the literature from 1988 to the present was surveyed. (This table has been updated from Lobao (2000) by adding all empirical studies published on the topic in *Rural Sociology* (the major scholarly journal in this field) since 2000. A review of reviews in the *American Journal of Agricultural Economics* (the major scholarly journal in this field) over the past 5 years was undertaken but no empirical studies were found on the topic. In addition, the following journals were surveyed for reviews relevant to the topic: *Agriculture, Food and Human Values, Culture and Agriculture, Sociologia Ruralis, Southern Rural Sociology, American Journal of Alternative Agriculture* (now the *Renewable Agriculture and Food Systems* journal), *Journal of Rural Studies* and the *International Journal of the Sociology of Agriculture and Food*. Two scholarly search engines – *Google Scholar* and *Agricola* were also used to find relevant reviews. Some reviews were located serendipitously. The programs and abstracts for the 2000–05 Annual Meetings of the Rural Sociological Society also were reviewed.) **Table 1** shows the classification of findings by research design of 56 studies conducted since the 1930s on the effects of industrialized farming on community well-being. In most studies (all of the sociological studies), the authors hypothesize that where farms are of larger- scale or industrialized in terms of organizational characteristics, they have a detrimental impact on the indicator(s) of community well-being, relative to family owned and operated farms. These relationships are expected to be found across communities and over time.

Types of Detrimental Impacts Reviewed by Social Scientists

Social scientists review that industrialized farms are related to relatively worse conditions for the following community impacts:

Socioeconomic Well-Being

- Lower relative incomes for certain segments of the community: Greater income inequality (income polarization between the affluent and the poor) or greater poverty (Tetreau, 1940; Goldschmidt, 1978a; Heady and Sonka, 1974; Rodefeld, 1974; Flora *et al.*, 1977; Wheelock, 1979; Lobao, 1990; Crowley, 1999; Deller, 2003; Crowley and Roscigno, 2004; Peters, 2002; Lyson and Welsh, 2005; Durrenberg and Thu, 1996).
- Higher unemployment rates (Skees and Swanson, 1988; Lyson and Welsh, 2005).
- Lower total community employment generated (Marousek, 1979; Thompson and Haskins, 1998).

Social Fabric

- Population: Decline in local population size where family farms are replaced by industrialized farms; smaller population sustained by industrialized farms relative to family farms (Goldschmidt, 1978a; Heady and Sonka, 1974; Rodefeld, 1974; Wheelock, 1979; Swanson, 1980).
- Class composition: Social class structure becomes poorer (increases in hired labor) (Gilles and Dalecki, 1988; Goldschmidt, 1978a; Harris and Gilbert, 1982).
- Social disruption:
  - increases in crime rates and civil suits NCRCRD (1999);
  - general increase in social conflict (Seipel *et al.*, 1999);
  - greater childbearing among teenagers (Lobao, 1990);
  - increased stress, social-psychological problems (Martinson *et al.*, 1976; Schiffman *et al.*, 1998);
  - swine CAFOs located in census blocks with high poverty and minority populations (Wilson *et al.*, 2002);
  - deterioration of relationships between hog farmers and neighbors (Jackson-Smith and Gillespie, 2005; McMillan and Schulman, 2003); and
  - more stressful, less neighborly relations (Constance and Tuinstra, 2005; Smithers *et al.*, 2004).
- Civic participation: deterioration in community organizations, less involvement in social life (Goldschmidt, 1978a; Heffernan and Lasley, 1978; Poole, 1981; Rodefeld, 1974; Lyson *et al.*, 2001; Smithers, 2004).
- Quality of local governance: less democratic political decision-making, public becomes less involved as outside agribusiness interests increase control over local decision-making (Tetreau, 1940; Rodefeld, 1974; Goldschmidt, 1978a; McMillan and Schulman, 2003).
- Community services: fewer or poorer quality public services, fewer churches (Tetreau, 1940; Fujimoto, 1977; Goldschmidt, 1978a; Swanson, 1980).
- Retail trade: Decreased retail trade and fewer, less diverse retail firms (Goldschmidt, 1978a; Heady and Sonka, 1974; Rodefeld, 1974; Fujimoto, 1977; Marousek, 1979; Swanson, 1980; Skees and Swanson, 1988; Foltz *et al.*, 2002; Foltz and Zueli, 2005, Smithers, 2004; Gomez and Zhang, 2000).
- Reduced enjoyment of property: Deterioration of landscape, odor in communities with hog CAFOs (Schiffman *et al.*, 1998; Wing and Wolf, 1999, 2000; Constance and Tuinstra, 2005; Reisner *et al.*, 2004; Wright *et al.*, 2001; Kleiner, 2003; McMillan and Schulman, 2003).
- Health: neighbors of hog CAFOs review upper respiratory, digestive tract disorder, eye problems (Wing and Wolf, 1999, 2000; Constance and Tuinstra, 2005; Reisner *et al.*, 2004; Wright *et al.*, 2001; Kleiner, 2003).
- Real estate values: residences closest to hog CAFOs experience declining values relative to those more distant

NCRCRD, 1999, p.46; Seipel *et al.*, 1998; Constance and Tuinstra, 2005; Reisner *et al.*, 2004; Wright *et al.*, 2001).

Environment

- Ecosystem strains: depletion of water, other energy resources (Tetreau, 1940; Buttel and Larson, 1979; NCRCRD, 1999).
- Environmental consequences of CAFOs: increase in Safe Drinking Water Act violations, air quality problems, and increased risks of nutrient overload in soils (NCRCRD, 1999).

The studies indicate the types of community conditions associated with industrialized farming. To what extent do the studies overall provide evidence of detrimental impacts? With regard to the public policy interest in the topic, a count of studies where any detrimental impacts were found was conducted. The studies were classified according to whether the researchers review: Largely detrimental impacts; mixed findings (i.e., researchers review only some detrimental impacts were found); and no detrimental effects. Classifying the studies is somewhat complex because each may test a number of relationships about industrialized farming. The studies were placed into detrimental/no detrimental outcome categories based on whether the findings for the majority of relationships tested consistently fell into either of these two categories. Remaining studies are those in which the researchers found some detrimental impacts but other relationships were mixed, as described further below.

Out of the total 56 studies, researchers review largely detrimental impacts in 32, some detrimental impacts in 14, and no evidence of detrimental impacts in 10. Thus, 82% (46 out of 56) of the studies review finding some negative impacts of industrialized farming. This analysis provides quantitative evidence of the consistency in past research which has led to the working hypothesis that industrialized farming jeopardizes community well-being.

Of the 32 studies where social scientists found predominantly detrimental impacts, the following points should be noted. First, these studies use the four major types of research designs described earlier, comparative case study, macrosocial accounting, regional economic impact models and surveys. Studies reviewing detrimental impacts exist across all time periods and regions of the country. These studies review adverse outcomes for socioeconomic well-being, social fabric, and environmental conditions, using both scale and organizational measures of industrialized farming. In sum, the studies provide a great deal of evidence, produced over many years by researchers using different research designs, on the negative impacts of industrialized farming.

Of the 14 studies where social scientists review some, but not consistently negative impacts of industrialized farming, the following points should be noted. These studies provide mixed findings, in that though adverse effects on some community indicators were found, at least one of the following also occurred: Industrialized farming had no statistical relationship with other indicators (i.e., there was an absence of any relationship); industrialized farming had a trade-off effect, with beneficial effects on certain indicators; industrialized farming did not consistently produce negative impacts for all time periods or regions; or industrialized farming produced beneficial effects for some groups but detrimental to other groups. Mixed findings are evident to a greater degree in regional economic impact and macrosocial accounting studies (**Table 1**).

Regional impact studies tend to show costs–benefits for economic performance indicators, with larger farms injecting greater total income into the community, but also producing less employment relative to smaller farms (e.g., Heady and Sonka, 1974; Marousek, 1979). Macrosocial accounting studies often test a number of relationships, adding to the greater potential of mixed findings. Lobao's (1990) study is an example. For counties in the 48 contiguous states, industrialized farming had no relationship with poverty and median family income at either of the two single time points (1970 and 1980); however, industrialized farming was related to higher income inequality at both time points and also to lower family income, higher poverty, and higher income inequality over the 1970–80 decade (i.e., counties with greater industrialized farming in 1970 experienced relative declines in socioeconomic well-being over the decade).

Other research designs also provide examples of mixed findings. An example of a case study showing mixed effects is Wright *et al.* (2001) conducted in six counties with CAFOs in Minnesota. This study found that CAFOs had positive effects for farmers who expanded their operations; detrimental effects for neighbors to CAFOs whose ability to enjoy their property deteriorate; detrimental effects for younger and midsized producers unable to expand because expansion by others had restricted their access to markets; and no effects for those who were not neighbors or who were not expanding. A survey (Jackson-Smith and Gillespie, 2005) also found mixed effects for the impacts of large-scale, hired–labor–dependent dairies on community social relations. Farm size was the strongest predictor of neighbors' complaints about dairy operations, but demographic attributes of dairy farm owners had a greater affect on their relationships with neighbors than did farm size or use of hired labor.

The 10 studies that found no detrimental impacts of industrialized farming used mainly macrosocial accounting designs and tended to analyze only indicators of socioeconomic well-being. Lobao's and Schulman's (1991) study is an example. They examined whether industrialized farming was related to higher family poverty across agricultural regions in the US for the period 1970–80. They found no significant relationship in any of the four regions analyzed. Finally, a recent survey design study (Foltz and Zueli, 2005) found no evidence that large farms are unlikely to purchase locally once the presence of local suppliers was taken into consideration. Instead, they demonstrated that purchasing patterns are commodity specific and determined by community attachment, and local supply considerations.

Summary and Conclusion

Social scientists often debate whether empirical research should be oriented around disciplines' accumulated body of

Table 1 Summary of studies examining the effects of industrialized farming on community well-being

Research design	*Findings with regard to detrimental effects*		
	Detrimental	*Some detrimental*	*No detrimental*
Case-study	5[a]	2[f]	0
Macrosocial accounting	13[b]	7[g]	8[j]
Regional economic impact	3[c]	3[h]	1[l]
Survey	9[d]	2[i]	1[k]
Other design	2[e]	0	0
Total (N=56)	32 (57%)	14 (25%)	10 (18%)

[a]Goldschmidt, 1944, 1968, 1978a, original; Small Farm Viability Project, 1977; Constance and Tuinstra, 2005; Whittington and Warner, 2006; McMillan and Schulman, 2003.
[b]Fujimoto, 1977; Goldschmidt, 1978b; Buttel and Larson, 1979; Swanson, 1980; MacCannell, 1988; Durrenberg and Thu, 1996; Lyson *et al.*, 2001; Peters, 2002; Wilson *et al.*, 2002; Crowley and Roscigno, 2004; Smithers *et al.*, 2004; Lyson and Welsh, 2005; Crowley, 1999.
[c]Gomez and Zhang, 2000; Foltz *et al.*, 2002; Deller, 2003.
[d]Tetreau, 1938, 1940; Heffernan, 1972; Rodefeld, 1974; Martinson *et al.*, 1976; Poole, 1981; Wing and Wolf, 1999, 2000; Reisner *et al.*, 2004; Seipel *et al.*, 1999; Kleiner, 2003.
[e]Seipel *et al.*, 1998; Schiffman *et al.*, 1998.
[f]North Central Regional Center for Rural Development (NCRCRD), 1999; Wright *et al.*, 2001.
[g]Flora *et al.*, 1977; Wheelock, 1979; Harris and Gilbert, 1982; Skees and Swanson, 1988; Flora and Flora, 1988; Gilles and Dalecki, 1988; Lobao, 1990.
[h]Heady and Sonka, 1974; Marousek, 1979; Thompson and Haskins, 1998.
[i]Heffernan and Lasley, 1978; Jackson-Smith and Gillespie, 2005.
[j]Heaton and Brown, 1982; Swanson, 1982; Green, 1985; Buttel *et al.*, 1988; van Es *et al.*, 1988; Lobao and Schulman, 1991; Barnes and Blevins, 1992; Irwin *et al.*, 1999.
[k]Foltz and Zueli, 2005.
[l]Otto *et al.*, 1998.

knowledge or, conversely, address the public interest and provide critical knowledge to build civil society (Burawoy 2005). Social science research on industrialized farming accomplishes both objectives. This study addresses the long-standing question, does industrialized farming jeopardize the well-being of communities, through systematically evaluating the findings of studies from the 1930s to the present. On the basis of a sample of 56 studies, 82% provide evidence of adverse impacts (57% reviewing largely detrimental effects and 25% some detrimental effects). These impacts were reviewed in studies using various research designs and across different time periods and regions.

The types of community impacts reviewed by social scientists were detailed earlier and are seen in the following general relationships. For socioeconomic well-being, researchers noted that industrialized farming was related to higher income inequality and to lower community employment, relative to moderate-sized family farming. Higher income inequality indicates that industrialized farming is less likely to sustain middle-class communities. Places with higher income inequality also are prone to other social problems because the gap between the affluent and the poor is greater. With regard to other socioeconomic impacts, such as total income injected into the community, regional economic impact models were likely to review beneficial impacts. The findings for income inequality, however, suggest that income growth is impeded in trickling down to families.

Studies assessing consequences for the social fabric of communities were likely to find detrimental impacts. Industrialized farming affects the social fabric of communities through altering population size and social composition which affect crime, social conflict, family stability, the local class structure, community participation, and local shopping patterns. Case studies reviewed the loss of local autonomy, in which communities become increasingly subject to the influence of external business owners, whose interests may not be compatible with their own. More recent studies reviewed environment impacts. As large animal confinement operations house densely concentrated livestock, they are prone to a host of negative environmental impacts on water, air, and human health.

Given the relative consistency of past research, four sets of impacts of industrialized farming for farming-dependent communities in Heartland states can be anticipated: Impacts on socioeconomic well-being, social fabric, the environment, and regional imbalances. Communities that receive industrialized farming are likely to increase population relative to other communities (i.e., if local family farmers are not displaced). These communities may increase employment and per capita income, but as shown by the NCRCRD (1999) study, this may not be at a rate significantly different from comparison locales. Communities with industrialized farms are likely to experience greater income inequality; government services for the poor and other disadvantaged groups are likely to be needed in these locales. Communities that gain new industrialized farming will encounter stresses in the social fabric; community decision-making is likely to be more subject to corporate farm interests; and in the case of large livestock confinement operations, communities will be at risk for environmental and health problems, entailing the need for state and local government intervention. Communities that lose moderate-sized family farms, in part because of transaction cost advantages (e.g., volume buying–selling) and public incentives given to industrialized farms, will lose a base of middle class producers and experience rifts in social fabric, including population decline. These communities are likely to have declines in other businesses and in the local property tax base and may require government aid for social and public services.

Not discussed in this review are alternative economic development strategies that farming-dependent communities can pursue. Notwithstanding arguments that vertical integration into farming and production contracts are the only options left to keep American farmers farming, there are alternatives and some working examples are discussed in NCRCRD (1999). Deller (2003) suggested that if the results of their analyses held true for other time periods, then policies aimed at preserving family farms in the name of economic growth might be misplaced. Instead, policy should be aimed at the promotion of alternative sources of income for farm families.

During the time frame in which previous studies have been conducted, Welsh (2009) notes that the structure of agriculture has changed dramatically toward a bimodal distribution of large and small farms each operating in different market structures. He recommends that new studies examining the relationship between agriculture and community should examine the impacts of changed market structure as well as how public policies can mitigate the negative impacts of agricultural industrialization.

From a sociological standpoint, government plays a role in the types of consequences that industrialized farming will have for community well-being. It establishes the legal–institutional framework for regulating these farms. It establishes the incentive structure offered to agribusiness firms in their location decisions. It provides the public services needed to mop up the destabilizing impacts of industrialized farming, such as a rising crime rate, increased social conflict, and the need for social services to cope with a changing population. Moreover, government will need to provide the social services related to population decline and poverty alleviation in communities which lose family farming. (In nonfarm-dependent communities, government intervenes in a number of ways when paid employment, such as in manufacturing and mining declines: through programs such as unemployment insurance, various income transfers, such as welfare payments, for which independent farm operators are generally not eligible due to property ownership; through retraining programs, such as for workers who lose jobs because of North American Free Tree Agreement; and through enforcement of community rights in plant closure laws. Owing to their farming base, farm-dependent communities usually cannot make as full use of these social safety nets as can other communities.)

The role that laws regulating corporate farms have in countering detrimental community impacts of industrialized farming had only been alluded to by some researchers. Lobao and Schulman (1991, p. 596) postulated that one of the reasons why a few studies have found that industrialized farming has had less adverse effects in the North Central Heartland Region (relative to the South and West) is due to its agrarian history of protection of family farming and regulation of corporate farming. NCRCRD (1999) also indicated that 'relatively lax anticorporate farming laws, weak environmental regulations and permissive groundwater access laws' not surprisingly encouraged large, animal confinement operation to locate in Kansas.

The role that corporate farming laws play in protecting rural communities has been alluded to in past research NCRCRD (1999) but only recently addressed by Lyson and Welsh (2005). When they examined states with anticorporate farming laws (Iowa, Kansas, Minnesota, Missouri, North Dakota, South Dakota, Oklahoma, and Wisconsin), they found that agriculture-dependent counties in states with such laws fare better on economic measures, that is, less families in poverty, lower unemployment, and higher percentages of farms realizing cash gains. In the comparison of states with less restrictive versus states with more restrictive laws, they generally found the same results as with the comparison of states with anticorporate farming laws and states without such laws. Additional research is needed to explain these findings, such as whether corporate farming laws *per se* or broader aspects of the institutional regulatory environment are protecting the fortunes of local communities.

It is clear, however, that within states, remote communities distant from metropolitan centers particularly need state-level protection. Remote rural counties appear to be targeted as recent operating sites by large animal confinement operations. Research by Wilson *et al.* (2002) demonstrated that census blocks in Mississippi with high percentages of African Americans or people in poverty were much more likely to be the locations of swine CAFOs. Of all local governments, remote rural counties have the least resources (staff, economic development, and social service budget) to cope with industrialized farming. They are in weak positions to bargain successfully with external corporations, to regulate their operations once they are in place, and to protect community social life and environment overall. State protection from industrialized farming is most critical in remote communities due, in part, to the fragility of local government (Lobao and Kraybill, 2005). From a social science standpoint, the farming system in place today has been created from both market forces and government policy and programs. It is thus logical that government can also be an instrument in transforming this system toward greater public accountability.

See also: Agribusiness Organization and Management. Agricultural Mechanization. Changing Structure and Organization of US Agriculture. Government Agricultural Policy, United States. Rural Sociology

Disclaimer

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Integrated Pest Management in Tree Fruit Crops

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Glossary

Active ingredient A chemical or chemicals in a pesticide formulation that kills, repels or otherwise provides control of a pest.

Degree-day A degree-day is the heat experienced by an organism when the temperature is one degree more than the lower development threshold for 24 h. Degree-days are a measure of heat units or physiological time. Insect development rate is driven by physiological time, degree-days, and not chronological time.

Ecology The science of the relationships between organisms and their environments.

Invasive pest An invasive pest, or exotic pest, is a species that has been introduced to an area where it is not native. Invasive pests often cause serious problems in the region where they are introduced because their populations are not suppressed by natural factors that limit them in their native home.

Molecular marker (genetic marker) A fragment of DNA sequence associated with part of the genome. Molecular markers are used to identify a particular sequence of DNA.

Natural enemy An organism that utilizes another organism as a food source. Natural enemies of insect pests (herbivores) are predators, parasites, pathogens, and nematodes.

Pesticide A substance used for controlling pests or other organisms harmful to plants or animals.

Phenology The study of relationships between cyclical or seasonal biological processes and climate, such as insect development.

Pheromone A chemical produced and released by an animal, which influences the behavior or development in other members of the same species.

Treatment threshold The number of pests that triggers a control action preventing a level of damage that would exceed the cost of the control action.

Introduction

Integrated Pest Management (IPM) was born in the late 1950s primarily out of a crisis in agriculture from the overuse of synthetic pesticides and an increasing concern over the ecological consequences of these pest-control tools. Rachel Carson's, 1962 book 'Silent Spring' highlighted ecological concerns over synthetic pesticides. Stern *et al.* (1959) articulated the philosophy of IPM, which was further developed by Geier and Clark (1961). Two books, Entomology and Pest Management (Pedigo, 1989) and Introduction to Insect Pest Management (Metcalf and Luckmann, 1982), and an annual review of entomology article (Kogan, 1998) are recommended as resources introducing the principles and examples of IPM from an arthropod perspective. The purpose of this article is to briefly introduce basic concepts of IPM with an emphasis on IPM of arthropods in perennial crops, and a specific examination of the outcome of more than 40 years of research and implementation on apple in Washington State.

IPM is an approach that applies the principles of ecology, especially population biology, to the management of pests in agricultural, forest, or urban environments. There are many definitions of IPM, but the one proposed by Rabb (1972) that "pest management is the intelligent selection and use of pest-control actions that will ensure favorable economic, ecological, and sociological consequences," captures the basic elements used in most definitions. The simple image of a structure can help show how the elements of IPM work together (**Figure 1**). An IPM program is built on a foundation that includes the knowledge of pest and natural enemy biology, their correct identification, and ecology. Intervention against a pest should be based on the risk of crop injury and is only taken if the pest's population exceeds a level where the cost of preventing injury exceeds the cost of the intervention. Therefore, sampling to estimate the pest's population level is required. Control actions are not implemented unless the pest's population exceeds a specified level, a treatment threshold. Phenology models are valuable tools that make sampling activities more efficient and the implementation of tactics more effective. IPM does not rely on a single tactic but utilizes multiple tactics to mitigate the negative impacts of pests. Tactics are used in an integrated approach with the goal of limiting or relegating the use of tools that disrupt natural controls to options of last resort.

General Principles of Integrated Pest Management

Identification

The correct identification of pests and their natural enemies is core to an IPM program. Although many pests of agriculture are well known, there are challenges associated with the accurate identification of some organisms. Plant pathogens like fungi, bacteria, and viruses can represent a special challenge for identification. For example, fungal diseases of apple expressed as rots in storage seemed to be well established until Dr. C. L. Xiao looked more closely. He found two fungi, one a new species and the other an expansion of the geographic distribution of the fungus, that had been misidentified and not previously recognized as problems (Xiao *et al.*, 2004, 2005). Some insects, such as parasitic wasps and temperate fruit flies in the genus *Rhagoletis*, are difficult to identify because external appearance of individuals within these groups are so similar.

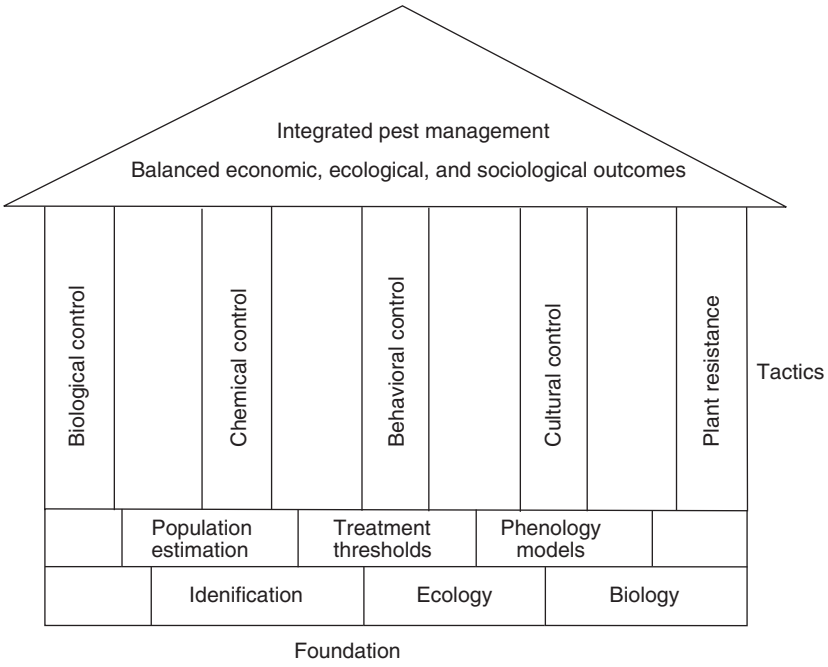


Figure 1 Representation of an Integrated Pest Management (IPM) system built on a foundation of sound biological understanding and tools that inform the integrated use of tactics.

The use of molecular techniques has helped with the identification of many disease organisms as well as species of insects that are morphologically identical.

Example of Identification:

Important pests of grapes grown in California are two species of leafhoppers: *Erythroneura elegantula* Osborn and *Erythroneura variabilis* Bearmer. A small parasitic wasp identified as *Anagrus epos* Girault attacked the eggs of these leafhoppers. This parasitoid was found to overwinter successfully in wild blackberry (*Rubus* spp.) on an alternative leafhopper host, *Dikrella cruentata* (Gillette), and the closer the association of blackberry patches to grape plantings, the higher the potential for biological control of leafhoppers in grapes (Doutt and Nakata, 1973). A similar association has been reported between prune trees that support an alternative leafhopper host, *Edwardsiana prunicola* (Edwards), of *A. epos* (Murphy *et al.*, 1996). However, in 1998, Triapitsyn reported that parasites previously identified as *A. epos* were actually a composite of three species in the genus *Aegagrus* Halliday, including a new species he identified (Triapitsyn, 1998). The importance of this new information will help researchers to sort out which species of *Anagrus* are using alternative overwintering leafhopper hosts and to better characterize and manage alternate hosts in and around commercial grape plantings that will enhance biological control of pest species.

Biology

Understanding the biology of pests and their natural enemies is the key to IPM. Without information on life cycle and seasonal development, it is impossible to effectively implement tactics to limit pests or conserve natural enemies. Being able to predict when a pest is present, and in which life stage, is also fundamental to the implementation of IPM. The life history of a pest usually follows a similar annual pattern, especially in temperate production zones, but because the rate of pest development is governed by environmental conditions, that is, by physiological time and not chronological time, the temporal occurrence of life stages can vary considerably from year to year.

Insect Ecology, Population Biology, and Sampling

Insect IPM is built on the concepts of ecology and it is, therefore, valuable for anyone desiring to understand the principles of IPM to become familiar with insect ecology. A good general resource on insect ecology is Peter Price's (1997) book by the same name. Following an introduction, this book deals with trophic relationships, populations, communities, and distributions. IPM deals with managing populations of pests and natural enemies so an understanding of population biology is especially important.

The largest population of an organism that can be supported on a crop over time is referred to as the carrying capacity. Insect populations are seldom observed at a carrying capacity in natural systems, like forests, and, of course, cannot be tolerated in managed systems like agriculture. It is most common for the population of a pest insect to be limited, by the plant itself (e.g., nutritional quality and resistance mechanisms), by their own interactions (competition – over utilizing the plant resource), or by actions of other organisms (predators, parasites, and pathogens) that use pests as food.

Pest populations can be impacted by factors that are density dependent or density independent. Density-independent factors

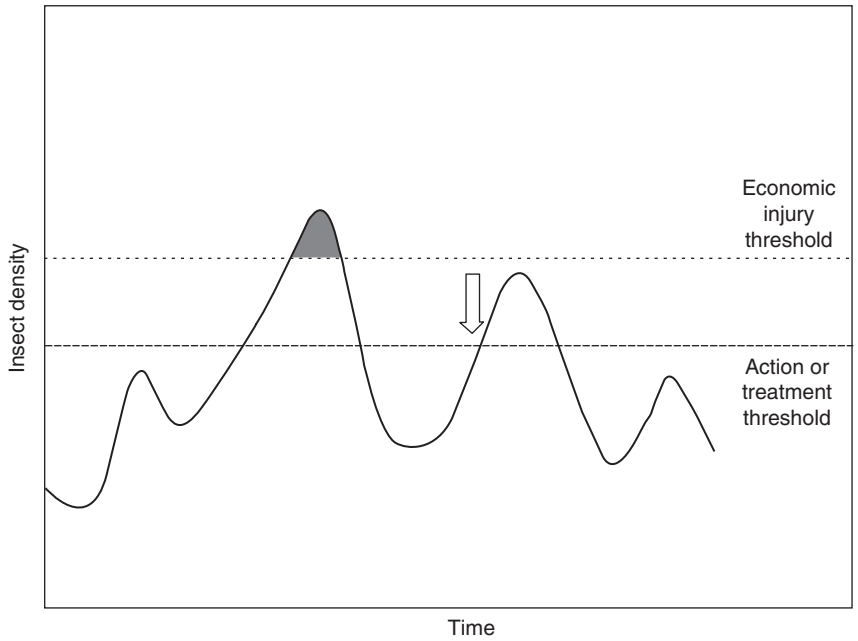


Figure 2 The economic injury level is the pest density above which crop loss equals the cost of taking a control action. The treatment or action threshold is the pest density at which a control is applied (arrow) to prevent the pest's population from exceeding the economic injury level.

are those that impact a proportion of the pest's population regardless of its size. Weather (freezes, droughts, etc.) or catastrophic events like fires are examples of density-independent factors that can impact a pest's population. In agriculture, the most useful density-independent factors are pesticides. When pesticides are applied, they kill a fixed proportion of the pest's population. Although pesticides are powerful tools in managing pest populations, they, and other density-independent factors, do not exert a regulatory impact on populations. Density-dependent factors are those that increase or decrease in response to the pest's population. Natural enemies of insects are examples of density-dependent factors. Their populations track changes in their prey or host. In many cases, density-dependent factors can regulate the population of a pest below levels, economic injury thresholds, that cause crop injury.

Knowing the level of a pest or natural enemy population is a core principle of IPM. This information is required to make decisions on the need to apply control tactics and to assess the effectiveness of those actions. As it is not possible to obtain an absolute measure of a pest or natural enemy population, sampling (monitoring) activities that estimate the level of a pest's population is fundamental to an effective IPM program. There are various means of estimating populations of organisms, which are outlined in *Ecological Methods* (Southwood and Henderson, 2000).

Economic Injury and Action Thresholds

All pests of agricultural crops cause some impact to the crop plant or product of that crop, but these effects are negligible until pest populations exceed a certain level. In IPM, this level is referred to as the economic injury level, which is defined as the pest population that causes crop loss equal to the cost of control. Conceptually, the relationship between the pest density, economic injury level, and action (treatment) threshold is shown in Figure 2.

For many diseases of agricultural crops, there is an assumption (sometimes incorrect) that the pathogen is always present. When the pathogen is present, all that are needed for the organism to cause levels of disease that exceed an economic injury level are environmental conditions conducive to rapid disease development and spread. For such plant pathogens, it is very difficult, if not impossible, to use a measure of inoculum levels before the application of control measures. Therefore, in most cases treatment thresholds for these pathogens are determined and controls applied when environmental conditions favorable for the pathogen are present. An example of this is the disease apple scab, *Venturia inaequalis* (Cke.) Wint. Controls are applied for this disease on the basis of a model driven by environmental factors of temperature and duration of leaf wetting (MacHardy and Gadoury, 1989).

For most insect pests, there is a population level, that is, the action or treatment threshold, where a control must be applied so that the economic injury level is not exceeded. While the concept of an economic injury level is helpful, in reality, its implementation is challenging because the value of a crop is seldom known, especially for high-value specialty crops, at the time a pest control decision is made. If the economic value of the crop is not known, then determining the level of injury that would equal the cost of control cannot be known. In addition, the impact on fruit or nut crops of pests that attack the foliage, such as spider mites or aphids, can be difficult to assess because resource reservoirs in the tree compensate for, and thus can delay, the effects of these pests for a year or more (Welter *et al.*, 1984).

Phenology and Degree-Day Models

Phenology is the study of relationships between environmental conditions and biological processes such as insect development. Phenology or degree-day models are used in IPM to predict the seasonal occurrence of plant pathogens and arthropod pests. These models associate environmental conditions with the development of pest. For insects, degree-days are used as a measurement of heat units or physiological time. A degree-day is the heat experienced by the insect when the temperature is one degree more than the lower threshold for 24 h.

The upper and lower temperature thresholds are usually determined by laboratory studies where an insect is reared at different constant temperatures. Lower and upper thresholds are estimated from the development rate data as shown in Figure 3. Development thresholds differ for each insect and often for each stage in an insect's life cycle. A fixed number of degree-days are required to complete each life stage. Once development thresholds are known, this information can be used to calculate physiological time, or degree-days, using simple formulas that utilize daily maximum and minimum temperature information (Baskerville and Emin, 1969).

Access to environmental data in or near agricultural plantings is important in predicting disease development and the life cycle of insects. A more specific discussion of degree-day models and their implementation in an online decision support system occurs later in this article.

Tactics

Chemical Control

Chemical controls (pesticides) are often the dominant tactic used in IPM programs. Chemical controls are designed to reduce pest (insect, pathogen, rodent, etc.) populations below levels that will not negatively impact the crop. Before the development of synthetic insecticides, which occurred after World War II, pesticides included horticultural oils, lead arsenate, soaps, lime sulfur, nicotine, and a few other inorganic elements like sulfur and copper. The modern pesticide era began with the discovery of chemicals like dichlorodiphenyltrichloroethylene and organophosphate (OP) insecticides that had high efficacy against insects. Their dramatic effect against pests of agriculture resulted in their overuse leading to a crisis that eventually resulted in an alternative approach, the development of IPM. IPM viewed chemical controls as one tool integrated into an overall strategy to mitigate the negative impacts of pests on a crop. Because of the high and often immediate impact of chemical controls on a pest population, their appropriate place in an IPM program was as a last resort in a multitactic approach.

The regulation of pesticides through the US Environmental Protection Agency (EPA) has changed the availability of chemical controls over the past two decades. The US federal Food Quality Protection Act (FQPA) of 1996 required the EPA to review and reregister all pesticides on the basis of risk. In addition, all uses of a pesticide were considered in determining risk, not just agricultural uses. This represented a significant shift from the previous regulatory approach, which balanced risks and benefits of pesticides. The highest priority for the reregistration of pesticides under FQPA was the OP insecticide class. Specialty crops were one of the biggest users of this insecticide class, so they were especially impacted by FQPA. Progress of EPA toward the implementation of FQPA can be found on their web site.

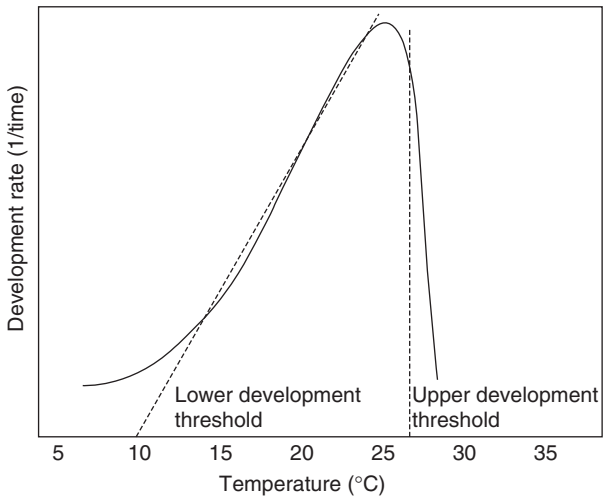


Figure 3 The rate of insect development increases as temperatures; they are exposed to increase, up to a point where development is suppressed, the upper development threshold. An estimate of the lower development threshold is established by extending a straight line through the ascending development curve to the temperature access.

Biological Control

In natural ecosystems, populations of different organisms are regulated by many different factors, including biological ones. Plant populations are regulated by herbivores, natural enemies regulate herbivore populations, and natural enemies of herbivores are regulated by their own natural enemies. In agricultural systems, herbivores (arthropods, fungi, and bacteria) are considered pests. Natural enemies that attack pests provide what is called biological control. Natural enemies of insects include predators, parasitoids, pathogens, and nematodes.

Examples of biological control of insect pests fall into three categories: classical, augmentation, and conservation. When a pest is introduced into a new location, its populations can increase rapidly due to a lack of natural controls that most often do not accompany the introduction. Classical biological control involves finding and introducing one or more natural enemy of the new invasive pest from its country of origin. After establishment, the introduced natural enemy can often provide complete or partial biological control of the invasive pest. Augmentation biological control occurs when a natural enemy of a pest is reared and released or moved from one place where it occurs to another where it is absent. This method of biological control is used most commonly in greenhouse environments for control of pests like spider mites and whiteflies. Conservation biological control occurs by following

management practices that preserve already existing populations of natural enemies. This is the most common form of biological control practiced in perennial cropping systems like tree fruit.

A core principle of IPM is that biological control can often keep pest populations below levels that would result in crop losses. For many pests, biological control will occur if the natural enemies are conserved, that is, they are not disrupted. In high-value crops like tree fruits, biological control has its primary value against pests that attack the foliage, such as aphids and spider mites. To establish and sustain biological control in these crops, IPM strives to use insecticides as a tactic of last resort or to use those that are known to have minimal impact on natural enemies.

Behavioral Controls

Insects communicate in a number of different ways, for example, visually, through sounds, and chemically. Pheromones are used as communication cues between individuals of the same species. Ants use trail pheromones to help other members of the colony get from their nest to a food source and return to the nest again in an efficient manner. Alarm pheromones are used by aphids to warn other aphids that a predator is on the prowl. Aggregation pheromones attract individuals of the same species to locations for purposes of feeding and mating. Sex pheromones are produced and released by one sex to attract the opposite sex for purposes of mating. Sex pheromones are highly species specific, making them potential tools for monitoring and controlling pests.

Adolph Butenandt and colleagues identified the chemical structure of the first sex pheromone in 1959 from the silk worm, *Bombyx mori* L. (Butenandt *et al.*, 1959). Sex pheromones may be a single compound or a blend of several compounds each in a specific ratio that optimize attraction. Soon after the discovery of moth sex pheromones, it was suggested that these chemicals might be useful as tools to control pests in managed systems like agriculture (Gaston *et al.*, 1967). The use of sex pheromones as a form of pest control has been referred to as mating disruption because the mechanism of control was associated with the disruption of male orientation to the female, thus preventing or disrupting the mating process (Cardé, 1990; Cardé and Minks, 1995).

Once the chemical structure of a sex pheromone was identified, they were synthesized in the laboratory. Synthetic pheromones are chemically identical to those produced by the insect and are highly attractive. When placed in lures, these synthetic sex pheromones attract males of the same species to traps where they can be captured and counted as a means of estimating the population of the species. However, the most important use of sex pheromones has been their use as controls for many key pests of forest and agricultural crops.

When sex pheromones are placed into dispensers that release them over a long period of time (several months), the normal behavior of the targeted pest is disrupted and mating is prevented, suppressed, or delayed. The release rate of pheromone coming from dispensers varies but is always many times higher than the amount of pheromone released by the insect. For example, the codling moth female releases approximately 6.5 ng h^{-1}, whereas a single pheromone dispenser releases approximately 1000 times that amount or approximately 50 mg ha^{-1} h^{-1} (Witzgall *et al.*, 2008). Because sex pheromones only impact one insect species, they are an excellent selective control for pests.

Pheromones have been used to control several pests in forests, vegetable, and perennial crops. More than 660 000 ha are treated with pheromones as controls for codling moth in pome fruit (apple and pear); Oriental fruit moth, *Grapholita molesta* (Busck), in stone fruit (peach and nectarine); European grapevine moth, *Lobesia botrana* (Denis & Schiffermuller); European grape berry moth, *Eupoecilia ambiguella* (Hübner), in grapes; pink bollworm, *Pectinophora gossypiella* (Saunders), in cotton; leafroller (Tortricidae) species in tea and other crops; and the Gypsy moth, *Lymantria dispar* (Linnaeus), in deciduous forests (Witzgall *et al.*, 2008). Witzgall *et al.* (2008) provide a review of the chemical ecology and management of codling moth. A specific case for the successful use of codling moth sex pheromones in apple IPM in Washington State is discussed later in this article.

Plant Resistance – Genetics

Plants have natural defenses against organisms that attack them, for example, herbivores and pathogens. Painter (1951) broadly classified plant resistance to insects into three categories: nonpreference, antibiosis, and tolerance. Nonpreference refers to factors in a plant that make them unattractive to pests. Antibiosis refers to factors in a plant that adversely affect pest development or mortality. Tolerance refers to plants that have an ability to overcome or compensate for injury inflicted by pests. Plants grown for food are often selected for traits that enhance yields and quality, often at the expense of factors that protect the plant from attack by pests.

Naturally occurring pest resistance factors can sometimes be found and utilized. A classic example of plant resistance to a pest that helped to save the French wine industry involved the grape phylloxera, *Daktulosphaira vitifoliae* (Fitch), a root-feeding insect. The grape phylloxera was accidentally introduced into Europe in the late 1800s. French wine grape plants were highly susceptible to this pest and it threatened to ruin the entire industry. American grapes were known to be resistant to the grape phylloxera and by grafting American grape roots onto French wine varieties the problem was solved.

Understanding the genetics of crop plants can help plant breeders incorporate desired traits of resistance into crop. Perennial crops like apple represent a particular challenge for breeders because of the long time required to grow trees and evaluate fruit for desired qualities. At Washington State University (WSU), the apple breeding program has expedited the process by utilizing rootstocks that result in apple trees bearing within 2 years. Even so it takes a minimum 15 years to find an apple variety good enough for consideration as a commercial variety, and then it takes several additional years to plant enough trees to generate sufficient production to gain a significant share of the market. As more is known about the apple genome, breeders are using modern molecular methods, like genetic markers for resistance to diseases (Stankiewicz *et al.*,

2002), to screen seedlings from parental crosses and discard those that do not carry the desired genes for resistance. As more becomes known about the location of genes and their role in apple, it will be possible for breeders to identify parents that carry genes for pest resistance and incorporate these traits with those for high yield, fruit quality, and other horticultural attributes.

Cultural Control or Ecological Management

Cultural control or ecological management refers to practices that modify the agricultural environment in ways that favor the crop's health relative to that of the pest. The concept involves finding weak links in the pest's life history that can be exploited. In annual cropping systems, cultural control can take the form of changing planting dates such that the seasonal life cycle of a pest is avoided or by crop rotations that reduce the buildup of a pest population in the same location on the same crop. Sanitation is another management practice that can be used to reduce a pest's population by eliminating overwintering habitats. In dry land wheat production, the practice of alternating a year of wheat with a year of summer fallow can help reduce certain pests while conserving water. Trap cropping is another possible cultural practice that can be used to attract a pest away from the primary crop. Trap crops can also be treated with an insecticide to reduce the pest's population without having to treat the primary crop.

There are fewer options for implementing cultural controls in perennial crops as annual strategies like those cited above are not readily available or possible. It is possible to manage plant nutrition to reduce vegetative growth that favors insect pests like aphids or pear psylla. However, this approach is a difficult balance between practices that make the tree less favorable for pests and the need to enhance fruit size and quality. Sanitation is useful for pests like the shothole borer, which colonizes pruned wood left in an orchard or piled up near the orchard border (Doerr *et al.*, 2008). A cultural practice designed to enhance or conserve biological control in orchards is the establishment of plants in or near the orchard, which provides alternative prey or hosts for natural enemies. In apple, the establishment of wild rose and strawberry gardens has been used to enhance biological control of leafrollers.

Example of Cultural Control:

The discovery of a small parasitic wasp, *Colpoclypeus florus* (Walker), in Washington (Brunner, 1996) prompted studies on the biology of this natural enemy. *Colpoclypeus florus* originally was brought from Europe to Canada and released in hope that it would provide biological control of leafrollers in forests or agricultural crops. This parasitoid was found to need large leafroller larvae in order to overwinter, but the leafroller species that are pests of orchards in Washington overwinter as small larvae that are unsuitable as hosts for *C. florus*. An alternative host, the strawberry leafroller, *Ancylis comptana* Frölich, turned out to provide a good overwintering host for *C. florus*, but this leafroller only occurred on wild rose in riparian habitats at some distance from most apple orchards (Pfannenstiel *et al.*, 2010; Unruh *et al.*, 2012). Dr. Tom Unruh, USDA-ARS scientist, found that by planting gardens of wild rose and commercial strawberries near orchards, he could provide an overwintering site for *C. florus* and enhance the levels of parasitism of leafroller larvae in the orchard. Many Washington growers have established and maintained these overwintering refuges for *C. florus* as a means of conserving this important natural enemy.

Integrated Pest Management in Tree Fruit with Focus on Apple as Example

Unique Challenges and Opportunities of Perennial Cropping Systems

Annual crops can take advantage of their transitory nature to manage pests, like crop rotation or planting dates, but because they are annually disturbed systems, it is more difficult to accumulate and sustain components in the crop environment that would stabilize IPM programs. By contrast, there are opportunities in high-value perennial crops to manage the crop environment and reduce long-term impacts of pests. For instance, conserving natural enemies of pests in an orchard provides stable biological control of several insect or mite pests, thus reducing the need to intervene with insecticides.

Perennial high-value crops, like tree and small fruits, citrus, nut crops, and grapes, have specific challenges and opportunities to the implementation of IPM programs. Challenges are tied to the high value of the product and the high expectation of quality, both external (cosmetic) and internal. The high value of the fruit results in a low tolerance for losses due to pests. The consequence of a low pest tolerance is too often the overuse of crop protection technologies, primarily pesticides.

Side Bar Example:

Modern high-density apple orchards (2500 or more trees ha^{-1}) in Washington State can produce a yield of 70 000 kg ha^{-1}. The cost of growing, harvesting, storing, packing, and marketing these apples varies by variety, but costs are high, approximately \$30 000 ha^{-1}. Not all apples harvested are packed and sold, primarily due to high demands for fruit quality; however, growers are usually able to market 80% of their harvested crop. If the net return to the grower were \$0.13 kg^{-1}, then, based on production of 70 000 kg ha^{-1}, net return to the grower would be approximately \$10 200 ha^{-1}. If a pest increases crop loss by 0.5%, the grower's profit would be reduced by roughly \$200 ha^{-1}. The cost of an additional pesticide to prevent this level of crop loss would be approximately \$125 ha^{-1}. In this scenario, there is little incentive for a grower to take the risk of crop loss by not applying a pesticide. The challenge for IPM is to develop tools that assess the risk of a pest causing crop loss that allows the grower to make informed decisions about applying a pesticide. If the pesticide is needed on the basis of the level of the pest's population, then the investment pays off by increasing grower profit by \$75 ha^{-1}. If the pesticide is not needed but the grower treats anyway, profit is reduced by approximately \$200 ha^{-1}.

According to the US Department of Agriculture, National Agricultural Statistics Service (USDA-NASS) report, Noncitrus

Fruits and Nuts 2012 Preliminary Summary, there are 1.84 million ha of tree fruit in the US. Different tree fruit crops are produced in different regions and therefore face different challenges when implementing IPM programs. The eastern US faces more problems with diseases compared with the western US because of a wetter and more humid climate. In addition, several key insect pests occur in the eastern US, which are not present in the west.

The key pest in an agricultural production system is that organism, or small number or organisms, for which most controls are directed to prevent crop loss. For tree fruit crops, key insect pests are direct pests, those that feed on the fruit. A direct pest can cause high levels of crop loss if management practices are not used to reduce its population (see Key pest example). Key pests for different tree fruit crops are listed in Table 1 (Figure 4).

Key Pest Example:

The codling moth, *Cydia pomonella* (Linnaeus), is the key pest of apple in the western US. The adults lay eggs on or near the apple. On emergence from the egg, the small caterpillar bores through the skin of the apple. It then moves toward the apple core, where it consumes the seeds. A codling moth population can increase rapidly from low levels where less than 0.2% of the crop is affected to where, in just two generations or one growing season, up to 25% of the crop can be injured. If uncontrolled for longer periods, the codling moth will destroy up to 80% of the crop each year. Based on USDA-NASS pesticide-use survey information, roughly 50% of insecticides applied to apple in Washington is used for control of codling moth.

Table 1 Key insect and disease pests of different tree fruit crops

Tree fruit crop	*Key insect pest*	*Key disease pest*
Apple	Codling moth (W)	Apple scab (E)
	Apple Maggot (E)	Powdery mildew (W)
	Plum Curculio (E)	
Cherry	Cherry fruit fly (E,W)	Brown rot (E)
	Plum curculio (E)	Powdery mildew (W)
Pear	Pear psylla (E,W)	Fire blight (E,W)
Peach, Nectarine	Oriental fruit moth (E,W)	Brown rot (E)
Plum	Plum curculio (E)	Brown rot (E)

Abbrevations: E, Eastern US; W, Western US.

Apple Integrated Pest Management in Washington

The remainder of this article will focus on apple IPM in Washington and specifically deal with arthropod pests. This approach will allow for a more detailed inspection of specific examples of apple IPM programs and the changes that have occurred over several decades and will address specific concerns that threaten to undo advances made in IPM programs over the past five decades. Although limiting discussion to the specifics of apple IPM in Washington narrows the focus, many of the principles addressed are relevant to tree fruit and other perennial cropping systems in the US and around the world.

The best resource describing the arthropod pest complex attacking tree fruit in Washington is the book Orchard Pest Management (Beers *et al.*, 1993), which is available online with updated articles. The key arthropod pest in Washington apple production is the codling moth. If not controlled, even a small codling moth population can result in crop loss that is economically unacceptable to a grower. Because tolerance of codling moth is low, there is little opportunity to rely on biological control (predators, parasites, or diseases) as a primary tactic. In addition to the codling moth, there are several other pests that directly attack apple fruit. These include



Figure 4 Image of codling moth adult and fruit injury. Photo of (a) a codling moth adult and (b) an apple cut open to show a codling moth larva and the feeding damage it causes.

leafrollers, thrips, scales, and true bugs like stink bugs and the mullein plant bug. While this latter group of pests can cause severe crop loss, they tend to be localized geographically and their impacts are not the same on all apple varieties.

Another group of arthropods (aphids, leafhopper, leafminer, and spider mites) are referred to as indirect pests because they do not directly attack apple fruit, rather they feed on foliage, bark, or roots. Often referred to as secondary pests they indirectly impact fruit quantity or quality when their populations become too high. Because higher populations of indirect pests can be tolerated in orchard compared with direct pests, there is a greater potential that biological control can be more effective. Apple IPM strives to conserve natural enemies of these pests by implementing selective chemical control programs.

Integrated Mite Control

The introduction of synthetic insecticides and miticides into the tree fruit production systems in the 1950s resulted in outstanding control of pests. Initially, control was so good that one or two applications of an insecticide provided control of all pests for an entire growing season. However, this phenomenon was short lived. Some insects and spider mites soon developed resistance to the miracle pest-control products, resulting in the need for more frequent applications and the use of higher rates.

Example of Resistance — Pesticide Treadmill:

Pests develop resistance when they are exposed to pesticides that eliminate most of their population. Some of the individuals in the population have a genetic predisposition to tolerate the effects of the pesticide. Therefore, these individuals survive in higher numbers than those that are susceptible to the pesticide. As pesticide use continues, those individuals that survive make up a higher and higher proportion of the pest's population, which then reduces the efficacy of the pesticide in suppressing the pest. Eventually, higher concentrations of the pesticide are needed to keep the pest population below levels that will cause crop loss; however, the battle is eventually lost as resistance to the pesticide continues to increase. Often, the strategy to rescue a crop from a pest that has developed resistance to a pesticide is to switch to a pesticide with a different mode of action, that is, a different mechanism of killing the pest. Although this approach can work for a while, there are individuals in the population that are less susceptible to the new pesticide. These individuals survive and eventually more frequent use and higher concentrations of the new pesticide are required to protect the crop. This cycle can be repeated over and over again and is referred to as the pesticide treadmill.

The pesticide treadmill scenario (see example of resistance) was played out in Washington apple orchards in the 1960s. Spider mites increased as a problem because they had developed resistance to synthetic insecticides used to control the key pest, codling moth, and there were no natural enemies of spider mites surviving in orchards. Apple growers were forced to use miticides, specific chemicals that control spider mites. However, the spider mites soon developed resistance to these products. The situation was in crisis mode; growers were using multiple miticide applications per year, but spider mite populations were still high enough in many orchards that apple foliage a turned brownish color in late summer.

Dr. Stan Hoyt, WSU entomologist, discovered that the use of low rates of certain OP insecticides provided control of the codling moth but at the same time allowed populations of the western predatory mite (WPM), *Galendromus occidentalis* (Nesbitt), to survive in the orchard (Hoyt, 1969). After a year or two of implementing Dr. Hoyt's discovery, the predatory mite suppressed spider mite populations to nondamaging levels. This program became known as integrated mite control because it integrated two tactics, chemical and biological control, and brought about a stable IPM program (**Figure 5**).

A key reason why his program was successful was that the WPM developed a tolerance to certain OP insecticides and could, therefore, survive in the orchard, even when these products were used for control of other pests. Integrated mite control is an example of an IPM program born out of crisis. It occurred because of the careful observations and research of an outstanding scientist and the willingness of a tree fruit industry to trust the results of sound science and adopt a new way of doing things. The economic value of integrated mite control to the Washington apple industry is in the millions of dollars. For example, most of the apple acres in the US use miticides to provide suppression of spider mites. The National Agriculture Statistics Service surveys of pesticide use in apple over the past 20 years show that Washington growers apply a miticide to an average of 24% of apple acres. By comparison, the average percentage of apple acres treated with miticides in Michigan and New York are 76% and 70%, respectively. If integrated mite control saved Washington apple growers a half of one miticide treatment annually, the savings would be about $7.5 million, or more than $300 million over the past four decades.



Figure 5 Photo of the western predatory mite (WPM) feeding on a pest, the European red mite. Image provided by Dr. E.H. Beers, Professor of Entomology, Washington State University.

The development of integrated mite control in Washington attracted the interest of other regions in the US and around the world as a model for integrating chemical and biological controls in orchard and other production systems. In eastern apple orchards, the integration of chemical and biological control of spider mites looked different from Washington because the natural enemies adapted to that climate were different. In Pennsylvania, growers adopted the use of low rates of OP insecticides and applied them to every other row. This approach protected a small predacious beetle, *Stethorus punctum* (LeConte), that fed on spider mites (Asquith and Hull, 1979). In recent years, however, a predaceous mite, *Typhlodromus pyri* (Scheuten), has become more common in Pennsylvania orchards and is more effective than *S. punctum*. In Michigan, a predatory mite, *Neoseiulus* (=*Amblyseius*) *fallacis* (Garman), was also shown to provide suppression of spider mites when combined with selective pesticides and orchard ground cover management (Croft and McGroarty, 1977). In other parts of the world with climates similar to Washington, the WPM was imported and established in orchards, thus replicating integrated mite control that mirrored in many respects that of apple production in Washington.

In the OP era, two additional apple pests were controlled biologically, namely the western tentiform leafminer, *Phyllonorycter elmaella* Doganlar & Mutuura, and white apple leafhopper, *Typhlocyba pomaria* McAtee. The leafminer developed resistance to OP insecticides and became a serious pest of apple in the mid-1980s. Research showed that a small parasitic wasp, *Pnigalio flavipes* (Ashmead), was present in orchards that did not use certain OP insecticides, namely chlorpyrifos and methyl parathion. When these two OPs were removed from the apple pest-control program, *P. flavipes* provided biological control of the leafminer, even when other OP insecticides were used in orchards. Like the WPM, *P. flavipes* was able to survive in apple orchards because it had developed a tolerance to azinphos-methyl. During the same time period, and as apple growers implemented the use of pheromones for codling moth control, a small parasitic wasp, *A. epos*, became more common in orchards. This parasitoid attacks the egg of the white apple leafhopper and after 3–5 years of programs that reduced the use of OP insecticides, populations of the leafhopper were reduced to levels that did not require additional insecticide intervention.

Pheromone Technology

It was nearly 20 years after the sex pheromone of the codling moth had been identified (Roelofs *et al.*, 1971) that the first product, Isomate®-C, was registered as a control for codling moth in the US. Early research demonstrated the value of pheromones (mating disruption) as a control for codling moth in Washington apple orchards; however, that research also revealed that if initial codling moth populations were too high, then pheromones alone were not sufficient to provided adequate crop protection (Gut and Brunner, 1998). In addition to not being a stand-alone control for high codling moth populations, pheromones were also considered to perform better when the area treated was large, that is, 8 ha or more, and the shape of the treated area was not long and narrow.

In 1995, the USDA provided funding for a codling moth area-wide management project (CAMP). The goal of the project was to demonstrate the value of pheromones using an area-wide approach. The project's objectives were to demonstrate that pheromones would provide control of codling moth, reduce the amount of insecticides applied for codling moth control by 70%, and improve biological control of secondary pests. Five CAMP sites were established: three in Washington, one in Oregon, and one in California (Calkins and Faust, 2003; Brunner *et al.*, 2002). All of the CAMP sites were successful in meeting the objectives of the project.

The Howard Flat CAMP site was a predominantly apple growing area located near Chelan, Washington. Howard Flat was approximately 480 ha of mostly contiguous apple plantings, but with a few plantings of cherry and pear. There were 36 growers operating orchards at Howard Flat, who took their fruit to four different warehouses where fruit were stored, packed, and marketed. In addition, there were 16 crop consultants, who assisted growers in making horticultural and pest management decisions.

An advisory committee was established of key growers and crop consultants to work with CAMP personnel at Howard Flat. This group met weekly during the growing season for the first 3 years of the project, then less frequently over the past 2 years. Information collected by CAMP personnel was distributed to all growers and was posted on a large board near the Howard Flat site, where all growers could access the information. Before the start of CAMP, data were obtained from crop consultants on codling moth captures in pheromone trap and growers provided spray records and information on fruit injury caused by codling moth in 1994. These baseline data showed that growers applied an average of 2.7 insecticides for codling moth control and there was an average of 0.9% fruit injury by codling moth. In addition, an average of 33 codling moths was captured in pheromone traps over the 1994 growing season. Together, these data indicated that apple production at Howard Flat was dealing with relatively high populations of codling moth (**Figure 6**).

At the start of CAMP, hand-applied pheromone dispensers were the only products available for codling moth mating disruption. These dispensers cost approximately \$250 ha^{-1} plus another \$38–63 ha^{-1} for application costs. The cost of the mating disruption treatments was subsidized by \$125 ha^{-1} for the first 3 years of the project to encourage growers to participate. In the past 2 years, growers were required to pay the full cost of the mating disruption treatments. In the first year of the Howard Flat CAMP, all but two growers agreed to participate. In the final 4 years, all growers participated in the project.

CAMP personnel monitored codling moth and leafrollers in all orchards to maintain a consistent assessment of the seasonal activity and relative densities of these pests. For codling moth, pheromone traps were used at a rate of 1 ha^{-1}. Lures (10X) used in traps had ten times the normal amount of codling moth pheromone in order to make them more attractive in orchards treated with high levels of pheromone. Traps were checked weekly and lures changed as needed. CAMP personnel assessed crop injury in most orchards every year just before harvest. Crop consultants made recommendations to growers on pesticides needed to control pests,

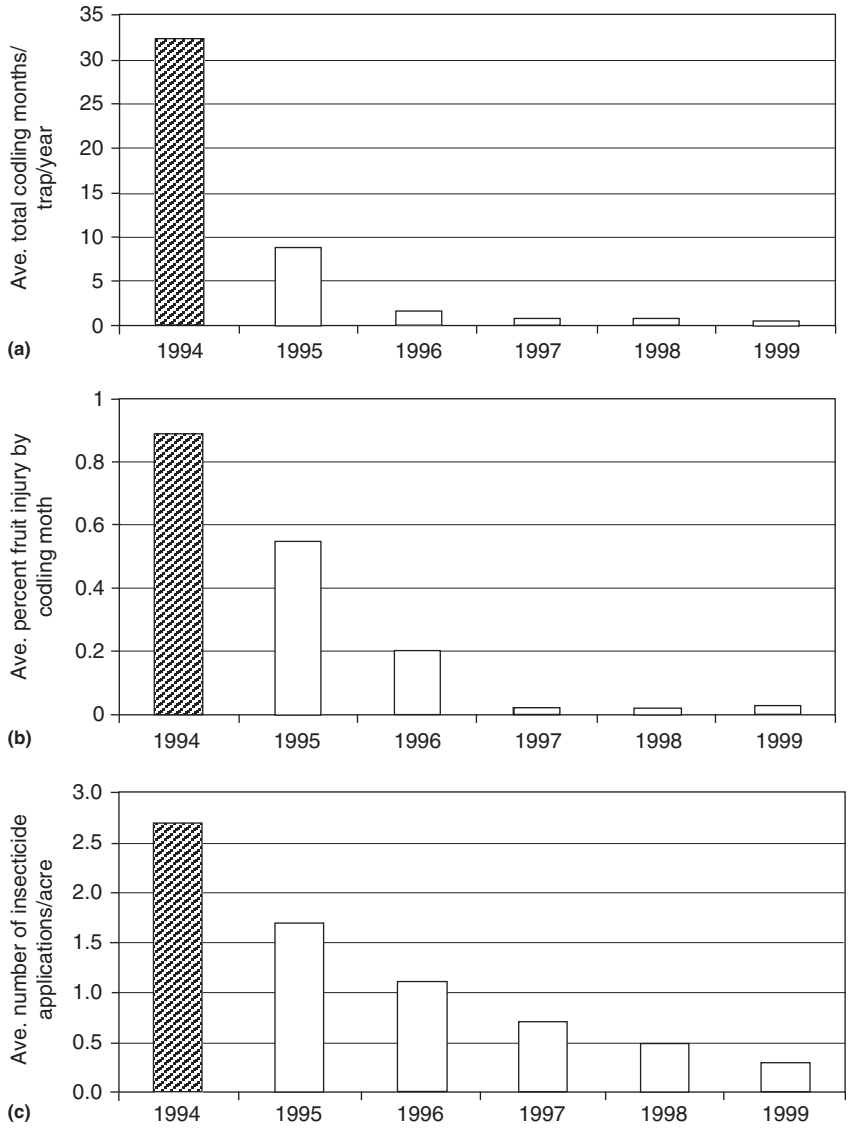


Figure 6 Results from the codling moth area-wide management project (CAMP) at Howard Flat, WA; (a) average capture of codling moth per trap per year, (b) average percentage fruit injury each year, and (c) the average number of supplemental (in addition to pheromone treatments) insecticides applied to control codling moth each year.

including insecticide applications as needed for codling moth to supplement the mating disruption treatments.

In the first year of the Howard Flat CAMP, the average number of codling moth adults captured in traps declined from 33 to 10 per trap. This decline was not unexpected because the use of mating disruption products is known to suppress capture of male moths in traps. However, in years 2–5, the average number of codling moths captured per trap continued to decline and in the past 3 years of the project, most traps (80–90%) captured no moths for the entire season (Figure 6). These data are evidence that the codling moth populations had declined substantially in the first 2 years of the project.

The percentage fruit injury after the first year averaged 0.55%, down from the preproject level of 0.9%. The number of insecticides applied for codling moth, as a supplement to mating disruption treatments, averaged 1.7 ha^{-1}, down from the preproject average of 2.7 ha^{-1}. After the second year of the project, fruit injury had declined to an average of 0.2% and the number of supplemental insecticides to an average of 1.1 ha^{-1} (Figure 6). In years 3–5, the percentage fruit injury varied between 0.01% and 0.03%. The number of supplemental insecticides applied for codling moth control also continued to decline, and by the last year of the project, the average number of applications was 0.3 ha^{-1}. Most growers did not apply any insecticides to supplement the control of codling moth provided by mating disruption in this year (Figure 6). Based on the preproject data at Howard Flat, insecticide use targeting control of codling moth was reduced by 85%, exceeding the project goal of 70%.

The CAMP at Howard Flat, and two other locations in Washington that showed similar results, demonstrated to

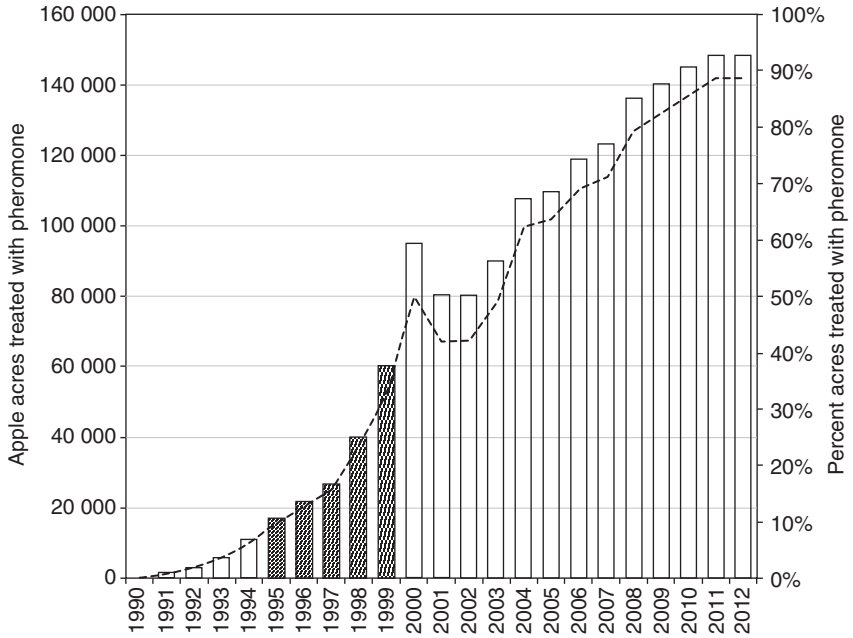


Figure 7 The number of apple acres treated with codling moth mating disruption products (pheromones) and percentage of bearing apple acres treated.

apple growers that codling moth mating disruption was a powerful selective control for their key pest. Although pheromone technology was more expensive than the use of insecticides alone, its added value by reducing fruit injury and eventually reducing the need for supplemental insecticide treatments convinced many growers that it was a good investment. The method of actively involving the grower and crop-consulting community in the planning and execution of the project at Howard Flat is an excellent example of how to extend a new technology into an agricultural system. As a result of CAMP, the adoption of codling moth mating disruption grew dramatically as growers learned about the success of the project. The percentage of bearing apple production area in Washington treated with pheromone technology for control of codling moth continued to increase after CAMP. In 2012, nearly 90% of bearing apple production area was treated with mating disruption products for the control of codling moth (Figure 7).

Phenology Models and Decision Aid Systems

Models that predict the development of a disease or arthropod pest are valuable tools in IPM programs. The Predictive Extension Timing Estimator, developed at Michigan State University, represented an early effort to automate the delivery of pest models (Welch *et al.*, 1978; Brunner *et al.*, 1980). In Washington State, the development of the WSU Agriculture Weather Network (AWN) made automation of model delivery a possibility. AWN maintains and provides accesses to environmental data from more than 132 stations throughout the state. A team led by Dr. Vince Jones from WSU developed the Decision Aid System (WSU-DAS). This web-based system currently delivers information on 10 insect, 4 disease, and 2 horticultural models (Jones *et al.*, 2009).

The power and utility of WSU-DAS comes through the integration of phenology model output with management recommendations and links to a WSU database of pesticides recommended for control of tree fruit pests. This automated delivery system allows users to create a personal profile where they specify the weather stations and models they wish to access. When the user logs onto WSU-DAS, only the weather stations and models they are interested in appear. The user can add weather stations and/or models to their personal account at anytime.

A screen-capture example of WSU-DAS output for the codling moth model is shown in Figure 8. In this example, the current conditions of codling moth development are shown along with appropriate management recommendations. A powerful feature of WSU-DAS is the capacity to predict pest phenology from 1 to 10 days by using temperature data derived from NOAA forecasts. Information on pest phenology can be viewed in different graphical formats or as a table. WSU-DAS also allows growers a choice of filters that automatically restrict pesticide options to those that fit different kinds of programs like organic or no-OP.

The WSU-DAS represents a state-of-the-art technology for delivering critical information in real time to assist growers and crop consultants in making pest management decisions. It represents the kind of decision support system that Washington tree fruit growers and crop consultants have said they want more of. WSU-DAS is now available to users through their smart phone or tablet.

WSU-DAS also provides an important link to other WSU online educational materials. For example, the front page of the WSU-DAS has a series of temporally relevant short stories that allows the user to access more information on the subject if desired. There are more than 120 such stories that automatically appear at appropriate times during the growing

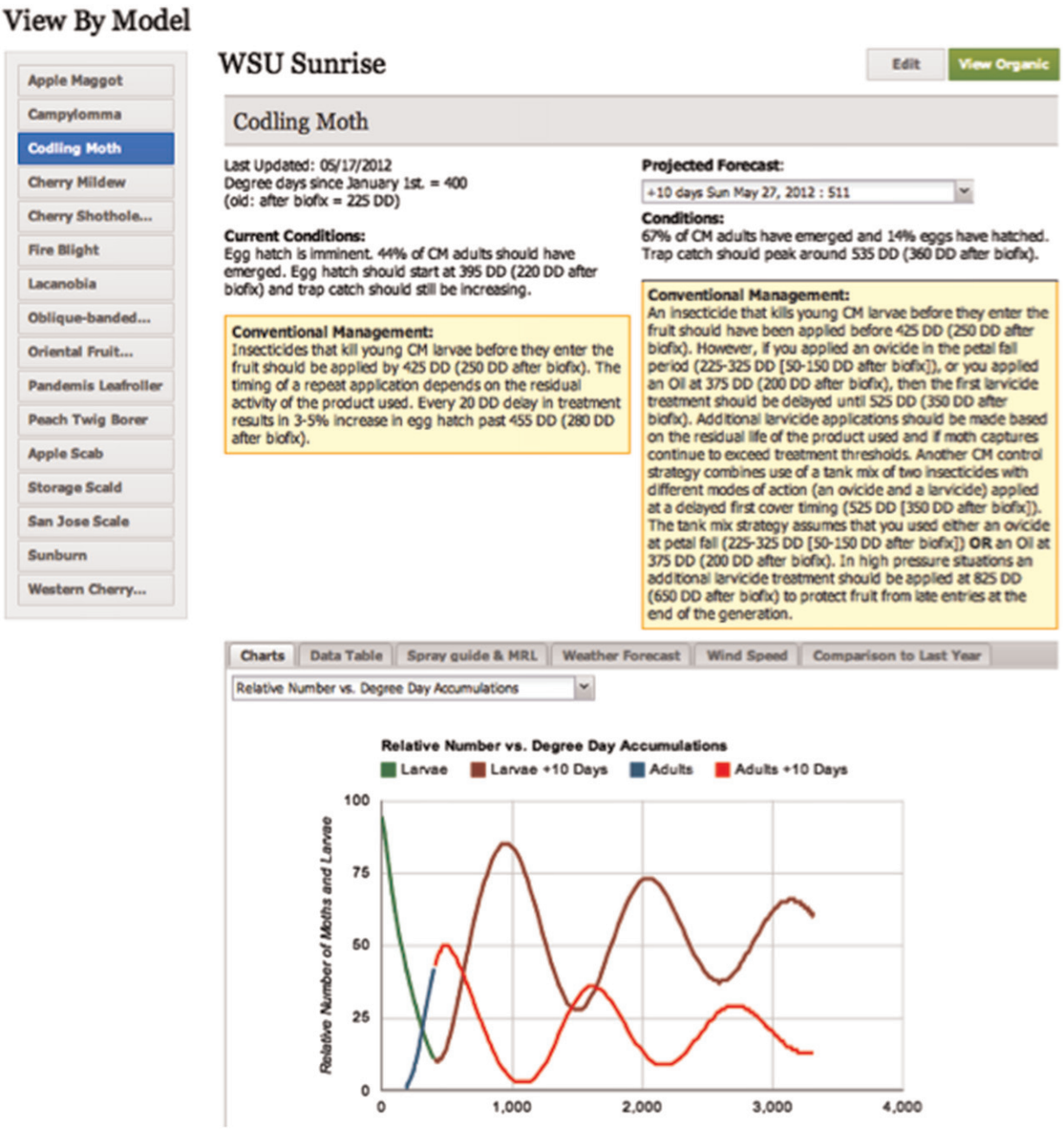


Figure 8 Screen capture of the codling moth model output from the Washington State University-Decision Aid System (WSU-DAS) showing current and forecast phenology and management recommendations.

season, thus leading users to important information about pests or horticultural practices.

Apple Integrated Pest Management Transition Project

In 2006, the EPA announced a decision to phase out, over 5 years, the use of the OP insecticide azinphos-methyl (AZM) from most agricultural uses. AZM had been the most used insecticide for codling moth control in Washington apple production for more than 40 years and was also important for control of other pests in tree fruit production throughout the US (Jones *et al.*, 2010). In response to this regulatory action, WSU implemented a 4-year Pest Management Transition Project (PMTP). Funding for this project was provided initially by the Washington state legislature, then later by Washington State Department of Agriculture through Specialty Crop Block Grants. The private pesticide industry had been in the process of developing and registering alternatives to OP insecticides and, through research, WSU had developed a good understanding of how these OP-alternatives fit apple IPM programs (Doerr *et al.*, 2012). The emphasis of PMTP was on

education: How to use OP-alternatives in apple IPM so that growers and crop consultants would not experience failures in their crop protection programs.

The primary education vehicles used in PMTP were Implementation Units (IU), which were made up of a small number (10–15) of growers and crop consultants. The IUs met four to five times in the first 2 years of the project. At these meetings, participants were given the PMTP handbook, which was used as a guide and knowledge source about OP-alternatives and how they best fit into an apple IPM program. The PMTP handbook is available online in both English and Spanish. The IU participants represented approximately 50% of the bearing apple production area in Washington, so the influence of information transfer from these groups was significant.

Additional ways of distributing information on OP-alternatives was through the project's web site, e-newletters, workshops, field days, winter grower meetings, and popular press articles. The PMTP employed an assessment and documentation specialist to assist with surveys and to interface with nonagricultural and farm worker communities. PMTP conducted surveys of crop consultants in 2007 and 2009 and of apple growers in 2008 and 2010. Information from these surveys allowed the project to assess perceptions and practices and changes over time.

Survey results pointed out concerns of both growers and crop consultants. For example, in the first survey, both crop consultants and growers (97.5% and 92.5%, respectively) agreed or strongly agreed that the cost of codling moth control would increase due to the phaseout of AZM, and these concerns changed little in the second survey (90.9% and 93.3%). Crop consultants were more confident that WSU had developed good information on alternatives to AZM in first and follow-up survey (82.5% and 84.0%) than were growers (65.6% and 66.1%), most likely because crop consultants were more in tune to changes in pest control products coming onto the market, and they participated more actively in meetings where research on new products was presented. Between the first and second surveys, growers indicated that their use of OP insecticides decreased by 9%, whereas crop consultants said that their recommendations for use of OP insecticides decreased by 40%. In addition to the comprehensive mail surveys, PMTP also conducted online surveys of IU participants and implemented use of the Turning Point™ audience response system as a means of gathering information from audiences at various meetings. Results of all these surveys along with questions asked can be found on the PMTP web site.

Outreach to the farm worker community, primarily Hispanic workers, provided important information on the safety of OP-alternative products being used in apple orchards. The project produced a poster, which has been used by growers, orchard managers, and pesticide applicators to explain the relative safety of OP-alternatives and why workers are allowed to reenter an orchard sooner than when OP insecticides were used.

Enhancing Biological Control

Biological control has been a key component of apple IPM since the establishment of integrated mite control in the late 1960s. When changes are made in practices in any cropping system, there is always a possibility that they will cause changes in IPM programs, positive or negative. When the use of OP-alternatives was implemented in apple IPM, prevailing thinking was that because these products were safer to humans and wild life, and were more selective in their control of pests than previous pesticides, they would also have little impact on natural enemies of pests. In part, this expectation was based on the way insecticides are typically screened for their impact on natural enemies, that is, by assessing acute mortality against the adult stage. Soon after the OP-alternatives were registered and used on a significant number of hectares in Washington, and other areas around the world, reports began to surface about the disruption of biological control of spider mites and aphids.

A multistate, multiinstitution research project funded through the USDA-National Institute for Food and Agriculture (NIFA) Specialty Crop Research Initiative program, Enhancing Biological Control in Western Orchards (EBCWO), had as one of its objectives examining the effects of selected OP-alternatives on a group of natural enemies found in tree fruit and walnut orchards. The project discovered that although OP-alternatives had little or no impact on adults of natural enemies, some showed significant sublethal effects, that is, the reproductive ability of the natural enemies was significantly impacted. These findings reveal why screening for acute toxicity of adult natural enemies alone does not reveal the true negative impacts of many OP-alternatives, and for that matter other pesticides. For more information on this project's findings on pesticide effects on natural enemies, and other information generated by the project, readers are directed to refer to the web site.

Another way EBCWO project is helping to enhance biological control in orchards is through the development of new monitoring methods and phenology models for natural enemies. Natural enemies are often very difficult to sample. Their presence is usually lower than that of pests and many are active at night. The EBCWO project has shown that different combinations of traps (color and shape) and lures (herbivore-induced plant volatiles) can attract different kinds of natural enemies. Some of the lure–trap combinations are highly selective, primarily capturing only one or two natural enemy species. Use of these new monitoring tools makes the presence of natural enemies in orchards much more apparent. In addition, they can be used to show the impact of IPM practices, such as the use of a toxic pesticide, on the abundance of a natural enemy.

In general, the phenology of natural enemies in orchards is not well understood. By using the natural enemy-monitoring tools developed by the EBCWO project, detailed information on the seasonal abundance of some natural enemies has become available. These data are being used to develop phenology models of these natural enemies. Once validated, the natural enemy models will be incorporated into WSU-DAS so that growers and crop consultants will know when natural enemies are present in the orchard and therefore when to avoid use of pesticides that would be most detrimental to their populations. New knowledge on the effects of OP-alternative on natural enemies, phenology models that predict when natural enemies will be present, and new monitoring tools that would confirm their presence or their absence are all

contributions that will help Washington growers conserve the free services provided by biological control in their orchards.

Impact of Integrated Pest Management on Use of Insecticides in Apple

NASS has conducted national surveys every other year starting in 1991 on pesticide use in tree fruit crops. These data include the percentage area treated, average number of applications, the pounds of active ingredient of each pesticide used and the total pounds of active ingredient used on each tree fruit crop in each state. The active ingredient is the chemical in a formulated pesticide that is responsible for control of the targeted organism.

Tree fruit crops are often reported as having the highest pounds of insecticide active ingredient applied per unit area relative to other agricultural crops. A primary reason for this is that tree fruit crops use horticultural mineral oil (HMO), which is classified as an insecticide in NASS surveys. HMO makes up the highest proportion of pounds of active ingredient of insecticides applied to tree fruit crops. This is due to the way the active ingredient for HMO is calculated. NASS assigns eight pounds of active ingredient to each gallon of HMO applied. HMO is typically used before bloom in tree fruit crops control of overwintering eggs of the European red mite and aphids, as well as various scales, most notably the San Jose scale. In most tree fruit crops, HMO is applied only once per season, and not all orchards are treated. Although some HMO is used in summer, the amount used is much lower than in the prebloom period.

In Washington, HMO (plus from 1999 on kaolin, a clay product used for sunburn but registered as an insecticide) made up an average of 83% of the total pounds of active ingredient of insecticides applied to apple (range 77% in 1995 and 1997–92% in 2011). Of all other insecticides used on apple in Washington, the OP insecticides made up an average of 51% (range 62% in 1995 and 41% in 2009) of the total pounds of active ingredient between 1991 and 2011. The active ingredient of OP insecticides applied averaged 4.48 kg ha^{-1} pounds between 1991 and 2011, but there was a significant decrease over this period. For example, between 1991 and 1997, the active ingredient of OP insecticides averaged 6.8 kg ha^{-1}, whereas the average between 2007 and 2011 was 2.2 kg ha^{-1}.

The amount of active ingredient in different insecticide formulations varies considerably. For example, 1.8 kg ha^{-1} of AZM active ingredient is applied when using the high label rate, whereas only 0.33 kg ha^{-1} of chlorantraniliprole (Altacor®) active ingredient, an OP-alternative insecticide, is applied when using the high label rate. Thus, comparing pounds of active ingredient of a pesticide makes it difficult to capture changes in the number of applications of different kinds of pesticides used over time. By calculating an area application, it is easier to follow the change in the average number of applications of all or different kinds of pesticides over time. An area application does not take into account the weight of active ingredient. It can be calculated from the NASS data by multiplying the average number of applications ha^{-1} by the proportion of ha treated. For example, if an insecticide is applied 2 times to 40% of an area

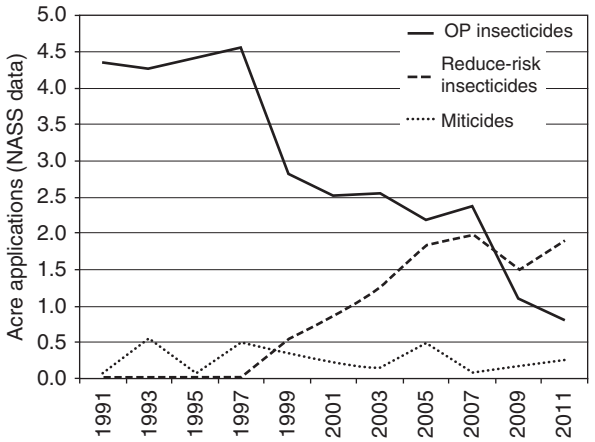


Figure 9 The acre applications of organophosphate (OP), OP-alternatives, and miticides used on apple in Washington State between 1991 and 2011 based on data from National Agricultural Statistics Service (NASS) surveys.

(acre or hectare), the number of area applications is 0.8 (2.0 × 0.4 = 0.8). By using area application values, HMO and kaolin data can be included in an assessment, because the number of times they are applied per area does not skew the information in the same way it does if the weight of active ingredient is used. The average number of area applications between 1991 and 2011 for all insecticides, including pheromones, HMO, and kaolin, was 8.1 (range of 10.8 in 1993 to 6.8 in 2001).

Figure 9 shows the number of area applications of OP and OP-alternative insecticides, miticides, and pheromones in Washington apple between 1991 and 2011. The drop in the area applications of OP insecticides between 1995 and 1999 is partially due to regulatory action restricting use of certain OP products during the growing season but can also be attributed to the adoption of mating disruption for control of codling moth. The area applications of OP insecticides remain relatively constant at approximately 2.5 until 2007, just after the EPA made the decision to phase out AZM. The dramatic drop in area applications of OP insecticides in 2009, and again in 2011, was due to apple growers shifting their programs to OP-alternatives. While regulatory action no doubt influenced the shift from OP to OP-alternative insecticides, the PMTP helped growers and crop consultants make the transition with minimal difficulty. The use of miticides in Washington apple orchards has remained relatively stable over time, with an average of 0.26 area applications between 1991and 2011. The increase in area applications of pheromones is attributed to the value apple growers saw in this selective control for their key pest.

New Threats to Integrated Pest Management

All IPM programs are subject to continual change as government regulations limit use of practices or technologies, especially pesticides, and as new technologies are developed to manage pests. A change that can result in an immediate and profound impact on an IPM program is the introduction of a new pest from a foreign country. One approach in dealing with a foreign pest is to find and introduce natural enemies from the pest's land of origin. This classical biological control approach

can at times provide sufficient suppression of the invasive pest so that additional controls are not required. However, even if such an approach is successful, it typically takes several years to find, culture, and then introduce natural enemies and, in most cases, the level of biological control is only partially successful and chemical controls are often still required.

The discovery of the brown marmorated stink bug (BMSB), *Halyomorpha halys* (Stål), in Pennsylvania signaled the establishment of what has become a very serious pest of tree fruit crops and many other agricultural crops (Hoebeck and Carter, 2003). The BMSB has more than 300 reported host plants including all tree fruit crops. It can, therefore, move from many different sources into or between agricultural crops. The BMSB feeds on fruit causing severe distortions and internal damage making them unmarketable. In 2010, in the Mid-Atlantic States, large populations of BMSB were reported in fruit orchards and, even though pesticides were used, crop losses were high. The evaluation of insecticides for control of the BMSB has shown that very few currently registered products are effective at preventing crop losses. Most of the insecticides that have shown promise against BMSB are in the synthetic pyrethroid class. This class of insecticide has a broad spectrum against pests and is known as being highly toxic to many natural enemies of agricultural pests.

The BMSB is known as a hitchhiker, that is, it likes to crawl into vehicles and packaging, especially in the fall of the year. The BMSB has spread from the eastern states to the western states of Oregon, Washington, and California. It is well established in the Willamette Valley of Oregon and southeastern Washington, where large populations have been reported. The first detection of BMSB in eastern Washington, where a majority of commercial tree fruit is grown, occurred in 2012. Although this first detection does not signal an immediate change in tree fruit IPM programs, it does not bode well for the future. If the only effective control of BMSB are synthetic pyrethroid insecticides, the Washington apple IPM program could lose five decades of progress and return to an era of repeated use broad-spectrum insecticides and a highly disrupted biological control system. Hopefully, research will provide alternative management tactics, including the introduction of natural enemies of BMSB from Asia, or effective pheromone trapping systems that would reduce its movement into crops. A large national research and extension project is currently underway with funding from a USDA-NIFA Specialty Crop Research Initiative grant. The web site of the project provides good information on the progress being made to combat this new and serious threat to IPM in all agricultural crops.

Summary

IPM as a philosophy strives to utilize all available tactics to mitigate the negative impacts of pests. The use of the most powerful and quick-acting tactic, pesticides, is the last line of defense after biological control, behavioral controls, or other tactics have failed to keep pests below levels that result in significant crop loss. Use of tactics, primarily pesticides, is based on the level of a pest present in the crop; therefore, sampling protocols and an understanding of the relationship between a pest level and crop injury is foundational to IPM.

IPM in tree fruit provides a good example of multiple tactics used to suppress key pests while conserving natural enemies that provide control of indirect or secondary pests. IPM programs in tree fruit have changed over the past five decades in response to regulatory action that has limited use of certain pesticides and to the development of new pest control technologies like pheromones and OP-alternative insecticides. IPM is information intensive, requiring an underpinning of sound science coupled with creative and technology-assisted delivery of information. A reduction in human resources in Extension activities at state land-grant institutions makes decision support systems like WSU-DAS even more important to the future of IPM information delivery.

See also: Plant Health Management: Biological Control of Insect Pests. Plant Health Management: Biological Control of Plant Pathogens. Quarantine and Biosecurity

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Intellectual Property in Agriculture

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Glossary

Biotechnology The use of biological methods (often genetic engineering and related advanced molecular biology applications) to produce products, processes, and related services. Generally, these are patentable under US patent law.

Commercialization The process of taking an invention or discovery to the marketplace. It involves working the idea into a business plan, consideration of protection options, and determining how to market and distribute the finished product.

Freedom to operate The ability to undertake research or commercial development of a product without infringing the unlicensed intellectual or tangible property rights of others.

Intellectual property (IP) Creative ideas and expressions of the human mind that have commercial value and are entitled to the legal protection of a property right. The major legal mechanisms or protecting IP are copyrights, patents, and trademarks. IP rights enable owners to select who may access and use their IP and to protect it from unauthorized use.

Patent (US) A grant by the federal government to an inventor of the right to exclude others from making, using, or selling his or her invention. There are three kinds of patents in the United States: a standard utility patent on the functional aspects of products and processes; a design patent on the ornamental design of useful objects; and a plant patent on a new variety of a living plant. Patents do not protect ideas but protect only structures and methods in which technological concepts are applied. Each type of patent confers the right to exclude others from a precisely defined scope of technology, industrial design, or plant variety. In return for the right to exclude, an inventor must fully disclose the details of the invention to the public so that others can understand it and use it to further develop the technology. Once the patent expires, the public is entitled to make and use the invention and is entitled to a full and complete disclosure of how to do so.

Plant breeders' rights Rights given to plant breeders to protect new varieties of plants by giving exclusive commercial rights to market a new variety or its reproductive material.

Plant patent In the United States, the Plant Patent Act of 1930 provides a grant of exclusive IP rights to applicants who have invented or discovered a new asexually propagated variety of plant. Tuberous plants are not covered by plant patents.

Plant variety protection A form of patent-like protection for sexually propagated plants as well as hybrids, tubers, and harvested plant parts. The Plant Variety Protection Act of 1970 is administered by the US Department of Agriculture and not the US Patent and Trademark Office (which does issue plant patents).

Public domain The status of an invention, creative work, commercial symbol, or any other creation that is not protected by some form of IP right. Items that have been determined to be in the public domain are available for copying and use by anyone.

Introduction

In the overall agricultural innovation system, there needs to be a balance between exclusive accesses to certain technologies and at the same time ensuring broad access to other technologies. An iconic example of this is the case in the early 1980s when recombinant DNA methods were patented by Stanford University and the University of California (Cohen and Boyer, 1980). This patent, covering the fundamental tool of modern biotechnology, was nonexclusively licensed under reasonable financial terms, a strategy that resulted in licenses to 468 companies (Feldman, 2005). Broad innovation was encouraged through access to the key enabling technologies; many companies became successful by using these tools to develop proprietary products based on other patented technologies that they exclusively held. Ultimately, the licensing strategy enabled US$35 billion in worldwide product sales and brought in US$255 million in licensing revenues (Feldman, 2005).

In agriculture today, the innovation system benefits by a balance of both exclusive and nonexclusive access to patented technologies to effectively support new technology development and to provide both commercial growers and subsistence farmers with the best technology possible for their crops. The ownership of critical IP and the rights to practice or use certain technologies is becoming a major issue confronting researchers in this area. Even purely fundamental academic research is not protected by an 'experimental use' exemption from patent infringement and may become increasingly entangled in issues involving access to IP rights (Eisenberg, 2003). Although the importance of IP in agriculture is becoming better recognized in both the public and the private sectors, many researchers, business people, research and development decision makers, and policy makers are still relatively uninformed about how to find, understand, and utilize IP information, including published patents and patent applications. Here an overview of the major issues and what a research scientist needs to be aware of when navigating the

agricultural IP landscape is provided. This topic had been reviewed previously and additional information can be found in those reviews (Chi-Ham and Bennett, 2011; Chi-Ham *et al.*, 2010; Bennett *et al.*, 2008).

What Is Intellectual Property?

IP is a form of property that applies to your ideas or the 'products of the mind' and gives the owner a set of rights that are, in some ways, comparable to tangible property rights. The concept of IP was insightfully addressed by Thomas Jefferson when he said: "If nature has made any one thing less susceptible than all others of exclusive property, it is the action of the thinking power called an idea, which an individual may exclusively possess as long as he keeps it to himself...Inventions then cannot, in nature, be a subject of property. (However) society may give an exclusive right to the profits arising from them, as an encouragement to men to pursue ideas which may produce utility" (Jefferson, 1903). Jefferson's concept of society providing a legal mechanism for inventors to have an exclusive right to profits from their ideas was subsequently integrated into the US Constitution, Article I, section 8, which states that "The Congress shall have power... to promote the progress of science and useful arts by securing for limited times to authors and inventors the exclusive right to their respective writing and discoveries." This forms the basis for IP rights and has become the cornerstone of the innovation process in the United States and more recently in many other countries throughout the world.

Intellectual Property and Agricultural Research

The impact of public sector research in agriculture has been very significant. In the United States, this dates back to the establishment of the Land Grant system of universities that has led the development of improved crop varieties, which were transferred to farms and the agricultural industry through cooperative extension services. Internationally, the system of crop research centers sponsored by the Consultative Group on International Agricultural Research has had a similarly large impact in developing new crop cultivars and agronomic practices that were delivered as a public good to support global food production (Table 1).

This model of public sector agricultural research has been slowly changing and the rate of change is now accelerating. At the core of this change is the increasing role of IP protection over agricultural inventions as well as the development of a research-intensive private sector in agricultural biotechnology. Thus, both United States and global agricultural systems are experiencing a change from research results being developed primarily in the public sector and the resulting technologies delivered for free as a public good to a system that is increasingly dominated by private companies who protect and treat results as a private asset. This has been accomplished through a much more intensive use of the patent system to protect agricultural innovations than was previously the case. The trend in patents awarded related to plant biotechnologies between 1980 and 2000 (Graff *et al.*, 2003) clearly illustrates the overall increase in patenting activity in this sector and this trend has continued in the authors' recent analysis (Figure 1).

In the past 25 years, other fundamental changes in the nature and ownership of innovations in basic and applied agricultural research have complicated the mission of public research institutions. The primary change was galvanized by the passage of the Bayh–Dole Act that effectively encouraged US universities to patent their innovations and license them to private sector companies in order to encourage their commercial use. Since that time, patenting by public research institutions and universities as well as the development of formal technology transfer mechanisms has accelerated. Although, by the 2000s, public sector institutions were contributing only approximately 2.7% of patents overall, their contribution to agricultural biotechnology patents is nearly an order of magnitude greater – contributing approximately 24% of all patents (Graff *et al.*, 2003). Although this trend has contributed to many positive economic outcomes, these new policies have created challenges for public research institutions and universities in supporting broad innovation, particularly for agricultural applications that address small markets, such as specialty crops, or that support humanitarian, rather than commercial, purposes.

Types of Intellectual Property in Agriculture

The main types of IP protection applicable to agricultural inventions include patents, plant variety rights, trade secrets, trademarks, and copyrights (Kesan, 2007; Dodds *et al.*, 2007). Tangible property rights are another class of property and are often captured in material transfer agreements (MTAs), bailments, or legal contracts that protect the exchange and use of physical materials. These forms of IP rights are the cornerstone of the innovation process in the United States and Europe, and the rights are increasingly expanding into other countries in the world.

Patents provide the legal rights to exclude others from using your invention. Patent rights are conferred by national governments for a specified period of time, usually 20 years, and are limited to the country in which the patent is granted. In exchange for exclusivity, the inventor makes a public disclosure of the invention. The monopoly that a patent provides to an inventor can be a powerful economic right and, as a consequence, the invention must meet a relatively high set of legal standards, which include (1) novelty, (2) nonobviousness, and (3) utility; that is, the invention (1) must be original and not previously known or published, (2) it must not be an obvious extension of previously known information, and (3) the invention must have some useful purpose. The legal standard of novelty has an important implication for public sector researchers because the primary means of scientific communication is through broad publication that, if done carelessly, can make an invention 'known' and thus destroy its patentability. The section of US patent law that lays out the novelty standard says that a patent application can be rejected on lack of novelty grounds if "the invention was… patented or described in a printed publication in this or a foreign country, before the invention thereof by the applicant for patent, or… More than one year prior to the date of the application for

Table 1 Overview of IP protection system

Means of protection	*What can be protected*	*How to protect*	*Term of protection*	*The rights of the owner*
Utility patent	Any useful, novel, and nonobvious invention	USPTO	If filing date is after 8 June 1995, 20 years from filing date; if filing date is before 8 June 1995, 17 years from issue date	Right to exclude others from making, using, manufacturing, selling, and offering to sell
US Plant Patent	Asexually produced plants (excludes uncultivated and tuber-propagated plants)	USPTO	If filing date is after 8 June 1995, 20 years from filing date; if filing date is before 8 June 1995, 17 years from issue date	Right to exclude others from asexually reproducing, selling, or using claimed plant
US and PVP	Sexually produced plants (excludes first generation hybrids and uncultivated plants)	USDA	20 years for most crops; 25 years for trees and vines	Right to exclude others from importing or selling, sexually or asexually reproducing, distributing without proper notice, producing a hybrid or new variety, and using the claimed patent
UPOV91	All genera and species	UPOV	20 years for most crops; 25 years for trees, shrubs, and vines	Prevents others from producing or reproducing, conditioning for the purpose of propagation, offering for sale, selling or other marketing, importing, exporting, and stocking for any purposes
Trademarks	Words, phrases, and logos that can distinguish the goods and services from those of others	Use or have a bona fide intent to use and apply for a federal registration	Unlimited duration as long as the mark is in use; the mark has to be renewed every 10th year	Right to exclude others from using the mark and other marks so similar that they cause confusion
Copyright	Literary works, software, dramatic works, music, pictures, sound recordings, architectural works, and movies	Apply for federal registration	Life of the author plus 70 years	Right to prevent unauthorized copying or public performance
Trade secrets	Any technical or business information that is secret and that gives the holder an advantage over a competitor who does not have the information	Keep secret; no registration available	Unlimited duration as long as the subject matter is secret	Right to prevent unlawful use

Source: Reproduced from Chi-Ham, C.L., Bennett, A.B., 2011. Intellectual property and the development of transgenic horticultural crops. In: Mou, B., Scorza, R. (Eds.), Transgenic Horticultural Crops: Challenges and Opportunities. Boca Raton, FL: Taylor and Francis, pp. 219–231; Modified from Dodds, J., Krattiger, A., 2007. The statutory toolbox: An introduction. In: Krattiger, A., Mahoney, R.T., Nelsen, L., *et al.* (Eds.), Intellectual Property Management in Health and Agricultural Innovation: A Handbook of Best Practices. Oxford, UK: MIHR. Davis, CA: PIPRA, pp. 337–350; and Dodds, J., Krattiger, A., Kowalski, S.P., 2007. Plants, germplasm, genebanks, and intellectual property: Principles, options, and management. In: Krattiger, A., Mahoney, R.T., Nelsen, L., *et al.* (Eds.), Intellectual Property Management in Health and Agricultural Innovation: A Handbook of Best Practices. Oxford, UK: MIHR. Davis, CA: PIPRA, pp. 389–400.

patent in the United States." The 1-year grace period provided in the United States does not exist in most other countries and public disclosure of an invention immediately bars patentability in those countries. This has especially been important since 16 March 2013, when the Leahy–Smith America Invents Act (AIA) was implemented as US patent law. The AIA transformed the US patent system from a first-to-invent system to a first-to-file system involving changes that make US patent law more consistent with the European Union and other nations to yield greater consistency and predictability in obtaining and enforcing patent rights across countries. Overall, the new first-to-file regime provides an incentive to file a patent application as early as possible. In addition to the timing of public disclosures, a researcher should consider the meaning of the words printed and publication. For example, is a report, a meeting proceeding, or a slide presentation posted on the Internet considered printed, such that the document bars future patentability? Any disclosure of a potentially patentable idea should be made thoughtfully and in consultation with an attorney or technology transfer office. In some cases, an intentional public disclosure can be purposely designed to bar patentability by others, in order to ensure that an invention remains in the public domain and available for everyone to use without IP restrictions (Boettiger and Chi-Ham, 2007).

In the United States, the two forms of patents most pertinent to the agricultural industry are plant patents and utility

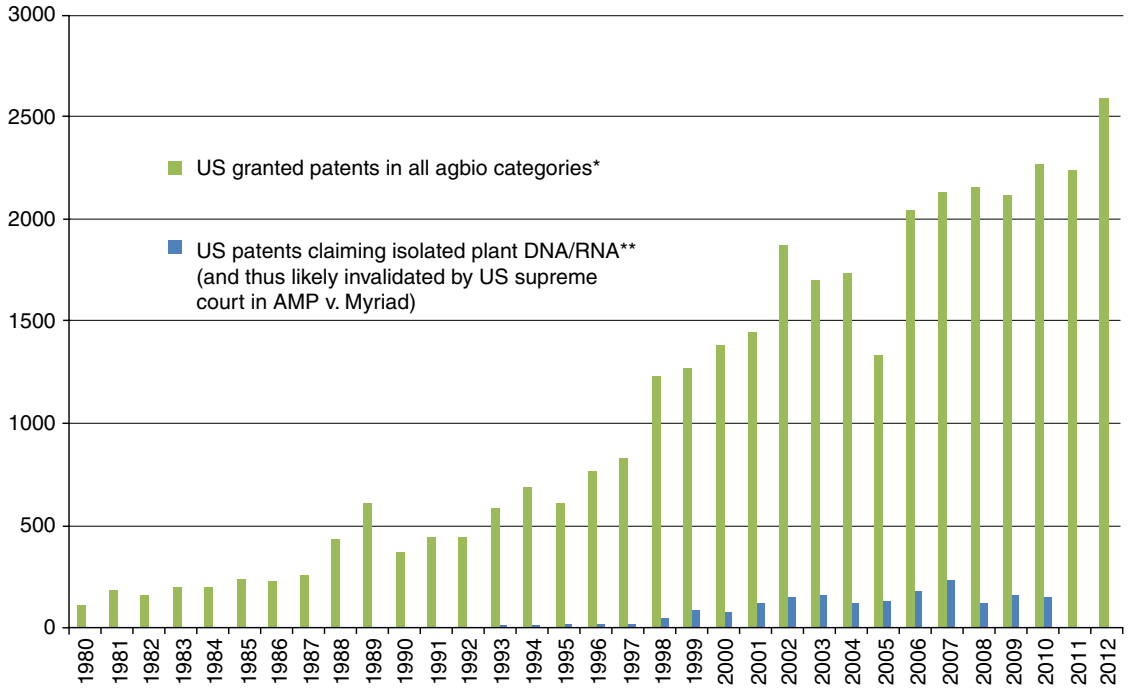


Figure 1 Annual Trends in Plant Biotechnology based on patents granted between 1980 and 2012. *Note*: Analysis includes *US patents granted and corresponding to the international patent class categories considered relevant in agricultural biotechnology (green bars, reproduced from Thomson Innovation, 2013, Available at: http://info.thomsoninnovation.com/en/features/search (accessed 07.05.14).). **US patents claiming isolated DNA/RNA sequences that are likely to become invalidated by the US Supreme Court, Reproduced from Graff, G.D., Phillips, D., Lei, Z., *et al.*, 2013. Not quite a myriad of gene patents. Nature Biotechnology 31, 404–410.

patents. Plant patents are unique to the US legal system and are granted only for plants that are asexually propagated, by cuttings or other means, such as strawberries or grape vines. At the time the US Plant Patent Act was enacted in the 1930s, sexually produced plants were believed to be unstable and nonuniform and as a result were excluded from plant patent protection. Utility patents offer one of the most robust forms of IP protection. In agricultural biotechnology, utility patents can be used to protect the genetically modified seeds or plants and the methods embodied in the invention, such as plant transformation and selection methods. Utility patents may protect different aspects of the invention. For instance, in the 1990s, Calgene Inc., now a part of Monsanto Company, used utility patents to protect the first agricultural biotechnology crop, the FlavrSavr™ tomato, which was genetically engineered to suppress expression of the tomato fruit-ripening polygalacturonase enzyme. Using a portfolio of patents, the company protected the DNA sequence of the enzyme, a DNA construct to suppress the enzyme expression in plants, the transgenic tomato cell, and even the overall method for antisense-based gene suppression of this or any other gene. In the United States, the US Patent and Trademark Office (USPTO) awards both plant and utility patents.

Plant Breeder's Rights (PBR) are a somewhat weaker form of IP for plant breeders, which, like patents, are granted nationally. In the United States, PBR are provided by plant variety protection (PVP) certificates issued through the US Department of Agriculture. PBRs are defined by a widely employed international agreement initiated by Europe, called the International Union for the Protection of New Varieties of Plants but commonly referred to by its French acronym UPOV (Lesser, 2007; Kesan, 2007). The original International Convention that established UPOV was held in 1961 and the treaty has been subsequently revised in 1972, 1978, and more recently in 1991. UPOV provides an international standardized framework according to which each member government can establish its own national legal system for PBRs. UPOV requires that a plant variety meets a set of criteria known as the DUS requirements: it must be distinct, uniform, and stable.

The agricultural industry can use a combination of plant patents, utility patents, PVP, and PRBs to protect and market new crop varieties in most parts of the world. Notably, in the United States it is possible to get dual protection for plant varieties through a utility patent and a plant patent, or through a utility patent and a PVP certificate, but not a plant patent and a PVP certificate as these cover either asexually or sexually propagated plants, respectively (Pardey *et al.*, 2013). For example, the University of California relies on US plant patents domestically and UPOV-based PBRs internationally to manage a successful Strawberry Licensing Program in domestic and international markets. The Strawberry Licensing Program has expanded internationally into countries with strong IP protection and the California-bred strawberry cultivars now represent up to 60% of the worldwide production (Bennett and Carriere, 2007).

In some cases, the dual protection through utility patents and PBRs has generated tensions because exemptions in one system are often not available under the other. For example, under PBR systems there is commonly an exemption for farmers to save and replant seed, which is not acceptable under

patent law. This was recently reinforced by the US Supreme Court in the decision Monsanto v. Bowman, which held that patent rights extend to the progeny grown by a farmer if those progeny still contain the patented genetic traits.

Trade secrets are an additional form of IP protection and one of the oldest. Trade secrecy is used to protect confidential business information, processes, know-how, data, and materials. However, a trade secret does not protect against the reverse engineering of a product by competitors. In the seed industry, trade secrets are used to protect parent inbred corn lines that are used to produce hybrid seed but are clearly not useful for the protection of a variety that can be directly propagated asexually or with open-pollinated seeds. Where appropriate, however, trade secrets can be maintained indefinitely so long as confidentiality is never breached.

Another form of IP protection, however, of limited utility in agriculture, is copyright. Copyright protects the expression of an idea, such as such as descriptions or diagrams, or other materials such as might be displayed in catalogs or seed packages. This form of IP protection is weaker than others because anyone is free to use the actual plant or the underlying depicted idea. Also, anyone is permitted to use the copyrighted information for the development of a product. In the United States, copyright protection is awarded for the life of the author plus an additional 70 years. Copyright use in plant sciences is, however, increasing because the plant genome information in electronic database can be subject to copyright protection.

Trademarks are another form of IP protection applicable to brand names of agricultural products; however, as with copyright it does not protect the underlying technology itself. In the United States, trademarks are registered at the USPTO. A searchable database of trademark registrations is available on the USPTO website at the Trademark Electronic Search System. For crops, trademarks are often used to protect any word, phrase, symbol, or logo that represents brand varieties or products, such as Dole® (a registered trademark of Dole Fruit Company), Sunkist™, and Monsanto Company's Roundup Ready® products.

Tangible property rights reside with the property owner and the terms of tangible property transfer are usually captured in MTAs or bailments, which both are legal contracts that allow the transfer of the 'physical' property while ensuring that the initial owner retains rights of physical ownership of the material. In research, MTAs are often used for transfer of materials for only research use, allowing scientists to perform academic research. However, there is typically no guarantee or promise that the owner will give rights for commercial applications. Also, the property owner can establish the time period and geographical limitations. Research use only MTAs are typically easier to obtain, especially between public or nonprofit research institutions but could represent considerable obstacles downstream if the materials cannot be used for commercial applications.

The patenting of plant and animal genes has been particularly controversial and critics have argued that genes are not patentable because they exist in nature. The USPTO has maintained since the 1980s that an isolated and purified deoxyribonucleic acid (DNA) molecule that has the same sequence as a naturally occurring gene is eligible for patent protection because it does not occur in its isolated form in nature. However, on 13 June 2013 the Supreme Court ruled in the case AMP v. Myriad Genetics that even if isolated, natural DNA is still a product of nature and therefore cannot be patented. The rationale of the ruling was that the location and order of the nucleotides existed in nature before anyone discovered them. This ruling has major implications because it will no longer be possible in the United States to patent or exclude others from using a naked genomic DNA molecule. However, interestingly the Court also ruled that a complementary DNA (cDNA) sequence is patent eligible because it is created from an messenger ribonucleic acid (mRNA) molecule as an exon-only DNA molecule that is not naturally occurring; more importantly the decision does not eliminate the ability to patent more complex DNA constructs.

Already in 2001, the USPTO began tightening the standards for granting of gene patents, by modifying and adopting a higher standard of 'utility' in its guidelines for evaluating gene patents, requiring that the applicant demonstrates that the 'utility is specific, substantial, and credible.' In spite of this specific utility requirement some patent applications have continued to seek to claim the sequences of hundreds of genes for which the utility is only broadly defined. For example, US patent application 20070022495 defines the utility of several hundred claimed genes as conferring an 'improved trait relative to a control plant' and "the improved trait is selected from the group that consists of larger size, larger seeds, greater yield, darker green color, increased rate of photosynthesis, more tolerance to osmotic stress, more drought tolerance, more heat tolerance, more salt tolerance, more cold tolerance, more tolerance to low nitrogen, early flowering, delayed flowering, more resistance to disease, more seed protein, and more seed oil relative to the control plant." The USPTO, however, significantly limited the scope of the claims of this broad application on granting the patent in 2010.

Based on the ruling by the US Supreme Court in AMP v. Myriad, a number of US-granted patents that include claims to isolated nucleic acids are likely invalidated (**Figure 1**).

Proliferation of Patents in Agricultural Biotechnology

The proliferation of patents in medical biotechnology led to the development of a metaphor to explain why people overuse or under use resources. The 'tragedy of the commons' was a term coined by Garrett Hardin to explain why people overused shared resources, such as common pastures, because they have no incentive to conserve or extend to the life of the resource (Hardin, 1968). By analogy, Heller and Eisenberg (Heller and Eisenberg, 1998) described the 'tragedy of the anticommons,' which, as a result of a proliferation and fragmentation of IP ownership across multiple owners, prevents any single institution or company from assembling all of the necessary rights to produce a product, resulting in underuse (or nonuse) of resources. Interestingly, although patents and IP generally are intended to encourage investment in research and development, the development of an anticommon has the opposite effect of blocking innovation. Although this concept of the anticommons was initially described in relation to

biomedical research, it also has direct relevance to agricultural biotechnology.

A prominent example of the complexity resulting from fragmented technology ownership and the potential for anticommons to arise was exemplified in the development of *β*-carotene-enriched rice by public-sector researchers who used at least 40 patented or proprietary methods and materials belonging to a dozen or more different owners in the gene transfer process (Kryder *et al.*, 2000). Some examples of the types of patented technologies that are required for developing a genetically engineered crop are discussed in the following sections.

Transformation Methods

The development of transgenic varieties has typically relied on either *Agrobacterium*-mediated or biolistic-mediated gene transfer methods (Herrera-Estrella *et al.*, 1983; Klein *et al.*, 1987). The breakthrough achievement in developing *Agrobacterium*-mediated gene transfer technology earned Van Montagu, Chilton, and Fraley the 2013 World Food Prize. Fundamental methods related to both processes of gene transfer into plant cells were developed in the public sector (Barton *et al.*, 2000; Sanford *et al.*, 1991), but key patents for *Agrobacterium*-mediated transformation are owned exclusively by Monsanto and others were licensed exclusively to Ciba-Geigy (now Syngenta) and the biolistic technology was licensed exclusively to DuPont for most fields of use. In addition, both private and public sector research and development organizations have patented a number of fundamental transformation methods as well as improvements, including vectors, species-specific protocols, and novel strategies to remove selectable markers and other 'foreign' DNA from the plant to be commercialized (Hamilton, 1998; Hoekema *et al.*, 1992; Frayley *et al.*, 1991; Rogers and Fraley, 2001). As a result of a variety of transactions, fundamental methods of gene transfer to plant cells were invented either by private sector companies or by the public sector but then licensed exclusively to private companies and represent a key technology area where patents have the potential to block new innovations. An example is the recently granted US 8,273,954 (Rogers and Fraley, 2001) patent covering a broad *Agrobacterium*-mediated transformation method for dicotyledonous plants, which is owned by Monsanto and has an anticipated expiration date in 2029. The effective filing day of the initial patent application was 17 January 1983; however, the pending application was not granted for approximately 30 years due to an interference case in which two applicants had claimed the same invention. Finally, in September 2012, Monsanto was granted the patent, which has a term of 17 years from the issuance date under US patent law, based on the fact that the original patent application was filed before 8 June 1995, the pre-General Agreement on Tariffs and Trade Treaty (GATT)–Agreement on Trade Related Aspects of Intellectual Property Rights filing date (**Figure 2**). The scope of Monsanto's patent is a method for transforming dicotyledonous plant cells with any coding sequence genes, including selectable markers, using *Agrobacterium* and a Ti plasmid with *Agrobacterium* transfer DNA borders. Monsanto Company announced that it would provide a royalty-free research license to the academic community and other nonprofit research institutions for the *Agrobacterium* transformation method newly issued patent US 8,273,954. The company also announced that it would continue to make commercial licenses available.

There has been a growing interest in non-*Agrobacterium*, bacterial-mediated transformation. One of the first viable alternative plant transformation methods to *Agrobacterium*-mediated transformation and biolistics was the Transbacter™ suite, developed by the Center for Application of Molecular Biology for International Agriculture (CAMBIA). Transbacter™ was introduced in 2005 by CAMBIA as a new plant transformation technology using non-*Agrobacterium* bacteria. CAMBIA filed a number of patents; however, the portfolio has been abandoned and the technology is now in the public domain. Recently, a research group based at Teagasc Crop Research Center (The Irish Agriculture and Food Development Authority) discovered an alternative bacterial plant transformation method to the classical *Agrobacterium*-mediated transformation using Ensifer adhaerens, a Gram-negative soil bacterium capable of a horizontal gene transfer that is genetically distinct from *Agrobacterium* (Mullins *et al.*, 2013; Wendt *et al.*, 2012).

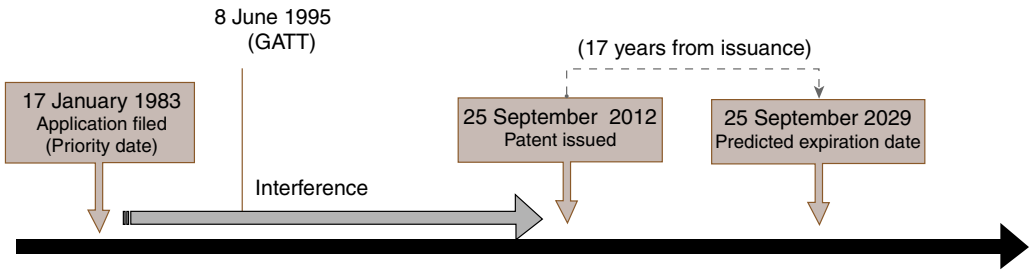


Figure 2 Prosecution of Monsanto's *Agrobacterium*-mediated transformation of dicot plants US patent 8,273,954. Although the patent application was filed in 1983, prosecution was delayed due to an interference case. The patent was awarded on 25 September 2012; however, because the application date was before 8 June 1995, the expiration date is calculated 17 years from the issue date. On 8 June 1995 the US patent law passed a major change to harmonize US law with other countries' law, the GATT. Before 8 June 1995 a US patent had a term of protection lasting 17 years from the date of issuance. Under GATT changes, an unexpired issue patent or a patent application pending on 8 June 1995 has a term of protection of 17 years from the date of issuance of the patent or 20 years from the filing date of the patent application, whichever is longer, which is the case for the US 8,273,954 patent. Any patent application filed on or after 8 June 1995 has a term of protection that begins on the date of the grant of the patent and ends on a date 20 years after the filing date of the patent application.

Ensifer-mediated transformation (EMT) exhibits transformation efficiencies that are comparable with *Agrobacterium*-mediated transformation, and more importantly can be directly substituted into existing *Agrobacterium* protocols without further optimization and may be used with both dicot and monocot plants. The Tegasc EMT patent portfolio currently includes an international patent application WO 2011076933 and two pending patent applications, US 20130078706 and CA 2784550 in the United States and Canada, respectively. These public sector inventions may represent alternatives for plant transformation.

Selectable Markers

The most commonly utilized plant selectable marker genes include the neomycin phosphotransferase II (*nptII*) and hygromycin phosphotransferase (*hpt*) genes that confer antibiotic resistance as a basis to select cell transformation (Miki and McHugh, 2004). Several other selectable markers conferring herbicide resistance or positive selection based on novel carbon utilization pathways provide important alternatives to the antibiotic-based selection strategies (Roa-Rodriguez and Nottenburg, 2003).

Historically, Monsanto held the broadest patent portfolio for use of selectable markers for plant transformation. Until 2008, Monsanto's patent on kanamycin-based plant selection (US 6,174,724) limited freedom to operate (FTO) for this enabling technology (Chi-Ham *et al.*, 2012). Because kanamycin is Generally Recognized as Safe, it is a desirable selection method from a technical, regulatory, and, now, and IP position.

Novartis AG (formerly owned by Eli Lilly & Company) owns an international patent portfolio protecting the method of selecting hygromycin-resistant plants, which includes two active issued US patents, US 5,668,298 and US 6,048,730, with a predicted expiration date of September 2014. Bayer CropScience (formerly Aventis CropScience) holds a patent portfolio with active issued US patents covering different components of the phosphinothricin-based herbicide selection method, including US 5,561,236, US 5,648,477, and US 5,646,024, which have predicted expiration dates of October 2013 and July 2014 for the latter two, respectively.

Selection strategies appear not to have been the topic of public sector research programs and there are just a few examples of either public domain or public sector-patented selectable markers for use in plant transformation (Dirk *et al.*, 2001; Dirk *et al.*, 2002; Mentewab and Stewart, 2005b; Mentewab and Stewart, 2005a; Hou *et al.*, 2006). Although there is potential to invent new selectable markers for plant transformation, at this point most of the broader patents have expired and there is potential to obtain FTO using public domain selectable markers.

Constitutive Promoters

Genetic regulatory elements are required to drive the expression of selectable marker genes and of specific transgenes. Selectable marker genes are typically driven by high-level constitutive promoters with the most common constructs utilizing the cauliflower mosaic virus (CaMV) 35S promoter derived from a viral genome and patent rights formerly owned by Monsanto, now expired (Chi-Ham *et al.*, 2012; Odell *et al.*, 1985). There are many promoters that confer constitutive gene expression which were developed in public sector organizations and either are in the public domain or can be licensed for nominal fees. These alternatives include: monocot and dicot actin promoters (Lemaux *et al.*, 2005; McElroy *et al.*, 1990; An *et al.*, 1996), an figwort mosaic virus (FMV) 34S promoter (Comai *et al.*, 2000), mannopine/octopine synthase (Gelvin *et al.*, 1999), or FMV and peanut chlorotic streak caulimovirus full-length transcript promoters (Maiti *et al.*, 1997; Maiti and Shepard, 1999). The FMV 34S has been used to drive constitutive gene expression and reported to be essentially equivalent to the CaMV 35S promoter (van der Fits and Memelink, 1997; Romano *et al.*, 1993) but has not been widely distributed to the public sector research community. Each of these promoters provides a strategy for driving constitutive transgene expression using public sector-derived or public domain components.

Tissue- or Developmental-Specific Promoters

Although many genes can be expressed under the control of constitutive promoters, targeting of expression to plant organs or tissues is typically desirable to minimize nonspecific effects of the introduced gene. For example, seed-specific promoters (Blechl *et al.*, 1999; Harada *et al.*, 2001) have been patented with claims directed toward their use to drive expression of heterologous genes in developing seeds. Public sector institutions have also patented a relatively large number of tissue- and developmental-specific promoters. Examples include the root-specific CaMV 35S fragment A promoter (Benfy, 1992), a root cortex-specific promoter (Conkling *et al.*, 1998), the Pyk10 root-specific promoter (Grundler *et al.*, 2001), an epidermal cell-specific Blec promoter (Dobres, 1998), and a vascular tissue-specific promoter rice tungro bacilliform virus (Beachy, 1998). In addition, there exists a large number of tissue and developmental specific promoters that have been characterized and placed in the public domain through publication. A wide range of constitutive and regulated promoters have been tabulated in a promoter database that includes information on expression characteristics as well as their IP status.

Subcellular Localization

In addition to specificity in tissue-level transgene expression, it is also often important to direct the targeting of the new protein to a specific subcellular location. For example, because β-carotene is produced in the plastids, the development of β-carotene-enriched rice utilized a transit peptide derived from the small subunit of Rubisco to target proteins to this subcellular compartment (Ye *et al.*, 2000). This and other transit peptides have been the topic of intense study, and several companies have patented their use to direct proteins into plastids (Herrera-Estrella *et al.*, 1983). For example, Plant Genetic Systems (now owned by Bayer) owned a broad patent family, including US 5,717,084 patent, covering a chimeric

DNA sequence that comprises any plant origin transit peptide for chloroplast targeting, with a predicted expiration date of February 2015. In addition, a French company, Rhone Poulenc Agrochimie, owns a US patent recently reissued, USRE 36,449, with narrower scope covering a plant carrying a DNA construct using a double transit peptide with an N-terminal domain of Rubisco. Therefore, in spite of several early publications from public sector research organizations describing alternative transit peptides that were not subsequently patented and thus should be accessible in the public domain, due to the broad claims of the Bayer patent family, using the alternative transit peptide would likely still fall within the scope of Bayer patent family as long as they are of plant origin. Targeting other subcellular locations has been the topic of intense research in both the public and the private sectors and there are many examples of public sector research describing unpatented sequences targeting proteins to a variety of subcellular sites, including the cell wall, vacuole, plastids, and peroxisomes (Komarnytsky *et al.*, 2000; Tague *et al.*, 1990; Volokita, 1991; Hayashi *et al.*, 1996; Bednarek *et al.*, 1990).

Developing a new genetically engineered crop requires the assemblage of a number of patented technologies through in-licensing or, potentially, by a series of strategic mergers and acquisitions. Several companies have effectively done this and have used platforms of proprietary technologies to develop new varieties of major crops. However, work on crops of less commercial interest has progressed slowly with few of the benefits of biotechnology having been realized in specialty crops (Clark *et al.*, 2004). Based on the requirement for assembling a large number of patented technologies to produce genetically engineered crop and the fragmentation of IP ownership, it appears that the preconditions for the development of an anticommons exist in this technology sector. In addition, the observed slowdown in the development of new agricultural biotechnology products may be, at least in part, an effect of such an IP anticommons (Graff *et al.*, 2009).

Freedom to Operate for Agricultural Research and Commercialization

Navigating the complex IP landscape of a research project in agriculture requires some analytical tools and specialized analytical capabilities (Fenton *et al.*, 2007). Although the importance of FTO analyses apply to all areas of agricultural research, they are especially important in the area of agricultural biotechnology where there are a large number of patented technologies. The analysis requires both legal and scientific knowledge as well as access to both patent and literature databases and typically takes the form of what is known as a FTO opinion. The FTO opinion is a legal assessment about whether research project or the development of a new product can proceed with a low, or tolerable, likelihood that it will not infringe existing patents or other types of IP rights. It is important to note that the FTO determination is not absolute but reflects an evaluation of risk because there is typically some uncertainty around the interpretation of patent claims as well as uncertainty as to whether new IP may issue or be discovered at a later date. The FTO opinion may lead to a range of options: identifying in-licensing targets, considering the substitution of technologies, deciding to ignore the potential infringement, investing in work-around technologies, or perhaps deciding to abandon the project all together. Although private firms are more likely to engage in FTO analysis because any infringement risk may directly affect their ability to develop new products and their ultimate profitability, public and not-for-profit private institutions are becoming increasingly aware of the need for better FTO information. This is particularly true for research projects undertaken by universities or not-for-profit research centers for the specific purpose of developing new crops for developing countries. In these cases, it is critical that IP considerations be taken into account early in the research process.

Although patents are the most common type of IP rights encountered, a thorough FTO analysis will assess all types of existing property rights for the likelihood that the research project or the product being commercialized infringes. Of particular concern are tangible property rights, such as cell lines, transgenic plants, germplasm, and plasmids. Because, the transfer of tangible property often occurs under the terms of a MTA that has no geographic or temporal limitation, these terms can be particularly problematic and directly impact FTO.

Enabling technologies for plant transformation or transformation vectors combines several components, such as promoters, selectable markers, marker removal systems, and more. Because of the fundamental role of these technologies, they have been extensively patented. In addition, the FTO surrounding plant enabling technologies is further complicated because these technologies are not used individually but are combined with a suite of related enabling technologies and specific trait technologies and are deployed in many different plant species. A single component of a transformation vector is a relatively simple example that illustrates the elements of an FTO analysis.

The target technology for this case study was a fruit-specific promoter from the tomato *E8* gene. The E8 promoter has been used to improve fruit quality, to extend fruit shelf life, and to express edible human vaccines specifically in ripening tomato fruit. The first step in an FTO investigation is to clearly define the target technology. In this hypothetical case, the fruit-specific promoter will be used exactly as described in the initial publications by Deikman and Fischer (1988), Deikman and Fischer (1988), Giovannoni *et al.* (1989), and Giovannoni *et al.* (1989). The promoters in these publications are virtually identical and consist of approximately 2100 nucleotides upstream of the *E8* structural gene. Further promoter characterization identifying the location and sequence of functional elements within the promoter and upstream nucleotide sequence was reported in Deikman *et al.* (1992). These publications draw the technical boundaries surrounding the target promoter technology and provide important prior art to subsequently filed patents.

To establish the relationship of publications and patents that describe or claim the E8 promoter, a patent landscape must first be established. The patent landscape should include patents and patent applications closely related to the technology. Keywords and authors of key publications are used to search for patents or patent applications. A separate search should then be conducted to identify patents or patent applications that referenced the scientific publications describing

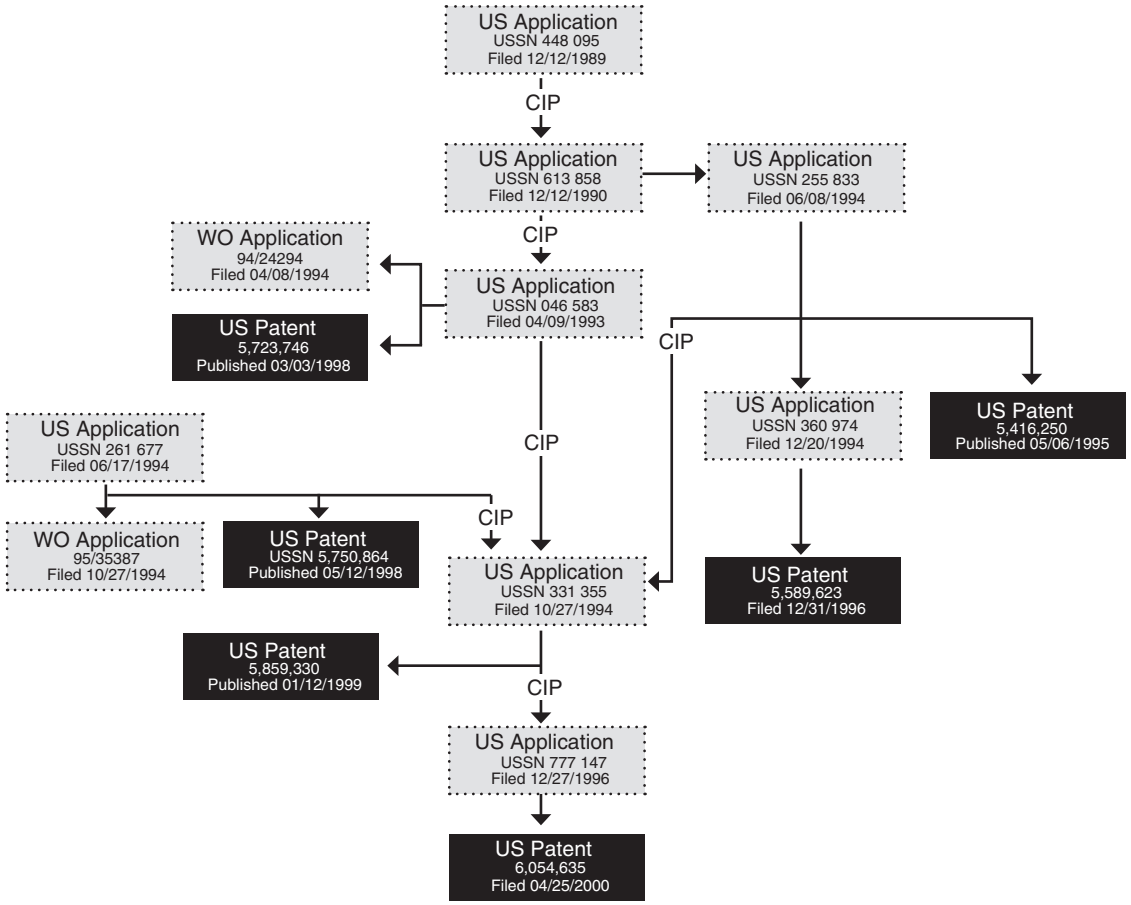


Figure 3 The Epitope/Agritope Patent Family related to the tomato E8 promoter. Patent applications are shown in gray, including US and WO or PCT applications; and issued US patents are shown in black. Modified from Fenton, G., Chi-Ham, C., Boettiger, S., 2007. Freedom to operate: The law firms approach and role. In: Krattiger, A., Mahoney, R., Nelsen, L., *et al.* (Eds.), Intellectual Property Management in Health and Agricultural Innovation: A Handbook of Best Practices. Oxford, UK: MIHR. Davis, CA: PIPRA, pp. 1363–1383.

the technology. Additionally, in the E8 case, patented DNA and protein sequence databanks were searched using the promoter's DNA sequence as a query. The patent landscape will reveal 'family' relationships among different patents and published patent applications. Patent families include later patent applications that claim the benefit of an earlier, related application or later, patent applications that arise from foreign filings of the patent application. Figure 3 illustrates a patent family arising from a 1989 patent application related to the E8 promoter filed by Agritope, an agricultural biotechnology company.

An informative way of analyzing the FTO search results is to construct a timeline of scientific literature, patent applications, and issued patents on the specific technology and on potentially overlapping subject matter. Ordering the patents and published applications according to their priority dates (also known as effective filing dates) reveals important relationships. For example, it reveals what publications or patents are prior art against newer patents. As patents may only be granted if the claims are both novel and nonobvious over the prior art, this analysis reveals the relative dominance of earlier, broader patents over later, narrower patents. Figure 4 illustrates the IP priority timeline for the E8 promoter. A thorough FTO analysis may require direct contact with the researchers and, in this analysis, it was learned from the authors of the Deikman and Fischer publication (1988) (Deikman and Fischer, 1988) that they did not apply for patent protection before their publication. This information was also confirmed by searching patent databases. Based on this information, it was presumed that the basic E8 promoter technology was in the public domain, but this conclusion required thorough review and documentation of the published literature or 'prior art' relative to the subject matter of subsequent patents.

As shown in the priority timeline, the Deikman and Fischer (1988), Deikman and Fischer (1988), Giovannoni *et al.* (1989), and Giovannoni *et al.* (1989) publications initially describe the E8 promoter technology. This precluded the novelty of any subsequent patent claims on the E8 promoter per se (e.g., applications filed by Agritope and Epitope). Counsel concluded that the tomato E8 promoter constructs per se could be reasonably considered to be in the public domain. However, some of the subsequent patents claim chimeric constructs that comprise the E8 promoter and heterologous genes and use of the E8 promoter in conjunction with other promoter elements. Thus, certain specific uses of the E8 promoter may infringe these subsequent patents.

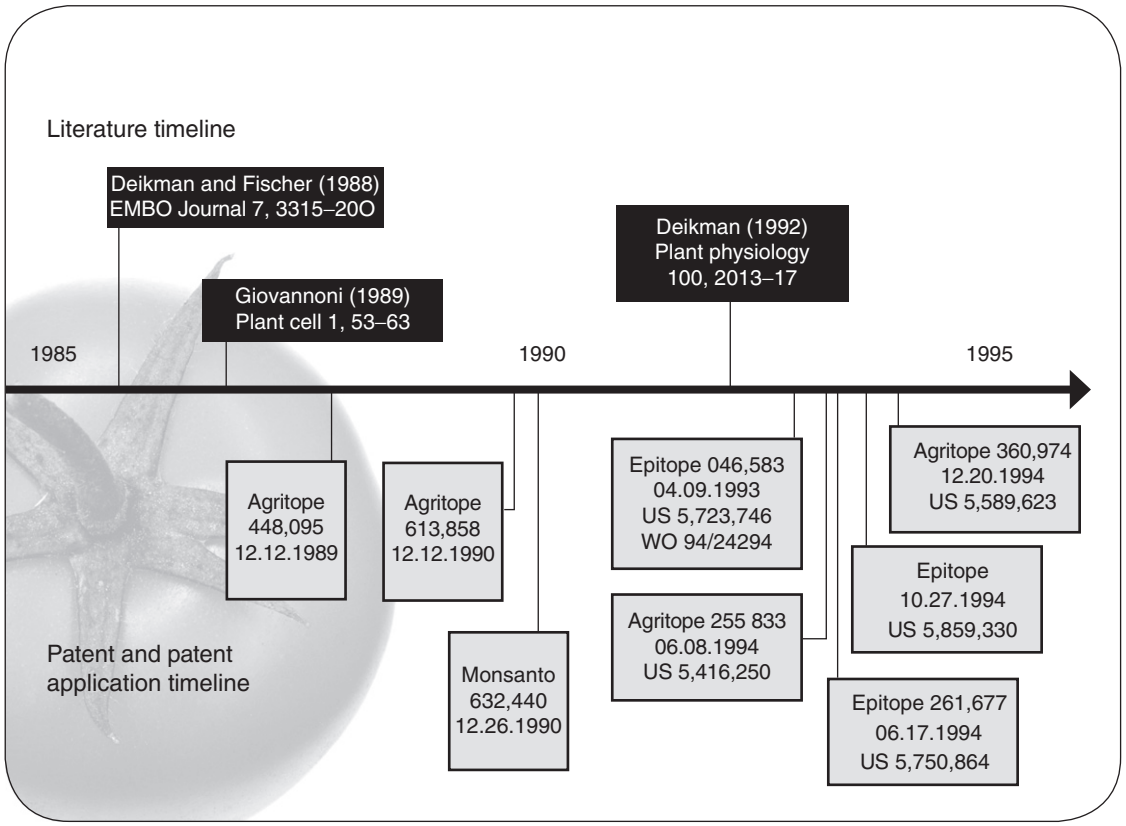


Figure 4 Timeline of the Tomato E8 promoter scientific publications and patents. Dates of publication of research articles are shown in black boxes above black timeline arrow, and priority date or effective flinging date of the issued US patents associated to the Tomato E8 promoter are shown in gray below the back time line. Modified from Fenton, G., Chi-Ham, C., Boettiger, S., 2007. Freedom to operate: The law firms approach and role. In: Krattiger, A., Mahoney, R., Nelsen, L., *et al.* (Eds.), Intellectual Property Management in Health and Agricultural Innovation: A Handbook of Best Practices. Oxford, UK: MIHR. Davis, CA: PIPRA , pp. 1363–1383.

This example provides an overview of the data and information that should be considered in an FTO analysis. It is not difficult to imagine how the complexity of an FTO analysis would grow dramatically with the inclusion of multiple enabling technologies, one or more trait technologies, and proprietary germplasm. This is one of the challenges of understanding IP constraints and developing FTO strategies in plant biotechnology where multiple complementary technologies are necessarily integrated to develop new crop varieties.

Strategies for Access to Technologies for Agricultural Research

The complex IP environment surrounding agricultural biotechnology research and development, exemplified by even a relatively simple FTO opinion, has spawned some new strategies and organizations committed to lower the IP barriers to new crop developments and provide more open access to patented technologies. These issues are critical for small private companies attempting to enter this sector but can also be important for public or not-for-profit research institutions. For example, a Federal Circuit Court of Appeals ruling in the Madey v. Duke case emphasized that academic research is not protected by an 'experimental use' exception from patent infringement, even when the research is purely fundamental (Eisenberg, 2003). Most plant biotechnology laboratories routinely use patented technologies in their research without permissions. Although patent owners have rarely been concerned about academic research infringement in agriculture, there are many examples where fundamental biomedical research has been challenged because of IP issues (Marshall, 2002). In addition to IP considerations in basic research, projects carried out in public or not-for-profit institutions that are targeted toward the development of crops for developing country farmers must consider the IP inputs to the project.

Most researchers are still relatively unfamiliar with how to find, understand, and utilize IP information, including published patents and patent applications. In addition, the ability to obtain the rights to use patented technologies has remained uncertain even for projects that have little commercial importance but, for example, may have large impacts in developing country agriculture. Several organizations have now emerged to address the relative inaccessibility of IP information and to provide a framework to ensure that IP does not block applications of agricultural biotechnology and, in particular, to facilitate projects that can have broad humanitarian benefits.

Several public sector and not-for-profit agricultural research institutions, including the University of California, the Donald

Danforth Plant Science Center, North Carolina State University, The Ohio State University, Boyce Thompson Institute for Plant Research, Michigan State University, Cornell University, the University of Wisconsin–Madison, the University of Florida, the USDA, Rutgers University, Texas A&M University, and Purdue University, developed the Public Sector IP Resource for Agriculture (PIPRA). These institutions made a public commitment to participate and promote strategies to collectively manage public sector IP in support of both United States and developing country agriculture (Atkinson *et al.*, 2003). This initial founding group of PIPRA members has grown to more than 45 institutional members in 13 countries, illustrating the widespread concern and interest in working collectively to remove and avoid IP barriers that might slow development of new crops.

A number of strategies have been implemented to enhance FTO using public sector IP for agricultural biotechnology projects. For example, informed decisions regarding dissemination of new knowledge via open publication or protecting it with a patent are clearly important and FTO can be improved if public sector institutions systematically consider how, when, and if to use the patent system to support broad innovation (Boettiger and Chi-Ham, 2007). Even when using the patent system, PIPRA encourages its members to reserve rights to use their newest and best technologies for humanitarian purposes, particularly when they issue exclusive commercial licenses (Bennett, 2007). For US agriculture, it is also important to retain rights to use patented technologies in development of small specialty crops that are not currently within the commercial interests of large private sector companies. The anticipated benefits of a collective IP management regime are to enable an effective assessment of FTO issues, to overcome the fragmentation of public sector IPR and reestablish the necessary FTO in agricultural biotechnology for the public good, and to enhance private sector interactions by more efficiently identifying collective commercial licensing opportunities.

In addition to PIPRA's core activities in developing a clearinghouse of public IP information and analytical resources, PIPRA is developing consolidated technology packages, or patent pools, particularly in the area of enabling technologies for plant transformation. Patent pools have been used effectively by companies to expedite the development and diffusion of innovations that draw on many complementary technology components protected by multiple patents, which are owned by multiple technology developers. In PIPRA's case, the development of a patent pool that provides FTO for plant transformation, which incorporates patented technologies from multiple owners was facilitated by its broad membership and their shared commitment to make these technologies widely available. This strategy is likely to create commercial licensing opportunities as well to support humanitarian projects.

Other initiatives have been established to manage IP issues and facilitate access to technologies in the agricultural and livestock areas, CAMBIA, the African Agricultural Technology Foundation (AATF), and the Global Alliance for Livestock Veterinary Medicines (GALVmed). CAMBIA was modeled after the 'open source' approach that is well developed in the IT software sector. This initiative was named Biological Innovation for Open Society or BiOS and is built on a broad philosophical foundation "to democratize problem solving to enable diverse solutions to problems through decentralized innovation." At the heart of BiOS was licensing language designed to preserve a pool of patented technologies from private appropriation. The idea was to create a 'protected commons' of enabling agricultural biotechnologies that are made freely available and whose use cannot be restricted by third-party patent rights. Even when a patent is granted on a new technology and broadly licensed, accessibility and utility could be reduced as subsequent patents stake proprietary claims for specific uses of the technology or combinations of the technology with other technologies (these are often called improvement patents). By signing the BiOS license, a researcher or an institution agrees to contribute back to the pool, for free distribution, data on the use of the technology and the patent rights to any improvements made to the technology. Over time, based on the improvements invented and contributed back to the pool by a set of researchers, the pool grows. CAMBIA abandoned the BiOs model and adopted a new technology access strategy whereby it abandoned its patent and tangible property rights.

GALVmed is a nonprofit global alliance for the development of livestock vaccines to improve livelihood in developing countries. Their IP asset management strategy anticipates and mitigates IP risks throughout the value chain for the development of livestock health products (Geoola and Boettiger, 2012). Similarly, AATF has implemented a public–private partnership model to access and deliver proprietary agricultural technology to smallholder farmers in Africa. Although many of the technologies are not patented in sub-Saharan Africa, AATF's model recognizes the value in know-how and strategic partnership. In 2008, AATF launched an ambitious initiative to develop Water Use Efficient Maize (WEMA). WEMA is a public–private partnership funded by the Bill and Melinda Gates Foundation, the Howard G. Buffett Foundation, and the USAID. WEMA's key partners include the National Agricultural Research Institutes in Kenya, Mozambique, South Africa, Tanzania, and Uganda; the International Maize and Wheat Improvement Center; and Monsanto. In terms of IP, Monsanto contributed commercial drought-tolerant and insect protection traits on a royalty-free basis and technical expertise.

Conclusions

IP as a tool to foster innovation has been important for hundreds of years but has become a much more prominent feature of research in the life sciences and in agricultural biotechnology in particular in just the past 25 years. This trend is unlikely to be reversed and, indeed, the importance of IP as an intangible asset contributing to the value of life science companies continues to increase. However, robust and sustained innovation in agricultural biotechnology, as in many technology sectors, requires a balance of both exclusive and nonexclusive access to proprietary technologies. This balance should ensure that the fundamental research tools are broadly available to support research and development in many application areas and at the same time provide the exclusivity to

specific trait or trait–crop combinations that will allow the developer of new varieties to recoup their substantial investment. The public sector has a role to play alongside agricultural biotechnology companies, particularly in providing research tools and broad enabling technologies and in addressing biotechnology applications in specialty crops whose market size may not justify commercial investment. The most powerful approaches, however, will come from public–private partnerships that mobilize proprietary technologies to address agricultural biotechnology product developments, which have a high social but low commercial value, including strategies to feed some of the world's poorest populations.

See also: Agricultural Ethics and Social Justice. Agricultural Law. Agricultural Policy: A Global View. Breeding: Plants, Modern. Genomics: Plant Genetic Improvement. Government Agricultural Policy, United States

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International and Regional Institutions and Instruments for Agricultural Policy, Research, and Development

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Glossary

Consultative Group of International Agricultural Research (CGIAR) A consortium of 15 centers that generate and disseminate knowledge, technologies, and policies for agricultural development in order to reduce rural poverty, increase food security, and improve human health and nutrition.

Food security Food security exists when all people, at all times, have physical, social, and economic access to sufficient safe and nutritious food that meets their dietary needs and food preferences for an active and healthy life.

Genetic resources Genetic material (any material of plant, animal, microbial, or other origin containing functional units of heredity) of actual or potential value.

International Agricultural Research Centers (IARCs) They include the CGAIR Centers, and some other institutions which engage in research and development activities for benefit of a region or the world. IARCs receive their funding from governments, philanthropies, and private sources, and their products and services generally are of the global public goods in nature.

International instruments These are treaties, conventions, and agreements among nations for development and implementation of legally binding or voluntary codes of conduct, norms, procedures, or standards.

Regional and international institutions and organizations facilitate cooperation and collaboration among nations, so that they can more efficiently meet the needs of their people provided by the agricultural sector. Exchange of knowledge, experiences, technologies, and products saves them valuable time and resources in facing the challenges to food security and environmental degradation. In a recent exercise, the Food and Agriculture Organization (FAO) of the United Nations, without claiming to be exhaustive, identified 62 instruments it supports related to agricultural production arena alone. Such instruments and organizations differ in their mandates and capacities – some are global and some are regional in their mandates; some focus on policy development and implementation and some on research or technology generation; and some set standards related to food quality and safety and some facilitate trade of agricultural products, etc. The following is a brief description of some relatively more widely known instruments and institutions selected to reflect this diversity in their mandates and functions.

Major International Research and Policy Institutions and Instruments

Food and Agriculture Organization of the United Nations

In 1943, 44 countries agreed to establish a permanent organization of food and agriculture that held its first conference as a specialized agency of the United Nations in 1945. The initial mandate of the FAO was to 'raise levels of nutrition and standards of living of the people under their respective jurisdictions; secure improvements in the efficiency of production and distribution of all food and agricultural products; better the condition of rural populations; and thus contributing toward an expanding world economy and ensuring humanity's freedom from hunger.' An Independent External Evaluation of the FAO in 2007 essentially confirmed the relevance of these goals for the FAO and recommended 'Reform with Growth' for it to continue to deliver its services to members. Today, the FAO's mandate continues to be 'to raise levels of nutrition, improve agricultural productivity, better the lives of rural populations, and contribute to the growth of the world economy.'

In 2011, the FAO's membership constituted 191 countries, 2 associate members, and the European Union. FAO Members meet every 2 years at their conference to 'review global policy issues and international frameworks, as well as to evaluate the work carried out and to approve the budget for the next biennium.' Supervision of technical and budgetary activities of the organization is carried by a council elected by the conference, with assistance from its Program and Finance Committees.

With its headquarters in Rome, 74 country offices, 5 regional and 11 subregional offices, the FAO was present in 130 countries. In April 2011, 53% of its 1835 professional and 1856 support service staff were based in Rome. The FAO serves its members through six technical departments: Agriculture and Consumer Protection, Economics and Social Development, Fisheries and Aquaculture, Forestry, Natural Resource Management and Environment, and Technical Cooperation. The FAO provides its members independent and reliable technical information, a forum to meet and discuss critical issues, policy expertise, and field projects that take technical knowledge to farmers' fields. It hosts a number of international instruments and agreements relevant to agriculture, including International Plant Protection Convention (IPPC), International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA), Agreement for the Establishment of

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the Regional Commission for Fisheries, and Convention Placing the International Poplar Commission within the framework of FAO.

International Agricultural Research Centers

Among the first International Agricultural Research Centers (IARCs) that specialized on crops important to food security were the International Rice Research Institute (IRRI) established in 1960 in the Philippines and the International Maize and Wheat Improvement Center (CIMMYT) established in 1966 in Mexico. Both centers were largely funded by the Rockefeller and the Ford Foundations and their contributions to the Green Revolution in the Indian subcontinent in the 1960s led to the creation of the Consultative Group on International Agricultural Research (CGIAR) in 1971. In turn, this led, by the turn of the century, to the establishment of 16 independent centers working on technologies and policies relevant to improvement and utilization of crops, livestock, forests, and fisheries.

The reform of the CGIAR in 2008 has led to creation of a consortium that now hosts 15 independent IARCs that conduct their research and development activities with other public, private, and nongovernmental organizations around the world. Establishment of a funding mechanism through CGIAR Fund improves dialog and collaboration among Centers to focus on important goals. The 15 CGIAR Centers are:

Africa Center: A pan-African rice research organization that conducts research and development activities for increasing rice productivity and profitability in a sustainable manner;

Bioversity International: An organization with a global focus that 'places the use and conservation of biodiversity in smallholder farming systems at the center of its work';

Center for International Forestry Research: An organization with a global focus, whose research 'enables more informed and equitable decision making about the use and management of forests in less-developed countries';

International Center for Agricultural Research in the Dry Areas: Conducts research on major food crops for nontropical dry areas in developing countries in order to improve food security and livelihoods of rural poor;

International Center for Tropical Agriculture: Focuses its research to generate knowledge on beans, cassava, and tropical forages in order to improve crop production, income, and natural resource management, especially in smallholder systems;

International Crops Research Institute for Semiarid Tropics: Focusing its research on chickpea, pigeon pea, sorghum, groundnut, and pearl millet in order to generate knowledge for farmers in the semiarid and arid tropical regions of the world;

International Food Policy Research Institute: 'Identifies national and international policies and strategies for meeting the food needs of the developing world on a sustainable basis';

International Institute of Tropical Agriculture: Works especially to address the needs of poor in the tropics through knowledge to 'enhance crop quality and productivity, reduce risk to producers and consumers, and generate wealth from agriculture';

International Livestock Research Institute: Conducts research that 'helps people in developing countries to keep their farm animals alive and productive, increase and sustain their livestock and farm productivity, find profitable markets for their animal products, and reduce their risk to livestock-related diseases';

CIMMYT: Conducts research 'to sustainably increase productivity of maize and wheat systems and thus secure global food security and reduce poverty';

International Potato Center: A global center that 'seeks to achieve food security, increased well-being, gender equity for poor people in root and tuber farming, and food systems in the developing world';

IRRI: Develops 'new rice varieties and rice crop management techniques that help rice farmers to improve the yield and quality of their rice in an environmentally sustainable way';

International Water Management Institute: Works 'to improve the management of land and water resources for food, livelihoods, and the environment' in order to help the poor in developing countries;

World Agroforestry Center: Generates and applies 'the best available knowledge to stimulate agricultural growth, raise farmers' incomes, and protect the environment'; and

World Fish Center: Works to improve livelihoods of poor who depend on fisheries and aquaculture and 'to achieve large-scale, environmentally sustainable increases in supply and access to fish at affordable prices for poor consumers in developing countries.'

There are a few other IARCs such as the World Vegetable Center and the International Fertilizer Development Center that are not a part of CGIAR but operate along the same principles as the CGIAR.

Committee on World Food Security

The Committee on World Food Security (CFS) was established by the FAO Conference in 1975 as a Committee of FAO Council in response to the food crises of the 1970s. 'It is the United Nation's forum for reviewing and following up on policies concerning world food security.' It currently has 123 members, who meet twice during even years. Its terms of reference include:

- Coordination of food security issues at the global level by providing a forum for discussion and coordination of action among public, private, nongovernmental, and other organizations dealing with food security issues,
- Promote greater policy convergence and coordination by developing and adhering to guidelines on food security and promotion of best practices and lessons learned by its members,
- Support and advice to countries and regions for the elimination of hunger, achievement of food security, and application of Voluntary Guidelines for the Right to Food.

The CFS is currently undergoing reform and the reformed CFS will reinforce the above actions and also develop a Global Strategic Framework for Food Security and Nutrition to promote coordination and synergistic actions.

International Plant Protection Convention

IPPC was established almost 60 years ago and now has 177 signatories (members). IPPC 'aims to protect cultivated and wild plants by preventing the introduction and spread of pests.' Its secretariat is provided and hosted by FAO in Rome. The governing body of IPPC is the Commission on Phytosanitary Measures (CPM) that facilitates cooperation among its members. CPM is assisted by a Standards Committee and a Subsidiary Body on Dispute Settlement. Major activities of IPPC include setting international standards on phytosanitary measures, build member capacity to set and implement the standards, and assist countries in assessing their plant protection activities and needs. The work of IPPC is also complemented by several regional plant protection organizations. An independent evaluation of IPPC in 2005–06 highlighted the importance of the Convention and recommended that it pay greater attention to the needs of its developing country members, so that they can better participate in the process of setting international standards and benefit from implementing them.

Commission on Genetic Resources for Food and Agriculture

Commission on Genetic Resources for Food and Agriculture was established by the FAO Council in 1983 at the request of the FAO Conference. It is mandated to cover policies and technologies dealing with conservation and sustainable use of all components of biodiversity dealing with food and agriculture. The Commission's terms of reference are as follows and its 173 members meet once every 2 years:

- To keep under continuous review all the FAO activities related to conservation and sustainable use of genetic resources for food and agriculture and keep the Director-General and relevant FAO Committees informed about them;
- To ensure development of appropriate global systems for genetic resources for food and agriculture in harmony with Convention on Biological Diversity and other such instruments;
- To provide an intergovernmental forum for negotiation of issues dealing with genetic resources for food and agriculture;
- To facilitate and oversee cooperation and coordination with other international bodies dealing with conservation and sustainable use of genetic resources for food and agriculture.

International Treaty on Plant Genetic Resources for Food and Agriculture

In 2001, the FAO members approved establishment of the ITPGRFA which was brought into force in 2004 to support 'conservation and sustainable use of plant genetic resources for food and agriculture and the fair and equitable sharing of the benefits arising out of their use, in harmony with the Convention on Biological Diversity, for sustainable agriculture and food security.' The birth of the Treaty was due to recognition among the FAO members that no country was self-sufficient in its own plant genetic resources to meet its food, feed, and other needs, and they all depended on each other for them. The Treaty also aimed at keeping much of the world's plant genetic resources in the public domain. The Treaty also recognizes the role farmers have played in conserving and improving the plant genetic resources for food and agriculture while also utilizing it. It has a fast-growing number of contracting parties, which stood at approximately 130 in 2012. The contracting parties of the Treaty constitute its Governing Body, whose 'basic function is to promote the full implementation of the Treaty, including the provision of policy guidance on the implementation of the Treaty.' The governing body of the Treaty meets once every 2 years. Much of the plant genetic resources currently listed under the mandate of the Treaty come from CGIAR centers; however, increasingly, other contracting parties are also including their germplasm under the Treaty.

International Rice Commission

The International Rice Commission (IRC) was established by the FAO members in 1949 'in order to promote national and international action in matters relating to the production, conservation, distribution, and consumption of rice.' At present, IRC has 62 members including most rice-growing countries as well as some nonrice producers. Its activities include analysis and provision of rice-related information, recommend national and international actions related to sustainable intensification of rice production, and organization of regular sessions of IRC in order to discuss recent developments in science and policy issues and challenges affecting rice production, distribution, and consumption. In recent years, interest in IRC has waned with the emergence of alternate providers of some of its services. However, an effort is underway by members to reevaluate its future, given the status of rice as the world's number one food, and its relevance to climate change adaptation and mitigation. An independent international forum may be necessary to provide countries an opportunity to discuss issues of global importance in relation to rice.

Rotterdam Convention on Prior Informed Consent Procedure

Rotterdam Convention on Prior Informed Consent (PIC) Procedure for certain hazardous Chemicals and Pesticides in international trade was adopted in 1998 and came into force in 2004 'to promote shared responsibility and cooperative efforts among parties in the international trade of certain hazardous chemicals in order to protect human health and the environment from potential harm; and to contribute to the environmentally sound use of those hazardous chemicals, by facilitating information exchange about their characteristics, by providing for a national decision-making process on their import and export, and by disseminating these decisions to parties.' It creates 'legally binding obligations for the implementation of the PIC procedure.' It currently has 149 Parties. The Annex III of the Convention lists 43 chemicals, of which 32 are pesticides and 11 are industrial chemicals. The secretariat of the Convention is currently jointly provided by

the FAO (for pesticides) and United Nations Environment Programme (for industrial chemicals).

Major Regional Organizations

Some research and collaboration organizations and institutions have emerged in different regions that promote cooperation among members. They normally operate on funds received from assessed contributions from their membership and on additional donor support for specific activities and projects. As member countries are from a region, they have greater similarities in their natural resource and ecological, social, and cultural assets and values, making cooperation easier and more rewarding. The following are examples of such institutions/organizations.

Inter-American Institute for Cooperation on Agriculture

Founded in 1942 and with its headquarters in San Jose, Costa Rica, the Inter-American Institute for Cooperation on Agriculture (IICA) is the 'specialized agency of the Inter-American System for promotion of agriculture and rural well-being' and 'making agriculture competitive and sustainable in the Americas.' With its offices in each of the 34 member countries, the institute works on meeting the needs of its member countries in areas such as 'technological innovation, agricultural health and food safety, agribusiness and commercialization, territorial management and rural well-being, food security, natural resources, and climate change.' More specifically, the institute focuses on (1) Designing, analysis, and evaluation of public policies and strategies; (2) Strengthening and modernizing institutions; (3) Capacity building; (4) Knowledge management for agriculture and rural well-being; and (5) Supporting countries on specific issues and investment projects.

New Partnership for Africa's Development/Comprehensive Africa Agriculture Development Programme

The Comprehensive Africa Agriculture Development Programme (CAADP) is an initiative of the New Partnership for Africa's Development (NEPAD) to eliminate hunger and reduce poverty in Africa through agriculture. This is an Africa-led and Africa-owned initiative that enjoys broad international support. It has four pillars: (1) Land and water management that aims to 'extend the area under sustainable land management and reliable water control systems.' Three initiatives under this pillar include TerrAfrica (addresses land degradation issues across the region through coordinated action); conservation agriculture (a Norway-funded program of countries and the FAO to improve soil health, promote water use efficiency, and lower the cost of production); and water and irrigation (to improve irrigation infrastructure in the region). (2) Market access that aims to 'increase market access through improved infrastructure and other trade-related interventions.' Major issues addressed include transportation, storage and packaging, retail facilities, information, and supply chains. (3) Food supply and hunger 'aims to increase food supply and reduce hunger across the region by raising smallholder productivity and improving responses to food emergencies.' The work under this pillar directly relates to the first Millennium Development Goal (MDG-1) as it focuses on chronically food insecure and vulnerable populations. The major thrust is on increasing domestic food production and marketing capacity, building trade, and improving household income. (4) Agricultural research aims to 'improve agricultural research and systems in order to disseminate appropriate new technologies.' Major focus is on improving relevance and effectiveness of agricultural research conducted by countries, Conseil pour la Recherche Agricoles en Afrique in West Africa, and the Association for Strengthening Agricultural Research in East and Central Africa, as well as others operating in the region.

Forum for Agricultural Research in Africa

The Forum for Agricultural Research in Africa (FARA) forms a coalition of national, regional, and international agricultural organizations working in Africa in order to 'sustainably reduce African food insecurity and poverty and enhance environmental conditions.' It aims to specifically achieve broad-based agricultural productivity, competitiveness, and market sustainability. It delivers its results through four networking support functions, viz., advocacy and policy, access to knowledge and technologies, capacity strengthening, and partnerships and strategic alliances. The FARA is governed by a general assembly that sets its overall vision and direction. An elected executive committee supervises the work of its secretariat.

Conclusions and the Future

International instruments and institutions have played a significant role in feeding the world over the years. Their impact varies with the clarity of their mandate, the vision and determination of their members in ensuring that they play their role, and the availability of financial support. Recent critical independent evaluations of some of these instruments and institutions (e.g., the FAO, CGIAR, and IPPC) have affirmed their importance to global food security and trade and made critical suggestions for their continued relevance and effectiveness. They have emphasized the need for instruments and institutions to work more closely to serve their members as well as to improve their efficiency. They have also urged their members and the donor community to provide additional financial resources and guidance so that the institutions and instruments can play the roles mandated to them. There have been suggestions that perhaps there are already too many instruments and institutions and some of them have lost their relevance and are overly bureaucratic; however, new ones will continue to emerge depending on the needs perceived by countries and their politics. In the future, it may be well worth examining the roles, functioning, and efficiency of the existing institutions and instruments, and appropriately assigning emerging new needed roles to them, before developing additional ones.

See also: Advances in Pesticide Risk Reduction. Biodiversity: Conserving Biodiversity in Agroecosystems. Food Security: Food Defense and Biosecurity. Food Security, Market Processes, and the Role of Government Policy. Genebanks: Past, Present, and Optimistic Future. Regulatory Conventions and Institutions that Govern Global Agricultural Trade

Relevant Websites

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International Trade

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Glossary

Antidumping duty A tariff levied against a country that is dumping.
Countervailing duty Tariff imposed by the importing country in response to export dumping by exporters (i.e., the exporter either sells below cost of production or sells abroad at a price below that charged in the home market).
Gains from trade The net benefits to agents from allowing an increase in voluntary trading with each other.
Import quota Specifies the maximum amount of a good that can be imported per year.
Optimal revenue tariff Set by the government to maximize government tariff revenue from imports; this tariff has the effect of restricting trade even more than for the optimal large country tariff.
Optimal welfare tariff One that is set by the government to maximize a large country's total welfare.
Scientific tariff One that raises the price of an imported good to the level of the domestic price, so as to leave domestic producers unaffected.
Tariff Policy instrument that drive a price wedge between what the exporters receive and what the importer pays.
Tariff rate quota A combination of an import tariff and an import quota in which imports below a specified quantity enter at a low tariff or nonexistent level and imports above that quantity enter at a higher tariff.
Voluntary export restraint A restriction on a country's imports that is achieved by negotiating with the foreign exporting country for it to restrict its exports. In some cases, a voluntary export restraint can actually increase the welfare of foreign producers.

Introduction

Tariffs on agricultural traded goods are widespread worldwide. From theory and empirical evidence, one can deduce why certain producers and other special interest groups lobby for tariffs.

> Almost every nation protects its industries from foreign competition. One such protectionist instrument is the tariff. This is an instrument used by importers of a specific commodity; it drives a wedge between export and import prices. For example, if a country imposes a dollar per pound tariff on beef imports, excluding all other factors such as transportation costs, the price in the exporting nation is one dollar below the price producers receive in the importing country. (Schmitz and Schmitz, 1994, p. 269).

First, the theory of tariffs is explored and the empirical data relating to their importance is examined. For many years, global agricultural trade negotiations under both the General Agreement on Tariffs and Trade and the World Trade Organization (WTO) have been stalled because of tariffs.

Import Tariffs

A common trade barrier is the import tariff (e.g., Canadian tariffs on dairy products and US tariffs on beef imports). Import tariffs are a way for governments to protect their domestic industries (Josling *et al.*, 2010). Two of the most common types of tariffs are: (1) a specific tariff based on per unit cost and (2) an *ad valorem* tariff based on a percentage of the price of the product.

There is a rich history on the use of tariffs (Schmitz *et al.*, 2002). In the United States, for example, tariffs of 5% were established as early as 1789. In 1816, US tariffs were increased to between 15% and 20%. After 1870, the sentiment for tariff reform in the United States grew rapidly. The Dawes Bill of 1872 lowered tariffs by 10%; however, the see-saw approach to tariffs gave rise to the McKinley tariff of 1890, which gave the United States the highest protection afforded by any of the previous tariff acts. After a brief move to lower tariffs in 1913, the United States returned to a protectionist policy in 1921. The most dramatic increase in US tariffs came with the introduction of the Smoot–Hawley Tariff in 1930. Canada immediately responded by placing its own higher tariffs on US imports, which increased Canada's trade with Britain even more than after the well-known removal of the Corn Laws in 1820. Canada remained a significant agricultural exporter to Britain until the end of the Second World War (Marchildon, 1998).

Small Country Tariffs

In Figure 1, the effects of a specific import tariff on different groups, including producers and consumers, are shown. In Figure 1(a), the small-country case, the domestic supply schedule is S, whereas the domestic demand schedule is D. The free trade price is P_w. If tariff T is introduced, the internal price in the small country will increase to P_1 and imports will be reduced to $(Q_2 - Q_1)$. The net loss from the tariff is $(acb + dfe)$. Producers will gain (P_1P_wca), consumers will lose (P_1P_wed), and the government will collect$(abfd)$ in tariff revenue.

Now, consider Figure 1(b), the large-country case. The free trade price P_w is set in the world market where excess supply ES equals excess demand ED_0. Suppose tariff T is again introduced. This tariff will shift the excess demand curve downward

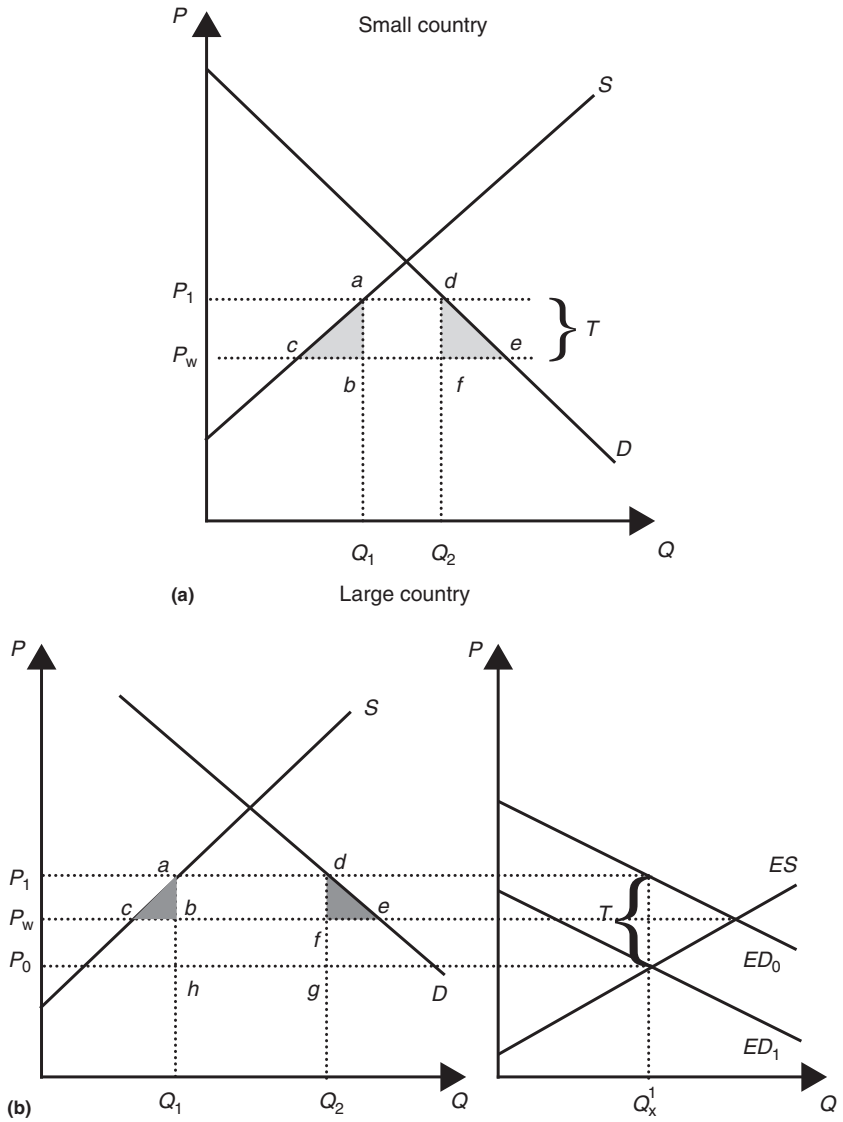


Figure 1 Import tariffs in (a) a small country and (b) a large country. *D*, domestic demand curve; ED_0, initial excess demand curve; ED_1, final excess demand curve; *ES*, excess supply curve; and *S*, domestic supply curve. Reproduced from Schmitz, A., Moss, C.B., Schmitz, T.G., Furtan, H. W., Schmitz, H.C., 2010. Agricultural Policy, Agribusiness, and Rent-Seeking Behaviour, second ed. Toronto: University of Toronto Press.

from ED_0 to ED_1, the internal price will increase to P_1, and the import price (world price) will fall to P_0. In this case, there is a net gain to the large country from the use of a tariff in the amount of $[(bhgf) - (acb + dfe)]$. If $bhgf > (acb + dfe)$, the tariff generates a net gain for the large country; in either case, the exporter loses.

From the above, producers in importing countries always gain from tariffs, and therefore spend considerable sums of money rent-seeking politicians to support tariffs. However, consumers in the importing countries lose from tariffs. As there are typically a large number of consumers and a small number of producers of any specific product, the incentive for an individual producer to lobby the government to increase tariffs on a particular product is much higher than the incentive for an individual consumer to lobby the government to reduce tariffs on that same product. This is the main reason why agricultural producer groups are typically more politically influential than food-related consumer advocate groups.

Optimal Welfare Tariffs

Optimal welfare tariffs have a long history in international economics. The optimal welfare tariff is welfare improving for the importing country, but in aggregate there is a net loss when all countries are taken into account. In Figure 2, the excess supply curve of country A is given by ES_A, and the excess demand curve of country B is ED_B. The free trade price is P_w. The optimal welfare tariff $(P'_B - P'_A)$ is determined where the marginal outlay curve *MO* intersects the excess demand curve ED_B. If country B imposes an optimal import tariff $(P'_B - P'_A)$, it behaves as a monopsonist with respect to country A by

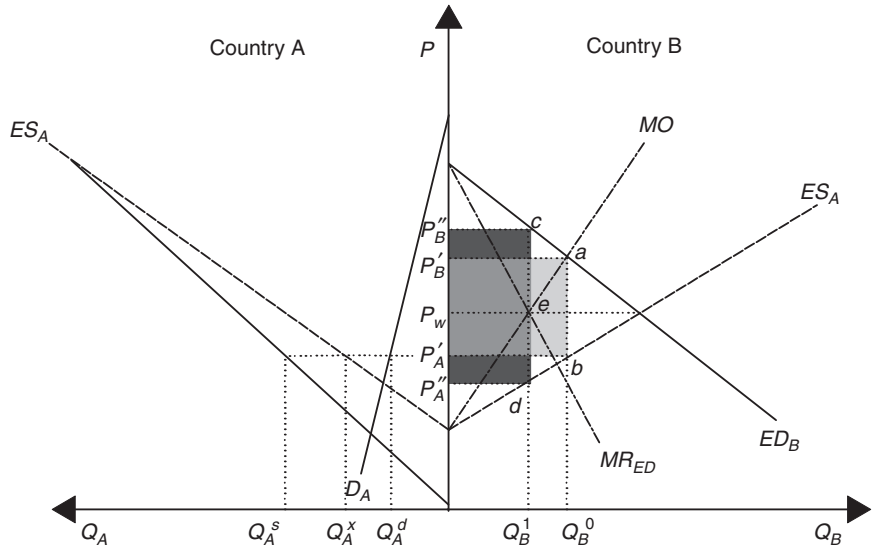


Figure 2 Optimal welfare and revenue tariffs. D_A, domestic demand curve of country A; ED_B, excess demand curve of country B; ES_A, excess supply curve of country A; *MO*, marginal outlay with respect to the excess supply curve of country A; and MR_{ED}, marginal revenue with respect to the excess demand curve of country B. Reproduced from Schmitz, A., Moss, C.B., Schmitz, T.G., Furtan, H.W., Schmitz, H.C., 2010. Agricultural Policy, Agribusiness, and Rent-Seeking Behaviour, second ed. Toronto: University of Toronto Press.

reducing imports to $Q_B{}^0$. The total tariff collected is $(P'_BP'_Aba)$. Consumers lose from the tariff whereas producers gain.

Optimal Revenue Tariffs

Governments use revenue tariffs to collect revenue from imports. These types of tariffs have been used by the Japanese Food Agency and by the European Union (EU) (Carter and Schmitz, 1979; Schmitz *et al.*, 1981). Conceptually, these tariffs are set, so the government can exploit both exporters and domestic consumers. The optimal revenue tariff is determined where *MO* and the marginal revenue to the excess demand curve MR_{ED} intersect (Figure 2). The optimal revenue tariff is $(P''_B - P''_A)$ per unit of import. The tariff revenue collected is $(P''_BP''_Adc)$. Note that imports are always lower ($Q_B{}^1$ compared with $Q_B{}^0$) and the tariff revenue is always higher under the optimal revenue tariff when compared with the optimal welfare tariff.

General Equilibrium Tariffs

Figure 3 shows the effects of tariffs for more than one country. The aggregate production possibility for agriculture and manufacturing is represented by X_1X_2. At relative prices (terms of trade) represented by P_1, the output of manufacturing is M, whereas A of agriculture is produced. This is under no trade. At free trade, the relative price is P_2. Output of agriculture increases to $\overline{A}$ but production of manufacturing decreases to $\overline{M}$. Welfare is improved under free trade because consumption occurs at C_2, which is on a higher indifference curve than C_1.

A tariff causes production to fall between the free trade and no trade points. For example, for a tariff that changes the terms of trade to P_3, agricultural output is A_0, and M_0 represents the manufacturing output. The tariff drawn in Figure 3 is welfare improving (C_3 lies above C_2).

In cases where tariffs are welfare improving, the important assumption is that the trading partner does not retaliate. Under extreme retaliation (i.e., retaliatory tariffs), the outcome can be very different as both the countries jointly can lose from tariffs.

Optimal Byrd Tariff

The Continued Dumping and Subsidy Offset Act (CDSOA) attached as an amendment in 2001 by senator Robert Byrd of West Virginia stipulated that the tariff revenue should be reimbursed to the petitioners for the tariff. The Byrd Amendment (which the CDSOA is commonly referred to) provided additional incentives for rent-seeking behavior by special interest groups (Schmitz and Schmitz, 2012); Schmitz *et al.* (2006) derived the optimal Byrd processor tariff in a vertical market structure. They considered a group of processors, referred to as the processing industry, who buy inputs for processing from abroad and from domestic producers. The excess supply curve for the exporter of an input for processing is *ES* (Figure 4). The importer's domestic supply schedule for producing the same input is S_d. The demand curve for the processor's output is D_c. The processor's derived-demand curve for the input is D_d. The free trade price for the input is P_f and exports are Q_f.

Under free trade, the raw-product processor will purchase Q_f from abroad at price P_f and will purchase Q_1 domestically at price P_f. In essence, the processor uses $(Q_f + Q_1)$ inputs so that its total outlay for the raw product is $(P_fQ_f + P_fQ_1)$. A portion of the processed input comes in the form of imports, and the remainder is produced domestically. Under constant processor costs, given the consumer demand for the final product D_c, the processor will produce Q^* and will sell the final product at P^*.

Under the optimal processor tariff $(P_t - P_p)$, the processor now imports only Q_t (which equals Q_x of exports) of the input

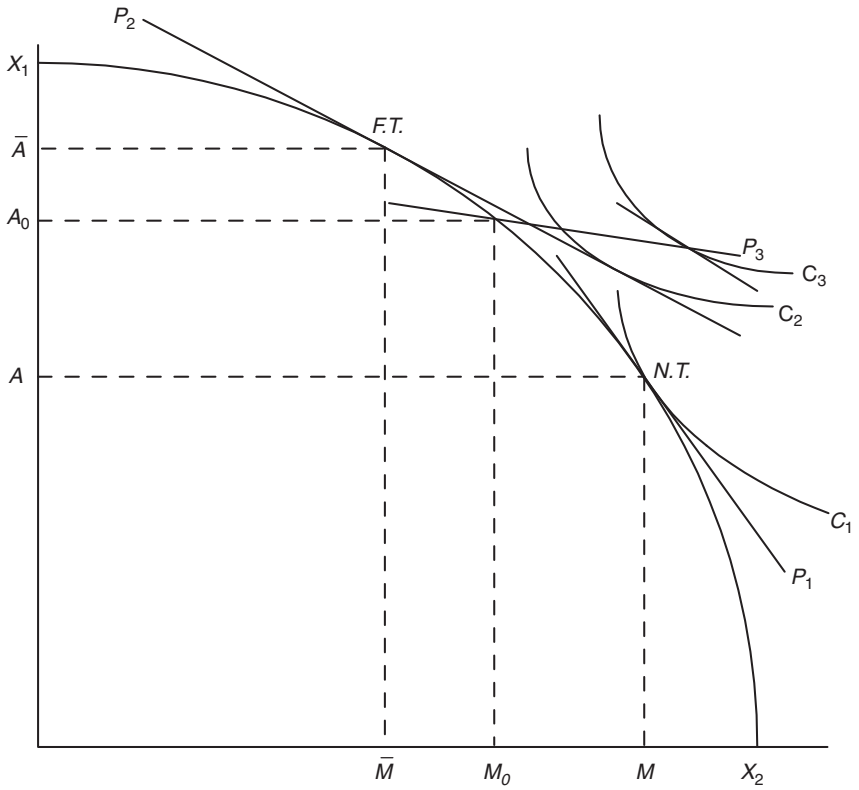


Figure 3 Tarriffs in general equilibrium. (A_0, M_0), amount of X_1 and X_2 consumed in equilibrium under a tariff; $C_{1,2,3}$, community indifference curves; *F.T.*, FREE TRADE equilibrium point where the country consumes A bar of X_1 and M bar of X_2; *N.T.*, NO TRADE equilibrium point where the country consumes A of X_1 and M of X_2; P_1, terms of trade under no trade; P_2, terms of trade under free trade; and P_3, terms of trade under a tariff. Reproduced from Schmitz, A., Schmitz, T.G., 1994. Tariffs and trade. In: Encyclopedia of Agricultural Science, vol. 4. Waltham, MA: Academic Press.

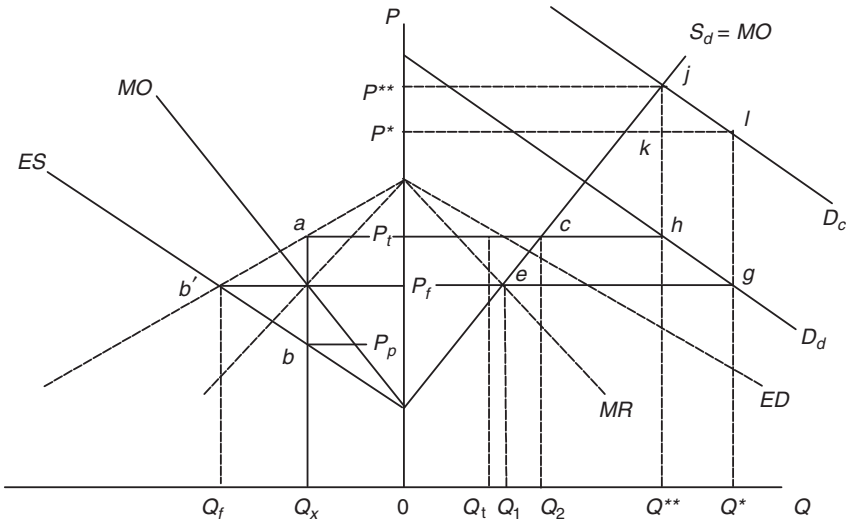


Figure 4 The optimal Byrd processor tariff. D_c, demand curve for the processor's output; D_d, processor's derived demand curve for the input; *ED*, excess demand; *ES*, excess supply; *MO*, marginal outlay with respect to the excess supply curve; *MR*, marginal revenue with respect to the excess demand curve; and S_d, importer's domestic supply schedule for the input. Reproduced from Schmitz, A., Moss, C.B., Schmitz, T.G., Furtan, H.W., Schmitz, H.C., 2010. Agricultural Policy, Agribusiness, and Rent-Seeking Behaviour, second ed. Toronto: University of Toronto Press.

to be processed at price P_t. The tariff revenue abP_pP_t will be reimbursed to the processor; hence, its effective outlay on imports is reduced to P_pQ_t. However, raw product processor expenditures on domestic inputs will increase from P_fQ_1 to P_tQ_2. Total expenditures by the processor on purchases of both imports and domestic raw product will actually decrease when the tariff revenue is rebated to the processor. Compared with free trade, the optimal Byrd tariff $(P_t - P_p)$ results in a gain to

both processors (abP_pP_t) and domestic producers (P_tP_fec). (The optimal processor tariff is derived where the marginal outlay curve *MO* intersects the marginal revenue curve *MR* at the excess derived-demand curve *ED* as in **Figure 4**.)

Trade Remedy Actions

The WTO allows for trade remedy actions including antidumping (AD) and countervailing duties (CVDs). AD actions can be imposed when two conditions are met: (1) the US Department of Commerce (USDOC) determines that foreign goods are sold, or likely to be sold at less than fair value (LTFV) and (2) the US International Trade Commission (USITC) determines that an industry in the United States is injured materially, or threatened with injury, from the sale of the goods. Dumping, or sales at LTFV, typically occurs when a company exports a product at a price lower than the price it normally charges in its own home market.

The WTO agreement allows governments to act against dumping when there is genuine material injury. A government must show that dumping is taking place, calculate the extent of dumping (the dumping margin), and show that dumping is causing injury. Typically, an AD action means charging extra import duties in order to bring the price closer to normal value. The dumping margin is the difference between the price or cost in the home market (the normal value) and the price in the export market.

The WTO agreement stipulates three methods for calculating the normal value: (1) a comparison of the export price with the price in the exporter's home market; (2) a comparison of the export price with the price charged in a third-country market; or (3) a calculation based on the combination of the exporter's production costs, other expenses, and normal profit (constructed value).

CVDs can be imposed when (1) the USDOC determines that the government of a country, or any public entity within a country, provides a countervailable subsidy on the manufacture, production, or export of goods sold into the United States, and (2) the USITC determines that an industry in the United States is injured materially or threatened with injury by reason of these imports. The types of subsidies covered by CVD actions are specified in the WTO Agreement on Subsidies and CV Measures (WTO, 2003). Only specific subsidies that apply to a specific enterprise or industry group are usually actionable. The WTO Agreement identifies three types of actionable subsidies: (1) subsidies that provide an advantage over rival exporters in a third-country market, (2) subsidies that advantage the domestic industry over exporters to that country, and (3) subsidies that damage the domestic industry in the importing country.

The Scientific Tariff and Multifunctionality

Tariffs are used to promote noneconomic objectives of various kinds through their influence on domestic production and consumption of certain products (Schmitz and Schmitz, 1994). Examples include tariffs to promote (1) national self-sufficiency and independence, (2) diversification and industrialization, (3) a way of life, (4) military preparedness, (5) bargaining, and (6) food security. Earlier scholars labeled these as scientific tariffs (Johnson, 1960). More recent literature categorizes these under the label of multifunctionality.

Of the tariffs listed above, the most popular one appears to be the tariff that promotes food security. Strong arguments for food security have been made because of world famines that are natural or manmade. However, a word of caution is needed. Much of the literature discredits the notion of scientific tariffs because other policy instruments are often superior to tariffs to achieve specific policy objectives (Schmitz and Moss, 2005).

Tariff Rate Quotas and Importer/Exporter Agreements

Often, protection takes the form of tariffs in conjunction with quotas. For example, the United States restricts sugar imports through a tariff rate quota (TRQ) system. High tariffs are applied to US imports of sugar that exceed the quota-level specification. According to USDA/ERS (2013),

> A TRQ is a two-tiered tariff for which the tariff rate charged depends on the volume of imports. A low-tier (in-quota) tariff is charged on imports without the quota volume. A high-tier (over quota) tariff is charged on imports in excess of the quota volume. Almost all raw cane sugar, refined sugars and sugar syrups, and sugar-containing products are imported under TRQs for those products.

As of 1 January 2008, sugar from Mexico enters the United States duty free under the North American Free Trade Agreement (NAFTA) and is not subject to quota restrictions. Since then, US sugar imports from Mexico have both increased significantly and become more volatile due to weather and other factors.

In agriculture, there are cases where the prices for traded commodities are agreed to by governments. A classic example is the outcome of negotiations between Mexico and the US on trade in tomatoes. In response to years of tariff-related disputes over tomatoes (Bredahl *et al.*, 1987), the two countries agreed in 1996 to a suspension agreement where a minimum price was set below which Mexico could not export tomatoes to the US. This suspension agreement was renewed in 2013.

According to the USDOC (2013),

> On March 4, 2013, the United States Department of Commerce and producers/exporters accounting for substantially all imports of fresh tomatoes from Mexico signed an agreement suspending the antidumping investigation on fresh tomatoes from Mexico. The basis for the agreement was a commitment by each signatory producer/exporter to sell the subject merchandise at or above the reference price, which will eliminate completely the injurious effects of exports of fresh tomatoes to the United States.

These types of agreements often take the form of either a voluntary export restraint on trade shipments or an import/export cartel between the two countries.

Equivalence of Tariffs and Quotas

Agricultural trade is often restricted by both tariffs and nontariff barriers. Consider an import quota. This trade instrument

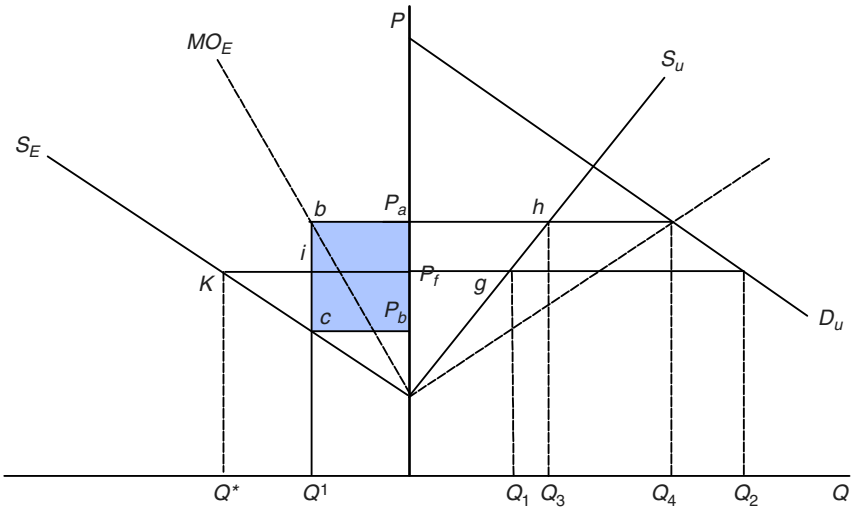


Figure 5 The equivalence between tariffs and quotas. D_u, domestic demand curve for the importing country; MO_E, marginal outlay with respect to the exporter's excess supply curve; S_E, excess supply curve of the exporting country; and S_u, domestic supply curve for the importing country.

can have the same effect on trade flows as can a tariff, but the income distributional effect is very different. Consider Figure 5, where import demand is D_u, import supply is S_u, and export supply is S_E. The free trade price is P_f and imports total (Q_1Q_2). Under an optimal tariff, the import price becomes P_a. Production in the importing country increases from Q_1 to Q_3, and producers gain P_aP_fgh from the tariff. The tariff revenue collected by the government in the importing country totals (bcP_bP_a).

Suppose, instead of a tariff, the importing country imposes a quota in the amount (Q_4-Q_3). The effect on production and trade flows is the same, but note that the government no longer collects the tariff revenue. As a result, there is a net loss from the quota for the importer. However, the exporter can gain from the import quota. Even though the producer price falls to P_b, there is a revenue gain of (bcP_bP_a), which can be larger than the loss from a fall in the price of the export good. On net, the exporter gains, from the import quota, an amount $(biP_fP_a) - (kci)$.

A key element of US sugar policy has been import quotas on sugar from abroad. In certain periods of history, these have resulted in US internal prices for sugar being well above export prices. However, there are preferred sugar exporters who are able to sell sugar to the United States at price P_a, but there are others who sell at prices below the US internal prices to countries not included in demand D_u.

Empirical Work

There are empirical estimates of the impact of agricultural trade barriers. Quite often, however, the estimates are a result of combined policy instruments that include tariffs. Often agricultural policy instruments, such as price supports, are used in conjunction with barriers to trade, such as tariffs (Schmitz and Schmitz, 2012). Moreover, because of retaliatory action by an importer in response to a tariff policy by an exporter, a situation can arise where trade ceases. In addition, under retaliatory action, tariffs can give way to production subsidies. As a result, even if one correctly measures the impact of production subsidies in a trade context, the policy instrument that gives rise to the subsidies can be a tariff.

Overall Agricultural Distortions

Anderson (2009), Anderson and Martin (2009), Anderson and Masters (2009), Anderson and Swinnen (2009), and Anderson and Valdes (2009) give an in-depth analysis of the many agricultural trade and policy distortions that exist worldwide. This work, which includes 75 countries that together account for more than 90% of the world's farmers, concludes that without the agricultural price and trade policy reforms of 2004, global welfare would be lower by US$233 billion annually. Owing to the 2004 reforms, low-income economies have benefited more than high-income economies; the world has moved closer toward global free trade in goods (annual global welfare cost of policies at US$168 billion in 1980, compared with an estimated gain of US$233 billion in 2004); and all high-income economies have lowered price supports for their farmers, with some countries replacing price supports with assistance partially decoupled from production. Their work is consistent with the authors' earlier finding (Schmitz *et al.*, 1997) that the gains from trade can be negative even though the volume of trade can be large. Quite often, the welfare impact from removing government domestic policy distortions far outweighs the classic gains from trade.

Case Studies

Tomatoes

For many years, the United States attempted to restrict tomato imports from Mexico through the use of import tariffs, but on many occasions failed. Bredahl *et al.* (1987) demonstrated that the imposition of tariffs is a competitive strategy, as producers on both sides of the border cannot gain from tariffs. They demonstrated two alternative strategies where gains are possible: (1) voluntary export restraints or (2) an import–export

cartel on tomatoes. Interestingly, the United States gave up on the strategy to impose tariffs, and instead agreed with Mexico on a suspension agreement. The first suspension agreement was put in place in 1996 and was replaced with a new agreement in 2013. Little analysis has been done on the impact of this agreement, both in terms of its effect on US and Mexican producers and consumers.

The cotton controversy

In an ongoing trade dispute that was a major reason for the breakdown of the Doha Round of WTO trade negotiations in Cancun in September 2003, Brazil challenged the United States on the use of cotton subsidies that allegedly interfere with cotton exports from Brazil. Schmitz *et al.* (2007) estimate that US cotton policy lowered world cotton prices by 10–15%. Brazil won part of its case against US cotton subsidies in 2003. As of 2013, the United States continues to make payments to Brazil of approximately US$100 million per year. This is likely to continue as in June 2013 the price of cotton dropped below the US$71.25 cents per pound target price. The same issue revolves around sugar. Brazil sued Europe over EU sugar policy (Powell and Schmitz, 2005) and forced Europe to lower its sugar subsidies. This takes on added interest in view of the 2013 trade talks between the EU and the US over further trade liberalization.

Ethanol tariffs

The United States launched several controversial programs to promote the conversion of corn into ethanol. In the 1980s, a 54-cents-per-gallon tariff was imposed on imports. In 2004, US blenders of transportation fuel received a tax credit of 46 cents per gallon. The trade barrier and subsidy were the source of an ongoing ethanol dispute between the US (a country that produces ethanol from corn) and Brazil (a country that produces ethanol from sugarcane). On 31 December 2011 both the tariff and the tax credit were removed and these changes complemented the tariff elimination enacted by Brazil in 2010. The US program changed from the government providing subsidies to ethanol processors to a blend ethanol/gasoline ratio requirement (de Gorter and Just, 2009; Just and de Gorter, 2009). It remains to be seen whether or not the US can satisfy its ethanol mandate in the absence of the subsidies but there is evidence that recently, Brazil and the US have begun collaborating in an effort to promote the global use of not just ethanol, but also biofuels in general.

US shrimp imports from China

According to Adams *et al.* (2005), p. 225,

> The warm-water shrimp-harvesting industry in the Gulf of Mexico and South Atlantic (GSA) region represents the most economically important component of all the domestic commercial seafood-harvesting sectors in the United States.

Since 1975, shrimp harvesters in the GSA region have sought regulatory relief from imports on several occasions. Examples include:

1. In 1975, the USITC responded to the International Shrimp Congress, which led to adjustment assistance permitted under Title II of the Trade Act of 1974.
2. US Senator Breaux authored a bill to formulate a policy to provide for domestic shrimp industry protection. A temporary 5-year import quota combined with a 30% *ad valorem* tariff was proposed. The bill failed.
3. In 1985, the USITC responded to public hearings on imposing trade restrictions on shrimp imports, but did not take any concrete action (USITC, 1994).

US imports of garlic from China

China is one of the world's leading producers of garlic, a product used for cooking and medicinal purposes. In 1994, the Fresh Garlic Producers Association of the United States alleged that fresh garlic from China was being imported to the US market at LTFV. The USITC ruled in favor of the United States in the garlic AD case (Yamazaki and Paggi, 2005). Three 5-year reviews have been initiated by the USITC since 1999 to examine whether the AD duties should be revoked. They continue to conclude that its removal would likely lead to the continuation or recurrence of the material injury to the US domestic garlic industry and, in April 2012, the United States announced that it would maintain the existing AD duty on fresh garlic from China. The duty margin is set at 376.67%.

United States sugar disputes with Mexico and the European Union

For years, the United States restricted imports of sugar from Mexico by imposing an import quota. However, with the passage of NAFTA in 1994, the US converted the import quota into a TRQ and agreed to phase out the over quota tariff over a 15-year period. During the period that the US restricted sugar imports from Mexico there were several retaliatory policies implemented by Mexico. For example, in 2002, the Mexican government imposed a 20% 'soda tax' on all beverages sold in Mexico that were not sweetened with its own cane sugar. This effectively eliminated the use of US high fructose corn syrup in Mexican soda production. The WTO ruled in favor of the US and Mexico eliminated the tax in 2007. Mexico also imposed other retaliatory duties to support freer trade during this time.

In 2008, free trade in sweeteners between the US and Mexico began. As a result, US sugar imports from Mexico increased from 0.054 million metric tons (mmt) in 2005–06 to 0.63 mmt in 2006–07 to 1.27 mmt in 2008–09. In general, US sugar imports from Mexico increased significantly after 2007 but also became much more volatile, reaching a low of 732 000 mt in 2009–10 and a high of 1.55 million mt in 2010–11.

The EU, historically, has provided the highest support for sugar producers. High price supports were accompanied by sugar export subsidies. In an interesting case in 2004, Brazil launched a WTO investigation against the EU sugar regime. The WTO supported Brazil's case, with several actions being taken by the EU to deal with Brazil's concerns (Powell and Schmitz, 2005).

The beef dispute between the United States and Canada

In 1999, the Rancher-Cattlemen Action Legal Foundation (R-CALF) filed an AD petition with the USITC alleging that Canada was dumping live cattle onto the US market. The USITC ruled in Canada's favor that live cattle from Canada were not being dumped on the US market. In addition, R-CALF filed a CV complaint against the Canadian cattle industry, contending that

Canadian cattle were being fed cheap barley subsidized by the Canadian Wheat Board. Again, the USITC ruled in Canada's favor. The defense argued that neither case had an economic or empirical base (Wohlgenant and Schmitz, 2005). As a result, USITC ruled in favor of the Canadian cattle industry. However, the USDOC sided with R-CALF and imposed temporary duties on Canada (Schmitz *et al.*, 2005).

Conclusions

Trade distortions that include tariffs have declined significantly since the early classic written by Johnson (1973) titled 'Agriculture in Disarray.' As emphasized, there are many trade barrier instruments, including tariffs, and the empirical evidence presented above includes the effect of removing several trade instruments at the same time. Even so, the increased liberalization, because of removing trade barriers, is significantly impacted by the tariff component of trade distorting policy instruments.

The effects of a country's retaliatory use of CV and AD duties have been discussed. However, over time, lowering or removing tariffs that exist may have little to do with retaliatory actions by importers under either AD or CVD legislation.

See also: Agribusiness Organization and Management. Agricultural Cooperatives. Agricultural Law. Agricultural Policy: A Global View. Asian Aquaculture. Beef Cattle. Biotechnology: Regulatory Issues. Changing Structure and Organization of US Agriculture. Food Chain: Farm to Market. Food Security: Development Strategies. Food Security, Market Processes, and the Role of Government Policy. From Foraging to Agriculture. Global Food Supply Chains. Government Agricultural Policy, United States. International and Regional Institutions and Instruments for Agricultural Policy, Research, and Development. Markets and Prices. Policy Frameworks for International Agricultural and Rural Development. Production Economics. Regulatory Conventions and Institutions that Govern Global Agricultural Trade. Simulation Modeling: Applications in Cropping Systems. Sugar Crops. Tree Fruits and Nuts

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Invasive Aquatic Animals

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Glossary

Ballast water Water carried in tanks on ships in order to maintain ship stability during voyages.
Ballast water exchange Replacing coastal water with ocean water during a voyage.
Ecosystem The network of interactions of living organisms as well as the physical and chemical components of their environment within an area than can be defined.
Habitat suitability rating When habitats are compared with a rating model where unsuitable is zero (0.0) and optimum is (1.0) using parameters including water temperature, salinity, gradient, cover, substrate, etc.
Species displacement When a species is replaced by another within a habitat due to space occupation, behavior activity, or other competition.
Subtropical Habitats that are tropical in nature but located above or below the latitudes of tropical environments.
Temperate Characteristic of climate between the tropical and polar latitudes.
Tropical Characteristic of climate between the Tropic of Cancer and the Tropic of Capricorn.
Vector As in dispersal vector, an agent that transports an organism from one place to another.

Introduction

Movement of aquatic animals from their native range into other locations constitutes an invasion, often with damaging consequences in the new location. Humans are responsible for movement of many aquatic animals into new locations. Unintended and negative consequences of their release have occurred in many cases due to species displacement, ecosystem destruction, and sometimes from diseases carried by the invasive aquatic animal. In some instances the potential for using exotic animals as human food or as biological control for other invasive organisms returns economic benefit from the introduction.

The degree of concern about aquatic animal invasions depends on the impact of that species on human activities or ecosystem diversity in the specific area of invasion. The potential for spreading into other locations increases the importance of that species globally. An aquatic species that has spread widely over several centuries can still be invasive even though it may be almost ubiquitous. Recent invaders may be no less important, because of their ability to expand their range quickly and displace less competitive species.

Historic Introductions of Aquatic Species

Aquatic species introductions, leading to invasive spread, may have begun with the common carp, *Cyprinus carpio*. Common carp are presumed to be two subspecies which were documented to live in Europe and Asia more than 10 000 years ago, then domesticated independently (Balon, 1995). Recent genetic evidence confirms the existence of the two subspecies of common carp (Zhou *et al.*, 2003). Domestication involves animal movement and therefore the first spread of invasive common carp may be attributed to the Romans for moving them from the Danube across Europe (Balon, 1995). Now, common carp are one of the most important invasive aquatic animals in the world. More than 3.5 million tonnes of common carp are produced by aquaculture each year (Statistics and Information Service of the Fisheries and Aquaculture Department, 2012) for use as human food. Yet damage to world ecosystems from common carp invasion exemplifies the problems of exotic species introduction, the efforts to reduce the negative effects of invasions, and the length of time that invasive aquatic species remain as nuisances.

Considerations over intentional introduction of exotic aquatic animals are studied in order to weigh the consequences of introduction versus benefits. Notably, tilapia, Chinese carp, and ornamental fish are important commercial fish with invasive reputations in aquatic ecosystems. Over the course of human history, more than 50 000 nonnative species, including many aquatic animals, have been introduced into North America. Some of these species, such as wheat, rice, cattle, and poultry were introduced as sources of food and now provide more than 98% of the US food system valued at approximately US$800 billion year^{-1} (Pimentel *et al.*, 2005).

Methods for Slowing or Reversing the Effects of Aquatic Invasions

Once an invasion starts, control of further invasion and reversal becomes difficult if not impossible to attain. Water is a difficult medium to operate a species location and for removal operation. Therefore, few aquatic invasive introductions have been reversed, unless in small confined water bodies where toxic substance or draining are used to eliminate the species (Clearwater *et al.*, 2008). More complex methods include release of sterile males; release of species-specific disease or predators; or removal by netting, angling, or electrofishing.

Responses to Aquatic Invasive Animals Have Included the Following Ideas

(1) Coordination of local, state, regional, federal and international activities, and programs pertaining to invasions; (2) control and manage the introduction and spread of invasive

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species through education and outreach; (3) prevent the establishment of invasive species populations through early detection and rapid response programs; (4) control or eradication of established invasive species through cooperative management activities designed to minimize impacts to nontarget species; (5) monitor the distribution and impacts of invasive species to determine management priorities; (6) develop needed research on impacts and control of invasive species; and (7) prevent the introduction and spread of invasive species by national and international regulatory efforts.

Policies regulating invasive aquatic animals are complicated by international trade pressures. Decisions made to improve food availability or to improve economic status may cause damages that last for 500 years. Risk assessment models are needed in order to determine regulatory policy (Keller *et al.*, 2007).

Examples of Aquatic Invasive Animals of Global Importance

Salt Water

Asterias amurensis *(northern Pacific sea star)*

Originally from coastal waters from Russia to Japan, the sea star has moved into new locations, further south, where it preys on a wide variety of commercial and ecologically important species. This sea star is native to cool waters but has adapted to waters up to 20 °C and a wide range of salinity. Severe damage to bivalve fisheries is predicted due to invasion of the northern Pacific sea star (Ross *et al.*, 2002). A large part of the northern Pacific sea star diet is the blue mussel, *Mytilus edulis*, but in the absence of this preferred food, many other benthic animals are eaten (Barkhouse *et al.*, 2007). Eradication of the northern Pacific sea star in open water would be difficult and probably impossible; therefore, a system of prevention and exclusion has been adopted in order to prevent further introductions (Dommissee and Hough, 2004). Targets for regulation include ballast water, water intakes on ships, marine-based aquaculture gear and stock, fishing gear, recreational gear and vessels, mooring lines, and vessel hulls. Ballast water exchange, where 95% of the original water is replaced with deep ocean water, has been accepted as a possible means of northern Pacific sea star exclusion. Monitoring programs are in place with hope to identify the invader in new locations so that eradication efforts might be used.

Impact from invasive northern Pacific sea star amounts to billions of dollars of impact to commercial fisheries and potential extinction of marine species found in the invaded areas. Tasmania has already experienced fisheries reductions. Japan, near the native range of the northern Pacific sea star, must deal with this pest to their mollusk culture industry. Spread to the coast of North America by debris from tsunamis and typhoons is also anticipated. As monitoring programs are established by more countries (Bax *et al.*, 2006), there is hope that future expansion of the range of the northern Pacific sea star may be limited, possibly using genetic sex-ratio distortion.

Carcinus maenas *(green crab)*

Moved from Europe and north Africa primarily by ships since the 1800s, the green crab eats important mollusk species including Manila clam (*Venerupis philippinarum*) and displaces native crustaceans (Dungeness crab, *Cancer magister*). Note that the Manila clam is an introduced species in North America but has become an important addition to commercial shellfish harvesting. The dispersal of the green crab is mainly by ships, but other human activities are to blame, including intentional stocking (Klassen and Locke, 2007). Once introduced, the green crab can be moved by ocean currents into areas with suitable salinity (above 22 ppt) and temperature (10–22.5 °C) (Hitchcock *et al.*, 2004).

Dramatic reduction in soft clam (*Mya* sp.) and other mollusk harvests have followed invasion of the green crab. Mollusks are vulnerable to green crab at <15 mm sizes (Sanchez-Salazar *et al.*, 1987) and the reduction of spat limits mollusk populations. Green crab foraging changes the estuary bottom in such a way that erosion or saltwater grass damage may occur (Lafferty and Kurvis, 1996; Davis *et al.*, 1998). Minor uses for harvested green crabs are small compared to the value of lost shellfish harvest as approximately 40% of shellfish may be lost to green crab predation in a single year (Grosholz *et al.*, 2001). Trapping remains a possible suppression method for green crab, but evaluation of economic benefits of controls is lacking. Historic losses between US$719 million and US$805 million to the shellfish harvesters on the East Coast of the United States occurred over a 30-year period (Abt Associates, Inc, 2008).

Eriocheir sinensis *(Chinese mitten crab)*

Native to Asia, the Chinese mitten crab has been introduced to Europe and North America. A voracious eater, it eliminates invertebrate populations during mass migration. It contributes to shoreline erosion by burrowing. Managing crab populations by capture during environmental changes (salinity or temperature) may cause a population decline; however, ballast water remains a vector for reintroduction and spreading (Garcia-de-Lomas *et al.*, 2010). Chinese mitten crabs have spread to the West and East Coasts of North America where damage from the crabs is only recently reported (Dittel and Epifanio, 2009). Tolerant of freshwater, the Chinese mitten crab is a danger to freshwater stream and river ecology and has been observed in the Great Lakes of North America (Nepszy and Leach, 1973). Rice growing areas near the coastal streams are vulnerable to damage from Chinese mitten crab invasion as migration of 1000 km from salt water is possible.

Established populations of Chinese mitten crab, after causing damage, have been observed to decline due to a nearly complete reduction of adult crabs. Evidence of mated females does not necessarily indicate established populations (Benson and Fuller, 2014). Well established populations exist in Europe and Asia. Migrations downstream occur in the fall in Northern Hemisphere locations and young crabs travel back upstream the following year. Worth more than US$1.25 billion year^{-1} as food in China, few countries allow legal possession of Chinese mitten crab (Veilleux and de Lafontaine, 2007). Therefore, legal status changes must occur in order to use trapping as a control method.

Mnemiopsis leidyi *(American comb jelly or sea walnut)*

Introduced to eastern European seas from estuaries of North and South America by ballast water discharge, the American

comb jelly or sea walnut competes with commercially and ecologically important young aquatic animals for food. Destruction of the Baltic Sea ecosystem is an example of the danger of American comb jelly introduction. Decline, by half, in zooplanktivorous fish populations can open the ecosystem to invasion by the American comb jelly (Purcell *et al.*, 2001). Widely distributed, the American comb jelly is deemed improbable to eradicate but many studies of biological controls have been undertaken with the eventual determination that nontarget damage will occur. One genus, *Beroe*, feeds on gelatinous zooplankton and may serve as a control (Galil, 2008). In the Black Sea, *Beroe ovata* increased as American comb jelly population declined – a possible cause and effect that could lead to biological control measures (Shiganova and Malej, 2009). *Beroe* sp. and *M. leidyi* are sometimes moved simultaneously in ballast water.

Potamocorbula amurensis *(Amur River clam)*

Recently introduced to cool waters off California in North America, large populations of Amur River clam develop without predator pressure. The Amur River clam has established as 95% of the biomass in some locations and is the dominant benthic species in San Francisco Bay. This efficient filter-feeding mollusk has caused significant reduction in plankton in the infested estuary (Greene *et al.*, 2011). Birds can almost eliminate the clam in shallow water, but deepwater populations reestablish the shallow water population in later seasons. Crabs and fish will eat the clam when their mouths are large enough, notably Dungeness crabs and white sturgeon. The Amur River clam may be suppressed by cool water temperatures in its native range, but can thrive in warmer water and over a wide salinity range. However, early life stages suffer from very low salinity. Pelagic life stages are moved in water currents, but spread has occurred due to the influence of shipping (Thompson and Parchaso, 2012). Densities as high as 10 000 per m^2 can exist and harvesting of high density populations provides animal and aquaculture food in some countries (Carlton *et al.*, 1990).

Fresh Water

Clarias batrachus *(Asian walking catfish)*

Established in southeast Asia to Australia and accepted as an aquaculture species, the Asian walking catfish was introduced to the United States in the 1900s. Rapid spread occurred in Florida south of the frost line from 1968 to present. A carnivorous catfish, it displaces native fish and preys on native aquatic animals (Barber and Babbitt, 2003). The Asian walking catfish has been spread primarily as an aquaculture species, in the aquarium trade, or stocked intentionally in natural waters. It has been declared established and invasive in Florida, USA, but is established elsewhere and not considered invasive (Courtenay *et al.*, 1974; Welcomme, 1988). The Asian walking catfish rapidly spread to 24% of freshwater in Florida where it began to displace native sunfish and catfish species.

The Asian walking catfish is a tropical species with euyhaline ability surviving to 10 °C and 18 ppt salinity. Prevention of introduction is the best control. Carnivorous and aggressive feeding behavior places the Asian walking catfish without competition in most ecosystems. Relatively easy reproductive needs allow spawning in cavities in static waters near 25 °C. The characteristics that make the Asian walking catfish a suitable aquaculture species also enhance its invasive qualities. Where commercial fishing has waned, the Asian walking catfish has little pressure to control population expansion as long as fish, amphibian, or invertebrate food sources are available. Regulation of Asian walking catfish intends to limit distribution and along with education efforts may help restrict the catfish to existing locations (Brogan, 2003).

Ctenopharyngodon idella *(Grass carp)*

Spread by government agencies and private individuals for aquatic plant control by biological means, the green carp (**Figure 1**) has escaped and become established in river systems that have a high habitat suitability rating (depth, current, temperature, and length). A native of the Amur River area of Russia and China, the grass carp has been released or escaped into most temperate and tropical areas of the world. Grass carp impact on the environment is largely an alteration of the environment that leads to decline of vascular aquatic plants and an increasing in phytoplankton with corresponding effects on native fish species (Bain, 1993). Grass carp are recommended as a biological control for succulent aquatic plants and triploid populations have been produced in order to limit reproduction after escapement (US Army Corps of Engineers, 2012). High value for grass carp has allowed successful development of functionally sterile fish for stocking as aquatic plant control agents. Population expansion has continued as some governing entities allow stocking of diploid grass carp. Therefore, electric gates and exclusion devices have been installed on rivers in efforts to restrict fish migration away from existing locations.

Cyprinus carpio *(common carp)*

Popular in Europe and across Asia, the common carp has spread as an aquaculture species but escapes into natural waters of temperate and tropical climates. Rapid reproduction and survival in a broad range of habitats allows the continued spread of common carp. A few isolated watersheds remain free of this species. Eventually most temperate and high mountain tropical ecosystems will be invaded by common carp



Figure 1 Grass carp. Courtesy of USDA APHIS PPQ Archive, USDA APHIS PPQ, Bugwood.org.

(Zambrano *et al.*, 2006). Common carp are part of the carp-polyculture system, so have been cultured for more than 6000 years. Ornamental koi are common carp strains with popularity for aquarium and water garden enthusiasts. Widespread in the eighteenth century before concerns for invasive introductions, common carp have been established in populated areas of most continents. Commercial fisheries are developed in Europe, North America, and Asia for common carp. Carp pituitary glands are a secondary product collected and used to induce spawning of cultured fish. Still, prolific spawning has insured that common carp populations will continue to spread throughout suitable habitats. Saunders *et al.* (2010) discussed Koi herpesvirus as a possible control for *Cyprinus carpio*. However, nontarget impact may affect valuable cultured koi, ghost, and common carp stocks. Also, common carp that were not killed would recover to be lifetime carriers of the virus. Predatory fish including pike and bass suggested as controls for confined populations of common carp. Predatory fish are a nonselective control that may have a place in common carp management, so management objectives that insure healthy native predator fish populations may limit exotic invasive fish impact. However, dense populations of common carp may not be controlled or may reach sizes that exceed predator gape width so that control is not possible (Drenner *et al.*, 1997). Largemouth bass are considered invasive species when outside their native range.

Dreissena polymorpha *(zebra mussel)*

Introduced by ballast water discharge into fresh waters around the world, the zebra mussel (**Figure 2**) causes displacement of native mollusk species, competition for food, and biofouling damage (Benson *et al.*, 2012). Canal systems in Europe allowed zebra mussels to spread to almost all drainages during the eighteenth and nineteenth centuries. Able to populate at 700 000 per m^2 zebra mussel fouling affects power generation, maritime industries, and water supplies. Potential exists for zebra mussels to spread to all freshwater navigation waters in temperate regions of the world. Phytoplankton filtered and consumed by zebra mussels competes with zooplankton and other aquatic animal larvae (Frischer *et al.*, 2005). Water clarity increases over zebra mussel reefs (Ackerman *et al.*, 2001; Holland, 1993). Lakes change from phytoplankton-dominated to macrophyte-dominated communities after zebra mussel invasions.



Figure 2 Zebra mussel. Courtesy of Amy Benson, US Geological Survey, Bugwood.org.

Monitoring and control of zebra mussel cost an average of US$30 million per year in the Great Lakes area of the United States during the mid-1990s. One thousand four hundred and ninety water-using companies used monitoring, chemical treatment, retrofitting, or mechanical removal and in some cases did not use surface water due to zebra mussel presence (Park and Hushak, 1999). Prevention is proposed as the best method to contain zebra mussels in current locations. However, monitoring and enforcement regulations are needed and must be applied diligently. Eradication works in closed systems but is always costly. Open system treatments would cost tens of millions of dollars, even if the technology were available (Western Regional Panel on Aquatic Nuisance Species, 2010).

Lithobates catesbeianus *(American bullfrog)*

Intentional introductions and escape from aquaculture have moved the bullfrog from North America to many countries across the world. As carriers of the chytrid fungus, they could contribute to the decline of native amphibians. Bullfrogs, outside their native range, compete with and eat endangered amphibians and fish. Direct removal and habitat elimination may be useful methods to reverse bullfrog invasions (Adams and Pearl, 2007). Trapping and electro shock efforts may be effective for controlling invasions in localized habitats (Orchard, 2011). These methods require a substantial investment of labor in order to achieve control of bullfrogs.

The chytrid fungus, *Batrachochytrium dendrobatidis*, is present in at least two strains. The bullfrog is susceptible to one but may carry the other. However, over time infection load decreases in bullfrog skin so that the bullfrog may not be an efficient carrier of this fungal disease of amphibians (Gervasi *et al.*, 2013). It has been proposed that the global trade in amphibians has led to development of a hypo virual strain of the chytrid fungus. This hybrid of strain is made possible by sexual reproduction of the chytrid fungus (Schloegel *et al.*, 2012) and may be one of the reasons the fungus is devastating in one location but not in another. Also, decline in fungus presence on bullfrog skin may explain some of the variation in chytrid fungus expression during bullfrog invasions.

Micropterus salmoides *(largemouth black bass)*

Introduced in many parts of the world as a sport fish, largemouth bass are predatory fish adaptable to temperate and tropical lakes and streams. The largemouth bass eats and sometimes eliminates native fish and crustaceans (Gratwicke and Marshall, 2001). Largemouth black bass, stocked in ponds or lakes as sport fish, will travel upstream and downstream into habitats of native carnivorous fish. Competition for food

sources including forage fish and crustaceans can have damaging effects on native bass, trout, and pike. As a result more homogeneous fish communities alter plankton and habitat to the exclusion of diverse native aquatic ecosystems (Jackson, 2002). Sport fish, including lake trout, brook trout, and walleye are affected when *Micropterus* are established. Although government agencies have been responsible for introductions in the past, unauthorized introduction of largemouth black bass are more likely to cause damage to sensitive ecosystems. Therefore, educational and regulatory policies should be developed and enforced as a means to limit expansion of largemouth black bass range.

Oncorhynchus mykiss *(rainbow trout)*

Rainbow trout was introduced from western North America across the rest of North America and much of the cool water habitats in the world. A popular sport fish that can displace native trout and consumes ecologically important fish and invertebrates. An example is the displacement of cutthroat trout (Seiler and Keeley, 2007). Escapement from aquaculture facilities may carry disease to native fish, lower vigor by hybridization with resident trout populations, or compete for limited forage in oligothrophic water bodies (Patterson and Blanchfield, 2013). Rainbow trout disperse rapidly after escape and may travel 350 km in a short period of time.

Increased aquaculture of rainbow trout in Europe and mariculture in Chile and Norway intensify the danger of escape and impact on native fish. Study of rainbow trout infected with sea louse observed movement between farms near the source of escapement and a reduction of sea louse abundance over several months (Skilbrei, 2012). Rainbow trout remained in the farm area but did not rely on eating wasted feed from the farm, rather subsisted on local forage and contributing to the impact of the farm on local fauna. Recapture of escaped rainbow trout has been suggested as a means to reduce invasive impact (Skilbrei and Wennevik, 2006). Gillnets are one means of recapture that appears to catch more escaped fish than wild fish.

Oreochromis mossambicus *(Mozambique tilapia)*

Mozambique tilapia and its hybrids are popular aquaculture fish noted for tolerance to harsh environments in warm and tropical waters. Tilapias spawn prolifically and are voracious omnivores. The Mozambique tilapia was stocked in aquaculture ponds and natural waters during the last half of the twentieth century, escaping into tropical and subtropical fresh and estuarine ecosystems (Courtenay and Robins, 1989). In the Philippines, Mozambique tilapia are established in brackish water farms, rivers, and swamps. An endemic fish, the snarapan, has been reported extinct at least partly due to invasive Mosambique tilapia (Canonico *et al.*, 2005). Research observations, while significant, are generally incomplete for comparing conditions before and after Mosambique tilapia introductions. Policy needed to manage established populations and to protect native fisheries require more research in order to settle ambiguous observations and to show the cost versus benefit of introductions. The argument that tilapia feed in their own niche with little damage to other fish seems to ignore the effect of introduced tilapia on native tilapia and cichlids that share food sources. Introduction of Mozambique tilapia after careful consideration of competitors, food availability, and temperature barriers may be accomplished with proper government oversight; however, uncontrolled introductions are most dangerous to ecosystems.

Oreochromis niloticus *(Nile tilapia)*

The Nile tilapia (**Figure 3**) has been intentionally spread across the world as an aquaculture food fish. Sometimes confused with the Blue tilapia (*Oreochromis aurea*), the Nile tilapia has escaped aquaculture facilities to warm water river systems and lakes. Nile tilapia eat small benthic organisms and detritus, so may not compete directly with native fish that eat other food items such as larger invertebrates and fish (Peterson *et al.*, 2006). Competition for space forces native forage fish into closer contact with predators (Martin *et al.*, 2010). Nile tilapia may invade most tropical waters and establish reproducing populations (Zambrano *et al.*, 2006). Estuarine waters are potential habitats and pathways for travel to other watersheds during Nile tilapia escape (Lowe *et al.*, 2012). Diluted salinity during wet years increases migration potential between coastal habitats. Nile tilapia have established feral populations in most, if not all, countries where it has been introduced (Vicente and Fonseca-Alves, 2013). Temperature limits must be well outside the tolerance range of Nile tilapia in order to limit establishment.

Impact of Nile tilapia on native ecosystems is controversial due to the ability of Nile tilapia to feed at a different trophic level than many native fish. Fish biomass may increase after Nile tilapia establishment without significant effect on diversity of native fish assemblies, even after 7 years (Arthur *et al.*, 2010). Long-term effects are difficult to predict and objective impact observations are limited. In Nicaragua, 80% of native cichlids were lost after Nile tilapia introduction and in Madagascar, decline in native fish diversity was correlated to tilapia introduction. Examination of the stomach contents of nonnative Nile tilapia in Mississippi, USA revealed food organisms outside its traditional detritivorous niche (Canonico *et al.*, 2005). Attempts to eradicate introduced Nile tilapia have failed except in isolated ponds and pools.



Figure 3 Nile tilapia. Courtesy of US Geological Survey Archive, US Geological Survey, Bugwood.org.

Pomacea canaliculata *(channeled apple snail)*

Native to South America, the apple snail was transferred by the food and aquarium traders to North America and Asia. Damage to crops (rice and taro) and sensitive wetland vegetation has been extensive. Apple snails can carry diseases transmissible to humans such as the rat lungworm (*Angiostrongylus cantonensis*). Introduced to Taiwan in the 1980s, apple snails have spread through southeast Asia and southern China and now into Australia. The channeled apple snail was introduced as a human food into the Hawaiian islands in 1989 (Cowie, 1998). North America has also experienced uncontrolled apple snail establishment largely because suitable predators are not present in numbers adequate to control this snail (Howells, 2003).

Rhinella marina *(cane toad)*

Native to Central and South America, the cane toad (**Figure 4**) was utilized as a biological control for agricultural insect pests in the early 1900s. When introduced, it spreads over wide ranges, as in Australia where it moved more than 2000 km over 75 years. Cane toads are poisonous and predator populations decline in cane toad-infested areas while prey populations increase (Shine, 2010). Some Australian predators recovered 10 years or more after cane toad invasion by learning to avoid the toads. So, no evidence of species extinction has been reported from cane toad infestation in Australia. Barriers to expansion of cane toad infestations include restricting access to water by fencing or draining (Tingley *et al.*, 2013). Using the cane toad poison to lure tadpoles to traps may improve removal efforts (Crossland *et al.*, 2012). Lungworms (Nematoda) may be useful parasites for cane toad control due to differential susceptibility between cane toad and native amphibians (Phillips *et al.*, 2010). Other promising controls include the use of hormones to lure cane toad tadpoles to eggs so that cannibalization will reduce that invading population (Crossland *et al.*, 2011).

Salmo trutta *(brown trout)*

Transported from Europe in the late 1800s, the brown trout is used for aquaculture and fisheries stocking. The brown trout may displace native and endangered fish by competition and predation. Genetic dilution of native salmonids occurs when brown trout cross with salmon (Krueger and May, 1991). Brook trout and golden trout are vulnerable to brown trout competition (Pister, 1991). Prey species, similar to the Modoc sucker, have gone into decline due to brown trout predation.

Containment efforts are regulatory and educational in nature. An integrated approach to improve the status of competitive species, like brook trout, has begun in New York, NY, USA. Habitat improvements and water quality improvements, favoring brook trout, are expected to limit brown trout (Neumann and Wildman, 2002). Piscicides have been applied to kill brown trout in areas of golden trout habitat, then fish barriers were installed to isolate golden trout and exclude brown trout (Pister, 1991). In Australia, regulations governing introductions and fish movement are intended to keep brown trout from spreading beyond existing locations. Repeated electrofishing can selectively reduce brown trout, provided labor and equipment resources can be made available (Caudron and Champigneulle, 2011).



Figure 4 Cane toad. Courtesy of US Geological Survey Archive, US Geological Survey, Bugwood.org.

See also: Asian Aquaculture. Domestication of Animals. Land Use: Management for Biodiversity and Conservation. Regulatory Conventions and Institutions that Govern Global Agricultural Trade

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https://nas.er.usgs.gov/
The Geological Survey of the United States.
http://giasipartnership.myspecies.info/
The Global Invasive Alien Species Information Partnership.

Invasive Species: Plants

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Glossary

Biotic resistance hypothesis The hypothesis that competition and other biotic interactions with native plant species explain the tendency for less disturbed plant communities to suffer relatively low rates of invasion.

EICA hypothesis The hypothesis that the lack of native pathogens, predators, and herbivores experienced by nonindigenous plant species in new habitats allows re-allocation of resources away from defense and toward development and growth, in turn resulting in increased invasiveness.

Exposure studies Studies that are conducted to determine the level of risk posed by an organism to the environment, often involving tiered assessment of the likelihood of each step of a given hazard scenario occurring.

Invasion barriers Biotic, abiotic, and geographical factors that prevent nonindigenous plant species from moving between invasion stages.

Naturalization The process during which a plant species establishes viable populations in a new location.

Nontarget environments Environments that may be placed at risk by the unwanted effects of a novel organism that lies outside the area originally targeted for its release.

Phenotypic plasticity The ability of an organism to alter its phenotype in response to changing environmental conditions.

Polyploid An organism containing more than two sets of homologous chromosomes.

Preadaptation In the context of invasive species, referring to the ability of nonindigenous species to survive in newly colonized habitats by expressing preexisting adaptive traits.

Propagule pressure A measure of the number of individuals of a nonindigenous species released into a given region, incorporating both the number of release events and the number of individuals per event.

Introduction

As human societies have developed they have increasingly broken down the spatial barriers that historically separated species, communities, and ecosystems. The result has been an ever-increasing rate of long-distance dispersal of both animal and plant species to new habitats and the concomitant taxonomic homogenization of previously distinct floral and faunal assemblages. Today, this process continues virtually unabated, and invasive species are considered to pose one of the primary contemporary threats to biodiversity conservation and agricultural productivity in both native and agricultural systems on a global scale. Indeed, it is no exaggeration to state that synergistic interactions between invasive plants and other agents of global change, including anthropogenic global warming (AGW), rising atmospheric carbon dioxide concentrations, nitrogen deposition, habitat fragmentation, and disturbance, are likely to leave few if any natural or agroecosystems unchanged over the next century.

The economic costs of plant invasions alone are staggering. It has been estimated that in 2005 the direct annual economic impact of weedy plants on US agricultural production exceeded US$ 25 billion, with losses mainly caused by reduced crop and pasture yields and the cost of weed control (Pimentel *et al.*, 2005). Similarly, a thorough assessment of the economic impact of weeds in Australia in 2004 revealed annual losses associated with agriculture of AU$ 4 billion, and costs of invasive species management in natural systems of at least AU$ 19 million. A further AU$ 80–90 million was spent on weed management and research by public authorities and the Australian government (Sinden *et al.*, 2004). The direct impacts of nonindigenous species on natural and seminatural ecosystems are also severe: In addition to direct negative impacts on biodiversity such as species extinction, many of the most aggressive nonindigenous species alter the structure, composition, and function of recipient plant communities, processes that are driving change in ecosystems on a global scale.

For these and other reasons, plant invasions have long been of interest to ecologists. In the five decades since Charles Elton published his classic 1958 book 'The Ecology of Invasions by Animals and Plants' (Elton, 1958), ecologists and agronomists have sought to develop a unified understanding of how, why, and under what circumstances plant invasions occur, and the strategies that may be most successfully adopted for their control. Although much of this research has proved extremely fruitful, leading to successful systems for both identifying potentially invasive species and managing their impacts once established, some areas remain difficult or controversial or are compromised by a lack of data. Indeed, at the most basic level our understanding of the biological mechanisms that allow some species to dominate plant assemblages following introduction to new habitat remains limited, and integrating new data and theory from across ecology, evolutionary biology, and ecophysiology will be a critical ongoing challenge for invasion biologists in coming years (Richardson and Pyšek, 2008).

This article is intended to provide a basic overview of current knowledge in invasion biology and to highlight active areas of research. The authors first describe the basic invasion

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pathway, and consider the barriers that nonindigenous species must overcome before becoming invasive in a new geographic range. They illustrate key principles associated with the invasion pathway using data from Australia, which provide an excellent case study of invasion of a geographically isolated land mass by introduced plants. Then they consider evolution and other genetic processes associated with the establishment and spread of invasive species and turn our attention to the mechanisms of their impact on natural ecosystems and their roles as ecosystem engineers. They then discuss two current questions of great importance in contemporary invasion biology. The first is whether climate change is likely to confer an overall fitness advantage on nonindigenous species relative to cooccurring native plant species, and why. The second is whether genetically modified crops or their adoption is likely to cause increased weed pressure on target and nontarget natural and agricultural ecosystems – a matter of great controversy over the past decade. They conclude by briefly discussing opportunities for future research.

Unfortunately, invasion biology has long been plagued by the use of vague or contradictory terminology to describe processes or stages of the invasion pathway and the plants involved (Richardson *et al.*, 2000). The authors begin, therefore, by defining some important terms that will be used throughout the article. The term nonindigenous plant species (NIPS) refers to species occurring outside of their native range, and is used interchangeably with terms such as 'alien' and 'exotic' species. Invasion refers to the process in which introduced plants reproduce outside of the original immediate area of introduction and does not include reference to any damage cause by the plant. Weeds are invasive species, especially in agricultural systems, that cause harm or are otherwise undesirable.

The Biology of Plant Invasions

The Invasion Pathway and the Australian Experience

The end result of the successful introduction of NIPS to new regions can be a situation where introduced species become geographically widespread, overabundant, and cause an enormous amount of ecological and economic damage. To get to this situation, however, plant species require the ability to traverse several invasion stages (Theoharides and Dukes, 2007) and to surpass several important 'invasion barriers' (see **Figure 1**; Satai *et al.*, 2001).

The first stage of the invasion pathway, 'Transport,' is associated with NIPS overcoming a significant natural barrier of geography, one that NIPS could not disperse across naturally. Somehow, NIPS must cross vast distances over land and/or sea. The most striking characteristic of modern-day plant invasions is that this transport stage is facilitated by a diverse range of human activities. For instance, many plant species are deliberately brought into new regions for ornamental purposes (Groves *et al.*, 2005). A good example of global translocation of NIPS is the Singapore Daisy (*Sphagneticola trilobata*), which was originally brought into Australia as a garden ornamental and deliberately planted as a roadside and railway embankment stabilizer in the north-east of the

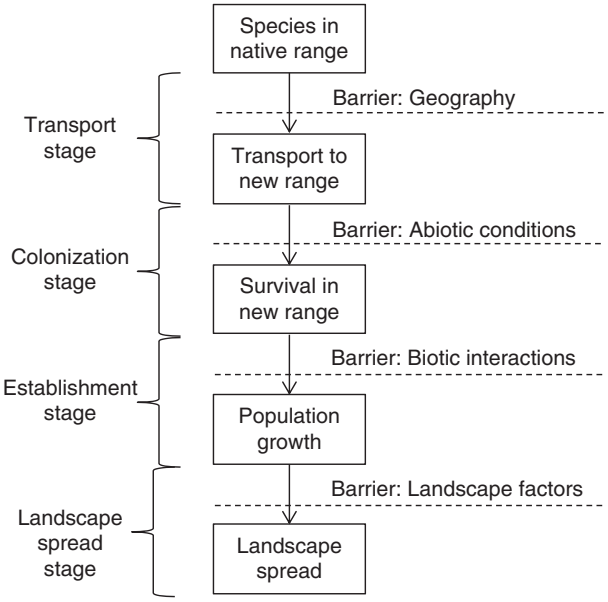


Figure 1 Typical invasion pathway showing the four main invasion stages (transport, colonization, establishment, landscape spread) and barriers faced by plants associated with each stage. Adapted from Hellmann, J.J., Byres, J.E., Bierwagen, B.G., Dukes, J.S., 2008. Five potential consequences of climate change for invasive species. Conservation Biology 22, 534–543.

continent. Some NIPS have been introduced to new regions to be used for a variety of purposes. For example, Mesquite species (*Prosopis* spp.) were introduced to Australia as fodder for livestock and as ornamental species in station homestead or town gardens, and were also used in mine dumps and other soil stabilization programs. Importantly, a large number of NIPS can be introduced to new regions outside their natural geographic ranges accidentally, and thus can be considered unintentional introductions. For instance, Whiskey Grass (*Andropogon virginicus*) was introduced accidentally to Australia when it was used as protective packaging for American bottles of whiskey.

It would appear that irrespective of the reason for introduction, there is the potential for any NIPS to become a serious agricultural weed, whether introduced purposefully or accidentally. Indeed, all three plant examples provided above are now considered serious weeds of Australian agriculture.

The second stage of the invasion pathway, 'Colonization,' or 'Introduction,' can be successfully traversed by NIPS in one of two ways. First, some species need to overcome a barrier in the form of cultivation. For example, many NIPS exist in cultivation beyond the limits of their native ranges, but they do not form self-sustaining populations outside of cultivation. The key concern here is the fact that some species can escape cultivation to become established in the wild. Using Australian examples to illustrate this idea, two extreme examples of escapees from cultivation, which are considered to have 'jumped the garden fence,' are Paterson's curse (*Echium plantagineum*), which costs agriculture AU$30 million per year, and Lippia (*Phyla canescens*), which costs the grazing industry an estimated AU$38 million per year. The second way NIPS can traverse the colonization stage is by avoiding the cultivation

barrier; this happens when a species has been introduced accidentally by humans directly into the new environment.

More than 27 000 NIPS are known to have been introduced to Australia; however, only approximately 10% of these species have surpassed the third stage of the invasion pathway, the 'Establishment' stage. For plants, this is also commonly referred to as the 'Naturalization' stage. An invasion ecology generality that appears to be fairly consistent globally is the Tens rule (Williaimson and Fitter, 1996), whereby only approximately 10% of the introduced flora of a region will ever become naturalized (although it is worth noting that this is an average figure and recent studies have documented much higher percentages in some regions of the world). Furthermore, approximately 10% of naturalized NIPS will transition to become invasive weeds (see below, the 'Landscape spread' stage). Interestingly, NIPS introduced as garden ornamentals are the dominant source of new naturalized plants and weeds in Australia. Of the roughly 2700 NIPS now known to be established in the Australian environment, approximately 1800 species are escaped garden plant species. The rate of increase in the number of naturalized plant species in Australia has tended to be linear until recent times. Recent work has reported an increase in the number of species naturalizing in Australia, leading to the conclusion that the rate of naturalization is increasing.

What does it take for NIPS to become naturalized? A species is generally considered naturalized when there is evidence for the existence of a self-sustaining population over a period of time corresponding to multiple generations. It is rare to find published work that compares the attributes of species that have become naturalized with other species introduced to the same region that have not become naturalized. Recent comparative work, however, for North American plant species that have become naturalized in Europe has shown that introduction history, in particular increased planting frequency, is an important determinant of current naturalization success among these exotic invaders in Europe (Bucharova and van Kleunen, 2009). Life-history traits of species can also be important, but this depends on plant growth form. For example, the naturalization success of trees was found to increase positively with maximum plant height and seed spread rate. This was not the case for other life forms.

The fourth and final stage of the invasion pathway is 'Landscape spread.' Arguably, this is the most important part of the invasion pathway. If NIPS fail to get past the barriers of dispersal and subsequent survival during population spread in the introduced range, then they do not have the potential to become serious weeds of the environment and/or agriculture. Few species pass through this invasion stage successfully. Indeed, current estimates of the number of invasive NIPS in Australia put the number at approximately 130 species. This figure is currently being reviewed, and it is likely to nearly double in the future to nearly 250 species. Interestingly, this puts the number of invasive NIPS in Australia at 10% of the total number of naturalized species, a percentage that follows the aforementioned Tens rule.

A fundamental question of invasion ecology is just how long it takes NIPS to shift from the state of naturalization to become invasive. The length of time between these two states is referred to as the lag time or lag phase (although it can sometimes refer to the period of time between introduction and invasion). Lag times are notoriously difficult to determine, as it is not often known when a species has become naturalized. Nevertheless, some studies have described lag times and it is clear that these can vary considerably. The majority of species do go through a lag phase, which appears to be approximately 50 years as a minimum for NIPS in Australia. Recent work examining 23 NIPS introduced to Hawai'i that eventually became invasive pests has revealed that the average lag time between introduction and first evidence of spread is 14 years for woody plants and 5 years for herbaceous plants. Such short lag times provide equally worrying short times for managers attempting to manage the spread of new invaders.

Perhaps one of the most important questions for invasion ecology and for the quest for an understanding of just what it is that makes species invasive is what traits invasive NIPS possess that allow them to become successful invaders (Drenovsky *et al.*, 2012). One approach that has been adopted over the years has been to compare the traits of invasive NIPS with resident native species. Unfortunately, this approach has yet to reveal any globally consistent biological differences. A more relevant approach has been the exploration of traits that differ between naturalized noninvasive NIPS and invasive NIPS. The idea here is that by using a 'target-area' approach, one can compare NIPS that cooccur within their introduced range for fundamental differences in their attributes. Given its long-term geographic isolation, but relatively recent settlement by nonindigenous peoples, Australia provides a unique opportunity to study the invasion process and the factors that contribute to invasion success in NIPS (Murray and Phillips, 2010; Phillips and Murray, 2012). A substantial body of evidence is emerging to show that invasive NIPS differ from noninvasive NIPS in both their introduction history and life history. Introduction history refers to traits of species related to where they have been introduced from, why they were introduced, and how long they have been resident in the novel range. Indeed, residence time has emerged as a highly important trait for successful invasion. NIPS that have been present in the new range for longer periods of time are more likely to have become invasive. Life-history traits of species refer to those characteristics of species related to growth, survival, and reproduction. Interestingly, recent work for Australia has shown that species with small seeds (correlated with increased reproductive output) are more likely to become invasive than larger-seeded species. Furthermore, the seeds of invasive NIPS are more likely to have had more resources invested by the parent plant into their dispersal adaptations (e.g., wings for wind dispersal, fleshy fruit for dispersal by vertebrate foragers).

Evolution in Invasive Species

One of the most interesting paradoxes of invasion biology is that many invasive species, despite originating from numerically small founder populations, adapt extremely well to new environments and undergo rapid population growth and range expansion. Because bottlenecked populations typically have low genetic diversity and hence should have reduced evolutionary potential, it is argued that this phenomenon could be simply explained by high levels of 'preadaptation'

among the most successful exotic species with traits that lead to high fitness in new environments (e.g., high dispersal rates and competitive ability). Such species may remain highly invasive despite suffering some diminishment of genetic diversity in response to inbreeding.

Although this may be broadly true, the fact remains that many of the best examples of rapid evolution come from invasive NIPS, and the critical role that evolutionary adaptation can play in the invasion process is now becoming widely recognized among biologists (Whitney and Gabler, 2008). Indeed, mounting evidence suggests that a range of genetic processes, even among small founder populations, can facilitate plant invasion of new habitats (Lee, 2002). Most of these involve increases in additive genetic variance, which must be present for evolution to occur in response to selection pressure. Two of the most important mechanisms include hybridization of invasive species with close relatives in the new range (interspecific) and admixture of previously separated genotypes in the introduced range (intraspecific). One of the most widely cited examples of interspecific hybridization leading to increased hybrid invasiveness is that of *Spartina anglica* in the British Isles (Raybould *et al.*, 2008), an allopolyploid derived from *Spartina maritima* and *Spartina alterniflora*. *Spartina anglica* is now a noxious weed, whereas the parental species have relatively limited distributions. 'Polyploid' hybrids usually have greater fitness than diploid hybrids, and allopolyploidy has been linked to invasiveness in a number of taxa.

Intraspecific genetic admixture is most likely in species with a history of multiple introductions, and can result in genetically diverse populations of invasive NIPS that have an increased evolutionary capacity (Frankham, 2005). Several other genetic processes can also apparently increase the fitness of invasive species. Additive genetic variance can be increased by conversion of epistatic or dominance variance by genetic drift following population bottlenecks; epistasis itself (interaction between different gene) provides a source of variance that could respond to selection pressure. In some species a small number of genes instead of total additive variance may play a critical role in determining plant fitness under new selection regimes. Of course, not all introduced species benefit significantly from these genetic processes; for instance, some invasive NIPS are known to have limited genetic diversity and evolutionary capacity as a result of small founder population size. All are also influenced to a greater or lesser extent by a range of factors such as genetic drift, small population size, trade-offs among fitness-related traits, and swamping of adapted genotypes by migration (i.e., migration-selection balance) that limit population adaptation and expansion in range-edge or marginal habitats.

Evolutionary theory suggests that adaptation should occur following selection for fitness-related traits that have a heritable source of genetic variation. Sources of selection in new habitats are myriad, including climatic factors, competition with resident species, or new grazing or predation regimes. There is compelling evidence (Colautti *et al.*, 2010) that many invasive species have undergone population differentiation or evolution in response to broad-scale climatic gradients within a matter of decades (e.g., *Echium plantagineum*, *Hypericum perforatum*, *Solidago altissima*, *Senecio inaequidens*, and *Lythrum salicaria*; Konarzewski *et al.*, 2012; Monty and Mahy, 2009), although the establishment of such clines is not ubiquitous. Mimicry is a fascinating evolutionary adaptation exhibited by some crop weeds in response to the strong directional selection typical of agricultural cultivation (Barrett, 1983). Under these predictable and repetitive selection regimes mimicry can develop in seed, which increasingly resembles that of the associated crop species in terms of weight, size, and overall appearance, or vegetative growth traits, which also can converge. Studies have shown that *Echinochloa crus-galli* var. *oryzicola*, for instance, is closer to rice in phenology, growth, and morphology than to its close relative *Echinochloa crus-galli* var. *crus-galli*. Rapid evolutionary responses to agricultural herbicide application also occur frequently, with crop weeds developing herbicide resistance. The implications of this process associated with the cultivation of genetically modified crops are discussed in another section of this article.

Over the past decade there has been much focus on the potential for plants to experience release from specialist natural enemies (herbivores and diseases) when moved outside of their native range, resulting in increased fitness (the enemy release hypothesis; Keane and Crawley, 2002). Theory suggests that plants experiencing reduced rates of herbivory will reallocate resources away from resistance or tolerance strategies to increased growth, provided that the production of defense chemicals or tolerance mechanisms comes at a fitness cost. Evidence for evolution of increased competitive ability involving this mechanism (known as the 'EICA hypothesis'; Blossey and Nötzold, 1995), along with other evolutionary processes, has been postulated as explaining the tendency for some NIPS to exhibit a lag phase before becoming invasive. Evidence for the EICA hypothesis was first observed in *Lythrum salicaria* but since then has only found partial experimental support; recently it has been suggested that resource allocation under enemy release may affect many fitness-enhancing traits, not just those relating to growth and competition.

Traditionally, much of the focus of research of invasion biology has been on developing an understanding of the demographic and life-history predictors of invasiveness, on their impacts on native and agricultural ecosystems, and on means for more efficient weed control in different settings. However, given the strong emerging links between genetic background, evolutionary capacity, and invasion dynamics, it is clear that treating invasive species as uniform entities with fixed genotypes will fail to adequately capture their likely behavior when faced with changing environmental conditions and selection regimes. One area where this clearly applies, for example, is in the modeling of weed spread under future climate change scenarios. Successful integration of evolutionary and ecological concepts into a more detailed and predictive understanding of the process of plant invasions will remain one of the most interesting but challenging aspects of invasion research for years to come.

Impacts of Invasive Species on Natural and Agricultural Systems

Invasive NIPS can have an impact on individual species to entire landscape scales through a wide range of genetic,

demographic, and evolutionary mechanisms (Levine *et al.*, 2003). These impacts can be direct, such as competition for light, water, and nutrients with native community associates, or indirect, involving complex changes to ecosystem processes. As with other components of the invasion process (Ehrenfeld, 2010), however, invasive NIPS differ significantly in their capacity to directly and indirectly drive change in recipient ecosystems. Determining when and how impacts arise, which species are likely to significantly transform ecosystems, and which communities are most susceptible to change has direct application to more effective management of extant invasive species and efficient restoration of degraded ecosystems once they have been removed.

Arguably the most obvious and socioeconomically damaging direct impacts of invasive NIPS occur in agricultural systems where competition for light, water, and nutrients by weedy species reduces crop yields to a point where intensive and costly control is required. These systems, which are characterized by both impoverished faunal and floral assemblages and abundant supply of resources, are especially prone to invasion, and many crop weeds are ruderal, r-selected (fast growing) species that are generally intolerant of competition and abiotic stress. It is estimated that globally weeds reduce crop yields by approximately 9%, although figures vary across crops and depend strongly on the crop protection measures used to reduce potential losses: less developed regions suffer considerably higher losses. Along with other crop pests, weeds are expected to pose a significant challenge to global food security in coming decades, and thus a range of strategies including the development of genetically modified herbicide- and pest-resistant crops (see Section Transgenic Plants as Invasive Species) are being adopted to enable more efficient weed control.

A great many ecological studies have quantified changes in the composition and diversity of terrestrial plant assemblages following invasion by NIPS, usually by comparing invaded with uninvaded communities. In many cases, competition is cited as the reason for loss of native species. This a plausible explanation because virtually all plants compete for a limited set of common resources (e.g., light, water, nutrients), but relatively few studies have investigated the implied competitive relationships among native and exotic species using formal removal or addition experiments, and the link between specific resources and competitive exclusion is often unclear. However, water and light competition associated with invasive species is a frequent driver of vegetation decline or change. *Carpobrotus edulis*, for example, is an invasive succulent plant that, by competing for water, affects the morphology and growth of cooccurring native shrubs in coastal California, while competition with annual exotic species for light during spring has been proposed as a key mechanism that has led to the decline of the native bunchgrass *Nassella pulchra* in Californian grasslands. Interestingly, the competitive advantage experienced by invasive species is highly dependent on resource availability; many invasive species are fast-growing species with high biomass production when resource supply is adequate but perform less well than native species in low-resource environments. Biomass production, in fact, is perhaps the most widespread process by which invasive species both directly and indirectly impact on native associates.

Invasive NIPS that are taller or denser than native associates or have novel traits can alter ecosystem attributes such as light regimes, soil moisture patterns, litter composition, and sediment deposition to such an extent that they become ecosystem engineers (also called transformers or keystone species). NIPS capable of fixing atmospheric nitrogen (nitrogen fixation) are one widely studied group that transform ecosystems by increasing soil nitrogen availability, which can significantly alter plant community structure and composition, especially in environments where soil nitrogen is low and there are few or no native nitrogen fixers. An excellent example is *Myrica faya*, an invader of volcanic soils in Hawai'i (Vitousek and Walker, 1989). The rate of nitrogen fixation of *M. faya* is two orders of magnitude higher than that of associated native species, leading to overall increases in nitrogen availability at the ecosystem level. Such processes can also facilitate invasion by other nonnitrogen-fixing species, such as the stimulation of *Bromus diandris* growth in soil obtained from patches of the invasive nitrogen-fixing shrub *Lupinus arboreus*. Other NIPS alter soil chemistry through salt concentration or produce allelopathic chemicals that negatively impact on native species.

Morphological and physiological differences between NIPS and associated native species can also alter the spatial and temporal distribution of water through the soil profile, in turn affecting ecosystem composition and structure. Grasses such as *Pennisetum setaceum*, an invader of tropical dry forests in Hawaii, can reduce water availability in the upper rhizosphere, in turn reducing the health of coexisting native tree species (Cordell and Sandquist, 2008). In contrast, deep-rooted woody or taprooted species can alter soil water balances by drawing water from deeper in the soil profile, changing subsoil drainage patterns and patterns of primary production. Differences in phenology can also be critical; for example, the displacement of the summer-active C4 species *Themeda australis* by the invasive spring-active C3 species *Nassella neesiana* is believed to have altered the timing of peak soil water availability in temperate grasslands and pastures of south-eastern Australia. Similarly, exotic species including the winter-active grass *Bromus tectorum* shift soil water extraction in semiarid shrub-steppe ecosystems in western North America to earlier in the growing season, reducing later availability for native species. Similar interference patterns occur in crops and pastures invaded by agricultural weeds.

At broader scales, NIPS can significantly alter ecosystem processes by changing nutrient pools, the flow of energy though plant communities, or the structure and behavior of entire food webs and trophic levels. One frequently observed effect of increased biomass production by invasive species is an increase in the size of above- and below-ground carbon pools, and associated fluxes. Carbon inputs are generated by plant net primary productivity, which is often, although not always, greater in invasive species, and litter produced by invasive species typically decomposes faster due to lower C:N ratios and lower lignin:N ratios in plant tissue. As noted previously, soil N pools and fluxes can be radically altered by invasive species, especially N-fixers, although significant changes have also been observed in response to invasion by grasses. Soil and plant respiration are the major pathways of

carbon loss in terrestrial systems, and these can also be altered by plant invasion, as can N loss via nitrification and denitrification. However, the magnitude and direction of these changes often vary significantly across different habitats and different invasive species, and more work is needed to determine whether any broad patterns can be discerned across invaded systems and species more generally.

One dramatic way in which invasive species can significantly alter both the structure and processes of entire ecosystems is by inducing change in fire regimes. Because plant species have multiple strategies for maximizing fitness in fire-prone habitats (e.g., resprouters vs. obligate seeders), changes in the timing, intensity, frequency, and extent of fires in response to elevated fuel loads have the potential to drastically change vegetation composition and structure. These changes to vegetation can in turn alter fire behavior in self-perpetuating positive feedback loops. An excellent example of such a process is the 'grass-fire cycle' in which high biomass production by invasive grasses results in hotter fires, which increases mortality in overstorey vegetation. This in turn allows further invasion, leading to the eventual replacement of savanna, woodland, or forest plant communities by grassland – a process that is occurring in northern Australia where savanna vegetation is being invaded by the highly productive Gamba grass (*Andropogon gayanus*). Interestingly, the high-severity fires generated by Gamba grass and associated loss of tree species significantly reduce above-ground carbon storage and may increase greenhouse emissions (Setterfield *et al.*, 2010), demonstrating the impact that invasive species can have on ecosystem processes that are critically important at the global scale.

The authors have discussed some of the direct and indirect mechanisms by which invasive plants can alter the composition and diversity of plant communities and the processes that structure entire ecosystems. NIPS, however, can also have profound genetic effects on native or agricultural species. One important mechanism involves the mixing of gene pools of formerly distinct taxa; in this context the authors are mainly concerned with hybridization and introgression between previously isolated native species and NIPS, known as genetic assimilation or genetic swamping (Antilla *et al.*, 1998). This process can potentially lead to extinction, especially if the native species is rare, and is of increasing concern to conservation biologists due to the high levels of sexual compatibility observed among plant species in general. Perhaps the best documented example is of sunflowers in North America, where introgression between weedy *Helianthus annuus* and rarer endemic species (e.g., *Helianthus bolanderi)* threatens the endemic species with local or even range-wide extinction. In the case of *H. annuus* and *H. bolanderi*, more recent introgression has led to the development of populations that are morphologically more similar to *H. annuus* (Carney *et al.*, 2000). This process can occur even if the invasive species is rarer relative to the native species, as is the case in *Spartina alterniflora* in California, which, due to high male fitness, threatens to assimilate the more widespread native *Spartina foliosa*. In this example, competition between *S. alterniflora* and *S. foliosa* pollen tubes is thought to favor *S. alterniflora* on the stigmas of both species, which is an interesting form of reproductive interference. Introgression can range from primarily unidirectional, as with gene flow from introduced Siberian elm (*Ulmus pumila*) to red elm (*Ulmus rubra*) in the eastern US, to bidirectional. Interestingly, recent studies indicate that biparental introgression can lead to the replacement of parental lineages by hybrid genotypes (e.g., California radish; *Raphanus* sp.), provided hybrids and hybrid descendents do not suffer from outbreeding depression. It should also be mentioned that hybridization can pose a threat to small plant populations even in the absence of introgression.

Genetic effects of NIPS on recipient plant communities and ecosystems are not restricted to those associated with gene flow and hybridization. For example, evolution can occur in other trophic groups, especially insects, in response to the establishment of novel plant populations, and the mixing of biota may lead to the generation of new kinds of mutualistic interactions that stimulate further coevolution (Mooney and Cleland, 2001). The dramatic decline in populations of native species in response to incursion by invasive species is likely to increase the probability of genetic drift, inbreeding, and other genetic consequences associated with population bottlenecks. Finally, given that many invasive plants differ in phenology and morphology from associated native species, shifts in the timing, severity, and resource specificity of competitive relations among native and exotic plants are likely to significantly alter the intensity and direction of selection, and hence evolution, in both groups.

Ecosystem Invasibility

The concept of 'invasibility,' which refers to the vulnerability of an ecosystem to invasion, arose in response to the basic observation that plant communities and biomes differ significantly in their tendency to be invaded by NIPS (Lonsdale, 1999). Explaining why this is so has been one of the most heavily researched areas in invasion biology. One commonly observed pattern is that invasions tend to be promoted by disturbance, fragmentation, high resource availability, and slow recovery of native vegetation, such that late-successional plant communities tend to be invaded by few NIPS compared with those that have been highly modified. As noted previously, a large proportion of invasive species worldwide can be classified as r-strategists, characterized by rapid growth and biomass accumulation and high reproductive potential, and these species tend to be favored by disturbance and high nutrient availability. It is therefore not surprising that disturbed or modified systems tend to be heavily invaded, and that so many agricultural systems suffer invasion by weedy species – both cropping and pasture-based agricultural systems create homogenous, highly modified environments characterized by high resource availability, low competition, and recurring disturbance. Indeed, disturbance-driven intermittent resource enrichment or release leading to differences between resource supply and resource uptake has been proposed as a general process that increases the susceptibility of plant communities to invasion by alien species.

The 'biotic resistance hypothesis' has long been advanced to explain why less disturbed systems tend to be less invaded

by exotic species. Competition with native species is well known to represent a major barrier to invasion, especially when resources are limited, because nonindigenous competitive advantage appears to be strongly linked to overall resource availability. Functional similarity between native and nonindigenous species can increase competitive interference, and based on associated niche-packing models it has therefore been argued that more diverse or species-rich native assemblages should be less invasible than impoverished ones. Indeed, depauperate communities may even contain vacant niches that allow preadapted species to readily establish invasive populations – *Ammophila arenaria* in Californian coastal dunes ecosystems is a frequently cited example. This has proved, however, to have been a contentious idea in invasion ecology, because the empirical data inconsistently show a negative relationship between native and exotic species diversity. Indeed, a frequently observed pattern is that native and exotic plant diversity tends to be negatively correlated at small spatial scales, due to competitive exclusion, but positively correlated at large scales, where differences in the diversity and availability of resources affect both native and exotic species in similar ways. The diversity of species and functional groups occurring within different trophic levels may also impact on community invasibility in some ecosystems.

Abiotic resistance is also seen as an important driver of invasibility. At the biome scale, for instance, deserts, savannas, and other harsh environments tend to be less invaded by exotic plants than more mesic habitats, the latter being more generally favorable for seedbank germination and seedling survival. However, these patterns also to some extent reflect the specific nature of the pool of nonindigenous species that are potential sources of invasive species – for example, some extreme environments face little 'propagule pressure' from species that are adapted to those conditions. This can arise from the history and composition of introductions in a given region, which reflect patterns of agricultural development, seed movement, ornamental plantings, and many other social and economic factors. An excellent example of this occurs in temperate south-eastern Australia, where numerous introductions have occurred through agricultural practices including the long-distance transport of seed and hay from other temperate areas. Given their provenance, these species are typically unable to survive in intact Australian alpine vegetation, which appears to be less invasible than lowland temperate ecosystems. However, pressure from species that are better adapted to such conditions is now also increasing, and it is likely that such systems will turn out to be more invasible than was initially suspected.

Collectively, these lines of evidence indicate that variation in the diversity and abundance of invasive plants in different habitats, which may at first glance be causally linked solely to invasibility, in fact reflects differences in species traits, characteristics of the recipient community, and propagule pressure. Untangling the interactions between these drivers will continue to be a focus of invasion biology research with capacity to improve our management of agricultural and natural landscapes in the face of an increasingly large pool of potentially invasive species.

Contemporary Issues in Invasion Ecology

Climate Change and Plant Invasions

There is now overwhelming evidence that anthropogenic emission of CO_2 is altering the climate of the earth. Over the past century global temperatures have risen by approximately 0.75 °C and it is estimated that 1.8–4.0 °C of warming (relative to 1980–99) is likely to occur by the end of the twenty-first century, depending on the emissions scenario. A major emerging concern is that future climate change linked to anthropogenic global warming (AGW) could increase the fitness of NIPS relative to native species, thus magnifying their impacts on natural and agricultural ecosystems.

There are very good reasons to suggest that many extant invasive NIPS will have an enhanced capacity relative to native species to respond to changes in abiotic and biotic stressors (Dukes and Mooney, 1999). To become successful invaders, all exotic species must pass through a series of environmental filters (**Figure 1**); those that fail to do so ultimately lack the ability to establish populations in new environments and undergo landscape-level spread. Barriers to success include geographical limits to colonization, abiotic limits to establishment and survival of founder populations, biotic limits to population expansion, and landcape-level limits to population spread. Only exotic plants that possess certain combinations of traits associated with dispersal, growth, competition, and adaptation can pass through these filters, and those that do tend to become widespread and abundant.

These filters select for successful invaders that contrast with native species in a number of key ways. First, most native species are rare or have restricted geographical ranges, whereas invasive species tend to have broad physiological tolerances to abiotic stress and occupy large ranges (Hellmann *et al.*, 2008). Rare species usually have slower population growth rates, lower competitive ability, and a reduced capacity to cope with abiotic and biotic change. Exotic species also often exhibit high levels of genetic diversity in their native range, which increases the chance of matching specific, locally adapted genotypes to climatic conditions of the invaded range (preadaptation). Opportunities for preadaptation are enhanced in exotic species with a history of multiple introductions, which has occurred in many of the worst ornamental and pasture weeds. A prime example is St. John's wort (*Hypericum perforatum*), which has been introduced into North American from Europe on multiple occasions, and which displays climate matching of source genotypes in the invasive range.

Populations of invasive species also frequently undergo rapid evolution, including for climate-related traits that increase fitness in new environments. Adaptive differentiation of populations along broad climatic gradients has been observed in many species, including purple loosestrife (*Lythrum salicaria*), invasive North American populations of which have developed strong latitudinally based clinal variation for phenological traits (flowering time and size at flowering time) that are similar to those that are found in native European populations. Other examples include ragweed (*Ambrosia artemisiifolia*), African ragwort (*Senecio inaequidens*), and sunflower (*Helianthus maximiliani*; Kawakami *et al.*, 2011). Adaptive evolution can also arise from the admixture of previously

separated and distinct genetic lineages and subsequent generation of novel genotypes, providing invasive species with added capacity to invade new habitats.

'Phenotypic plasticity' has also been suggested as a key driver of plant invasiveness, because having the ability to maintain positive population growth rates in a wide range of environments is likely to confer an advantage over more specialized native or crop species (Hulme, 2008). Enhanced niche breadth linked to phenotypic plasticity can be striking: Brazilian pepper (*Schinus terebinthifolius*), for example, a highly invasive species in the southern US, can grow as a tree, vine, or scrambling shrub, depending on growing conditions. Plasticity in reproductive allocation, dry matter partitioning, and growth have been observed in numerous crop and pasture weeds (e.g., *Echium plantagineum*; *Ammannia* spp.), and can alter competitive relationships among plants when grown under conditions of limited resource availability. By allowing plants to more efficiently exploit a wide range of environments and by compensating for the low genetic diversity that typifies many founder weed populations, phenotypic plasticity is also likely to place at an advantage plant populations subjected to increasing climatic variability or enhanced abiotic stress (Nicotra *et al.*, 2010).

Seeds produced by invasive NIPS often have specific morphological adaptations for wind, water, or animal dispersal that increase the rate and distance of propagule movement into new habitats (Murray and Phillips, 2010). For example, low seed mass often facilitates wind dispersal, while many ornamental species produce fruit that are spread long distances by birds and animals (zoochory). Some species have multiple modes of seed production: An excellent example is the invasive South American tussock grass *Nassella neesiana*, which produces seeds in panicles, stems, and at the base of the tussock. This gives *N. neesiana* the capacity to spread rapidly via multiple vectors (e.g., grazing animals, roadside mowing), and as a result it has become one of Australia's worst invaders of native grassland and grazed pastures. Rapid generation time, typical of many r-selected species, is another life-history adaptation that facilitates the growth and spatial expansion of plant populations. Shifting climatic envelopes are expected to benefit species that can rapidly extend populations into new climatically suitable ranges, and it is likely that many invasive species, especially those that are already efficient dispersers, will benefit.

One of the most often-cited differences between native and invasive NIPS is in competitive ability and overall growth and biomass production (Vilà and Weiner, 2004). Typically, invasive species have rapid growth rates, and numerous studies suggest that most are highly competitive in both natural and agricultural settings. However, in most circumstances the magnitude of any growth or competitive advantage enjoyed by invasive species depends on resource availability: in resource-poor environments native species often have superior or equal fitness (Daehler, 2003). In typical high-fertility cropping situations such conditions are unlikely to arise, but nutrient limitation often negatively impacts on the performance of exotic species in seminatural (e.g., unimproved pasture) and natural vegetation. In these environments, disturbance favors invasive species because it frees up resources that would otherwise be exploited by existing native vegetation. It is therefore clear that interactions between climate change and other drivers of global change (Marini *et al.*, 2012), including anthropogenic disturbance and habitat fragmentation, will determine the relative fitness of invasive species in the coming century.

Rising atmospheric carbon dioxide concentrations [CO_2] associated with the burning of fossil fuels is another driver of global change that will impact on all plant populations. Because trade-offs exist between acquisition of atmospheric CO_2 and water loss, altering [CO_2] changes physiological processes taking place in plant tissue, in turn altering plant growth and water use efficiency. Many invasive and native plants increase biomass production and fecundity under elevated [CO_2], a response known as the CO_2 fertilization effect (Godfree *et al.*, 2013). This process has been implicated in the success of a number of invasive species, including cheatgrass (*Bromus tectorum*) in semiarid rangelands of the US. However, although the high phenotypic plasticity of invasive species may increase their ability to shift their physiological optimum to take advantage of CO_2 fertilization, at present it appears questionable whether invasive species should in general disproportionately benefit more from rising [CO_2]. Indeed, a large proportion of the world's worst weeds are C_4 species, and many compete with C_3 crops, which in general tend to be more responsive to CO_2 fertilization.

Overall, developing a level of knowledge sufficient to answer the question of nonindigenous advantage under AGW with any certainty is likely to be a challenging task, especially given the somewhat chequered history of predicting the success of invasive species in general. Nonetheless, understanding the links between the traits and attributes of NIPS and key climatic drivers will underpin our ability to manage or avoid the detrimental impacts of NIPS on a global scale.

Transgenic Plants as Invasive Species

The impact of genetic modification (GM) or engineering on the biosafety of recipient organisms has been one of the most contentious issues in ecology of the past two decades (Hails, 2000). Genetic modification involves the transfer of genetic material (a transgene), usually coding for a beneficial trait, from one organism into a target organism (the genetically modified organism or GMO), which then expresses the trait. Since 1996 GM technology has been rapidly adopted across the globe, and in 2011 over 160 million hectares of GM crops were grown across 29 countries, a figure that is currently increasing at a rate of approximately 8% per year. A small number of widely grown species (cotton, corn, soybean, and canola) expressing herbicide tolerance (HT) and virus and insect resistance (VR and IR) still dominate global plantings of transgenic crops.

In the late 1970s to mid-1980s arguments were widely put forward that no GMOs should pose any risks to the environment. These were based on a range of premises, such as that genetic modification does not produce any genetic novelty that could not otherwise be generated by traditional selective breeding, or that all GMOs will suffer metabolic costs associated with transgene expression leading to reduced environmental fitness. This view, however, was challenged shortly

after when it became clear that genetic engineering had the potential to create truly novel combinations of potentially adaptive traits, especially where phylogenetic leapfrogging was involved. Pleiotropic or other unintended effects associated with the transformation process could also impact strongly on plant phenotype in unpredictable ways. Since then, the development and release of GMOs has been placed under strong regulatory oversight in most countries, and methods for quantifying risk associated with GMO deployment have been the focus of sustained scientific endeavor (Hilbeck *et al.*, 2011).

One of the most widely discussed potential risks associated with GMO release involves transgenic organisms or wild relatives becoming weedy either in crop or nontarget environments. This can occur via two main pathways (**Figure 2**): either the GMO itself can spread into nontarget areas outside of the cropping area and become invasive, or gene flow can occur into wild relatives growing in nontarget habitats, which then become invasive. For the majority of transgenic crops, the highest-risk situations occur when the transgene confers a clear fitness advantage under natural selection regimes and where hybridization with wild relatives is possible. Many transgenes are unlikely to increase the fitness of either crop plants or wild relatives in noncrop situations, for example, herbicide (glufosinate or glyphosate) tolerance in natural ecosystems. However, other traits such as pathogen or insect resistance could increase the fitness of plants containing the transgene significantly. Probably the most widely studied transgenic plants that fall into this category contain *cry* genes *Bacillus thuringiensis* (*Bt*) that express endotoxin proteins that provide resistance to insect pests.

Many crops such as maize and cotton that express *cry* genes are unlikely to become themselves invasive because they are highly domesticated and lack critical demographic traits that are essential for establishment of feral populations in nontarget environments, such as seed dormancy or the ability to compete with native vegetation for light, water, and nutrients. Of much greater concern in these crops is the potential for gene flow to wild relatives, a process involving pollen flow, the formation of viable wild-crop hybrids, and (usually), if the transgene present confers a selection advantage, gene introgression into wild populations (**Figure 2**). Given that virtually all the world's most important crops hybridize with wild relatives somewhere in the world (Ellstrand *et al.*, 1999), it seems virtually inevitable that gene flow from transgenic crops to wild relatives will occur, although this does not mean that a significant risk will be posed to the environment in all cases. Examples of GM crops in which the potential for hybridization with sexually compatible wild species or wild genotypes have been investigated include sorghum (with *Sorghum halapense*), maize (with teosinte), sunflowers, canola (with *Brassica rapa* and other species), sugar beet, and cotton (with other *Gossypium* species).

Transgenic pasture plants probably pose a greater invasive risk to the environment than most crop species because they have a wide range of traits that allow them to persist in mixed plant communities in which competition for limiting resources and abiotic stresses is more intense. Pasture species have a history of invasiveness, and many have shown the capacity to rapidly undergo range expansion and local adaptation following introduction. An increase in fitness arising from the presence of disease or pathogen- or stress-related transgenes in such species could therefore have serious consequences for nontarget plant communities. One of the best studied cases is that of virus-resistant white clover (*Trifolium repens*), which in south-eastern Australia, in addition to being an important pasture plant, is also an invader of endangered native grassland and woodland communities. Studies have shown that a range of viruses including *Clover yellow vein virus* limit the growth rate of wild *T. repens* populations, and thus the introgression of transgenes for virus resistance from sown pastures could increase the invasiveness of wild populations in these habitats (Godfree *et al.*, 2007). Another example is creeping bentgrass (*Agrostis stolonifera*), a highly competitive turf grass species. Flow of transgenes from HR genotypes to wild *A. stolonifera* populations and another related species, *Agrostis gigantea*, has been observed under field trial conditions, potentially making their control in other agronomic settings more difficult.

Ecological and evolutionary processes associated with the use of GM technology can also lead to weed problems within agricultural settings. GM plant lines can themselves volunteer in subsequent crops, especially if they produce a persistent seedbank. This is of particular concern in farming systems that rely on sequential rotations of crops that all express the same type of HT (e.g., glyphosate tolerance). Gene stacking can also lead to the development of plant lines resistant to multiple herbicides, as has been demonstrated in canola in Canada. Evidence suggests that the repeated use of a single herbicide group for control of weeds in GM crops can also lead to the development of herbicide-resistant crop weed biotypes, for example, Roundup resistance in *Conyza canadensis*. Both situations have significant implications for farm management and economics. Finally, the use of GM technology allows for greater control of weeds, but this may adversely affect other faunal associates that depend on plant biodiversity as a resource.

Over the past two decades, increased regulation of GMOs around the world has necessitated the development of new strategies for quantifying the potential direct and indirect risks posed to human health and the environment. Risk is defined by the equation risk=f(hazard, exposure) (Wilkinson *et al.*, 2003), where the hazard is the severity of the unwanted change and exposure is the probability of the hazard occurring. In the scenarios described above, hazard refers to the severity of the impact of increased invasiveness of GM crops or associated wild relatives on natural or agricultural systems. Hazards are normally identified using structured hazard identification studies in which potential scenarios leading to hazard realization are identified; several such scenarios are shown in **Figure 2**. In most cases, the efficacy of the genetic transformation and the potential impact of GM plants on target and nontarget organisms are initially evaluated by direct comparison of transgenic lines with genetically similar or identical isolines so that the impact of the introduced trait on plant phenotype and fitness can be directly quantified. Detailed 'exposure studies' are then conducted to determine the probability of each step in a given hazard scenario occurring following release of a transgenic plant into the environment. Risk assessments are often conducted in a carefully structured tiered procedure in which hazards are first indentified under

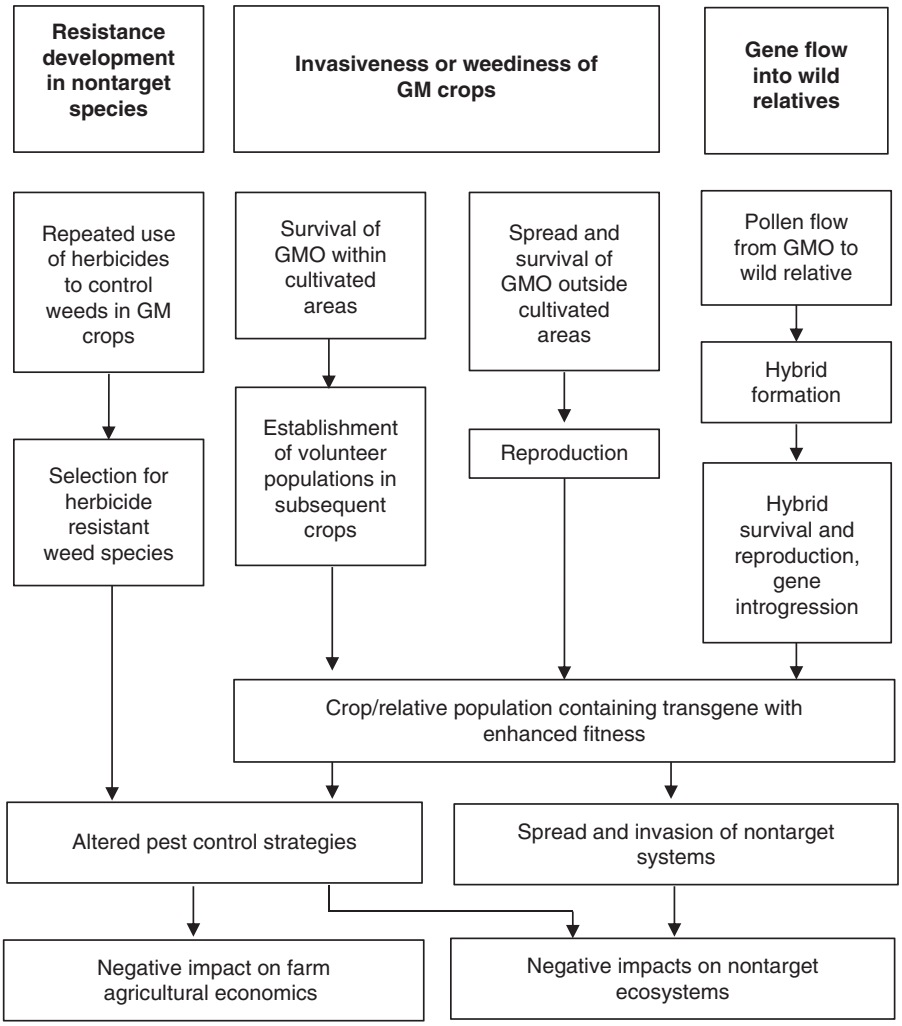


Figure 2 Framework for identifying some possible invasion hazards (bold) to nontarget and agricultural systems associated with the release of transgenic plants into the environment. Potential direct and indirect pathways leading to realization of hazard are shown; the risk assessment processes seek to quantify the probability of each stage in the hazard pathway occurring. Adapted from Sanvido, O., Romeis, J., Bigler, F., 2007. Ecological impacts of genetically modified crops: Ten years of field research and commercial cultivation. Advances in Biochemical Engineering-Biotechnology 107, 235–278.

'worst-case scenario' conditions using first-tier laboratory experiments and then more detailed second- and third-tier semifield and field experiments aimed at refining probabilities associated with specific steps within a given hazard scenario.

The combined experience from the past two decades suggests that the relatively small number of mainly herbicide-tolerant and insect- or pathogen-resistant GM crop species currently grown on a wide scale pose only a limited direct threat as invasive species. Although gene flow to weedy relatives will occur in some species, there are few examples to date of where this has led to realization of hazard in nontarget systems. However, a wide variety of 'new generation' GM crops engineered for oil and pharmaceutical production, drought tolerance, fungal resistance, altered phenology, bioremediation, and many other traits are also now in development or commercial adoption worldwide. Interactions between these plants and nontarget species and ecosystems are certain to be complex, and risk assessments that explicity test for increased invasiveness under field conditions will remain central to their successful, hazard-free release into the environment.

Using the Past to Inform the Future

Directions for Study and Management of Invasive Species in a Changing World

As this article has shown, invasion ecology is a dynamic, rapidly evolving field of research that continues to provide novel insights into the ways in which plants establish and maintain viable populations in new habitats and how they impact recipient agricultural and natural systems. Yet, many questions remain, and new approaches are being developed to better understand the role of plant invasions of agents of global change. For example, very recently, a small number of studies in invasion ecology have examined historical patterns

of introduction of invasive NIPS to particular regions of the world. Such comparative analyses of NIPS introductions can pinpoint periods in history when different regions of the world have received particularly high numbers of species. Such knowledge can provide an important historic baseline for determining the factors driving the successful spread of NIPS. An understanding of temporal introduction patterns can inform management aimed at limiting the ecological, economical, and social impacts of invasive NIPS on native biodiversity. Such a historical approach is somewhat analogous to using historical information on climate variation to predict future climate scenarios.

Australian work in this context has revealed distinct peaks since permanent European settlement of the continent began in the late 1700s. Peaks during early European settlement (1810–20) and human range expansion across the continent (1840–60) both coincided with considerable growth in Australia's human population. It is likely that human population growth during these times increased the likelihood of NIPS becoming invasive as a result of increased colonization and propagule pressure. Although this sort of research is in its infancy, there are many promising avenues to pursue, and valuable information to be gleaned from better understanding previous temporal patterns of NIPS introductions. Hopefully, such approaches will further increase our ability to predict and manage the impacts of NIPS globally in years to come.

See also: Climate Change and Plant Disease. Invasive Aquatic Animals. Plant Biotic Stress: Weeds. Regulatory Challenges to Commercializing the Products of Ag Biotech

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Investments in and the Economic Returns to Agricultural and Food R&D Worldwide

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Glossary

Benefit–cost ratio The ratio of the discounted present value of a stream of research benefits relative to the associated stream of research costs.

Internal rate of return The discount rate that equates the present value of the stream of research benefits and the present value of the stream of associated research costs.

Modified internal rate of return The compounding rate of interest that equates the future value of the stream of research benefits and the present value of the stream of associated research costs, given a particular value for the external rate of return on reinvested flows of benefits and a particular value for the rate of interest paid on borrowed funds.

Research and development expenditures Comprise expenditures on creative work undertaken on a systematic basis to increase the stock of knowledge and its use to devise new applications.

Research and development (R&D) spillovers The benefits conferred on a given geopolitical entity (e.g., a state or nation) from research conducted elsewhere.

Research intensity The ratio of national expenditures on public R&D relative to a measure of the corresponding value of output (often denominated as the value of agricultural gross domestic product).

Stock of knowledge An estimate of the accumulated stock of scientific knowledge currently in use, usually denominated in dollars of constant purchasing power.

Introduction

For most of farming's 10 000-year history, progress in agriculture was largely by trial and error, sometimes involving serendipity, other times involving astute observation, tinkering, and experimentation by farmers. This produced some gains in crop yields over the long haul but at a much slower pace than has been evident in recent decades (e.g., it appears that English wheat yields increased more than 15-fold during the past 800 years: beginning at approximately 0.5 tons ha^{-1} in the first half of the thirteenth century (Stanhill, 1976) to 3.5 tons ha^{-1} in 1961, and averaging 7.7 tons ha^{-1} in 2011 (FAO, 2013). Approximately 80% of the increase occurred in the past 200 years, with more than half of the increase occurring since 1961, although rates of gain in the UK wheat yields have slowed dramatically since the early 1990s). For much of this history, increases in crop production came mainly from increasing the land used in agriculture. This did not mean innovation was absent. Expanding the physical footprint of agriculture meant changing the agroecological attributes (soils, terrain, temperature, rainfall, and so on) that affected agricultural production, so simply to maintain average yields farmers had to scout, trial, and choose varieties of crops (or the crops per se) best adapted to these changed local circumstances (Olmstead and Rhode, 2002; Beddow and Pardey, 2014).

Scientifically bred crop varieties and livestock breeds, and their associated agricultural management practices, have a history of barely 100 years. In the middle of the nineteenth century and especially at the beginning of the twentieth century, a number of important changes occurred. Specifically, Darwin's theory of evolution, the pure-line theory of Johannson, the mutation theory of de Vries, and the 'discovery' of Mendel's laws of heredity all contributed to the rise of plant and animal breeding in the beginning of the twentieth century (In 1900, the Dutch botanist Hugo de Vries, the German botanist Correns, and the Austrian agronomist Tschermark independently and about the same time published studies on the laws of heredity that had been anticipated in the 1866 paper by the Austrian monk Gregor Mendel. When Mendel's paper was published in the *Proceedings of the Natural History Society of Brünn*, it had little impact and was cited very few times over the subsequent 35 years.). The mid-nineteenth century work of organic chemists like von Leibig led to substantial improvements in the understanding of the role soil fertility plays in plant growth (Von Liebig's book Organic Chemistry in Its Application to Agriculture and Physiology published in 1840 in both Germany and Great Britain triggered widespread interest in the application of science to agriculture. Within 8 years of its publication, von Liebig's book had gone through 17 different editions, translations, and revisions, mostly in Germany, England, France, and the United States but also in Denmark, Italy, the Netherlands, Poland, and Russia (Rossiter, 1975; Russell, 1966; Salmon and Hanson, 1964). Like others, Ruttan (1982) viewed von Liebig's book as the critical dividing line in the evolution of modern agricultural science.). Pasteur's germ theory of disease, together with other fundamental insights gained from bacteriology, virology, and related microbiological sciences, spurred the development of animal vaccines and more broadly promoted the development of methods to manage and mitigate production losses associated with crop and livestock diseases. Along with genetic innovations, this growing body of scientific

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knowledge fostered a host of other innovations in pest and disease management, animal husbandry, and the like, which accompanied 'labor-saving' innovations that augmented and replaced human labor with wind and water mills and livestock draft power with tractors and other machines.

Organized research is itself a relatively recent innovation and has been an element of public policy for less than 200 years (Ruttan and Pray, 1987). Similarly, intellectual property rights (IPR) have existed in some form for centuries, but effective patents and patent-like rights have been formalized only relatively recently in most countries (e.g., in 1790 in the United States). Extending the scope of intellectual property (IP) protection to include the biological innovations used in agriculture is an even more recent phenomenon (Wright and Pardey, 2006).

Investments in agricultural research – irrespective of whether it is research conducted by private firms or public entities – now account for the lion's share of the technical progress in agriculture. However, it still takes a considerable time (typically decades not merely years) for the agricultural productivity consequences from investments in research to be fully realized. For this reason, this article presents and interprets new data on agricultural research and development (R&D) investments over the past half century, highlighting the changing public sector versus private sector roles. Research in the general biological sciences, genomics, informatics, and other sciences also affects progress in the food and agricultural sectors; so the article begins with a consideration of the changing global structure of overall investments in R&D.

International agricultural R&D and technology spillovers have long played important growth-promoting roles in agricultural economies around the world. The cost of communicating new ideas and tapping into technologies developed elsewhere in the world has been falling rapidly, such that access to other people's knowhow and innovations could well play an even bigger role in promoting future growth in agricultural productivity than in the past, both absolutely and relative to investments in homegrown R&D. With this in mind, this article presents measures of the potential for countries to tap scientific knowledge developed elsewhere in the world for the furtherance of their own agricultural sectors.

Finally, agricultural R&D pays handsome dividends. The article ends with a discussion of the evidence from hundreds of benefit–cost studies of returns to agricultural R&D and what it all means. It concludes that the evidence should be interpreted with care – the most common statistics quoted are likely to be misleading – but that there can be no doubt that the returns have been remarkably high in the past, a clear indication of an underinvestment from the point of view of the broader society, and there is no reason to think that the returns will be lower looking forward.

Investments in Science Worldwide

(This section draws heavily on Dehmer and Pardey (2014a).). Increasingly, innovations – in areas like genomics or precision agriculture and other informatics technologies – that affect agricultural productivity arise from R&D done in or for sectors other than agriculture. To place food and agricultural R&D in this broader innovation landscape the article begins with a brief look at the changing structure of science spending worldwide over the past three decades (Unless otherwise stated, throughout this article research expenditures in current, local currency units were first deflated to base year 2005 using country-specific implicit gross domestic product (GDP) deflators from the World Bank (2012) and United Nations (2011). The resulting series in constant currency units were then converted into 2005 international purchasing power parity (PPP) conversion factor dollars using the corresponding PPP from the World Bank (2012) and Heston *et al.* (2012). See Pardey *et al.* (1992) for an assessment of this approach.)

Dehmer and Pardey (2014a) estimated that the world spent a total of US$1.1 trillion (2005 PPP prices) on all types of public and private R&D in 2009 (For consistency with the reported global food and agricultural R&D totals to follow, spending by the eastern European and Former Soviet Union countries has been excluded from this 'world' total. In 2009, R&D spending by these countries was estimated to be approximately US$44 billion (2005 PPP prices).). This is roughly a threefold increase in (inflation adjusted) total R&D spending worldwide since 1980. Yet the global divide in this spending is stark. Eighty-one percent of the world's 2009 science spending was performed in just 10 countries, with the United States alone accounting for almost 33% of the world total (**Figure 1**). The 152 remaining countries of the world accounted for the remaining 19% of global spending. Notably, the middle-income countries of Brazil, India, and China (the BICs) are among the top 10 countries in terms of R&D spending and accounted for 17% of the world's 2009 total. The low-income countries (those 32 countries with gross national income (GNI) per capita averaging less than US$1005 per person and striving to support 11.7% of the world's population) accounted for a mere 0.26% of the world's science spending in 2009 (Low-, middle-, and high-income designations are based on the World Bank (2011).). To underscore the magnitude of these spending differences, in 2009 the high-income countries invested US$840 per person (2005 PPP prices) in R&D, whereas the middle-income group spent US$52 per person and the low-income group committed just US$4 per person.

The large economic disparities in the distribution of investment in R&D are plainly evident in **Figure 1**. China, a lower middle-income country, by 2009 accounted for 12.6% of the world's R&D spending in that year. The rest of Asia and Pacific (including India) had a global market share of just 3.4% – about the same share as Latin America and Caribbean (including Brazil) – whereas sub-Saharan Africa (where, of the countries for which R&D data are available, 47 are low-income countries) accounted for less than 1% of the world total.

Although the United States and other high-income countries still make up by far the largest share of global science spending, there are signs of an inexorable shift in the global R&D landscape. Growth in real spending from 2000 to 2009 in high-income countries, at just 3% per year, was the lowest of all income groups. Spending in low-income countries grew by 8.4% per year during this same period (albeit from a small base), whereas real R&D expenditures in middle-income countries grew by a remarkable 12.4% per year.

Approximately 66% of the world's R&D was done by private firms in 2009, with an especially marked concentration (81%) of that private research being performed in rich

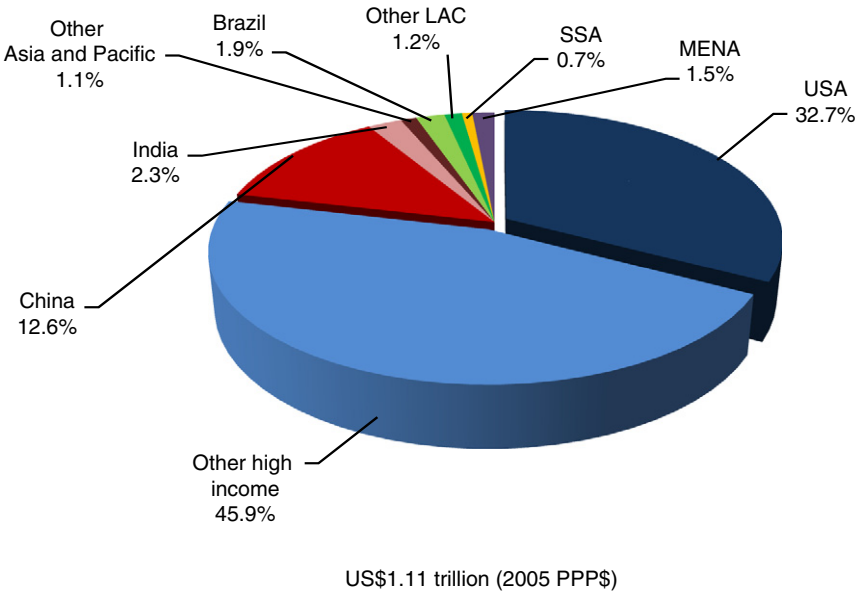


Figure 1 The geography of R&D spending worldwide, 2009. LAC, Latin America and Caribbean; MENA, Middle East and North Africa; PPP$, purchasing power parity conversion factor dollar; SSA, sub-Saharan Africa. Data include private and public spending estimates for 162 countries. Eastern European and Former Soviet Union countries are excluded. Reproduced from Dehmer, S., Pardey, P.G., 2014a. 'Global science spending, 1980–2009.' International Science and Technology Practice and Policy (InSTePP) Center Report. St Paul, MN: University of Minnesota.

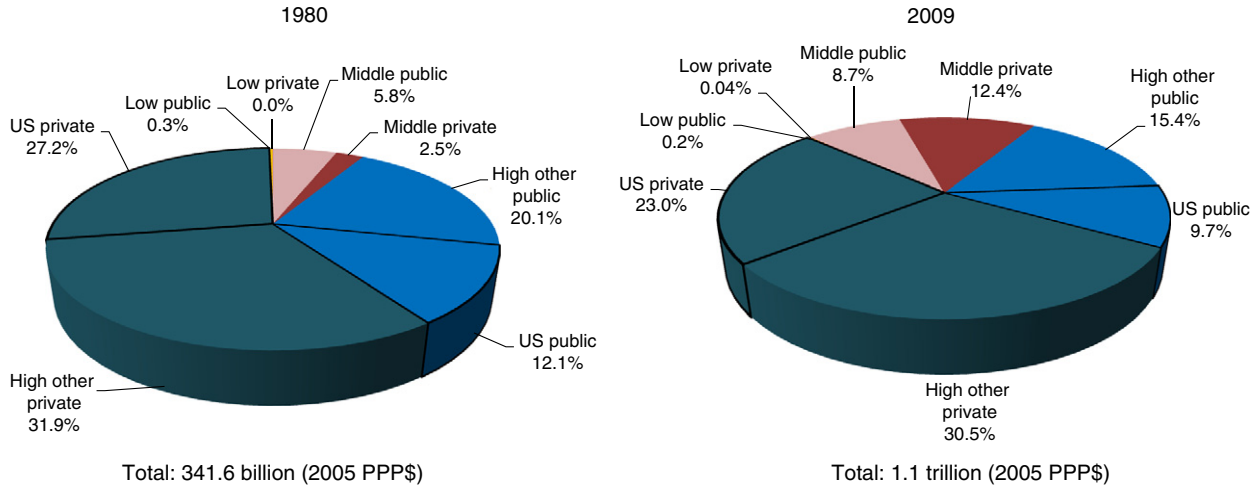


Figure 2 Global public and private R&D spending, 1980 and 2009. PPP$, purchasing power parity conversion factor dollar. Eastern European and Former Soviet Union countries are excluded. Countries are grouped into income classes using contemporary World Bank schema. High-income countries are those with 2010 GNI per capita of US$12 276 or more; middle-income countries had 2010 GNI per capita between US$1006 and US $12 275; and low-income countries had 2010 GNI per capita less than or equal to US$1005 (World Bank 2011, p. 389). Reproduced from Dehmer, S., Pardey, P.G., 2014a. 'Global science spending, 1980–2009.' International Science and Technology Practice and Policy (InSTePP) Center Report. St Paul, MN: University of Minnesota.

countries (Figure 2). Consequently, private sector research accounted for 68% of the total research spending in high-income countries, compared with 58% in the rest of the world.

Agriculture accounts for a modest share of total R&D. In 2009, global total (public and private) investments in food and agricultural R&D were approximately US$53 billion (2005 PPP dollars), just 5% of the overall science spending in that year (This estimate assumes that 90% of the world's 2009 private food and agricultural R&D spending occurred in high-income countries. See Section Private Sector Food and Agricultural R&D below, and especially Dehmer and Pardey (2014b) and Pardey and Chan-Kang (2014).). Nonetheless, that investment has realized demonstrably high returns (see Section Conclusion below) and is undergoing significant

changes in terms of where in the world that research is being carried out and who performs it. These changes could well have profound consequences for the nature and pace of innovation and productivity growth in global agriculture over the decades ahead, and it is to these investment trends the article now turns its attention.

Private Sector Food and Agricultural Research and Development

(This section draws heavily on Dehmer and Pardey (2014b) and Pardey and Chan-Kang (2014).). Although the empirical handle on private investments in food and agricultural research worldwide is far from certain, the available evidence indicates that the private share of global food and agricultural R&D is in the 35–41% range (Pardey and Beintema (2001; **Table 2**) estimated that the private share of global agricultural R&D was almost 35% in c. 1995, and approximately 94% of that research occurred in developed countries. Beintema and Stads (2008) (**Figure 4**) put the private share of the total at 41% in 2000, of which 94.4% took place in high-income countries. Fuglie *et al.* (2011, Table 1.2) estimated the private share of total to be 39% in 2000, with the high-income country share of global private food and agricultural R&D being 89%.). Like R&D in general, the lion's share of food and agricultural R&D (estimated to be in the 89–94% range) takes place in the high-income countries. The limited private sector participation in agricultural research done in or for developing countries stems from several factors, many of which are likely to persist for some time (except perhaps in countries experiencing relatively rapid economic growth, such as Brazil, China, and India). A significant share of food produced in developing countries is consumed by the household that produced it. Even when commodities enter the marketing chain, in developing countries they are often purchased in less-processed forms for preparation and eating at home. Consequently, a much smaller share of the food bill in developing countries accrues to postfarm food processing, shipping, and merchandising activities, areas where the incentives for private innovation are relatively pronounced.

Likewise, on the supply side, purchased inputs (such as herbicides, insecticides, improved crop varieties or animal breeds, and all sorts of agricultural machinery) constitute a comparatively small share of the total costs of production in many agricultural market segments in many parts of the developing world. Although this is likely to change as incomes rise and infrastructure improves, the pace of change will likely be uneven and more gradual in the poorest areas where (semi-) subsistence farming still predominates. The cost of doing business in places with small and often remote farms subject to poor market access, lack of farm credit, and limited communication services also undercuts private participation in agribusiness, in turn reducing the private incentives to invest in R&D targeted to these markets. In addition, a plethora of regulations, many times inefficiently enforced, combined with an uncertain and incomplete legal environment (especially related to contract law and intellectual property protection) make it difficult for local and multinational private interests to profitably penetrate agricultural markets with new seed, chemical, or other agricultural technologies in substantial parts of the developing world.

These many impediments notwithstanding, private investment will be critical to agricultural development and increased productivity in important parts of the developing world. However, the current obstacles to investment make clear the importance of public investments, which can make private investment in these areas more attractive. Publicly performed R&D continues to play a pivotal, and typically complementary, role to private R&D in the rich countries and will remain the principal if not sole source of agricultural innovations for many of the world's (poorer) farmers for many years to come.

Rich-Country Trends

Approximately 90% of the world's private food and agricultural R&D is performed in rich countries. Pardey and Chan-Kang (2014) reported that privately performed food and agricultural R&D in rich countries grew from US$4.3 billion (2005 PPP prices) in 1970 to US$17.5 billion in 2009, an average real rate of growth of 3.7% per year (**Figure 3**, inset) (The countries in this rich-country grouping include Australia, Austria, Belgium, Canada, Denmark, Finland, France, Germany, Greece, Iceland, Ireland, Israel, Italy, Japan, the Netherlands, New Zealand, Norway, Portugal, the Republic of Korea, Spain, Sweden, Switzerland, the United Kingdom, and the United States.). The spatial concentration of this research is also especially pronounced. Just two countries, the United States and Japan, accounted for more than half (55%) of this rich-country private food and agricultural total in 2009, with the top five countries (also including France, Germany, and the United Kingdom) accounting for three-quarters of the corresponding spending total.

The growth in private food and agricultural R&D spending in rich countries was faster than the corresponding real rate of growth of public sector spending among these countries (which averaged 2.1% per year for the period 1970–2009), such that the average ratio of private to public spending increased from 0.62 in 1970 to 1.08 in 2009. The drift toward an increasing share of food and agricultural R&D being performed by private firms was fairly widespread: 79% (19 of 24 rich countries) had higher private-to-public spending ratios in 2009 versus 1970. However, in only 11 countries did private food and agricultural R&D spending in 2009 exceed public spending (compared with five countries in 1970) – ranging from 87% of the food and agricultural R&D total in Switzerland to 50% in Japan. In 2009, the private share of total spending averaged 34% for the remaining 13 rich countries, with Greece having the smallest private share at 11%.

There is a tendency to think of private food and agricultural R&D as being mainly investments in research on agricultural chemicals, crop breeding, and machinery. Important as those areas of innovation are, research targeted to the food, beverages, and tobacco subsector accounted for 46% of the rich-country private food and agricultural R&D total in 2009 (**Figure 3**). The share of food, beverages, and tobacco R&D has shrunk a little over the past four decades (from 53% of private food and agricultural R&D in rich countries in 1970), and this

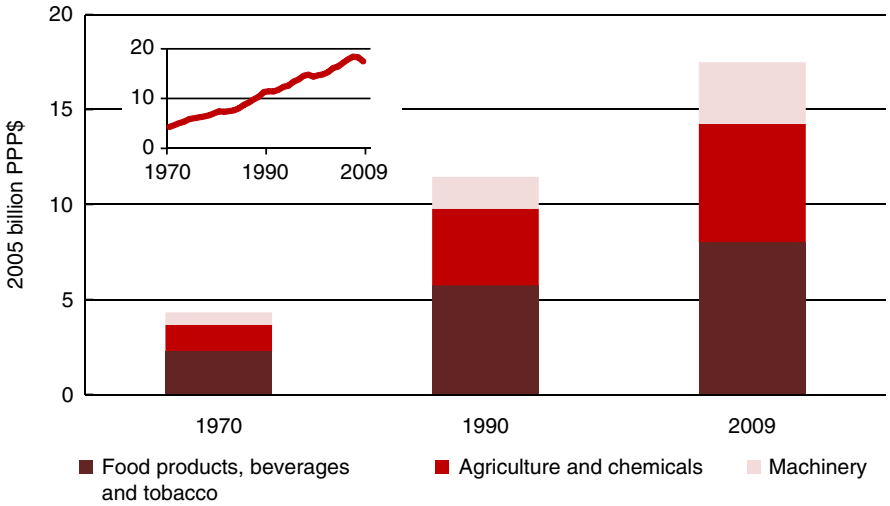


Figure 3 Private food and agricultural R&D in the rich countries, 1970–2009. PPP$, purchasing power parity conversion factor dollar. There are 24 countries included in the total presented. They are Australia, Austria, Belgium, Canada, Denmark, Finland, France, Germany, Greece, Iceland, Ireland, Israel, Italy, Japan, the Netherlands, New Zealand, Norway, Portugal, the Republic of Korea, Spain, Sweden, Switzerland, the United Kingdom, and the United States. Inset plots real annual spending from 1970 to 2009. 'Chemicals' and 'machinery' represent estimates of agriculturally related chemicals and machinery research, respectively. 'Agriculture' includes crop breeding and other areas of research of relevance to production agriculture. Reproduced from Pardey, P.G., Chan-Kang, C., 2014. Public and private R&D for food and agriculture in rich countries, 1960–2009. InSTePP Report. St Paul, MN: University of Minnesota.

trend is evident in 15 of the 24 rich countries in Pardey and Chan-Kang (2014).

These overall shares of rich country spending mask substantial cross-country differences in the orientation of their private food and agricultural R&D investments. For example, in Ireland and Portugal, food, beverages, and tobacco R&D accounted for more than 80% of the private food and agricultural R&D total in 2009, whereas in Sweden, Germany, and Austria more than two-thirds of private agricultural R&D was focused on machinery, agriculture (including crop breeding), and chemicals-related research.

United States Developments

Like many other rich countries, the United States has a long history of private innovation in agriculture and public policies to incentivize private R&D effort. The introduction of IPR, beginning in the United States with patents, trademarks, and copyrights in the eighteenth century, rates among the more prominent public policy measures intended to stimulate the creation and dissemination of US inventions. Many of the agricultural patents in the middle of the nineteenth century dealt with agricultural machinery, implements, and devices. Even something as seemingly simple as farm fencing material was heavily patented. Beginning with patent number 63,482 issued on 2 April 1867 to Alphonzo Dabb from Elizabethport, New Jersey for 'Improvement in Pickets for Fences and Walls,' more than 400 patents were issued for designs and manufacturing methods related just to barbed wire (Clifton, 1970; Krell, 2003).

In the United States, as elsewhere in the world, changes in the scope of intellectual property protection have been associated with a rise in agricultural innovations coming from the private sector. For example, legal forms of plant varietal rights have been on offer in the United States since 1930 and the private sector share of the rights issued has risen from 55% in the 1930s and 1940s to 82% of the rights in more recent times (Pardey *et al.*, 2014a). The intellectual property landscape evolved hand in hand with important changes in the genetics and genomics sciences that support crop varietal development.

Dehmer and Pardey (2014b) estimate that in 2009, US $6.8 billion of privately performed research was conducted in the United States directed toward food and agriculture (including forestry), compared with a total in 1950 of just US $67.9 million (US$463.5 million in 2005 prices) (**Figure 4**, inset). This implies an annual average rate of growth in private food and agricultural R&D of 9.0% per year over the period 1950–2009 or 4.9% per year when deflated by the implicit GDP deflator. The highest sustained real rate of growth (6.6% per year) was realized in the period 1950–80, a period of correspondingly rapid growth in public investment in agricultural R&D. Real growth slowed during the 1980s and early 1990s but picked up pace during the latter part of the 1990s (7.7% per year during the period 1993–98) as large agricultural chemical, machinery, and food companies ramped up their investments in agricultural research in the United States, along with a substantial number of smaller, new entrants (King, 2001; King and Schimmelpfennig, 2005). Private food and agricultural R&D spending declined immediately thereafter – from US$5.2 billion (nominal dollars) in 1998 to US$4.6 billion in 1999 – a prelude to the more general reduction in private research spending overall. It then recovered (even after adjusting for inflation) beginning in 2001.

Food, beverages, and tobacco research conducted by companies, including Kraft, Kellogg, and PepsiCo, is the largest category of private food and agricultural research in the United

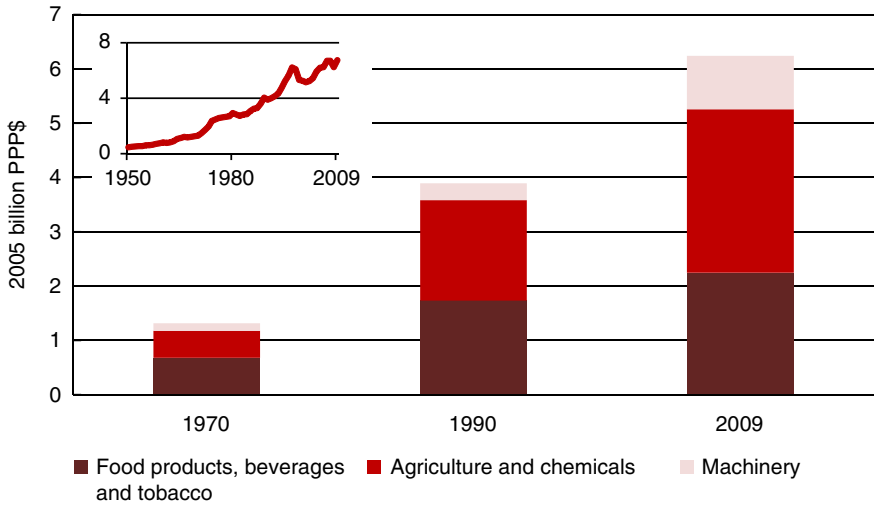


Figure 4 US private food and agricultural R&D, 1950–2009. PPP$, purchasing power parity conversion factor dollar. Inset plots real annual spending from 1950 to 2009. 'Chemicals' and 'machinery' represent estimates of agriculturally related chemicals and machinery research, respectively. 'Agriculture' includes crop breeding and other areas of research of relevance to production agriculture. Reproduced from Dehmer, S., Pardey, P.G., 2014b. 'U.S. private food and agricultural R&D spending, 1950–2009.' International Science and Technology Practice and Policy (InSTePP) Center Report. St Paul, MN: University of Minnesota.

States, accounting for 36% of the 2009 total. With 84.5% of the value of 2011 US food sales accruing to postfarm activities, this is to be expected (USDA, ERS, 2013) (Moreover, between 1939 and 2011, food consumed away from home rose from 19.2% to 48.7% of total US food expenditures (USDA, ERS, 2012).) Agriculture and chemical research (which includes biological research intended to develop new crop varieties as well as innovations designed to develop new herbicides, pesticides, fungicides, and veterinary medicines) account for the next largest share of private research, followed by research on new agricultural machinery and equipment.

Public Sector Food and Agricultural Research and Development

Important as private agricultural R&D has been, for much of the world the greatest part of the agricultural R&D effort that drove farm productivity growth was in the public domain. The public sector will likely continue to play a pivotal role, both as a complement to private R&D and as a substitute for private research in areas that lack the incentives for a sufficient private presence. A long-run perspective on investments in publicly performed R&D is presented here.

Trends in National Spending

(This section draws heavily on Pardey *et al.* (2014b,d), whose data were compiled in accordance with the guidelines spelled out in Organisation for Economic Cooperation and Development (OECD) (2002). Earlier compilations of global public food and agricultural R&D spending include Evenson and Kislev (1975a,b, Appendix 1), who reported research and extension expenditure and personnel estimates for 84 countries for c. 1965; Oram and Bindlish (1981), who developed annual agricultural R&D expenditure estimates for 51 developing countries for the period 1970–80; Pardey and Roseboom (1989), who reported a documented series of R&D spending and (full-time equivalent) personnel employed by national agricultural research systems (NARSs) that includes data on 154 developed and developing countries spanning the period 1960–86; and Beintema *et al.* (2012), who summarized estimates for 179 countries for the period 1980–2008. See also Pardey and Beintema (2001); Pardey *et al.* (2006) and Beintema and Stads (2008).). Over the past half century, and especially during the past decade or so, the global structure of public agricultural R&D spending has undergone a seismic shift. In 1960, just US$5.37 billion (2005 PPP prices) was spent on nationally conducted public agricultural R&D worldwide (**Figure 5**). By 2009 that total had climbed to US $33.6 billion: an average rate of (inflation adjusted) growth of 3.4% per year (Pardey *et al.* (2014b) reported an estimate for public agricultural R&D conducted in the Former Soviet Union (FSU) and Eastern European countries of US$1.14 billion (2005 PPP prices) in 2009. This figure includes estimates for the Czech Republic, Hungary, Poland, Romania, the Russian Federation, and 23 other countries from this region.). Big, and of late accelerating, geographical shifts in the location of performance of this R&D have been seen. In 1960 the high-income countries – classified according to average per capita incomes in 2009 (World Bank, 2011) – accounted for 56.2% of the world's total spending by national agencies: almost 50 years later, in 2009, that share had dropped to 48.5%. The United States has lost significant global market share, accounting for 21.5% of the worldwide total in 1960 but just 13.4% in 2009. If recent trends continue, the US position will continue to shrink. Pardey *et al.* (2014c) showed that the growth in real public sector agricultural R&D spending (i.e., intramural spending by the United States Department of Agriculture, USDA, and the state agricultural experiment

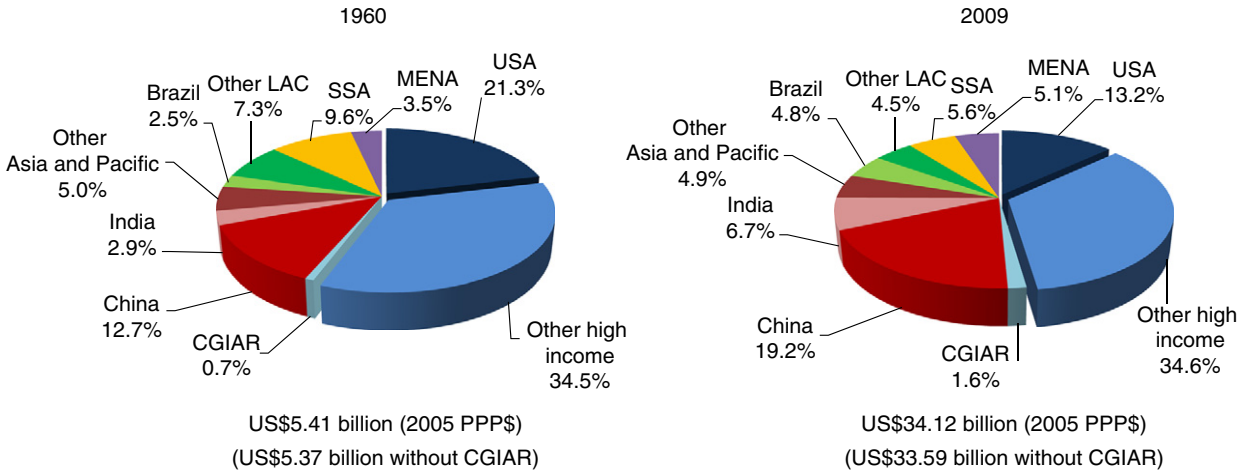


Figure 5 Structure of public food and agricultural research worldwide, 1960 and 2009. LAC, Latin America and Caribbean; MENA, Middle East and North Africa; PPP$, purchasing power parity conversion factor dollar; and SSA, sub-Saharan Africa. These estimates are for 126 countries, excluding countries from Eastern Europe and the Former Soviet Union. High-income countries are excluded from each geographical region. For example, Asia and Pacific excludes Japan and Singapore; MENA excludes Qatar and the United Arab Emirates. Reproduced from Pardey, P.G., Chan-Kang, C., Dehmer, S., 2014b. Global food and agricultural R&D spending, 1960–2009. InSTePP Report. St Paul, MN: University of Minnesota.

stations) has transitioned from an extended period of slowing down to one of no growth or negative growth (Using the implicit price deflator for GDP to adjust for inflation (as is done for almost all of the R&D data reported in this article) indicates that real spending on publicly performed agricultural R&D in the United States has flatlined since 2004. Using a purpose-built US agricultural R&D deflator (which grew at an annual average rate of 3.83% per year from 2004 to 2009, compared with 2.61% per year growth for the implicit GDP deflator) indicates a cut back in real spending since 2004.).

Sub-Saharan Africa has also lost market share, declining from 10% of the world's total in 1960 to 6% in 2009. So too has the Latin America and Caribbean region; although Brazil's share increased from 3% to 5%, the rest of that region lost ground relative to the rest-of-the-world aggregate. The notable expansion in market share was in the Asia and Pacific region: China's share grew from 13% in 1960 to 19% in 2009, whereas India's grew from 3% to 7%. In 2009, 31% of the world's public agricultural R&D took place in the Asia and Pacific region compared with just 21% in 1960.

Figure 6 plots the trends in real spending from 1960 to 2009 by region. Particularly in the past decade or thereabouts, spending by today's middle-income group of countries (which includes Brazil, India, and China – BIC) grew rapidly. By 2009 this group of countries had caught up with the high-income countries as a group in terms of their agricultural R&D spending; both groups of countries spent approximately US $16 billion on public agricultural R&D in 2009 (As a group the BIC countries spent US$10.5 billion (2005 PPP) on public agricultural R&D in 2009, 2.3 times the corresponding amount spent by the United States in that year.). Over this same time period, the 28 countries in today's low-income group (of which 24 are from sub-Saharan Africa) made little headway vis-à-vis the rest of the world. In 2009 they collectively spent US$0.82 billion (2005 PPP) on agricultural R&D, equivalent

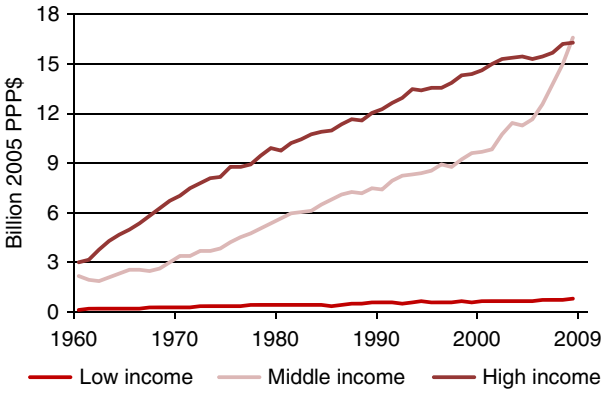


Figure 6 Public agricultural R&D spending by income class, 1960–2009. PPP$, purchasing power parity conversion factor dollar. Eastern European and Former Soviet Union countries are excluded. Reproduced from Pardey, P.G., Chan-Kang, C., Dehmer, S., 2014b. Global food and agricultural R&D spending, 1960–2009. InSTePP Report. St Paul, MN: University of Minnesota.

to just 2.5% of the respective high- or middle-income totals that year.

Figure 7 highlights key elements in the changing structure of global public agricultural R&D worldwide. The share of total R&D done by China, and thus the BIC aggregate, shrank substantially throughout the 1960s, a response to the turmoil of the Great Leap Forward and the subsequent Cultural Revolution (and causing the initial decline in the middle-income totals plotted in Figure 6). As Fan and Pardey (1992) described, during 1960–61, one-third of the Chinese Academy of Agricultural Sciences (CAAS) institutes were moved to rural areas or disbanded and the Academy's total number of staff declined by 70% from 7500 to 620 personnel (CAAS was established in 1957 (Fan and Pardey, 1992, p. 31).). From a

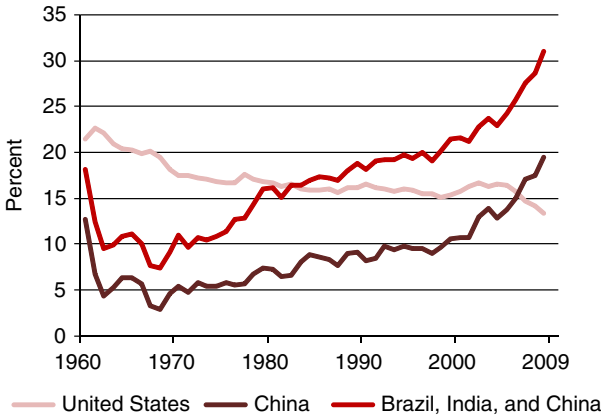


Figure 7 Shifting shares of global public agricultural R&D spending, 1960–2009. Reproduced from Pardey, P.G., Chan-Kang, C., Dehmer, S., 2014b. Global food and agricultural R&D spending, 1960–2009. InSTePP Report. St Paul, MN: University of Minnesota.

50-year low of 3.0% of global agricultural R&D spending in 1968, China's share of the total grew steadily to 10.7% in 2001 and thereafter grew rapidly to 19.5% by 2009. The BIC trend followed a similar path, such that by 2009 these three countries alone accounted for 31.2% of the world total and 60.5% of the low- and middle-income total. The flip side of these developments is a declining share of the world's total both for today's high-income countries as a group and for most of the countries within this group (specifically 20 out of 33 countries) as illustrated by the US share plotted in Figure 7.

These changes in the global structure of public agricultural R&D reflect a shifting pattern of growth in R&D spending among countries and regions of the world. Figure 8 shows the average rate of inflation-adjusted growth in spending by decade since 1960 for five regions of the world. A pronounced and persistent trend is the long-run ratcheting down in the rate of growth of public spending in the high-income countries: from an average rate of 9.1% per year in the 1960s to just 1.0% per year for the decade beginning in 2000.

The generally slower pace of spending growth in Latin America and sub-Saharan Africa compared with the Asia and Pacific region is also evident. All three of these regions saw real agricultural R&D spending growth rebound in the last decade of the data presented here, but the recovery is much more marked in Asia and Pacific than the other two regions. Moreover, the 1980s and 1990s were dismal decades in terms of spending growth in Africa and Latin America and especially so in Africa during the 1990s when overall spending shrank (in real terms). For sub-Saharan Africa and the Latin America and Caribbean regions the recent recovery was not widespread and appears fragile. In sub-Saharan Africa, more than half the increase in spending from 2000 to 2009 came from just two countries (Nigeria and Angola), whereas Brazil accounted for more than half the increased spending in the Latin America and Caribbean region during this same period.

In the early 1960s, the top 10 countries ranked by public agricultural R&D spending accounted for 62% of the world's total spending; by 2007–09, they accounted for 67%. Not only has the spatial concentration in the conduct of public

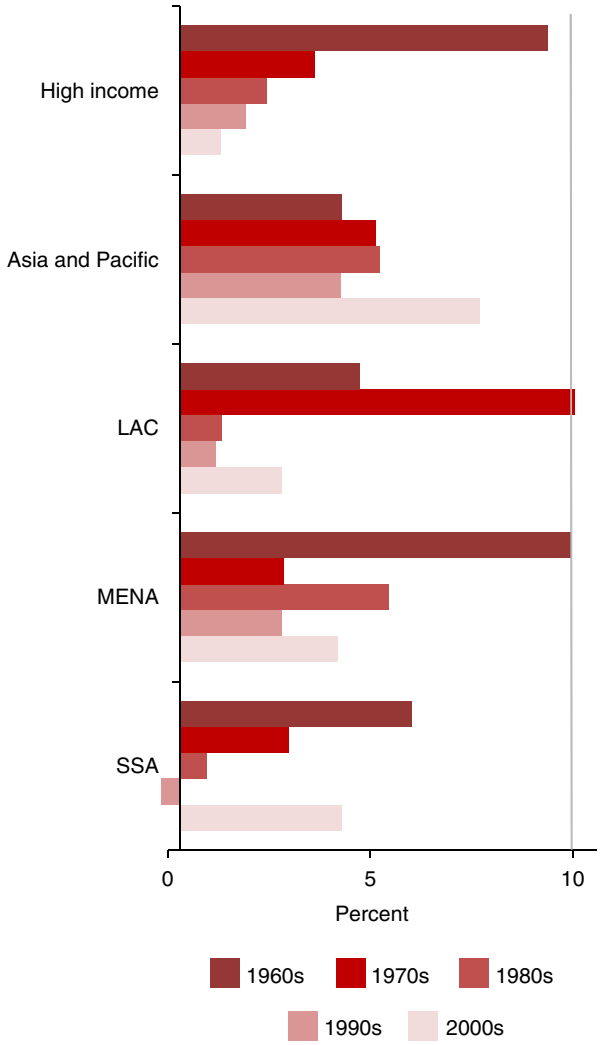


Figure 8 Rates of growth in public agricultural R&D spending by decade, 1960–2009. Eastern European and Former Soviet Union countries are excluded. All growth rates were adjusted for inflation and were calculated using the least-squares method (i.e., as the slope of a regression of logarithms of variables against trend) described in World Bank (2011, p. 409). The 1960s indicates the period covering 1960–1970 and likewise for other decades. Adapted from Pardey, P. G., Chan-Kang, C., Dehmer, S., 2014b. Global food and agricultural R&D spending, 1960–2009. InSTePP Report. St Paul, MN: University of Minnesota.

agricultural R&D become more pronounced over the past half century, but also the ranking of countries in terms of the amounts spent on public agricultural R&D has changed markedly. In the early 1960s, the first-ranked United States spent almost three times more than the second-ranked China (Table 1). By 2007–09, China was spending measurably more than the United States. Germany dropped in the ranking, as did the United Kingdom (5th in 1960 vs. 13th in 2009). By 2007–09, Australia had also dropped out of the top ten (down to 16th). New entrants into the top ten are Brazil (11th in 1960–62 and 5th in 2007–09), Spain (38th to 9th), and South Korea (14th to 10th). India also moved markedly up the

Table 1 Top ten agricultural R&D spending countries, 1960 and 2009

1960–62				*2007–09*			
Rank	*Country*	*2005 PPP$ in million*	*Rank in 2007–09*	*Rank*	*Country*	*2005 PPP$ in million*	*Rank in 1960–62*
1	United States	1213	2	1	China	5 767	2
2	China	433	1	2	United States	4 487	1
3	Germany	339	6	3	Japan	3 223	4
4	Japan	310	3	4	India	2 071	8
5	United Kingdom	268	13	5	Brazil	1 473	11
6	South Africa	205	24	6	Germany	974	3
7	Canada	197	7	7	Canada	871	7
8	India	162	4	8	France	867	12
9	Australia	157	16	9	Spain	795	38
10	Argentina	137	19	10	South Korea	792	14
Top 10		3422		Top 10		21 320	
Top 20		4298		Top 20		26 406	
Bottom 100		944		Bottom 100		4 241	

Source: Data underlying Pardey, P.G., Chan-Kang, C., Dehmer, S., 2014b. Global food and agricultural R&D spending, 1960–2009. InSTePP Report. St Paul, MN: University of Minnesota.

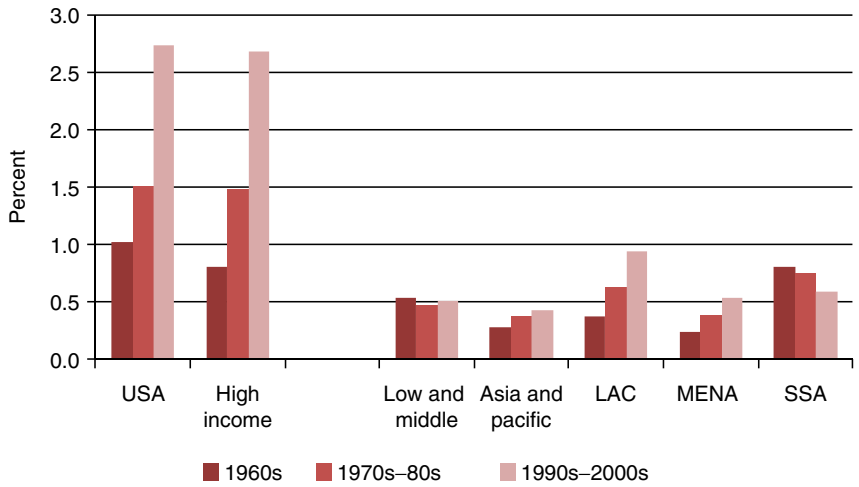


Figure 9 Agricultural research intensities by region, 1960–2009. Agricultural GDP from World Bank (2012) and United Nations (2011). These agricultural research intensity ratios express food and agricultural R&D spending relative to agricultural GDP. Agricultural R&D data details given in Pardey, P.G., Chan-Kang, C., Dehmer, S., 2014b. Global food and agricultural R&D spending, 1960–2009. InSTePP Report. St Paul, MN: University of Minnesota.

ranking from eighth to fourth. This represents a significant change in the geoeconomic order of public agricultural R&D investments, with the historically richer countries ceding ground in more recent years to those with rapidly rising per capita incomes.

Research Intensities

Countries with larger (smaller) agricultural economies are likely to invest more (less) in agricultural R&D simply because of a congruence effect (Pardey *et al.*, 1989). For this reason, normalizing agricultural research expenditures with respect to the size of the agricultural economies they serve gives one indication of the intensity of research spending. The research intensity ratios summarized in Figure 9 are (weighted) averages by decades of the amount of public agricultural R&D spending relative to the corresponding agricultural GDP (ag GDP).

Over the past 50 years, the high-income group has progressed steadily toward an evermore research-intensive mode of agricultural production (Figure 9). Compared with an average of just 56 cents for every UA$100 of agricultural output in 1960, these countries invested an average of US$3.59 per year into public agricultural R&D per hundred dollars of output in 2009. R&D intensity has increased in spite of a slowdown in the rate of growth of agricultural R&D spending, an indication of an even more pronounced slowdown in the rate of growth of agricultural output in these countries. In contrast, the intensity with which the Asia and Pacific region invests in agricultural R&D has grown much more modestly from 0.40% of ag GDP in 1960 to 0.54 in 2009. Although this region has sustained growth in agricultural R&D spending at a

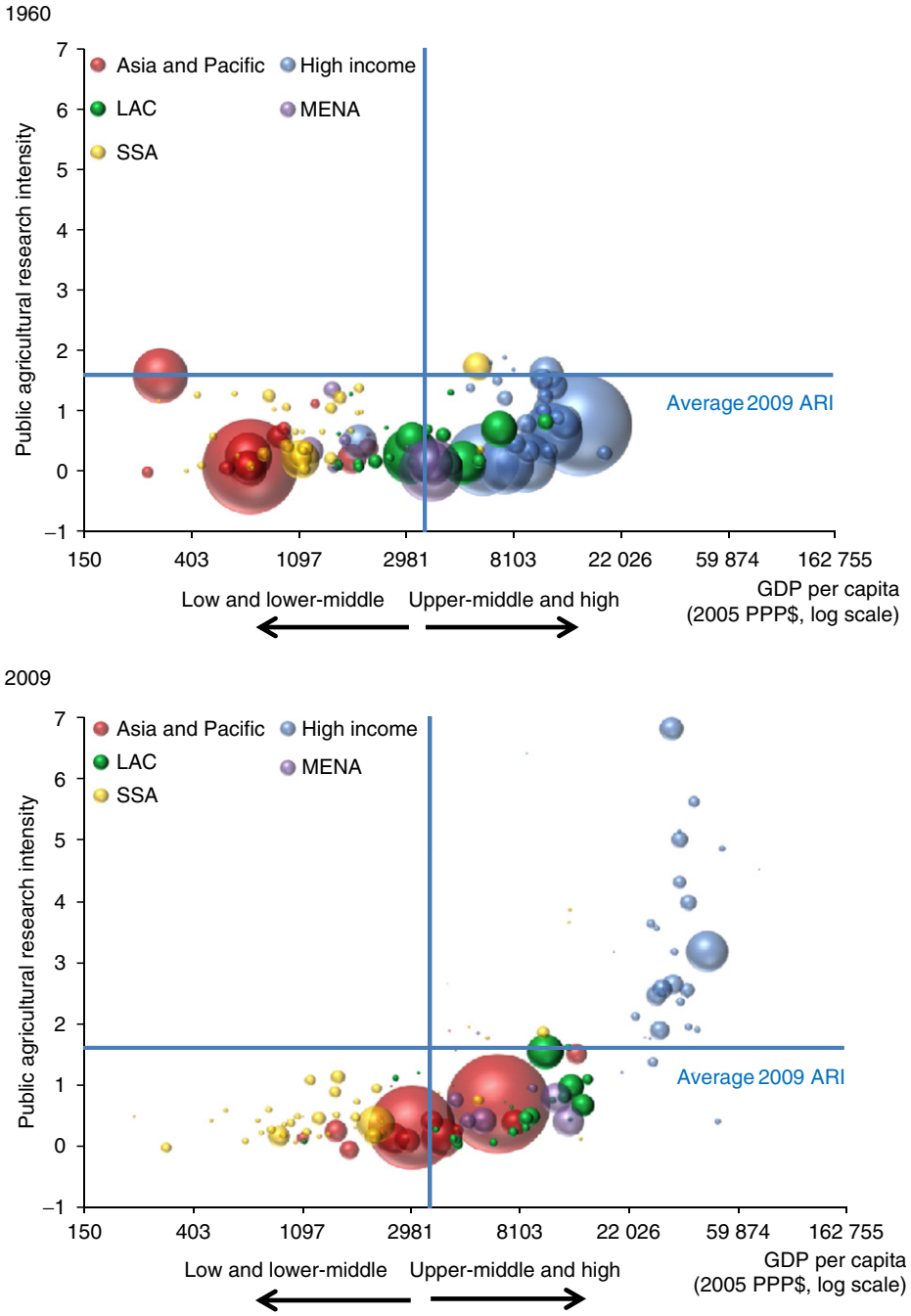


Figure 10 Agricultural research intensities and stage of development, by country 1961 versus 2009. PPP$, purchasing power parity conversion factor dollar. The area of the circle that represents each country is proportional to that country's agricultural GDP in the respective year. Reproduced from Pardey, P.G., Chan-Kang, C., Dehmer, S., 2014b. Global food and agricultural R&D spending, 1960–2009. InSTePP Report. St Paul, MN: University of Minnesota.

comparatively rapid pace – averaging 5.0% per year since 1960 – agricultural output has grown at reasonably rapid rate as well (3.85% per year). Thus, even though the growth in spending on agricultural R&D outpaced the corresponding growth in the value of output, the growth rate differentials were comparatively modest such that the region's research intensity only inched up over time, although increasingly so after the mid-1990s. In sub-Saharan Africa, research intensities have been slipping, especially in the past couple of decades: with 51.2% (22 countries) of the 43 countries in sub-Saharan Africa having lower research intensities in 2009 than what they had in 1980. The same pattern is evident in the low-income countries more generally, with 53.6% of the 28 low-income countries for which relevant data are available similarly losing ground.

Figure 10 offers further insight into the changing world order in terms of agricultural production and the corresponding

investment in public agricultural R&D. In this figure, each bubble represents a country, colored according to its region of production, and the size of the bubble represents that country's share of global agricultural output (ag GDP). In 1960, the high-income countries dominated agricultural production and public agricultural R&D. In the 50 years since then, the higher-income countries have shrunk in relative importance as agricultural producers, and their agricultural intensities have risen. The most striking change though is the increase in relative importance of the middle-income countries – especially China, India, and Brazil – both as agricultural producers and as performers of agricultural R&D. These countries are now poised to play a role in the coming 50 years that was played by today's high-income countries in the past 50 years. At the same time, many of the world's poorest countries continue to lag behind, both in terms of their share in global agricultural production and the relative intensity by which they invest in agricultural R&D.

Stocks of Knowledge and International Research Spillovers

(This section draws heavily on Pardey and Beddow (2013).). Trends in public sector national spending on agricultural R&D may misrepresent the cross-country gaps in scientific knowledge (Stocks of privately held knowledge are also economically important but are not quantified here, partly because of a lack of data.). Science is a cumulative endeavor, with a snowball effect. Innovations beget new ideas and further rounds of innovation or additions to the cumulative stock of knowledge. The mutually beneficial effects of accumulating and exchanging ideas is why lone innovators have largely given way to institutional approaches to research, why scientific disciplines formed professional organizations and spawned journals to capture and carry forward findings, and why scientists seek out other scientists and their ideas at conferences, via the internet and other venues. And so the size of the accumulated stock of knowledge, not merely the amount of investment in current research and innovative activity, gives a more meaningful measure of a country's technological capacity.

The current stock of productive knowledge and the contribution of past research spending to that stock are sensitive to the types of science being done, the institutional structures surrounding the science, and the economic context that affects the use of this stock. Some science spending makes persistent and even perpetual contributions to the changing stock of locally produced knowledge: the same spending in societies ravaged by wars, institutional instability, and outright collapse may have a much more ephemeral effect. Here two types of knowledge stocks are developed. One is a measure of the accumulation of productive knowledge from a country's own R&D (dubbed 'homegrown' knowledge) and the other a measure of the potential stock of knowledge spill-ins from R&D done elsewhere in the world.

Homegrown knowledge

To the public, agricultural science seems to progress through a series of breakthroughs, irrespective of whether it is the invention of tractors, hybrid corn, bioengineered pest or herbicide-resistant crops, or drip irrigation. The occasional genius does make a great leap forward, but the magic of science stems from the slow and steady accretion of new knowledge. Today's scientists stand firmly on the shoulders of those who went before them. Although investments in research give rise to new ideas, knowhow, and innovations in the near term, these innovations draw directly on the efforts of past research. Thus, innovation is a cumulative process. Stocks of productive knowledge, representing an accumulation of the past and present R&D used in agriculture, can thus be viewed as a metric of the state of innovation.

Pardey *et al.* (2014e) developed money measures to quantify the stocks of productive knowledge that resulted from spending on publicly performed agricultural R&D in the United States and around the world. In calculating own-country knowledge stocks, they accounted for the lag between research spending and the production of useful knowledge: expenditures in a given year do not only make immediate or near-term additions to the knowledge stock, but also continue to generate a stream of knowledge over the subsequent half-century. In one of the models applied by Pardey *et al.* (2014e), the productivity benefit of a given R&D investment increases each year for 24 years, then begins to decrease as the knowledge depreciates until it essentially no longer adds to the stock of knowledge by approximately 50 years after the investment. Using the data on country-by-country R&D spending from 1960 to 2009 summarized above (and taken from Pardey *et al.*, 2014b), along with this lag structure (initially developed by Alston *et al.*, 2010b), the global, public pool of productive scientific agricultural knowledge used in agricultural production in 2009 was estimated to be approximately US$18.6 billion (2005 PPP dollars). Approximately one-third of the world's agricultural knowledge stock was generated by three countries, the United States (14.9%), Japan (11.2%), and China (7.1%); nearly half of the world's agricultural knowledge stock was generated by seven countries (the three listed previously, plus Brazil, Russia, the United Kingdom, and Italy).

To aid in interpretation, the world is divided into six groups. First, the 33 high-income countries are separated out regardless of where they are located. The remaining middle- and low-income countries are grouped by region: Asia and Pacific (19 countries), Eastern Europe and the Former Soviet Union (EE&FSU, 28 countries), Latin America and Caribbean (LAC, 24 countries), the Middle East and North Africa (MENA, 7 countries), and sub-Saharan Africa (SSA, 43 countries). The 33 high-income countries account for approximately 56% (an average share of 1.7% per country) of world agricultural knowledge stocks, whereas the sub-Saharan African countries account for approximately 6%, or an average of 0.14% per country. The regional breakdown of world agricultural knowledge stocks is shown in **Figure 11**, where the size of each rectangle represents a region's share of the global stock of agricultural knowledge. Each region is subdivided into its constituent countries, with each country's rectangle scaled accordingly. Of particular note is that although some regions account for a relatively small share of world agricultural knowledge stocks, there are still countries within the regions that play an important role in generating new knowledge. For example, China, Brazil, Russia, South Africa, and Nigeria all account for relatively large shares of the global public stock of productive agricultural knowledge.

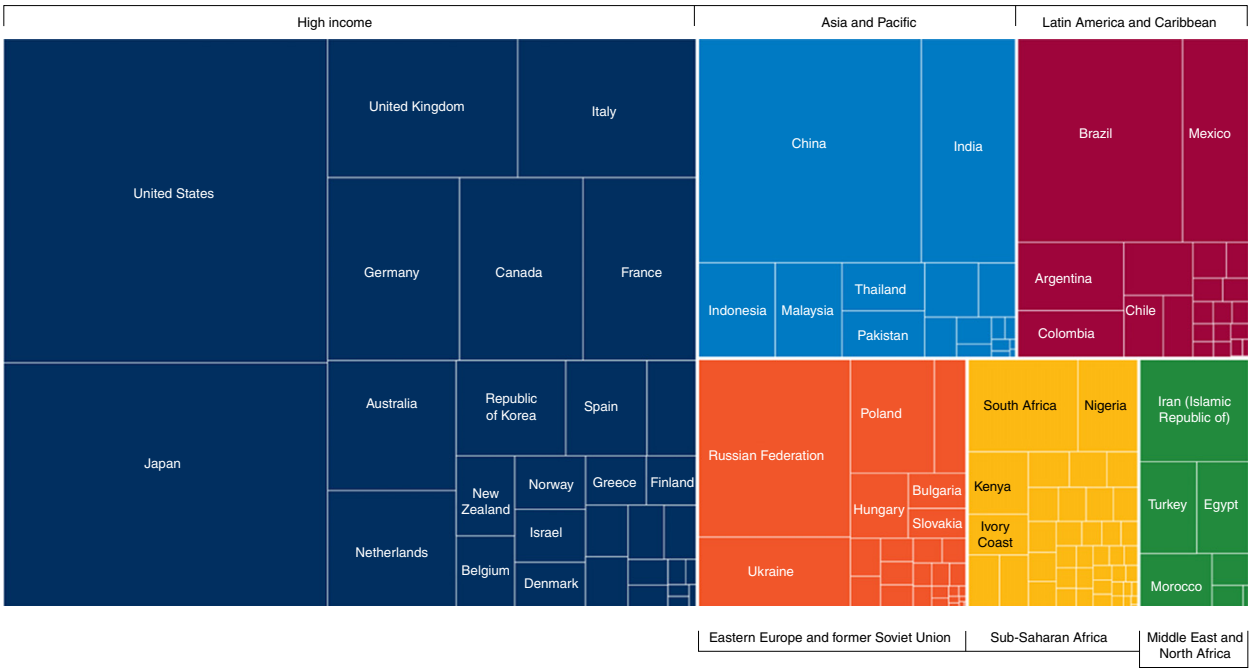


Figure 11 Cumulative homegrown knowledge stocks, by region and country, 2009. Reproduced from Figure 17 in Pardey, P.G., Beddow, J.M., 2013. Agricultural innovation: The United States in a changing global reality. CCGA Report. Chicago, IL: Chicago Council on Global Affairs.

Other peoples' knowledge

Before the modern scientific age, great advances in American agricultural productivity resulted from the efforts of plant prospectors who imported new and improved crop varieties from foreign lands. Walter Burling of Mississippi imported a new cotton variety from Mexico in 1806 that would become the mainstay of the early American cotton industry; Agoston Haraszthy helped to transform the California wine industry by importing several hundred grape varieties from across Europe, North Africa, and the Middle East in the 1860s. In addition to the efforts of private citizens, the USDA sent its scientists to the far corners of the globe in search of better plant varieties (As early as the mid-1850s the federal government employed 'agricultural explorers' to scout the globe for new plant and seed material for shipping back to the United States (Ryerson 1933, p.117). US Navy expeditions and Consular staff were also regularly used to collect new plant material from countries around the world and ship that material back to the United States. Juma (1989) placed these early seed-scouting endeavors in an international context, which is then linked to contemporary interests concerning genetic resources and modern biotechnologies. (See also Olmstead and Rhode (2008).). These efforts were particularly fruitful in introducing varieties of wheat and other crops suitable for the relatively arid and harsh conditions on the Great Plains.

R&D spillovers are still of substantial if not increasing economic importance to US agriculture. For example, foreign entities accounted for 64% of all the plant varietal rights in the United States in 2008 (compared with just 21% in 1984) (Pardey *et al.*, 2014a). By the early 1990s, approximately one-fifth of the total US wheat acreage was sown to varieties with CIMMYT ancestry, and in 1993 virtually all the California spring wheat crop was grown with varieties from CIMMYT or CIMMYT-based ancestors (Pardey *et al.*, 1996). The United States' reliance on wheat varieties from CIMMYT and elsewhere in the world persists (Pardey and Beddow (2013, p. 10) examined the genetic pedigree of the hard-red wheat variety Jagger, released commercially in 1995 as a joint product of the Kansas agricultural experiment station and the USDA's Agricultural Research Service (USDA-ARS). By 2005 this was the most widely planted variety in the United States, occupying 11% (i.e., 5.5 million acres) of the total US wheat area and more than 25% of the area in states such as Kansas and Oklahoma. They found that almost 70% of Jagger's antecedent varieties came from places and breeding efforts outside the United States.).

The reliance on R&D spillovers goes well beyond wheat varieties. A comprehensive study by Alston *et al.* (2010a) of the state-by-state returns to all the state-level investments in agricultural R&D performed in the United States estimated that, on an average, one-third of the economic benefits from research-induced productivity gains in agriculture in each state were attributable to spill-ins from research done in other states or by the federal government. A myopic view of innovation policy would consider only recently and locally performed R&D. A more nuanced approach is to recognize that R&D findings spill across national borders (typically in both directions, in and out of a country) and to be explicit about these spillovers when forming innovation policies, particularly when deciding how much to invest in agricultural R&D and who should pay for it.

Drawing on a concept of 'technological proximity' first used by Jaffe (1989), Pardey *et al.* (2014e) calculated the potential for agricultural knowledge to spill into each country from each other country, averaging the potential based on agroecological similarity and production similarity. For

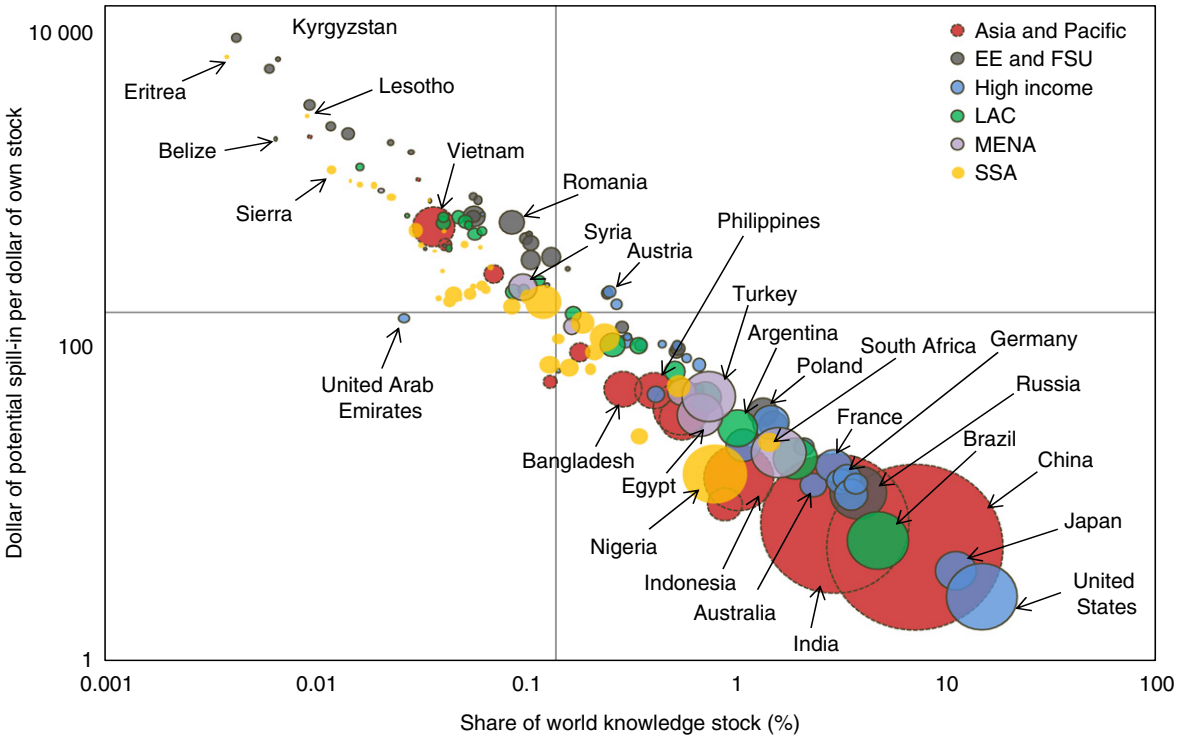


Figure 12 Potential spill-in leverage versus world share of knowledge stock, by country, 2009. The area of the circle that represents each country is proportional to that country's agricultural GDP in 2009. Reproduced from Figure 19 in Pardey, P.G., Beddow, J.M., 2013. Agricultural innovation: The United States in a changing global reality. CCGA Report. Chicago, IL: Chicago Council on Global Affairs.

example, by this measure approximately 49% of US agricultural knowledge could be applicable to Danish agriculture, whereas only approximately 29% of its agricultural knowledge might be applicable to South Africa. For a given country, the total knowledge that could spill in from another country is given by the percentage similarity multiplied by the stock of knowledge in the other country. Summing these values for all countries provides an estimate of the total global stock of knowledge that might be relevant to each country – the amount that could spill-in.

In Figure 12, each country is represented by a circle, and once again the area of which is proportional to the corresponding country's agricultural GDP in 2009. The colors of each circle represent geopolitical groupings of countries. Just five countries (China, India, the United States, Indonesia, and Nigeria) accounted for approximately one-half of the entire world's agricultural output. The horizontal axis of Figure 12 shows each country's share of the world's pool of productive, public agricultural knowledge, whereas the vertical axis shows the ratio of the total amount of relevant knowledge that could spill-in relative to each country's own stock of knowledge. The United States is positioned on the far right of the horizontal axis, with the largest share (14.9%) of the 2009 global public stock of knowledge: Eritrea is on the far left with the smallest share (just 0.004%) (Countries with very small agricultural knowledge stocks or with insufficient data to estimate knowledge stocks are not shown in Figure 12.). Reading of the vertical axis, a ratio of, for example, 1000 indicates that for each dollar a country invests in agricultural R&D, it could potentially tap US$1000 of spill-in knowledge. All countries have positive spill-in ratios – ranging from approximately 2.6 for the United States to 15 for Nigeria and more than 7000 for Eritrea – and therefore all countries can potentially benefit from knowledge generated elsewhere.

There are a few agricultural technologies that can be transplanted from one country to another without modification. Alston and Pardey (1999) broached the idea of diseconomies of economic distance in R&D and its implications for R&D spillovers, and their core idea holds here as well. As a region, by some measure, is more distant (technologically different) from another, the costs of adapting R&D increase. A high spill-in ratio indicates that a large pool of knowledge could potentially be adapted to the local environment, and that much technology could likely be used with little or no modification. Decline in spill-in ratios indicates that relative to the domestic stock, there is less foreign knowledge to tap.

Most of the sub-Saharan African countries have above-average potential spill-in ratios, and all but Nigeria and South Africa could potentially access at least 25 times their locally produced agricultural knowledge by adapting and adopting technologies produced in other countries. Thus, these areas show great potential for tapping foreign knowledge. Countries with relatively low spill-in ratios, such as the United States, Japan, China, and Brazil, could also potentially tap large knowledge stocks, but the relative cost of importing versus producing knowledge locally might be higher on average (Pardey *et al.*, 2014e). Thus, it is not clear that countries with both low potential spill-in ratios and large domestic

agricultural R&D enterprises would be as successful in adapting foreign knowledge as would countries with high spill-in ratios and small domestic R&D systems. Nonetheless, all countries have sizable spill-in potentials that should be integral to domestic decisions about the orientation and operational details of their own R&D efforts.

Internationally Oriented Agricultural Research and Development

(This section draws heavily on Pardey and Beddow (2013). See also Alston *et al.* (2006).). Progress in agriculture has always been an inherently international affair. The global diffusion of agriculturally significant plants and animals, their accompanying pests and diseases, and the tools and techniques used in production agriculture has been a pivotal part of the history of agricultural innovation. An important event in this history was the 'Colombian Exchange' that was initiated when Columbus first made contact with native Americans in the 'New World' (Crosby, 1987; Diamond, 1999; Olmstead and Rhode, 2008). Most of the commercial agriculture in the United States today is based on crop and livestock species introduced from Eurasia (e.g., wheat, barley, rice, soybeans, grapes, apples, citrus, cattle, sheep, hogs, and chickens), although with significant involvement of American species (e.g., corn, peppers, potatoes, tobacco, tomatoes, and turkeys).

More formal forms of international collaboration in the development and diffusion of agricultural innovations, designed to enhance the international spillovers of technologies and techniques, crystallized in the first half of the twentieth century. Baum (1986, pp. 5–6) and Culver and Hyde (2000) attributed the original idea of providing rich-country research assistance to developing-country agriculture to Henry A. Wallace, who founded the Pioneer Hi-Bred International Company in 1926 and served as US Secretary of Agriculture from 1933 to 1939 and as Vice President of the United States in the Roosevelt administration from 1940 to 1944 (Perkins (1997, p. 106) and Wright (2012, p. 1720) also pointed to the pivotal role played by Wallace in seeding the Green Revolution.).

Efforts to develop formal centers of international collaboration began in the 1940s and continued through the 1960s with the founding of four international research centers that would become the core of the Consultative Group on International Agricultural Research (CGIAR, or CG for short) system. By 1970 the budgets of the four founding centers totaled US$15 million. With the creation of the CGIAR in 1971, the system began expanding over the next two decades (**Figure 13**). The total number of centers increased, as did the funding per center, with funding reaching US$305 million in 1990 (US$422 million in 2005 dollars). After an abrupt cessation of growth in funding during the 1990s, funding began increasing again after 2000, reaching US$643 million (US$580 million in 2005 dollars) by 2010.

Over time, as agricultural productivity increased and donor priorities began to change, the allocation of funding among centers also changed. Throughout the 1970s and 1980s overall CG spending in real terms grew at a substantially faster rate (9.7% per year) than the spending by the four founding centers (5.6% per year) (Through 1971, all funding went to the four founding CG centers. During the 1970s, real funding for the four founding centers grew 9.9% per year. During the 1980s, however, the rate of growth of real funding slowed to an average of 2.5% per year and then declined for the following 15 years, before beginning to grow again in 2005 at an average annual rate of 6.5 per year from 2005 to 2010.) At the same time there was a broadening of the scope of the system beyond the main staple food crops, which was the focus of the founding centers, to include commodities, such as potatoes, livestock, sorghum, millet, bananas, and plantains. Funding was also targeted to agricultural development issues, such as food policy and the management of NARS. Mirroring domestic agricultural research policy developments in the rich countries that mainly fund the CG, during the 1990s the scope of the system broadened further to encompass forestry, fishery, water, and other issues. As a consequence, CG activities now

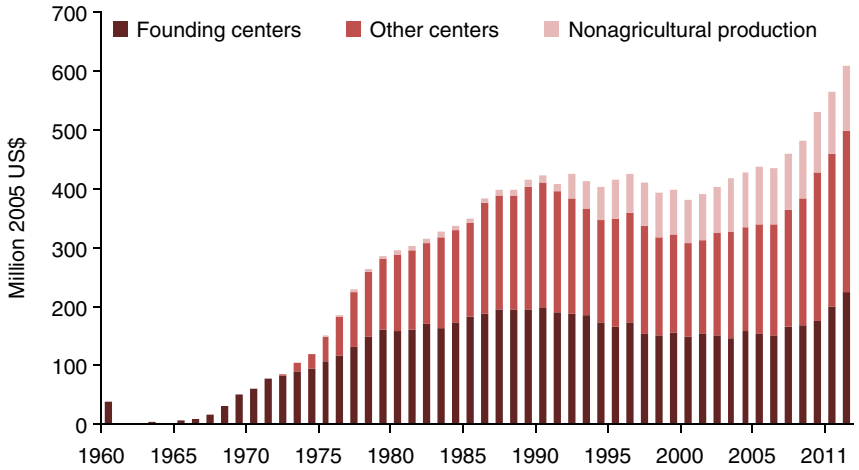


Figure 13 Real expenditures of the CGIAR, 1960–2011. Data in US dollars deflated to 2005 prices with implicit GDP deflator from the Bureau of Economic Analysis (2012). Reproduced from Figure B6 in Pardey, P.G., Beddow, J.M., 2013. Agricultural innovation: The United States in a changing global reality. CCGA Report. Chicago, IL: Chicago Council on Global Affairs.

give less weight to directly enhancing the productivity of the main staple food crops, relative to other activities (This is in line with similar trends in rich countries that provide the majority of funding for the CG. For example, in 1976 approximately 65% of the research conducted by the state agricultural experiment stations in the United States was targeted to increasing, or at least maintaining, farm productivity. By 2009, only 56% of the research had this orientation, as research into human nutrition, the environment, energy, and other areas of policy and social concern gained ground (Pardey *et al.*, 2014c).).

The long-run shift in CG priorities has been dramatic. Of the total increase in funding for the CG since 1990 (US$158 million in inflation-adjusted 2005 dollars) only 1.3% of that increased funding went to the four founding centers (or 36.0% if other centers that do research on specific agricultural commodities are also included, such as the International Potato Center, the International Center for Agricultural Research in the Semi-Arid Tropics, the International Network for the Improvement of Banana and Plantain (now merged with Bioversity International), and the International Livestock Research Institute. The overwhelming majority of the additional funds (64%) were directed to issues other than productivity improvements in crop and livestock production. In 1990 the four founding centers constituted 47.2% (almost one-half) of the total CG funding. By 2010 their share had fallen to 34.7% (just more than one-third) (Unfortunately, the CG has not maintained a set of science indicator statistics that enable funding trends to be meaningfully parsed into commodity-specific or other research program areas. Here the shift in center-specific funding is being used to illustrate the shift away from 'research' on staple food crops. The extent to which CG funds are used for research vs. other purposes (e.g., outreach- or extension-type activities, training, agricultural development efforts, or even administrative overhead) is also difficult to determine, impossibly so it seems for meaningfully examining long-term trends in these attributes.).

The size and scope of CGIAR activities vis-à-vis investments globally in food and agricultural research has also changed markedly. Although the CG substantially accelerated the spread of new varieties of wheat, rice, and other technologies (commonly called the Green Revolution), it now receives only a small, and of late, declining fraction of the global agricultural research investment dollars. In 2009, it represented just 1.6% of the US$34.12 billion spent on public sector agricultural research worldwide – or 3.1% of the research spending of the low- and middle-income countries combined (**Figure 5**) (In 1990, the CG constituted 5.3% of public agricultural R&D spending by the low- and middle-income countries.).

Perhaps even more dramatic is the shift in the size of the CG relative to particular rich and middle-income countries. In 1970, public spending on agricultural research in the United States was 31 times more than that of the CGIAR (US$1883 million against US$60.7 million for the CG in 2005 dollars), falling to just 8.5 times larger than the CG in 2009. In contrast, Brazil, India, and China as a group spent 19.6 times more than the CG in 1970, increasing slightly to 19.8 times more than the CG in 2009 (If private sector research is also factored in, the United States was 52.7 times larger than the CG in 1970 and 20.3 times larger in 2009.).

The Returns to Investments in Agricultural Research and Development

(This section draws heavily on Hurley *et al.* (2014a,b).). What is the economic worth of these substantial investments in food and agricultural R&D worldwide? It takes time – often many years – for research to generate tangible technologies and commercially useful ideas, and it takes time after that to fully realize the resulting economic benefits, not least as the uptake of new agricultural technologies often takes a decade or more. To estimate the economic worth of agricultural R&D, economists have developed summary measures that take account of the timing of the flows of costs and benefits. One such measure is the benefit–cost ratio (BCR): the (discounted) present value of the benefits divided by the (discounted) present value of the costs. This measure requires the choice of a suitable discount rate to be used to convert the streams into present values. Another popular summary statistic is the internal rate of return (IRR): the discount rate that equates the present value of the benefits and the present value of costs. An investment is deemed profitable if its benefit–cost ratio is greater than one (i.e., the present value of the benefits exceeds the present value of costs) or if the computed IRR is greater than the required (market) rate of return. Both of these conventional measures have been applied to evaluating agricultural research investments, but some issues have been raised about the interpretation of the results.

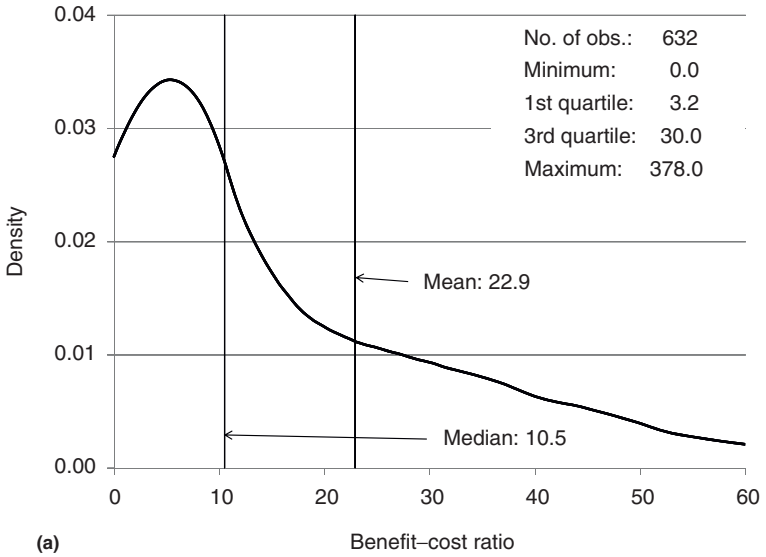
Conventional Measures of the Returns to Research and Development

Zvi Griliches published the first formal economic estimate of the rate of return to agricultural R&D more than half a century ago (Heckman (2006) wrote that "early empirical work on the social rate of return to research activity (Griliches, 1958), and on the role of economic incentives in determining the distribution of benefits from new technologies (Griliches, 1957), laid the foundations for scientific study of these topics." Schultz (1953) gave the earliest known economic estimate of the overall benefits attributable to public agricultural research in the United States but did not report a formal benefit–cost ratio or an internal rate of return.). Since then many economists have published a large number of estimates. Hurley *et al.* (2014a,b) reported a compilation of 2242 evaluation estimates from 372 separate studies published between 1958 and 2011 (Prior compilations include Alston *et al.* (2000), Evenson (2001), and Fuglie and Heisey (2007). After correcting some errors (and dropping several studies that reported only producer or consumer surplus estimates) in the compilation developed for Alston *et al.* (2000), the authors added 81 new studies published during the period 1999–2011 that reported 392 additional IRRs or BCRs.). This includes a total of 2049 IRR estimates and 632 BCR estimates, with 76 studies (20% of the total) reporting both BCRs and IRRs for the same program of research. Nearly half of the studies (and 42% of the estimates) were published in the 1990s. Around 38% of the studies were published in refereed journals. The rest were published in books, graduate dissertations, conference papers, and a good deal of gray

literature, including reports published by various international and national agencies.

The preponderance (99%) of the published evaluation evidence pertains to research carried out by public agencies (including either state or national government or international organizations along with universities). Approximately one-third of the reported evaluations for publicly performed R&D pertain to research done jointly, say by a government agency in collaboration with a university, whereas 28% of the estimates pertain to research that involved universities. Approximately 7% cover joint public and private research, whereas just 0.9% involves privately performed R&D. The CGIAR centers carried out the research encompassed by 12% of the evaluation estimates (and approximately 18% of the studies).

One-third of the evaluation estimates refer to research performed by federal or state agencies (including land-grant universities) in the United States. Research conducted by institutions from the Asia-Pacific, Latin America-Caribbean, and sub-Saharan Africa regions account for 14%, 13%, and 12% of the evaluation estimates, respectively. Almost 6% of the



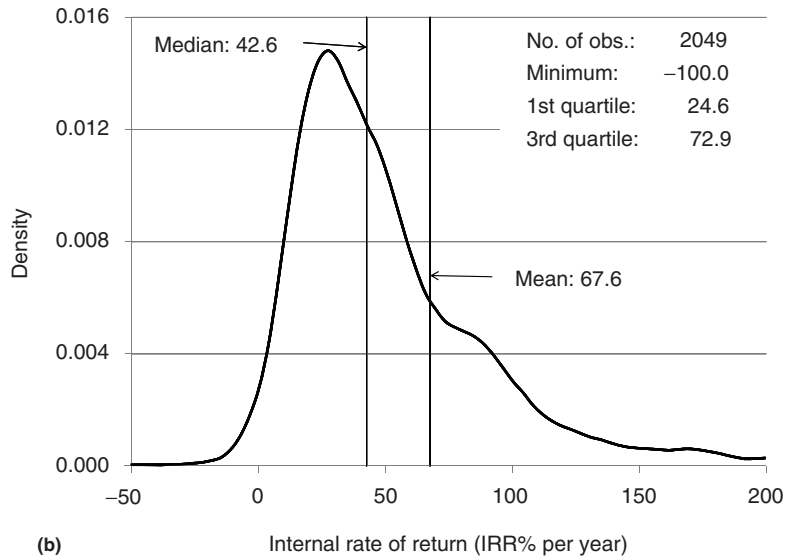


Figure 14 Distribution of reported benefit–cost ratios and internal rates of return. (a) Benefit–cost ratios and (b) internal rates of return. (a) Plot represents a Kernel density estimate (kernel = epan2, bandwidth = 4.9) fitted across 632 BCR estimates. For presentation purposes the plotted observations were truncated at 60. (b) Plot represents a Kernel density estimate (kernel = epanechnikov, bandwidth = 7.0) fitted across 2049 IRR estimates. For presentation purposes the plotted observations were truncated at 200. Reproduced from Hurley, T.M., Rao, X., Pardey, P.G., 2014a. Re-examining the reported rates of return to food and agricultural research and development. American Journal of Agricultural Economics, with permission from Oxford University Press.

estimates pertain to multinational research (i.e., research spanning multiple countries), with nearly 40% of these estimates dealing with research carried out by the CGIAR.

More than half of the estimates refer to joint research and extension activities. Around 38% of the estimates refer to broadly defined research investments that included both basic and applied research. Only a limited number of the estimates (close to 1%) refer exclusively to either basic research or extension. A little more than one-quarter of the estimates refer to research related to cereal crops, with maize and wheat research getting the most attention followed by rice. Assessments of aggregate investment in research for 'All agriculture' make up another fifth of the estimates, followed by livestock research, which accounts for approximately 10% of the estimates. This compilation also includes a small number of assessments of natural resources research, forestry research, and joint crop and livestock research.

Griliches' seminal 1958 study reported both the IRR and the BCR, although Griliches expressed a preference for the BCR. This preference appears to have eluded many subsequent researchers: 93% of the compiled studies report IRRs, with only one in three studies reporting BCRs and only one in five reporting both. Figure 14 (a) and (b) show the distribution of BCRs and IRRs, respectively, and other common descriptive statistics. The average BCR is 22.9 (i.e., in present value terms, on an average agricultural R&D yields US$22.9 of benefit for every dollar invested in R&D), although the distribution is right skewed and so the median (10.5) provides a more robust measure of the centrality of the estimates. The average IRR is 67.6% per year. Again the distribution is right skewed, with a median of 42.6% per year. The minimum is a dismal −100% per year, whereas the maximum is an incredible 5645% per year. Seventy-five percent of these IRRs exceed 24.6% per year, whereas a quarter exceed 72.9% per year.

Table 2 provides summary measures that characterize the distribution of the reported IRRs stratified by the type, commodity focus, and geographical orientation of the R&D. It includes measures of the central tendency of these distributions (specifically their mean and median values, the latter perhaps a more informative measure given the highly skewed

Table 2 Attributes of the reported internal rates of return

	Number of observations	*Number of publications*	*Central tendency*			*Range*			
			Mean	*Median*	*Standard deviation*	*Minimum*	*Maximum*	*5th Percentile*	*95th Percentile*
	(count)		*(percentage per year)*			*(percentage per year)*			
R&D orientation									
Basic	16	8	42.9	29.8	34.1	–1.3	110	–1.3	110
Applied	208	51	139.5	43.5	528.1	6.0	5645	17	321
Extension	17	9	77.0	47	85.2	1.3	350	1.3	350
Basic and applied	752	140	50.3	40	45.7	–56.6	526	5	116
Research and extension	1045	175	66.2	44	83.3	–100	1219	11.61	197.6
Commodity orientation									
Crop total	1177	207	56.2	42	72.3	–100	1736	9	143
Cereals	589	116	52.7	39	47.8	–100	466	11	135
Maize	170	37	53.4	43.5	46.3	–100	291.4	4	135
Wheat	201	51	48.8	40	37.1	–47.5	290	14.2	110
Rice	87	30	75.1	60.1	72.4	0.0	466	17	215.8
Fruits, vegetables, and nuts	99	21	76.6	33.4	196.8	1.4	1736	3.91	260
Livestock total	211	41	129.3	56	504.7	2.5	5645	10	158.5
Poultry	83	13	256.0	85.1	789.9	14	5645	25.5	526
Other livestock	128	33	47.2	38.4	32.2	2.5	143	6.8	111
Natural resources	32	9	44.6	37.9	32.1	0.0	111.2	7	111.2
All agriculture	468	72	64.5	37.9	101.8	–22.0	1219	6.9	219.4
Geographical orientation									
United States	644	72	82.8	41.3	298.0	–14.9	5645	7.4	207.3
Other developed	388	69	75.0	50	132.6	–1.3	1736	12	220
Asia and Pacific	314	54	76.9	52.8	83.0	–1	1000	17	201
Latin America and Caribbean	273	55	47.9	41	30.0	–22	191	15.2	100
Sub-Saharan Africa	255	57	42.7	35	42.1	–100	350	–3.4	122.5
Multinational	133	43	47.7	32.4	72.1	–47.5	677	8.3	94.9
Global	30	11	34.5	33.6	19.5	9	84.2	9	79
All studies	2049	346	67.6	42.6	182.2	–100	5645	9	166

Notes: 'Natural resources' includes evaluations of forestry research; 'All agriculture' includes evaluations of aggregate investments in programs of research; 'Multinational' includes evaluations of investments that span several countries; and 'global' includes evaluations that encompass a large number of countries (typically spanning multiple continents).

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nature of the distributions) and indications of the dispersion of the estimates (specifically minimum and maximum values and the 5th and 95th percentiles). The substantial variation in the methodological details used to estimate the reported IRRs summarized in Table 2 cautions against overinterpreting the apparent differences in the returns to different types, commodities, or location of performance of research.

Modified Internal Rates of Return to Research

Using IRRs to summarize R&D benefit and cost streams is problematic. Alston *et al.* (2011) criticized the IRR as a measure of investment returns, pointing to a conceptual flaw in the method, the implausibly high values that are typically obtained as a result, and the questionable implications of these values – a dollar invested at an annual rate of return of 50% per year would be worth in excess of US$11 million after 35 years and US$600 million after 50 years – and they suggested using a BCR or a modified internal rate of return (MIRR) instead. As subsequently elaborated by Hurley *et al.* (2014a,b), the implausibly high estimated values are the result of two key assumptions used in the IRR calculation. First, the calculation assumes that the beneficiaries (i.e., farmers and consumers) can reinvest their benefits at the same rate of return (i.e., the computed IRR). Second, the cost of the investment over time is discounted at the same rate (i.e., the computed IRR). These two assumptions are generally questionable and are empirically problematic when the computed IRR is very large, as is typically true for investments in agricultural R&D. In computing the MIRR the analyst chooses values for the rates of discount for research costs and rates of return to reinvested research benefits. If more reasonable assumptions are made about rates of discount for research costs and rates of return to reinvested research benefits, the computed MIRR will be much smaller than the conventional IRR, and typically much more plausible, as demonstrated by Alston *et al.* (2011) and Andersen and Song (2013).

Hurley *et al.* (2014a,b) developed a methodology for using information reported in previous studies to recalibrate a subset (270) of the previous IRR estimates using the MIRR. With this recalibration, the mean MIRR is 13.6% per year, which is 82% lower than the mean corresponding IRR of 67.9% per year. The interquartile range of the MIRRs is less varied, just 15% of the corresponding range for the IRRs, and with a much reduced median of 9.8% per year. The minimum MIRR is −2.0% per year, whereas the maximum MIRR is 107.0% per year, well below the corresponding IRR estimate of 1736% per year.

Conclusion

Agricultural R&D is a crucial determinant of agricultural productivity and production and therefore food prices and poverty. In this article, the authors present new evidence on investments in public agricultural R&D worldwide as an indicator of the prospects for agricultural productivity growth over the coming decades. The agricultural R&D world is changing, and in ways that will definitely affect future global patterns of poverty, hunger, and other outcomes. The overall picture is one in which the middle-income countries are growing in relative importance as producers of agricultural innovations through public investments in R&D and have consequently better prospects as producers of agricultural products, although the important role of privately performed R&D gives a substantial innovative edge to the higher income countries where most of this R&D takes place.

The economic impact of this research has been much studied, and the overwhelming conclusion drawn from this evidence is that the returns to agricultural R&D have been large. However, some have questioned the evidence, and there are reasons to be skeptical about some aspects of it (e.g., Alston and Pardey, 2001). The reinvestment rate assumptions implicit in the calculations used to derive internal rates of return (IRRs) – the statistic of choice used to summarize the returns associated with a given cost of research – are part of the estimation problem, which can be addressed by using a MIRR to summarize the same research benefit–cost streams. The recalibrated MIRR estimates of the rates of return to public agricultural R&D are more modest but still substantial compared with the opportunity cost of the funds used to finance the research. This still suggests that society has persistently underinvested in public agricultural R&D, notwithstanding the distorted view of the evidence created by reliance on the IRR to represent the returns to this investment that has characterized the literature for the past 50 years. If this underinvestment continues and the supply of important agricultural staples fails to keep pace with the growth in aggregate demand, increasing food prices will further stress the world's most vulnerable populations.

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See also: Advances in Animal Biotechnology. Biotechnology Crop Adoption: Potential and Challenges of Genetically Improved Crops. Biotechnology: Herbicide-Resistant Crops. Biotechnology: Pharming. Biotechnology: Plant Protection. Biotechnology: Regulatory Issues. Intellectual Property in Agriculture. Production Economics

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Land Use: Catchment Management

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Glossary

Denitrification The process of microbially facilitated reduction of nitrate into nitrogen (N_2) gas and other nitrogen oxides.
Ecosystem service Benefits to humankind from a multitude of resources and processes that are supplied by natural ecosystems.
Gray water Water output of a food production (or other) system that is degraded in comparison to the fresh (blue and green) water inputs.
Hydromorphology Hydrological, habitat, and structural processes and features of rivers, lakes, and coastal waterbodies.
Nitrate vulnerable zone A term used in Europe for areas of land that drain into nitrate-polluted waters, or waters which could become polluted by nitrates.
Pollution swapping The outcome of mitigation practices is positive for one natural resource but negative for another.

Agricultural Catchment Water Quality

Surface Water Quality Problems

Freshwater is a scarce and valuable resource (FAO, 2011). Conservation and equitable distribution of freshwater is therefore critical to sustaining ecosystem services and global food production (Rockstrom *et al.*, 2009). Agriculture uses 70% of global freshwater and so optimizing water use through advanced irrigation, farm, and food processing systems is paramount to meeting the globally increasing demands for food, particularly in the face of a changing climate. With the quantity of freshwater available, all human activities affect the quality of freshwater resources, and degradation of water quality in turn increases the scarcity of freshwater (Peters and Meybeck, 2000). Impaired water quality also limits ecosystem services, and human welfare and livelihood (Ongley, 1996; FAO, 2011). Poor water quality can cause loss of aquatic and riparian biodiversity, ecosystem stability and recreation value, poor human health (e.g., due to unsanitary drinking water and toxins from harmful algal blooms), physical disruption to water supply systems, shellfish contamination, fish kills, and reduced aquaculture production (Carpenter *et al.*, 1998; Schindler, 2006; Withers and Haygarth, 2007; Kay *et al.*, 2009).

Eutrophication and sedimentation are two common processes leading to water quality degradation. Eutrophication is an increased rate of organic matter supply to a waterbody, which can lead to excessive algal growth, species composition changes, taste and odor problems, changes in aesthetics, and oxygen depletion when algal blooms decompose. Both natural and human-induced processes lead to hypoxic (reduced oxygen) and anoxic (no oxygen) conditions in waterbodies (Rabalais *et al.*, 2010). The main cause of eutrophication in waterbodies is the oversupply of nutrients. Nitrogen supply commonly limits eutrophication in marine waters and phosphorus supply commonly limits eutrophication in freshwaters. However, colimitation or the reverse scenarios also occur (Boesch *et al.*, 2001). Sedimentation is the deposition of suspended soil and other particulate matter on river, lake, and estuary beds. Accelerated levels of suspended and deposited sediment can disturb the habitats for macroinvertebrates, aquatic flora, and fish spawning (Donohue and Molinos, 2009). Other significant causes of water quality degradation include accumulation of pesticides, other persistent organic pollutants and heavy metals, and changes in salinity, pH, thermal regime, and hydromorphology (i.e., waterbody structure, habitat, and hydrological processes) (Tognetti and Lawrence, 2002).

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Impacts of Agriculture

Detrimental water quality impacts in rivers, lakes, groundwater, and coastal waters have been attributed to impacts from agriculture, forestry, urban, and industrial land use (Carpenter *et al.*, 1998). During the 1980s and 1990s, there was considerable success in reducing nutrient inputs to waterbodies from human wastewater and industrial discharge, such that agricultural inputs have become a higher total proportion of overall inputs in many cases (Schindler, 2006; Kronvang *et al.*, 2008). This is the case in Lough Neagh in Northern Ireland, where the dominant source of phosphorus gradually switched from urban discharge to agricultural inputs after controls on urban discharge were introduced in the 1980s (Foy *et al.*, 2003). Globally, agricultural 'gray' water (polluted freshwater) volumes are estimated to be large (53%) compared with industrial (26%) and domestic (20%) users of 'blue' (surface and groundwater) and 'green' (consumed rainwater) water (Mekonnen and Hoekstra, 2011). The current nitrogen use is estimated to far exceed the planet's boundaries of sustainability and phosphorus transfer from land to water has almost reached the planet's functionally sustainable threshold (Rockstrom *et al.*, 2009).

Pressures (i.e., stressors on the environment) on waterbodies in agricultural catchments include enhanced losses of nutrients and eroded soil, changes to the natural hydrologic regime, increased losses of agrochemicals, pathogens and organic compounds, and acidification (Carpenter *et al.*, 1998; Blann *et al.*, 2009; Quinton *et al.*, 2010; Carpenter *et al.*, 2011; Foley *et al.*, 2011).

In Europe, pressures from agriculture are significant in 40% of rivers and coastal waters, and in one-third of lakes and transitional waters (EEA, 2012). Brown tides in China have been linked to turbidity, dissolved organic carbon, and metals exports, which have been partly linked to intensification of agriculture (Gobler *et al.*, 2011; Qiu, 2012; Zhang *et al.*, 2012a). In the Aral Sea basin in Central Asia, overextraction of water for irrigation caused a 90% decline in the lake volume between 1960 and 2006 and an increase in lake salinity, leading to large-scale abandonment of fishing industries, land desertification, and to poor ecosystem and human health (Micklin, 2007). Other examples of where impaired water quality has been linked to agricultural land use include the Baltic Sea in Europe (Gustafsson *et al.*, 2012), Chesapeake Bay in the United States (Simpson, 2010), and the Great Barrier Reef in Australia (Waterhouse *et al.*, 2010).

Technical Options for Water Quality Mitigation

A range of stewardship approaches, including engineering solutions that treat the symptoms, and management practices that minimizes the pressures, is needed to mitigate against anthropogenic pressures on the planet's resources (Steffen *et al.*, 2011). In agriculture, practices aimed at mitigating environmental degradation are interchangeably referred to as 'mitigation measures', 'stewardship approaches' and 'best, recommended, conservation or sustainable' management practices and can be classified as cultural or structural measures. Cultural measures (e.g., fertilizer application rate, form, placement, and timing) are land management practices that modify the spatial and temporal availability of nutrients and pollutants for mobilization and transport to waterways. Structural measures (e.g., slurry storages, riparian fences, and vegetation) are those that modify the pathway of nutrients, pollutants, and water to a receiving waterbody. A range of structural and cultural mitigation measures can be applied at different stages of the link between land management and water quality impact. These stages can be conceptualized as a transfer continuum for materials that are mobilized from sources via pathways of transport and later delivered to a waterbody where they may cause an ecological impact (Haygarth *et al.*, 2005). **Figure 1** highlights the key components of the nutrient transfer continuum for nutrients. Many mitigation measures have benefits for both the off-farm environment and the farm system itself by sustaining the soil, animal, landscape, and water resource. For example, increasing output from similar or lower nutrient use, reducing soil compaction and erosion and enhancing farm water quality have both on- and off-farm benefits (Ridley, 2005; Gourley *et al.*, 2007; Zeckoski *et al.*, 2007; Simpson *et al.*, 2011; Soane *et al.*, 2012). Mitigation measures that target nutrient, agrochemical, sediment and pathogen losses, and greenhouse gas emissions at plot, field, and farm scales have been identified for a range of agricultural industries and climates (Ongley, 1996; United Nations Environment Program, 1998; Sharpley *et al.*, 2000; Campbell *et al.*, 2004; McKergow *et al.*, 2008; Kay *et al.*, 2009; Merriman *et al.*, 2009; Monaghan, 2009; Sharpley *et al.*, 2010; Newell Price *et al.*, 2011). The effectiveness of each mitigation measure described in this section is often highly site-specific and needs to be targeted to each agricultural landscape to avoid neutral or negative impacts on the environment.

Mitigating Sources

Structural and cultural practices that optimize the magnitude, timing, and spatial distribution of nutrient, contaminant, and sediment sources can mitigate losses to catchment waterways and in many cases also increase farm profitability, particularly when efficiency of the farming system is increased (Monaghan *et al.*, 2008). Source management is often more practical and feasible than water management in rain-fed farming systems. In the Republic of Ireland, for example, more than half of the mandatory agricultural mitigation measures are focused on managing point and diffuse nutrient sources (Statutory Instrument 610, 2010).

A EU-wide upper limit on the rate of organic nitrogen in manures that can be applied through spreading or animal grazing has been set at 170 kg ha^{-1} (with some exceptions allowed) in an effort to minimize nitrogen (and phosphorus) losses to receiving waterbodies. Practices that maintain agricultural production while decreasing the use of fertilizers are also encouraged. For example, to reduce inorganic fertilizer requirements, manures and slurries that are produced when stock are housed in farm yards can be captured, stored, and later redistributed to fields. However, investing in the infrastructure and spreading equipment and developing the skills required to utilize manures as fertilizers is an on-going

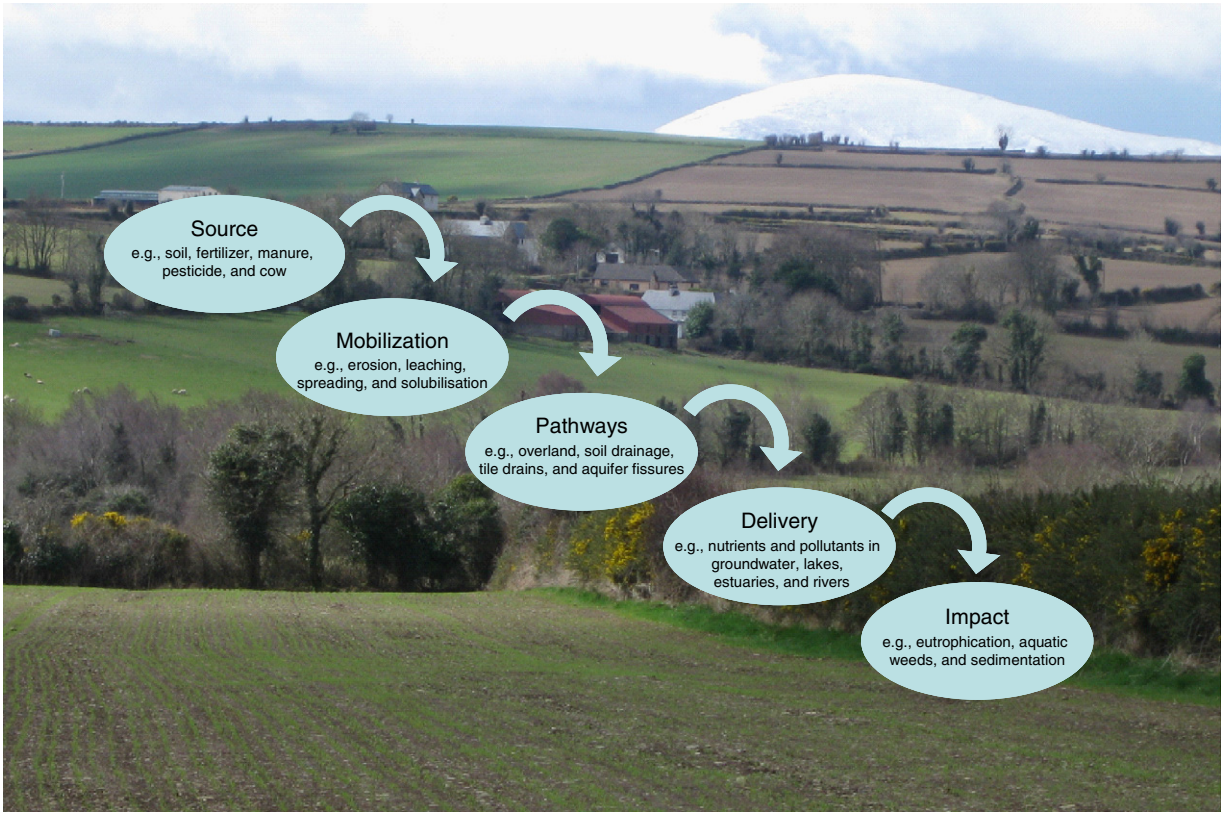


Figure 1 Good agricultural practices and targeted implementation of mitigation practices can reduce the mobilization and delivery, via flow pathways, of nutrient, agrochemical, and sediment sources so that detrimental impacts in receiving waterbodies are minimized. Imagery courtesy of Teagasc, Ireland.

challenge for livestock farmers (Kleinman *et al.*, 2012). To maximize the value of nutrient use, and minimize losses to the environment, manure and fertilizer should be applied at appropriate rates, timings, and locations to match crop requirement, maximize crop uptake, and minimize leaching of nitrate and volatilization of ammonium compounds (Di and Cameron, 2002; Lalor *et al.*, 2011). Soil management practices that minimize nitrogen leaching include use of cover crops, minimal plowing of pasture (particularly in early autumn), improved stock management, and precision farming (Di and Cameron, 2002). Certain fertilizer formulations can also be used to reduce nitrogen losses from cropping systems to the environment (Chen *et al.*, 2008).

Comprehensive reviews of measures suitable for mitigating phosphorus sources in a range of farming systems are provided by Kronvang *et al.* (2005), Nash and Halliwell (1999), and Sharpley *et al.* (2000). Availability of phosphorus sources for loss to waterways can be minimized by matching fertilizer and manure application rates to match crop needs, and not applying fertilizers to soils that have stores of plant-available phosphorus higher than crop requirements (Richards, 2006). Timing phosphorus applications to fields in ways that avoid forecast heavy rain, choosing appropriate fertilizer formulations, and placing fertilizer away from the main water flow pathway (e.g., subsurface placement of phosphorus fertilizers and manures) can reduce the risk of losses in runoff and drainage (Hodgkin and Hamilton, 1993; Nash *et al.*, 2004). Avoiding stocking or fertilizing areas within fields that seasonally saturate can reduce losses because the wettest parts of the landscape contribute a disproportionately large amount of runoff and nutrients to downstream waterbodies (Melland *et al.*, 2008; Sharpley *et al.*, 2011).

A range of soil amendments (e.g., gypsum, lime, bauxite mining residues, siderite, refuse ash, dredged river sediments, alum hydrosolids, ferrous sulfate, and cement kiln dust) increase the soil's capacity to retain phosphorus against leaching, mostly due to their iron, aluminum, or calcium content (Summers *et al.*, 1996; Callahan *et al.*, 2002; Murphy and Sims, 2012), however, these amendments are not widely applied. Soil management practices that maintain a threshold level of groundcover and minimize compaction will minimize erosion and runoff of nutrients. Practices include rotating stock between fields and optimizing stock densities to efficiently utilize but not overgraze pasture, controlling farm machinery traffic, and minimizing tillage operations (McCaskill *et al.*, 2003; Agouridis *et al.*, 2005; Deasy *et al.*, 2010; Godwin, 2012).

Mitigating Pathways

A key mitigation strategy for reducing nutrient and contaminant loads in surface and subsurface pathways is to reduce the interaction between water, as a transporting

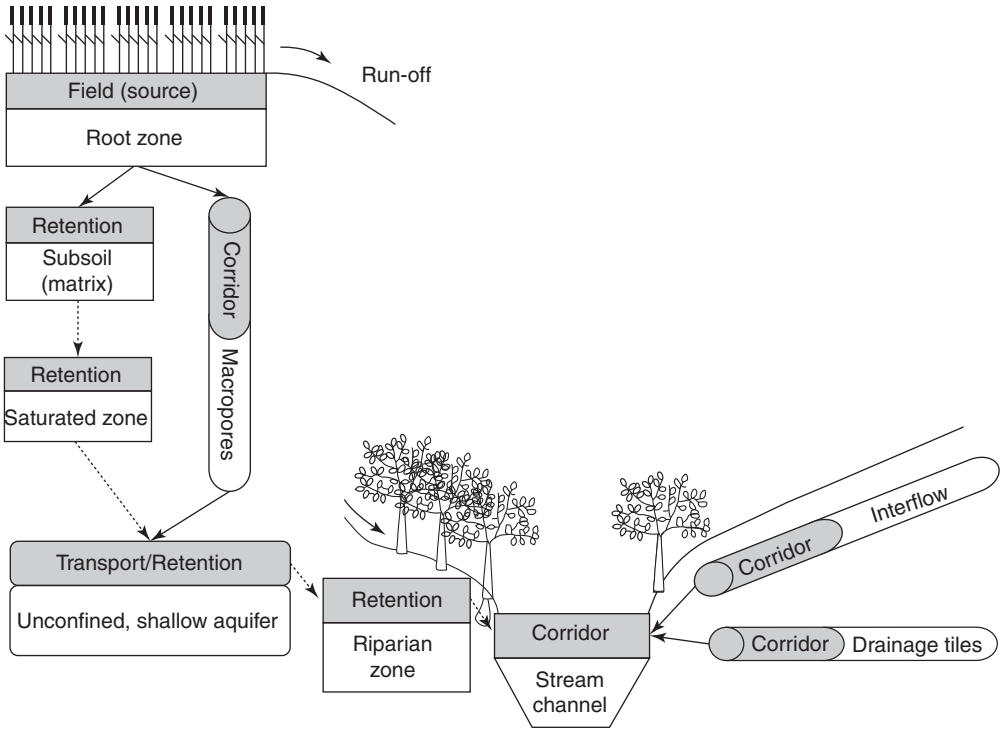


Figure 2 Pathways of nitrate movement from fields to a stream. Nitrate can be transported in water rapidly to streams through natural pipes (corridors) such as tile drains and old root channels and can also flow more slowly through soil and groundwater aquifers and be taken up by plants or biologically transformed into other nitrogen forms (retention). The retention processes attenuate, or deplete, the amount of nitrate reaching the stream. Reprinted from Haag, D., Kaupenjohann, M., 2001. Landscape fate of nitrate fluxes and emissions in Central Europe: A critical review of concepts, data, and models for transport and retention. Agriculture, Ecosystems and Environment 86, 1–21.

medium, and the source of the nutrient or contaminant. Interaction can be reduced by reducing the volume or energy of water flow, by redirecting the pathway of water flow, or by removing the source from the water flow pathway, either in space or time. For example, nitrate nitrogen that drains from the root zone via old root channels or subsurface drains (i.e., high energy flow) may rapidly reach a stream without attenuation (**Figure 2**). In contrast, nitrate that flows through lower energy water pathways such as soil drainage and riparian zones may be retained and naturally attenuated (depleted) by plant uptake or by biological transformation (e.g., via denitrification) into gaseous nitrogen forms (see Section Pollution Swapping). For phosphorus, the optimum spatial arrangement of mitigation practices on a farm can be guided by identifying areas that transfer disproportionately high amounts of phosphorus. These areas usually have both a high source of phosphorus and a high potential for surface runoff and are termed critical source areas (Sharpley *et al.*, 2011). A range of phosphorus and nitrogen loss risk assessment indices and models have been developed to identify the critical source areas in farmed landscapes (Buczko and Kuchenbuch, 2007, 2010) and are the subject of continuing research (e.g., Shore *et al.*, 2013).

The volume of soil drainage can be decreased through increasing plant water uptake by planting deep-rooted perennial forage crops instead of shallow-rooted annual crops (White *et al.*, 2003). Efficient irrigation management can also decrease volumes of surface runoff and subsurface drainage (Wilcock *et al.*, 2011). Slowing water in drainage ditches using vegetation and low-grade weirs allows attenuation of nitrogen and phosphorus (Ensign *et al.*, 2006; Kröger *et al.*, 2011). Retention of runoff water in constructed wetlands can also enable denitrification of nitrate and uptake and sediment adsorption of phosphorus, sedimentation, degradation, and decay of pathogenic bacteria (Scholz *et al.*, 2010; Wilcock *et al.*, 2012) and pesticides (Moore *et al.*, 2007; Gregoire *et al.*, 2009). Sediment traps and flow diversion terraces in fields facilitate deposition of sediments entrained in field runoff (Yang *et al.*, 2009; Ockenden *et al.*, 2012). Vegetated riparian buffers have some potential to mitigate inputs of nitrogen, phosphorus, sediment, and fecal inputs (Lovell and Sullivan, 2006; Collins *et al.*, 2007; Kay *et al.*, 2009). Buffers are most effective for reducing sediment and sediment-associated nutrients in cases where surface runoff is slowed allowing for enhanced deposition of sediment. Where infiltration is enhanced, some attenuation of dissolved nutrients and contaminants also occurs.

Separation of clean and dirty water by using appropriate guttering and drainage in farm yards reduces the potential for nutrients and sediment to become mobilized, and diverting runoff from farm lanes can prevent nutrients directly entering streams (Wilcock *et al.*, 2007).

A range of technologies have the potential to remove nutrients from water. Phosphorus is adsorbed and precipitated by aluminum, iron, or calcium compounds in natural, industrial byproduct, or artificial media such as iron oxide,

limestone, steel slag, melter slag, and bauxite mine red mud residue (Buda *et al.*, 2012; Klimeski *et al.*, 2012). Nitrate is removed by denitrification using permeable carbon reactive media (Fenton, 2008), and concentrations of suspended solids, chemical oxygen demand, and total nitrogen are decreased through physical filtration, as well as by absorption and biological uptake in aerobic woodchip filters (Ruane *et al.*, 2011).

Mitigating Direct Delivery

Limiting direct contact between nutrients and other contaminants and a waterbody itself provides a direct means for mitigating losses. Fecal contamination of waterways and erosion from trampled stream banks can be reduced if stock are excluded or discouraged from entering a waterbody. Partial or total stock exclusion can be achieved by riparian vegetation, fencing, providing bridges for crossing, and providing alternative shade and water sources and by managing grazing rotations (Agouridis *et al.*, 2005; Collins *et al.*, 2007; Kay *et al.*, 2008). Minimum distances to watercourses are routinely included in fertilizer spreading and pesticide spraying codes of practices.

Mitigating Impacts

In some cases, the impact of eutrophication can be mitigated through engineering, chemical treatment, and hydromorphological modification; however, these approaches are often prohibitively expensive and the mitigation effect is often temporary. The Mondego estuary in Portugal provides an example of where reducing the water residence time and redirecting inflows and associated nutrient loads to enter a deeper section led to improved water quality status according to some biological and physicochemical indicators (Lillebo *et al.*, 2007). Elsewhere, recovery of eutrophic lakes, dams, and estuaries has been accelerated by (usually costly) technologies that remove nutrients including chemical amendment (with lime, ferric aluminum sulfate, and other phosphorus binding products), aeration, dredging, harvesting macrophytes, flushing to reduce water residence times, and manipulation of the food web (Humphries and Robinson, 1995; Schindler, 2006; Gafsi *et al.*, 2009). Phosphorus binding and filtering products have also had some success situated near to and within streams (McDowell and Nash, 2012) and manipulating light and temperature through shading can also minimize eutrophic impacts (Bowes *et al.*, 2012).

Pollution Swapping

Pollution swapping is a term used to describe the outcome of mitigation practices that is positive for one natural resource but negative for another. Stevens and Quinton (2009) reviewed the pollution swapping potential of mitigation methods (cover crops, residue management, no-tillage, riparian buffer zones, contour grass strips, and constructed wetlands) in combinable cropping enterprises. They found potential for pollution swapping via increased greenhouse gas emission after retaining crop residues, establishing riparian buffer strips, or constructing wetlands for sediment loss control, via increased nutrient leaching due to crop residue retention, and via runoff of nutrients, particularly soluble phosphorus and dissolved organic carbon due to the reduced efficacy of riparian buffers and constructed wetlands over time. In another case, vegetated riparian buffers reduced eroded sediment inputs to streams, however, less suspended sediment was then available to adsorb phosphorus from the water so concentrations of the most algal-available phosphorus form increased as a result (McKergow *et al.*, 2006). The suitability of zero tillage cropping varies depending on the soil type and climate and can lead to increased greenhouse gas emissions from wet heavy clay soils and increased runoff of dissolved phosphorus from accumulation of phosphorus near the soil surface in some circumstances (Soane *et al.*, 2012). **Table 1** summarizes some of the advantages and disadvantages of zero-till cropping in Europe. Mitigation measures, therefore, need to be targeted to the desired outcome and to specific soil types and agricultural systems in order to optimize both mitigation and production.

Governance, Costs, and Benefits of Water Quality Mitigation

Costs and Benefits

The costs of implementation, the technical feasibility, and the adoptability of practices can all constrain the effectiveness of farm practice change measures related to water quality (Buckley *et al.*, 2012). In the European Union, the Water Framework Directive requires the member states to calculate the cost-effectiveness of policies that are implemented. Derogations from Water Framework Directive objectives are allowable where it can be demonstrated that achieving such objectives would involve disproportionate costs (Kallis and Butler, 2001). Calculating cost-effectiveness requires both a measure of the costs of implementation and a measure of the effect of the policies on water quality (Balana *et al.*, 2011). Owing to the complexities of estimating the costs of a suite of mitigation measures in a diverse agricultural socioeconomic and physical landscape, costs are often modeled for a range of actual or theoretical farming systems scenarios (Fezzi *et al.*, 2008). Similarly, physical effects of measures are difficult to measure with certainty (see Section Monitoring and Evaluation of Mitigation Effectiveness) and are therefore frequently modeled (e.g., as marginal abatement costs) rather than measured directly (Fezzi *et al.*, 2010). Importantly, the impacts of mitigation measures vary between agricultural landscapes and over time, so cost-effectiveness needs to be measured or modeled for each landscape and time frame of interest.

Cost-effectiveness of mitigation measures has been modeled for a range of farming systems and landscapes. Source mitigation approaches such as altering the way nutrients are managed at farm level are often cost neutral or cost beneficial (Ribaudo *et al.*, 2001; Zhang *et al.*, 2012b). For example, reducing the risk of nutrient transfer to the aquatic environment through a more efficient use of chemical fertilizer potentially has a double dividend effect of increased returns to agricultural production (Barnes *et al.*, 2009; Huhtanen *et al.*, 2011; Buckley and Carney, 2013). In the United Kingdom, optimal

Table 1 Advantages and disadvantages of plowing and no-till farming in Europe, although not universally relevant to all regions

Moldboard plowing		*No-till*	
Advantages	*Disadvantages*	*Advantages*	*Disadvantages*
Appropriate loosening of topsoil before seedbed preparation	Pan formation below the depth of plowing (from passage of plow sole and tractor wheels)	Lack of compaction below plow furrow	Crop establishment problems during very wet or very dry spells
Complete burial of weeds, crop residues, lime, other amendments and manure	Excessive looseness to depth of plowing	High work rates and area capability	Weed control problems
Inversion allows structural development of lower layers in the topsoil	Exposure of bare topsoil to wind and water erosion	Increased bearing capacity and trafficability	Cost of herbicides, herbicide resistance
Exposes soil compacted at harvest to loosening by weather	High susceptibility to recompaction of topsoil	Reduced erosion, runoff and loss of particulate P	Risks of increased N_2O emissions and increased dissolved reactive P leaching
Increased mixing of nutrients throughout profile	Buried weed seeds brought to the surface	Opportunity to increase area of autumn-sown crops	Reduced reliability of crop yields, especially in wet seasons
Promotes surface drainage leading to warmer, drier seedbed in spring	Reduced trafficability under wet conditions	Stones not brought to the surface	Unsuited to poorly structured sandy soils
Reduced risk of crop diseases	Low work rate and high costs	Drilling phased to take advantage of favorable weather conditions	Unsuited to poorly drained soils
Reliable agronomically in widely differing seasons	Increased CO_2 emissions (fuel and oxidation of SOC)	Increased area capability	Risk of topsoil compaction
Suitable for preparing a seedbed after grass	Greater oxidation of organic matter near surface	Reduced overall costs (fuel and machinery)	Problems with residual plow pans
	Disruption of macrofauna (earthworms, predatory insects)		Increased slug damage
			Unsuited for incorporation of solid animal manures

Source: Reprinted from Soane, B.D., Ball, B.C., Arvidsson, J., *et al*., 2012. No-till in northern, western and south-western Europe: A review of problems and opportunities for crop production and the environment. Soil and Tillage Research 118, 66–87.

cost-effective measures for reducing nitrate leaching were modeled as reducing stocking rates and annual grazing duration, and substitution of cropping area to grassland (Fezzi *et al.*, 2008; Cardenas *et al.*, 2011). For mitigation of phosphorus in runoff, measures that targeted pathways of loss were modeled as more effective than source management, and amongst the most cost-effective of the pathways measures were sediment traps and riparian buffers (£4–8 (US$6.5–13, conversion rate as of 15 December 2013) per kg phosphorus conserved) (Haygarth *et al.*, 2009). In contrast, to mitigate phosphorus exports from dairy farms in Australia and New Zealand, source management strategies were calculated to be more cost-effective (NZ$0–200 (US$0–165) per kg phosphorus conserved) than using amendments or edge-of-field methods to capture phosphorus (McDowell and Nash, 2012). Similarly, in Ireland, source management to deplete surplus P in the soil was identified as the most cost-effective long-term strategy for water quality improvement in the Lough Melvin catchment (Schulte *et al.*, 2009).

At the river basin scale, Roberts *et al.* (2012) identified, through modeling, that costs to implement agricultural, forestry and river management changes sufficient to meet aspired nutrient pollution reduction targets for the impaired Gippsland Lakes in eastern Victoria, Australia (AU$1 billion (US$0.9 billion) over 25 years) exceeded the available environmental budget. They proposed that discussion around environmentally acceptable mitigation measures should center on cost-effective, politically realistic, and technically feasible options. Optimizing the spatial arrangement of measures also increases the cost-effectiveness (Qi and Altinakar, 2011; Doole *et al.*, 2013). Cost–benefit analysis, which places monetary values on both costs and the effects of measures, identified that farmyard improvement and establishing vegetative buffers in critical source areas was effective in reducing phosphorus loss but only became cost beneficial 15 years after implementation in one study (Rao *et al.*, 2012).

Water Quality Governance

Rogers and Hall in Hoekstra (2006) define water governance as "the range of political, social, economic and administrative systems that are in place to develop and manage water resources, and the delivery of water services, at different levels of society." Recognition of the hydrological connection between upland and lowland parts of catchments has resulted in watersheds (river basin boundaries) frequently being used as administrative boundaries for water management (Ferrier and Jenkins, 2010). For example, natural resource management planning within river basin boundaries is an integral

component of the Water Framework Directive legislated in Europe since 2000 (Official Journal of the European Community, 2000). Many countries also share river basin resources (e.g., Mekong, Nile, and Danube), which leads to a high dependency on water quantity and quality governance upstream (Hoekstra, 2006; Murphy and Glasgow, 2009).

A range of policy instruments and mechanisms are used in water quality management, specifically to link upstream and downstream water users (Tognetti and Lawrence, 2002). These mechanisms include regulatory instruments (Statutory Instrument 610, 2010; Daroub *et al.*, 2011), economic instruments, and mechanisms to increase market access (Dabrowski *et al.*, 2009; BenDor and Riggsbee, 2011); modifying organizational structures (Ridley, 2005); education, awareness-building, and participatory approaches (Ridley, 2005; Ulén and Kalisky, 2005; Bergfur *et al.*, 2012; Doody *et al.*, 2012). **Table 2** shows an example of the suite of agricultural policies imposed since 1985 to reduce nutrient transfers to waterbodies in Denmark (Kronvang *et al.*, 2008). The choice of mechanism(s) can be usefully informed by an account of the likely ratio and type of public and private benefits that will occur as an outcome of structural or cultural practice change (Pannell, 2008). Adaptive planning and implementation approaches and fit-for-purpose governance structures are the key features of what is known as integrated catchment management (Hammer *et al.*, 2011; Pahl-Wostl *et al.*, 2012). The potential beneficiaries of mitigation practices such as land and water user groups and commodity boards are being increasingly involved in catchment and water governance (Millenium Ecosystems Assessment, 2005). Payments for ecosystem services (FAO, 2004), and farmer-led movements such as Landcare in Australia (Youl *et al.*, 2006), exemplify recognition of the multiple benefits (i.e., environmental, food and fiber, employment, and community) provided by farmers as stewards of the land.

Monitoring and Evaluation of Mitigation Effectiveness

Accounting for Investments in Environmental Management

Despite the large number of plot to farm-scale studies on technical mitigation options for water quality, there is a relative paucity of evidence that these measures improve water quality at larger spatial scales and also over long temporal scales. Evidence for the effects of mitigation measures on water quality is required to account for public and private funds spent implementing those measures, to inform the scientific foundation for the implementation of a measure, and to help inform expectations about the potential in time and space for those measures to achieve anticipated water quality targets. In some cases expectations of natural resource condition improvement are not realized despite expenditure on research, development, extension, incentives/subsidies, and penalties. In many cases insufficient monitoring exists to demonstrate whether change has occurred. Since 2002, a nationwide evaluation of more than 50 years of conservation practices and 38 catchment assessment studies (the Conservation Effects Assessment Project) was initiated in the United States to account for US$6 billion in expenditure on these practices (Weltz *et al.*, 2005). In Australia, AU$1.4 billion (US$1.25 billion) was spent for more than 7 years to remediate salinity of soils and groundwater; however, there was little evidence of mitigation as a result of this expenditure (Pannell and Roberts, 2010). In the European Union, monitoring the impact that policies affecting agricultural practice have on water quality is mandatory in zones declared as Nitrate Vulnerable Zones (e.g., in England, France, Sweden, Czech Republic, and the Walloon region of Belgium) and is a prerequisite for stocking rates above a European Union cap on manure-nitrogen loading to be permitted. Some member states have identified the whole country as a Nitrate Vulnerable Zone (e.g., The Republic of Ireland, Austria, Luxembourg, Germany, and Denmark) and have accordingly established national and agriculture-specific programs to monitor the impacts of farm practice regulations on water quality (Fraters *et al.*, 2011).

Water Quality Targets and Standards

To measure the effectiveness of mitigation measures, the target condition relating to the water resource needs to be defined. Targets may be defined as chemical load, concentration and exposure, degree of sedimentation, biological quality, hydromorphology, or a combination of indicators (Ongley, 1996). In the United States, total maximum daily loads are used as targets and are defined as the maximum amount of a pollutant that a waterbody can receive and still meet water quality standards. Legislation requires that total maximum daily loads are set for impaired waters; however, implementation of measures to achieve load reductions is largely voluntary or incentivized (Helmers *et al.*, 2007). The European Union Water Framework Directive (Official Journal of the European Community, 2000) set a target for all waterbodies to attain at least 'good' water quality status by 2015 (with 6-year review cycles if the first target could not be met). To monitor progress toward this target, an intercalibration process was conducted (e.g., McGarrigle and Lucey, 2009) so that the water quality status can be compared across the wide range of bioregions and waterbody types across Europe and to account for shared bioregions between jurisdictions. Individual member states have subsequently set their own chemical, biological, and hydromorphological water quality standards. For example, in The Republic of Ireland standards for drinking water and standards designed to protect ecological status have been legislated, with ecological status being constrained by the most limiting of a range of chemical, biological, and hydromorphological indicators (Bowman, 2009). The Australian and New Zealand guidelines for fresh and marine waters require threshold (or 'trigger value') chemical concentrations and biophysical status to be established based on conditions in reference waterbody types (Anon, 2000; McDowell *et al.*, 2013). The choice of indicator of system quality or change can influence assessments of whether mitigation measures have been successful or otherwise. For example, Lillebo *et al.* (2007) found that estuary quality either did not change, improved, or worsened in response to mitigation measures depending on the quality status indicator used in the assessment. Some indicators may not be able to pick up changes due to specific mitigation measures. For example, if loads of nutrients from diffuse sources of episodic overland flow are reduced by

Table 2 Agri-environmental policies implemented in Denmark since 1985 to reduce nitrogen loss from agriculture

Danish policy actions	*Policy measures imposed*
1985: NPo Action Plan to reduce N- and P-pollution	• Minimum 6 months slurry storage capacity • Ban on slurry spreading between harvest and 15 October on soil destined for spring cropping • Maximum stock density equivalent to 2 LU ha^{-1}. (1 livestock unit = 1 LU corresponds to one large dairy cow) • Various measures to reduce runoff from silage clamps and manure heaps • A floating barrier (natural crust or artificial cover) mandatory on slurry tanks
1987: The First Action Plan for the Aquatic Environment (AP-I), aiming to halve N-losses and reduce P-losses by 80%	• Minimum 9 months slurry storage capacity • Ban on slurry spreading from harvest to 1 November on soil destined for spring crops • Mandatory fertilizer and crop rotation plans • Minimum proportion of area to be planted with winter crops • Mandatory incorporation of manure within 12 h of spreading
1991: Action Plan for a Sustainable Agriculture, aiming to reduce N-loses from agricultural fields by 100×10^6 kg N	• Ban on slurry spreading from harvest until 1 February, except on grass and winter rape • Obligatory fertilizer budgets • Maximum limits on the plant-available N applied to different crops, equal to the economic optimum. The economic optimum is calculated annually, taking into account the mineral N in the soil (from a comprehensive soil sampling system) • Statutory norms for the proportion of manure N assumed to be plant-available (pig slurry: 60%, cattle slurry: 55%, deep litter: 25%, other types: 50%)
1998: The Second Action Plan for the Aquatic Environment (AP-II)	• Subsidies to establish 16 000 ha wetlands, designed to reduce nitrate leaching through denitrification and reduced demand for fertilizer • Subsidies to enable reduced nutrient inputs to up to 88 000 ha of areas designated as being specially sensitive with regard to the environment • An expectation that animal feeding practice would be improved to reduce N excretion • A reduction of the stock density maximum to 1.7 LU ha^{-1} • Subsidies to encourage the conversion of 170 000 ha to organic agriculture • The statutory norms for the proportion of manure N assumed to be plant available were increased from 1999 (pig slurry: 65%, cattle slurry: 60%, deep litter: 35%, other types: 55%) • Maximum limits on the application of plant-available N to crops reduced to 10% below the economic optimum • Mandatory 6% of the area with cereals, legumes, and oil crops to be planted with catch crops • Subsidies to encourage afforestation on up to 20 000 ha
2000: AP-II Midterm Evaluation and Enforcement	• Increased economic incentives to establish wetlands • The N assumed to be retained by catch crops must be included in the fertilizer plans • Further tightening of the statutory norms for the proportion of assumed plant-available N in manure. From 2001; pig slurry: 70%, cattle slurry: 65%, deep litter: 40%, other types: 60%; from 2002 pig slurry: 75%, cattle slurry: 70%, deep litter: 45%, other types: 65% • Reduced fertilization norms to grassland and restrictions on additional N-application to bread wheat
2001: Ammonia Action Plan	• Subsidies to encourage good manure handling in animal housing and improved housing design • Mandatory covering of all dung heaps • Ban on slurry application by broadcast spreader • Slurry spread on bare soil must be incorporated within 6 h • Ban on the treatment of straw with ammonia to improve its quality as an animal feed • Options for planning authorities to restrict agricultural expansion near sensitive ecosystems
2004: The Third Action Plan for the Aquatic Environment (AP-III). AP-III is very closely related to the EU-water Framework Directive and the EU Habitat Directive. N-leaching must be reduced by further 13% by 2015	• Further tightening of the request for catch crops

Source: Reprinted from Kronvang, B., Andersen, H.E., Børgesen, C., *et al*., 2008. Effects of policy measures implemented in Denmark on nitrogen pollution of the aquatic environment. Environmental Science & Policy 11, 144–152.

reducing agricultural soil's phosphorus levels, but instream biological quality responds mainly to low-flow nutrient concentrations, then the benefits of the overland flow mitigation measures may not be reflected by biological indicators.

Monitoring Methods

Many of the mitigation measures implemented on farms have been recommended to or by policy makers a result of process studies that relate action to response for individual or small groups of measures (Kronvang *et al.*, 2005; Carton *et al.*, 2008; McDowell *et al.*, 2009). Effectiveness of implementation of measures can also be informed by scenario analysis and modeling of the complex interactions of land management with environmental variables (Silgram *et al.*, 2008; Oenema *et al.*, 2009; Vigiak *et al.*, 2011; van Grinsven *et al.*, 2012). A growing number of studies have also directly measured the impacts of mitigation measures at the catchment scale.

A water catchment, often also referred to as a watershed, is the area of land from which rainfall eventually drains into a surface waterbody. Although surface water catchments are defined by topography and are separated by watersheds, or catchment divides, groundwater zones of contribution to surface waters do not always follow the same topographic boundary. Water catchments provide discrete biophysical spatial units that account for all the anthropogenic and natural chemical, biological, and physical processes that influence the mobilization, transfer, attenuation, and delivery of materials from their sources to receiving surface waterbodies. Headwater catchments that supply water to perennial streams have a significant influence on downstream water volumes and quality despite often being a large distance away (Alexander *et al.*, 2007). An understanding of the degree to which land use and management in these headwater catchments influences inherent hydrological and biogeochemical cycling is therefore important in terms of managing lake, groundwater, and coastal water quality.

Medium-sized headwater catchments, or meso-catchments (also referred to as microbasins (Yates and Bailey, 2006) or small watersheds (Meals *et al.*, 2010)), are commonly 1–100 km^2 and incorporate first- to third-order streams. Measuring the effects of agricultural mitigation practices on water quality in meso-catchments offers advantages over smaller and larger scales in that the size can minimize inputs from non-agricultural pressures, can enable adequate stakeholder involvement in implementing and monitoring agricultural practices, and the integrated and 'net' impacts of attenuating and mobilizing processes and farm types and practices are accounted for (Iital *et al.*, 2008; Fealy *et al.*, 2010). Larger catchments usually include other significant influences such as forestry, industrial, and municipal land use. Also, as the size and scale of the catchment increases, the effects on water quality of individual mitigation practices become more difficult to discern (Kiersch, 2002, **Table 3**).

Approaches for measuring water quality impacts of agricultural mitigation practices in meso-catchments range from measuring water quality over a time series, such as before and after a land management change (e.g., Jaynes *et al.*, 2004), or over a spatial series such as in paired catchments with and without agricultural practice change (e.g., Schilling and Spooner, 2006) or over a gradient of practices or catchment types, and by cause and effect studies that measure sources, pathways, and impacts of practices (e.g., Wall *et al.*, 2011, **Figure 3**).

Table 3 Measurability of land use effects by basin size

Impact type	*Basin size (km^2)*						
	0.1	*1*	*10*	*10^2*	*10^3*	*10^4*	*10^5*
Average flow	x	x	x	x	–	–	–
Peak flow	x	x	x	x	–	–	–
Baseflow	x	x	x	x	–	–	–
Groundwater recharge	x	x	x	x	–	–	–
Sediment load	x	x	x	x	–	–	–
Nutrients	x	x	x	x	x	–	–
Organic matter	x	x	x	x	–	–	–
Pathogens	x	x	–	–	–	–	–
Salinity	x	x	x	x	x	x	x
Pesticides	x	x	x	x	x	x	x
Heavy metals	x	x	x	x	x	x	x
Thermal regime	x	x	–	–	–	–	–

Note: x, measurable impact; –, no measurable impact.
Source: Reprinted from Tognetti, S., Lawrence, T., 2002. Synthesis report of the FAO electronic workshop on Land Water Linkages in Rural Watersheds. FAO Land and Water Bulletin 9. Rome: FAO Land and Water Development Division, with permission from the Food and Agriculture Organization of the United Nations.

A dose–response relationship is also sometimes used to describe the increasing impacts on water quality, where the agricultural pressure increases. The European Environment Agency uses the Drivers-Pressure-State-Impact-Response (DPSIR) framework to assess change in the state (S) of natural resources due to changes in specific drivers (D) and pressures (P) that can have an impact (I) and are the focus of policy responses (R) (EEA, 2012). These conceptualizations highlight the biophysical links in space and time between agricultural pressures and water quality in receiving waterbodies. Nutrients, for example, can be transferred from both point and diffuse sources. Point sources include discharges from intermittent or persistent discrete sources (such as a farmyard) to a water flow pathway or waterbody. Diffuse transfers are derived from nonpoint sources, which are spatially widespread, such as nutrients in soil. The connectivity of these sources with receptor waterbodies depends on the activity of, and attenuation potential along, the water flow pathway to the receptor. For example, overland flow transport of soil and nutrients tends to occur episodically during storms and from parts of a catchment that are prone to generate runoff (e.g., saturated areas and hard surfaces).

Effects of agricultural practice on water quality are challenging to measure at the meso-catchment scales because of (1) the resource constraints associated with establishing sufficient monitoring infrastructure and collecting land management information (Cherry *et al.*, 2008), (2) the uncertainty in cause–effect relationships due to the complexity of hydrological, climatic, biogeochemical, and anthropogenic processes occurring in time and space, and because (3) long time scales are normally needed to identify trends in data due to variation in responses through time and due to time lags between implementation of mitigation measures and responses in water

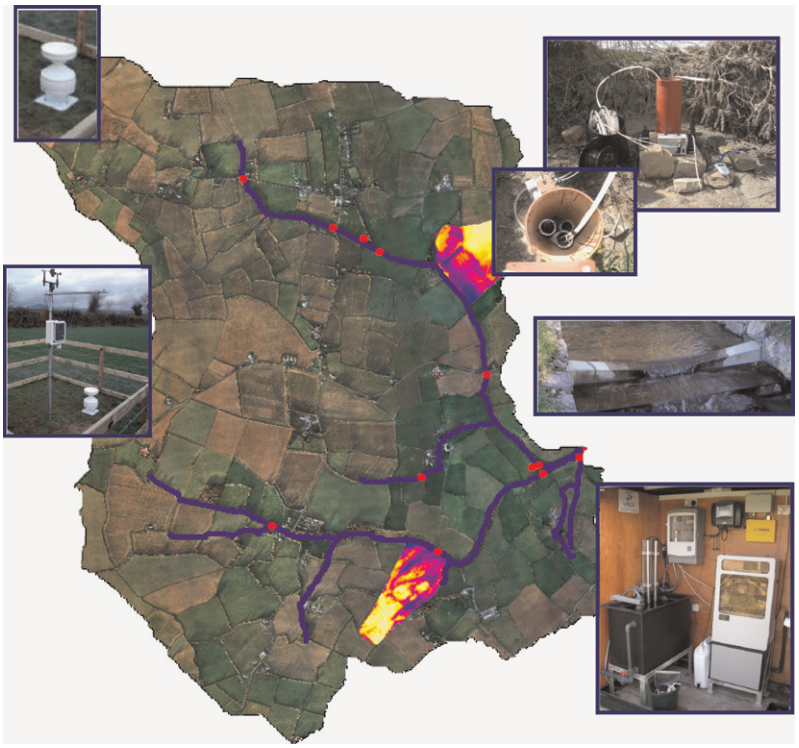


Figure 3 A meso-catchment study of the effects of agricultural nutrient management policies on water quality in Ireland (Wall *et al.*, 2011) includes measurements of subhourly stream discharge and water quality at the catchment outlet, monthly water quality at upstream locations, meteorological parameters, geophysical characteristics and groundwater dynamics and quality in two representative hillslopes, field by field soil nutrient levels, and surveys of farm nutrient management practice and financial data. Imagery courtesy of Teagasc, Ireland.

quality (Spooner *et al.*, 1987; Meals *et al.*, 2010). These challenges are discussed in the Sections Resource constraints, Uncertainty in cause–effect relationships, and Time lags between implementation of mitigation measures and responses.

Resource constraints

Owing to the sometimes 100-fold variation in phosphorus concentrations between baseflow and stormflow in streams, and the likelihood that phosphorus measures are aimed specifically to mitigate surface sources of phosphorus, sufficient sampling intensity of stormflow phosphorus concentrations is required to accurately measure flow-weighted concentrations and loads (Jordan and Cassidy, 2011). Stormflow samples are costly to collect and analyze on a continuous and highly spatially distributed basis. The cost of sampling one site every 7 h for 1 year and analyzing for nutrients was estimated at EUR5000 (US$6900) once-off for equipment and EUR 30 000 (US$41 200) for sampling at 2012 Euro values (Melland *et al.*, 2012). Technologies such as continuous bankside analysis provide opportunities for continuous analysis that importantly capture high flows but are still costly (EUR50 000 (US $68 700) once-off for equipment and EUR30 000 (US $41 200) for sampling) and are often impractical to deploy at multiple locations (Jordan *et al.*, 2007). Passive sampling may offer a compromise between increasing the spatial coverage of sampling and collecting continuous (integrated) nutrient concentrations over storm and baseflows, but the technology is still at the research and development stage (Jordan *et al.*, 2013).

Uncertainty in cause–effect relationships

Effects of measures are difficult to dissociate from potentially overriding/swamping attenuation effects such as groundwater denitrification and stream nutrient uptake and from counteracting effects such as increased intensification of agricultural production (Sutton *et al.*, 2009). The effect of mitigation needs to be large, compared with background processes, so that impacts can be measured and measures can be effectual (Tomer and Locke, 2011). Further to these factors, rates of implementation of mitigation measures are often difficult to control, particularly when there is reliance on voluntary adoption (Yates *et al.*, 2007). Uncertainty in measurement can affect estimates of cost-effectiveness and equity of cost sharing of mitigation (Khadam and Kaluarachchi, 2006). Gren and Destouni (2012) suggest that calculation and presentation of a range of estimates of nutrient loads based on different models is likely to reduce barriers to implementation of measures by identifying commonality in model outcomes (such as consistent attribution of nutrient source or apportionment of mitigation costs) and thus reducing arguments about model outcome uncertainty.

Time lags between implementation of mitigation measures and responses

The time between when a land management activity occurs, and when either a positive or negative response in water quality occurs depends on the type of pollutant and the potential for that pollutant to be mobilized or attenuated along the path it travels to reach a waterbody. Lag times for water

quality improvement in groundwater and groundwater-fed waterbodies after nitrate mitigation can be as long as decades (Fenton *et al.*, 2011), particularly where travel rates through aquifers are slow and there is little opportunity for denitrification (e.g., oxic chalk aquifers in Denmark (Collins and McGonigle, 2008; Fenton *et al.*, 2011; Windolf *et al.*, 2012)). To identify trends in acid-sensitive lake chemistry, 10 years of sulfate chemistry records were predicted to be sufficient for trend analysis but no trends in nitrate were detectable over this time frame due to the biological processes of nitrogen transformations (Skjelkvale *et al.*, 2005). For phosphorus and sediment movement via surface flow pathways, chemical fixation of phosphorus to soil particles and retention and remobilization of particulate and soluble phosphorus forms throughout landscape and channel beds can cause years to pass before water quality improvements from phosphorus mitigation practices occur (Walling, 1999; McDowell *et al.*, 2003; Stutter *et al.*, 2007; Schulte *et al.*, 2010).

Contaminant flow times can impact not only the timing of the response, but also the degree of response. Generally, the longer the contact time between a contaminant and its surrounding flow path media (in this case soils or geological strata), the longer the time available for attenuating reactions (such as sedimentation, denitrification, or phosphorus adsorption) or mobilizing reactions (such as phosphorus desorption and nitrification) to occur (Barrow and Shaw, 1975; Haag and Kaupenjohann, 2001). Even after water quality improvement, however, recovery of aquatic biological structure and function is not guaranteed and can be limited by a complexity of factors including, for example, extinction of endemic species during the eutrophication phase (Schindler, 2006; Carpenter *et al.*, 2011). Using modeling, no improvement in Baltic Sea eutrophication was predicted in response to decreased nutrient loads since the 1980s due to at least a 20-year time lag in water quality response (Gustafsson *et al.*, 2012). Further to time lags that occur in the biophysical response of waterbodies, implementation of cultural and structural changes to farms and farm practice takes time, even where measures are made mandatory by governments or industry (Kronvang *et al.*, 2008).

Observed Effects of Mitigation on Water Quality

Agricultural mitigation measures have had either no measurable effect, or positive, or negative effects on water quality over periods of 3–20 years in meso-catchments in North America, New Zealand, Europe, and Brazil (Melland *et al.*, 2013). Beneficial effects occurred over periods of 1.5–10 years whereas the time it took for these effects to be measured and identified as significant ranged from 4 to 15 years. These response times tend to increase with increasing catchment size. An increasing number of studies have integrated measurement of environmental impact in terms of biological water quality (Bergfur *et al.*, 2012) along with the more traditional hydrological and chemical indicators. In most catchments where beneficial effects of mitigation measures were successfully measured, combinations of measures that address nutrient or pollutant sources, pathways, delivery, and impact have been implemented. Successful farm measures included improved engineering and crop management to reduce runoff and drainage of nutrients and sediment, as well as high rates of implementation of measures across the catchments. In many cases, the potential to measure improvement in one or more water quality indicators was limited by the impact of a few management or weather events. Reasons that water quality did not improve in some studies included the uncertainty inherent in most nutrient flux measurements and a lack of high flow water quality samples that limited the ability of practice impacts to be measured. In other catchments, it was difficult to verify whether a lack of effect was the result of ineffective measures, or because time lags for improvement of water quality were longer than the monitored period. Pollution swapping was identified in some cases. A number of meso-catchment studies attribute water quality improvements largely to changes in land use from a more intensive system such as maize strip cropping to a less intensive system such as alfalfa or due to retirement of land from production altogether (Schilling and Spooner, 2006; Yates *et al.*, 2007; Makarewicz *et al.*, 2009). Where land is taken out of production, or where land use intensity is reduced to mitigate water quality impacts, a potential trade-off between water quality and agricultural output may occur. In contrast, and although environmental water quality targets have yet to be met (Windolf *et al.*, 2012), measures including setting minimum plant-available nitrogen percentages for manure nitrogen, and capping livestock density and allowable nitrogen fertilizer rates in Denmark, have led to a significant decrease in nitrogen concentrations in 84% of monitored streams (Kronvang *et al.*, 2008) and at the same time, crop yields have been sustained and livestock production has increased.

Sustainable Intensification

To feed the world's population, which is projected to increase to 9 billion in 2050, policies enabling 'sustainable intensification' are being promoted (Foley *et al.*, 2011). Sustainable intensification has been defined as "simultaneously raising productivity, increasing resource use efficiency, and reducing negative environmental impacts of agriculture" (Bolton and Crute, 2011). For example, De Klein *et al.* (2012) identified, through modeling of a database of farm system information, that by incorporating targeted mitigation strategies into pastoral dairy production systems increases in milk production without a concomitant increase in nitrogen leaching and greenhouse gas emissions is theoretically possible and needs to be tested in the field. Currently, there are few catchment-scale examples that demonstrate increased production and economic wealth while simultaneously maintaining high-quality surface waters in intensive agricultural settings, highlighting that sustainable intensification remains a continuing challenge.

Summary

All human activities, including agriculture, have an impact on the quality and quantity of freshwater resources. In turn,

maintaining good water quality is imperative for supporting human use of freshwater and sustaining ecosystem function. Agricultural activities can impair water quality through excess movement of soil, nutrients, salt, pathogens, and chemicals from land to water. When reaching waterbodies in excessive amounts, these often-essential components of agricultural systems can be considered pollutants. Plot and field-scale studies have identified a range of technical options that can mitigate off-farm water quality degradation and many options also improve the profitability and sustainability of the farming system. These technical options include limiting the source of pollutant that is available for transport, managing the pathways of travel that a pollutant takes before reaching the waterbody, reducing direct inputs of pollutants into a waterbody, and directly manipulating the waterbody where an impact has occurred.

To maintain or achieve good water quality in agricultural catchments, policies and management recommendations should be developed after consideration of the likely implementation rates (which includes an assessment of cost) and effectiveness of the practices. Consideration of the potential for pollution swapping is also necessary. Headwater river catchments provide useful spatial scales for measuring the effectiveness of practices because these catchments represent the complexity of activities and transport pathways occurring in agricultural landscapes. Catchments are also increasingly used to define administrative boundaries for water resource management. The cost, difficulties in monitoring and collecting information, uncertainty in relating cause to effect, and the long time frames needed to measure changes at these scales is challenging. There is, however, a growing body of evidence that water quality can be improved in intensively farmed landscapes. These studies, and other scientifically robust monitoring and modeling endeavors, are important for informing effective, socially acceptable, and cost beneficial strategies that can facilitate sustainable intensification of agriculture into the future.

See also: Advances in Pesticide Risk Reduction. Market-Based Incentives for the Conservation of Ecosystem Services in Agricultural Landscapes: Examples from Coffee Cultivation in Latin America. Natural Capital, Ecological Infrastructure, and Ecosystem Services in Agroecosystems. Soil: Conservation Practices. Virtual Water and Water Footprint of Food Production and Processing. Water: Advanced Irrigation Technologies. Water: Water Quality and Challenges from Agriculture. World Water Supply and Use: Challenges for the Future

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Land Use, Land Cover, and Food-Energy-Environment Trade-Off: Key Issues and Insights for Millennium Development Goals

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Glossary

Computable general equilibrium (CGE) A computer-simulated neoclassical macroeconomic model based on microfoundations of optimizing behaviors of representative agents, viz., firms, consumers, and governments. Typically, these are used for practical policy modeling of tax, trade, tariff, technology, and policies, among others. It uses popular software, like general algebraic modeling system and general equilibrium modeling package for model implementation.

Global trade analysis project A project housed in the agricultural economics department of Purdue University, West Lafayette, IN, USA. This is a trade model with 57 single and composite sectors with 129 regions (Version 8 of the database). It has 29 agency members, including the World Bank, US International Trade Commission, the Massachusetts Institute of Technology joint program on the Science and Policy of Global Change, and European Commission, among others.

Human capability The capability approach to economic development is pioneered by Nobel Laureate Economist Amartya Sen (Indian National, currently professor of Economics at Harvard University, USA) in the 1980s and developed further in the 1990s. It gave a new dimension to traditional welfare economics by broadening the definition in terms of functioning, entitlements, agency, and human development. The United Nations' human development index and the inclusive wealth index make extensive use of this aspect of human capability where 'freedom' from poverty, deprivation, and any form of degradation is of central importance. Thus, it is multidimensional in nature and could be useful for issues of food and nutritional security linked to land use and climate changes.

Immiserizing effects 'Pauperizing' effects of any policy. It was discussed in the context of trade-led growth. If a growth does not serve the purpose of benefiting the targeted poor, then the effect of such policy is said to be immiserizing. In case of land rush deals, the immiserizing effects refer to the adverse deleterious effect on the landless or marginal landholder of land acquisition for growing food–biofuel crop and feed and reexporting them.

Input–output model Usually known as I–O model, it shows interdependences between sectors of a national economy and different regions. It was developed by Wassily Leontief, and he was awarded the Nobel Prize for his contribution in this area. This is the basis of social accounting matrix and CGE models showing interindustry structure via intersectoral linkages in a square matrix form. It gives a linear system of equations from which solutions for final output, intermediate output, and input–output coefficients are obtained by satisfying Hawkins-Simon condition of nonnegative principal minors for Leontief inverse matrix.

Land rush Since 2009 especially, fueled by food–feed–fuel competition and food crisis, many countries were involved in land acquisition in other countries, such as Madagascar, Cambodia, Pakistan, and Ethiopia, among others. China, South Korea, India, and other emerging economies were active. This is called 'land grab' where most of these countries acquired farmland (and water resources) to grow crops and exported back to their country for consumption (often, it was called land outsourcing by 'The Economist' magazine). This created civil conflicts, riots, disturbances, and political backlash in many destination countries.

Millennium development goals Established by the Millennium Summit of the United Nations in 2000, it has eight goals for development, each having different targets to be achieved by 2015. As it is nearing the target year of 2015, evaluating these goals and achievements is need of the hour. In brief, these goals are the following: halving the extreme poverty, universal primary education, gender balance and women empowerment, reducing child mortality, maternal health improvement, environmental sustainability, and global partnership for development. Until 2013, the progress was uneven across regions.

Social accounting matrix (SAM) The backbone of the CGE model (described above). Every country's SAM captures the flows of major economic activities between agents, viz., firms, households, government, and rest of the economy with expenditure–sales flows, and corresponding flows in a matrix format based on National Income Accounts of a nation. Normally, every country brings out SAM for a particular year and hence it offers a static picture of the economy and is benchmarked so that row and column sums match. Column and row number entries add up to match. The United Nation (UN) standardized national accounts is the basis of extended SAM analysis and SAM multiplier under different scenarios.

Land and Land Resources refer to a delineable area of the earth's terrestrial surface, encompassing all attributes of the biosphere immediately above or below this surface, including those of the near-surface, climate, the soil and terrain forms, the surface hydrology (including shallow lakes, rivers, marshes and swamps), the near-surface sedimentary layers and associated groundwater and

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> geohydrological reserve, the plant and animal populations, the human settlement pattern and physical results of past and present human activity (terracing, water storage or drainage structures, roads, buildings, etc.). (FAO-UNEP, 1997)

> Global demand for agricultural land is on a collision course with environmental protection goals. We face a 'perfect storm' as we struggle to feed a burgeoning population on a diminishing supply of land, water, nutrients, and biodiversity. Despite global efforts, ambitious targets and massive expenditure, there are as yet no general and effective solutions for meeting both nature conservation goals and human needs. (Sayer *et al.*, 2013)

Introduction and Overview

The first quote that opens up the article suggests that the global economy is embedded in the earth's ecosystem and land use and cover is an essential element in ecological economics. On a different note, the second quote gives a cautionary message that land-use practice (e.g., deforestation, grazing, and agriculture) affects ecosystem, biodiversity, and climate and impacts on land cover. The crucial point is, however, anything associated with 'land' involves emotive issues. Anything disrupting its ownership, inheritance, and the change of land-use patterns is bound to create complex problems that could hardly evade one's attention. Economic development depends on land allocation as history of economic thought informs one since the days of the physiocrats who placed immense importance on agriculture sector as the primary source of value and later Ricardo (2004) [1817] expounding rent on land as reflective of its quality. Although the modern era has placed emphasis on industrialization and service sector growth, and land has attracted less than deserving attention, the issue is complex but challenging in its own merit. Green growth or economic development with low carbon emissions has been of immense research interest and great concern among the policy makers. Several factors cause the unprecedented rise in the level of the global carbon emissions and result in change in the status of habitat as well as natural resources. These are as follows: human impact, population growth, fossil fuel combustion, land-use changes, and natural resource depletion, to mention but a few. Vollan and Ostrom (2010) argued that:

> Sustainably managing common natural resources, such as fisheries, water, and forests, is essential for our long-term survival. Many analysts have assumed, however, that people will maximize short-term self-benefits…and warned that this behavior will inevitably produce a 'tragedy of the commons.'

An 'inclusive' approach is needed to understand the impact mechanisms of land use and forestry policies on macroeconomic variables, climate change, and food perils. Thus, it warrants a shift in the paradigm of economic development, based on sustainability and harmony or balance between economic growth and natural resource base. The issue of land use is fundamental to climate change, agricultural production, forestry management, bioenergy, and ownership and property rights tangled with recent rush for land acquisition (land grab and water grab). Food crisis and climate crisis are interrelated, if not two sides of the same coin, i.e., the aspect of natural resource management (NRM) in the broad sense of the term. The rising levels of traces of atmospheric greenhouse gases (GHGs), especially that of carbon dioxide, through greenhouse effects threaten a natural climate control system mechanism that maintains planet Earth's average temperature hospitable to living creatures – plants and animals. With escalation in the level and concentration of the GHGs, like methane, nitrous oxide, ozone, and carbon dioxide, the stability of this natural resource is jolted and the whole ecosphere is facing crisis. Synergistic combinations of climate change and land-use changes have potential to produce dramatic impacts on land cover.

Of late, no other issue has received more attention than the problems of climate change, food perils, global food insecurity, and spiraling of world food prices. Price spiraling in the food and feed stocks is inducing policy makers in developed and developing nations to rethink current agricultural, environmental, and trade policies. Climate change, food perils, global food insecurity, spiraling of world food prices, and economic crisis are affecting humanity. Recent food price crisis starting from 2008 till now shows that hunger and deprivation still remain a key challenge despite rise in agricultural productivity, and the millennium development goals (MDG) are not achieved in terms of balancing sustainable socioeconomic and environmental development and access to food. Global unrest and upheavals over food and feed prices have called for attention into the debate surrounding the food–feed–fuel trinity. With the onslaught of globalization and emergence of Southern Engines of Growth (e.g., Brazil, Russia, India, China, South Africa, and Mexico (BRICSAM) economies and rapidly growing dynamic emerging economies), what is driving the recent variability of land use is the increasing competition for land between burgeoning demand for food crops and growing energy crops based on biofuels. Less reliance on fossil fuels (coal, oil, and gas) and increasing reliance on renewable and environmentally sustainable energy or bioenergy are of paramount importance. In the face of fluctuating oil prices, more emphasis is on investment in innovation technologies related to renewable and environmentally friendly diverse energy mix (for instance, solar, wind, or biomethane power) and preventing depletion of natural resources at the same time. Development needs to be environment-inclusive with a focus on biodiversity. Obviously, this involves efficient management of natural resource, viz., land, coal, oil, and gas – the last three being the major source of fossil fuel combustion leading to emissions. Complex interplay between energy demand, economic growth, greenhouse effects, climate change, and food crisis needs a better multidimensional perspective for its pivotal role in poverty alleviation, human development, and inclusivity. Therefore, the role of agriculture and forestry for development gains due importance as the deadline of MDGs approaches soon, and needless to say, the issue of 'land use and land management' also deserves attention.

Spence Commission on Growth and Development Report (World Bank Commission on Growth and Development, 2008) and World Development Report (World Bank, 2008) have also emphasized on the preponderance role of climate issues and food security amidst unprecedented growth in

demand fueled by economic prosperity and inequality. According to Dell *et al.* (2008), mean global land temperatures have gone up by 1 °C with disparate warming effects across nations. Also, they showed that this affects growth rates and levels in poor countries more than the rich nations. Interestingly, they show the effect of socioeconomic and institutional factors in the wake of such climatic shift causing changes in soil quality, water/sea levels, natural disasters, etc. Thus, an 'inclusive' approach is needed to understand the impact mechanisms of land use and forestry policies on macroeconomic variables, climate change, and food perils. The major challenge is to enunciate the national and international policy approaches to tackle the shortage of food supply without depleting the natural resource base.

If these interconnected issues are not seen in proper perspective with a unified and broader approach, the perceptible gains from economic development will be submerged. After all, the earth's most important and largest reservoir of natural resources is the global ecosphere. For the purpose of this article, the authors focus on land-use changes and environmental degradation as one of the most important causes behind food insecurity. Increasing global integration, economic growth in emerging economies, i.e., BRICSAM, land-use changes, population growth, and increasing fossil fuel usage have led to high level of global carbon emissions leading to GHG effects. This, along with the oil crisis, has led to adoption of biofuel policies. Also, enacting the law of using biofuel and diversion of crops and land away from the usage for food supply has led to food insecurity. Thus, land-use changes and conversion of forest to nonforest use have led to the overall crisis.

All these speak volumes for the necessity of an approach and scientific understanding so as to derive significant policy debate about climate change and its human impact. As Turner II *et al.* (2007, p. 20666) has mentioned:

> Land change science has emerged as a fundamental component of global environmental change and sustainability research. This interdisciplinary field seeks to understand the dynamics of land cover and land use as a coupled human–environment system to address theory, concepts, models, and applications relevant to environmental and societal problems, including the intersection of the two.

Thus, the authors further argued (p. 20667), "Changes in land and ecosystems and their implications for global environmental change and sustainability are a major research challenge for the human–environmental sciences." This emergent land-change (system) science (LCS) research community takes environment as arrays of ecosystems where land-use decisions affect structure and functioning. Sayer *et al.* (2013) had offered a 'ten principle' guidelines for a landscape approach for reconciliation of competing land uses for growing food demand, growing bioenergy demand, conservation, and the ensuing food–fuel trade-off affecting land switching for alternative uses. By viewing land use/land cover changes as a 'coupled system,' LCS models are complex involving 'environmental dynamics' as well as agent-based decision making, technological innovation, socioeconomic issues (e.g., economic crisis), and biophysical disturbances (drought causing adverse effects on food supply and famine, soil degradation, tsunami, etc.). In the similar vein, the 'landscape approach' offers a guideline, in comparison with sectoral approach based on optimization principles and decision making, for an integrated people-centric view where decision-making process has a bearing on the decision-making outcome and also agriculture–environment synergy plays a key role.

Scientific investigation on this issue involves, generally, developing a compendium of database of information for understanding land-use change and land management across regions, building up models of land-use decisions for identifying factors, understanding dynamics, and also developing integrated assessment models (IAMs) encompassing global and regional models. Different modeling approaches are in vogue for studying the effect of climate change and impact analysis. For example, impact assessment models are major framework tools for analyzing climate change policy. As bioenergy is becoming an important factor for transition from fossil fuels to carbon-free energies (in addition to solar and nuclear sources), land use needs to be integrated in analysis of climate or energy policy. Several models have emerged, one of which is the computable general equilibrium (CGE) model that integrates land use changes in economic decision making in a neoclassical mainstream framework involving optimization exercises of economic actors, viz., producers or firms, consumers or households, and governments in a 'global trade analysis project (GTAP)' model. These models are insightful with deficiencies. As Pindyck (2013, p. 860) had said:

> A plethora of Integrated Assessment Models (IAMs) have been constructed and used to estimate the social cost of carbon (SCC) and evaluate alternative abatement policies. These models have crucial flaws that make them close to useless as tools for policy analysis: certain inputs (e.g., the discount rate) are arbitrary, but have huge effects on the SCC estimates the models produce; the models' descriptions of the impact of climate change are completely ad hoc, with no theoretical or empirical foundation; and the models can tell us nothing about the most important driver of the SCC, the possibility of a catastrophic climate outcome. IAM-based analyses of climate policy create a perception of knowledge and precision, but that perception is illusory and misleading.

Also, Vollan and Ostrom (2010) called for analytical research and empirical verification with a 'behavioral theory of human action' by incorporating 'microsituational' and 'broader contextual variables' for explaining cooperation in common resources.

In this article, the author addresses land use and land-use changes from the broader perspective of food perils and climate change causing vulnerability to humanity at large. As this aspect is dealt with in another part of the encyclopedia, the author does not discuss in detail about vulnerability and adaptation; however, in this article he situates the discussion in the wider context of: (1) triple crisis, (2) land-use changes induced by several drivers (e.g., economic growth, energy policy, etc.), and (3) land reforms and land acquisitions. Thus, this article purports to offer distinctive information maintaining continuity of broad themes of the book. In particular, the author has reviewed studies dealing with the aspects of land-use changes, land grab, and climate change from the angles of: (1) practical policy issues and (2) analytical studies modeling the interlinkages. Quite distinctively, this article differs from other articles dealing with different aspects of land

use, such as management, restoration, biodiversity, and conflict between agriculture and urban sprawl. Section Land Use, Land Cover: Reconciliation of Issues and Evidences offers a synoptic overview of basics of land use and land cover (LULC), and driving forces underlying changes in them are discussed in Section Proximate Causes behind Recent Land-Use Changes: Food–Energy–Environment Trilemma, whereas Section Changes in Land Use and Energy–Food Security Trade-Off: From the Perspective of MDG spells out the consequences of such changes in terms of global warming and food security. Section 'New' Lands: Myths and Realities of Land Deal discusses current spate of global land deal and aspects of land acquisition for economic development in some developing nations. The modeling lens of analysis of such issues offers snapshot view briefly in Section Land-Use and Land-Cover Change through the Modeling 'Lens': A Bird's Eye (Re-) View; Section Concluding Observations concludes with some highlighted challenges to date.

Land Use and Land Cover: Reconciliation of Issues and Evidences

Most of the land-use decisions based on economic considerations take into account the market values of land and such decisions could lead to damages to ecosystem services, such as reduction in land for wildlife habitat or recreational space or more GHG emissions leading to decline in human welfare resulting in deprivation in broader connotation of the term. To weigh the benefit and loss, it is needed to adopt the people-centric view of such changes, and human-devised policies should take into account the complexity of natural environment and biodiversity for improving land-use and land-cover changes in terms of arresting climate degradation, maintaining habitat and diversity, and balancing agriculture and forestry. LULC is central to any global environmental change and central to the UN MDG for food security, as they affect food entitlements, nutrition and nourishment, and level of human deprivation. However, it is needed to get a clear understanding of terminologies without using them erroneously interchangeably. In fact, given the huge dimension of work and complex nature of envisaged interactions, as mentioned by Turner II *et al.* (2007, p. 20667),

> …the absence of a universal land-use/cover taxonomy have given rise to metaclassifications of land-use/cover and translations between different classification schemes to compare case studies and aggregate their findings.

Taxonomy: Brief Overview

Land cover refers to the earth's terrestrial surface and subsurface covered by grass, trees, water, bare ground, asphalt, soil, and human structures, etc. Conversions or modifications of such cover means replacement of one cover type by another, for example, thanks to agricultural expansion, forestry, livestock herding, agroforestry practices, deforestation, or land switching, change in the urbanization sprawl, etc. affect features of land and its inherent properties. These changes cause alterations in biodiversity, productivity, soil quality, runoff, material and energy flows in the biogeospheres, gas emissions, carbon cycle, etc. All these are triggered by human action for purposeful activity, such as agricultural expansion or structural shift, like industrialization for economic growth. Therefore, land-use changes, driven by purposeful human activities exploiting the terrestrial surface, cause land-cover changes and hence their biophysical attributes and classification status. How people make use of land and socioeconomic activities defines broadly the land-use classes (e.g., urban land use, industrial land, agricultural land-use, etc.), and the changes in such uses, depending on definitions adopted, define land-cover types and their classification. However, there is no broad consensus on uniform definitions. According to Michigan State University Extension Service:

> *Land use* is commonly defined as a series of operations on land, carried out by humans, with the intention to obtain products and/or benefits through using land resources. *Land cover* is commonly defined as the vegetation (natural or planted) or man-made constructions (buildings, etc.) which occur on the earth surface. Water, ice, bare rock, sand and similar surfaces also count as land cover … In short, land use indicates how people are using the land, whereas land cover indicates the physical land type.

However, a change in one does not imply change in other or vice versa. In other words, having same land cover does not mean same land use as the use of the same land parcel might be for different economic uses; similarly, same land use does not imply identical land cover. According to Consortium for Atlantic Regional Assessment:

> Land use refers to how land is used by humans. In other words it refers to the economic use to which land is put. For example is the land being used for commercial purposes (stores, office buildings, apartments, etc.) or for industrial purposes (factories, assembly plants)? Or is the land being used for recreational or agricultural purposes? On the other hand, land cover refers to the vegetation, structures, or other features that cover the land. For example, is the land covered by grass, by trees, by water, or by large buildings surrounded by a lawn?

Therefore, for a particular land mass, both the aspects of 'use' and 'cover' provide a comprehensive idea about the proper land management so as to facilitate planning and decision making.

To get comprehensive worldwide overviews of the status, the role of Food and Agricultural Organization (FAO) of the United Nations in collecting and disseminating information on agriculture, forestry, food security, and land use–land cover is significant. According to FAO:

> Land use is characterized by the arrangements, activities and inputs people undertake in a certain land cover type to produce, change or maintain it. (FAO-UNEP, 1999) (*Adopted during the course of development of the Land Cover Classification System*, LCCS). A more inclusive definition of land-use is often used in practice. 'Land use' actually includes near-surface water (see the definition of land). Any given area of land is usually used to satisfy multiple objectives or purposes.

The land-use information contains dimensions of action covering 'what,' where,' 'when,' and 'why' aspects behind current land-use practices. Hence, this gives ideas on factors

influencing land-use patterns. Further as per Di Gregorio and Jansen (2000),

> The Land Cover Classification System (LCCS) is a comprehensive, standardized *a priori* classification system, designed to meet specific user requirements, and created for mapping exercises, independent of the scale or means used to map. Any land cover identified anywhere in the world can be readily accommodated. The classification uses a set of independent diagnostic criteria that allow correlation with existing classifications and legends.

They use environmental and technical attributes to further refine the definition. However, due to lack of space, it is not explained in detail in this article.

Land-Use and Land-Cover Data: Overview and Current Status

Land-use practices (e.g., deforestation, grazing, and agriculture) affect ecosystem, biodiversity, and climate and impacts on land cover. To get an impression about the current status, it is important to have information about the available datasets and their coverage across global regions. As mentioned by Hertel *et al.* (2013, p. 6),

> Empirical analysis and operational models particularly suffer from the lack of data. Nordhaus (2006) is a first step towards spatially explicit economic data. In the meantime, spatial down-scaling techniques are also being developed to generate gridded socio-economic data from regional aggregates. Validating these methods against actual spatial data will be necessary for assessing performance and reducing uncertainties across alternative methods.

As seen in Section Land-Use and Land-Cover Change through the Modeling 'Lens': A Bird's Eye (Re-) View, prerequisite for a successful modeling effort depends on good quality data covering the concerned variables. Nordhaus (2006) developed Geographically based Economic Data (G-ECON) database for countries measured with a resolution of 1° latitude and 1° longitude scale covering 25, 572 terrestrial grid cells. Criticizing the modern view of economic growth fueled by capital, labor, and technology, Nordhaus (2006) thought omission of geographical and climate variables makes the discussion on economic development incomplete. His novelty was to introduce the concept of 'gross cell product (GCP)' or 'gridded output,' where grid cell is the unit of data referring to surface bounded by 1° latitude and 1° longitude area with 64, 800 grid cells worldwide. GCP is value added in a specific geographic region and summed across all cells in a country/region. It converts into gross domestic product (GDP)/gross national product. Their estimates of per capita are used in economic modeling exploring climatic and geographic impact on economic activity. According to Nordhaus (2006, p. 3510), "The G-Econ database can be useful not only for economists interested in spatial economics but equally for environmental scientists looking to link their satellite and other geographically based data with economic data." Using annual maps of cropland, pastureland, harvest of wood, and urban land as inputs, Meiyappan and Jain (2012) characterized historical LULC changes and offered datasets useful for modelers for exploring the effects of changes in LULC effects on biogeophysics, biogeochemistry, and hydrological scale, and the datasets are downloadable from a webpage. This dataset is consistent for use with Integrated Science Assessment Model (ISAM). The data coverage is reproduced from the same paper in **Tables 1** and **2**.

However, there are global databases that have been developed for climate change and biofuel policy analysis. One of them is developed by Monfreda *et al.* (2013), who described the global agricultural land-use data of the global agricultural crop and grazing lands using data fusion technique with the collaboration of the Center for Sustainability and the Global Environment at the University of Wisconsin. Sohngen, *et al.* (2013) had developed global forestry data for land-use modeling. This database and model can handle sustainability issues related to forested ecosystem. Also, an integrated land-use database has been developed on the basis of GTAP CGE model by extending to incorporate 18 agroecological zones (AEZ).

Proximate Causes behind Recent Land-Use Changes: Food–Energy–Environment Trilemma

Typically, cross-sectional analyses (a posteriori) and detailed case studies (a priori) explored the reasons for land-use/

Table 1 Result of average estimates (in million km^2 units and rounded to one decimal places) of cropland and pastureland areas for 2001–05 based on datasets, as cited by authors, viz., RF (sourced from Ramankutty and Foley, 1999), HYDE (based on Klein Goldewijk *et al.*, 2011) and HH (based on Houghton, 2008)

Regions	*Cropland*				*Pastureland*			
	RF	*HYDE*	*HH*	*Range*	*RF*	*HYDE*	*HH*	*Range*
North America	2.1	2.3	1.9	1.9–2.3	2.4	2.5	0.0	0.0–2.5
Latin America	1.6	1.5	1.4	1.4–1.6	4.8	5.4	2.8	2.8–5.4
Europe	1.2	1.2	0.1	0.1–1.2	0.6	0.7	0.0	0.0–0.7
China	1.3	1.6	0.7	0.7–1.6	3.5	5.2	0.0	0.0–5.2
South & South-East Asia	3.0	2.9	1.5	1.5–3.0	0.3	0.4	0.0	0.0–0.4

Note: RF – Ramankutty, N., Foley, J., 1999. Estimating historical changes in global land cover: Croplands from 1700 to 1992. Global Biogeochem Cycles 13 (4), 997–1028, HYDE – Klein Goldewijk, K., Beusen, A., van Drecht, G., De Vos, M., 2011. The HYDE 3.1 spatially explicit database of human-induced land-use change over the past 12 000 years. Global Ecology and Biogeography 20 (1), 73–86, and HH – Houghton, R.A., 2008. Carbon flux to the atmosphere from land use changes: 1850–2005. In: A Compendium of Data on Global Change. Oak Ridge, TN: Carbon Dioxide Information Analysis Center. Oak Ridge National Laboratory, US Department of Energy.

Source: Adapted from Table 2 in Meiyappan, P., Jain, A.K., 2012. Three distinct global estimates of historical land-cover change and land-use conversions for over 200 years. Frontiers of Earth Science 6 (2), 122–139.

Table 2 Estimates of area of deforested and forest regrown (1765–2005), as derived using ISAM estimates mentioned in **Table 1** above, based on four kinds of land-use activities (Unit: million km^2)

Regions	*Forest area in 1765*	*Total deforested area*			*Total forest regrowth*		
		ISAM-RF	*ISAM-HYDE*	*ISAM-HH*	*ISAM-RF*	*ISAM-HYDE*	*ISAM-HH*
North America	9.6	3.3	3.5	3.3	2.4	2.0	2.2
Latin America	10.5	3.1	2.4	4.5	1.0	0.6	1.2
Europe	2.5	2.0	1.6	1.3	1.5	1.0	1.1
China	2.3	1.1	1.1	0.7	0.8	0.3	0.7
South & South-East Asia	5.8	2.0	2.1	2.4	0.7	0.4	1.2

Abbreviation: ISAM, Integrated Science Assessment Model.

Source: Adapted from Table 4 in Meiyappan, P., Jain, A.K., 2012. Three distinct global estimates of historical land-cover change and land-use conversions for over 200 years. Frontiers of Earth Science 6 (2), 122–139.

land-cover changes. For example, in different contexts, generally it has been found that deforestation, desertification, agricultural expansion and intensification, industrialization, urban sprawl, forest degradation, fossil fuel demand, etc. lie behind changes in LULC. Generally, proximate causes are direct causes related to actions of individual households, communities, farms recurrently affecting agriculture, forestry, and infrastructure (e.g., road, irrigation, etc.). The core causes underpinning them that trigger a chain of drivers are as follows: demographic, technological, economic growth, environmental factors like tsunami, cyclone, drought, energy crisis, socioeconomic and institutional factors, and biophysical variables. Distinctions between these variables are often blurred as web of factor work conjointly. Separation of exogenous factors and endogenous variables are often difficult. Ojima *et al.* (1994) offered a link between human action and LULC changes via land-use decisions (economic aspect) and biophysical factors (environmental aspect). According to Geist and Lambin (2002), the land characteristics-related biophysical features that impacte on forest conversion, deforestation, and modifications are as follows: soil quality, watercourse, vegetation, topography, forest fires induced by drought, and weed intrusion. The features can further be extended to climatic variability, like rainfall trends and changes in fire regime, dry/wet conditions, and matter for dry land zones such as Sahel or Senegal. In the case of cropland, McConnell and Keys (2005) had found that precipitation, soil fertility, erosion, and vicinity of watercourse matter for agricultural production intensification, often leading to land diversion from one location to another as those biophysical factors change. (Poverty often underlies the incidence of deforestation as nonrich people are involved in forest fragmentation, logging, fossil fuel use, and other activities disturbing bioecosphere (see Geist and Lambin, 2003)). On the basis of household surveys and expert interviews, Qasim *et al.* (2013, p. 146) had found evidence that 'technological and environmental factors, accessibility and proximity to local markets, immense use of firewood, conflicting property rights and other institutional weaknesses, and overgrazing of alpine pasture were the main driving forces for agriculture expansion and deforestation.' The study corroborates the conjecture about the factors affecting land-use changes in developing nations, but for policy insights the author felt the need for framework of a multisectoral, multiscale approach.

For the economic factors and policies, the complex web of interactions among variables, such as input and output prices, subsidies to agriculture, taxes, transportation cost, fertilizer cost, capital flows, credit access (e.g., via rural credit market or microfinance recently), technology, and land reforms, work together to affect land-use pattern and land relations. (In this article, for want of space, issues like land acquisition, share cropping, share tenancy, landless laborers in agriculture, or dual economy surplus labor case that are seen in developing economies like India, Bangladesh, Pakistan, or some Asian nations, are not discussed. These issues are so interesting and complex that they deserve a lengthy discourse, which is beyond the small volume of an article). Mostly, demand-driven causes boosted by recent economic growth, especially in Southern Engines of Growth (e.g., BRICSAM), have triggered a change in conspicuous consumption habits with diversion from cereals to cash crops or even dairy or meat products. Also, the Green Revolution (agrotechnological innovation) has led to the emergence of capitalist farming with high-yielding variety seeds, requiring different input combination as compared with subsistence farming. As Geist and Lambin (2002) had discussed, in Asia, Africa, Latin America, and in most of the regions, forest conversion and land degradation in dry land or cropland have been triggered by economic and technological factors, such as market growth, commercialization (consumption demand surge, sectoral diversification with economic growth, and structural transformation), market failures and nonmarket benefits (like conservation easement, agroforestry, ecotourism, etc.), urban industrial expansion, biotechnological change (biotechnology, GM Crops, Fertilizer, and Pesticide), poor timber/wood extraction techniques, economic deprivation and impoverishment, deficiencies in technical knowledge, and absorptive capacity (Das and Alavalapati, 2003; Das, 2007). Different geographical regions have different contributory factors. For example, in sub-Saharan Africa, changes in livestock practices, replacement of grazing with cropping, land intensification (operating at the intensive margin of land), access to capital and insurance markets, public investment in technology, water management, etc. played a role. However, in case of Latin America, as McConnell and Keys (2005) mentioned, market-driven agricultural expansion, technology adoption, shifting to new crops, credit market functioning and infrastructure (road and irrigation), etc. played a role. In contrast, for Asia, similar factors work, but more important role could be ascribed to adoption of agroforestry practices, land tenure structure, large-scale irrigation, frequency of cultivation and growth of

cultivars, labor bottlenecks, change in urban consumption habits due to economic growth, and agricultural policies like subsidies, tax, credits given to farmers with poor background, etc. in all these regions, phases of industrialization, and more recently, the service sector-led growth has caused dramatic shift in macroeconomic structure causing agriculture to shrink considerably. This causes changes in land use and land ownership, resulting in income distribution effects (see World Bank: World Development Report 2013 for grand overview of income inequality and occupational displacement in a macroeconomic context). (As this article introduces related aspects of land-use changes, discussion of this aspect is the subject matter of separate topics in the discipline of economics of poverty, income distribution, and inequality in the wake of structural changes. This does not undermine the purpose as the author touches on the important aspect for benefit of readers' familiarity with the important issue at this juncture of globalization and economic crisis inflicting rich and nonrich alike.) Demographic factors like population explosion in countries like India and China are a matter of concern; furthermore, aging population is another concern. Starting from Malthus (1798) and followed by Ehrlich and Holdren (1971), the negative impact is emphasized with controversial debate.

With global interconnectedness via trade and foreign direct investment, increase complexity and uncertainty looms large. For example, trade in forest products, rangeland modifications, urbanization led by migration, eco labeling and global organic food networks, trade in GM goods, land rush where foreign production is outsourced in the less-developed countries like Africa (Das, 2013) affect biodiversity via land-use changes (Geist *et al.*, 2006).

As Godfray *et al.* (2010, p. 812) had argued:

> Continuing population and consumption growth will mean that the global demand for food will increase for at least another 40 years. Growing competition for land, water, and energy, in addition to the overexploitation of fisheries, will affect our ability to produce food, as will the urgent requirement to reduce the impact of the food system on the environment. The effects of climate change are a further threat. But the world can produce more food and can ensure that it is used more efficiently and equitably. A multifaceted and linked global strategy is needed to ensure sustainable and equitable food security …

Moreover, Godfray (2011) argued that the threat of climate change and sustainability thwarts development and accentuates food crisis, pushing people more into food poverty. The need for sustainable intensification and global cooperation to close the yield gap is emphasized. Quoting Godfray *et al.* (2010, p. 813):

> Producing more food from the same area of land while reducing the environmental impacts requires what has been called 'sustainable intensification.' In exactly the same way that yields can be increased with the use of existing technologies, many options currently exist to reduce negative externalities. Net reductions in some GHG emissions can potentially be achieved by changing agronomic practices, the adoption of integrated pest management methods, the integrated management of waste in livestock production, and the use of agroforestry. However, the effects of different agronomic practices on the full range of GHGs can be very complex and may depend on the temporal and spatial scale of measurement. More research is required to allow a better assessment of competing policy options. Strategies such as zero or reduced tillage (the reduction in inversion ploughing), contour farming, mulches, and cover crops improve water and soil conservation, but they may not increase stocks of soil carbon or reduce emissions of nitrous oxide. Precision agriculture refers to a series of technologies that allow the application of water, nutrients, and pesticides only to the places and at the times they are required, thereby optimizing the use of inputs. Finally, agricultural land and water bodies used for aquaculture and fisheries can be managed in ways specifically designed to reduce negative impacts on biodiversity.

Global unrest and upheavals over food and feed prices have called for attention into the debate surrounding the food–feed–fuel trinity. Price spiraling in the food and feed stocks is inducing policy makers in developed and developing nations to rethink current agricultural, environmental, and trade policies. Obviously, this involves efficient management of natural resource, viz., land, coal, oil and gas – the last three being the major source of fossil fuel combustion leading to emissions. In short, higher food prices have been fueled by many factors starting in 2008–09; for example, dry weather in critical growing regions (like drought in Australia and Ukraine), a cyclone-hit Myanmar in 2009 causing further spiraling as it was siphoning off from other sources like Thailand and Vietnam, poor yields in countries like Bangladesh (hit by floods and devastating cyclone), increasing oil prices, rising production and delivery costs, etc. These are typically the natural supply shock. Rising oil prices coupled with growing demand for fertilizer has caused rise in fertilizer prices. However, supply of fertilizer has not picked up because of oil prices. Similarly, rising prices of pesticides and fuel are factors behind soaring prices. Fertilizer shortage is another factor underlying the proximate cause of dwindling supply factor for the latest rise in food prices. Growing demand due to population expansion, biofuel-led demand for corn palm oil, natural gas supply shortage, pollution factor for chemical fertilizer based on fossil fuels, tight supply due to expensive process of expansion of production, etc. have triggered a price rise.

However, growing demand from emerging economies, especially China and India, leads to higher food prices despite being unaffected by credit crunch. Surge in world demand spurred by growing world population, higher income, diet changes, and asymmetric global expansion has fueled the price hike to such an extent that with inadequate supply the impending crisis worsens for the people with less income.

Aside from these proximate conventional supply–demand factors, the underlying causes feeding into them are the concern for environmental factors, especially the GHG emission, global warming, and environmental degradation. Also, agricultural crops like soybeans, sugar (in Brazil), and corns are increasingly used to make biofuels – biodiesel and ethanol – as transportation fuels. Subsidizing and enforcing usage of biofuels have led to their widespread use as motor fuels and, in fact, people have argued about the possible contribution of diversion of food crops to fuels in causing food perils. According to Banse *et al.* (2013a, p. 59), following an equilibrium simulation model (Modular Applied General Equilibrium Tool (MAGNET), on which more in Section

Land-Use and Land-Cover Change through the Modeling 'Lens': A Bird's Eye (Re-) View) for policies to reduce emissions from deforestation, degradation, and energy crisis, the finding is summarized as:

> [At] the global level, the EU and US biofuel policies contribute to the increasing demand for biofuel crops. But other countries, such as Brazil, Canada, India, Thailand, Philippines and South Africa, that also introduced mandatory biofuel targets contribute to an even higher extent to increasing world prices for agricultural products driven by food use for fuel. With increasing agricultural output, total agricultural area is projected to increase by 5%, while production of biofuel crops increases by around 19% indicating a more intensive production of biofuel crops at the global level. Even the strong increase in crop production in countries implementing biofuel policies exceeds domestic supply, and the imports of these biofuel crops from other parts of the world which do not implement biofuel policies are projected to increase significantly. The analysis shows that apart from direct effects of an enhanced demand for bioenergy on production and land use, the indirect effects of biofuel policies dominates. Additional production of biofuel crops within and outside countries with voluntary and mandatory biofuel policies leads to strong indirect land use changes and associated GHG emissions. The systematical variation of factor mobility indicates that the 'burden' of global biofuel policies is not equally distributed across different factors within agricultural production. Agricultural land as the pre-dominant and sector-specific factor is regardless of different degree of inter-sectoral or intra-sectoral factor mobility the most important factor and limits the expansion of agricultural production.

Many studies using simulation general equilibrium models (recursive dynamic or comparative static CGE models as discussed in Section Land-Use and Land-Cover Change through the Modeling 'Lens': A Bird's Eye (Re-) View) have found this trade-off between biofuel feed/food stock and energy demand. For example, Birur *et al.* (2008) had identified six drivers behind biofuel boom as crude oil price hike, replacement of a chemical causing pollution (e.g., methyl-tertiary butyle-ether) by ethanol in the United States, subsidies for biodiesel and ethanol in the European Union and the United States, and performed historical simulation for 2001–06 to find that there is trade-off between feed and bioenergy crops. In a similar vein, Hertel *et al.* (2013) had found in a comparative static assessment under exogenously specified biofuel expansion forecasts over 2006–35 period that under International Energy Agency's 'New Policies' scenario, biofuels account for nearly one-fifth of global land-use change over 2006–35 period. In the absence of GHG regulation, the welfare-maximizing path for global land use allocates 170 Mha to biofuel-fed stocks by 2100, with the associated biofuel accounting for approximately 30% of global liquid fuel consumption. Villoria and Hertel (2011) considered two models under alternative land demand specification to show that geographic trade patterns matter under biofuel policies for indirect land-use effects depending on elasticity parameters.

As Tilman *et al.* (2009) found in the nature of the trilemma, they emphasized the need for third-generation biofuels based on microalgae and other sources in order to avoid 'biofuels done wrong!' According to them, land-use decisions for biofuel could affect both food–feed stocks and also, via indirect land-use effects biofuels could translate into negative effect on GHG reduction (the whole purpose of biofuel demand), biodiversity loss, and further food price escalation. Therefore, they call for (Tilman *et al.*, 2009, p. 271), 'dramatic improvements in policy and technology are needed to reconfigure agriculture and land use to gracefully meet global demand for both food and biofuel feedstocks.' In a similar vein, Godfray (2010, 2011) had called for 'more sustainable food system' on the basis of global cooperation between developed and developing countries in terms of technology transfer for closing the yield gap. It is quite apt to quote Godfray and Charles (2011, p. 19846),

> Increasing prices will reduce demand, but in a complex way, because food is not any other commodity. People literally have to eat to stay alive, so, as prices in- crease, an increasing fraction of poor people's incomes will be spent on food. However, between 0.75 and 1 billion people today do not have sufficient economic access to food, and even though populations in the future are likely to be wealthier on average, significant increases in food prices will hinder or re- verse progress in reducing hunger. Thus, if we do nothing, economic forces may prevent demand from increasing as high as Tilman *et al.* (2009) expect, but chiefly because people are forced to remain in food poverty – something most people would agree is unethical and would pose grave risks for global political security.

Concerned about land-use/land-cover changes, Godfray (2010, 2011) further argued,

> Producing more food with less effects on the environment requires a radical shift in thinking by the agricultural and environmental communities. The goal for agronomists and plant and animal breeders is not now simply to increase yields but to optimize across a much more complex set of objectives, with a particular emphasis on increasing input efficiency and reducing harmful outputs. Innovation in areas such as precision agriculture, soil science, and climate-smart agriculture are urgently required to make what has been called sustainable intensification a reality. In addition, it will be critical to align market incentives to promote more sustainable food production, i.e., to internalize the costs (or benefits) of the negative (or positive) externalities. For the environmental community, a major challenge is to accept the inevitable loss of some biodiversity that feeding 9 to 10 billion people will entail and to work to develop integrated land use policies that minimize this harm.

Aside from those, increasing urban uses of land surface also diverts land from agriculture, forestry, farmland, and that affects biodiversity. By doing meta analyses of 326 studies based on remote-sensed images, Seto *et al.* (2011) had estimated an increase in urban land expansion of 58 000 km^2 between 1970 and 2000. Highest rates of expansion have taken place in emerging economies and developing countries, like India, Africa, and China, whereas for the United States, it has been the largest in total urban land expansion. According to the study, 'by 2030, global urban land cover will increase between 430 000 km^2 and 12 568 000 km^2, with an estimate of 1 527 000 km^2 more likely.' The proximate causes are various, viz., growth in per capita GDP, increasing capital flows due to global integration, population growth, land use policy, and transport costs, etc.

Without any solution in vision, this leads to deprivation, starvation, and famine. Growth in incomes has led to increasing imports and restrictions or export bans and taxes or ceilings/quotas from the net exporter, thereby restricting availability of grain supplies on international markets, tightening supply conditions, and triggering further rise. There is a need for effective social and political processes to assure biotechnology's wise and wide usage in equitable way to develop

products available publicly so that the benefits accrue to all for adaptation and adoption, especially in developing countries. The role of public research systems (national innovation systems and policy) in promoting use of these technologies to produce new crop varieties is important. "We hope that world leaders coming to Rome will agree on the urgent measures that are required to boost agricultural production, especially in the most affected countries, and at the same time protect the poor from being adversely affected by high food prices," said Food and Agriculture Organization (FAO) Director-General Jacques Diouf. It calls for support to agricultural research that serves the needs of poor farmers. To prove the Malthusian predictions wrong again, the roles of science and technology for yield and fertilization are crucial. Typically, agricultural biotechnology encompasses sophisticated technologies, like tissue culture, DNA-based genetic markers, DNA chips, and other DNA-based diagnostic techniques to identify and create new varieties of traits in crops. These have immense potentials for benefits in developing countries where access to transgenic or genetically improved crop varieties can be used as a solution for addressing the difference between abject poverty, hunger, malnutrition, and a sustainable livelihood with appropriate calorie intake. Developing genetically altered new crop varieties with more micronutrients and essential nutritional value will compensate for deficient diets in poor nations. For example, soybean-derived biofuels are healthy substitute for petroleum-based home heating fuels. Norman Borlaug had also reiterated the necessity of global cooperation and collaborative system of international biotechnology research to meet the MDG by 2015. Inventions such as soybean cultivation with zero-tillage technology, use of lignocellulose-based plant feedstock and waste biomasses for conversion into biofuels, and increasing yields of bioenergy crop production, rice, and wheat could lead to net energy gain, environmental benefits, and economic efficiency without curtailing food supplies.

Thus, the policy responses could be: shifting to higher yields via engineered crops by investment in agricultural research, better chemical fertilizer, and better seed varieties, so that there is limited agricultural runoff causing environmental damage to ecosystem. Improving productivity could ease the constraint far better than the typical tax-mix policy – even for net food importer or net exporter, the agricultural technology improvement or production shifting could ease the supply constraint in the face of severe demand constraint. If government subsidizes biotechnology research or inputs, then the technological change could help the net food importer to become net producer and supplier in medium to longer run.

Changes in Land Use and Energy–Food Security Trade-Off: From the Perspective of MDG

Historically, economic development and standards of living were governed by socioeconomic variables as well as geographic (shaping institutions) and climatic factors (Acemoglu and Robinson, 2012; Diamond, 2005). As Nordhaus (1991, 2006, pp. 3510–3511) says,

> …one of the major factors in economic development has been the movement from climatic-sensitive farming and into climate-insensitive manufacturing and services. In 1820, 72% of U.S. employment was on farms, whereas by 2004, the share was down to1.2%. … Current theories and empirical studies of economic growth today give short shrift to climate as the basis for the differences in the wealth of nations. A review of a handful of textbooks on economic development shows that climate is confined to a few lines in hundreds of pages.

Thus, any discussion on LULC changes and associated climate change is incomplete without consideration of its impact on poverty, food security, and nutritional security affected by such changes in land use and lying at the core of human development. As per the MDG and FAO's definition of food–nutrition–environmental sustainability, it is imperative to address food security as part of environmental and climate change issue as well as the issue of food/feed trade-off. Nordhaus (1991, 2006) had shown the importance of having information on geographical variable (data on GCP as mentioned in Section Land Use and Land Cover: Reconciliation of Issues and Evidences) for studying impact of geography and poverty in the African context. Hertel and Rosch (2010) had mentioned that exploring the much ignored link between climate change and poverty is 'vital for the formulation of effective policy responses to climate change.' In particular, they show that climate change impacts are transmitted to the nonrich via agriculture and hence this sector is susceptible to climate change mitigation strategies.

According to Fan (2013), approximately 870 million people (1 in every 8) are undernourished and above 2 billion people lack severe deficiencies in macronutrients (IFPRI 'Walk the Talk'). The rising food prices and resultant food insecurity have a pernicious effect on human development via health damage as well as exacerbating inequality, leading to socioeconomic disturbances. Nordhaus (1991, 2006) had shown that 'geography handicap' could explain output differences between countries like Africa and developed countries. With the newly constructed database (G-ECON), it was shown that geographic conditions (e.g., temperature, precipitation, soil, and coastal proximity) determine economic disadvantage of nations like Africa compared with the temperate regions and also estimated negative impacts on world output due to doubling of CO_2 equivalent GHG emissions. Therefore, any change that causes land use/cover to change will impact on food–energy–environment equilibrium and might cause differences in output per capita via GCP.

As is well known, instead of conventional indicators of economic progress as GDP, the United Nations Human Development Report has developed the alternative concept and dimension of 'wealth' based on human capability, access to basic rights, and entitlement as well as, income, literacy, and gender balance (see Sen, 1995). Also, the UN's University (UNU) International Human Dimension Programme (UNU-IHDP) on Global Environmental Change echoes with the same concern as expounded by Stiglitz–Sen–Fitoussi Commission Report in 2009. Therefore, UNU-IHDP and UNEP (2012) focuses on human as well as natural capital as the basic ingredient of wealth. Developing an Inclusive Wealth Index (IWI) to include a human, physical, manufactured, and social and natural capital, a new dimension has been added to the

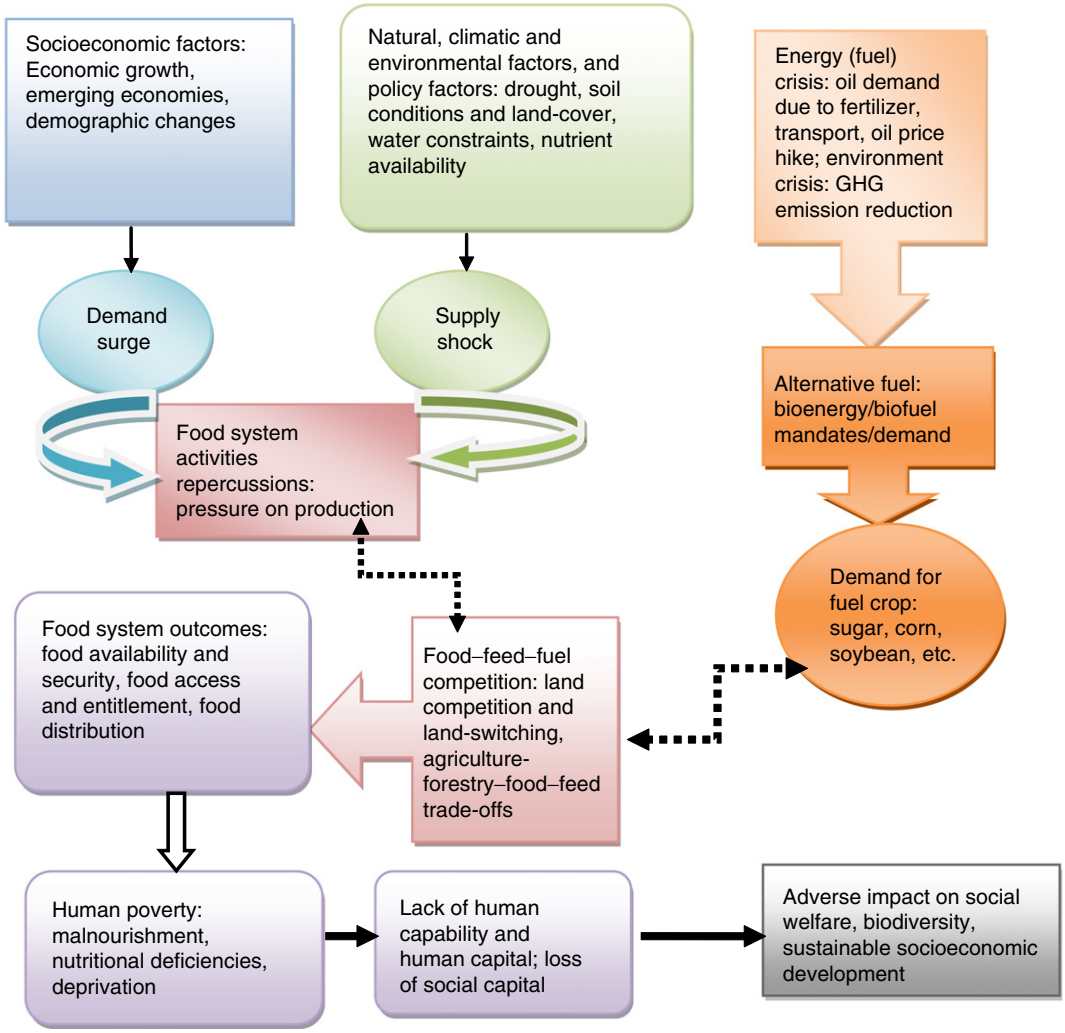


Figure 1 Drivers behind food–feed–climate change trilemma and its poverty impact.

concept of economic prosperity on a sustainable basis. As GDP is an inadequate measure, this new index captures all-round aspects of economic development. According to the report's balance sheet,

> While 19 out of the 20 countries experienced a decline in natural capital, six also saw a decline in their inclusive wealth, putting them on an unsustainable track, Russia, Venezuela, Saudi Arabia, Colombia, South Africa and Nigeria were the nations that failed to grow. The remaining 70 per cent of countries show IWI per-capita growth, indicating sustainability. 25 per cent of countries that showed a positive trend when measured by GDP per capita and HDI were found to have a negative IWI per capita. The primary driver of the difference in performance was the decline in natural capital. There are clear signs of trade-off effects between the different forms of capital.

Taking a holistic view, land-use change and climate policy could affect food and nutritional security and can endanger poverty impact. This nexus is described in Figure 1.

According to Wheeler and von Braun (2013), climate change has an adverse impact on controlling hunger and malnutrition. It hinders the progress toward a world free of hunger and deprivation. To quote them (Wheeler and von Braun, 2013, p. 508):

> Climate change could potentially interrupt progress toward a world without hunger. A robust and coherent global pattern is discernible of the impacts of climate change on crop productivity that could have consequences for food availability. The stability of whole food systems may be at risk under climate change because of short-term variability in supply. However, the potential impact is less clear at regional scales, but it is likely that climate variability and change will exacerbate food insecurity in areas currently vulnerable to hunger and undernutrition. Likewise, it can be anticipated that food access and utilization will be affected indirectly via collateral effects on household and individual incomes, and food utilization could be impaired by loss of access to drinking water and damage to health. The evidence supports the need for considerable investment in adaptation and mitigation actions toward a climate-smart food system that is more resilient to climate change influences on food security. Climate change and associated bioenergy policy will cause a shift in land-use thereby causing micronutrient deficiencies among children and adult alike. Moreover, as further emphasized, food security is illustrated by the United Nations' Food and Agricultural Organization (FAO) definition: (i) the availability of sufficient

quantities of food of appropriate quality, supplied through domestic production or imports; (ii) access by individuals to adequate resources (entitlements) for acquiring appropriate foods for a nutritious diet; (iii) utilization of food through adequate diet, clean water, sanitation, and health care to reach a state of nutritional well-being where all physiological needs are met; and (iv) stability, because to be food secure, a population, household or individual must have access to adequate food at all times. It is extremely challenging to assess precisely the current status of global food security from such a broad concept. However, the big picture is clear: About 2 billion of the global population of over 7 billion are food insecure because they fall short of one or several of FAO's dimensions of food security. Enormous geographic differences in the prevalence of hunger exist within this global estimate, with almost all countries in the most extreme 'alarming' category situated in sub-Saharan Africa or South Asia.

Following the discussion, the author offers a flow chart showing the trilemma and its impact on human development. As the diagram in **Figure 1** depicts, food security involves many dimensions, such as malnutrition, hunger, poverty, nutritional deficiencies, and promotion of environmentally sustainable green growth. As Sen (1995, p. 209) had argued: "Indeed the environmental challenge is not just that of food production – there are many other issues related to population growth and overcrowding. [In fact], a tendency to concentrate on food production only, neglecting food entitlement, can be deeply counterproductive." The diagram represents such complex holistic view.

'New' Lands: Myths and Realities of Land Deal

"Land is not just a resource to be exploited, but a crucial vehicle for the achievement of improved socioeconomic, biological, and physical environments." – Food and Agriculture Organization, United Nations (FAO) (1999), "Cultivating our Futures: FAO /Netherlands Conference on the Multifunctional Character of Agriculture and Land."

Here the author discusses the recent episodes of the rush for transborder land acquisitions in the wake of food scarcity; this is especially by emerging economic giants, with its aftermath like food riots, civil unrest, and backlash. This is linked to water grab issues, which are covered in other article in this encyclopedia. As international actors tap into lands beyond their borders, in the wake of a global systemic crises of food–feed–fuel, endangered by financial crisis, it is a contentious issue as land plays a central role in developing economies and least-developed countries, because of its insurmountable importance related to identity, property rights, livelihoods of the inhabitants, and most importantly, at this juncture, its inextricable linkages to the burning issues of the problem of 'unholy trinity' of food (in-) security, feed (in-) sufficiency, and fuel crisis (related to climate change). However, the entire picture is murky and lack of academic literature and analysis leads one to consider media reports – biased or impartial – concerning the impacts (see **Table 3**).

There are differences in size and terms of contract negotiations and often it does not involve direct land acquisitions, but rather involves food supplies via contract farming or investment in irrigation or agricultural/rural infrastructure. The latter is being welcomed to some extent, as expected, because that could generate beneficial effects to spillover to other segments (Von Braun and Meinzen-Dick, 2009). In other aspects, it has led to incidents like civil unrest and overthrow of the government in Madagascar in 2009 over the South Korean company Daewoo's attempt to acquire 1.3 million hectares for maize and oil palm; Mozambique resisted a Chinese lease deal; and some other incidents as well – to mention but a few (see Daniel and Mittal, 2009, 2010; Kugelman and Levenstein, 2009 for detailed unfolding of incidents). In this context, the author quotes Von Braun and Meinzen-Dick (2009):

Well-documented examples are scarce, and some reports are contradictory. This lack of transparency limits the involvement of civil society in negotiating and implementing deals and the ability of local stakeholders to respond to new challenges and opportunities.

It presents a table of media reports (**Table 3**) on such deals for the available range of countries, although the reports are not specific about the size of the land deals. Deininger *et al.* (2011) covers 14 countries, and it documents that the total amount of reported large-scale farmland deals sum to 45 million hectares even before the end of 2009 alone, in comparison with the average yearly rate of expansion of 4 million hectares spanning the decade up to 2008 (Deininger *et al.*, 2011, p. vi). However, all the reports unanimously agree that 'little is known so far (Von Braun and Meinzen-Dick, 2009, p. 3).' Below, the author reports the major 'observations' or evidence-based

Table 3 Examples of media reports on overseas land investments to secure food supplies, 2006–09

Country investor	*Country target*	*(Hectares)*	*Current status*	*Source*
Bahrain	Philippines	10 000	Deal signed	Bahrain News Agency (2009)
China (with private entities)	Philippines	1 240 000	Deal blocked	The Inquirer (2009)
Jordan	Sudan	25 000	Deal signed	Jordan Times (2008)
Libya	Ukraine	250 000	Deal signed	The Guardian (2008)
Qatar	Kenya	40 000	Deal signed	Daily Nation (2009)
Saudi Arabia	Tanzania	500 000	Requested	Reuters Africa (2009)
South Korea (with private entities)	Sudan	690 000	Deal signed	Korea Times (2008)
United Arab Emirates (with private entities)	Pakistan	324 000	Under implementation	The Economist (2008)

Note: A more extensive listing of media reports on overseas land investments is available on IFPRI's website at http://www.ifpri.org/ pubs/bp/bp013Table01.pdf. Well-documented examples are scarce, details on the deals are often murky, and some reports are contradictory. IFPRI invites observers to share evidence-based information on the listed and on new land deals by posting a contribution on IFPRI's blog at http://ifpriblog.org/2009/04/24/landgrab.aspx.

Source: IFPRI has compiled this table from media reports. The responsibility for the accuracy of the information presented here, however, lies with the reporting media.

information from them in order of their chronological appearances in the domain.

The study by Von Braun and Meinzen-Dick (2009) mentioned that the proliferation of land acquisitions are targeted by the countries with higher capital endowment and water scarcity (say the Gulf States) and high population with food insecurity (emerging engines like India or China) toward the host countries depending on their geographical proximity, but mostly, on the basis of their low labor cost, abundance of land and water, and favorable climate for crops. But aside from crops, biofuels (first or second generation) are also produced in these lands, causing shift in land-use patterns, and thereby defying the much-proclaimed objective motivating these deals. According to that study, approximately 15 to 20 million hectares of farmland have been negotiated or under transactions over last several years and more so. It is now at the 'systemic' crisis point. Also, Kugelman and Levenstein (2009) reported (quoting The Economist) that it is approximately one-fifth of the EU farmland and of the same size of France's farmland. (This is the study by Woodrow Wilson Centre for International Scholars on "Land Grab? Race for the World's Farmland.) Between 2006 and mid-2009, as reported by IFPRI, foreign actors had sought or secured approximately 37–49 million acres of farmland. With Ethiopia being one of the hungriest country in the world with population of 13 million, it is leasing out approximately 7.5 million acres of its fertile land to investors who are exporting food back to their own countries of residence (see Daniel and Mittal, 2009, 2010). The study by Cotula *et al.* (2009) covered qualitative interviews and case studies for five sub-Saharan African and other countries, viz., Ethiopia, Ghana, Madagascar, Mali, and the Sudan and Mozambique and Tanzania. As Cotula *et al.* (2009) mentions, "international land deals and their impacts remain still little understood."

To tackle the issue of conflicting objectives, Von Braun and Meinzen-Dick (2009) offered a 'dual approach.' First, by establishing a transparent code of conduct for the host and the foreign investors and second, designing appropriate policies by the host government to tap the opportunities and controlling the adverse effects, they fought to counter the immiserizing effects. Transparency, sharing the benefits with the locals, and adherence to national trade policies when domestic supply is at stake are emphasized. Moreover, the report mentions:

> At the root of foreign investments in agricultural land are the food crisis and the volatility in food markets that have undermined trust in trade on the side of importers. The combination of an international code of conduct, on the one hand, and improved domestic agricultural policies, on the other hand, would make a virtue of the investments that investors consider a necessity and facilitate win-win outcomes. Well-designed foreign direct investment could embed transfers of knowledge and institutional strengthening into the investment and related trade flows, thereby improving productivity in the target countries of these investments. In the longer run, a healthy trade relationship could grow out of such investment islands, building trust in trade, at least on a bilateral basis and potentially more broadly, in an increasingly volatile world food system.

According to Cotula *et al.* (2009), most of these countries lack proficient mechanism to ensure local rights, production for domestic supply over exports, protecting local interests, livelihood, and welfare and thus the 'win-win' situation should be viewed with cautious optimism rather than harping on myopic vision of potential benefits without serious study. (According to Olivier De Schutter, the UN Special Rapporteur on Right to Food, on his report to Committee on Sustainable Development: "the issue is not one of merely increasing budget allocations to agriculture, but choosing from different models of agricultural development the ones which may have different impacts and benefit various groups differently (quoted from Daniel and Mittal, 2010, p. 1).")

As emphasized by Von Braun and Meinzen-Dick (2009, p. 1):

> These land acquisitions have the potential to inject much needed investment into agriculture and rural areas in poor developing countries, but they also raise concerns about the impacts on poor local people, who risk losing access to and control over land on which they depend. It is crucial to ensure that these land deals, and the environment within which they take place, are *designed in ways* that will *reduce the threats and facilitate the opportunities* for all parties involved for a 'win-win' situation.

There are mixed reactions to the large-scale land acquisitions stemming from differences in perceived benefits as there is lack of transparency in the deal and design. As mentioned by Von Braun and Meinzen-Dick (2009), the foreign firms and the host or the 'local elites' share a commonality of interest and without the participation of the small holders or local communities. Given their underrepresentation, there is scope of 'unfavorable' terms of the deal and hence there is room for discord. The literature so far available provides evidence-based information on the pessimistic side, thus quoting Von Braun and Meinzen-Dick (2009), "unequal power relations in the land acquisition deals can put the livelihoods of the poor at risk." Whatever is the type of land – unused or unproductive under customary tenure agreements – having no formal arrangement or title to the land makes the small holders vulnerable to the deal. Therefore, by displacing from safety network of livelihood 'large-scale acquisitions jeopardize their welfare (Von Braun and Meinzen-Dick, 2009, p. 2).' (The issue of ecological diversity and sustainable development practices by the foreign investors being unaware of the local ecology and conditions are also mentioned. But, this aspect is set aside as it is beyond current scope of analysis.)

The Deininger *et al.* (2011) reiterates this apprehension that although investments could lead to higher productivity in longer run, the lack of transparency and secret or veiled tactics between the buyers and sellers (lack of governance) could be detrimental to this optimism. Thus, the report does not unequivocally lend support to the much-hyped 'benefits' of running such deal but warns against the mismanagement due to weak governance and corrupt underhand dealing. It presents evidences from 2004 to 2009 for 14 countries, mostly in Africa, and finds that 'desired benefits' were not achieved in all countries, especially in Africa where 'investments' did not achieve their full potential in terms of productivity and poverty reduction. This has been attributed to 4 factors: weak governance and failure to recognize land rights to local people, lack of capacity to manage and process large-scale investments properly, insufficient elaboration and technically nonviable investors proposals, and lack of properly formulated

development strategy to reflect development objectives of hosts and its proper focus, lack of transparency or information leaving rooms for corruption to flourish, and availability or access to information. It classifies countries on the basis of 'Yield Gaps' between actual and potential production and extent or scope for land expansion. Also, it refers to the 'significant gaps in the laws, policies, and institutions that govern such (large scale) investments' and that is the source of potential 'danger.' It calls for 'greater accountability on the part of governments and investors' and 'well-defined rights to use and occupy land.'

Moreover, by presenting a mixed picture across Africa, Latin America, Europe, and Asia, the report points out the failure on the part of most of the host governments to ensure rights to land and livelihood for the benefit of the local people and thus undermining the potential benefits via improved productivity. In fact, it mentions for some countries that there is room for potential productivity improvement on currently cultivated land, even without land available for expansion, for addressing food insecurity. Therefore, it is imperative for the host governments to make the land acquisition deals in a clear-headed and transparent way and also to invest in factors for boosting technological effort, skills, and proper institutions protecting own people. The report 'calls for a country-led approach to outside investment that sets clear criteria.' For such investments to have beneficial and sustained effect on host economies' pursuit of development, seven guiding principles have been outlined: (1) respect land and resource lights, (2) ensure food security, (3) ensure transparency, good governance, and a proper enabling environment, (4) consultation and participation, (5) responsible agroenterprise investing, (6) social sustainability, and (7) environmental sustainability. Quoting Deininger *et al.* (2011):

> Currently none of the African countries of interest to investors achieves even a quarter of its potential productivity. Rather than just focus only on an expansion of uncultivated land, it is important that investors and governments support improvements in technology, infrastructure, and institutions that can improve productivity on existing farmland.

As the World Bank (2010) mentioned, 'this debate has suffered from two main weaknesses, one among them is that there has been a dearth of rigorous, empirical analysis of what is happening on the ground (p. 1).' Das (2013) analytically, for the first time, presented a general equilibrium model capturing the immiserizing possibility of such deals.

Land-Use and Land-Cover Change through the Modeling 'Lens': A Bird's Eye (Re-) View

The preceding discussion shows that global land-use changes affect climate and is being affected by climate changes on a large scale. As human action over centuries has caused changes in land cover via land conversion for different purposeful productive activities, land-use changes need integration of agriculture, forestry, and environment with a human-centered focus. In fact, as Vollan and Ostrom (2010) mentioned, translating these 'social dilemmas' into a conditional cooperative behavior – modeled via designing via field experiment and economic games involving 'microsituational and broader contextual variables – could give valuable insights about long-term benefits of trust and cooperation in resource management. As these complex systems remain poorly understood, for practical policy implications a reasonable modeling framework to capture the interlinkages among these variables couched in terms of behavioral foundation and its subsequent empirical verification is necessary. As land-use changes cause changes in existing land cover (e.g., biofuel- or ethanol-driven conversion of cropland for sugarcane production in Brazil or India due to rise in demand for fuel for energy security leads land surface to change), it could result in atmospheric changes via variations in radiation forcing. Thus, any modeling effort for climate change policy must incorporate a land-use aspect. Below, the author gives a brief overview of major types of modeling efforts and their main thesis, without indulging in describing detailed structure and desiderata and classification of genre of models, so as to get a glimpse of distinction between modeling approaches. (Each of these models is so huge, multifaceted, and wider in scope that it is not worth evaluating each of them separately in one single article, as it goes beyond its scope. Each of them deserves separate discussion articles for their own merits (or points of demerits giving emergence to a variety of models from the breeding ground of respective criticism of each other). However, given the current focus (and length) of this article, this does not undermine the purposes at all. Given the immense practical and policy relevance, literatures abound in this area.)

According to Lambin *et al.* (2006, p. 5),

> [The] complexity of causes, processes, and impacts of land change has so far impeded the development of an integrated theory of land-use change. The need to distinguish between land-use and land cover to account for interactions between socio-economic and biophysical processes is one source of complexity. Moreover, land-use change processes are dominated by multiple agents, multiple uses of land, multiple responses to social, climatic and ecological changes, multiple spatial and temporal scales in the causes of and responses to change, and multiple ties between people and land. Causes and consequences of land-use changes depend on the social, geographic and historical context. Theory building has thus been-and still is-a difficult task.

Although no unified theoretical framework has emerged or even is possible to capture such complex interaction between socioeconomic and biophysical mechanisms and systems, the quote vindicates the necessity of a framework for analyzing LULC. Emergence of a box–arrow framework based on Turner *et al.* (1995) has shown qualitatively the linkages between social systems, ecological systems, land management, and LULC systems in a less-cluttered but informative theoretical framework. (see Lambin *et al.* (2006, p. 6)). There are other theories as well, such as multiphasic response theory (incorporating demographic changes on land-use pressures and economic responses) and complexity theory (based on complex holistic systems integrating the 'pixels' of relevant societal elements with focus on nonlinear relationship between components and their feedbacks to generate divergences from original to induced equilibrium changes in response to perturbations). LCS, as Turner II *et al.* (2007) mentioned,

simultaneously deals with human–environmental–geographical information (via remote sensing science) in an interdisciplinary, 'multiscaled coupled system' in an intensive way. Further, they (Turner II *et al.*, 2007, pp. 20667–20668) found, "Comparative and meta analyses of place-based land change studies have demonstrated the roles of such factors as markets, policy, transportation, governance, and household life cycles on different types of land covers." Therefore, they argue for inclusion of 'ambient factors,' such as biogeosphere-related variables affecting socioeconomic variables. Undoubtedly, this affects the human development through a multiplicity of channels, and to meet the MDG targets one needs to consider all the factors that might cause deprivation via food–feed availability and access, entitlement to land and food, and land degradation, drought, or desertification that intensifies the environmental channel of poverty impact.

The diversity of modeling approaches, as discussed, are driven by the need for addressing deficiencies of each model and also wide range of research agenda focusing on regional, national, or global level. Some of the models, dealing with different issues and research questions (but broadly focusing on environment–forestry–agriculture–LULC aspects), are as follows: deforestation models (Lambin and Ehrlich, 1997, Lambin and Geist (2003)), integrated urban models (U.S. Environmental Protection Agency (EPA), 2000), multiagent modes, (Bousquet and Le Page, 2004), biogeochemistry and biogeography models (VEMAP, 1995), the process-based terrestrial ecosystem model, and static and dynamic versions of global CGE model, such as dynamic timber supply model Sohngen and Mendelsohn (1998), Dynamic future agricultural resources model (FARM) (Ianchovichina *et al.*, 2001), Dynamic GTAP (GDyn, Das (2003, 2007), GTAP-E (Burniaux and Truong, 2002), Cintrafor Global Trade Model, the US Forest Services' timber assessment market model – aggregate timber land assessment system model, and last but not least, the nonlinear spatial equilibrium market structure-based sectoral Forest and Agricultural Sector Optimization Model. Unlike nonspatial models like Sahelian land-use (SALU) dealing with rate and magnitude of LULC, the spatial models like conversion of land use change and its effects (CLUE) model and geographical modelling (GEOMOD) consider pixels in spatial entities to consider spatial land-use changes owing to social and biophysical environmental changes. With regard to temporal dimension covering path dependencies, the temporal dynamics underlying land-use systems give projections or forecast over long-run LULC changes. Thus, there are static (comparative-statics comparing two snapshot equilibrium scenarios of policy impacts) models, like GTAP or regression models, and dynamic model versions, like CLUE, GEOMOD, FARM, or GDyn. Some of these models are descriptive (i.e., simulating the LULC system's functioning and future patterns of such changes), whereas others, based on the objective function of optimal land-use configurations given actual constraints of LULC and socioeconomic objectives, are prescriptive in nature and often take an agent-based bottoms-up approach (Verburg *et al.*, 2006; Piggott and Whalley, 1985; Lee *et al.*, 2013).

Verburg *et al.* (2006) mentioned that the land-use/land-cover (LUCC) project took the onerous task of developing a new generation of such models 'capable of simulating the major socioeconomic and biophysical driving forces' underpinning them with a spatial and temporal dimension. This kind of models takes a land-use systems view to include factors influencing land-use variables, such as economic, social, cultural, political, institutional, and biophysical. Most of these models are computer models performing simulation of policy scenarios on a 'what if' basis. Therefore, policy configurations affecting land-use/land-cover changes could be analyzed and their sensitivity could be tested to learn about impact.

The landscape approach is one approach to deal with these issues of competing land demands and climate change mitigation. According to Sayer *et al.* (2013, p. 8349),

> [it] seeks to provide tools and concepts for allocating and managing land to achieve social, economic, and environmental objectives in areas where agriculture, mining, and other productive land uses compete with environmental and biodiversity goals. [It] has been refined in response to increasing societal concerns about environment and development tradeoffs. Notably, there has been a shift from conservation-orientated perspectives toward increasing integration of poverty alleviation goals.

Thus, 10 principles (viz., continual learning and adaptive collaborative management, multiple scales to address diverse ranges of issues, multifunctionality of components and trade-offs, multiple stakeholders, logic and legitimacy of action via transparency, clear rights and responsibilities for conflicting claims, monitoring and participation, system-level resilience to threats and vulnerabilities of landscape, learning and improving stakeholders' skills and capacity to participate, etc.) of this approach emphasize achieving synergies between conservation and economic interests. According to this study, the typical sectoral approach is inadequate and hence 'optimal' solutions based on quantitative analyses might not capture the trade-offs between agricultural expansion, environmental change, and land competition. Models differ in terms of units of analysis – pixels or spatial units of parcel of land, individual interacting agents, and/or organizations – depending on the research questions and human–environment interaction to be analyzed.

Following the review of Turner *et al.* (2007), it can be said that LCS-based models are many. These include the following: Integrated Model to Assess the Global Environment capturing human–environment interface, CLUE model, and SALU model. However, there is agent-based modeling of individual decision making and interactions (conflicts or cooperation), statistical modeling linking household survey data with remote sensing-derived land-cover data, and simulation models where environmental change (exogenously occurring or endogenous in the system) and its impacts are analyzed under different counterfactual experiments. Integrating agent, or microeconomic units-based model with other methods, is an eclectic paradigm that is difficult to 'translate into useful land-change outcomes (Turner *et al.*, 2007, p. 20670).' For example, using explicit Dynamic Integrated Model of Forestry and Alternative Land Use, Rokityanskiy *et al.* (2007) modeled the effect of carbon sequestration policies inducing land-use and land management changes of landowners on climate change mitigation. They achieve the objectives by integrating emission scenarios and their dynamic development with the Model for Energy Supply Strategy Alternatives and their General

Environmental Impact, which operates with food security constraints and urban land usage. In particular, their findings suggested that landowners are motivated to afforestation and biomass usage substituting for fossil fuel consumption, and this results in land-use changes (i.e., via avoiding deforestation or conversion of forest land to nonforest usage) depending on carbon prices.

Among the climate change and energy models, IAM is a widely used framework. It is pluridisciplinary based on environmental science and policy modeling. It integrates knowledge from multiple domains into a single analytical framework and makes assessment or evaluation to decipher policy-relevant information on the basis of numerical model solutions. There are other models, such as simple climate models, three-dimensional more complex atmosphere–ocean general circulation models, and earth system models (ESMs), as well as coupled dynamic global vegetation models, to take into account global terrestrial carbon cycle and climate interactions. Another model for evaluating the regional and global effects of GHG reduction policies is based at Stanford University and it is a model for estimating the regional and global effects of GHG reductions. Several submodels include domestic and international open economy, emissions related to energy and nonenergy emissions of GHGs, and market and nonmarket damages due to global climate change where each economy is modeled neoclassically with Ramsey–Solow model of long-run economic growth (these models are solved using GAMS library, e.g., CONOPT3, or MINOS). All these models' successes depend on transparency and validations. Typically, these models are based on multitude of assumptions on biosphere, land use and cover, fossil fuel usage and GHG, technological progress, and future evolution of global economy. These are large scale, complex, and purport to integrate natural and social systems by quantifying different aspects, which are not amenable for quantification.

In a review, Parson and Fisher-Vanden (1997) mentioned that such models seek to 'combine knowledge from multiple disciplines in formal integrated representations' by combining socioeconomic and biophysical processes, human activities, and dynamics of human-induced emissions and their regulation. Challenges such as broadening disciplinary knowledge and informed policy and decision making have been reviewed. In another article, Van Vuuren *et al.* (2009) emphasized the necessity of understanding the uncertainties associated with quantification in the IAMs as these models are regularly used for evaluation of policies aimed at emissions controls. They consider various carbon cycle components and climate systems across different IAMs and compare them with ESMs. They find that although outcomes are more or less within ranges, large differences make them not so good for policy advice, and there is room for improvements for IAMs, for example, in terms of climate sensitivity, inertia in climate response, and carbon cycle feedback. The need for better communication between the IAM and the ESM development communities is stressed. Further, Van Vuuren *et al.* (2009) concluded:

> Given the uncertainty in climate feedback onto the carbon cycle, we recommend that IAMs should consider including these feedbacks in their uncertainty analysis. Our results also suggests a very pressing need for the climate modelling community to run their more complex, earth-system models for scenarios with aggressive mitigation and lower emissions than the IPCC SRES range, including scenarios where the concentration overshoots the eventual target level. This is because even the simple climate models cannot hope to capture the complex geographical nature of carbon cycle changes and local feedbacks, such as those involving local hydrology changes which are believed to have a significant interaction with local vegetation. The recent IPCC AR5 assessment will involve such ESM simulations, but it is important these are made available to the IAM community as early as possible. Finally, it is vital that policy makers, especially those involved in UNFCCC negotiations, are made aware of the large spread in the climate and earth system components of IAMs. More work is recommended to understand how these affect the economic outputs from current IAMs.

Another genre of model is the Integrated Global System Model (IGSM) based at Massachusetts Institute of Technology in the Joint Program on the Science and Policy of Global Change. As before, IGSM deals with human–climate system interactions and explores consequences for environment of global climate change.

The IAMs linking ecological and economic aspects of LULC got its boost from the Intergovernmental Panel on Climate Change (IPCC, 2001), which focused on improving global model analytics, integrating mitigation and adaptation, climate mitigation options in terms of sustainability, and development and equity considerations. The latest 5th IPCC was released recently. This has an important bearing on the joint modeling effort of 26 teams, viz., Coupled Model Intercomparison Project, as researchers from various disciplines try to estimate climate sensitivity of doubling of atmospheric carbon dioxide (CO_2) on the warming of the globe (Kerr, 2013; Kintisch, 2013). According to this report in Science (4th October 2013), although the sensitivity numbers have not changed since 1979 with a small margin of error, the model and data have advanced. However, 'the abstract quality of equilibrium sensitivity' is mentioned. The robustness of 'transient climate response' and its practical policy relevance is emphasized as it usually matches the simulated range generated from the models. However, in order to have a policy impact, modelers' research is often driven by IPCC's policy question (4th October 2013).

Regarding the geographical scope and capture of global interactions, especially as globalization has transformed organization of socioeconomic activities crossing boundaries, the models have evolved to take into account global spillovers. As Verburg *et al.* (2006, p. 121) argued:

> Only few global models of land-use land cover change have been developed and those global model analyses are not typically aimed at investigating land-use/land cover change issues per se, but, land-use/cover change can play an important role in analyses of climate change, biodiversity loss, agricultural production or world markets.

IAMs are examples of such models developed in the late 1980s–early 1990s and used for IPCC assessment of GHG emissions and global warming. These are also sometimes used in the IFPRI and the United Nations Environment Program for issues related to food and agriculture. However, models capturing economy-wide linkages between sectors and representative agents at the national level need to extend the

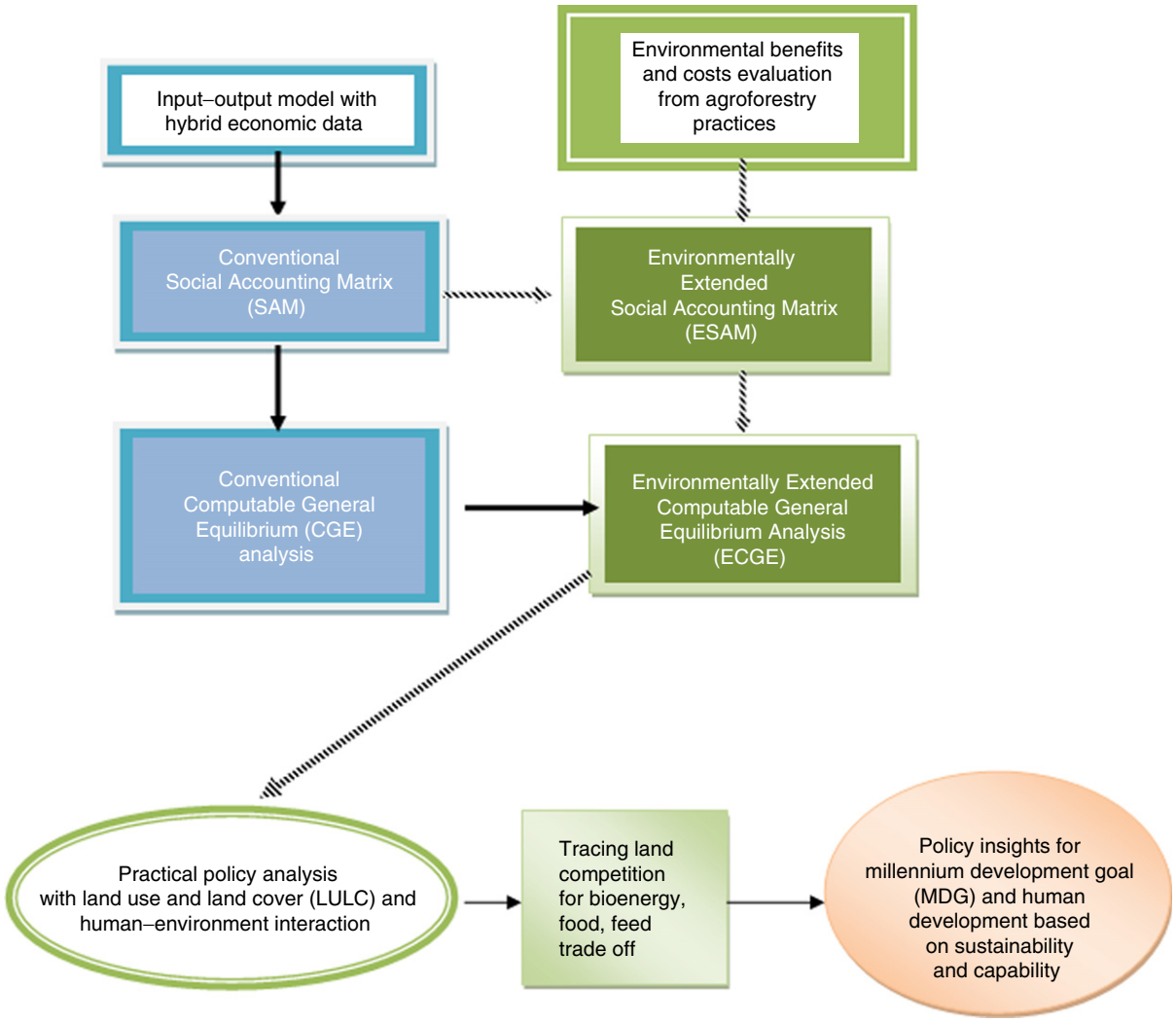


Figure 2 A stylized mechanism for environment–ecology–economy nexus and socioeconomic impacts.

framework to trace global impact, as many activities are not just confined to domestic boundary, rather they extend to global territory and causes climate spillover effects. Economy-wide economic effects of the policy changes are important as it generates spillover effects within the system. Hence, the CGE framework explicitly models the multisectoral linkage based on input–output models and the Social Accounting Matrix (SAM) and also focuses on goods and factor market interactions. Secondary impacts of development policy are assessed via the application of traditional input–output models (Leontief, 1986) with intersectoral transactions and different sets of multiplier effects. These are useful means of conducting the impact analysis. For modeling intersectoral transaction, Input–Output Models and SAM framework are used. SAM-based models are much detailed in the sense that in addition to intermediate input flows, they have a detailed institutional structure.

This kind of structure highlights on: (1) growing environmental concerns and preferences for biodiversity; (2) implications for socioeconomic benefits, equity, and distribution within income groups and environmental sustainability, (3) need for integration of Ecological, Environmental Benefits, and benefits with socioeconomic factors in an integrated approach for sustainable development, and (4) economic ecological nexus in an integrated framework. Figure 2 presents a mixed approach for ecological variable-augmented CGE framework.

The CGE models are equilibrium models where land allocation is done by demand–supply interactions of the land-intensive sectors. The GTAP is such a global economy model (Hertel, 1997) where land is immobile across globe; however, under the perfect competition assumption of factor and good markets, land is allocated as per its relative economic return in various uses. (In 1826, Von Thuenen gave a treatise on locational rent and his model for deforestation offers rationale for rent and perishability of goods to determine land use (Von Thuenen, 1826). There are also classical models that are not mentioned here, but they do not cover land-use information as detailed for lack of data.) In this macroeconomic model, with microeconomic foundations based on neoclassical optimization principles (e.g., utility maximization by household, profit maximization or cost minimization by the firms, and global savings being allocated to equate rate of return across

globe), heterogeneity of production processes across regions in the world and differences in global land-use patterns are not explicitly modeled.

In CGE models, the policy impacts on factor markets are studied, for example, trade policy impact on wage and factor returns and returns to land in case of agricultural policy shocks. In the context of the EU Common Agricultural Policy, the factor market project tries to predict the policy impact on agricultural factor markets, viz., for land, labor, and capital, which are not integrated like the food and agricultural markets. Banse *et al.* (2013a,b) studied such an aspect of factor market in MAGNET. This model is useful for studying the impacts of biofuel policies like Renewable Energy Directives and the United Nations Reduce Emissions from Deforestation and Degradation (REDD) programs, which cause change in land-use by limiting the land for agricultural and biofuel production and protecting and managing forest sinks and carbon sequestration. In particular, they studied this using GTAP Version 6 database with base year updated to 2010, and 45 regions and 26 sectors. Their headline results are, according to them (Banse *et al.*, 2013a,b, p. 41),

> …economic and population growth, together with biofuel policies, increases the demand for agricultural products and agricultural land use. The increased demand for land is met by increased yields and the conversion of forests and woodlands. The introduction of a REDD policy to protect forests and woodlands, limits the supply of land (6%) suitable for agricultural production, leading to the intensification of production and higher land prices.

As they find, for tropical regions this causes a rise in food prices and affects food security and vulnerability.

The economy-wide modeling has merits for public decision making as it enables simulation-based scenario analysis for ensuing policy changes and hence examining coherence of policy criteria. Thus, it provides a scientific understanding on the basis of judgments on social welfare and cost benefits. Hertel *et al.* (2013) had documented recent advances in the methodology of integrating LU in CGE models and incorporating a database of land use for agriculture, forestry, and biofuel policy mandates. This breaks ground in model development and is a reference work for work in the global land-use and climate change policy 'by offering a synthesis and evaluation of a variety of different approaches to this challenging field of research (Hertel *et al.*, 2013).' As Hertel *et al.* (2013) mentioned, development of such models is hindered by nonavailability of data on global land resource, non-CO_2 GHG and GHG emissions based on production activity, and sequestration drivers. These models take into account opportunity costs of land uses, trade-offs between agriculture and forestry, and the mitigation strategies. According to them, the FARM model by Darwin *et al.* (1995, 1996), which has disaggregated land resources into six heterogeneous classes based on length of growing period, offers rich ecological information based on spatial bioclimatic model. That was the first global CGE model with disaggregated land use information. Dynamic timber supply Model of Sohngen and Mendelsohn (1998) includes forest dynamics and incorporates the adaptive behavior of forest producers as well as the modeling of harvests and forest stocks. Other models are GTAP-AEZ model (Hertel *et al.*, 2013) with more extensive land-use database, forest carbon sequestration, and GHG emissions and GTAP-E and GTAP-L (Burniaux, 2002; Burniaux and Truong, 2002), which extend the static GTAP model by incorporating detailed features on energy production, demand, and substitution, for implementing Kyoto Protocol. It has interfuel substitution and a development of the underlying SAM to account for carbon tax revenues and expenditures, with a particular mechanism for trade in CO_2 emissions trading. As technological changes and productivity growth affects land use (e.g., biotechnology or bionanotechnology), this needs to be modeled. Das (2003, 2007) considered the impact of technological changes, especially information technology, forestry biotechnology in a comparative static and dynamic framework of GTAP-based augmented model to show the productivity gains and its benefits in terms of output and price affecting welfare. Das *et al.* (2005) simulated different forest conservation policies and spotted owl conservation in a multiregional applied general equilibrium model of the US economy. The Millenium Ecosystem Assessment (2005) has reiterated the growing interest in model building for researching land use-related effects and induced further effort in development of such joint modeling efforts. MEA shows the negative impact on crop yields due to adverse effects of environmental degradation as marginal productivity gains of technological progress decline. Different other models such as GTAP-AEZ (Hertel *et al.*, 2013), LEI Institute Trade Analysis Project, Kleines Land Use Model, etc. are briefly reviewed in Hertel *et al.* (2013). Baldos and Hertel (2012) developed a Simplified International Model of agricultural Prices, Land use, and the Environment in a partial equilibrium setup. This model – developed for better understanding of drivers changing global farm and food system and affecting agricultural land use, production prices, GHG emissions, and food demand – is used to simulate long-run changes of global farm and food system for historical validation for 1961–2006. This model is useful, as discussed in Section Land Use, Land Cover: Reconciliation of Issues and Evidences, for studying the impact of land competition for food demand and demand for land, thanks to ecosystem services, such as feedstock use by global biofuel/bioenergy demand.

Another genre of models is developed in a G-Cubed framework of dynamic nature. One of the important concerns in this technology-driven, high-growth world is about environmental sustainability. Many researchers have discussed the importance of addressing the climate change mitigation policies and the failure of Kyoto protocol so as to 'design a more durable post-2012 international agreement' or coordinated action (McKibbin and Wilcoxen (2008), to mention a few). This all depends not only on economics but also on national legal, accounting, and socioinstitutional structure in conjunction with international cooperation with a significant role being ascribed to economic theory as 'good guidance' for designing 'politically realistic policy' based on hybrid approach of multidisciplinary nature (McKibbin and Wilcoxen, 2002).

According to Stern (2007), aside from emissions trading and reduction of deforestation, technological cooperation, low-carbon technology invention, and investment in energy R&D are crucial. Analyzing impact of technological advances via biotechnology, ICT, and environmental technology on NRM, food security, and land use would be one of the major

focuses of the research. This would inform policy prescriptions to mitigate or facilitate adapting to global climate change initiatives. Analysis would address different policy designs, reduction incentives, conservation program, biodiversity issues, and climate and biofuel policies covering aspects such as broader impacts on the structure of (agricultural) production and interactions between climate and technology policies. Genetic engineering aided by IT development and combined with traditional practices produce sophisticated varieties adapted to local land and soil quality. In resource-poor nations, poverty, low productivity, and environmental degradation (deforestation and soil degradation) concatenate to cause a vicious spiral (see Das (2003, 2007)) in static and dynamic GTAP model).

Concluding Observations

This article has offered a broad view of the plethora of issues related to LULC and entangled with it the food–energy–environment trilemma. Climate change has been called a 'wicked problem' by Batie (2008). Climate change induces land-use change and vice versa. However, the changes are global and these worldwide changes cause repercussions to forests, cropland, waterways, and environment, and they are driven by the necessity to provide food–feed–shelter–bioenergy to almost 7 billion people. Challenges that are faced now involve trade-offs between human needs, economic prosperity, and managing global biosphere to maintain sustainably the capacity to provide burgeoning demand for goods and services in long run. The matter is complex and needs intensive research. The proposed analysis enlightened on the impacts of anticipated climate change on land use, agricultural production, food supply and availability, and other economic activities. This article is just a glimpse of the vast canopy of issues covering multidisciplinary perspective. As already seen, the issue crosses boundaries of natural science, social science, anthropology, and above all, the science for understanding the world as a complex adaptive system where land use and climate change should not be treated separately. As Sen (1995, p. 205) had stated: "The contemporary age is not short of terrible and nasty happenings, but the persistence of extensive hunger in a world of unprecedented prosperity is surely one of the worst.. However, food output must be one of the variables that can, inter alia, influence the prevalence of hunger." Further, Sen (1995, p. 209) argued: "Policy makers may be misled if insulated from the real situation of hunger – and even threats of famines – by favorable food output situations." Thus, the issue of land-use changes needs to be seen in broader perspective. Analytical models that capture these trade-offs could give some insight into the intricacies of such relationship. As Pindyck (2013, p. 870) had mentioned: "the physical mechanisms that determine climate sensitivity involve crucial feedback loops, and the parameter values that determine the strength of those feedback loops are largely unknown." These loops in the context of IAMs or complex models are important, as already seen in **Figures 1** and **2**, as 'feedback' is an inherent property of the human–environment interactive system. The tackling of the wicked problem needs a holistic approach.

See also: Biotechnology Crop Adoption: Potential and Challenges of Genetically Improved Crops. Climate Change, Society, and Agriculture: An Economic and Policy Perspective. Computer Modeling: Applications to Environment and Food Security. Computer Modeling: Policy Analysis and Simulation. Economics of Natural Resources and Environment in Agriculture. Food Security: Development Strategies. Food Security, Market Processes, and the Role of Government Policy. Land Use: Catchment Management. Land Use: Management for Biodiversity and Conservation. Land Use: Restoration and Rehabilitation. Virtual Water and Water Footprint of Food Production and Processing. Water: Advanced Irrigation Technologies. Water Use: Recycling and Desalination for Agriculture. Water: Water Quality and Challenges from Agriculture. World Water Supply and Use: Challenges for the Future

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Land Use: Management for Biodiversity and Conservation

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Glossary

Agroecology The science of understanding and enhancing the value of ecological processes in agriculture.
Conservation biological control (CBC) Enhancing the efficacy of biological control agents through habitat manipulation.
Ecosystem services Ecosystem functions provided by biodiversity that have value to humans.
Green revolution A system of enhancing crop yields through a combination of high inputs of water, fertilizers, and pesticides.
SNAP The four key resources that the natural enemies of pests need to increase for their ecological fitness and efficacy: shelter, nectar, alternative food, and pollen.

Introduction

"I am a photosynthesis manager and an ecosystem-service provider."
Peter Edlin, Swedish farmer

"Fuí por el mundo buscando la vida: pájaro a pájaro conocí la tierra"
"I've wandered the world in search of life:
bird by bird I came to know the earth"
Pablo Neruda, Chilean poet

The above quotations share and celebrate the vital importance of biodiversity for agriculture and human well-being. However, many people believe that agriculture is the greatest ecological experiment on Earth. Modern agriculture has high external costs and damages the natural environment. It is considered to be the biggest cause of climate change and is responsible for 24% of greenhouse gas emissions. Undoubtedly, modern food production is dependent on fossil fuels. In 2012, the International Energy Agency stated that no more than one-third of proven reserves of fossil fuels can be consumed before 2050 if the world is to limit climate change to 2 °C (IEA, 2012). Bearing this in mind, the Food and Agriculture Organization of the United Nations (FAO) showed that the current dependence of the food sector (including agriculture) on fossil fuels may limit its ability to meet future food demands. Recently, the University of Michigan, USA, has calculated that 10 cal. of fossil-fuel energy are used to produce 1 cal. of food energy on the plate (10:1). In 1940, the ratio was 1:2.3 whereas in 2000 it was 7.3:1 (Ahmed, 2013). Agriculture is in many ways in a state of tension; it minimizes and substitutes for processes, such as nitrogen fixation (substitute: urea), biological control (insecticides, herbicides, and fungicides), ecological succession (herbicides), soil formation and maintenance (exploiting action of soils), and plants' ecological traits matching ambient growing conditions, for example, water needs (irrigation) and food webs (one trophic level only).

Over the past century, as agricultural land use has intensified, ecosystems have been degraded and ecosystem services (ES) lost. In addition, biodiversity has been lost at a higher rate than during the last ice age. A consequence of biodiversity loss is reduced ES. In 1997, Costanza *et al.* estimated the value of global ES (based on a biome by biome approach) and suggested that the total ES value of the world was US$33 trillion. This figure was twice as high as the global gross domestic product (GDP) at the time. Although the article was criticized because of the many assumptions inherent in its value transfer approach, it did highlight the potential value of ES to the world. In the context of global agriculture, Costanza *et al.* (1997) ascribed a value of only US$92 ha^{-1} $year^{-1}$ for croplands. This is now considered to be a gross underestimate of the value of farm ES, as the economic value of earthworms alone well exceeds this figure.

International agencies are consistent in their view that modern, high-input, and substitution agriculture cannot meet the demands of a rapidly expanding world population, which is predicted to reach 9 billion in a few decades. Compounding that challenge is a current rapid global increase in meat consumption, especially chicken meat, which is largely driven by an increasing standard of living in parts of Asia. This is, in turn, driving a worldwide increase in demand for grain, which is likely to double in the next few decades.

A very relevant example of the threats to and opportunities for world food production is the report to the Human Rights Council of the United Nations in 2010 by Olivier De Schutter. He outlined agroecology as the key to ensuring the human right to food in a sustainable manner. Agroecology uses ecological principles to sustain and increase production while minimizing the impacts of substitution agriculture. Agricultural ecosystems based on agroecology are developed and managed by reinstating and enhancing natural processes, such as recycling nutrients and energy, integrating crops and livestock, and diversifying species, including noncrop ones. Internationally, agroecology is being seen as a way to improve the sustainability of food systems with several organizations now promoting its benefits, including the FAO (Food and Agriculture Organization of the United Nations, 2010); United Nations Environment Programme (UNEP, 2010); Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES, 2010) and Biodiversity International (2012).

A large-scale study, commissioned by the Foresight Global Food and Farming Futures project of the UK Government

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(Pretty *et al.*, 2011), reviewed 40 projects in Africa that employed agroecology in the 2000s. The projects included crop improvement, integrated pest management, soil conservation, and agroforestry. By 2010, crop yields were doubled on average and 10.39 million farmers documented improvements in farming and food yields (Pretty *et al.*, 2011). In fact, De Schutter (2010) predicted that agroecology could double crop yields in developing and developed countries over the next decade.

Biodiversity, Agriculture, and Well-Being

How can biodiversity make agriculture more sustainable? Luck *et al.* (2003) argued that loss of biodiversity is commonly characterized by species extinctions. However, substantial changes to ecosystems and the status of biodiversity can occur through community structural effects before species extinction takes place. Luck *et al.* (2003) suggest a new approach to make the concept of ES and the deployment of ES enhancement more tangible and to promote end-user uptake. This was the idea of a service-providing unit. This essentially produces an ES enhancement 'recipe' to facilitate uptake by end users.

Well-being is now an area of interest, with researchers recognizing that appropriate exposure to green places and the right type of agriculture can improve well-being. Work by Barton and Pretty (2010) at the University of Essex, UK, has quantified the benefits to mankind of green exercise or a 'dose of nature' on self-esteem and mood. Examples of this effect can be seen among people using the UK's Public Footpath Scheme, where people who have access to farmland for walks have lower stress levels. In fact, exercise in green areas, such as farmland, beaches, forests, and nature reserves, and the consequences on well-being are the key components of current thinking on Genuine Progress Indicators (GPIs). Work by Costanza and others in this area has shown that GPIs have been declining since 1978 even though the more orthodox and flawed measure, GDP, has been steadily increasing over that time (Kubiszewski *et al.*, 2013). It follows that returning appropriate, functional biodiversity to agriculture can generate tangible benefits to humans as well as 'softening' the impact of modern farming on the environment and human health.

Case Studies: The US Prairies and the New Zealand Greening Waipara Project

Agroecological methods, such as conservation biological control (CBC), can increase the ES value of agriculture, while reducing its externalities caused by energy, pesticide, fertilizer, and fossil fuel use (Jonsson *et al.*, 2008). CBC enhances natural enemy efficacy through modifying the habitat – an approach easily remembered by the acronym SNAP (shelter, nectar, alternative prey, and pollen). The provision of flowering plants to enhance natural enemy fitness is a key aspect of CBC. Fiedler *et al.* (2008) conducted a review of current habitat management strategies involving all or part of SNAP and found that this management relied heavily on the four plant species, whereas plants native to the area and perennial plants were largely underrepresented. Here, the authors examine two case studies: habitat management in southern Michigan (USA) and native plants in New Zealand vineyards, both of which address this imbalance.

In 2003, studies were conducted in southern Michigan to use habitat management to help reduce pests by enhancing natural enemy effectiveness (Fiedler and Landis, 2007). Plant species that grew in declining prairies and oak savannas were investigated. They were added to this existing vineyard as plants under the vines. The study revealed that a modest number of native plant species can enhance the efficacy of natural enemies as well as 'nonnatives.' Feeding on floral resources alone will not automatically enhance pest control when using floral subsidies to increase natural enemy success. This must be measured against a hierarchy that includes the use of floral resource by adult parasitoids, the compatibility of the agent with the use of some pesticides, improved fitness of individual agents, and if the improved fitness applies to males and females. A decrease in pest populations, reducing growers' costs, and improved marketing opportunities complete the picture (Wratten *et al.*, 2003).

Vineyards are typically monocultures with a low provision of ES. However, the Greening Waipara Project, a government-funded initiative in New Zealand, is aiming to combat this problem (Bio-Protection Research Centre, 2010; Norton and Reid, 2013). In this study, the vineyard ecosystem was modified by the interrow planting of buckwheat (*Fagopyrum esculentum*; **Figure 1**), phacelia (*Phacelia tanacetifolia*; **Figure 2**), and alyssum (*Lobularia maritime*; **Figure 3**) to provide nectar



Figure 1 Flowering buckwheat in a vineyard interrow. Courtesy of Waipara Hills.

resources for key parasitoid wasps (Berndt and Wratten, 2005). The increase in parasitoid numbers that resulted from this work decreased the number of pests to below the economic injury level. In addition to pest control, other ES were developed, such as using New Zealand endemic plants as living mulch to disrupt the life cycle of *Botrytis cinerea* (a fungus that causes gray mold disease) or to suppress weeds.



Figure 2 Flowering phacelia in a vineyard interrow. Courtesy of Waipara Hills.

Habitat modification is not only pertinent to CBC, but it also plays a key role in other ES, such as attracting pollinators and enhancing their fitness (Wratten *et al.*, 2012). Gillespie and Wratten (2013) showed that, in both field and laboratory trials, the plant species *Veronica* 'Youngii' and buckwheat enhanced the fitness of butterflies, *Lycaena salustrius*, fitness more than other exotic plant species. If these floral resources are provided in vineyards and farmlands, then populations of butterflies may increase, contributing to their conservation.

The Urgent Need for Changes in Policy and Practice

Starting in the 1940s and reaching its peak in the late 1960s, the Green Revolution increased agricultural production around the world. The initiative was started by Norman Borlaug, the 'Father of the Green Revolution,' who has been credited for greatly reducing world hunger (Tilman *et al.*, 2001). Research and technology during this time transformed farming from subsistence to commercial operations. Mass production of crops involved the development of high-yielding cereal varieties, expansion of irrigation, creation of hybrid seeds, and a dependence on synthetic fertilizers and pesticides.

Although the Green Revolution increased food supplies, it had negative effects on food security, environment, and health. The latter was impacted by heavy use of agrochemicals. Increased food production does not mean better food security,



Figure 3 Strips of flowering alyssum in an organic lettuce crop in California. Courtesy of Mission Organics.

and critics of the Green Revolution argue that it does not take into account natural occurrences, such as historical famines and the socioeconomic or political situations in developing countries. The negative impact on the environment is largely undisputed; from pesticide and fertilizer pollution to the loss of agricultural biodiversity as a result of monocropping. There is conflicting evidence on the long-term health impact of pesticide consumption by humans. However, pesticide poisoning through the use of improper safety equipment and techniques is well documented. The Punjab region has been strongly affected by water contaminated with pesticides. Studies show that groundwater in its cotton region is contaminated with low levels of applied pesticides; with carbofuran and monocrotophos almost reaching maximum contamination levels (Tariq *et al.*, 2004). Additionally, water use in the Punjab region has caused the water table to decrease by 1 m $year^{-1}$ and 90 of 138 blocks in the state have declared extreme water shortages (Singh, 2004). Critics of the Green Revolution all address one common end point: current techniques are unsustainable.

In response to criticisms of the Green Revolution practices, a new type of farming initiative called the Evergreen Revolution was founded, led by the Indian Prime Minister Manmohan Singh (Swaminathan, 2000; Wratten *et al.*, 2013). This initiative was triggered in response to the conditions in India, where there are problems with malnourishment (International Food Policy Research Institute, 2012), and one of the more famous cases of negative health implications from pesticides is in Punjab (Ejaz *et al.*, 2004). With support from the US President Barack Obama, the United States and India entered into an agreement to develop, test, and extend food security, and form the partnership for an Evergreen Revolution (Office of the Press Secretary, 2010). This partnership means cooperation between Indian and American researchers and scientists to investigate and improve technologies to extend food security in India, Africa, and around the world (USAID, 2013). This approach is eminently appropriate for developing and 'developed' countries, as pointed out by De Schutter (2010).

To further develop world food security at a time when sustainable intensification of agriculture is increasingly being demanded, the relatively new science of ecological engineering needs to be widely adopted (Gurr *et al.*, 2004). This approach identifies, quantifies, and enhances farmland ES. This range of methods still remains largely unexploited despite a large number of prominent and sustainable successes. For example, insects that deliver biological control of pests do not operate well in agricultural monocultures and need resources supplementary to those provided by their prey. In vineyards in New Zealand, Australia, and elsewhere, the annual flowering plant buckwheat is regularly deployed in early summer between the vine rows to provide SNAP. The attack rate and longevity of a parasitic wasp within those vineyards are markedly enhanced by the nectar from buckwheat, leading to longevity of approximately 40 days compared with 3–4 days with water as a control. This leads to the numbers of a caterpillar pest within the grape bunches declining to such an extent that they fall below the accepted economic injury level. This means that insecticides are no longer needed, saving NZ \$250 ha^{-1} $year^{-1}$.

Recent unpublished work by H. Sandhu and S. Wratten in New Zealand evaluated ES provided by mineralization of soil nutrients and biological control of soil–surface pest eggs in organic and conventional arable farmland. When the economic value of these two ES for the organic farms was calculated and extrapolated to the area of arable land in the European Union, the resulting potential economic benefit for that region exceeded the total annual value of European farm subsidies. This profound result shows clearly that some new thinking is required for the policymakers to achieve true future farming based on a sound knowledge of how to evaluate and enhance farmland ES (Wratten *et al.*, 2013). The key challenge is to develop appropriate policy changes, including paying for ES and enhancing farmer uptake of agroecological protocols. The latter requires a keen recognition of social learning through which farmers most readily acquire new knowledge (Warner, 2007). The work of Keith Warner at Santa Clara University, California, is key to work in this area.

See also: Air: Greenhouse Gases from Agriculture. Biodiversity and Ecosystem Services in Agroecosystems. Biodiversity: Conserving Biodiversity in Agroecosystems. Climate Change, Society, and Agriculture: An Economic and Policy Perspective. Green Revolution: Past, Present, and Future. Land Use: Restoration and Rehabilitation

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Relevant Website

www.bioprotection.org.nz
Bio-Protection Research Centre.

Land Use: Restoration and Rehabilitation

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Glossary

Biodiversity A contracted form of 'biological diversity' and referring to the genetic, species and ecosystem levels of life in a specified region or globally.

Ecosystem function Processes such as nutrient cycling and energy flow that are key to the viability and sustainability of ecosystems. When ecosystem functions are directly exploited by humans – for example, in the form of soil formation, pollination and pest suppression – they are recognised as ecosystem services and can be assigned a value.

Reallocation Action to bring about a change to a degraded area of habitat to a new use or state from the original state of biological complexity and ecosystem function after a natural or human-mediated perturbation such as tsunami or pollution event.

Rehabilitation Action to bring about the partial return of a degraded area of habitat to its original state of biological complexity and ecosystem function after a natural or human-mediated perturbation such as tsunami or pollution event.

Restoration Action to bring about the complete return of a degraded area of habitat to its original state of biological complexity and ecosystem function after a natural or human-mediated perturbation such as tsunami or pollution event.

Introduction

Nuclear accidents, oil spills, and tsunamis have in recent times dominated the world's headlines. These events produce sudden and dramatic ecological degradation over a restricted area. Other changes such as pollution, soil degradation, desertification, or deforestation occur chronically over large sections of each continent. Where catastrophic events occur, their major impact on biodiversity occurs instantaneously, even though the residual effects may last for several years. In contrast, the impacts of long-term ecosystem degradation may occur over a much longer time scale as individual species become threatened and eventually become extinct. Ecosystem degradation is often a result of the expansion of intensive agriculture in many parts of the world (Rey Benayas and Bullock, 2012). Human development has frequently changed ecosystems which has lead to a reduction in biodiversity, ecosystem functions, and agricultural outputs. Reversing the effect of degraded agricultural land is important to improve agricultural output and so reduce the pressure on remaining native ecosystems (Dobson *et al.*, 1997). Ecosystem degradation can be addressed by restoration efforts if undertaken before substantial losses of biodiversity have occurred (Dobson *et al.*, 1997). If ecosystem degradation has not progressed too far, a return to an original state is possible simply by removing anthropogenic stresses and allowing natural processes to operate. This is not possible when thresholds of irreversibility have been passed. When such a threshold, which may not always be easily detected or quantified, has been passed, the system cannot be restored without intervention to correct the specific changes that led to the threshold being crossed (Aronson *et al.*, 1993).

Restoration

The term restoration is often used synonymously with rehabilitation. In most situations, however, to restore implies that an area of habitat will be returned to its original state with all biodiversity and ecosystem function reinstated to the predegradation condition (Law, 1984; Bradshaw, 1988; EPA: Environmental Protection Agency, 1995; Bainbridge, 2007; Rey Benayas and Bullock, 2012). One view of ecological restoration is that the goal is to create "a living museum in which flora and fauna are put back as they once were, seeking a complete or near-complete return of a site to a preexisting state" (Aronson *et al.*, 1993) (**Figure 1**). The term is widely used in relation to climax ecological communities such as forests and certain freshwater systems. These often have economic or esthetic value which serve as the drivers for restoration. Further, because climax communities represent an end-point for ecological succession, nearby areas of undisturbed habitat may serve as a benchmark for exactly what is to be sought in the restoration program. The natural processes of ecological succession may be used in the restoration process, for example, a gradual change from shrubby to long-lived woody vegetation with associated changes in faunal components such as birdlife. Accordingly, restoration activity may be passive in nature; sought simply by removing or ameliorating the factors that led to the original degradation. For example, control of feral grazing animals or allowing a natural wild fire regime may allow the return of native plant species which may then support the reestablishment of native fauna. More commonly, however, such passive actions are complemented by active efforts to speed up the process or to make step changes that otherwise may not occur because of the operation of a threshold for irreversibility. An example of such a step change is the reintroduction of an original plant or animal species that otherwise would not be able to reach the new area because of geographical isolation. Other active restoration actions include implementing biological control of a weed, reintroducing natural woody debris into streams to serve as fish habitat, and earthworks to stabilize regolith and reduce erosion.

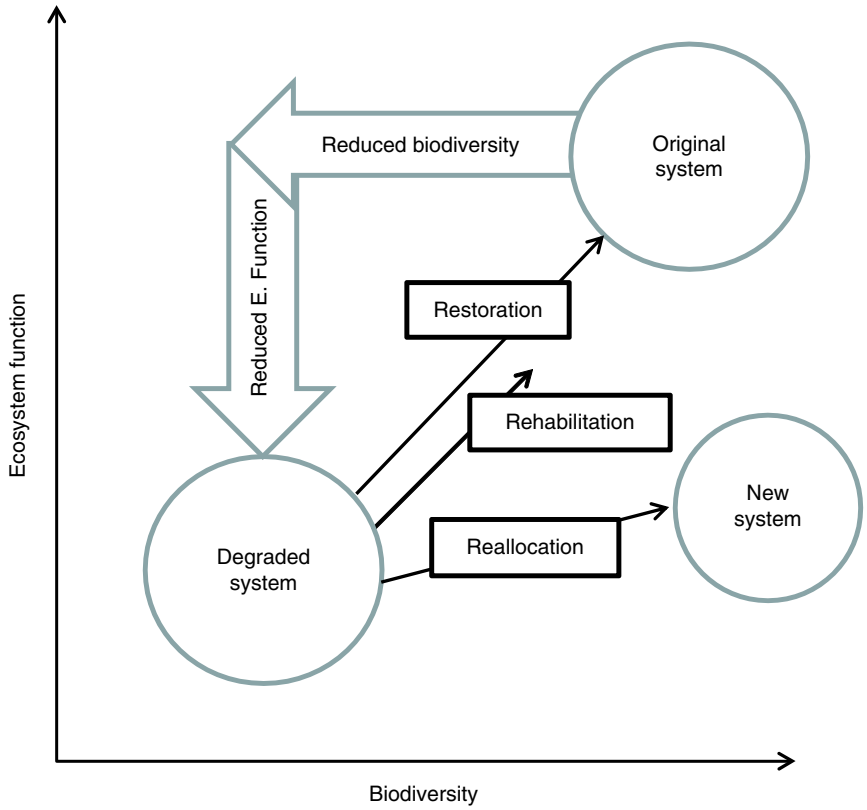


Figure 1 Degraded systems differ from the original state in typically having a lower level of biodiversity at the genetic, species, and community level and an associated lower level of ecosystem function. Restoration brings about a return to the original system, rehabilitation is a partial return to the original, whereas reallocation (or replacement) is a change to a third state. Adapted from Lugo, A.E., 1988. The future of the forest. Environment 30, 41–45.

In practice, restoration is difficult, expensive and slow; even when active restoration methods are implemented. This is because precise, ecological information on the goal of the restoration process may be lacking. Although restoring a patch of climax forest may be tractable when surrounded by undisturbed patches, a more common scenario is for the forest to be isolated and often remote from exemplar patches so information on key aspects such as the tree species and community composition have to be determined by extrapolation. Related to this, availability to the restoration project of biological propagules and founders is commonly a problem. Often the population density of original species in the degraded area is very low or nonexistent, even in more durable forms such as the soil seed bank. Any nearby habitat known to be similar to the original state of the restoration site may be able to donate seeds, tubers, and organisms. Otherwise, biological material from further afield needs to be obtained, introducing differences in provenance, a still greater issue when the taxonomy of species is poorly known as is common outside of North America and Western Europe. For invertebrates and microbes particularly, the poor state of taxonomic knowledge coupled with often high levels of endemism to small sites can be an important limitation of achieving full restoration to the original state. This lack of ecological information of historic or prehistoric ecosystems restricts restoration efforts as the goal is often ambiguous (Aronson *et al.*, 1993). A further major problem with restoration is that removal of species that have become established in degraded sites, such as weeds and small mammals, can be challenging. Many such species are reselected so have high powers of dispersal to new micro sites, are highly fecund so produce many offspring and rapidly reproduce after attempted control efforts, and may be invasive species that are freed from their natural enemies so lack important biotic regulators.

Complete restoration may also be inconsistent with society's current needs and values, this combined with the difficulties outlined above means that complete restoration of an ecosystem is often unachievable. The original ecosystem has taken centuries or millennia to develop so would be impossible to replicate faithfully (Bradshaw, 1988). Accordingly, many management efforts either aim for rehabilitation or reallocation, or are forced to settle for these outcomes when efforts to achieve restoration fail (Figure 1).

Rehabilitation

Rehabilitation is action intended to bring about the partial return of a degraded area of habitat to its original state of biological complexity and ecosystem function (Figure 1). This may occur after a natural or human-mediated perturbation such as a tsunami or pollution event. Essentially, many of the practices and challenges described for restoration apply also to rehabilitation; the latter is, however, made more tractable by

the fact that full restoration of the original system is no longer the aim. Rather, rehabilitation aims to improve to some degree a degraded site by increasing biodiversity at the genetic, species, and community levels and thereby reestablishing associated ecosystem functions such as trophic interactions, water, and nutrient cycles. Thus, to rehabilitate an area is to aim for something which is similar but a little less than full restoration. The goals are determined by what society wants and needs, the level of degradation, and the economical, political, and social environment (Law, 1984).

The diversity of land degradation whether it is pollution, soil degradation, desertification, or deforestation across each continent means that the end-point for rehabilitation is greatly varied. Rehabilitation can simply repair a damaged or blocked part of the ecosystem, which will restore some ecosystem productivity for the benefit of society. Rehabilitation seeks rapid change. Rehabilitation is like restoration, as it uses the indigenous ecosystem's structure and functioning as much as they can be determined (Aronson *et al.*, 1993). Rehabilitation often attempts to jumpstart a new ecosystem by removing the cause of the degradation that led to threshold of irreversibility being passed. Restoration, however, is usually attempted where no threshold of irreversibility has been passed (Aronson *et al.*, 1993). Rehabilitation is aimed at producing a stable productive ecosystem that is consistent with society's values (Law, 1984) but often with introduced species and less ecological complexity than complete restoration.

Reallocation

Reallocation, also known as replacement, is said to occur when management efforts do not seek to reinstate to any degree the original state of the ecosystem's structure and functioning (**Figure 1**). Rather, the nature or use of the site is deliberately targeted in some other direction. For example, a former mining site that led to the severe degradation of a natural grassland may be reallocated to a new use such as plantation forestry. Often, reallocation aims to achieve new landforms and landuses for society's benefit even when restoration is possible. For example wetlands, recreational areas, urban development, or agriculture (EPA: Environmental Protection Agency, 1995).

Degradation, Rehabilitation, and Restoration in Agriculture

Degradation

Both new and traditional demands for agricultural outputs are putting intense pressure on scarce land resources. Agriculture competes for land and water with growing urban settlements and industrial zones. There is also an increasing demand for bio-fuels (Food and Agriculture Organization (FAO), 2012). Agriculture is a major user of land (30% earth's surface) and water (70% extracted freshwater) and it is important to manage the quantity and quality of those resources (FAO, 2012). Despite efforts to conserve and recycle natural resources, the agriculture sector generates waste and pollution that can negatively impact ecosystems. For instance, agriculture is the main source of nitrate and ammonia pollution in both ground and surface water. It is also a major contributor to the phosphate pollution of waterways and the release of powerful greenhouse gases (methane and nitrous oxide) into the atmosphere.

Land degradation in the context of agriculture is the loss of the ability of land to produce food, fiber, and fuel either temporarily or permanently, or to maintain its natural ecosystem function. Land degradation can be caused by the removal of surface vegetation with the resulting loss of organic matter, soil, and plant and animal species (Cribb, 2010). Degradation of agricultural land is a problem as degraded land yields less and so contributes to rising prices as well as to declining viability of rural communities, value chains, and ultimately even to conflict and refugee crises (Cribb, 2010). Degradation also reduces other ecosystem services such as clean water, carbon dioxide absorption, and timber production. Saline or acid soils or those heavily polluted with industrial wastes are toxic to most plants and animals and can result in freshwater degradation resulting inland and water that is unfit for growing food. Pollution can be the result of heavy metals in runoff or fallout from the air from factories, spills, and leaks from transport accidents, the overuse of agricultural pesticides and fertilizers or in highly populated areas the poor disposal of sewage (Cribb, 2010). Potentially, harmful substances can cause a variety of illnesses in humans if polluted land is used to produce food (Cribb, 2010).

Salinity can be natural but agricultural activities, chiefly irrigation and clearing of perennial vegetation, can lead to or exacerbate salinity to the extent that this form of degradation now affects about a tenth of the earth's land surface (**Figure 2**).



Figure 2 Farm rehabilitation seeking to deal with soil salinity in Australia. Regenerating trees on the distant rise and saplings sown in fenced-off areas in middle distance access and use water, preventing recharge of the water table while perennial pasture species are used in place of annual species in the low lying foreground. Piezometers (white plastic tube) allows monitoring of the water table height and periodic measurement of electrical conductivity.

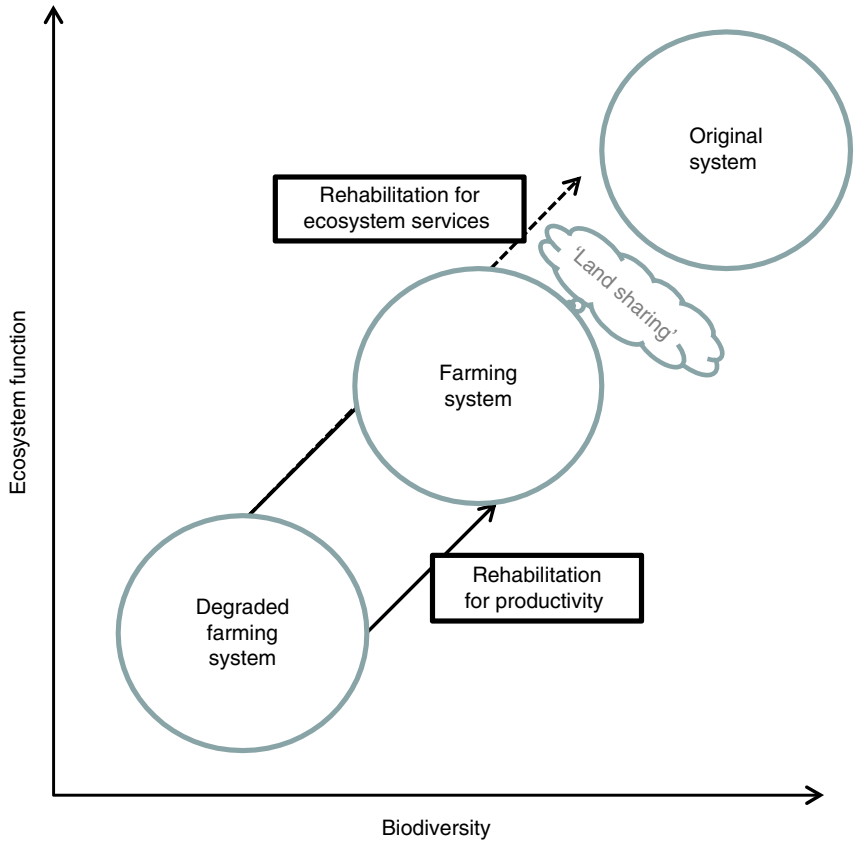


Figure 3 Farming systems are degraded natural systems with lower levels of ecosystem function and biodiversity. They are vulnerable to further degradation that frequently requires rehabilitation efforts to maintain farm productivity. Increasingly, agricultural rehabilitation goes further such that natural biodiversity and farming share the same area with agriculture benefitting from enhanced ecosystem function.

Soil acidity is associated with agricultural activity because most agricultural products are slightly alkaline in their chemical composition so their repeated removal from a site leaves the soil increasingly acidic. For example, the removal of one ton of alfalfa hay requires the application of 70 kg of lime (calcium carbonate) to neutralize the resulting soil acidity. Acidity can also result from fertilizer use, particularly the nitrogenous fertilizers ammonium sulfate and monoammonium phosphate. Further, when nitrates are leached from the topsoil to below the root zone, or from the site entirely, this leaves the soil acidic.

Removing the protective cover to reduce competition for water and nutrients, plowing, heavy grazing and deforestation leave the soil highly vulnerable to wind erosion, particularly during severe droughts. Heavy grazing around water points or during long droughts prevents or delays the regrowth of vegetation or favors only invasive shrubs. This problem is particularly acute in parts of subSaharan Africa, where inherently low soil fertility, severe nutrient depletion, and poor soil structure are prevalent. Heavy fertilizer applications are unaffordable and too risky in these low-potential rain fed cropping systems.

Improving land and water management techniques can rehabilitate agricultural land and restore productivity. Conservation agriculture, improving soil fertility, integrated pest management and other agronomic techniques such as crop rotation can all contribute toward rehabilitating agricultural land (FAO, 2012).

Restoration and Rehabilitation

In the context of agriculture, the concepts of restoration and rehabilitation as used in natural ecosystems need to be tempered by the fact that agriculture is a human activity that has replaced natural systems. Accordingly, agricultural systems constitute habitats with degraded ecosystems in terms of biodiversity and ecosystem function in all respects other than the production of agricultural products (**Figure 3**). This is reflected in the fact that modern agricultural systems are heavily reliant on inputs of allochthonous water, fertilizers, and fossil fuels to generate high yields, and on pesticides and managed honey bees to replace natural pest regulation and pollination. Globally, however, agriculture is widely affected by forms of degradation described above that may be a direct result of the agricultural activity or by external factors such as seawater inundation and pollution. Together, these types of degradation mean that rehabilitation efforts are frequently practiced on farmlands. Most commonly, the aim of these efforts is to address the degradation to restore the site's capacity for productive agriculture. Increasingly, however, the aim may be to take a farming system to a state somewhat closer to the type of

habitat that was present before agriculture was practiced at the site (Figure 3).

Rehabilitation for Agricultural Productivity

Agriculture dominates terrestrial land use in most areas of the globe where the land is inherently suitable for production. This reflects the pressure imposed by the burgeoning human population, predicted to reach 9 billion by 2050. Coupled with rising living standards and attendant need for animal proteins, population growth will mean that the global demand for food will increase for at least another 40 years (Godfray *et al.*, 2010). The human population is likely to plateau at some 9 billion people by roughly the middle of this century. This momentous challenge to agricultural technology illustrates the pressure on farmlands to achieve ever greater levels of productivity, underlies why degradation is increasingly common in these stressed systems and illustrates the importance of successful rehabilitation.

In this context, rehabilitation projects aim to deal with forms of degradation such as soil erosion (Figure 2) to restore farm productivity. Soil degradation resulting in reduced yields is estimated to affect 16–40% of land area and is expected to expand (Tscharntke *et al.*, 2012). Some soil losses around the world are in excess of 50 ton per hectare in a year which is up to 100 times faster than the rate of soil formation (Banwart, 2011).

When considering a rehabilitation approach, it is important to understand how the degradation occurred as removal of the cause can be the start of the solution (Oma, 1992). As well as understanding the cause of the disturbance, the degree of degradation, the productivity goal and economics and timing will determine the methods used (Bainbridge, 2007). Rehabilitation practices range from land surface shaping and drainage management to soil amendments, minimum or zero tillage practices or weed removal or other agronomy practices. Rehabilitating ecosystem services could also include the reestablishment of a single taxon or specific function such as a pollinator or improved drainage.

The soil is central to many forms of degradation in agriculture so many rehabilitation efforts focus strongly on management of soil chemistry, structure, and biology. For example, nutrient deficiencies can be overcome in the short term by the application of artificial or organic fertilizers though care needs to be taken to avoid fertilizer forms and application patterns that lead to acidification. In the longer term, the introduction of nitrogen-fixing plant species, use of perennial crops, pastures and noncrop vegetation, and a return to mixed farming systems that integrate cropping and livestock can provide more durable solutions. Improving the structure of the soil can take a long time and depends on the soil type and the climate; however, biological properties can be reinstated within 10 years (Dobson *et al.*, 1997). A more difficult problem is the decontamination of soils polluted with heavy metals, radioactive materials, or certain organic compounds. Costly approaches such as mass removal or covering with new topsoil are suitable only for small areas. This has led to interest in the potential of phytoremediation, the use of plants to take-up the pollutants from the soil. The plants are then harvested and removed. Even factoring in the costs of these actions and disposal of the contaminated plant material, this strategy is less expensive than traditional approaches. Future advances in plant breeding and processing technology may even allow the pollutants to be recovered and reused.



Figure 4 An example of an agri-environmental scheme feature in southern Britain that constitutes rehabilitation of farmland toward the original habitat. A mixture of flowers sown and managed specifically to support pollinator insects such as bumble bees replaces crop land but earns the farmer payments from a government-funded stewardship scheme.

From Agriculture toward a Former State

Despite the pressure imposed by the burgeoning human population and its expanding demands, there is a recognized need to preserve biodiversity if only for purely selfish reasons of the ecosystem services provided (e.g., carbon sequestration from the atmosphere). Reflecting this, many countries have introduced land sharing schemes whereby agricultural and biodiversity uses are balanced on a given site. Such agri-environmental schemes are often encouraged by payments from the government to farmers, usually for specific land stewardship activities such as planting trees or maintaining grassy or herbaceous vegetation for wildlife or pollinators (Wade *et al.*, 2008). In this context, rehabilitation projects generally involve taking an area of land out of agricultural production; often this is a minimum proportion of the farm as prescribed under a legal framework. Then, passive management may be used, relying on the natural regeneration or establishment of desired plant species. A problem with this approach is that propagates of desirable plant species may be dramatically outnumbered by those of weedy species, particularly if the area has been under cultivation for a long period and is remote from natural vegetation remnants. If weeds are allowed to flourish in areas take out of production they can threaten the productivity of other parts of the farm and neighboring properties. For this reason, rehabilitation of farmland is usually more active and this may be a requirement of agri-environmental schemes that involve financial incentives. Active restoration is practiced by planting trees, hedgerows or sowing desired, native grassy and herbaceous species (Figure 4). Together, such management efforts go beyond attempts to restore the productivity of the

farmland and constitute rehabilitation toward the original nature of the area before agriculture was practiced (Figure 2).

Case Study: Posttsunami Rehabilitation of Farmland

On the 26th December 2004 an earthquake of magnitude 9.3 generated a tsunami in the Indian Ocean affected more than 12 countries causing extensive loss of life (230 000 people in 9 countries) and damage to properties along the coastal areas of these countries (Prih Harjadi, 2008). The tsunami had a severe impact on the local environment, and caused extensive damage to the coastal ecosystem (Shaw, 2008). Tsunami also caused a massive inflow of seawater over the coastal inland agricultural systems and severely affected soil and water resources. The earthquake caused a drop in elevation on some parts of the coastline causing agricultural land to be submerged (Slavich *et al.*, 2008). Areas previously suited to intensive agriculture deteriorated very rapidly because of seawater inundation and deposits of salty sediments (Chandrasekharan *et al.*, 2008; Slavich *et al.*, 2008). In some areas, permanent inundation has resulted in some losing their livelihoods (Niino, 2008; Shaw, 2008). The most saline soils are present where tsunami water lay for longest and these areas suffer the greatest crop yield losses. Shallow groundwater sources were also affected, rendering them unfit for irrigation and domestic use in places (Shaw, 2008; Slavich *et al.*, 2008).

Immediate rehabilitation efforts include the repair of agricultural infrastructure including irrigation channels, clearing of debris, scraping surface salt from fields, and the application of gypsum to selected fields (Niino, 2008). Aid was provided in the form of farm implements, fertilizer, or compost and distribution of salt tolerant crop varieties in the form of seed, seedlings, or cuttings (Niino, 2008).

It is important to reduce the effect of soil salinity on agricultural land by having effective drainage networks to allow seawater to drain from fields. Irrigation and drainage channels had to be cleared of debris and reshaped. In areas where this was not feasible it was estimated it would take years for the land to be rehabilitated. Good rainfalls in the year after the tsunami flushed and leached salts from soils where drainage was adequate such that soil electrical conductivity fell to levels that allowed for crop growth (Abubakar and Basri, 2008; Chandrasekharan *et al.*, 2008).

Reducing salt accumulation can be facilitated by adding soil ameliorants to improve enhance structural stability of the soils and correct nutrient imbalances. Ameliorants can include gypsum, organic matter such as green manure or compost (Abubakar and Basri, 2008). Initial rehabilitation efforts were focused on land with light or medium damage, within 3–4 years most of this land was rehabilitated and under cultivation and work had begun on more heavily damaged land which included the rebuilding of paddy fields (Abubakar and Basri, 2008).

Vegetable, cereal, and tree crops can be grown in tsunami affected soils by selecting species and varieties that tolerate soil salinity. There are rice cultivars and tree crops that are tolerant of salinity and able to be planted in tsunami affected soils. Some of these are regularly grown in tidal swamp areas. (Chandra Mohan, 2008; Joshi, 2008).

Longer-term strategies include new investment in agricultural field drainage technologies, provision of water harvesting structures, and the desilting of drainage channels and watercourses (Chandrasekharan *et al.*, 2008). Further, unsustainable land use expansion combined with demographic growth into marginal areas are responsible for elevating the level of exposed to natural risks and increased the region's vulnerability to environmental impacts that extreme natural events, such as tsunamis, may cause (Shaw, 2008). Accordingly, responses should be directed toward the prevention and mitigation of the environmental impact of natural disasters as well as to the rehabilitation and reconstruction of sites damaged by such events. The capacity of a region to resist or ameliorate the impact of a disaster is related to the provision of environmental services based on the natural resources available in that region such as well preserved ecosystems (Shaw, 2008). Areas of mangroves in coastal zones (Hogarth, 2001) are one relevant example.

Earlier natural disasters such as volcanic eruptions have led to the short- or long-term abandonment of agricultural land and it was ultimately the overall economic and social 'health' of the farming system that determined the level and speed of recovery (Wilson *et al.*, 2011). Natural disasters may act as a catalyst, accelerating the rate at which adjustments in ongoing economic and social systems occur. Community resilience is largely dependent on preexisting social, economic, and political conditions as well as postdisaster responses, relief effort, mitigation strategies, and longer-term rehabilitation programs (Wilson *et al.*, 2011). A well-planned rehabilitation program will take the opportunity to improve agriculture such as introducing higher yielding crops and/or varieties and improving existing infrastructure and support systems (Chung, 1987). Responses from donor countries and international agencies with relief assistance are often immediate but agricultural rehabilitation, because of its long-term nature and high cost require ongoing efforts by the governments and communities of the affected countries (Chung, 1987). Many nongovernment organizations (NGOs) promote the idea of 'build back better,' for example, restoring natural ecosystems such as mangroves. Some such work has, however, been considered wasteful as it was implemented in some cases without proper postdisaster surveying (Cochard *et al.*, 2008). NGOs have also paid locals to implement natural ecosystems restoration schemes but this creates a false economy and can result in exacerbation of farm abandonment as rural workers prefer cash employment (Cochard *et al.*, 2008).

The Future of Rehabilitation in Farmlands

Many ecosystems have been transformed or degraded by human use, and restoration offers an opportunity to recover services and benefits as well as less tangible benefits such as aesthetic and recreational value (Aronson *et al.*, 2010). In farmland, ecological restoration can contribute to sustainable agriculture by directly addressing many forms of degradation whether caused by agricultural activities or by external perturbations. Increasingly, rehabilitation efforts undertaken in farmlands go further. Agri-environmental schemes in many parts of the world move degraded agroecosystems closer to

their original, preagricultural state thereby restoring significant amounts of biodiversity and associated ecosystem services (Wade *et al.*, 2008). Agroforestry represents an intermediate step between natural secondary forests and reclamation of severely degraded land in terms of high versus low provision of biodiversity and ecosystem services, state of degradation, and time and costs of forest restoration. Agro-successional restoration schemes have been proposed, which include agro-ecological and agro-forestry techniques as a step before forest restoration (Rey Benayas *et al.*, 2009).

Farmers are increasingly aware of the ecosystem services performed by agricultural biodiversity. These include pest suppression, conservation of pollinator species and wildlife, fixation of atmospheric nitrogen, nutrient cycling. Strategies for enhancing these are many and varied but adoption tends to be strongest when the right forms of diversity are selected and incorporated into farming systems with the minimum of disruption to normal farming practices (Gurr *et al.*, 2004). Examples of farming practices and landscape features that favor biodiversity include strategic revegetation of property boundaries, field margins, and track edges to create living fences, planting isolated trees to take advantage of their disproportionate positive value of biodiversity conservation and potential for seed dispersal, creation of pollinator friendly areas using specific plants and nesting habitat, the introduction of overwintering habitat, and nectar plants for natural enemies of pests (Rey Benayas *et al.*, 2009). An important current example is ecological engineering of Asian rice. Planthopper pests have devastated rice crops throughout Asia over the past 5 years, largely because of the overuse of insecticides which have reduced the diversity of natural enemies and led to the development of insecticide resistance in pest populations. Further, the widespread use of a relatively small range of rice varieties has meant that planthoppers have also evolved immunity to the traits in rice plants that previously conferred high levels of insect resistance. This erosion in efficacy of the two mainstays of pest control (insecticides and pest-resistant varieties) necessitated action to reinstate natural mortality of planthoppers imposed by a wide diversity of predatory and parasitic arthropods. A range of plant species was evaluated in laboratory experiments and led to the identification of sesame as one suitable for boosting the longevity, fecundity, and impact of parasitic wasps and predators. This was then promoted for use on the earthen banks around rice fields where it gave good control of pests (**Figure 5(a)**). This rehabilitation strategy has become widely used in China and Vietnam because it gives farmers a highly tractable method to rehabilitate their farms to a state similar to that of traditional rice production landscapes such as of Sanmen in eastern China, where rice is produced in mixed farming systems without the need for insecticides (**Figure 5(b)**).

In alignment with the value of biodiversity to agricultural production through greater operation of ecological goods and services and less reliance on synthetic inputs, the fact that 40% of terrestrial area is under agricultural management and just 12% is protected means that the protection of biodiversity requires a highly connected matrix made up of seminatural habitats, managed habitat including farmlands as well as reserves (Tscharntke *et al.*, 2012). Management of biodiversity, in habitats outside of farming systems can be used to benefit agricultural production and enhance ecosystems services (Rey Benayas *et al.*, 2009). This differs from any notion of a wholesale reversion to traditional agricultural methods which would reduce food production massively. Restoration and rehabilitation efforts to benefit wildlife and ecosystem services to agriculture can employ highly specific actions intended to benefit particular taxa or guilds and ecosystem services such as pollination and natural pest regulation. Relevant strategies often occupy only small fraction of the agricultural land, meaning that they compete to only a small degree with productive farmland use.

Some have found that the majority of plant biodiversity is found in small fragments of noncrop habitat suggesting that in ecosystems with little noncrop habitat, biodiversity can be improved by land sparing (Egan and Mortensen, 2012) where agricultural land is farmed intensively and remaining natural habitat is protected. According to Phalan *et al.* (2011), land sparing conserves biodiversity more effectively than land sharing where land is not protected but is managed in a wildlife-friendly manner. Many authors argue about land sparing, stating that it requires proper implementation and is not a system that can be transferred across different ecosystems



(a) (b)

Figure 5 (a) A rice crop in eastern China in which rehabilitation of natural pest control has been achieved by use of sesame on the bunds to provide nectar to enemies of pests, (b) a traditional rice production landscape in eastern China where the diversity of crop and noncrop vegetation allows production without the need for insecticides.

(Fischer *et al.*, 2011; Tscharntke *et al.*, 2012). Others also argue against land sparing approaches as agricultural intensification can result in increased land clearing or movement of agriculture into unsuitable areas and a high use of pesticides. Improved knowledge of biodiversity can lead to improvement in agricultural yields as well as improving biodiversity (Fischer *et al.*, 2011). Much of the food insecurity at present is caused not by insufficient agricultural production but by poverty and problems of socioeconomic access (Ratnadass *et al.*, 2012). Tscharntke *et al.* (2012) also argues that world food shortages are better resolved by less wastage and better distribution of the foods currently produced rather than increasing food production.

Although ecological restoration is challenging to achieve, rehabilitation is far more tractable and generally widely regarded as essential not only for conserving biodiversity, but also for promoting economic development and sustainable livelihoods, particularly in developing countries. Likewise, restoration within and around degraded ecosystems provides a powerful tool for increasing resilience and connectivity in natural environments, thereby reducing the vulnerability of these ecosystems and their resident biodiversity to the projected consequences of climate change (SER Society for Ecological Restoration, 2009).

See also: Biodiversity and Ecosystem Services in Agroecosystems. Biodiversity: Conserving Biodiversity in Agroecosystems. Climate Change, Society, and Agriculture: An Economic and Policy Perspective. Food Security: Yield Gap. Land Use: Catchment Management. Land Use, Land Cover, and Food-Energy-Environment Trade-Off: Key Issues and Insights for Millennium Development Goals. Land Use: Management for Biodiversity and Conservation. Soil: Conservation Practices

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Linkages of the Agricultural Sector: Models and Precautions

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Glossary

Basic economic sector Produces goods and services for consumption outside the local region (export consumption).

Cointegration A statistical property of time-series variables. Two or more time series are cointegrated if they share a common stochastic drift, such as stock market indices and the stocks that make up the indices.

Compensating variation The amount of money that just compensates a person, group, or whole economy, for the welfare effects of a change in the economy, thus providing a monetary measure of that change in welfare.

Consumer surplus The difference between the price a consumer pays for an item and the price he would be willing to pay rather than do without it.

Equivalent variation Measures the amount of money that, paid to a person, group, or whole economy, would make them as well off as before the specified change in the economy.

Kaldor–Hicks improvement Any alternative that increases the economic value of social resources. Kaldor–Hicks is related to Pareto efficiency. Under Pareto efficiency, an outcome is more efficient if at least one person is made better off and nobody is made worse off. Under Kaldor–Hicks efficiency, a more efficient outcome could leave some people worse off but an outcome is more efficient if those that are made better off could in theory compensate those that are made worse off and lead to a Pareto optimal outcome.

Nonbasic economic sector Serve the needs of the local basic sectors and local resident population or consumption.

Producer surplus Measures the difference between the amount that a producer of a good receives and the minimum amount that the producer would be willing to accept for that good.

Introduction

Rural America has realized rapid demographic and economic structural changes over the past several decades. By 2000, the last Census to report farm employment showed a decline from approximately 32.0 million in 1920 to approximately 3.0 million workers in 2000, its lowest value of all time (Dimitri *et al.*, 2005). Also from July 2011 to July 2012, nonmetropolitan population fell by 0.2%, which was the first ever decline in nonmetropolitan population recorded by the Census (USDA, 2013).

During this same period the structure of the nonmetropolitan nonfarm economy was also changing. Nonmetropolitan county economies have a strong resource base, and the proportionate share of farm sector employment in total nonmetropolitan employment declined from 14.4% in 1969 to 5.6% in 2011 (U.S. Department of Commerce, 2012). Although there is a perception even in nonmetropolitan counties that agriculture is the primary employment sector, by 2011 the manufacturing sector (10.0%), the retail sector (10.9%) and the health care and social assistance sector (10.0%) each had larger proportionate shares of total nonmetropolitan employment than agriculture (Goetz *et al.*, 2013).

It has also been suggested that even with economic structural change, the agricultural sector provides stability in many rural economies. As Moline *et al.* (1991) found in Wyoming, agricultural producers have fixed levels of operating expenditures that must be covered in a given year. Many agricultural sector expenditures involve purchases from local businesses and the fixed expenditure level provides some stability to the local economy. With lower output or higher input prices, most agricultural producers will realize lower returns while trying to maintain output levels and expenditures. Changes in production levels due to drought, rangeland fires, or government production reduction policies will impact the stability of these farm expenditures.

The overall structure of nonmetropolitan counties has been impacted not only by changing agricultural sector relationships in rural economies, but also by structural change in agriculture itself from greater vertical integration between producers, processors, and distributors. This vertical integration of agriculture or what has been characterized by Drabenstott (1995) as the 'broilerization of agriculture' produces a different linkage between agriculture and the rest of the rural economy. In fact, many states have targeted agriculture as a cluster industry but what they are really referring to is agribusiness as their economic target.

Given the changes in nonmetropolitan population and the restructuring of the agricultural sector, a number of state, and local studies have been commissioned to measure the contributions of the agricultural sector to the local, regional, or state economy. Leones *et al.* (1994) identified 14 states that completed contribution analyses of their state's agricultural industry. Of interest in all of these studies is how agriculture is defined. If the study extends beyond the farm gate, it becomes

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an agribusiness study which can include agricultural manufacturing, distribution, and retail. In this case a serious problem of double counting can arise, if agricultural sector impacts are counted twice.

As discussed in Section Introduction, agriculture has the potential to have substantial ripple effects on rural economies from changes in activity. Changes in agricultural economic activity may occur in response to drought or disasters (weather or fire), expansion of foreign trade or location of agribusiness firms, adoption of new technologies, or changes in public policies. These changes are felt throughout most rural economies because of the agricultural sector's economic linkages within the local economy. Because of these economic linkages, government officials, business decision makers, and concerned citizens are profoundly interested in the total and distributional impacts of changes in agricultural activity in their local economy, and in order to shed light on these ripple effects or impacts, economic models are often employed. If these models are incorrectly used, the resulting analysis will be misused, disregarded, or discredited by the public. Poorly executed studies can actually cast a shadow of doubt on agriculture, which can work against the industry within the larger community.

The principal objective of economic impact modeling is to identify changes in the local, regional, or state economy from positive or negative changes of a particular segment of the economy (Davis *et al.*, 1999; Cummings and Morris, 1997; Goetz *et al.*, 2009). These studies are often based on either economic base or input–output (IO) models but more advanced models have been applied which include social accounting matrix (SAM) models, computable general equilibrium (CGE) models and conjoined econometric/inter-industry models. Here the authors discuss the use of impact models for analysis of changes in agricultural activity and the potential misuses of these models. This article is divided into two major sections. The first section discusses the alternative models that can be used to derive economy-wide impacts from changes in agricultural sector activity. The second section discusses the different metrics of economic impact modeling as well as the impacts of the size of the study area. Social and public sector impacts can and should also be incorporated in a detailed analysis but are not addressed here. For social and public sector impacts early studies from the Western Rural Development Center provide excellent information (Weber and Goldman, 1979; Faas, 1980; Siegler and Meyer, 1980; Cooke *et al.*, 1996).

Models for Estimation of Impacts

Economic impact models' primary objectives are to derive overall and distributional impacts in the local, county, state, or national economy from positive or negative changes in a particular segment of the economy, such as agriculture (Davis, 1990; Cummings *et al.*, 1998). Impact studies, especially those investigating the distributional impacts of changes in agricultural sector activity have been either export/economic base, IO, SAM, conjoined econometric/IO models, or CGE models. The authors next review these in turn.

Economic Base Models

Export- or economic base models have a long history dating back to the 1940s. North (1959) pointed out that export sales, including agricultural exports, led to US growth from the 16th to 19th centuries. The premise of export/base economic models is fairly simple: to promote economic growth at the local level one must increase exports out of the region which in turn injects money into the region. Historically, this has caused policy makers to focus on goods-producing industries, such as agriculture, mining, forestry, and manufacturing as the 'engines of economic growth.' More recently, Kilkenny and Partridge (2009) questioned the reliance on export-base growth models for contemporary rural growth initiatives. For example, over the past 50 years the economy has moved from a goods-producing economy, a focal point of export-base analysis, to a services-producing economy. Export- or economic base models also have been criticized because of their theoretical weaknesses by Krikelas (1991) and Isserman (1980) (e.g., all regions export and none import).

Export- or economic base models are thus not without criticism or problems in their use or calculation. These criticisms or problems are (1) the identification or measurement of sector basic and nonbasic employment or income, (2) an oversimplified theory, (3) stability of multipliers over time (Brown *et al.*, 1992; Gerking and Isserman, 1981; Stabler and Howe, 1988; Williams, 1996).

Identification of economic base

The first criticism of base multipliers is the bifurcation of sectoral employment into basic (exporting) and nonbasic (nonexporting) employment or income. Sectoral employment and income are not reported separately as basic or nonbasic values, and therefore empirical procedures must be used to bifurcate the data into its two components. Four procedures have been suggested to bifurcate the data which are direct interviews, assumption procedure, location quotients (LQs), and minimum requirements.

The direct methods procedure employs surveys of local businesses and households to bifurcate the flow of local economic activity (Tiebolt, 1962). Interviewing local businesses and households, however, is expensive and time consuming. Also, with any interviews the representativeness of the sample may be questioned and the accuracy of replies by businesses and households as to proportions of total business activity or household consumption that are exported may be questionable.

To address problems of timeliness and expense, indirect procedures have been developed to bifurcate sectoral employment or income. One indirect method is the assignment procedure. For this indirect method, the researcher or focus group assume or agree on the proportion of total sectoral activity that represents exports. This procedure has no theoretical backing and depends on the researcher's or focus group's knowledge of the local economic sector. It is sometimes referred to as the 'expert assignment approach.'

Another indirect procedure to bifurcate sectoral employment or income is the LQ approach. This procedure's premise is that the more specialized a given region's sector, for example, agriculture, relative to total regional activity, the more

of the sector's economic output is exported. A LQ for a given sector i in a region r is estimated as:

$$\mathrm{LQ}\,i,r = \frac{\text{Percentage of total regional } (r) \text{ employment in sector } (i)}{\text{Percentage of total national employment in sector } (i)} \quad [1]$$

If the percent of employment or income in sector i, such as agriculture, in region r is greater than the percentage of agriculture in the nation, then part of that sector's employment or income is made up of exports. If the sector's proportionate share of total employment is less than the national share, however, the sector's employment or income is classified as nonbasic.

Minimum requirements are another indirect method to derive a sector's and region's export base or basic employment or income. The main difference between the LQ and minimum requirements approaches is that the region's employment or income structure is compared to a sample of similarly sized counties or regions rather than the nation as a whole. For each economic sector, the county within the size class (e.g., based on population) that has minimum share of its employment or income devoted to that sector is identified. Every other county within the size class is then assumed to produce exports, with its export activity consisting of the difference between a sector's share of employment or income in the region and the sector's share in that county where the minimum share occurred.

In addition to these methods being used to build impact assessment methods and tools, the simple methods have proven to provide powerful insights into the strengths, and weaknesses, of local economies. Because of their simplicity, local decision makers are likely to understand and hence use the information gained by their application. Still, even as these simple bifurcation methods have been criticized, they at the same time have been the focus of numerous refinement procedures (e.g., Pratt, 1968; Archer, 1976; Isserman, 1980; LeSage and Reed, 1989).

For example, researchers have employed dynamic location procedures to estimate basic employment or income or they have employed confirmatory factor analysis. Harris *et al.* (1998) employed confirmatory factor analysis to estimate sectoral basic employment and income for a given region. This procedure assumes that basic employment or income is unobservable and that procedures such as the assignment procedure, LQs, and minimum requirements are imperfect estimates of the basic sector activity. These indirect procedures, although not perfect, provide some indication of the unobservable latent variable which is export or basic activity. Using confirmatory factor analysis (Bollen, 1989), a relationship among a set of indicators of basic employment or income can be employed to derive the unobserved latent variable sectoral basic employment or income. Additional explanation of these procedures and enumeration of limitations are addressed by Shaffer *et al.* (2004).

Oversimplification

Base models have been criticized for being simplified in that they assume that a shift in export demand is the sole source of change in local economic activity. There are many additional factors that affect economic activity, including supply factors. Size of population, labor availability and skill level, and entrepreneurship activity, to name a few would likely influence local economic activity in contemporary America more than just expanded export sales. The notion of promoting economic growth through building stronger linkages within the local economy, for example, cannot be addressed in export-base theory. Also the theory neglects imports and the multiplier effect of 'import substitution.'

Stability of basic and nonbasic multipliers over time

Economic base models are justified by the existence of a long-run relationship between basic and nonbasic sectors: basic or export sectors buy inputs from local nonbasic and as the export sector grows, nonbasic sector activity also grows. Some past studies (Shahidsaless *et al.*, 1983; Braschler, 1972; Mandelbaum and Chicione, 1985; Mulligan and Kim, 1991) employed single-time period cross-sectional data. Cross-sectional studies, unfortunately, are static in nature and any examination of change during one period alone could be misleading.

Other studies employed monthly or quarterly time-series data to test for short-run and long-run multipliers (Henry and Nyankori, 1981; Spreen and Mulkey, 1980; Lego *et al.*, 2000; Harris *et al.*, 1999). With time-series models, cointegration is applied to test for long-run relationships between variables such as basic and nonbasic employment or income. Nishiyama (1997) found that economic base theory through cointegration holds strongly for the crudest definition of base such as the assignment method but not for other base definitions for the states of California, Massachusetts, and Texas. As noted in Section Oversimplification, the definition of the local economy or region matters: it has been argued that small isolated economies rather than large state or metropolitan economies are more appropriate for export-base models. Harris *et al.* (1999) and Lego *et al.* (2000) employed cointegration to show linkages between basic and nonbasic economic sectors and dynamic multipliers through vector autoregression models. Results of both studies show that export employment in a sector such as agriculture could yield negative short-run multipliers but employment multipliers that are positive in the long-run. Short-run negative multipliers could be due to the lag of labor migrating from other areas to the study area and the basic sectors offering above average wages thereby bidding away employment from local nonbasic sectors. Given a longer time period the study area labor force increases due to in-migration and both basic and nonbasic employment increases.

These previous base model studies aggregate basic and nonbasic employment or income into one sector. To derive differential sectoral impacts, differential export-base models were developed. Vias and Mulligan (1997) and Weiss and Gooding (1968) derived disaggregated multipliers for small areas but the number of disaggregated sectors were limited to four or fewer. The results of disaggregation were less than desirable in that the number of disaggregated base sectors was limited by degrees of freedom for statistical significance. Interindustry or IO models became more commonly used because of their ability to estimate detailed distributional impacts.

Vollet and Bousset (2010) employed meta-analysis to derive export/economic base multipliers. This procedure found

the area size, how the export/base sector was identified, and if the export/base sector was based on employment or income greatly impacts the multiplier estimation.

Although some export/base bifurcation procedures can appear to be overly simplistic, tools such as LQs have proven to be conceptually and empirically powerful for understanding local economies. Despite the limitations, these tools have stood the test of time and are still used for a range of economic development policy analysis in addition to impact assessment, such as industrial cluster analysis (e.g., Goetz *et al.*, 2009).

Input–Output Models

Given the need for more disaggregated sectoral information from impact analysis, IO models have been employed since they were first developed by Leontief (1936) in the 1930s. The original IO models developed by Leontief were national and used to derive impacts from national agricultural policy changes. Originally envisioned as a system of national income accounts, the power of the Leontief approach lies is in its ability to model ripples (i.e., impacts) throughout the economy and measure economic multipliers.

State, regional, and local policy decision makers requested similar analysis of potential local impacts of changes from public policies affecting their local agricultural sectors. At the time, however, national production functions could not be transferred to subnational study areas and resulting analysis was unsatisfactory. Desiring subnational IO models, a series of survey-based IO models were developed in Texas (Grubb, 1972), Washington State (Bourque *et al.*, 1967), West Virginia (Miernyk *et al.*, 1970), and Kansas (Emerson, 1969). These survey-based models were, and still are, expensive and required substantial time to be completed.

Given the dissatisfaction with direct survey models, several nonsurvey procedures were subsequently developed. These nonsurvey procedures employed traditional and alternative LQs procedures and supply–demand procedures to derive regional and county IO models. Researchers found that data collection and programming these indirect procedures were again time consuming and costly.

With increases in computing power the US Forest Service developed the IMPLAN IO modeling system (Alward and Palmer, 1993). IMPLAN provided software and data that could easily and inexpensively be used to create regional and county IO models for policy analysis. The IMPLAN modeling system was later commercialized as Minnesota IMPLAN. This software program became popular among government, university, and private sector users. The application of the IMPLAN software was expedited by a workshop sponsored by United States Department of Agriculture and the Regional Development Centers in 1988 in Ft. Collins, CO, USA. This training greatly expanded the use of IO models by University Cooperative Extension faculty to address impact issues from changes in agricultural policy. As noted, many studies have investigated the impacts of the agricultural sector on the state economy, and Leones *et al.* (1994) found that about half of these studies used IO models. IO models have also been employed to provide regional impacts from natural disasters and changes in public policies as they impact the agricultural sector.

Nonsurvey methods and models need to be verified and validated. Holland *et al.* (1997) provided a detailed procedure for doing this for IMPLAN. McKean and Spencer (2003) investigated the possibility that IMPLAN may understate agricultural sector impacts. Also some have found the agricultural sector scheme from IMPLAN to be too aggregated and that other secondary data procedures need to be employed to address specific agricultural sectors and agricultural policy questions. Procedures outlined by Coupal and Holland (1995) showed how University Cooperative Extension agricultural budget fact sheets can be used to develop disaggregated agricultural sectors for specific modeling analysis. The procedures have been applied to numerous studies to analyze crop and livestock specific policies and issues for impact analysis (Coupal and Holland, 1995; Fadali and Harris, 2006).

To complete the validation and verification of the IO model, procedures outlined by Lahr (1993) should be followed to develop what is called a hybrid or mongrel model. Lahr (1993) suggested completing direct interviews of resource sectors, miscellaneous sectors, and other key sectors of interest. Collecting sectoral information as a percentage of total output that are exports and total inputs that are imports increases the validity of the model. The IMPLAN model to its credit allows easy modifications to its database for this specific analysis.

Numerous studies investigating economic linkages and impacts of the agricultural sector have been conducted for single counties, regions, states, or even nations. Hughes and Litz (1996) developed an interregional IO model of the Monroe Louisiana Functional Economic Area employing the IMPLAN model. Their model estimated the contribution of agriculture in the rural periphery to the urban core. Their study showed economic linkages between the urban food processing sector and the rural periphery economy to be small. Interregional studies such as Hughes and Litz (1996) may become more important, as growing metropolitan populations may not understand the economic linkages between their cities and the rural agricultural periphery.

Social Accounting Matrix Model

Impact analysis from changes in agricultural activity from IO models primarily shows total output, employment, and income impacts. By the 1990s interest was not limited only to total impacts but also the distributional consequences of different agricultural policies and production levels on the regional economy. SAM models were developed to identify the distributional impacts of agricultural activity changes. One of the primary results of a regional IMPLAN derived SAM model is the disaggregation of households by income size. This allows one to derive the distributional impacts of agricultural sector output changes or public policies on a regional economy. Holland and Wyeth (1993) discussed similarities and differences in IO and SAM multipliers. SAM models have also been applied to agriculture and forestry for analysis of distributive economic impacts (Breisinger *et al.*, 2010; Bautista, 2001; Marcouiller *et al.*, 1993). Waters *et al.* (1999) employed SAM modeling procedures to estimate the agricultural sector's role in Oregon's economic base. The SAM allowed for federal

transfer payments into the base analysis, which provided unique insights.

Conjoined Econometric/Interindustry Model

With IO and SAM models, resulting impact analysis shows only total economic and distributional impacts. The analysis generally followed a 'with' and 'without' framework with no discussion of how these impacts proceed over time. Public policy questions arise as to impacts to local government revenues and expenditures, and demographics, and local government services. To include these additional factors conjoined econometric/IO, models have been developed. Rey (2000) and Shields (2006) showed the conjoined econometric/IO model provides several advantages over IO or SAM models and sophisticated econometric models. As noted in Shaffer *et al.* (2004) the use of the simple Keynesian system of economic accounts has provided the theoretical foundation for a wealth of statistically (econometric) derived models of national and state economies. These models are widely used for both policy or impact analysis (Shields *et al.*, 2001) and forecasting (see Johnson *et al.* (2006) for a detailed discussion of a particular family of conjoined models and their applications).

With the widespread use of IOs and SAMs at the local level, primarily through the application of IMPLAN, economists are exploring ways to leverage the power of IOs and SAMs with the power of statistical models. Because both IO/SAM and econometric approaches have attractive features, it was inevitable that economists would try to select the most promising attributes of each in developing a hybrid model. These models that use both IO/SAM and econometrics are often referred to as integrated or conjoined. In his 1977 presidential address to the American Economics Association, Nobel Laureate Lawrence Klein suggested that models that integrate IO/SAMs and econometric methods might become a new method or approach to guide our thinking about the performance of the economy.

In an integrated or conjoined model, the IO/SAM component is used to determine industry supply and primary factor demands. The econometric component determines final demands, factor prices (hence price endogenous), primary factor supplies, and financial market variables. The aim is to retain the sectoral detail of the IO/SAM and close the model with a system of endogenous econometric relationships. The closure mechanism links primary factors and final demand.

Hybrid conjoined models offer several important benefits from an applied perspective. First, the IO/SAM component allows for more sectoral detail, or disaggregation, than the traditional econometric or CGE approaches. Second, the econometric equations provide a better mechanism for introducing policy simulations by fully specifying the underlying components of final demand. Third, the full employment assumption of IO/SAM can be relaxed – the econometric component allows for unemployment or underutilization of local resources. Fourth, the econometric components can accommodate spatial issues that are of particular importance to communities, such as migration and commuting. Finally, the econometric components explicitly allow prices to fluctuate.

There are, unfortunately, limitations to these conjoined models. First, there is no commonly accepted way to link the IO/SAM and econometric elements of the model, specify the econometric equations, or choose among alternative econometric methods. Second, the required time-series data at the local level can be difficult to obtain. As a result, two competing models can yield different policy results depending on how the model builder approaches model construction and estimation.

Computable General Equilibrium Model

IO, SAM, and conjoined econometric/IO-SAM models cannot be used for welfare analysis. This is where CGE models can be employed. Just like the original IO models of the 1930s, the success of these national models for analysis of public policies led to a demand for similar work at the state, regional, and county levels. One of the problems with IO-SAM and export-base derived models is that prices are fixed and not allowed to vary. For economists this is particularly troublesome because prices are the market clearing mechanism. To use an economic model that does not readily allow prices to change is troublesome, and the advent of CGE models directly addressed this fundamental problem. Development of CGE models, however, was fairly complex and they were not widely used. The data from IMPLAN modeling of SAM's, the development of General Algebraic Modeling System and enhance computing power provided researchers and Cooperative Extension personnel the tools to develop subnational CGE models.

CGE models are based on the Walrasian general equilibrium structure. The models explicitly incorporate supply constraints, identify prices and quantities separately, and assume twice-differentiable production and preference surfaces. Thus unlike IO and SAM models, CGE models allow substitution effects in production and consumption. Factor and commodity markets attain their equilibrium through adjustment of prices. There are several CGE models in the literature (Seung *et al.*, 2000; Waters *et al.*, 1997; Schreiner *et al.*, 1996; Hoffman *et al.*, 1996; Kraybill *et al.*, 1992; and Berck *et al.*, 1991). Seung *et al.* (2000) analyzed water reallocation policies in rural Nevada and compared water reallocation policies employing compensating variation. Additionally, Schreiner *et al.* (1996) used CGE modeling as a framework for economic development and showed that policies for increased employment or higher aggregate output levels could produce results that were lower than welfare maximization policies. Given increased application of CGE models and potential advances by IMPLAN to produce synthesized CGE models the use of CGE models should increase.

CGE models, as with any economic model, have their limitations. Because of the complexity of these models industrial detail is lost compared to an IO/SAM model. For example, all of agriculture is commonly aggregated into one sector. Modelers must at times make heroic assumptions to operationalize the model. For example, exactly how sensitive are the demand for and supply of agricultural commodities? Or exactly how does the local economy interact with the larger surrounding economy? Exactly how do consumers and firms

respond to tax policies? Each of these plus dozens of other issues must be quantified in detail and often researchers must make strong assumptions to operationalize the models.

Alternative Metrics for Impact Analysis

With employment of various models to derive economic linkages of the agricultural sector to other sectors in the economy and resulting economy-wide changes from alternative agricultural production levels due to natural disasters, export expansions, or governmental policies, alternative metrics employed in the use of these models needs to be addressed. Watson *et al.* (2007) provided an overview of alternative metrics for assessing how changes in agriculture affect the study area economy. They discussed contribution analysis, impact analysis, and benefits or welfare analysis. An understanding of the differences in these metrics provides researchers and reviewers of economy-wide studies with a perspective on proper procedures for analyzing regional economic changes from agricultural activity. Incorrect application of an impact research metric can yield errors in the analysis which then undermines the analysis in the eyes of the funding agency and public.

Contribution analysis yields estimates of gross change in economic activity and the resulting respending of dollars in a local economy. The contributions metric as defined by Watson *et al.* (2007) is based on a purely descriptive analysis that simply tracks gross economic effects and does not address crowding out of other sectors or economic activity. Impact analysis, however, examines the effect of new revenues to the study area or of keeping revenues in the area that would otherwise leave. Especially in studies of tourism, impact analyses encompass the concept of 'displacement.' Displacement in this case refers to expenditures by local tourists that would have been spent on other sectors of the economy if the tourism activity had not existed. Given a fixed amount of money for recreational expenditures, how do local residents spend those dollars? Therefore, this would represent only recycling of dollars that already exists and not new dollars coming into the study area (if the tourists are not from outside the area). For example, does a local agritourism event draw from only the local community or does it attract tourists from a larger geographic area? If the local agritourism event draws from only the local community, what other recreational activities in the community are affected or displaced?

Cost–benefit analysis is yet another means of assessing changes in a rural economy. Cost–benefit is an overall economic efficiency or social welfare analytical concept which employs compensating or equivalent variation. Boardman *et al.* (2001) and Schreiner *et al.* (1996) discussed that benefit analysis usually draws on what economists call Kaldor–Hicks welfare analysis while applying CGE models. These CGE models are complex representations of simple supply and demand relationships. Shocks to the local economy, such as a change in agricultural exports, shift those supply and demand relationships resulting in different prices and quantities produced and consumed. The cost–benefits of those shifts are captured through consumer and producer surplus. Here consumer surplus is the difference between the maximum price a consumer is willing to pay and the actual price they do pay for a good or service. Producer surplus is the amount that producers benefit by selling at a price that is higher than the least that they would be willing to sell for. Although these concepts are intuitive to an economist, they often are less intuitive to policy makers and concerned citizens. This is an area for extension economists to address as to outreach programs to convey an understanding of welfare analysis with economy-wide models.

Differences in results from cost–benefit analysis, when compared to impact procedures, can arise when the public is better off in ways that are not tractable by economic activity. For instance, residents in a rural area may be happier spending US$50 for a local agritourism event than spending the same amount on a close substitute, for example a concert. If this is the case, as Watson *et al.* (2007) enumerated, the actual economic activity in the rural area has not changed but the net benefits, or welfare, to the rural residents has increased. For this reason, it is important to understand that contribution or impact analysis should not be confused or mistaken for cost-benefit analysis.

Additionally, the impacts by size of the study area should be addressed. Usually the study area is defined by groups funding the study. The study area is usually a county, a region defined by a grouping of counties, or an entire state. The geographic boundaries of a study area limit impacts to a given area. For example, a small rural ranching area which experiences a reduction in public cattle grazing will have large local economic impacts. If, however, the study uses the nation as a region, then the impacts from reduction of public grazing in one small rural county will have relatively small national impacts. Therefore, the area of study becomes profoundly important if public policy issues are to be formulated correctly from the results of economy-wide models.

Conclusion

Given the demographic and economic structural changes in nonmetropolitan economies as well as the structural changes in the agricultural sector itself, understanding and proper use and application of economy-wide models for public policy analysis is paramount. This article has attempted to provide a succinct review of models that have and can be used to analyze the economic linkages and impacts of the agricultural sector to a county, regional, interregional, or national economy. This article reviewed several historical quantitative procedures to estimate the agricultural sector's contribution to the economic base of an economy, and how these models can be modified to increase verification and validity. The article also addressed differences in economy-wide model metrics that can be used and how the incorrect application of a metric may provide erroneous results. Lastly, the importance of considering the size of the study area was stressed. Geographic boundaries limit the impacts that vary from the national to the local perspective. Proper metrics and study area are essential for ensuring that studies are publically accepted. The article did not address fiscal or social impacts that will arise from changes in agricultural activity. These activities must also be included

for a comprehensive analysis of changes in agricultural production or public policies that impact the agricultural sector.

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M

Marek's Disease and Differential Diagnosis with Other Tumor Viral Diseases of Poultry

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Glossary

Adjuvant A substance that enhances the body's immune responses to an antigen.

Aflatoxins A toxic compound produced by certain molds found in food, which can cause various pathological problems (liver and kidney damage, immunosuppression, and tumors).

Allele Each of two or more alternative forms of a gene that arise by mutation and are found at the same place on a homologous chromosome.

Apoptosis A genetically determined process of cell self-destruction that is marked by the fragmentation of nuclear deoxyribonucleic acid (DNA); is activated either by the presence of a stimulus or by the removal of a stimulus or suppressing agent; is a normal physiological process eliminating DNA-damaged, superfluous, or unwanted cells; and when halted (as by genetic mutation) may result in uncontrolled cell growth and tumor formation – also called programmed cell death.

Astrocytosis An increase in the number of astrocytes, frequently observed in an irregular zone of variable definition adjacent to degenerative lesions (encephalomalacia), focal inflammations (abscesses), or certain neoplasms in the brain; in some instances, astrocytosis may be diffuse in a relatively large region; it represents a reparative mechanism.

B haplotype Major histocompatibility complex of the chicken.

Bursa of Fabricius A primary lymphoid organ that opens into the cloaca of birds and functions in B-cell production.

Demyelination A degenerative process that erodes away the myelin sheath which normally protects nerve fibers.

Edematous Affected with edema (an excessive accumulation of serous fluid in tissue spaces or a body cavity).

Encephalomalacia The softening of the brain due to degenerative changes in nervous tissue (as in crazy chick disease).

Encephalomyelitis The inflammation of the brain and the spinal cord. In young poultry, encephalomyelitis is induced by a picornavirus (avian encephalomyelitis virus).

Feather follicle epithelium The layer of the epidermis surrounding the feather follicle (a small tubular invagination of the skin with a fleshy dermal papilla at the bottom from which the feather grows. The papilla is inserted in the opening at the end of the quill).

Feather pulp The remnants of vascular tissue contained in the core of each feather.

Flaccid paralysis A clinical manifestation characterized by weakness or paralysis and reduced muscle tone without other obvious cause (e.g., trauma).

Gliosis A nonspecific reactive change of glial cells in response to damage to the central nervous system (CNS). In most cases, gliosis involves the proliferation or hypertrophy of several different types of glial cells, including astrocytes, microglia, and oligodendrocytes. In its most extreme form, the proliferation associated with gliosis leads to the formation of a glial scar.

Heterophil Leukocyte in avian species equivalent to neutrophils in mammalian species.

Immunohistochemistry The microscopic localization of specific antigens in tissues by staining with antibodies labeled with pigmented material.

Immunomodulator The agents that alter the immune response by suppression (immunosuppressive) or enhancement (immunostimulant).

Infectious laryngotracheitis A respiratory disease of chickens caused by an alphaherpesvirus (*Gallid herpesvirus 1*). It is characterized by severe inflammation of the larynx and trachea that lead to coughing, sneezing, head shaking, lethargy, discharge from the eyes and nostrils (sometimes bloody), and difficulty breathing.

Keratitis The inflammation of the cornea.

Lymphoblastoid Resembling a lymphoblast.

Lymphodegenerative The degeneration of the lymphoid tissue.

Lymphohistiocytic Involving lymphocytes and histiocytes.

Major histocompatibility complex (MHC) A set of molecules displayed on cell surfaces that are responsible for lymphocyte recognition and 'antigen presentation.' The MHC molecules control the immune response through

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recognition of 'self' and 'nonself' and, consequently, serve as targets in transplantation rejection.
Oncogene A gene that causes normal cells to become cancerous either because the gene is mutated or because the gene is expressed at the wrong time in development.
Oncogenic Tending to cause or give rise to tumors.
Panolphtalmitis The inflammation of all the eye structures or tissues.
Parenchyma The specialized epithelial portion of an organ, as contrasted with the supporting connective tissue and nutritive framework.
Pathognomonic Characteristic or symptomatic of a particular disease or condition.
Pectenitis The inflammation of the pecten (a vascular pigmented membrane projecting into the vitreous humor within the globe of the eye in birds).
Perifollicular Surrounding a follicle (either hair or feather follicle).
Pleomorphic Occurring in various distinct forms. In terms of cells, having variation in the size and shape of cells or their nuclei.
Polyneuritis Neuritis involving several nerves simultaneously.
Quantitative trait loci (QTLs) Stretches of DNA containing or linked to the genes that underlie a quantitative trait.
Real-time polymerase chain reaction (PCR) A technique used to monitor the progress of a PCR reaction in real time.
Reticuloendoteliosis A group of pathological syndromes in several avian species caused by reticuloendotheliosis virus, a member of the avian retrovirus group.
Retinitis The inflammation of the retina.
Serotype A group of closely related microorganisms distinguished by a characteristic set of antigens.
Single-nucleotide polymorphism A DNA sequence variation occurring when a single nucleotide – A, T, C, or G – in the genome (or other shared sequence) differs between members of a biological species or paired chromosomes.
Spastic paralysis An abnormal condition characterized by the involuntary contraction of one or more muscles with associated loss of muscular function.
Torticollis A condition in which the head becomes persistently turned to one side, often associated with painful muscle spasms.
Toxoplasma A parasitic spore-forming protozoan (genus *Toxoplasma*, phylum Sporozoa) that can sometimes cause disease in humans and animals.
Uveitis The inflammation of the uvea.
Vasculitis The inflammation of a blood vessel or blood vessels.

Introduction

Marek's disease (MD) is a highly contagious lymphoproliferative disease of chickens caused by an alphaherpesvirus of the Genera *Mardivirus* (ICTVdB-Management, 2006). In the absence of proper control methods, MD constitutes one of the major threats for the poultry industry. Vaccination against MD has been used since the late 1960s with great success (Churchill *et al.*, 1969). However, Marek's disease virus (MDV) has evolved toward increased virulence within the last 50 years (Witter, 1997) and the ability of MD vaccines to control the disease has consequently decreased. Even using adequate vaccination, in 1984, Purchase estimated mortality and condemnation losses associated with MD at US$169 million in the US and at US$943 million worldwide (Purchase, 1985).

In addition to lymphomas, MDV is able to induce a variety of nonneoplastic syndromes, such as neurological syndromes, immunosuppression, and arteriosclerosis. The economical impact of the MDV-induced nonneoplastic syndromes is difficult to estimate but might be more relevant than initially thought, especially MDV-induced immunosuppression (MDV-IS).

Diagnosis of MD is sometimes complex due to the similarity between MDV-induced tumors and neoplasia induced by other viruses (i.e., avian leukosis virus and reticuloendotheliosis). In addition, some nonneoplastic syndromes, like peripheral neuropathy, are characterized by peripheral nerve lesions very similar to those induced by MDV. An accurate diagnosis is extremely important to establish the proper control methods. Besides confirming a diagnosis, in the event of an outbreak of MD, it is necessary to analyze the possible causes that might have led to the breach on MD vaccine immunity.

MD vaccines are cell associated and that makes their handling and storage difficult. Many outbreaks of MD have been related to failures on vaccination procedures that led to reduced vaccine doses. However, other factors have also been associated with MD outbreaks, such as early infection with MDV (before vaccines can establish immunity), concomitant immunosuppressive diseases, or presence of emergent more virulent MDVs in the area.

The goal of this article is to review the different syndromes induced by MDV focusing mainly on those of more economical relevance for the poultry industry. This article reviews the methods to diagnose MD and to differentiate MD from other related diseases. Finally, currently available vaccines and vaccine protocols are discussed.

Etiology

MDV is an alphaherpesvirus belonging to the genus *Mardivirus* and the subfamily Alphaherpesvirinae. According to the International Committee on Taxonomy of Viruses, members of the genus *Mardivirus* are divided into three species, viz. *Gallid herpesvirus 2* (formerly named MDV serotype 1), *Gallid herpesvirus 3 (*formerly named MDV serotype 2), and *Meleagrid herpesvirus 1* (formerly named MDV serotype 3). The original classification in serotypes was based on the recognition of common and distinct antigenic epitopes for each serotype

(Bülow *et al.*, 1976). Furthermore, each serotype has unique biological features. Serotype 1 MDVs are oncogenic viruses of chickens. Based on their virulence, serotype 1 MDV can further be classified into pathotypes (Witter, 1997). To date, four pathotypes have been described: mild (m), virulent (v), very virulent (vv), and very virulent plus (vv+). Serotype 2 MDVs are nononcogenic viruses of chickens (Schat and Calnek, 1978a). Serotype 3 MDVs are nononcogenic viruses of turkeys and are commonly named as turkey herpesvirus or HVT (Witter *et al.*, 1970). The original classification in serotypes has recently been justified on the basis of the complete sequence for serotype 1 Md5 and GA strains (Lee *et al.*, 2000; Tulman *et al.*, 2000), serotype 2 HPRS-24 strain (Izumiya *et al.*, 2001), and serotype 3 FC126 strain (Afonso *et al.*, 2001). In this article, the term MDV indicates serotype 1 MDV because virulence is unique for this serotype. Related herpesviruses of serotypes 2 and 3 are indicated by the serotype.

MDV has unique features that differentiate it from any other alphaherpesvirus (Schat and Nair, 2008). It is a cell associated with lymphotropic properties similar to those of gammaherpesvirus. It establishes latency in lymphocytes. Furthermore, it carries an oncogene (meq) and is able to transform latently infected lymphocytes into neoplastic cells. However, its molecular structure and genomic organization are similar to alphaherpesvirus (Buckmaster *et al.*, 1988); hence, it is classified into this group of viruses. The details on the genome structure of MDV exceed the objectives of this article and readers are encouraged to read other articles for detailed information (Schat and Nair, 2008).

MDV can establish three different kinds of interaction with the host cells: productive infection, latent infection, and transforming infection. Productive infection implies replication of viral deoxyribonucleic acid (DNA), synthesis of viral protein, and in some cases, production of viral particles. Based on the production of viral particles, there are two kinds of productive infection: fully productive infection and restrictive productive infection. Fully productive infection results in the development of large numbers of enveloped, fully infectious virus. This kind of infection occurs only in the feather follicle epithelium (FFE) and is of major importance in the epidemiology of the disease, as it is the main, if not the only, source of infectious MDV particles (Calnek *et al.*, 1970). Restrictive productive infection results in the development of nonenveloped virions. Several cell types are permissive for restrictive productive infection. *In vivo*, B cells are the principal target cells but activated T cells, macrophages, and transformed cells can also support restrictive productive infection (Calnek, 2001). *In vitro*, this kind of infection can be observed in chicken kidney cells, chicken embryo fibroblast, duck embryo fibroblast, B cells, and other cell lines from chicken origin. Latent infection is defined as the presence of viral genome with no or limited production of viral antigens or infectious virus (Morgan *et al.*, 2001). During latency, transcription of viral DNA is minimal and there are very few copies of viral DNA per infected cells. For serotype 1 strains, the distinction between latency and transformation is problematic and most of the studies of latency are conducted either using other nononcogenic serotypes or in transformed cell lines. Activated T cells are the target cells for latent infection, but latency has also been reported in a small proportion of B cells and in satellite cells and nonmyelinating Schwann cells of peripheral nerves and spinal ganglia (Pepose *et al.*, 1981). Transforming infection occurs only in cells infected with serotype 1, because other serotypes have no oncogenic potential. Transcription of viral DNA is still low but higher than in latent infection. Activated T cells, mainly of phenotype CD4+CD8−, are the target cells for transformation. Viral antigen expression during transforming infection is very restricted and is further discussed under the diagnosis section of this article.

MDV has increased in virulence within the past 50 years (Witter, 1997). Before the industrialization of the poultry industry in the 1950s, MDV strains were mild in virulence and were characterized for inducing a mild polyneuritis in older chickens with no major economical significance (Marek, 1907; Pappenheimer *et al.*, 1929). In the 1950s, a major switch in MDV occurred that jeopardized the onset of the poultry industry. MDVs became oncogenic and were able to induce not only a polyneuritis syndrome but also widespread lymphomas with mortality up to 50% of the flocks (Biggs *et al.*, 1965; Eidson *et al.*, 1968). Those viruses are currently known as virulent MDV (vMDV) (Witter, 1997). The introduction of MD vaccines in the late 1960s (Churchill *et al.*, 1969; Witter *et al.*, 1970) controlled the more severe form of the disease for approximately 20 years. The most widespread vaccine used at that time was serotype 3 MDV (HVT) (Witter *et al.*, 1970). However in the 1980s, a second switch of the virus occurred and led to decrease efficacy of HVT (Witter *et al.*, 1980). Those emergent viruses are currently known as very virulent MDV (vvMDV) and forced the poultry industry to introduce a new vaccine based on combination of HVT and serotype 2 viruses known as bivalent vaccine (Witter, 1982; Calnek *et al.*, 1983). The efficacy of the bivalent vaccine got reduced again in 1990s when another switch of the virus took place. Those are the currently existing viruses and are known as very virulent plus (vv+MDV) (Witter, 1997). The only vaccine currently available that can control vv+MDV is an attenuated serotype 1 MDV strain named CVI988 or Rispens (Rispens *et al.*, 1972; Witter *et al.*, 1995).

Biologically, the newly emergent more virulent MDVs differ clearly from less virulent MDVs. They are able to break vaccine immunity and this is the criteria for the gold standard pathotyping system (Witter *et al.*, 2005); they are more neurovirulent (Gimeno *et al.*, 2002); they might have expanded the host range (Gimeno, 2008); and they seem to be more immunosuppressive (Calnek *et al.*, 1998). Molecularly, however, there are minor changes among vMDV, vvMDV, and vv+MDV (Spatz and Silva, 2007) and at this point it has not been possible to establish a pathotyping system based on molecular features.

The causes of MDV evolution are not well elucidated but some hypotheses have been proposed. The changes in poultry production systems during the 1950s could be a major trigger for the initial changes in MDV leading to a new manifestation of the disease. The occurrence of all subsequent waves of evolution of virulence had been linked to the introduction of different generations of vaccines (Gimeno, 2008). The observation that viruses from each successive wave acquired the ability to overcome the immunity induced by the previously used vaccine strongly suggests that the evolution is primarily aimed at avoiding/overcoming the vaccine-induced response.

The fact that none of the current MD vaccines induce sterilizing immunity or prevent challenge viruses from being released could be a major trigger for the evolution of MDV.

Epidemiology

Chickens are the most important natural host for MDV, but quail, turkeys, and pheasants are also susceptible to virus infection and disease (Witter and Schat, 2003). It is suspected that more virulent MDVs have increased ability to induce disease in turkeys than less virulent MDVs. This work addresses the clinical and pathological manifestation of MD in chickens. A more detailed description of the disease in other species can be found in Gimeno *et al.* (2003) and Schat and Nair (2008).

MDV infection occurs by the airborne route. Transmission of the infection occurs readily between chickens by direct or indirect contact. Epithelial cells in the keratinizing layer of the FFE support fully productive infection and these cells serve as a source of contamination to the environment and to other chickens. Virus is generally associated with desquamated, keratinized FFE cells that are shed along with molted feathers and as dander. Virus excretion begins approximately 2 weeks postinfection (wpi) (Kenzy and Biggs, 1967), with a maximal shedding occurring between the third and the fifth wpi (Witter, 1972). Once the infection has been introduced into a chicken flock, regardless of vaccination status, infection spreads quickly from chicken to chicken. Replication of the virus in the feather follicle can be detected by the existence of nuclear inclusion bodies in the infected cells or by evaluation of the expression of MDV antigens. Vertical transmission of MDV has not been reported.

Vaccination does not prevent superinfection, which is a major factor in the evolution of MDV toward more virulence. Vaccinated chickens become a perfect ecosystem in which a variety of MDVs replicate and those better fit to avoid the immune system have an advantage to spread in the flock. Recently, Dunn *et al.* have evaluated the consequences of superinfection and the factors that influence the outcome of the infection when superinfection occurs (Dunn *et al.*, 2010).

Pathogenesis

MDV is able to induce a variety of syndromes that are divided into two categories: nonneoplastic and neoplastic. The latter is by far the most relevant for the poultry industry due to the economical repercussions and it is referred to normally as MD. The impact of the nonneoplastic syndromes is less understood and it is discussed in the section clinical signs and lesions of this article. Pathogenesis of MDV is a very complex process and a detailed discussion is beyond the scope of this article. Further details can be found in numerous review papers (Schat and Nair, 2008; Calnek, 2001). In this article only those events of the pathogenesis that are relevant to the development of the different MDV-induced syndromes are reviewed. The pathogenesis of MDV differs in chickens that have maternal antibodies (MAb) against MDV and those lacking MAb. In this section, events occurring after infection of chickens lacking maternal antibodies are described. **Tables 1** and **2** summarize the differences on the pathogenesis of MDV in chickens with and without MAb.

The natural route of MDV infection is via respiratory tract following inhalation of infectious cell-free MDV from a contaminated environment. The role of the lung in MD pathogenesis is not clear and it is presumed that phagocytes present in the lung pick up the virus and carry it to lymphoid organs, such as bursa of Fabricius, the thymus, and the spleen. At this early point in the infection, there is no associated pathology in the lung; however, viral antigen has been detected in

Table 1 Pathogenesis of Marek's disease virus in chickens lacking maternal antibodies

Days postinoculation	*Viral infection*	*Lesions*	*Clinical signs*
0	Lung	None	None
3–6	Lymphoid organs	Lymphodegenerative syndromes	Depression Transient immunosuppression
2–7 on	Blood	None	None
7–14	Brain	Brain edema and vasculitis	Transient paralysis
	Nerves	Neuritis	None
	Eye	Panophthalmitis	Blindness
	Other tissues	Inflammation	None
10-on	Feather follicle epithelium	None	None
14-on	Nerves, viscera, and brain	Tumors	Variable
21-on	Arteries	Arteriosclerosis	None

Table 2 Pathogenesis of Marek's disease virus (MDV) in chickens with maternal antibodies against MDV

Days postinoculation	*Viral infection*	*Lesions*	*Clinical signs*
0	Lung	None	None
3–6	Lymphoid organs	None	None
2–7	Blood	None	None
10-on	Feather follicle epithelium	None	None
14-on	Nerves, viscera, and brain	Tumors	Variable

parenchymal cells (Adldinger and Calnek, 1973; Phillips and Biggs, 1972; Purchase, 1970).

MDV reaches the lymphoid organs within 24–36 h after intratracheal inoculation. In the lymphoid organs, infection of lymphocytes seems to be assisted by splenic ellipsoid-associated reticulum cells in blood vessel walls (Jeurissen *et al.*, 1992). In unvaccinated chickens lacking material antibodies against MDV, a productive cytolytic infection is established in the lymphoid organs between 5 and 6 days postinfection (dpi). The initial target cells for the cytolytic infection are B lymphocytes (Shek *et al.*, 1982). This productive infection leads to necrosis and inflammation in the lymphoid organs, inducing what is known as lymphodegenerative syndromes. At this stage, antigens are present in infected cells and virus particles can be detected by electron microscopy. Lymphodegenerative syndromes are associated with a transient immunosuppression.

The necrosis of B cells in the lymphoid organs elicits an immune response and the recruitment of numerous inflammatory cells, especially macrophages, T and B lymphocytes, and some heterophils. The activation of T cells is of particular relevance in the pathogenesis of MDV as resting T cells are refractory to MDV infection. Activated T cells can also support productive infection, but in most cases infection becomes latent after T cells are infected. The switch from cytolytic infection to latency occurs very fast and by 7–8 days evidence of cytolytic infection in the lymphoid organs is minimal, if at all. Latent infection, however, can be detected by this time not only in lymphoid organs but also in peripheral blood lymphocytes (PBL).

Latently infected PBL probably are the disseminators of MDV to other tissues of the chickens. As early as 6 dpi, MDV can be detected in the eye, brain, and in peripheral nerves (Gimeno *et al.*, 2001; Pandiri *et al.*, 2008). Depending on the virulence of the virus and the genetic resistance of the chickens, MDV can reactivate in some of the lymphocytes infiltrating the brain tissue and induce an acute inflammatory response. The consequence of this inflammatory response in the brain is the development of vasculitis and vasogenic edema, responsible for the clinical signs of transient paralysis (TP) (Swayne, 1987; Gimeno *et al.*, 2001; Abdul-Careem *et al.*, 2006; Jarosinski *et al.*, 2005). In some cases, inflammatory lesions in the brain (perivascular cuffing and gliosis) are not associated with the development of TP. Early inflammatory lesions in the peripheral nerves (neuritis) are not associated with any clinical manifestation. Early inflammatory lesions in the eye can be detected as early as 6 dpi and can progress in extension and severity until they induce panophthalmitis with complete destruction of the retina (Pandiri *et al.*, 2008).

A second wave of cytolytic infection is detected in most tissue of epithelial origin by the end of the second week after infection. Because of its relevance in transmission, productive infection of the FFE is particularly important. Replication of MDV in the FFE occurs in genetically resistant as well as susceptible birds independently of the virulence of MDV strain. It also occurs in vaccinated chickens regardless of the level of protection that vaccines confer to a particular challenge. MDV most likely is transferred to the FFE by infected lymphocytes within lymphoid aggregates that develop in the perifollicular dermis as early as 7 dpi. The lymphoid aggregates can develop either into necrotic areas consisting of FFE cells and degenerating lymphocytes (dermatitis) or into cutaneous tumors (skin leukosis).

The secondary cytolytic infection is also associated with a permanent immunosuppression. The mechanisms behind permanent immunosuppression are poorly understood. MDV is able to affect the immune system in various ways: lymphodegenerative syndromes (Calnek *et al.*, 1998), immune dysregulation of the immune responses (downregulation of major histocompatibility complex (MHC) I (Gimeno *et al.*, 2001; Hunt *et al.*, 2001), upregulation of MHC II (Calnek *et al.*, 1984; Niikura *et al.*, 2007), increase of nitric oxide (NO) (Jarosinski *et al.*, 2002)), and neoplastic transformation of T cells. Both immune dysregulation and transformation of lymphocytes can lead to a permanent immunosuppression.

Vascular changes of the major arteries have been detected as early as 15 dpi, although evident lesions of vascular sclerosis do not occur until much later in the pathogenesis (Njenga and Dangler, 1995; Fabricant and Fabricant, 1999). MDV antigens can be detected in smooth muscle cells of affected arteries as early as 1 month after inoculation. Also, cells comprising arterial lesions were found to be latently infected with MDV (Fabricant, 1985). The exact pathogenesis of arteriosclerosis is unknown, but it is thought that MDV induces necrosis in the smooth muscle cells and this, together with the known alteration in lipid metabolism, might be the initial changes in the development of arteriosclerosis (Calnek, 2001). Arteriosclerosis occurs only in unvaccinated chickens lacking maternal antibodies against MDV.

Latently infected T cells can become transformed, leading to the development of lymphomas. Transformation can occur in lymphocytes infiltrating any tissue. Therefore, MDV-induced lymphomas can be detected in the nerves, brain, skin, and any internal viscera. Clinical manifestation of MDV-induced lymphomas depends on the location and extension of the tumors. For the purpose of this article, MD is referred to as MDV-induced lymphomas. Syndromes, other than lymphomas, induced by MDV will be referred by the syndrome name.

Clinical Signs and Lesions

Incidence and economic relevance of the different MDV-induced syndromes vary. Lymphodegenerative syndromes, panophthalmitis, TP, and arteriosclerosis occur only in susceptible chickens lacking maternal antibodies and unvaccinated against MD. This is a very unlikely scenario in field conditions and therefore these syndromes are most commonly reproduced in the laboratory. TP, however, was commonly observed in 8–18-week-old pullets before the use of MD vaccines and is still a problem in 30–40-day-old broiler chickens when they are unvaccinated. Neoplastic syndromes are the most commonly observed syndromes in the field and have important economic impact. The economic impact of MDV-IS is unknown. With the exception of lymphoid organ atrophy (if lymphodegenerative syndromes occur) no specific lesions or clinical signs are associated with MDV-IS. Therefore, MDV-IS is not discussed in this section.



Figure 1 Chicken suffering of paralysis.

Neoplastic Lesions and Associated Syndromes

Clinical signs

Signs associated with the development of MDV-induced lymphomas vary according to the location of the tumors and very few are specific to MD. Stunting, depression, lethargy, paleness, and diarrhea are nonspecific clinical signs that may be observed, especially when the course of the disease is prolonged. Torticollis and tremors are characteristics of the persistent neurological disease due to the neoplastic infiltration of the central nervous system. Asymmetric progressive paralysis that evolves to complete spastic paralysis of one or more of the extremities is the most characteristic sign of peripheral nerve dysfunction (Figure 1). Involvement of the vagus nerve usually is associated with crop paralysis and gasping. Blindness appears in birds with ocular involvement and can be uni- or bilateral.

Gross lesions

The gross changes commonly present in MD are enlargement of the peripheral nerves and spinal ganglia and lymphoma formation in various organs and tissues. Skin lesions are also observed and they are more common in meat-type than in egg-type chickens.

Visceral organs

Lymphomas may occur in virtually any tissue or organ. Distribution of the tumor in a tissue or organ can be diffuse, nodular, or both. When diffuse, viscera appear enlarged, sometimes to several times the normal size, and with grayish to whitish discoloration (Figure 2). When nodular, lymphomas appear as one or several white or gray firm foci with smooth cut surface.

Integument

Skin lymphomas are mainly associated with feather follicles and are more evident in dressed carcasses. A few or several follicles become enlarged, and in severe cases lesions from several follicles coalesce. Initially, there are whitish nodules, but in some cases they appear ulcerated with brown crust formation. Comb and wattles can also be affected. Lesions in the skin of the shanks start with reddish discoloration



Figure 2 Diffuse tumor in the liver tumor. Please note the severe hepatomegaly.

(Alabama Red Leg) and tend to progress into skin tumors with crusts (Figure 3).

Peripheral nerves

Enlargement of peripheral nerves is one of the main lesions associated with MD and has important diagnostic value to differentiate between MD and lymphoid leukosis. Although visceral tumors can occur in the absence of gross nerve lesions, if nerves are affected, the diagnosis is very much simplified. Any nerve or root ganglia can be affected and the enlargement can affect a nerve uniformly along its length or it might be nodular. Lesions can be uni- or bilateral. Affected nerves or affected areas of the nerves are usually up to 2–3 times the normal thickness. In severe cases, the enlarged nerves lose their normal glistening cross-striations, have a gray or yellow discoloration, and sometimes an edematous and hemorrhagic appearance (Figure 4).

Microscopic lesions

Regardless of the location, lymphomas induced by MDV have the same microscopic characteristics. Therefore, a general description is made followed by specific characteristics of the different tissues. MD tumors can be focal, well demarcated from the normal parenchyma of the viscera, or can infiltrate and destroy the normal parenchyma. MD lymphomas consist of a mixture of small and medium lymphocytes, lymphoblast, and macrophages (Payne, 1985). Plasma cells are rarely



Figure 3 Skin tumors in the skin of thighs and shanks.

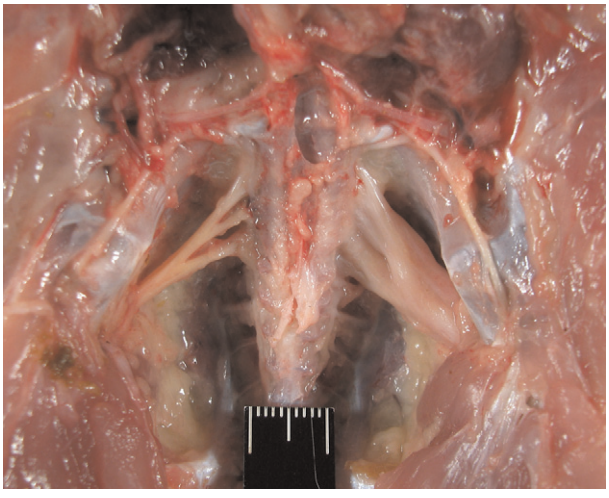


Figure 4 Unilateral tumor in sciatic plexus.

present. The lymphoid tumor cells are pleomorphic, with abundant cytoplasm containing few organelles other than mitochondria and ribosomes. The nuclei are fairly large, irregular in shape, and nucleoli are apparent. Because of the inflammatory component in MD lymphomas, it is particularly difficult to differentiate initial stages of the neoplasm from normal lymphoreactive areas or with severe inflammatory lesions induced by MDV.

Peripheral nerve

Peripheral nerve lesions have been classified in two types – A and B (Payne and Biggs, 1967). Type A is characterized by a massive infiltration of neoplastic cells that destroy the structure of the nerve. Microscopic characteristics of the lymphomas in nerves are the same as those described in other tissues. Type B lesions are inflammatory in nature and are characterized by infiltration of the plasma cells, edema, and different degrees of demyelination. The pathogenesis of type B lesions is poorly understood, but chronological studies have showed that they occur late in the pathogenesis of MD and appear after type A lesions, may be as an immune response against them (Lawn and Payne, 1980).

Antigen expression

Tumor cell phenotype

The complex composition of MD tumors makes the evaluation of the phenotype of the neoplastic cells difficult. Immunohistochemical analysis of MDV-induced tumors reveals that the majority (60–80%) of lymphoma cells are T cells, and most of the other cells (10–20%) are B cells, with small proportion of nonlymphoid cells, such as macrophages (Payne, 1985). It is considered that neoplastic cells are included in the T cell component because lymphoblastoid line cells and transplantable lymphoma cells derived from primary MD lymphomas are all T cells, carry MATSA, and contain multiple copies of MDV genome. Tumor cells also express high amounts of the antigen AV37, an analogous to the human CD30 antigen (Burgess *et al.*, 2001; Ross *et al.*, 1997). Although experimentally MDV is able to transform cells of a variety of cell types, under natural conditions most of the neoplastic transformed cells are considered to be CD4 + CD8 − T cells expressing the antigens MATSA and AV37.

Marek's disease virus antigens

Expression of MDV antigens is quite restrictive in transformed T cells. Sporadically, a few cells in the tumors express early antigens, such as pp38 and ribonucleotide reductase. The expression of these antigens is inconsistent and varies greatly from tumor to tumor. It is now considered that cells expressing those early antigens might be undergoing a reactivation of the infection (Witter and Schat, 2003). The oncogene meq, however, is consistently highly expressed in lymphomas as well as in lymphoblastic cell lines.

Nonneoplastic Lesions and Associated Syndromes

Lymphodegenerative syndromes

Clinical signs

Lymphodegenerative syndromes occur only in unvaccinated chickens lacking maternal antibodies against MDV. Therefore, the relevance of these syndromes in the field is minimal. Under experimental conditions, 5–6 dpi chickens become depressed, with ruffled feathers and reluctant to move.

Gross lesions

Bursa of Fabricius and thymus appear atrophic and yellowish in color as early as 4–6 dpi. Atrophy of bursa and thymus might be reversible after infection with low virulence virus, but

these lesions persist after infection with highly virulent MDV. The spleen is enlarged and in many cases marbled at 4–6 dpi. After infection with highly infected MDV, necrotic abscess can be observed not only in the spleen but also in other tissues (i.e., liver) at approximately 7–10 dpi (Witter *et al.*, 1980). Necrosis in lymphoid organs is more evident when 1-day-old susceptible chickens are inoculated with highly virulent MDV (early mortality syndrome).

Microscopic lesions

The productive infection in lymphoid organs reaches a peak at 5–6 dpi and is accompanied by cytolysis of lymphocytes and other cells, a hyperplasia of reticulum cells, accumulation of macrophages, and infiltration by granulocytes. In the thymus, the cytolytic infection and hyperplasia of reticulum cells occur mainly in the medulla, and the cortex is markedly regressed. Similar changes occur in the bursa, with destruction of the normal architecture. When regression of the bursa and thymus is not reversible, connective tissue replaces the main parenchyma and there is luminal lining epithelial infolding or undulation.

Antigen expression

Early cytolytic infection in lymphoid organs is characterized by the production of abundant viral antigen, as can be detected by a variety of techniques. Most of the antigens in the bursa and thymus can be detected in the medullary areas where necrosis is evident.

Transient paralysis

Clinical signs

As for lymphodegenerative syndromes, TP occurs only in unvaccinated chickens without maternal antibodies. In field conditions, TP was described in young pullets (8–18-week-olds) before the widespread use of vaccines (Zander, 1959; Cho *et al.*, 1970; Kenzy *et al.*, 1973). In those countries where vaccination of broilers is not a common practice, TP can be a problem in broilers chickens (30–40-day-olds) (Gimeno *et al.*, 1996). Clinically, TP is characterized by the development, 8–12 days following infection with an oncogenic MDV (Zander, 1959; Cho *et al.*, 1970; Kenzy *et al.*, 1973) of a flaccid paralysis that initially affects neck muscles and later tends to become generalized. The onset of TP is very abrupt and most chickens with TP recover completely within 24–48 h. An acute form of TP occurs after infection with highly virulent MDV (Witter *et al.*, 1999). In acute TP, most chickens die within 24–48 h.

Gross lesions

TP is not associated with any gross lesions. However, most of the chickens suffering TP have bursa of Fabricius and thymus atrophy because of concomitant lymphodegenerative syndromes.

Microscopic lesions

The development of vasogenic edema subsequent to vasculitis is the lesion responsible for the establishment of TP. Several chronological studies of the changes occurring in the brain after MDV infection have been conducted (Gimeno *et al.*, 2001; Swayne *et al.*, 1989). Endothelial cells of the brain capillaries are among the first altered element in the brain of infected chickens. As early as 6–8 dpi, endothelial cells become hypertrophic and hyperplastic (Gimeno *et al.*, 2001). Following these early alterations, macrophages and lymphocytes cross the blood–brain barrier, forming perivascular cuffing and extending into the neuropil. Reactivation of the infection in some of the infiltrative lymphocytes has been associated with the development of vasculitis characterized by severe damage and infiltration of heterophils in the vascular wall. Leakage of immunoglobulin G and albumin around affected vessels result in vacuolization. The edema and vasculitis is expressed coordinately with clinical flaccid paralysis and resolved in 2–3 days. Other brain lesions (perivascular cuffing, lymphocytosis, and gliosis) can be detected after recovery of TP or in MDV-infected by clinically normal chickens (Swayne *et al.*, 1989).

Antigen expression

MDV antigen expression can be detected in the brain as early as 6 dpi. Replication of MDV seems to be incomplete as early antigens (i.e., pp38 and meq) but not late antigens (gB) are expressed. Time course and level of expression of MDV antigens are related with the establishment of brain lesions and development of TP.

Panophthalmitis (Gray eye)

Clinical signs

Birds with ocular involvement may show evidence of blindness (Ficken *et al.*, 1991); (Pappenheimer *et al.*, 1929; Spencer *et al.*, 1992). The blindness can be uni- or bilateral, although recognition of clinical blindness requires careful observation and is usually overlooked in the field. Affected eyes gradually lose their ability to accommodate to light intensity.

Gross lesions

Gross ocular changes, including the loss of pigmentation in the iris ('gray eye') and irregularity of the pupil, are caused by mononuclear infiltration of the iris. Cataracts; conjunctivitis, occasionally with multifocal hemorrhages; and corneal edema have also been observed (Ficken *et al.*, 1991).

Microscopic lesions

Pandiri *et al.* (2008) classified MDV-induced lesions in the eye as early lesions (6–11 days postinoculation, dpi) and late lesions (26 and 56 dpi) based on the location and severity of the lesions. The early lesions involved iris, ciliary body, and choroid layer and are characterized by endothelial cell hypertrophy, vasculitis, and infiltration of lymphocytes (mainly CD8 +), plasma cells, macrophages, and heterophils. Late lesions consisted of severe lymphohistiocytic uveitis, keratitis, pectenitis, vitreitis, retinitis, and segmental to diffuse retinal necrosis.

Antigen expression

Pandiri *et al.* reported expression of MDV antigen pp38 in the cells infiltrating choroid layer at 11 dpi and within the retina, uveal tract, and corneal epithelium during later stages of infection (Pandiri *et al.*, 2008). No expression of late antigen gB or oncoprotein *meq* was detected, which rules out the possibility that infiltrated cells were transformed.

Inflammatory lesions in various organs related to Marek's disease virus infection

MDV induces inflammatory and degenerative lesions in various organs that do not get accompanied by the development of clinical signs and that might or might not develop into neoplastic lesions. It is important to differentiate between those inflammatory lesions (indication of MDV infection) and proliferative lesions (indication of MD).

- Inflammatory lesions in the brain are not always related to the development of TP. Perivascular mononuclear infiltration (perivascular cuffing), gliosis, and astrocytosis are common findings in MDV-infected chickens regardless of the onset of TP. These lesions appear as early as 6 dpi and in most cases persist.
- Inflammatory lesions in the nerves can occur as early as 6 dpi. They are not associated with the development of clinical signs and often occur in the absence of gross enlargement of nerves. Pathogenesis and nature of inflammatory nerve lesions are very similar to the ones described in the brain for TP. The development of nerve lesions have been studied chronologically (Lawn and Payne, 1980). Initial lesions include mainly perivascular cuffing composed of macrophages and small lymphocytes and occur as early as 6 dpi. Sometimes vasculitis occurs and severe damage of the blood vessel wall is observed. In severe cases, lymphocyte infiltration is not only restricted to perivascular location but can also affect the neuropil. Mild inflammatory lesions in the nerves can be induced by all three MDV serotypes and can regress without inducing clinical signs. However, when these lesions are induced by an oncogenic virus, they might progress to the development of lymphomas.
- MDV-induced lymphoid infiltration and inflammatory lesions occur in a variety of other visceral organs and tissues during the second cytolytic infection. These lesions are not associated with any clinical manifestation. However, it is important to differentiate those inflammatory lesions that only indicate infection with MDV from neoplastic lesions that determine the development of disease. Also, mild inflammatory lesions in many tissues can also be induced by a variety of infectious and noninfectious agents. Under field conditions, it is very difficult to associate these lesions with MDV infection.
- Early lesions in the skin are not normally associated with clinical signs or gross enlarged follicles and in general have to be identified by microscopic analysis. They are important as they seem to be necessary for the infection of the FFE and therefore for the transmission of the disease. Early pathological changes in the skin can be classified as inflammatory (perifolliculitis and inflammatory infiltration in the feather pulp) and degenerative due to the replication of MDV in the FFE. Inflammatory lesions in the dermis and in the feather pulp can either regress or progress to the development of tumors. Chronological studies have shown that lesions in the feather pulp resemble those in the nerves (Cho *et al.*, 1998).

Vascular syndromes (Arteriosclerosis)

Experimentally, infection with MDV has been associated with increased rates of arteriosclerosis (Fabricant *et al.*, 1978). However, the development of arteriosclerosis is a multifactorial phenomenon and the practical relevance of arteriosclerosis induced by MDV is not clearly determined. It, however, seems unlikely that MDV-induced arteriosclerosis has an important impact in the poultry industry because vaccination with turkey herpesvirus protects chickens against it (Fabricant *et al.*, 1981). No clinical signs have been associated with MDV-induced arteriosclerosis.

Diagnosis and Differential Diagnosis

MDV is ubiquitous and under field conditions, most, if not all, chickens are infected with oncogenic MDVs regardless of their vaccination status. Most of them, however, are properly protected by vaccination and never develop MD or any of the other syndromes induced by MDV. Therefore, detection of MDV by itself cannot be used for diagnosis of MD or any of the other MDV-induced syndromes.

This section focuses mainly on the diagnosis of MD and the differential diagnosis with other poultry tumor diseases. Diagnosis of nonneoplastic syndromes induced by MDV is presented at the end of the section.

Diagnosis of Marek's Disease (Neoplasia) and Differential Diagnosis with Other Poultry Viral Tumor Diseases

The diagnosis of lymphomas is fundamentally different from the diagnosis of many other diseases of chickens and presents numerous challenges to the diagnostician. Three distinct viruses can induce lymphoma in poultry: one herpesvirus (MDV) and two retroviruses (Avian leukosis virus (ALV) and reticuloendotheliosis virus (REV)). Lymphomas induced by the three viruses appear similar on superficial inspection because, by definition, they are all composed of lymphocytes. Although organ and tissue tropisms differ, there is no truly pathognomonic lesion for any of the lymphoma types. Each virus can induce tumors in many different tissues. In the case of ALV and REV, two different viruses can induce identical bursal lymphomas that, in all important respects, constitute the same disease. Perhaps the most confusing issue is the high probability of multiple infections. The three virus types are each widespread in nature and, once infection occurs, may reside in infected chickens for long periods. Moreover, most infected chickens never develop tumors. In some retroviral lymphomas, the fully infectious form of the causative virus disappears. Thus, the presence of the virus does not necessarily indicate the presence of the disease, and in some cases the disease can be present in the absence of the virus. A review of differential diagnosis of poultry tumor diseases has been recently published (Witter *et al.*, 2010) and readers are encouraged to read it for further details.

The diagnosis of MD is a multistep process. The tentative diagnosis can be done in the farm and includes the evaluation of epidemiological, clinical, and pathological parameters. Confirmation of the diagnosis in the laboratory could be done by histopathology, immunohistochemistry, and real-time polymerase chain reaction (PCR). **Table 3** summarizes the

Table 3 Differential diagnosis of tumor viral diseases in poultry

Age (weeks)	*Gross lesions*	*Differential diagnosis*	*Test to confirm diagnosis*	
			Aid in the diagnosis	*Confirm diagnosis*
<14	Enlarged nerves	Marek's disease Peripheral neuropathy	Histopathology	Real-time polymerase chain reaction (PCR)
	Tumors in viscera + enlarged nerves	Marek's disease	Not necessary in most cases	Not necessary in most cases
	Tumors in viscera	Marek's disease Acutely transformed retrovirus	Histopathology Immunohistochemistry	Real-time PCR
>14	Enlarged nerves	Marek's disease Peripheral neuropathy Reticuloendotheliosis (neuritis)	Histopathology	Real-time PCR
	Tumors in viscera + enlarged nerves	Marek's disease Reticuloendotheliosis virus (REV)-induced tumors	Histopathology Immunohistochemistry	Real-time PCR
	Tumors in viscera	Marek's disease Avian leukosis virus (ALV)-induced tumors REV-induced tumors	Histopathology Immunohistochemistry	Real-time PCR
	Tumors in the Bursa of Fabricius	Marek's disease ALV-induced tumors REV-induced tumors	Histopathology Immunohistochemistry	Real-time PCR

main differential diagnosis to consider and the necessary test to confirm a diagnosis.

Tentative diagnosis

Epidemiology

Age has been used traditionally as a criterion to differentiate MD from retrovirus-induced tumors. Both REV and ALV requires longer time to transform lymphocytes than MDV. Therefore, if a chicken younger than 14 weeks develops lymphomas, MDV is the most likely etiology. However, MDV is able to induce tumors in young as well as old chickens; hence, this criterion has its own limitations.

Clinical signs

Retrovirus does not induce specific clinical signs. Chickens with retrovirus-induced tumors develop nonspecific signs, such as depression, lethargy, ruffled feathers, etc. MDV can affect the brain and peripheral nerves and if tumors develop on those tissues, chickens will develop neurological clinical signs (paralysis, ataxia, tremors, torticollis, etc.). However, if MDV-induced lymphomas are not affecting nervous system, clinical signs will be nonspecific, just like those induced by retroviruses.

Gross pathology

Involvement of the peripheral nerves is normally associated with MDV-induced lymphomas. If peripheral nerve enlargement is present, MDV is the most likely cause of the tumors. However, this assumption has two limitations. Peripheral neuropathy (PN) syndrome is a nonneoplastic syndrome that induces enlargement of peripheral nerves just like MDV does (Bacon *et al.*, 2001b; Witter *et al.*, 2010). In the absence of visceral tumors and if only nerve lesions are present, further diagnostic tests have to be done to differentiate between MD and PN. If there are both nerve and visceral tumors, PN is ruled out. However, REV can induce lymphoma in viscera and neuritis that could easily be confused with MD. In this case, further diagnostic tests are needed.

- Detection of bursal tumors is a common feature in tumors induced by retroviruses (both ALV and REV). However, they are not presented in all chickens with retrovirus-induced tumors. Also, MDV can induce bursal tumors that grossly look identical to those induced by retroviruses.
- Eye lesions have been used as criterion to diagnose MD because retrovirus does not affect eyes. As mentioned in other sections of this article, MDV-induced eye lesions are not neoplastic in nature and therefore are only indicative that those chickens are infected with MDV.
- Skin lesions, especially in meat-type chicken, are more common in chickens with MD than in chickens with retrovirus-induced tumors. Nonetheless, if only skin lesions are present, it is necessary to differentiate between MDV-induced skin lesions and other skin lesions, such as squamous cell carcinoma and inflammation due to infectious agents and ectoparasites.

Laboratory diagnosis

1. Histopathology: Samples of tumors and peripheral nerves of animals freshly killed should be collected and fixed in buffered formalin at 10% for an adequate histopathological evaluation. Two criteria are evaluated by histopathologists – distribution of lesions and characteristics of the tumor cells.
   a. Distributions of the lesions:
      - Lymphomas in visceral organs accompanied with lymphoma in nerves. Those lesions are characteristics of MD and diagnosis can be confirmed by histopathology. However, it is important to confirm that nerve lesions are indeed neoplastic (Type A) and not

inflammatory. Inflammatory lesions in the nerves are an indication of infection but not of MD.
- Lymphomas only in nerves. In this case, the diagnosis of MD can be done by histopathology if lesions are type A. If lesions are type B, it is necessary to differentiate between MD and PN by other methods.
- Lymphomas only in viscera. Those lesions could be due to retrovirus or to MDV, and further tests are needed.
- Lymphomas in the bursa. This lesion can be very helpful in the diagnosis by histopathology. Retrovirus-induced tumors induce intrafollicular lymphomas. MDV induces extrafollicular lymphomas.

b. Tumor cells morphology can also aid in the diagnosis if samples were collected from animal freshly killed and fixed properly. ALV-induced lymphomas are formed by homogeneous population of lymphoblast, whereas MDV-induced lymphomas are formed by a heterogeneous population of cells, including large, medium, and small lymphocytes and macrophages. REV-induced lymphoma normally are identical to those induced by ALV but sometimes can be very similar to those induced by MDV.

One of the major challenges in the diagnosis of MD by histopathology is the differentiation between inflammatory lesions induced by MDV and development of lymphomas also induced by MDV. First, MDV is the etiology of both kinds of lesions. Also, inflammatory lesions can progress to the development of neoplastic lesions, but this is not always the case. Finally, lymphomas are composed by a mixture of neoplastic and inflammatory cells. It is a fact that inflammatory lesions not always lead to the development of lymphomas and that even MDV vaccines (i.e., HVT) can induce them (Witter *et al.*, 1976). Interpretation of borderline inflammatory/neoplastic lesions has to be done carefully based on other evidence of the disease (i.e., clinical signs, gross lymphomas, etc.). In many cases, further diagnostic tests are necessary to differentiate between inflammation and MDV-induced tumors.

2. Immunohistochemistry: Characterization of the phenotype of tumor cells by immunohistochemistry can be very useful in the differential diagnosis of poultry tumor diseases. MD tumors are composed of T cells, whereas ALV-induced lymphomas are composed of B cells. REV tumors are generally composed of B cells, but sometimes they can be T cells instead. The major drawback of phenotypic characterization of tumor cells is that most commercially available antibodies against chicken's antigens do not work very well in formalin-fixed samples; moreover, samples have to be snap frozen in liquid nitrogen.
   a. Detection of oncogene meq in tumor cells by immunohistochemistry is another option more specific than identification of cell phenotype (Gimeno *et al.*, 2005). MD-induced tumor cells express high levels of meq, but this is not present in retrovirus-induced tumors or in PN lesions. The limitation of this technique, however, is that antibodies against meq are not commercially available.
   b. Expression of other cell markers, such as MATSA and AV37, is high in MD tumors (Gimeno *et al.*, 2005). However, they are not specific and can also be present in other tumors or even in inflammatory lesions (Gimeno *et al.*, 2005; Schat and Calnek, 1978b). Therefore, its use in diagnostic is limited.
3. Real-time PCR: Quantification of the MDV DNA by real-time PCR is highly useful for confirmation of MD tumors, because tumorous tissue contains 100-fold higher levels of MDV DNA than latently infected tissue (Gimeno *et al.*, 2005). The same assay can be used for early diagnosis as early as 3 weeks of age (Gimeno *et al.*, 2008). Quantification can be done by using a standard curve (absolute quantification) or by the Ct method (relative quantification). However, the Ct method (relative quantification) is recommended as it is easier to standardize at different laboratories and does not require the use of a standard curve. Diagnosis of MD can be done using tumors, blood, and feather pulp (Cortes *et al.*, 2011). Samples can be stored frozen at $-70\ ^{\circ}C$ or can be collected in Flinders Technology Associates (FTA) cards (Cortes *et al.*, 2009). The latter has several advantages for storing and shipping.

Diagnosis of Nonneoplastic Syndromes

1. Lymphodegenerative syndromes: Diagnosis of lymphodegenerative syndromes in the field is very difficult. Besides MDV, a variety of other diseases of infectious (infectious bursal disease, chicken infectious anemia, etc.) and noninfectious (aflatoxins and stress) etiology induce necrosis and atrophy of the lymphoid organs. Moreover, expression of MDV antigens is very high during the peak of the productive infection (5–6 dpi) but is transient and often no MDV antigens can be detected in atrophied lymphoid organs. An important point to consider is that lymphodegenerative syndromes do not occur in MDV-vaccinated chickens or in chickens bearing maternal antibodies against MDV.
2. TP: Diagnosis of TP can be made in most cases by the characteristic clinical signs. Healthy chickens suddenly develop flaccid neck paralysis that become generalized and in a short time (24–48 h) either recover or die. TP appears only in unvaccinated chickens that lack maternal antibodies against MDV. In field cases, TP has been diagnosed in unvaccinated flocks of broilers at 3–4 weeks of age, when maternal antibodies have disappeared. Evaluation of the microscopic lesions in the brain can confirm the existence of vasculitis and brain edema. Detection of MDV DNA in the brain is not an adequate method of diagnosis for TP as it can also be detected in infected chickens without TP (Witter *et al.*, 1999). TP has to be differentiated from other diseases producing paralysis (i.e., botulism and peripheral neuropathy) and brain lesions (i.e., Newcastle disease, avian influenza, west Nile virus, encephalomalacia, encephalomyelitis, toxoplasmosis, and bacterial encephalitis). Both TP and botulism produce flaccid paralysis, but no brain lesions can be found in botulism. Peripheral neuropathy is characterized by the enlargement of peripheral nerves, which is not present in chickens with TP. Brain lesions induced by other viral encephalitis (Newcastle disease, avian influenza, west Nile virus, and encephalomyelitis) could be confused with those induced

by MDV in chickens with TP. The transient nature of TP aids in the diagnosis. In addition, in the other viral encephalitis, neurons are affected, but this is not the case for TP. Finally, vascular lesions in TP are slightly different because along with the endotheliosis and perivascular cuffing (common with the other viral encephalitis) there is severe vasculitis and brain edema. Toxoplasma, bacterial encephalitis, and encephalomalacia are characterized by severe infiltration of heterophils, necrosis, and in the case of encephalomalacia thrombosis. None of these lesions are detected in chickens with TP. Finally, it is important to differentiate TP lesions from other MDV-induced lesions in the brain that are not related with the development of TP. Perivascular cuffing, gliosis, and lymphocytosis can occur at the same time as the development of TP but are not related with the development of the syndrome (Swayne *et al.*, 1989).

3. Immunosuppression: MDV-IS is very complex and other than atrophy of lymphoid organs, at the moment, there is no any method to diagnose MDV-IS. Further studies are warranted for better understanding of MDV-IS, methods of detection, and methods of control.

Control

Control of Marek's Disease

MD control is based on three criteria: good biosecurity, selection for genetic resistance, and vaccination. Biosecurity and genetic resistance are currently used as important adjuncts to vaccination rather than as primary control strategies. The focus of this article is mainly on vaccines and vaccination protocols. Recent reviews on MD vaccines and control procedures are available for further details (Bublot and Sharma, 2004; Gimeno, 2008; Schat and Baranowski, 2007).

Genetics

The relevance of genetic resistance in the control of MD was observed several decades ago (Cole, 1968) and indeed was the first method for controlling the disease. Primary breeder companies frequently include MD resistance as one of the criteria for selection. The strategies to select MD resistance have been reviewed (Bacon *et al.*, 2001a) and include mainly mass selection (i.e., breeding from survivors) and family selection utilizing pedigreed offspring as breeders. There are two groups of genes in the chicken that influence MD resistance: MHC genes and non-MHC genes. The relevance of MHC genes in MD resistance has been amply demonstrated (Bacon *et al.*, 2001a) and is well characterized. Particularly remarkable is the influence that the B haplotype has on the efficacy of MD vaccines and how this influence depends on the serotype of the vaccine (Bacon and Witter, 1992, 1994a,b). Theoretically, one could select the most appropriate vaccine based on the predominant B haplotype of a particular strain. This issue has not been exploited in the practice because of the difficulties in determining the predominant B haplotype, especially in meat-type chickens. However, it is now technically possible to identify the predominant B haplotype in meat-type chickens, and as molecular techniques improve it might be economically feasible for commercial lines (Li *et al.*, 1997; Goto *et al.*, 2002).

Several non-MHC genes may also be involved in resistance. For example, line 6 and line 7 chickens differ markedly in MD susceptibility, but both lines are homozygous for the MHC B^2 allele (Crittenden *et al.*, 1972). Numerous studies have identified and mapped several quantitative trait loci (QTL) (Bumstead, 1998; Vallejo *et al.*, 1998; Xu *et al.*, 2011). The studies are still ongoing but the rapid technological advances in complete genome sequencing and single-nucleotide polymorphism analysis will identify several specific genes associated with resistance to MD.

Biosecurity

Taking the example of specific pathogen-free flocks, MD can be eradicated from a farm if ideal conditions of biosecurity are followed. Unfortunately, the use of filtered air and positive pressure housing is not economically feasible for the poultry industry. However, a proper biosecurity plan will be of great help for controlling MD. There are two critical points that any biosecurity plan should consider: Reduce initial levels of MDV in the farm by preventing entry of MDV into the building and avoid contamination of the environment by preventing MDV from leaving the building. Measures to reduce initial levels (all in–all out systems, single-age buildings, etc.) of MDV have been widely stressed, although not always followed. Measures to avoid contamination of the environment, however, are not always well recognized and there are two issues that deserve more attention: air management and disposal of chicken carcasses and manure. Biofilters designed to remove odors from air emanating from livestock facilities might be a solution to decrease the level of MDV contamination in the air exiting poultry farms (Spencer and Guan, 2004). Carcasses are usually burned or buried, but disposal of manure does not normally receive the attention it requires. Composting has been shown to be a satisfactory alternative procedure for discarding both carcasses and manure (Spencer and Guan, 2004).

Vaccination

Vaccination protocols

- Types of vaccines
  Modified live vaccines are the cornerstone for protecting against MD. There is a large selection of licensed MD vaccines representing three MDV serotypes. In general, three types of formulation in ascending order of efficacy are as follows: HVT alone, HVT plus a serotype 2 strain, and CVI988 (Rispens) with or without viruses of serotypes 2 and 3. A decade ago, a novel serotype 1 MDV vaccine (strain BH16) was introduced in Australia and seems to confer at least as much protection as CVI988 (Karpathy *et al.*, 2003; Karpathy *et al.*, 2002). Recently, several recombinant vaccines using HVT as a vector have become available and are widely used alone (mainly in broiler chickens) or in combination with vaccines of serotypes 1 and 2. In addition, recombinant vaccines using serotype 1 strains (either as a vector expressing other viruses' genes or by deleting complete or partially the oncogene meq) have been developed and are still under experimental evaluation

(Zelnik *et al.*, 1995; Morgan *et al.*; 1998; Cui *et al.*, 2005; Lupiani *et al.*, 2004).

MDV is highly cell associated and as a result, vaccines are produced in chick embryo cells, stored in liquid nitrogen, and administered as viable cell suspension. HVT, although not serotypes 1 and 2 MDV, can be produced as a cell-free suspension and stored in a lyophilized state. However, the cell-associated form of HVT vaccine has been most widely used because it is more effective than cell-free virus in the presence of maternal antibodies.

- Vaccine administration
  Early immunity is essential because most chicks face challenge from MDV within a few days of being introduced into their brooding pens. Therefore, MD vaccines are administered to chicks at hatch by subcutaneous or intramuscular inoculation or *in ovo* at ED18 via amniotic or intraembryonic route (Sharma and Burmester, 1982). Cell-associated vaccines are very labile. Only viable infected cells are capable of transmitting the vaccine virus, so handling is of crucial importance for a vaccine to retain its efficacy (Halvorson and Mitchell, 1979). Failures in the cold chain (MD vaccines have to be kept in liquid nitrogen and maintained under refrigeration), improper thawing conditions, and reconstitution in inadequate diluents can severely reduce vaccine titers. Other factors such as mixing with antibiotics (Colwell *et al.*, 1975; Eidson *et al.*, 1978), joint administration with other vaccines (Rosenberger, 1983), or long delays in vaccination after reconstitution can also decrease vaccine titers. Finally, dilution of vaccines to reduce vaccination cost is a common practice worldwide, especially in the broiler chicken industry. The negative effects of administered suboptimal doses of vaccine have been recently reported (Gimeno *et al.*, 2011a).

  Besides suboptimal vaccine dose, there are other factors that influence the efficacy of vaccines, such as early challenge with MDV before vaccine-induced immunity has been elicited; decreased immune competence of the chicken by either infectious or noninfectious causes; and presence of highly virulent viruses.

- There are three strategies (protective synergism, revaccination, and the use of adjuvants) that are commonly used to augment vaccine efficacy:
  1. Protective synergism: Combination of the SB1 strain (serotype 2) and the FC126 strain (serotype 3, HVT) provides better protection than either vaccine alone (Schat *et al.*, 1982; Witter, 1982). This phenomenon, termed protective synergism, is the basis for the bivalent vaccines developed in the 1980s. Synergism is strongly serotype-specific and is especially evident between combinations of serotypes 2 and 3 (Witter, 1992). No protective synergism has been reported between combinations of serotype 1 with serotypes 2 or 3. However, augmentation of protection for MD vaccines has been observed with two additional systems. Combinations of HVT and glutaraldehyde-inactivated serotype 1 MDV obtained from feather follicles was reported to improve protection (Pruthi *et al.*, 1987). Combinations of HVT and a recombinant fowlpox virus expressing gB and other glycoproteins of serotype 1 MDV also provided improved protection (Nazerian *et al.*, 1996). The mechanisms involved are poorly understood and represent an overlooked but important area for future research.
  2. Double vaccination: The practice of administering MD vaccine a second time has been used in commercial poultry flocks for many years. It became popular in the United Kingdom and was adopted by many growers in Europe and other countries but has not been common in the United States. The author has recently conducted several experiments to develop a model that allows to reproduce the benefits for the second vaccination under laboratory conditions. Her results indicate that the benefit of double vaccination can be achieved by using a less efficient first vaccine followed by a more efficient second vaccine (Gimeno *et al.*, 2011b). *In ovo* vaccination followed by a second vaccination at the day of age seems to be the most beneficial protocol (Gimeno *et al.*, 2011b). An early and strong activation of T cells following the *in ovo* vaccination has been suggested to be, at least partially, responsible for the benefits of double vaccination (Gimeno *et al.*, 2012).
  3. Use of adjuvants and immunomodulators: MD vaccines are administered in embryo or in 1-day-old chicks. The use of immunomodulators, such as cytokines and adjuvants, along with MD vaccines could enhance the innate immune response and induce an earlier maturation of the immune systems of the chickens. Acemannan, a polysaccharide, has been licensed as an adjuvant of MD vaccines in the US since 1992 but is not widely used. Several studies have been conducted to include cytokines in MD vaccines to enhance the cellular immune response (Djeraba *et al.*, 2002; Tarpey *et al.*, 2007). This area of research will continue in the future and may be a solution to increase the protection conferred by current vaccines.

- Monitoring vaccination
  Because of its cell-associated nature, MD vaccines are labile and failures in the administration might occur. Monitoring replication of the vaccines in the chicken can ensure that vaccination was correctly administered. Evaluation of MD vaccines in the chickens has been traditionally done by plaque assay (Cho, 1981). Recently, primers specific for each MD serotype have been designed and real-time PCR has slowly overtaken the traditional plaque assay. It has been recently demonstrated that feather pulp is an adequate sample to monitor MD vaccination for vaccines of all three serotypes (Cortes *et al.*, 2011; Baigent *et al.*, 2005). Spleen can also be used, but that requires euthanizing animals. The use of blood is not advisable due to the high numbers of false negative (Cortes *et al.*, 2011). Sample can be taken fresh and stored frozen until processed or in FTA cards (Cortes *et al.*, 2009). The latter has the advantage of an easy storage and shipping. It is recommended to sample chickens between 1 and 3 weeks of age to monitor how vaccine was administered. After 3 weeks of age, the levels of MD vaccines achieve a plateau even if very low dose of vaccine was administered (Gimeno *et al.*, 2011a; Baigent *et al.*, 2007).

Control of Nonneoplastic Syndromes

Development of lymphodegenerative syndromes, TP, and arteriosclerosis is severely limited or abolished by vaccination with HVT regardless of the virulence of the challenged MDV strain. Control of MDV-IS is uncertain. Recent studies have demonstrated that vaccination (albeit able to control the development of MD) does not protect completely against the permanent immunosuppression induced by MDV. Further studies on the mechanisms behind MDV-IS are warranted to develop better methods to detect and control it.

See also: Poultry and Avian Diseases

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Market-Based Incentives for the Conservation of Ecosystem Services in Agricultural Landscapes: Examples from Coffee Cultivation in Latin America

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Glossary

Agricultural intensification The increase of yield (i.e., amount of commodity produced per unit area) in agricultural areas through increased inputs of labor, fertilizer, pesticides, etc.

Certification The programs in which farmers contract third-party certifiers to confirm their adherence to specific production criteria, with the cost of certification outweighed by the ability to sell agricultural products at a price premium to consumers.

Ecosystem services The direct and indirect benefits of natural ecosystems for human livelihoods; these are also known as environmental services.

Market externalities A cost or benefit of the production or sale of a product that affects other parties not involved in the transaction and that is not generally reflected in the cost of the product.

Market failure In the context of ecosystem services, when the prices of goods and services do not reflect their true costs of production or consumption (e.g., the true cost of fossil fuel production with respect to impacts on global climate is not reflected in its cost, resulting in environmental degradation).

Nonexcludable service An ecosystem service that a beneficiary will receive regardless of whether or not they compensate the provider (i.e., there is no way to exclude those who do not pay providers for the service).

Opportunity costs The financial benefits that are foregone by making one choice over another (e.g., the potential revenue lost by choosing to grow crops in less productive manner that is more likely to maintain ecosystem services).

Payments for environmental services The voluntary agreements between purchases and sellers by which the beneficiaries of ecosystem services pay those who produce or manage such services in order to incentivize their protection and maintenance.

Shade coffee The practice of growing coffee under a canopy of native or introduced trees to shield the plants from excessive sunlight.

Technification of coffee The process of reducing or eliminating shade cover and at the same time increasing the density of coffee plants; initially promoted by the United States Agency for International Development in the 1970s as a method to reduce impact of coffee leaf rust.

Introduction

Virtually all aspects of human livelihoods and well-being are dependent on the resources and processes provided by natural ecosystems. Known as 'ecosystem services' or 'environmental services,' these are the direct and indirect benefits of natural resources and ecosystem processes for human economies (Millennium Ecosystem Assessment, 2005). Environmental services encompass a diverse range of products and processes, from carbon cycling to cultural and spiritual renewal (**Figure 1**). In addition to providing tangible or intangible benefits for human societies, the majority of environmental services share another characteristic: they are positive externalities, providing a net benefit to society whose value is not reflected in the cost of the direct products and services affected (Polasky, 2012; Salzman, 2009). The positive externalities of environmental services provide an example of market failure (Salzman, 2009); spontaneously arising markets fail to reflect the true value of these services, leaving them vulnerable to overexploitation and degradation.

Agricultural production is itself a provisioning service (Zhang *et al.*, 2007) reliant on a diverse suite of ecosystem services operating at a variety of spatial and temporal scales (Kremen and Miles, 2012). Given that agricultural production comprises approximately 40% of land cover (Foley *et al.*, 2005), managing agriculture in order to maximize the provision of ecosystem services, while minimizing disservices (e.g., soil degradation and pesticide contamination), is a key component of moving toward sustainability in the twenty-first century (Robertson and Swinton, 2005). Diversified agricultural systems are more effective in supporting ecosystem services and minimizing disservices (Kremen and Miles, 2012); however, low-diversity and high-intensity conventional systems have become the norm throughout the world. This situation results from interactions between local history, policy, lack of research, and market failures that compensate farmers for yields but not for positive (or negative) externalities involved in production. In this article, the authors have described relationships between agricultural management and ecosystem service provision for a single crop – coffee, the most important tropical agricultural commodity crop, which is responsible for US$15 billion in exports annually (International Coffee Organization, n.d.). Using this example, the attempts to incentivize biodiversity conservation and compensate producers for the production and maintenance of ecosystem services were investigated. To provide a broader context for this discussion, the article begins with a description of the currently existing market-based mechanisms for conservation in agricultural landscapes, highlighting the advantages and disadvantages of voluntary and regulatory approaches.

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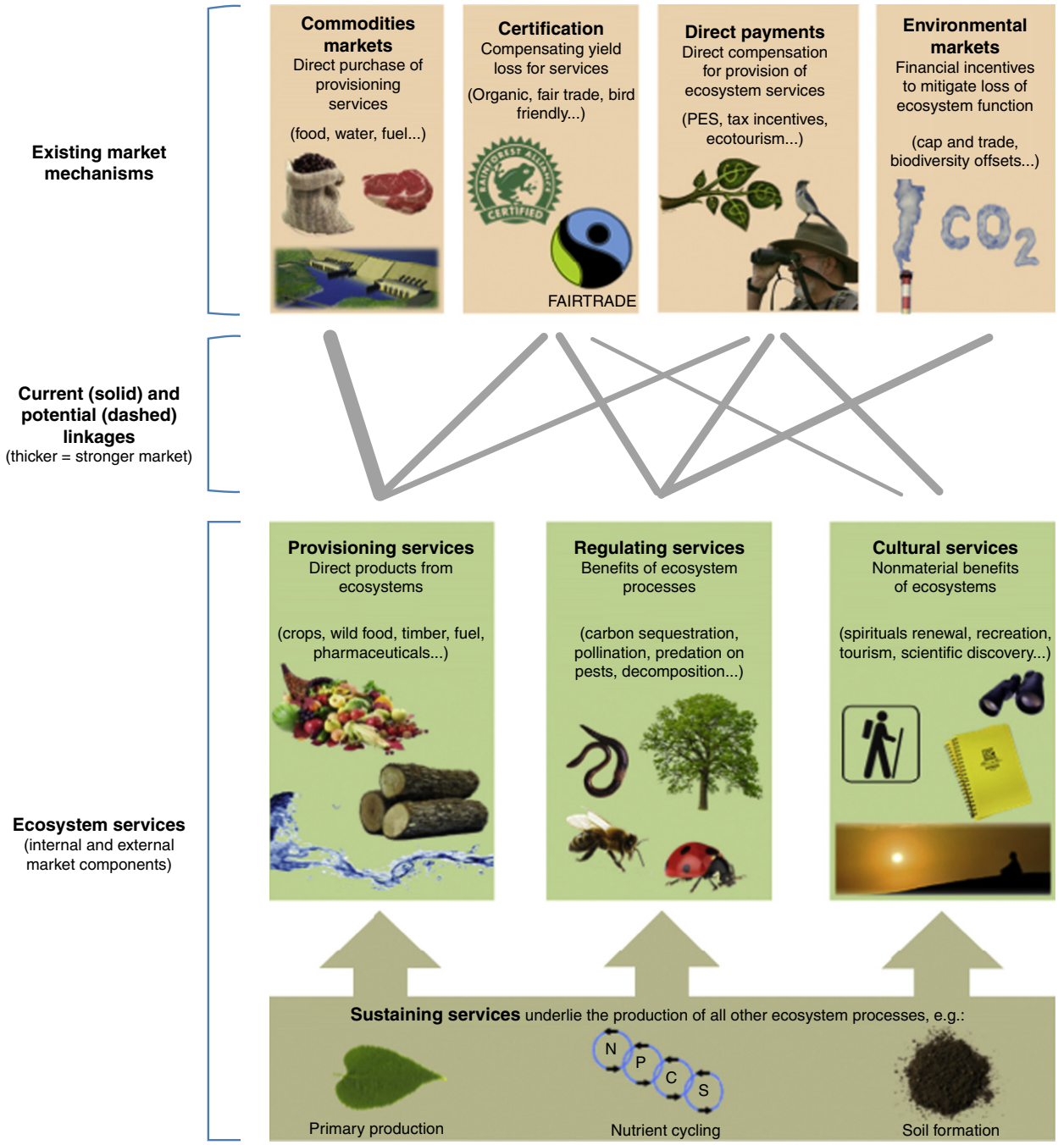


Figure 1 Ecosystem services (ES) and linkages to existing and potential markets (arrayed left to right from voluntary to policy driven); thickness of lines indicates strength of linkage between ES and market. Framework of ecosystem services adapted from Millennium Ecosystem Assessment, 2005. Ecosystems and Human Wellbeing: A Framework for Assessment. Washington, DC: Island Press.

Market-Based Incentives: Promise and Pitfalls

Although the importance of ecosystem function for human well-being has long been acknowledged, the ecosystem services framework was first articulated in the 1970s and elaborated in the 1980s (Mooney and Ehrlich, 1997). The development of the service framework came about not necessarily due to the desire to explicitly value services, but rather as a response to the failure of conservation efforts based on appeals to nature's intrinsic value (Norgaard, 2010). Nevertheless, the ecosystem services framework provides a structure in which these functions can be valued and incentivized.

Existing market-based incentives exist along a continuum from entirely voluntary mechanisms to mechanisms dependent on regulatory interventions that integrate market externalities into economies (Figure 1). Commodity markets

(e.g., market for timber, agricultural products, etc.) are themselves dependent on provisioning services. However, for the purposes of this article, the focus is on markets for the various sustaining, regulating, and cultural services that comprise the market externalities whose conservation has not been captured by spontaneously arising markets.

Voluntary Mechanisms

Among existing voluntary mechanisms, certification schemes, which indirectly incentivize biodiversity conservation and maintenance of ecosystem services, are the most widely available and applied incentives. These market-based approaches that compensate producers for ecosystem services are widely considered effective at promoting conservation in agriculture, although there are few empirical examples of such markets (Kroeger and Casey, 2007). Producers generally participate in third-party certification schemes with the expectation of a price premium in exchange for compliance with international standards of quality and fairness in production. Dozens of certification schemes exist within the agricultural sector, including well-known examples, such as organic and fair-trade certifications. Although a few of these certifications focus specifically on conservation of biodiversity or ecosystem services, most include related environmental criteria that presumably benefit biodiversity and ecosystem function. For example, organic agriculture appears to have limited, but highly heterogeneous, benefits for biodiversity of certain taxa, such as birds, bats, and invertebrates, that provide regulating services of pest control within farms (Bengtsson *et al.*, 2005; Hole *et al.*, 2005; Fuller *et al.*, 2005).

Despite the widespread adoption of some certification programs, the approach presents many weaknesses in the context of conservation. Certification schemes themselves reflect a shift from compulsory to voluntary participation in market mechanisms for conservation (Hatanaka *et al.*, 2005), in that responsibility for monitoring of standards that has traditionally rested with government agencies is shifted to third-party certifiers; consumers are free to 'opt out' by purchasing less expensive (and less sustainably produced) commodities. A review of major agricultural certifications found that most standards fail to provide specific guidelines for targeting the protection of endangered species and none specifically seek to prevent habitat loss (UNEP-WCMC, 2011). Additionally, the cost of certification and the price are a major barrier for small and medium producers to participate in these schemes, thus excluding many producers in the developing tropics. Without wide adoption, the conservation value of certification schemes may be very limited (Gullison, 2003).

Policy-Driven Mechanisms

The ability to opt out of voluntary schemes, such as certifications, necessarily limits the impacts of these approaches in terms of conservation of biodiversity and ecosystem services. Higher impact approaches generally involve national or international governmental mechanisms that compel participation on the part of producers, consumers, or both. One emerging approach in these situations is direct payments for conservation (In some cases, voluntary direct payments are made to producers for the provision of ecosystem services, such as water and erosion control, but these payments generally take place locally and are not sold on a competitive market.). Direct payments for conservation outcomes may be the most efficient means to incentivize conservation of biodiversity (Ferraro and Kiss, 2002) and, by extension, ecosystem services. Direct payments in agriculture may be made to farmers and landowners who through sound management practices may demonstrate a contribution to environmental services, such as water cycling, pollination, and soil. Although a number of small-scale, voluntary payment agreements have arisen (Pagiola *et al.*, 2004), larger scale programs generally occur through government subsidies (based on taxes, grants, or a combination of these two) for conservation or through payments for certain ecosystem services (Pagiola, 2008).

Environmental markets – in which biodiversity conservation interventions or ecosystem services are themselves sold as commodities – are often hailed as the next frontier in conservation practice; however, in practice there are very few examples of functioning environmental markets. Given that these are markets attempting to commodify externalities that are public goods without clear ownership, such mechanisms are unlikely to develop in the absence of national or international regulations limiting use of a readily available public good. Kroeger and Casey (2007) outlined three main reasons for the small number of ecosystem service markets: (1) absence of low cost and easily applicable approaches to quantifying ecosystem service flows, (2) difficulties in estimating the economic value of ecosystem services, and (3) the nature of the ecosystem flows as a public good. Thus, existing environmental markets rely on governmental regulation that creates a demand for ecosystem services. For example, in the United States, mitigation banking for wetlands and endangered species habitat exists as a direct result of government oversight of the issuance of credits and the sale and trade of such to potential buyers wishing to offset negative impacts of development (Bayon, 2008). Similarly, mitigation markets for greenhouse gases exist as a result of state legislation in the United States and regional legislation in Europe, in which farmers and other land managers may apply published standards to cap or capture carbon, selling these credits on voluntary or regulated carbon markets. For example, under the State of California climate change legislation AB-32, agricultural producers are able to sell carbon offsets within the regulatory market through sequestration and 'additional' sequestration gained through biodiversity friendly practices, such as minimal tillage and the use of cover crops (Sumner and Rosen-Molina, 2010). Participation in environmental markets is currently limited because of a lack of regulatory pressure, but in the case of existing markets, it is limited because of high transactional costs due to monitoring. Thus, as with certification, these up-front costs may serve as barriers to the small and medium producers who comprise the majority of agriculturalists in the developing world.

As one of the world's most important agricultural commodities, coffee provides a valuable lens for exploring

relationships between conservation, commodification, and globalization. In the following sections of this article, the authors have described various methods of coffee cultivation, focusing on Latin America ('Coffee Cultivation in Latin America'); effects of coffee cultivation on biodiversity and ecosystem service provision ('Coffee, Biodiversity, and Ecosystem Services'); and the existing voluntary and regulatory market mechanisms that have been used to incentivize the conservation of ecosystem services in Latin American coffee cultivation ('Market Incentives to Conserve Ecosystem Services in Coffee'). The authors have focused on the strategies that have shown the most success for conservation of biodiversity and ecosystem services in this important tropical crop and have made suggestions for future directions in market-based methods to incentivize conservation in agricultural landscapes in the tropics.

Coffee Cultivation in Latin America: Management Practices, Biodiversity, and Ecosystem Function

Introduced to the New World in the early eighteenth century, coffee cultivation expanded throughout Latin America after countries in the region gained independence from Spanish and Portuguese rule in the 1820s and 1830s, respectively (Pendergrast, 1999). In 2010, coffee plantations comprised more than 5.2 million ha in Central and South America (nearly 4% of total crop area) with a production value exceeding US$5 billion annually (Food and Agriculture Organization of the United Nations, n.d.). Two coffee species are widely cultivated in the Neotropics: arabica (*Coffea arabica*), sought after for its superior flavor, which grows at middle elevations (600–1500 m); and robusta (*Coffea canephora*), used primarily for manufacture of instant coffee due to its harsh flavor and high caffeine levels, which grows below 800 m elevation (Jha *et al.*, 2011). The following discussion applies to arabica coffee, drawing primarily from Latin American examples.

Traditional Coffee Management

Within Latin America, coffee is notable not only for its economic and social importance but also for its variety of growing systems. These various management types can be ordered along a gradient of increasing intensification (Moguel and Toledo, 1999). As intensification increases in coffee systems, the diversity and complexity of tree cover decrease, and coffee plant density rises (**Figure 2**). Depending on a variety of factors (local climate, coffee variety, and use of chemical inputs), yield may also increase with intensification (Soto-Pinto *et al.*, 2000; Perfecto *et al.*, 2005).

As the descendent of an understory plant, coffee is a shade-tolerant species; in traditional coffee production systems, shade trees are maintained to shield the coffee plants from receiving too much direct sunlight. The simplest coffee management systems in Latin America essentially replace the understory of a forested area. Although trees may be thinned, the shade cover is comprised entirely of native species with a multistratum canopy structure (Moguel and Toledo, 1999; Philpott *et al.*, 2008a). These 'rustic' systems generally occur on small scales as part of indigenous management practices (Moguel and Toledo, 1999). More common among small-scale producers are polycultural systems in which coffee is cultivated alongside fruit and timber trees mixed with native forest tree species that provide relatively high-shade cover and a thinner, but still multistratum, tree canopy. In these multicropping systems, noncoffee products may comprise up to one-third of the value derived from a coffee agroforest (Rice, 2008). In addition to producing multiple value streams, these systems are relatively low input. Transitional between traditional and intensive coffee systems are 'commercial polycultures' (**Figure 2**), in which a shade canopy is still maintained over the coffee, but mostly comprised of reduced diversity of planted trees subject to pruning to regulate shade levels.

'Modernization' of the Coffee System

Traditional coffee cultivation escaped the post World War II 'green revolution' largely intact. However, in the 1970s, coffee cultivation in Latin America underwent a rapid process of modernization, with conversion into reduced shade canopies, high-yield coffee varieties, and an increase in chemical inputs and the density of coffee plants (Perfecto *et al.*, 1996; Perfecto and Armbrecht, 2003). This process of 'technification' in Latin America initially began as a response to the arrival of coffee leaf rust (*Hemileia vastatrix*), a devastating fungal disease of coffee. Reducing shade was initially seen as a way to reduce moisture, and hence the spore formation, of the fungus (Perfecto *et al.*, 1996). Supported by funding from the United States Agency for International Development, governments in Latin America implemented modernization programs of shade removal coupled with dense plantings of high-yield coffee varieties that respond well to direct sun and chemical inputs; by 1996, 40% of Latin America's coffee area had been modernized (Rice and Ward, 1996). As the coffee leaf rust has proven less devastating than initially anticipated, the motivation for adopting low-shade systems has shifted to increasing yields (Perfecto *et al.*, 1996).

Intensified coffee systems may include some shade (**Figure 2**), but the height and shade cover is greatly reduced. The shade trees themselves may be a near monoculture of fast-growing trees. In Latin America, these are commonly native nitrogen-fixing species (*Inga* spp. and *Erythrina* spp.), although exotics (e.g., *Grevillea robusta*) may also be used (Perfecto *et al.*, 1996; Jha *et al.*, 2011). These trees may be subject to substantial pollarding and removal of epiphytes to decrease shade cover. In sun coffee, the shade layer is eliminated altogether, with dense plantings of high-yield coffee. Despite the widespread belief that reduced shade increases coffee production, the actual relationship between shade and production on a per plant basis is highly variable and inconsistent across studies (Perfecto *et al.*, 2005). Intensive systems generally do produce more coffee per ha; however, it is unclear whether these increases result from increased planting densities, use of sun-tolerant varieties, or other aspects of management. Low- or no-shade systems generally require higher chemical and labor inputs (Jha *et al.*, 2011).

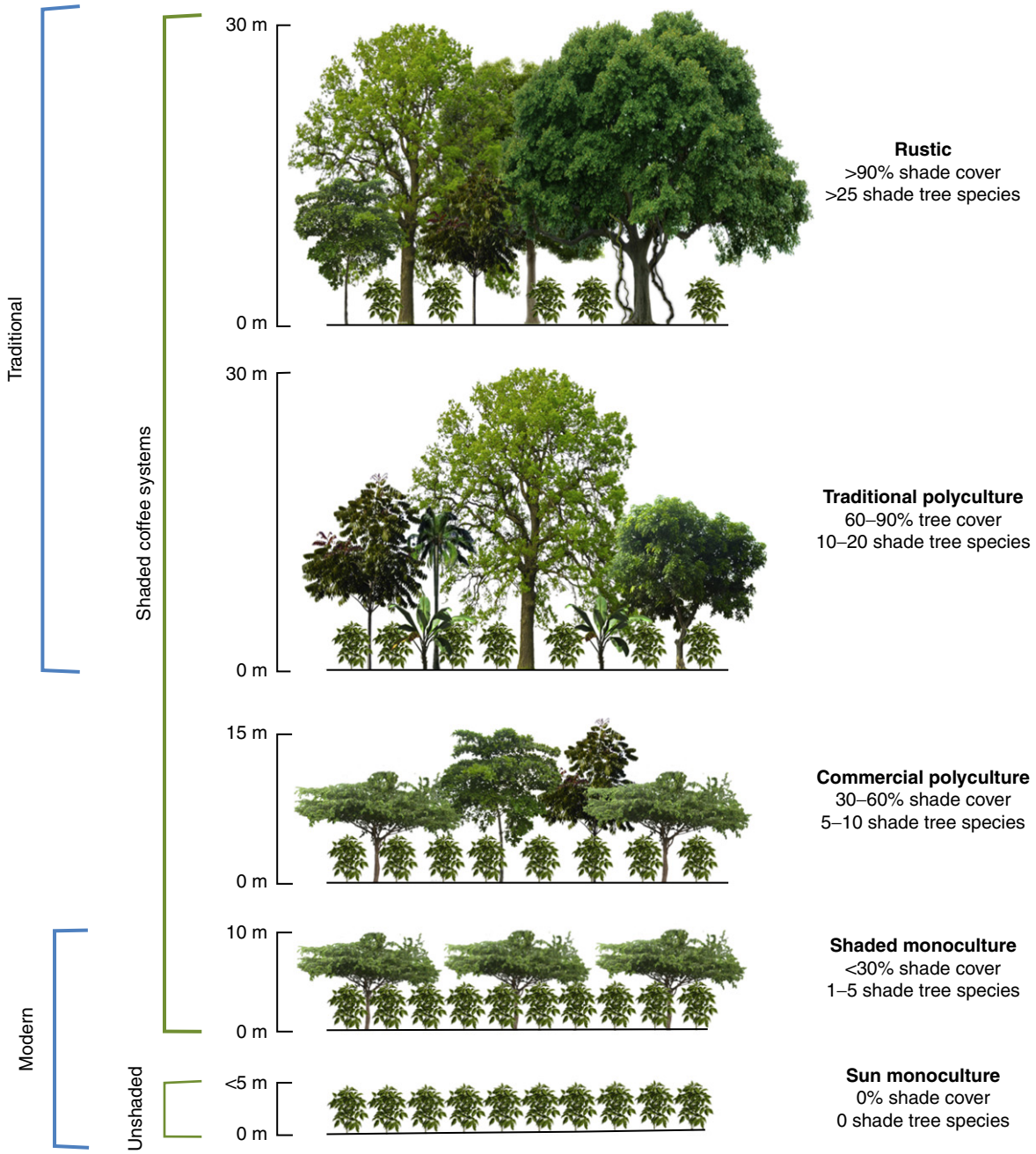


Figure 2 Schematic representation of coffee management systems from the least (top) to the most (bottom) intensive. As intensification increases, canopy height and structural complexity, tree basal area, and shade tree diversity decrease, whereas the density of coffee plants increases. Adapted from Moguel, P., Toledo, V., 1999. Biodiversity conservation in traditional coffee systems of Mexico. Conservation Biology 13(1), 11–21 and Perfecto, I., Vandermeer, J., Mas, A., Soto Pinto, L., 2005. Biodiversity, yield, and shade coffee certification. Ecological Economics 54 (4), 435–446.

Coffee Cultivation, Biodiversity, and Ecosystem Services

Biodiversity conservation in shade coffee plantations

Not surprisingly, these different coffee production systems vary not only in inputs (i.e., labor and agrochemicals) but also in their conservation value and their provision of ecosystem services. The maintenance of biodiversity is one of the most extensively studied ecosystem services provided by shaded coffee plantations (Perfecto *et al.*, 1996; Moguel and Toledo, 1999; Perfecto and Armbrecht, 2003; Donald, 2004; Somarriba *et al.*, 2004; Philpott *et al.*, 2008a).

By definition, traditional shaded coffee systems include a higher diversity of woody plants than modernized coffee plantations (Soto-Pinto *et al.*, 2001; Philpott *et al.*, 2008a; Williams-Linera and López-Gómez, 2008). Similarly, the epiphyte richness is higher in diverse shade coffee than in

intensive shade coffee and species numbers are similar between the most traditional systems and forests (Pendergrast, 1999; Hietz, 2005; Solis-Montero *et al.*, 2005; García-Franco, 2008). However, the richness and abundance of herbaceous understory plants may be substantially reduced as a result of coffee layer management (Saldaña-Vázquez and Sosa, 2010). Shaded coffee also facilitates bee-mediated pollen dispersal of native trees within coffee landscapes (Jha and Dick, 2008; Jha and Dick, 2010).

Both migratory and resident birds have been the focus of multiple studies that have demonstrated that the species richness, abundance, and functional diversity of birds decline with increasing management intensity in Latin American coffee plantations (Greenberg *et al.*, 1997; Matson *et al.*, 1997; Calvo and Blake, 1998; Perfecto *et al.*, 2003; Philpott *et al.*, 2008a; Philpott *et al.*, 2009). Several studies have demonstrated high species richness and abundance of bats in traditional coffee systems (Pineda *et al.*, 2005; García Estrada *et al.*, 2006; Sosa *et al.*, 2008; Williams-Guillén and Perfecto, 2010, 2011). Howler monkeys can use diverse shade coffee plantations as foraging habitat (McCann *et al.*, 2003; Estrada *et al.*, 2006; Williams-Guillén *et al.*, 2006). A variety of medium-sized mammals exploit high-shade coffee plantations in Mexico (Gallina *et al.*, 2009) and show a negative response to intensification (Gallina *et al.*, 2008). However, available evidence suggests that small mammal richness is reduced in coffee plantations and does not clearly relate to management intensity within coffee plantations (Gallina *et al.*, 2008). The effect of management intensity on herpetofauna remains largely uninvestigated. Amphibian species richness declines from cloud forest to shade coffee (Pineda *et al.*, 2005), although forest shade coffee ecotones conserve higher amphibian diversity than higher contrast forest corn edges (Santos-Barrera and Urbina-Cardona, 2011).

The effect of agricultural intensification in coffee plantations on invertebrate groups has also received substantial attention. Coleopteran groups show divergent responses: in some cases, richness and abundance in shade coffee actually exceeds that of primary forest (Pineda *et al.*, 2005). In contrast, scarab beetles show decreases in species richness and evenness in sun versus shade coffee, with shade coffee retaining only a quarter of the species richness observed in forests (Nestel *et al.*, 1993). For a variety of arboreal, ground-nesting, and twig-nesting ants, the richness and abundance is reduced in shade coffee and declines with increasing agricultural intensification (Perfecto and Vandermeer, 2002; Perfecto *et al.*, 2005; Philpott *et al.*, 2008a; Larsen and Philpott, 2009). Nevertheless, ants experience significant declines in richness in coffee versus forest in all but the most rustic coffee systems, and forest-adapted species show particularly strong declines (Philpott *et al.*, 2008a). The diversity of native bees is higher in coffee systems with greater tree species richness and canopy cover (Jha and Vandermeer, 2010). Diurnal Lepidoptera are particularly sensitive, as even the small changes in arboreal diversity and structure in traditional shade coffee plantations are associated with substantial declines in species richness (Perfecto *et al.*, 2003).

Fungal and microbial responses to intensification remain understudied, particularly given the importance of these groups in ecosystem function. Mycelial cord-forming fungi decline substantially between cloud forest and shade coffee (Guevara, 2005). Although saptrotrophic fungi have similar diversity and abundance in forest and different coffee systems, there is substantial species turnover between systems; in contrast, endomycorrhizal richness and abundance decline with increasing management intensity (Heredia Abarca *et al.*, 2008). Published information on soil bacteria is virtually nonexistent, although a study in Indonesia demonstrated increased bacterial diversity in shade versus sun coffee (Evizal *et al.*, 2012).

The role of shade coffee in maintaining biodiversity extends beyond the immediate conservation of species richness within coffee plantations. In many regions of Latin America, shade coffee represents the majority of remaining mid-elevation range forest cover (Perfecto *et al.*, 1996; Perfecto and Armbrecht, 2003); agricultural intensification within these zones could result in the loss of habitat for disturbance-tolerant species in this altitudinal zone. Shade coffee also comprises high-quality matrix that facilitates dispersal between forest fragments; as forests become increasingly fragmented in the tropics, highly permeable matrix like shade coffee will be key to countering biodiversity loss resulting from local extinctions by facilitating dispersal between fragments (Vandermeer and Perfecto, 2007; Perfecto and Vandermeer, 2010). The high-quality agroforestry matrix formed by diverse shade coffee plays a key role in maintaining biodiversity at landscape and regional scales (Perfecto and Vandermeer, 2008, 2010). For example, forest fragments in Colombia maintain significantly greater bat species richness than coffee plantations in a landscape dominated by unshaded coffee; however, in a nearby region dominated by shaded coffee, no significant differences were observed in species richness between forest fragments and coffee (Numa *et al.*, 2005).

Coffee plantations occur in a broader landscape context that can also affect their productivity and provision of ecosystem services. Even landscapes dominated by intensified coffee production often conserve forest fragments, at least in areas too steep to cultivate (Williams-Guillén, personal observation), and farmers may maintain forest fragments specifically for the provision of ecosystem services (Chandler *et al.*, 2013). In northern Costa Rica, members of a local cooperative have adopted an 'Integrated Open Canopy' system, in which smallholder farmers intensify production in a 2–3 ha area and maintain forest on an area of equal size (Arce *et al.*, 2009). At the farm scale, these IOC systems have higher productivity and harbor significantly higher bird diversity than nearby shade coffee systems (Chandler *et al.*, 2013). However, the extent to which this farm-scale diversity translates into increased provision of ecosystem services (e.g., pest control in the case of birds) remains unknown.

Biodiversity and ecosystem function in shade coffee plantations

Less-intensive coffee production systems contribute to a variety of local-, regional-, and global-scale ecosystem services (Jha *et al.*, 2011). As with other agricultural crops, coffee production is dependent on processes, such as pollination, predation, and climate and water regulation. Diverse shade canopies contribute to nitrogen cycling and soil nutrient content (Aranguren *et al.*, 1982; Beer, 1988; Grossman, 2003). High-shade systems are also buffer against variable climates

through increased soil moisture (Lin, 2010) and by reducing variability in microclimate variables (Lin, 2007). Increased shade cover and complexity correlate with reduced disturbance from extreme weather events (Philpott *et al.*, 2008b). These factors directly affect the production and quality of coffee fruits. Although production is widely believed to be higher in lower shade systems, high- and medium-shade systems show few differences in overall yield (Lin, 2009); when controlling coffee plant density, moderate-shade produces the highest yields (Soto-Pinto *et al.*, 2000). Shade cover can increase the quality of coffee produced (Muschler, 2001; Vaast *et al.*, 2005), particularly at lower elevations; this is an important consideration as climate change reduces the optimal areas for coffee cultivation (Jha *et al.*, 2011). Shade coffee can also reduce labor and herbicide inputs, as shade cover decreases the growth of competing herbaceous vegetation (Beer *et al.*, 1997; Muschler, 2001).

A variety of regulating services mediated by animal biodiversity also increase coffee production. Although coffee can be wind pollinated, its fruit set and quality is increased in the presence of nonnative (Roubik, 2002) and native (Klein *et al.*, 2003; Ricketts, 2004) bees. As a result of proximity to forest fragments that harbored increased diversity of native bees, the pollination services to a single coffee plantation in Costa Rica were valued at approximately US$60 000 per year (Ricketts *et al.*, 2004). Pollination services provided by native bees are associated with increased bee diversity (Klein *et al.*, 2003; Ricketts, 2004). The richness and diversity of native bees is increased in diverse shade coffee systems (Jha and Vandermeer, 2010); pollination services are, therefore, presumably enhanced in traditionally managed shade coffee, although the interaction between coffee management intensity and the presence of forest fragments in the landscape remains unexplored.

Although coffee is a well-defended plant, it is vulnerable to attack by a variety of insect pests that are, in turn, limited by the diverse assemblages of predators found in shade coffee. Exclosure experiments have demonstrated that birds, bats, and lizards limit the abundance of herbivores in coffee plantations (Borkhataria *et al.*, 2006; Williams-Guillén *et al.*, 2008; Johnson *et al.*, 2009). The abundance of bat predators increases with decreasing management intensity (Williams-Guillén and Perfecto, 2010, 2011), and the effectiveness of bird-mediated predation decreases in low-shade coffee (Perfecto *et al.*, 2004), suggesting that biocontrol by these generalist vertebrate predators is negatively impacted by intensification.

The coffee berry borer (*Hypothenemus hampei*, Coleoptera: Curcolionidae) is the most devastating insect pest of coffee (Damon, 2000). Native to Africa, the life cycle of this pest makes it difficult to control, as it spends the majority of its lifespan within coffee beans (Vega *et al.*, 2009). However, a variety of generalist predators impact the populations of this pest. In Jamaica, exclosures designed to keep birds from foraging in shade coffee resulted in doubling the proportion of coffee berry borer infestation (Kellermann *et al.*, 2008; Johnson *et al.*, 2009). The pest control services provided by vertebrate predators in coffee plantations have been valued at US$75–310 ha^{-1} $year^{-1}$ in terms of pest damage prevented (Karp *et al.*, 2013; Kellermann *et al.*, 2008); several bird species identified as important for berry borer and insect pest control, such as the Tennessee warbler (Philpott *et al.*, 2009) and rufous-capped warbler (Karp *et al.*, 2013), rely on trees in coffee farms for foraging or are more abundant in farms with more tree cover and most likely would provide limited benefits in intensive sun coffee systems due to the lack of shade cover.

The ecosystem services produced by shade (vs. sun) coffee production extend far beyond the local farm scale. Coffee cultivation contributes to watershed conservation, soil protection, and buffering negative effects of extreme weather events (Jha *et al.*, 2011). Shaded systems have more favorable and stable microclimates and suffer reduced water loss (Lin, 2007). Higher shade systems also suffered reduced landslides in the wake of a major hurricane (Philpott *et al.*, 2008b). Shade coffee also forms high-quality matrix that facilitates the dispersal of native wildlife across longer distances and between protected areas (Jha *et al.*, 2011). Increased permeability of matrices of shade versus sun coffee increases movements of key pollinators, seed dispersers, and predators, enhancing the ecological stability of protected areas in mountainous regions and at the same time providing increased opportunity for provision of ecosystem services within farms.

At a global level, one of the most critical ecosystem services that shaded coffee systems can provide is the sequestration of carbon, thus mitigating climate change. Tropical agroforestry systems may sequester more than 200 MT of carbon per ha (Albrecht and Kandji, 2003) in plant biomass and soil. In Mexico, carbon stocks were 22 times higher in coffee plantations than in maize cultivation (Soto-Pinto *et al.*, 2010), whereas in Togo, inclusion of even a simple shade layer over coffee increased carbon stocks by 3.5 times to 81 MT per ha (Dossa *et al.*, 2008). However, practices, such as fertilization and use of nitrogen-fixing shade trees could increase the emissions of other greenhouse gasses from coffee plantations, indicating that careful consideration of inputs and shade trees must be made in order to evaluate the overall impact of shade coffee on climate change mitigation (Jha *et al.*, 2011). Nevertheless, in a warming world, shade cover will most likely play a critical role in maintaining coffee cultivation as current growing regions become suboptimal due to increasing temperatures, changes in precipitation patterns, and more frequent hurricanes, all of which can be buffered through a shade canopy (Jha *et al.*, 2011).

Despite the system's reputation for sustainability, coffee cultivation can generate substantial ecological disservices. Deforestation, erosion, nutrient loss, and instability of microclimate can all result from the conversion of forest or high-shade systems to low-shade or sun coffee. In Latin America, coffee cherries are commonly processed via a 'full wash' method to remove coffee pulp and mucilage from the fruit before drying; although this produces a higher quality bean, the process produces large amounts of effluents that can contaminate local water supplies (von Enden *et al.*, 2002). Use of agrochemicals in coffee plantations presents immediate threats to workers applying chemicals (often without the use of adequate protective gear) as well as to local communities living with runoff. The most commonly used insecticides for coffee berry borer control, endosulfan and chlorpyrifos, are highly toxic (Jaramillo *et al.*, 2006). Plantings in extremely steep areas may lead to erosion, and replacement of forest with

coffee leads to biodiversity loss and potentially reduced watershed protection and climate mitigation.

Market Incentives to Conserve Ecosystem Services in Coffee

Existing Mechanisms

Given its economic and social importance, not surprisingly a number of mechanisms falling under the broad umbrella of Payments for Ecosystem Services exist for coffee. These schemes include certification of preferred production systems, direct payments to producers from governments or individuals, and participation of farmers in environmental markets.

Certification schemes

Certification programs are the most widespread and well-recognized mechanisms for compensating farmers for conservation of biodiversity and provision of ecosystem services. Under such programs, farmers adopt specific production criteria established by third parties, contract auditors to inspect and verify adherence, and receive in return the right to sell and market their product as certified. Although such systems may involve substantial costs for producers, the expected benefit is the ability to sell their crops at a price premium to consumers willing to spend more to support such systems. Certified coffee (e.g., organic, fair trade, etc.) accounts for approximately 10% of global production (Jha *et al.*, 2011). These certification and labeling initiatives are voluntary and private, without governmental mandate (Raynolds *et al.*, 2007).

Certified organic agricultural production is an example of a certification scheme familiar to most readers, in which production without the use of agrochemicals results in a more valuable crop. Organic certification is applied to a variety of crops globally; in case of coffee, organic certification generally involves the use of composting organic material, improvement of soil nutrient content, and prevention of erosion and soil runoff (Giovannucci and Koekoek, 2003); organic certification makes no demands with respect to tree cover or maintenance of forested areas. Thus, although organic production may improve provisioning of ecosystem services related to soil conservation, intensive organic systems may provide reduced regulating and provisioning services than traditional – but not organic – shade coffee plantations. For example, when canopy structure is held constant, organic production had no effect on the diversity or abundance of trees or birds in Nicaraguan shade coffee (Martínez-Sánchez, 2008).

A second widespread certification program applied to coffee is Fair Trade, which promotes price premiums for smallholder farmers and cooperatives exporting from the developing to the developed world. Although Fair Trade criteria focus on social and economic aspects of production, they also include limitations on the use of toxic agrochemicals, buffer zones around water resources, and ban the use of genetically modified crops (Jha *et al.*, 2011; Raynolds *et al.*, 2007). As is the case with organic certification, there are few provisions to ensure the maintenance of shade cover that enhances the provision of ecosystem services, although Fair Trade certification may have positive impacts on the provision of water and reduce agrochemical contamination as a result of measures meant to insure worker safety. Nevertheless, the focus on small producers may indirectly promote shade coffee, because smallholder farmers tend to use less labor-intensive shaded systems (Perfecto *et al.*, 2005). More recently, UTZ certification has become available for coffee and other tropical export crops with broadly similar criteria to those of Fair Trade (Giovannucci and Koekoek, 2003) focused on compliance with local labor and environmental laws.

In the 1990s, coffee certification programs that emerged focused on the certification of 'eco-friendly' coffee, more explicitly taking into account production methods and their effects on biodiversity and ecosystem service provision (Raynolds *et al.*, 2007). The Smithsonian Migratory Bird Center's Bird-Friendly® program is among the most stringent of these, requiring organic production, the use of at least 10 shade tree species with minimum heights of 12 m, three canopy layers, maintenance of lianas, and a minimum shade cover of 40% (Smithsonian Migratory Bird Center, 1998). Participants are small producers, and this certification comprises a small proportion of exports in the certified coffee market (Raynolds *et al.*, 2007). Although the provision of ecosystem services in Bird-Friendly® versus noncertified shade coffee has not been quantitatively evaluated, such management would presumably provide the widest variety of services. Rainforest Alliance's 'Sustainable Agricultural Network' standards include a variety of social and ecological criteria; the latter are less stringent than those of the 'Bird Friendly' program but include provisions for maintenance of diverse shade trees on farms with a minimum shade cover of 40%, protection of natural ecosystems and riparian buffers, wastewater treatment, use of integrated pest management techniques, and reduced agrochemical use (Hughell and Newsom, 2013). A recent contrast of certified and noncertified plantations in Columbia suggests that such certification has a positive impact on the provision of ecosystem services: certified farms had higher water quality and healthier streams, increased arthropod species richness, increased use of 'best management' practices, and increased revenues (Hughell and Newsom, 2013).

Direct payments

With direct payments, rather than receiving a price premium for coffee produced using methods that maintain ecosystem services, coffee producers receive direct payments from beneficiaries, usually through an institutional intermediary. Thus, incentives for maintaining ecosystem services are not tied to coffee commodity prices, which can undergo large and rapid price fluctuations (Jha *et al.*, 2011).

Although Payment for Environmental Services (PES) schemes have received widespread attention and are considered a promising approach, relatively few real-world examples exist from the tropics (Wunder, 2006). Despite widespread recognition of the potential to incorporate shade coffee production into PES for carbon sequestration and watershed protection (Rosa *et al.*, 2004; Montagnini and Nair, 2004), only a few initiatives specifically target small-scale shade coffee production (Méndez *et al.*, 2010a). Moreover, coffee plantation owners who maintain forest fragments on their properties could conceivably receive payments under

Costa Rica's PES program that rewards landowners for maintaining forested areas.

An example of a localized PES scheme involving coffee production comes from Honduras, where the community of Jesús de Otoro relies on water from the Cumes River (Kosoy *et al.*, 2007). This source of drinking water was becoming contaminated due to coffee cultivation upstream. A local grass roots water council of elected representatives (JAPOE, Council for Administration of Water and Sewage Disposal) created a PES scheme with the assistance of the nonprofit organization PASOLAC (Program for Sustainable Agriculture in the Hillsides of Central America), in which downstream users pay a fee of approximately US$0.06 per household per month to compensate upstream farmers for adoption of improved waste management practices and protection of forests (Kosoy *et al.*, 2007). Although downstream users report improvements in water quality, the low payments to upstream producers have hampered adoption, covering only 70 of the 200 ha identified as high priority for participation (Porras and Neves, 2010).

Tax incentives and agrotourism may also be seen as forms of direct payments in exchange for ecosystem services. The latter in particular is well developed in coffee plantations. In the Soconusco region of Chiapas, Mexico, several of the large coffee plantations have established tourist hotels and restaurants catering to weekend visitors and international tourists interested in bird watching and hiking (Anonymous, 2009).

Environmental markets

In the case of environmental markets, the ecosystem service itself is marketed and sold as a commodity to a beneficiary (usually an institution rather than individual) in the context of a dedicated market, usually subject to oversight by a regulatory body (Stuart *et al.*, 2010). Carbon credits and offsets are the most prominent example of such markets and the one with great potential but limited implementation in agroforestry systems, such as shade coffee.

One of the few success stories involving the sale of carbon from coffee plantations comes from the Scolel Te' program in central Chiapas, Mexico. The program was designed for researchers at the University of Edinburgh with the express goal of creating a market for the ecosystem services generated by agroforestry systems (Tipper, 2002). In this program, participating farmers develop plans for sustainable agroforestry and reforestation; based on estimates of carbon sequestered, they receive ex-ante carbon offset payments (US$12 MT^{-1} C in 2002; Tipper, 2002). The program is managed by the nonprofit AMBIO, which evaluates farmer management plans and estimates the amount of carbon to be sequestered as a result of the planned management and reforestation interventions. The program has grown rapidly: as of 2010, nearly 2500 registered producers managing more than 9500 ha of land had enrolled, and approximately US$109 500 worth of payments were made in 2010 (Quechulpa Montalvo and Esquivel Bazán, 2011). The program has additional social and educational benefits for producers through training and educational opportunities. This community-based carbon credit framework has since been consolidated as the Plan Vivo Standard, with registered projects across the globe subject to long-term third-party monitoring and selling Plan Vivo Certificates representing 1 MT of reduced or avoided carbon emissions (Anonymous, 2008). The up-front costs of entry into certification plans and green markets are often a deterrent to the participation of smallholder farmers; thus, the Plan Vivo standard represents one of the few success mechanisms by which the majority of producers in developing nations have access to these emerging markets. Nevertheless, the short fallings of these mechanisms are as numerous as their successes.

Failure and Weakness of Current Market Mechanisms to Conserve Ecosystem Services

Although market-based mechanisms for incentivizing the provision of ecosystem services have shown some early successes (Hughell and Newsom, 2013; Quechulpa Montalvo and Esquivel Bazán, 2011), the limited number of programs as well as the failure of well-established certification programs speaks of the weakness of currently existing schemes. Aside from the single study commissioned by Rainforest Alliance (Hughell and Newsom, 2013), no other research that has explicitly contrasted the provision of ecosystem services (or reasonable proxies, such as bee diversity as an indicator of pollinator services) in certified versus noncertified coffee farms is known. Thus, despite the sound and fury, the certification that serves to protect biodiversity or ecosystem services with coffee farms or other agricultural systems remains largely an article of faith. There is a clear research need for studies to investigate the ecological (rather than socioeconomic) effects of certification schemes.

As mentioned previously, certification schemes, such as Fair Trade and organic, may do little to directly safeguard a variety of ecosystem services, which is a weakness of the major certification programs if they are not explicitly linked to parallel programs that emphasize conservation of ecosystem function (Philpott and Dietsch, 2003). The volatility of current agricultural markets contributes to undermining the efficacy of certifications in maintaining biodiversity and ecosystem services. In the late 1990s, coffee prices underwent a precipitous decline in the wake of market liberalization, the dissolution of agreements setting international coffee prices, and a glut of production from Southeast Asia (Bacon, 2005); as a result, the labor costs of harvesting coffee exceeded the prices the cherries could fetch, with the result that coffee crops were left to rot on the plants (Williams-Guillén, personal observation). At one Costa Rican shade coffee farm, pollination services had been valued at >US$60 000 per year (Ricketts *et al.*, 2004); nevertheless, in the wake of the 'coffee crisis,' the plantation was transformed from coffee to intensive pineapple production (McCauley, 2006). Ecosystem services tied to the valuation of a crop are as vulnerable to market fluctuations as the crop itself.

It has been suggested that coffee certification itself could lead to more deforestation (and hence reduced provision of ecosystem services at regional scales) because an increase in coffee prices could incentivize expansion of coffee production into forested areas (Rappole *et al.*, 2003; Tejeda-Cruz *et al.*, 2010). However, despite price premiums received by smallholder producers of organic and Fair Trade certified coffee, overall impacts on household livelihoods are insignificant for most metrics as a result of limited per household production

and inability to sell entire harvests at certified prices (Méndez *et al.*, 2010b). Many types of certification are outside of the reach of small-scale producers due to up-front costs associated with enrollment (Gobbi, 2000). Although certified coffee is a growing sector, at present it comprises less than 2% of global coffee production (Méndez *et al.*, 2010b), and production for some markets currently outpaces demand (Giovannucci and Koekoek, 2003). Thus, although certification produces financial benefits for large-scale producers and highly organized cooperatives, as a measure for incentivizing the maintenance of ecosystem services in coffee plantations (and other agricultural landscapes), it is inadequate to protect ecosystem services as currently practiced – price premiums in general fail to offset increased production costs, and relatively few consumers in developed nations are interested in voluntarily paying for the 'real' cost of their coffee that integrates the externalities of human and ecosystem health.

The dearth of examples of the use of direct payments for ecosystem services speaks to some of the main challenges in the use of this system in developing nations. Such schemes depend on strong, transparent government agencies or institutions capable of regulating payment mechanisms; however, weak governance and corruption are the norm in the global south. Sustainable funding for direct PES is a second challenge, even for well-established programs: despite taxes to beneficiaries, Costa Rica's PES program relies partially on loans and grants from development agencies (Pagiola, 2008). The example of direct PES to coffee producers in Honduras highlights the need for payments to realistically offset the opportunity costs (i.e., the revenue lost by making a different choice, in this case, choosing not to invest in wastewater treatment). Low payments to producers have hampered adoption, resulting in low adoption rates and limited protection of the watershed. This example speaks of the broader issue of valuation within the design of PES schemes. Without accurate estimates of the monetary benefits of provisioning of ecosystem services, it is difficult to assess appropriate payments to providers (Kroeger and Casey, 2007). Given the impossibility of carrying out quantitative studies to estimate ecosystem service value in every local context, the development of spatially explicit modeling tools to estimate values and trade-offs between services is a key advance that will facilitate small-scale PES implementation (Kroeger and Casey, 2007; Tallis and Polasky, 2009). Initiatives, such as InVEST, promise to provide such tools (Nelson *et al.*, 2009), although their utility in real world situations remains largely untested.

Kroeger and Casey (2007) outline additional weaknesses in market-based approaches, which are apparent even in the relatively successful example provided by Scolel Te' example. Carbon sequestration provides an example of a nonexcludable service: beneficiaries will receive the service of carbon sequestration whether or not they pay to support reforestation and agroforestry. Thus, voluntary markets and programs will often fail to produce the funding needed to provide adequate payment to farmers, because it easy for beneficiaries to avoid payment and 'cheat the system.' For example, market fluctuations, the effects of economic recession, and other factors can result in low sales of carbon credits and hence reduced payments to Scolel Te' participants (Quechulpa Montalvo and Esquivel Bazán, 2011). Such market fluctuations effectively cause an increase in opportunity costs; if payments do not increase in tandem to offset these increases, producers may leave programs to pursue more intensive or expanded agriculture. The limited standards and monitoring protocols, coupled with a lack of global leadership to institute cap-and-trade programs, form a major limitation of environmental markets. Because large-scale environmental markets are unlikely to develop in the absence of regulations compelling participation on the parts of beneficiaries, such market-based mechanisms will remain limited in the current climate of market liberalization and deregulation.

Strategies and Opportunities for Improving Conservation of Ecosystem Services through Market Incentives

Lessons from Successful Programs

The Scolel Te' program provides one hopeful example for a successful PES approach in the developing Latin America. Because the program was designed to seek payments for traditional agroforestry practices already familiar to many producers (as opposed to seeking to radically change production techniques), adoption rates were high (Tipper, 2002). Nevertheless, other PES programs focused on modifying production systems have also met with success. For example, a program in Nicaragua used PES to incentivize the adoption of silvopastoral systems by ranchers, funded by the global environment facility; the program was well received by participants and produced improvements in indicators of ecosystem health (Pagiola *et al.*, 2007). Most participants maintained the improved systems after the end of the official project period and guaranteed payments, and the municipal government introduced tax incentives for producers (Svadlenak-Gomez, 2009). However, sustained funding for payments and weak local governance remain challenges for the long-term survival of the program (Svadlenak-Gomez, 2009).

PES schemes related to food systems can also serve to fill gaps in service and enforcement in the case of weak institutions with limited resources. A second example of a successful PES program comes from southwestern Nicaragua, where the Non-governmental organization (NGO) Paso Pacífico partnered with a government-administered wildlife reserve and local fishing communities to develop a performance-based incentives program to curtail the poaching of sea turtle eggs for local and national consumption (Smith and Otterstrom, 2009). Through this program, would-be turtle egg poachers are offered a modest payment in exchange for committing to protect a turtle nest by becoming 'nest protectors.' On successfully protecting a turtle nest, 'nest protectors' are then given a payment for each nest successfully protected. The price paid is above the market price for eggs. These performance-based incentives are a form of direct payments for conservation with the buyer being the environmental NGO. During the course of the program, poaching on the participating beaches dropped from nearly 100% to 15%. A key component of the program's success was participation of local community representatives in developing payment mechanisms, timely payment of incentives that were on a par with

opportunity costs, and transparency on the part of Paso Pacífico in the administration of the program. As with many PES programs, a key limitation was sustained funding: despite the program's success, it continues in a limited capacity on only one beach due to limited funding streams from granting agencies. Future options for developing sustainable funding streams include linking to incipient biodiversity markets, in which fisheries companies could, for example, purchase 'turtle credits' to fund the protection of nesting beaches to offset the accidental mortality of juvenile and adult sea turtles incurred during fishing.

Opportunities and Future Directions for Payments for Environmental Services in the Agricultural Landscapes of Latin America

Although the past years have seen some development of market-based mechanisms for conservation of ecosystem services in agricultural landscapes, such schemes remain a promise rather than a reality for the vast majority of producers in developing regions even when considering only the relatively valuable crop of coffee. A variety of factors, from volatile markets to weak governance, remain a barrier in using such incentives to promote conservation among agriculturalists of the global south. A recurring theme in the success of PES programs in Latin America has been the involvement of local nongovernmental institutions with close ties to the communities targeted for payments; these communities often present well-organized, semiautonomous governance, echoing arguments that local social movements must play a key role in successful conservation in developing nations (Perfecto *et al.*, 2009). Partnership with academic institutions in the development of program structures has also played a key role in successful examples, particularly in larger scale programs. Finally, programs designed with systematic input from local communities have been a clear component in success, particularly when the involvement of local governmental bodies reinforces norms and incentives. 'Top–down' approaches have produced some success, particularly when based on modifications of already-established policies (Pagiola, 2008). However, when such approaches overlook meaningful community participation, they often fail, whereas 'bottom–up' approaches based on interventions suggested by target communities tend to fail due to lack of resources; this situation highlights the need for 'hybrid' approaches that unite the resources of larger institutions with the insight and momentum of local, grassroots organizations (Méndez *et al.*, 2010a). In Latin America's developing nations, NGO intermediaries with close connections to local producers and relationships with institutional representatives are a key link in the design and effective implementation of PES schemes.

Given the limited availability of environmental markets and the technical and economic barriers to certification schemes, direct payments for conservation may be the most feasible approach in Latin America, at least in the short term. It is believed that small NGOs with conservation goals, meaningful relationships with small-scale producers, and the knowledge necessary to negotiate agreements with private industry and government stakeholders are a key nexus in uniting a variety of stakeholders to generate demand for the conservation of biodiversity and ecosystem services and biodiversity in the working landscapes that will most likely characterize much of the tropics in the twenty-first century.

Conclusion

Ecosystem services are fundamental to the success of agriculture, and agricultural production can produce a number of ecosystem services and disservices at local, regional, and global scales; nevertheless, examples of market-based mechanisms to conserve these services are limited (Kremen and Miles, 2012; Kroeger and Casey, 2007; Power, 2010). Although several existing mechanisms have the potential to compensate farmers in the developing world for conserving and maintaining ecosystem services, at present these programs are at incipient stage and have demonstrated both promise and pitfalls.

The most successful programs involve participation of governmental, nongovernmental, and academic institutions; integration of top–down and bottom–up solutions and mechanisms; and buffering smallholder producers against fluctuations in market prices (of both agricultural and ecological commodities). Demand for agricultural products in low- and middle-income countries is expected to double by 2050 (Food and Agriculture Organization of the United Nations, 2011); without concerted attempts to internalize the market externalities of ecosystem services, this increased demand will undoubtedly result in massive environmental degradation and the ultimate failure to provide adequate resources for the majority of the world's human population. Market-based incentives can play a key role in safeguarding ecosystem services in agricultural areas, but their implementation is limited by lack of adequate policy and regulatory mechanisms, sufficiently large incentives to offset opportunity costs, and the failure of stakeholders to unite top–down and bottom–up approaches that integrate the regulatory capacity of governments with participatory action from producers to design appropriate local models for compensation.

Within the developing world, weak governance and inequitable distribution of resources are fundamental barriers to the optimal function of market-based mechanisms. In these cases, nonprofit organization, academic institutions, and grassroots community organization play vital and complimentary roles in developing appropriate and effective methods to protect interests and sustainability of local and global populations. Much of the current degradation in ecosystem services has resulted from the market failures inherent to neoliberal priorities of deregulation and privatization; expecting market-based interventions to resolve problems caused by markets themselves is more likely a losing proposition. Ultimately, market-based approaches to conservation are only one component of a larger toolkit that incorporates concepts of the intrinsic value of nature and also a focus on economic productivity, social equity, and sustainable livelihoods (Perfecto *et al.*, 2009).

See also: Agroforestry: Complex Multistrata Agriculture. Agroforestry: Practices and Systems. Biodiversity and Ecosystem

Services in Agroecosystems. Biodiversity: Conserving Biodiversity in Agroecosystems. Natural Capital, Ecological Infrastructure, and Ecosystem Services in Agroecosystems

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Markets and Prices

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Glossary

Demand Quantity of a particular commodity which a consumer is willing to purchase as its price varies, assuming all other factors are held constant.

Market Place (perhaps a physical place but not necessarily) where buyers (demanders) and sellers (suppliers) of a commodity come together to negotiate an exchange at a price.

Money The numerable commodity or asset in an economy that serves as the most common means of exchange for goods and services.

Price The basic signal of exchange in economic systems. Price represents the rate at which one commodity (good) is exchanged for another commodity.

Supply Quantity of a particular commodity which is offered for sale per time period as price varies, assuming all other factors are held constant.

Price Functions

Price serves two major functions: first, to ration scarce commodities (who gets what) and second, to motivate (direct) future production of commodities (what products will be produced). The manner in which price carries out these functions differs according to the institutional rules (rules of the game) placed on the market. These rules range from very little regulation (asset prices in auction markets, e.g., futures markets for crops, livestock, and financial instruments in the US) to extreme forms of regulation where price is fixed by governmental authority. Two forms are described – free markets with little or no regulation except legal requirements of enforcement of contracts and type of communication among buyers and sellers (double oral auction vs. posted prices) and fixed price markets. The efficiency with which price is able to carry out the above mentioned functions is determined by the institutional rules placed on the market.

Some criteria useful for measuring the efficiency and performance of a pricing system include (Forker, 1975):

1. Allocation efficiency including short-run market clearance, inventory adjustments, production adjustments, and marketing efficiency.
2. Welfare considerations regarding price level and stability, price dispersion, and sharing of gains or losses within the marketing channel.
3. Competitive considerations on market access, bargaining power, structure, and information flow.
4. Cost considerations including waiting time and transportation and system costs.
5. The level of buyers' and sellers' satisfaction with the operation and results of the system.

Equilibrium Price

In free markets, price adjusts according to changes in supply and demand; the market price is that which just clears the market – the amount of the commodity suppliers want to supply (give up title to) equals the amount of the commodity demanders want to purchase (Mankiw, 2012). Generally, quantity supplied is a positive function of price, so that suppliers (those who hold title to the commodity) offer more for exchange (are willing to give up more of the commodity, possibly because they produce more of it) when price increases, whereas quantity demanded is a negative function of price, as demanders (people who do not have title to the commodity but may perhaps want to acquire title to it) offer to buy less when price increases. If the quantity that suppliers offer at a specific price is greater than the quantity that demanders wish to purchase at that price, price will fall, inducing demanders to take more. The reverse will occur if the quantity that suppliers wish to supply at a given price is less than the quantity that demanders wish to acquire at a specified price. Price arrived at in free markets by this interaction of supply and demand is called an equilibrium price, as there will be a tendency for price to return to this level if there is some small perturbation away from it.

Price arrived at through the interaction of demand and supply reflects the marginal valuation of the group (society) for the particular commodity. This explains the seemingly odd fact that a commodity as useful as water (say an acre foot of water) has a price much lower than an apparently less useful commodity, say a one carat diamond of high quality. The latter is of limited supply, whereas the former is of much greater supply. However, if constraints are placed on the availability of water, it would be seen, rather quickly, that its price would be equal to or much greater than that of a diamond. The marginal utility of a unit of water is much less than that of a diamond, but the total utility of water is much greater.

In free markets, those individuals who are willing to pay the market price will be able to acquire the commodity, whereas those who are neither willing nor able to pay the price do without. The entire amount brought to the market (amount suppliers are willing to put on the market) is rationed (allocated) among users by price. If the price arrived at in free market equilibrium is high (relative to the cost of producing the product), suppliers in future periods will have an incentive to bring forth additional supplies of the commodity. If the price is below the cost of production, suppliers will bring forth smaller quantities in future periods. Thus, price serves its

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second function: directs (motivates) what and how much is to be produced.

Planning Prices

In regulated markets, the extent to which price can accomplish its two functions is blurred. In extreme cases where price is held fixed by government authority, both the rationing and direction functions are stifled. For example, in centrally planned or command economies, where price is not allowed to adjust according to market demand and supply, rationing is accomplished on a first come, first served basis. Once the entire supply of the product is sold at the fixed price, waiting lines form, until additional product is brought to the market. Here price does not perform the rationing function. Rather, time spent in line does the rationing. In such cases, it is common for parallel or black (illegal) markets to form, which mimic the behavior of a free market.

The direction of production is also impaired in fixed price markets. If the price is set above the free-market equilibrium price, suppliers will have an incentive to produce more of that product (more than demanders wish to purchase). Such products will sit in inventory (wait to be sold). If price is set below the equilibrium price, producers will have no incentive to produce additional units of that commodity, even though demanders would be willing to pay more for additional quantities of that commodity. Thus, surpluses and shortages occur too high and too low, respectively, at fixed prices.

In centrally planned economies, provisions for changing price and production have been devised which rival market prices, at least, in theory (related works of Lange, 1936 and Lerner, 1934 develop this model and a critical comment is offered in Friedman, 1947). Prices in centrally planned economies were modeled to provide much of the same information as prices from free markets offer. Essentially, this model works by accounting prices and information interchanges between managers and the central planning authority. The central planner sends information to the managers in the forms of a set of price signals; the manager returns information to the central planners in terms of his/her output, if this planned output was greater than needed, a new set of accounting prices would be communicated to the managers. This process continues until a particular set of production levels are realized. Lerner (1944) argued that such a system could replicate the market pricing system. Although the Lerner model was never actually tested, the late 1980s to early 1990s collapse of the centrally planned economies of Eastern Europe suggests that the system may have suffered in application. It is difficult for central planners to gather even a fraction of the information relevant to production and consumption decision making that is conveyed by price in a free-market economy (Landsburg, 2011).

The price emanating from these planning models is a 'shadow price' which gives the marginal valuation of the resource (production constraint) in the model. As these prices are not necessarily seen in the market (but are the output from the mathematical model), they are labeled 'shadow prices.' Those constraints for which all of the resource is utilized will have nonzero shadow prices.

Price in Agricultural Markets

Agricultural markets are interesting because their demand functions (described generically above) are believed to have particularly inelastic form. When a demand function is inelastic, the percentage changes in quantity demanded due to a percentage change in price is small compared with a more elastic demand schedule (see **Figure 1**). The reader may grasp the relevance of this point by understanding that certain commodities have few substitutes. Food (as a composite commodity) is one such commodity. Consumers are not likely to change their previous level of food consumption due to a change in the price food. Food is quite habit forming and perishable.

Weather uncertainty leads to variable production which interacts with the inelastic demand, resulting in highly variable agricultural commodity prices. In markets characterized by inelastic demand functions, relatively small change in supply can have a large price impact (see **Figure 2**). Accordingly, market institutions which deal with high price variability, directly or indirectly, have found extensive use in agriculture.



Figure 1 Impact on quantity demanded with a decrease in price, comparing inelastic and elastic demand functions.

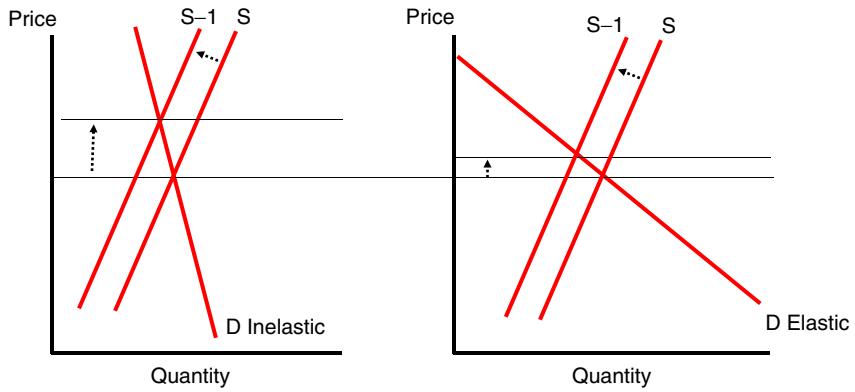


Figure 2 Impact on price with a decrease in supply (S), comparing inelastic and elastic demand functions.

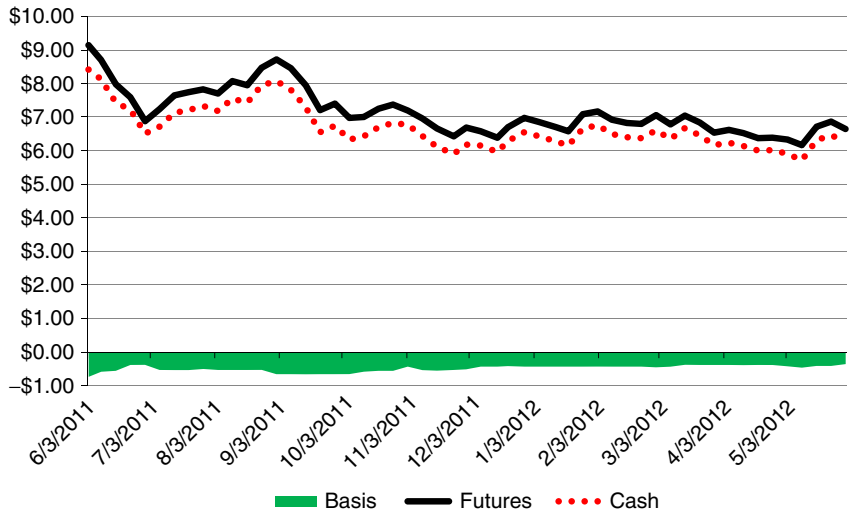


Figure 3 Wheat prices: Kansas City futures, Texas cash (spot, USDA-Ag Market News Service, www.ams.usda.gov/mnreports/AM_GR100.txt), and Texas basis.

The major market risk-bearing institutions are agricultural commodity futures markets, insurance contracts, and federal government programs.

Futures Prices

Organized futures markets which allow both producers and consumers to reduce market price uncertainty through hedging have existed in the US for well more than 100 years. Holbrook Working (1953) aptly defined hedging as using the futures market as a temporary substitute for the cash market. A futures market is a centralized market where futures contracts are traded in organized exchanges, either by open outcry, electronically, or both. A futures contract is a legally binding standardized agreement (conditions set by the exchange) to buy or sell a commodity specifying quantity, quality, and date and place of delivery. The only nonestablished variable is the price. In this way, the futures price is a statement of a commodity's value at a specific point in time at a particular location.

Forward pricing using futures contracts is based on the premise that, over time, the local cash price and futures prices move together. Therefore, adjusting for local conditions, pricing in the futures market is a close approximation to pricing in the cash market. The amount that the local cash (spot) price of a commodity is above or below the futures price for a particular month is called the basis (basis = local cash price minus futures). Although most of the differential between the local cash price and the futures price can be explained by storage and transportation costs between a user's or producer's local cash market and the exchange-specified futures market delivery point, local supply and demand conditions can also affect the amount of the basis.

Basis risk, the variability between local and futures prices, is generally much less than the price risk associated with the commodity. Figure 3 shows the relationship between the price of hard red winter wheat grown in Texas and the Kansas City Board of Trade exchange futures price (with delivery points of Kansas City, Missouri, Hutchinson, Kansas at a 9 cent discount, Salina/Abilene, Kansas at a 12 cent discount, and Wichita, Kansas at a 6 cent discount). In the 2011–12

marketing year, the average amount by which the Texas cash price of wheat was below the Kansas City futures price was 48 cents per bushel, in a 38 cent range from US$0.35 to US$0.73. Over this same period of time, the highest futures price was US $9.14 per bushel and the lowest was US$6.18 per bushel, a price range of US$2.96.

Very few buyers or sellers of futures contracts actually make or take delivery of physical commodities. Instead, they offset their positions in the futures market (buying back contracts if they sold and selling back contracts if they bought). Because futures and cash markets move together, any loss in the cash market is offset by gains in the futures market and vice versa.

Take the case of a Texas wheat farmer who plants in October and will harvest wheat the following June. He/she observes that the July futures contract for Kansas City wheat (the nearest, but not before, harvest-time contract offered) is US$8.00 per bushel. He/she is concerned that prices will fall between now and harvest and decides to hedge. He/she calls his/her commodity broker and sells the equivalent number of futures contracts to cover his/her expected production. His/her local basis at harvest is normally US$0.60/bushel. This action establishes an expected hedged cash price of US$7.40 per bushel (US$8.00 futures plus US$0.60 basis) (Ignoring brokerage commissions). At harvest, the price of the July Kansas City wheat contract is US$7.00 per bushel; the local basis is US$0.60. He/she sells his/her wheat in the local cash market for US$6.40 per bushel (US$7.00 futures plus US $0.60 basis) and buys back his/her futures contracts for a profit of US$1.00 per bushel (US$8.00–7.00=US$1.00). Adding the dollar profit from his/her futures transactions to his/her cash wheat price returns US$7.40 per bushel, the price he/she sought to lock in with his/her hedge. Had the futures price increased, say to US$9.00 per bushel, and the basis held steady at US$0.60, he/she would have sold wheat at harvest in the cash market for US$8.40 per bushel and subtracted a net loss in the futures market of US$1.00 per bushel from his/her wheat returns, again leaving him/her with a hedge price of US $7.40 per bushel. The uncertainty in the cash market price has been reduced by his/her equal but opposite participation in the futures market. The farmer remains subject to yield uncertainty which may not be particularly easy to forecast but can be partially covered by crop insurance.

The farmer who protected against a drop in his/her local cash market price by creating a short hedge with futures, also 'protected' against the benefit of a price increase during the course of the hedge. In 1984, a type of 'price insurance' in the form of commodity options on futures contracts became available for a premium. An option is the right, but not the obligation, to buy or sell something at a predetermined price (the strike price) at anytime within a specified time period. A put option gives the buyer the right to sell the underlying commodity; a call option gives the buyer the right to buy the underlying commodity. In the present case, the underlying commodity is a futures contract.

If the futures price falls below the option strike price before the option expires, the buyer of the put option could exercise his/her right to sell futures at the predetermined strike price. If price rises, the producer would not use (exercise) the option but simply sell the crop at the higher cash price level at harvest. Options in agricultural commodities typically expire at the end of the month before futures contract expiration, for example, the latter part of June for a July futures contract. At option expiration, the only value the option contract will have is the positive difference between the strike price and the underlying futures price. If the futures price is equal to or greater than the strike price, the option will expire worthless.

Instead of hedging and locking in a net expected hedged price of US$7.40 per bushel for his/her wheat, the farmer could have bought a put option. If a put with an US$8.00 strike price were selling for US$0.50 per bushel, he/she would have purchased the right, but not have the obligation, to sell (take a short futures position) July Kansas City wheat for US $8.00 per bushel anytime between the purchase date and option expiration. For that right, he/she would pay the option seller US$0.50 per bushel. Assuming he/she holds on to that option until harvest (and option expiration) in June, and the price of wheat falls to US$7.00 per bushel and the basis is US$0.60, he/she would sell his/her wheat in the cash market for US$6.40. His/her option position would have profit of US$1.00 (US$8.00 strike price minus US$7.00 futures) less the premium paid (US$0.50). His/her net wheat returns would be US$6.90 per bushel (US$6.40+1.00−0.50). This compares to wheat returns of US$7.40 if he/she hedged and US$6.40 by doing nothing (see **Figure 4**). If the price of wheat at harvest was US$9.00 per bushel, his/her option would expire with no value because the underlying futures price is greater than the strike price. In this case his/her returns from selling wheat would be US$8.40–0.50 premium paid or US$7.90 per bushel (US$8.40−0.50). This compares to a price of US$8.40 had he/she done nothing and US$7.40 with hedging.

The put option provides a price floor (subject to basis risk) but no ceiling against the possibility of higher prices. Unfortunately, as with any insurance policy, the benefits come at a cost of the premium, which is significant. Similar futures and options market operations can be defined for a user of agricultural products as inputs into other productive activities in order to protect against unforeseen increases in input prices, say a cattle feeder who feeds corn.

Futures markets have two categories of participants: (1) hedgers – those users and producers of commodities who seek protection from price risk and (2) speculators – investors willing to accept price risk in order to make profits. Speculators in futures markets, by their availability at the time of need to assume risk, perform an important economic function: they provide liquidity.

However, in the past several years, a new class of commodity investor has emerged, the financial index investor, who has diversified his investment portfolio to include commodity investment as an asset class. By pouring billions of dollars into commodity futures markets, the concern has been raised that these institutional investors are contributing to food price inflation by creating massive bubbles in agricultural futures prices. This issue continues to be a topic of research but a number of recent studies have failed to find a direct link between index trading and agricultural futures price movements (Irwin and Sanders, 2011; Etienne *et al.*, 2013).

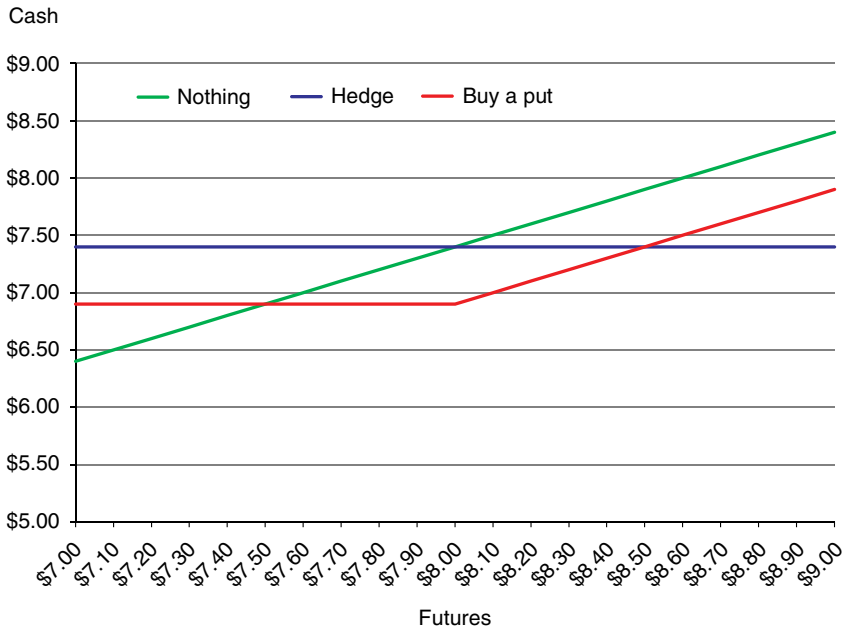


Figure 4 Net wheat returns from cash sales at harvest, hedging, and buying a put at various futures prices at option expiration.

Government Regulations on Prices

Government programs designed to influence prices of the US agricultural products have been in effect since the 1930s. Until the late 1990s, many products, including corn, cotton, wheat, barley, soybeans, milk, tobacco, wool, rice, and sugar, were subject to government programs. The motivation for such programs was to influence both the level and variability of prices within and between production cycles. Government programs in support of agriculture have historically been in the form of direct payments to producers and commodity price supports that effectively established a minimum price that producers would receive. Recently, such programs have either fallen out of favor with legislators or lost significance as commodity price levels have risen far above legislated levels of support. For example, in the 2008 farm bill, the target price for wheat (the national average price below which farmers would receive price support payments, less direct payments) was set at US$3.92 per bushel for 2008–09 and US$4.17 per bushel for 2010–12. This level of price support was below the life of contract lows of the July Kansas City wheat contracts, much less than the average price for the year (see **Figure 5**).

Another subsidy program, a federal cost-share program for crop insurance premiums, is gaining prominence as a major feature of the US farm policy. Crop insurance products that protect against both production and price risk are available, providing US producers with some degree of income security.

Efficient Price

The notion of an efficient price relates to its ability to quickly transfer new information. Thus, one would expect price in an efficient market to respond to new information in a timely manner. Notions of pricing efficiency have temporal, spatial, and form dimensions. All can be summed under the heading of 'the law of one price.' In its most simple form, it says that identical commodities should have the same price. Undoubtedly, the cost of making the commodities identical must be taken into account, so that wheat next month is not the same as wheat today – the two commodities are connected by storage. Wheat in Texas is not the same as wheat in Kansas – the two commodities are connected by transportation. And finally, wheat is not the same as bread – the two commodities are connected by processing. More directly, in an efficient market, prices reflect information such that the marginal benefits from acting on additional information are not greater than the marginal cost of acting on the information (Fama, 1970). Costs of acting on a new information signal must be taken into account when assessing the efficiency of a particular market.

This notion has been given formal treatment in terms of three forms of market efficiency: weak, semistrong, and strong. These forms focus attention on predictability of prices under particular information sets: weak form conditions on past prices (past own prices), semistrong conditions on all publicly available information, and strong form conditions on all information. Violations of weak-form and semistrong-form efficiency have been demonstrated for several agricultural commodities (Bessler and Brandt, 1992).

The law of one price (Ardeni, 1989) suggests that prices for the same commodity (similar commodities) differing only by time, space, or form will themselves tend to an equilibrium relationship. For short periods of time such prices may deviate from one another, but in the long run, they are brought back into their 'normal' equilibrium relationship with the difference reflecting the cost of making the commodities identical. Under some rather simple conditions, such prices will be cointegrated (Engle and Granger, 1987). Cointegrated prices will reflect the

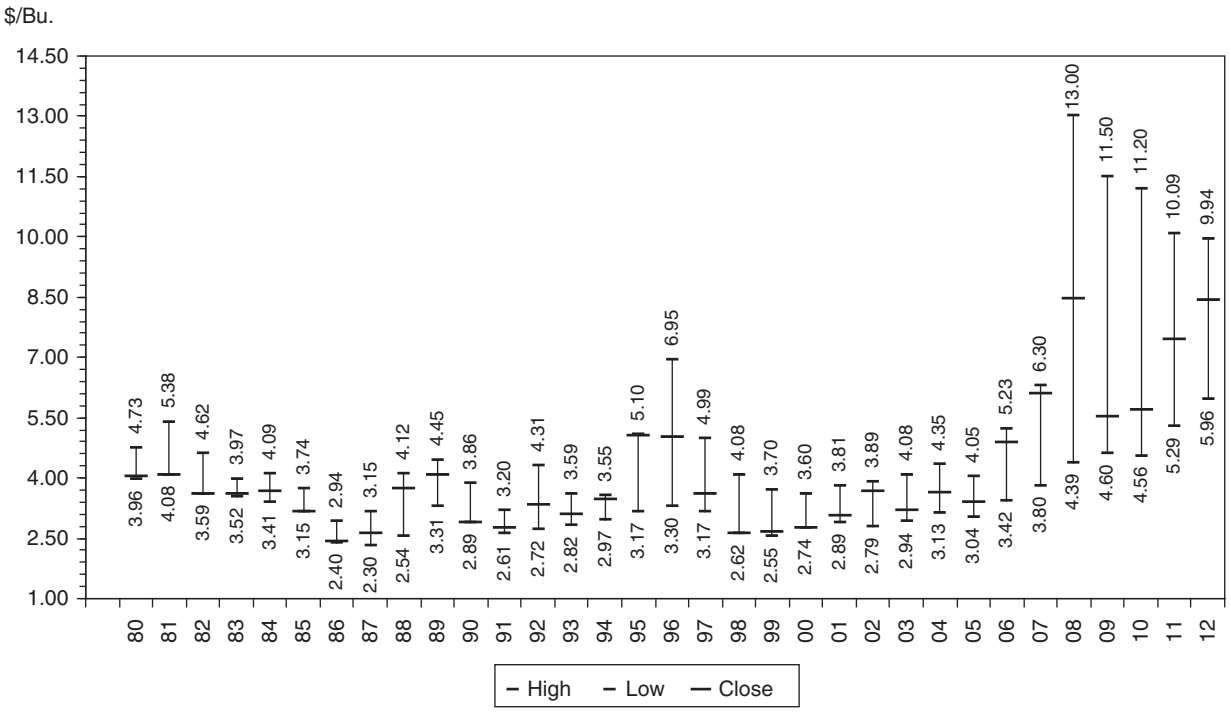


Figure 5 July Kansas City wheat prices: high, low, and close.

extent to which the market is defined. Government interventions will serve to effectively block such cointegrations by restricting the 'free flow' of information or product. Recent advances in modeling prices from markets use the notion of threshold cointegration (Blake and Fomby, 1997) to reflect that small differences in prices of commodities separated by space, time, or form may persist, as they are less than the threshold embedded in the cost of transactions.

Price Level

The foregoing discussion centers on relative prices. They are defined in terms of exchange for money (the numeraire good). The quantity of money in the economy will define the nominal level of these prices. In periods following substantial growth or contraction in the quantity of money, the price level may change quite rapidly. This is defined as a period of inflation or deflation – a period when the general price level increases or decreases. Historically, such periods have been at the heart of social and political turmoil, as witnessed by the late 1800s and the silver coinage (bimetallism) political campaign of William Jennings Bryan in the US, the hyperinflation in Germany in the 1920s, the great depression of the 1930s, and the inflation during the 1970s in the US. Each of these periods is characterized in terms of increases or decreases in the general price level. Further, each period experienced contractions (the US in the late 1800s and 1930s) or expansions (Germany in the 1920s and the US in the 1970s) in the quantity of the numeraire good (money).

The equation of exchange is helpful in understanding such periods: $MV=PQ$. Here, M is a measure of the money stock, V is a measure of the velocity of money (the number of times per unit of time that a unit of money turns over), P is a measure of the general price level (changes in the general price level are measured by broad-based price indexes such as the consumer price index or the wholesale price index), and Q is a measure of real value of transactions. For V constant and the economy at full employment (the economy is operating such that all resources are fully employed), an increase in M will result in an increase in P; decreases in M result in decreases in P. During the late nineteenth century, the US was on the gold standard. This tied the quantity of money (defined as the amount of currency and bank deposits) to the quantity of gold held by the government. From 1870 to 1896, there were few new gold discoveries to support the rapidly growing US economy. Bordo and Schwartz and Bessler (1984) argue that the relatively fixed money stocks (M) and an expanding economy (Q) had to result in either increased velocity (V) or a decrease in the price level (P), or both. In fact, Bessler provides empirical evidence that the price level actually fell in response to the contracting money supply.

A similar argument is behind explanations for the Great Depression, the inflation of the 1970s in the US, and the hyperinflations in Latin American in the mid-twentieth century.

It is generally believed that in the long run changes in money supply do not affect changes in relative prices, that is to say, the traditional view is that money is a veil, which merely covers, but is not a part of the real workings of the economy. However, recent work has at least questioned the short-run relevance of this view. Bordo (1980) discusses the short-run nonneutrality of money. Differing market institutions are offered as explanations for money showing nonneutral effects.

Agricultural products and other basic commodities (metals) are sold in auction-type markets, whereas other goods and services are often sold in posted price markets or under contracts which cover long periods of time. Pulses in the money supply will find their immediate effect in agricultural and other basic commodity market prices and show lagged (sluggish) effects throughout the rest of the economy.

See also: Agricultural Policy: A Global View. Food Marketing. Government Agricultural Policy, United States. Production Economics

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Mathematical Models to Elaborate Plans for Adaptation of Rural Communities to Climate Change

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Glossary

Adaptation to climate change The strategies that must be adopted to make the changes in the processes, practices, and structures to moderate the potential damages or to benefit from the opportunities associated with the change.

Climate change mitigation Mitigate climate change by reducing the sources or enhancing the sinks of greenhouse gases and other factors.

Hierarchy A representation of a complex problem in a multilevel structure, whose first level is the goal followed successively by levels of factors, criteria, subcriteria, and so on down to a bottom level of alternatives.

Multicriteria decision analysis (MCDA) An activity that helps making decisions mainly in terms of choosing, ranking, or sorting the actions with the basic ingredients: finite or infinite set of actions (alternatives), at least two criteria, and at least one decision maker.

Multicriteria decision making To make decisions in the presence of multiple, usually conflicting, criteria.

Multicriteria decision methods Mathematical methods to support MCDA.

Multiobjective mathematical programming General formulation of decision problems where a set of objective functions representing different criteria have to be optimized.

Outranking methods Multicriteria methods based on pairwise comparison of actions.

Scope and Objectives

Climate change is on the policy agenda at the global level, with the aim of understanding and reducing its causes and to mitigate its consequences. As in all natural, technological, and social changes, the best prepared countries will better support their specific effects of climatic change and will recover more rapidly. Therefore, it is essential to know those areas that are more sensitive to the negative effects of climate change, the parameters to be taken into account for its evaluation, and comprehensive plans to deal with it.

The adaptation to the climate change is now in the international sphere and is discussed in this article.

The authors try to understand, like adaptation to the climate change, the strategies that must be adopted to make the changes in the processes, practices, and structures to moderate the potential damages or to benefit from the opportunities associated with the change. These strategies must contemplate all the factors intervening into the environment including the collectivities that dwell in. The costs must be evaluated and also the negative repercussions for the sustainable development that are likely to appear.

Adaptation to climate change is a natural process, but man must anticipate, analyze, and quantify it. The development of strategies and the choice of alternatives, as well as to assess the costs of adaptation plans are a must. These plans may not be the same across the globe and each plan would depend on the geographical area. However, this article is intended to develop a common methodology and models, which can be adaptive and flexible.

The aim of this article is to show mathematical models based on multicriteria decision methods that could be applied to different geographical areas. In principle, the authors focus on Latin America.

These methods support decisions making, enable to develop and evaluate integrated plans for adaptation of different communities. European and Latin American areas are particularly vulnerable to climate change. They need to take into account all the factors involved, their side effects, and the diversity of the members of the network. The models will have to take into account criteria of physical type (meteorological, soil, and water resources), for the use of soil (agricultural, livestock, forestry, mining, industrial, urban, and tourism), economic (revenues, costs, benefits, and infrastructure), social (population and decision makers), political (implementation, legislation, and votes), education (educational programs and dissemination), and environmental.

General Objective

The objective of this article is to present a mathematical model that will allow the development and evaluation of integral plans for adaptation of communities to the climate change, in vulnerable areas of Europe and Latin America and to help select the most suitable alternative, evaluate the costs and design strategies of application, formation and diffusion of knowledge, and the education of the society.

The results will lay the basis of economic and social sustainable development, by means of a suitable planning and territorial arrangements, including not only the rational and sustainable use of the Earth, but also other natural resources. One of these is water resources that needs consideration for the arrangement of the hydrographic river basins and an integral management of these resources, as much as for the superficial water as well as underground water. All this will help, without a doubt, to promote a change in the social behavior of the involved area and the interrelated ones, by means of the opportune programs of information and education.

The authors' mathematical model named 'weighted PROMETHEE' is used for the generation processes, analysis, and evaluation of strategies of adaptation to the climatic change. It is supported by the use of multicriteria methods to aid decision making, developed by members of the GASC-UPM group based on the classic ELECTRE, PROMETHEE, and Analytic Hierarchy Process (AHP) method. It will be used to elaborate a General Plan of Adaptation to Climate Change, to serve as framework for the development as Regional Plans of Adaptation to Climate Change, management of water resources, and control of desertification.

The State Of The Art

Currently in most countries, international forums and institutions, universities, and research groups are studying methods and planning for the fight against climate change and, more recently, for adaptation to climate change. This has been possible thanks to the fact that groups of researchers have been trying to convince public opinion and the institutions that they must not expend efforts in the fight against climate change and that they have to divert them to the study of adaptation to climate change. However, still the majority of studies and models that are emerging target item to resolve specific problems and to predict the behavior of natural or human factors such as the elevation of the sea level, the increase in CO_2, etc., but without obtaining a global model that could give guidelines to make decisions appropriate in time and space.

The Framework Convention of the United Nations on Climate Change (UNFCCC) has created in most countries an Observatory or Commission on climatic change that is elaborating national plans of adaptation to climate change, but always on evaluation of impact on certain factors like water resources, biodiversity, the level of the sea, ozone layer, etc., without including any model like the one that is set out in this article (see European Commission, 2008; United Nations, 1992; Green Book (UE), 2007; Dresden, 2011).

The UNFCCC has organized annual conferences. In the last one (COP 15 – Copenhagen 2009, COP 16 – Cancun 2010, COP 17 – Durban 2011, COP 18 – Doha 2012, and COP 19 – Bonn 2013) only intention agreements have been obtained, but no imperative actions.

The Intergovernmental Panel on Climate Change was established in 1988 by the World Meteorological Organization and the United Nations Environment Program (UNEP). It has presented several reports about the causes and consequences of climate change but without an integral approach for adaptation.

Multicriteria analysis for climate change (MCA4climate) is a major new UNEP initiative providing practical assistance to governments in preparing their climate change mitigation and adaptation strategies (UNEP, 2011). It is designed to help governments, particularly in developing countries to identify policies and measures that are of low cost, environmentally effective, and consistent with national development goals. Many developing countries are still at an early stage of developing formal climate change policy plans and identifying specific nationally appropriate mitigation actions and national adaptation plans and actions.

This is a challenge for multicriteria decision analysis (MCDA). The principal way in which MCA4climate seeks to assist governments is through the application of the MCA4-climate policy evaluation framework – a powerful step-by-step analytical tool that has been developed by UNEP with assistance from international experts. This framework is based on a multicriteria analysis (MCA) approach – a well-established technique for identifying multiple impacts and aiding decision making. It ensures that the different dimensions of climate policies, including those that cannot be easily measured in monetary terms are taken into consideration. It also facilitates the engagement of stakeholders in the policy-planning process. Three case studies – Mumbai (in India), South Africa, and Sana'a Basin (in Yemen) – were carried out in order to demonstrate the practicalities of applying the framework.

The well-known Kyoto Protocol, not yet signed by all important countries, is focused, only to reduce CO_2 emissions.

There are organizations like Oxfam doing basic reports directed at the controversy on who causes CO_2 emissions and who has to pay the cost of reducing it, rich countries or poor countries. With the results of this article it will be possible to put in evidence affirmations interested or erroneous as well as to provide a greater social support on the proposed solutions (Oxfam, 2007).

The Forums of the Earth, also called UN Conference on Environment and Development, were held in Stockholm (Sweden) in 1972, Rio de Janeiro (Brazil) in 1992, and Johannesburg (South Africa) in 2002.

In the Rio Conference (Conference on Environment and Development, 1992) the participating countries agreed to adopt a development approach to protect the environment while ensuring economic and social development. At this summit, various documents were approved by 178 governments, which are as follows:

- Program 21: This is an action plan which aims at environmental and development goals in the twenty-first century.
- Rio Declaration on Environment and Development: Defining the rights and duties of States.
- Statement of principles on forests.
- Convention on Climate Change, Biodiversity, and Desertification.

The Earth Summit +5 took place in a Special Session of the General Assembly in 1997. The main objective was to analyze the implementation of Agenda 21 adopted at the Summit of 1992. After intense debate due to differences among States on how to finance sustainable development at the global level, various agreements were obtained, which were reflected in the final document of the session. These agreements are the following:

- To adopt legally binding targets for reducing emissions of greenhouse gases which are causing climate change.
- Move more vigorously toward sustainable patterns of production, distribution, and use of energy.
- Focus on poverty eradication as a prerequisite for sustainable development.

The World Summit on Sustainable Development, also known as the Johannesburg Summit (2002), was a follow up to Agenda 21 and its main objective was the adoption of specific commitments in relation to Agenda 21 and achieving sustainable development.

During 2001 a series of national consultations and preparatory meetings by regional and subregional organizations were conducted to assess the opportunities and challenges posed by sustainable development and to establish priorities, initiatives, and commitments needed to achieve this development.

The intergovernmental program was the central part of the summit, but attention was also paid to all sectors of the population who are committed to sustainable development, including those defined in Agenda 21, namely enterprise and industry, children and youth, farmers, indigenous people, local authorities, nongovernmental organizations, scientific and technological communities, women, workers, and unions.

Most countries, like Peru, are preparing National Plans for Climate Change adaptation and Risks management in Agricultural Sector (PLANGRACC) (see Agricultura Perú, Ministerio, 2011).

Methodology

The framework is based on a MCA approach that is a well-established technique for aiding decision making and it has already been successfully deployed in many areas of policy-making for the authors and other experts. The methodology uses a practical step-by-step tool for identifying and prioritizing mitigation and adaptation policies that are consistent with developmental goals. It ensures that all the different dimensions of climate policies, including those that cannot be easily measured in monetary terms, are taken into consideration. It also facilitates the engagement of stakeholders in the policy-planning process.

To test the models and to provide inputs to the general model, four case studies have been included.

Several steps have been established:

- To establish a consortium among mainly Research Groups of Europe and the Latin American countries to establish synergies that allow to obtain a common approach to develop and maintain the models.
- To create a climatological, edaphic, economic, sociological database, common for all the members, in compatible formats and scales to elaborate the initial matrix (IM).
- To analyze the present situation of the country members of the consortium in relation to the impacts of climate change, the battle against erosion and the management of water resources, and to forecast future scenes of climate change.
- To integrate in the model those models already made for erosion and desertification and those of integral management of water resources and planning, arrangement of hydrographic river basins, and urban waste management.
- To model the incidences of the possible solutions adopted in other areas with and without performance plans.
- To design and to reproduce material on the causes and effects of climatic change, incorporating the results of the project, to be distributed between local institutions and schools.
- To study the incidence that the project results will have in an improvement in the environment and with climatic change, education, sanitary improvement, and in the fight against poverty.
- To analyze the incidence that the integration of the society may have in the plans proposed by means of suitable campaigns of information, education, etc.
- To define case studies in relation to mitigation and adaptation actions to test different elements of the framework and to consider that the lessons learnt will be useful to the development of the overall model.
- To integrate the results of investigations made by the members of the partnership via a common model that will reduce costs, avoid duplications, enrich the knowledge, and make possible the development of the communities involved.

The actual 'climatic change,' activated more rapidly by emissions caused by humans, could have important effects on different countries that have diverse soils, populations, and use of lands. Let us consider a region that will support effects, maybe unfavorable with increase of temperature and decrease on rain. It is expected to require planning to change the actual status for adaptation to new situation or to mitigate its effects. For example, the change of use of lands can be made in different ways. In this case, the use of MCDA is required. The authors' experiences on multicriteria decision methods (MCDAM) and the application of some of these methods, in relation with climate change, are shown as cases studies located below. Some of the MCDAM, selected and used by authors, will be presented now in their main lines.

Multicriteria Decision Methods

MCDAM are models to aid decision making when there is a situation with several alternatives that should be optimized with respect to some criteria. The first thing to do, when applying a multicriteria approach to a project, is to analyze the feasible alternatives that exist. Then set the criteria and pseudocriteria and finally adopt the normalized weights that meet the decision maker preferences.

One criterion is used to discern if an alternative is at least as good as another to the decision maker. Usually, it is expressed by a value higher than zero. A criterion is called a pseudocriterion when the difference between the utility functions is higher than zero but small we cannot say that the alternative higher for that criterion preferred. Thresholds are involved here.

Pseudocriteria concept is widely used in the outranking methods. Preference threshold p and indifference threshold q are introduced for each criterion. They help the decision maker to show the preferences between alternatives.

The MCDAM can be continuous if the number of alternatives is infinite, with continuous functions to optimize and restrictions. When the number of alternatives and criteria are finite and generally small in number, the methods used are the discrete ones and within them, we have the outranking methods. They are based on knowing whether an alternative

dominates another or not. One should know if in relation to a criterion, an alternative is, at least, as good as another.

Following, the IM is elaborated. It is also called decisional matrix. It is a matrix formed by alternatives in rows and criteria in columns. They shall show utilities as positive numbers and a file will be added below with the weights of the standard criteria (sum 1) and another with the indexes, that will be $(+1)$ if that criterion is of the kind 'more is better' and (-1) if it is of the kind 'more is worse.'

Discrete Multicriteria Decision Methods are used in this article. The most important are the outranking methods. They consist of a compromise between the too poor dominance relation and the excessive ones generated by utility functions. The most significant methods in this area are ELECTRE due to B. Roy, PROMETHEE presented by Brans, and AHP by Saaty.

ELECTRE method

It is due to B. Roy, who in 1985 published 'Méthodologie multicritère d'Aide à la Décision' in the journal *Economica*. It is an acronym for Elimination Etchoix Traduisant la Realité. From that date Roy and his disciples were improving and getting new versions of the method ELECTRE I, they are II, III, IV, V, VI, and Tri. It is an outranking method that is based on the concepts of concordance and discordance. A threshold concept is introduced. Roy's team has developed in Paris an application software, although MATHCAD or other programs such as MATLAB or MAPLE can also be programmed for this use.

Standardized weights are applied to the criteria for setting decision-maker preferences. Dominance relations are put into a graph and alternatives that are not dominated and dominating others are included in the core. From these data, following the proposition (Roy, 1985), an alternative i outranks the alternative k, i.e., ELECTRE preferable to it, if two concordance and discordance conditions are both satisfied. For the first a concordance matrix should be obtained, from a decisional matrix 'standardized and weighted.' To consider discordance, a discordance matrix is also obtained.

PROMETHEE method

PROMETHEE methods are a family of Discrete Multicriteria Decision Aiding inside of the well-known outranking methods. J.P. Brans, professor at the University of Brussels, presented the PROMETHEE I and II methods in 1982. Brans and Vincke (1985) published an important paper on these methods. These methods are referred to as 'Initial PROMETHEE.' Brans and other authors added new methods to this family. One of them is named by the authors as 'Weighted PROMETHEE.' Brans, Vincke, and B. Mareschal published papers, a few years later and developed PROMETHEE III (ranking based on intervals) and IV (continuous case), and a software called PROMCALC and later PROMETHEE-GAIA and Visual PROMETHEE (Brans *et al.*, 1986; Brans and Mareschal, 1992a, 1994, 2002). In 1992 and 1994, Brans and Mareschal suggested PROMETHEE V (MCDA including segmentation constraints) and PROMETHEE VI (representation of the human brain) (Brans and Mareschal, 1992b, 1995). Other authors followed adding new methods to this family (Figueira *et al.*, 2004; Corrente *et al.*, 2013; Mousseau *et al.*, 2000). The most known and applied of PROMETHEE Methods are PROMETHEE I and II.

PROMETHEE is an acronym for Preference Ranking Organization Method for Enrichment Evaluation.

They used the concept of pseudocriterion as B. Roy and defined six types of pseudocriterion: type I: the usual, type II: quasicriterion, type III: with linear preference, type IV: level or in stairs, type V: with linear preference and indifference area and type VI: Gaussian.

They define a preference index. This index gives a measure of the preference of one alternative over other for all the criteria. From these indexes outgoing and incoming flows are defined. The outgoing flow is a measure of the dominance of one alternative over other. The incoming flow is the measure of how much that alternative is dominated.

The results in form named PROMETHEE I give a partial preorder from outgoing flow and ingoing flow, and in form PROMETHEE II a total order from the total flow that is the difference from both, outgoing minus ingoing.

The PROMETHEE III, IV, V, and VI, weighted, Tri, Cluster, etc. have other characteristics and applications. For example, V considers alternatives with restrictions and the weighted used weights, as done in this study.

Analytic hierarchy process method

It was presented by Saaty (1980). It is based on pairwise comparisons. It establishes three levels of comparison: the objective, alternatives, and criteria levels. It gets total weights and the heaviest alternative is preferred. The Saaty group has developed an excellent software, called Expert Choice, used in the Section Case Studies.

Case Studies

To obtain the inputs for the integral model the authors have studied different actions that have a high influence in climate change.

Territorial Planning in La Colacha River Basin (Córdoba Province, Argentina)

Introduction

Agriculture in developed countries must take into account food production, profitability, as well as environmental impacts. Environmental impact assessment covers infrastructure investment. Its integration in the decision-making process makes it an important environmental policy tool for influencing the location of projects. The river basin management plans will require coordination of all measures aimed at water protection including designation of catchment areas subject to or vulnerable to pollution from nutrients. To aid decision makers to adopt the best river basin management plans, the discrete multicriteria decision methods appear to be the most appropriate. La Colacha is a subbasin at the south of Arroyos Menores basin of Rio Cuarto city, formed by the junction of La Colacha and El Cipion streams, both being tributary of Santa Catalina stream (see **Figure 1**).

It includes an area of 416 km^2, which ranges between altitudes of 560 and 1000 m above sea level. The monsoon rainfall is on average at 830 mm $year^{-1}$, and is concentrated between October and April. The use of the land is mainly

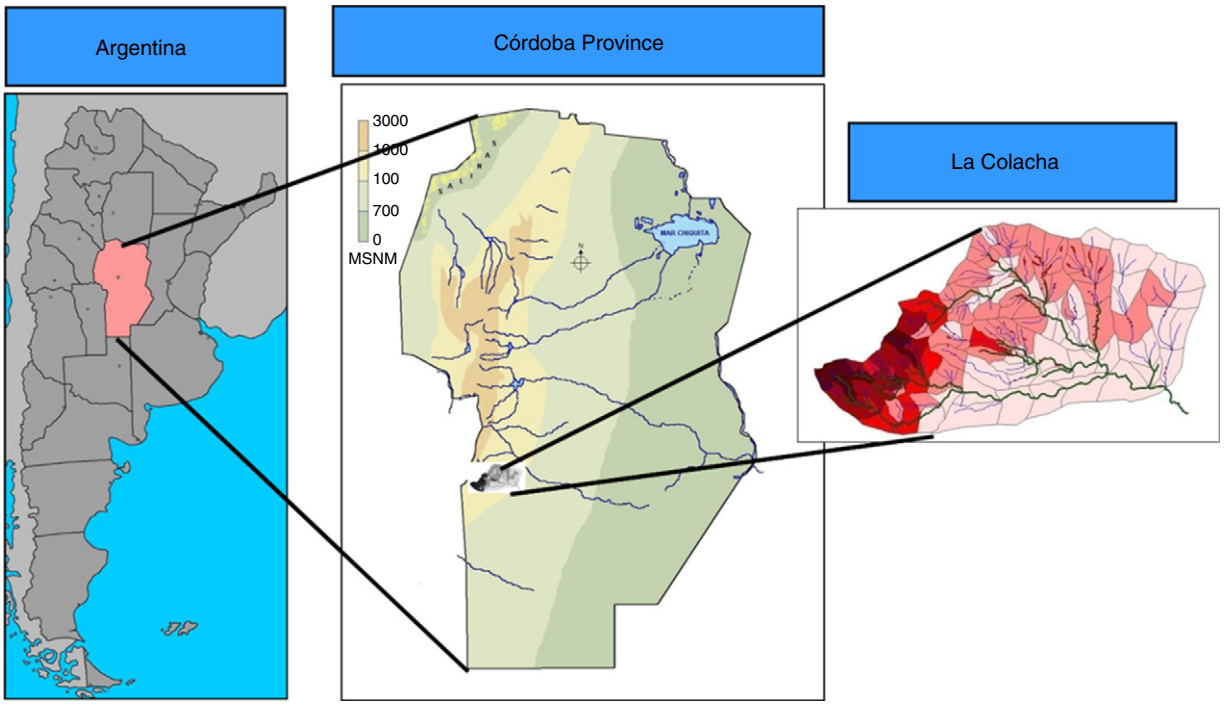


Figure 1 La Colacha basin in Argentina.



Figure 2 Gullies ('*cárcavas*') in La Colacha.

agricultural–livestock farming on the plains and extensive farming along the mountain ranges. The main degradation processes are the hydrologic erosion originating in furrows and with big gullies or ditches ('*cárcavas*') (see Figure 2), erosion in permanent rivers, and sediments being carried down to the lower basin areas.

Alternatives

Twelve alternatives (see Table 1) have been selected from the following combinations:

1. Land use.
   - Agrosilvopastoral use (ASP).
   - Actual soil use (ACT).
   - Intensive agricultural use (INT).
2. Soil conservation practices (SC): Use of techniques for erosion control and to reduce water pollution (terraces and filter strips).
3. River basin actions (HM): To reduce flooding, sediment, and contaminant load and avoid ditch and stream erosion.

Table 1 Twelve alternatives for La Colacha

No.	*Alternatives*	*Description*
1	ASP	Agrosilvopastrol use
2	ASP + SC	ASP with SC
3	ASP + HM	ASP with HM
4	ASP + SC + HM	ASP with SC and HM
5	ACT	Actual use (*status quo*)
6	ACT + SC	ACT with SC
7	ACT + HM	ACT with HM
8	ACT + SC + HM	ACT with SC and HM
9	INT	Intensive use (soybean)
10	INT + SC	INT with SC
11	INT + HM	INT with HM
12	INT + SC + HM	INT with SC and HM

Abbreviations: ACT, actual soil use; ASP, agrosilvopastoral use; HM, river basin actions; INT, intensive agricultural use; SC, soil conservation practices.

Criteria

Thirteen criteria and its respective weights have been applied to the 12 alternatives as follows:

- Field research,
- Expert panels,

- Social investigation, and
- Personal interviews.

The consequences of the alternatives would be felt from different points of view conducting to the adoption of the following criteria, that are enough independent, and that include all the possible effects. Their relative importance will be considered in discrete MCDM by setting sets of weights. Some criteria will get valuations from measures with units, and others are qualitative, and will get a qualifying index (*qi.*) of valuation in the range (1–10) of the kind 'more is better' as elicited by authors from their experience. All the criteria have indices I_j elements of a vector I, being $I_j=1$ if the criterion j is taken of the kind 'more is better' and being $I_j=-1$ if it is of the kind 'more is worse.'

Environmental criteria

1. Peak runoff (PRU), in $m^3\ s^{-1}$, is the maximum runoff of a basin for 80 mm rain in 6 h, that has an approximately 25 years return period, of the kind 'more is worse.' Runoffs were estimated with a model HEC-HMS (USACE (US Army Corp of Engineers), 2009). To estimate alternatively a basic winter volume of flow was found too imprecise and hence that different criterion was not used.
2. Average annual erosion (ERO), being the mean expected annual soil loss, in Mg ha^{-1} $year^{-1}$, assesses the sustainability of the use of soil with an alternative; hill-slope erosion. It is an indicator of long-term soil productivity and quality (Agrell *et al.*, 2004; Antoine *et al.*, 1997; Lakshminarayan *et al.*, 1995). The authors used RUSLE 2 (USDA-ARS, 2009) to estimate it, with aids for gullies such as by Dabney *et al.* (2008). It is of the kind 'more is worse.'
3. Sediment delivery (SED), in thousands of Mg (metric tons), indicates soil losses getting into a permanent stream, containing also pollutants, of the kind 'more is worse.' This was estimated using modified universal soil loss equation model (MUSLE model) (Williams, 1975), also for deposits in filter strips with (Muñoz-Carpena and Parsons, 2005). Measured differently from ERO.
4. Index of Environmental Quality (CAM), is in (qi.) range, of the kind 'more is better,' derived in the ways of Gómez Orea (1999), by considering the percentage of area for pasture, the percentage for agriculture, diversity in the types of vegetation, characteristics of streams, biodiversity, scenic attributes of landscape, margins and corridors with trees. This is adapted to be used to compare alternatives, not to compare basins.

Economic criteria

1. Investment (INV), in millions of argentine pesos (ARS). It is of the kind 'more is worse,' deduced from the cost of possible actuations in the subbasin. It was transformed into an annuity in standard ways, not differentiating between public and private sources. The opportunity cost under Argentine conditions was taken as 12%.
2. Maintenance (MAN), in millions of ARS $year^{-1}$, of the kind 'more is worse,' being the annual cost for reparation of works and rural roads, and estimated for roads with peak runoff (De Prada *et al.*, 1994).
3. Loss of agrosurface is the percentage of the agrosurface, of the kind 'more is worse,' estimated from HEC-HMS and VFSMOD (Muñoz-Carpena and Parsons, 2005). It is an important concept for such good large agrolands.
4. Benefits (BEN), in ARS ha^{-1} $year^{-1}$, being private and short term, of the kind 'more is better,' from the margin in a typical exploitation (De Prada *et al.*, 2008). The crop-weighted gross margin and the cost values were considered at 2010 prices. A monoculture may increment BEN and degrade more soil, but it influences farmers' decisions (Groot *et al.*, 2007; Gil *et al.*, 2008).

Social criteria

1. Ease for implementation (FIM), of the kind 'more is worse' for the MCDM in this article, is taken as the 'time needed for actions' (Degioanni *et al.*, 2000); sometimes indicated otherwise in the form of an (id.) as in Grau *et al.*, (2008, 2009), Anton *et al.* (2010), or otherwise as in Gonçalvez *et al.* (2007).
2. Externalities (EXT), of the kind 'more is worse,' are the effects of agriculture in other ecosystems, mainly caused from erosion of water from plots and used for multicriteria studies (De Prada *et al.*, 2008; Paneque Salgado *et al.*, 2006), effects on wetlands below (Cantero *et al.*, 1998; De Prada and Penna, 2009), and on roads (Cristeche, 2009).
3. Social acceptability (ACE) is necessary for regional planning, (e.g., see Zhen *et al.*, 2007), and includes sensibility to environment effects such as in Smith and McDonald, (1998) and considers remediation techniques (Gil *et al.*, 2008), as measured in Grau *et al.* (2008, 2009) with a valuation of 'more is better' scale as (*qi.*) in the range (1–10).
4. Employment impact (EMP), as measured by the number of jobs generated by the alternative. This is a principal social criterion and considered of the kind 'more is better.' The employment estimates considered the labor requirements of each crop rotation and forestation. This was used similarly with multicriteria in Grau *et al.* (2008, 2009), Simonovic and Akter (2006), and Paneque Salgado *et al.* (2006). This was estimated following Llach *et al.* (2004), depending on the type of activity and on the yields of the crops.
5. Legislation in force (LEG) is to be in accordance with adopting the solutions in an alternative, and it was measured by a valuation (*qi.*) in the range (1–10) 'more is better' scale. The *status-quo* alternative ACT is well for LEG, and actually INT is also well. The conservation of soils is backed by law (Law 8359, Arg., for conservation of soils), but action is voluntary and scarce (Cristeche, 2009). The alternative ASP when shifting from farming to forest has legal difficulties, and also hydraulic management often needs expropriation of lands.

Multicriteria methods applied

The following discrete MCDM have been applied:

- ELECTRE I, see Roy (1985), Roy and Bouyssou (1993).
- For initial PROMETHEE, see Brans and Vincke (1985), Brans *et al.* (1986); from it is derived the adopted weighted PROMETHEE, which seems preferable to introduce indication of relative importance of criteria, for it see Brans and

Mareschal (1994); it has been used previously by authors, see Anton *et al.* (2006, 2010) and Grau *et al.* (2008, 2009).
- AHP, see Saaty (1980, 1996a,b).

Initial matrix

Following the studies to prepare the doctoral thesis (Cisneros, 2010), the authors have the IM (see **Table 2**).

Systems of weights

The methods ELECTRE and weighted PROMETHEE depend on the weights for the respective criteria by elicitation using experience (Grau *et al.*, 2010). There is some literature on the methods to obtain these elicitations and some of them are used also in common software, but that requires comparing for calibration with other well-confirmed valuations of results, which were inexistent here. Three sets of weights that are given in **Table 2** have been used:

1. Based on an entropy method as in Zeleny (1982), Barba-Romero and Pomerol (1997), and Zhen *et al.* (2007). They were deduced from the IM of **Table 2**. The authors did a comparison, in a precedent case, with elicited weights and have felt that the resulting weights did not change essentially. These weights result were favorable for the environment criteria; they were used considering an 'environment trend.'
2. Based on equilibrium, all the criteria have similar weights, $1/13 = 0.77$ (or 0.769230…) in **Table 2**. These weights are in comparison more favorable for social criteria, they were used considering a 'social trend.'
3. Compromised for economy, is influenced by the fact that the farmer follows mainly that trend (Gil *et al.*, 2008), giving more weight to benefits, and eliciting the others as in **Table 2**. They were used considering an 'economic trend.'

In **Table 2**, the weights with entropy are oriented for environment, the weights inclined for benefits are more of economic kind, and with equivalent weights the trend is toward considering social effects. All these weights were already normalized so as to get one.

ELECTRE method

For La Colacha with ELECTRE does not get complete classifications and the alternative ASP + SC + HM is best for environmental and for social weights. After that is the ACT + SC + HM, but economic weights give preference for INT + SC + HM and for lower thresholds also to INT + SC, and for equilibrium weights other alternatives enter, ASP + SC and for lower thresholds ASP + HM and INT + SC. All the alternatives in kernels have some SC or HM. The graph and Kernel are shown in **Figure 3**.

PROMETHEE methods

When using MCDAM for these study areas the authors use different criteria and different weights. Hence, the results are more with weighted PROMETHEE than with nonweighted ones.

In **Figure 4** the results obtained using Weighted PROMETHEE I and II programmed by MATHCAD is shown. With Weighted PROMETHEE II the alternative 6 (ACT + SC) has a maximum total flux of 0.839, i.e., it is preferred.

Table 2 Initial matrix for La Colacha

			Criteria												
			1 PRU	*2 ERO*	*3 SED*	*4 CAM*	*5 INV*	*6 MAN*	*7 SAG*	*8 BEN*	*9 FIM*	*10 EXT*	*11 ACE*	*12 EMP*	*13 LEG*
Alternatives	1	ASP	337.2	4.2	11.4	6.2	2.3	0.3	41.9	603.7	5.0	30.5	5.0	854.5	6.0
	2	ASP + SC	278.1	1.7	4.2	6.6	2.7	0.4	41.9	629.7	9.0	25.1	8.0	854.5	4.0
	3	ASP + HM	242.7	3.3	3.0	6.4	3.4	0.6	41.9	603.7	6.0	21.9	6.0	861.9	5.0
	4	ASP + SC + HM	213.2	1.0	1.2	6.7	3.9	0.6	41.9	629.7	13.0	19.3	8.0	861.9	3.0
	5	ACT	420.5	7.3	23.5	4.6	0.3	0.1	21.0	661.0	1.0	38.0	7.0	382.0	9.0
	6	ACT + SC	353.3	3.5	9.7	5.0	0.9	0.2	21.0	705.6	4.0	31.9	9.0	382.0	7.0
	7	ACT + HM	278.8	4.7	4.9	4.8	1.4	0.3	21.0	661.0	4.0	25.2	6.0	389.5	6.0
	8	ACT + SC + HM	249.8	1.3	1.7	5.0	2.0	0.4	21.0	705.6	8.0	22.6	9.0	389.5	5.0
	9	INT	477.3	9.2	33.9	3.6	0.4	0.1	13.0	785.7	3.0	43.1	6.0	382.7	8.0
	10	INT + SC	401.6	3.9	11.2	4.1	1.2	0.3	13.0	823.2	6.0	36.3	8.0	382.7	7.0
	11	INT + HM	298.8	6.2	7.3	3.8	1.5	0.3	13.0	785.7	6.0	27.0	7.0	390.1	7.0
	12	INT + SC + HM	271.8	1.4	1.9	4.1	2.3	0.5	13.0	823.2	10.0	24.6	5.0	390.1	5.0
Systems of weights (W_j)		Entropy weights (Environmental trend)	0.045	0.112	0.209	0.043	0.108	0.077	0.080	0.036	0.089	0.045	0.041	0.066	0.049
		Equilibrium weights (Social trend)	0.077	0.077	0.077	0.077	0.077	0.077	0.077	0.077	0.077	0.077	0.077	0.077	0.077
		Economy weights (Economic trend)	0.045	0.113	0.077	0.043	0.108	0.036	0.08	0.21	0.089	0.042	0.041	0.066	0.049
		(I_j) - Indexes	−1	−1	−1	+1	−1	−1	−1	+1	−1	−1	+1	+1	+1

Abbreviations: ACE, social acceptability; ACT, actual soil use; ASP, agrosilvopastoral use; BEN, benefits; CAM, index of environmental quality; EMP, employment impact; ERO, average annual erosion; EXT, externalities; FIM, ease for implementation; HM, river basin actions; INV, investment; INT, intensive agricultural use; LEG, legislation in force; MAN, maintenance; PRU, peak runoff; SAG, loss of agrosurface; SC, soil conservation practices; SED, sediment delivery.

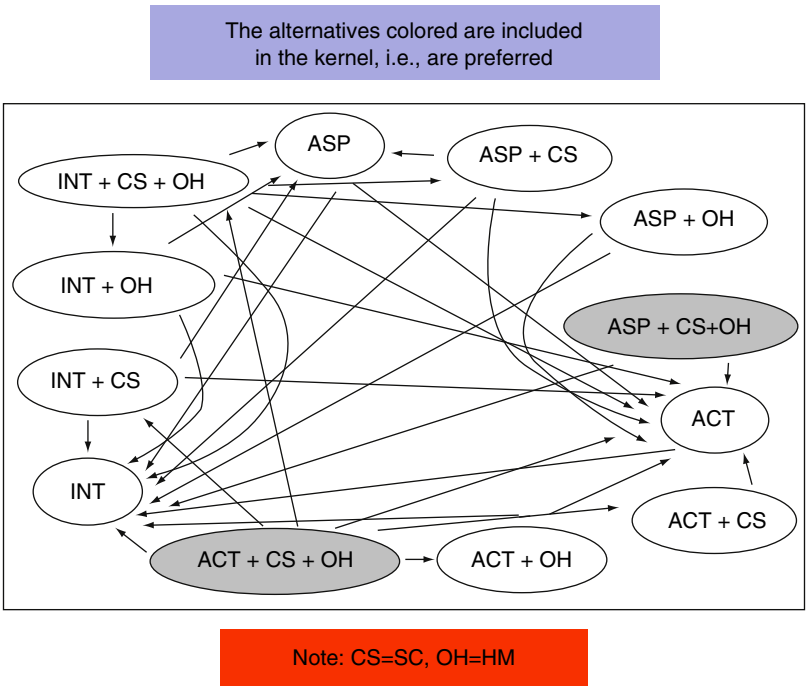


Figure 3 Graph and kernel (ELECTRE) for La Colacha. ACT, actual soil use; ASP, agro-silvo-pastoral use; HM, river basin actions; INT, intensive agricultural use; SC, soil conservation practices.

In Figure 5 the results obtained using Initial Brans PROMETHEE II programmed by MATHCAD are shown.

In Figure 6 the results obtained using Brans Initial PROMETHEE I programmed with MATHCAD8PRO are shown. A partial preorder has been obtained and the alternative 6, 2, and 4 are incomparable but 6 dominates more and it would be preferred.

Analytic hierarchy process method

The authors have used the Expert Choice PC software, by introducing pairwise comparisons of the criteria with relative considerations as for the weights of Table 2. In Figure 7, the EXPERT CHOICE graphical interface shows the results.

It can be seen from Figure 7 that the alternative 4 (ASP + SC + HM) is the preferred one.

Conclusions

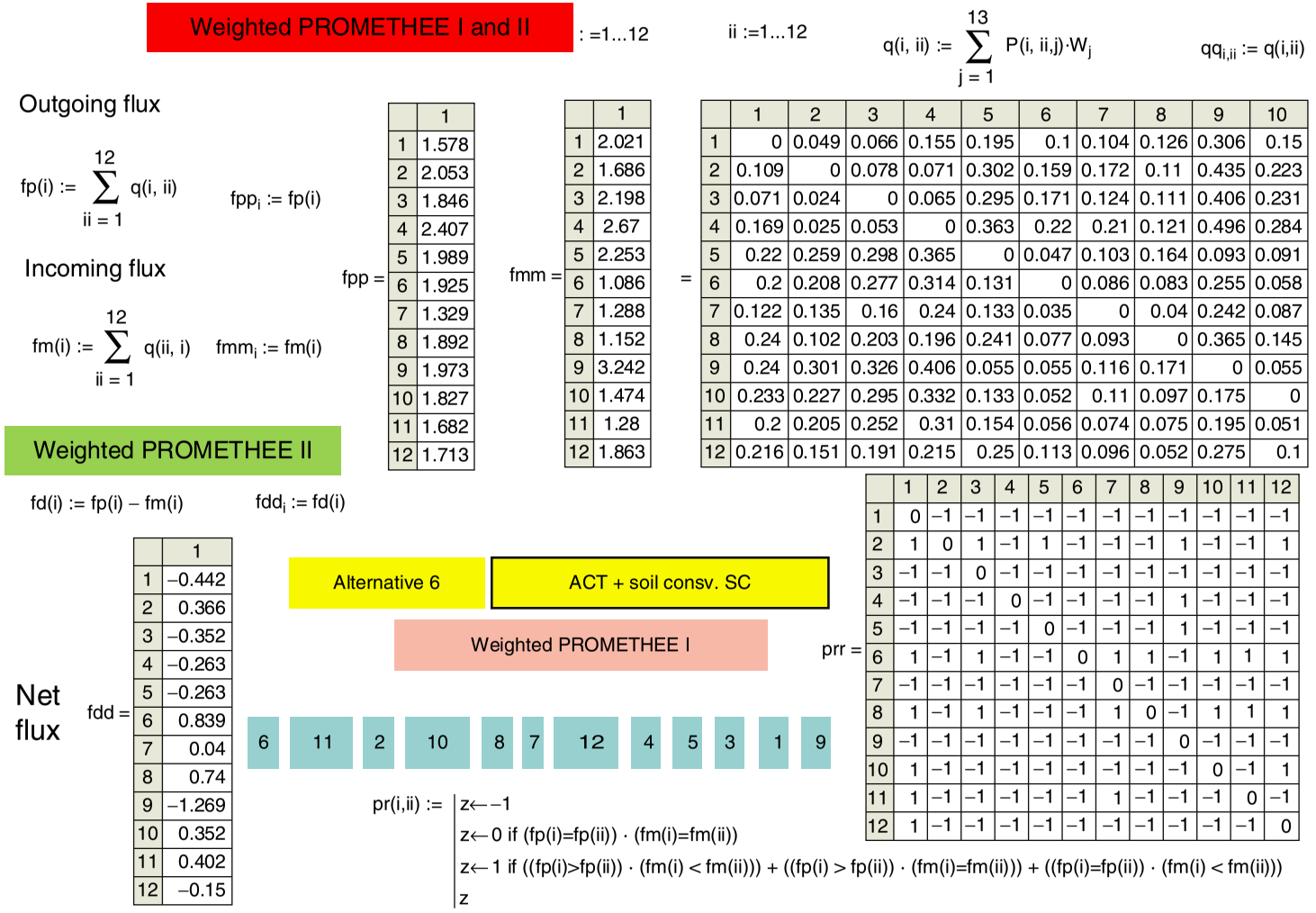
A combined extract from these results with discrete multicriteria methods is given in Table 3.

There are some variations with methods or with trends through systems of weights, but in general the SC and the actions for Hydraulic Management HM are recommended together, and if only one SC enters before HM. Moreover, the weighted PROMETHEE method is favorable to ACT, and the ELECTRE also, but more to ASP or INT depending more on weights due to the effect of discordances. The authors found ELECTRE better for the present studies, but the results of weighted PROMETHEE are in a more clear form, for every alternative, as in Figure 4 that includes results obtained with MATHCAD. The results of the different AHP are compatible with the adaptation from the IM used in the other methods as an indication to assess preference levels for pairwise comparisons about the criteria, and it gives comprehensive graphic results as in Figure 7 favorable for environmental criteria. With the weights with the trend for Economy the alternatives with INT become more important, but not with all methods.

The examination of such tradeoffs indicates that the alternative ACT + SC + HM is more efficient as being preferable for almost all the criteria, and that the alternatives ASP and INT are differently less efficient. These comparisons are best expressed using the discrete MCDAM to get influence of all the criteria.

The authors have considered in the studies the effects of changes in alternatives for plots, naming them tradeoffs and obtaining numerically various results, which is commented as:

1. A total change from ACT to INT would deteriorate all environmental criteria variables, some 15% in PRU, 26% in ERO and CAM, and 44% in SED, increasing costs included in INV and in MAN, the cost of maintaining roads in 44%, the offer of agrolands up to 60%, and the income of land operators in 18%. In social criteria, EXT would worsen by 16%, also LEG and EMP through a more mechanized production.
2. Changing from ACT use of soil to ASP improves the environment and social criteria variables at a serious cost in economic variables, reducing favorably (PRU, ERO, and SED) and increasing the CAM index. That would require high INV and MAN, the loss of many hectares of agrosurface and of some BEN. The EXT would be reduced in good sense the employment, EMP would increase considerably.
3. Changing ACT to ACT + SC, making soil conservation works maintaining actual use of lands, will ameliorate



	1
1	1.578
2	2.053
3	1.846
4	2.407
5	1.989
6	1.925
7	1.329
8	1.892
9	1.973
10	1.827
11	1.682
12	1.713

	1
1	2.021
2	1.686
3	2.198
4	2.67
5	2.253
6	1.086
7	1.288
8	1.152
9	3.242
10	1.474
11	1.28
12	1.863

	1	2	3	4	5	6	7	8	9	10
1	0	0.049	0.066	0.155	0.195	0.1	0.104	0.126	0.306	0.15
2	0.109	0	0.078	0.071	0.302	0.159	0.172	0.11	0.435	0.223
3	0.071	0.024	0	0.065	0.295	0.171	0.124	0.111	0.406	0.231
4	0.169	0.025	0.053	0	0.363	0.22	0.21	0.121	0.496	0.284
5	0.22	0.259	0.298	0.365	0	0.047	0.103	0.164	0.093	0.091
6	0.2	0.208	0.277	0.314	0.131	0	0.086	0.083	0.255	0.058
7	0.122	0.135	0.16	0.24	0.133	0.035	0	0.04	0.242	0.087
8	0.24	0.102	0.203	0.196	0.241	0.077	0.093	0	0.365	0.145
9	0.24	0.301	0.326	0.406	0.055	0.055	0.116	0.171	0	0.055
10	0.233	0.227	0.295	0.332	0.133	0.052	0.11	0.097	0.175	0
11	0.2	0.205	0.252	0.31	0.154	0.056	0.074	0.075	0.195	0.051
12	0.216	0.151	0.191	0.215	0.25	0.113	0.096	0.052	0.275	0.1

	1
1	−0.442
2	0.366
3	−0.352
4	−0.263
5	−0.263
6	0.839
7	0.04
8	0.74
9	−1.269
10	0.352
11	0.402
12	−0.15

	1	2	3	4	5	6	7	8	9	10	11	12
1	0	−1	−1	−1	−1	−1	−1	−1	−1	−1	−1	−1
2	1	0	1	−1	1	−1	−1	−1	1	−1	−1	1
3	−1	−1	0	−1	−1	−1	−1	−1	−1	−1	−1	−1
4	−1	−1	−1	0	−1	−1	−1	−1	1	−1	−1	−1
5	−1	−1	−1	−1	0	−1	−1	−1	1	−1	−1	−1
6	1	−1	1	−1	−1	0	1	1	−1	1	1	1
7	−1	−1	−1	−1	−1	−1	0	−1	−1	−1	−1	−1
8	1	−1	1	−1	−1	−1	1	0	−1	1	1	1
9	−1	−1	−1	−1	−1	−1	−1	−1	0	−1	−1	−1
10	1	−1	−1	−1	−1	−1	−1	−1	−1	0	−1	1
11	1	−1	−1	−1	−1	−1	1	−1	−1	−1	0	−1
12	1	−1	−1	−1	−1	−1	−1	−1	−1	−1	−1	0

Figure 4 Results with weighted PROMETHEE I and II methods for La Colacha.

$$q(i, ii) := \sum_{j=1}^{13} \frac{P(i,ii,j)}{12}$$

$qq_{i,ii} := q(i,ii)$

qq =

	1	2	3	4	5	6	7	8	9	10	11	12
1	0	0.053	0.072	0.168	0.211	0.108	0.113	0.136	0.331	0.162	0.156	0.197
2	0.118	0	0.084	0.077	0.327	0.172	0.187	0.119	0.471	0.242	0.21	0.215
3	0.077	0.026	0	0.07	0.319	0.185	0.134	0.121	0.439	0.25	0.198	0.179
4	0.183	0.027	0.057	0	0.393	0.238	0.228	0.131	0.537	0.308	0.272	0.233
5	0.238	0.281	0.322	0.395	0	0.051	0.112	0.178	0.101	0.098	0.115	0.262
6	0.217	0.226	0.299	0.34	0.142	0	0.093	0.09	0.276	0.063	0.106	0.233
7	0.132	0.146	0.173	0.26	0.144	0.038	0	0.043	0.261	0.094	0.034	0.11
8	0.259	0.11	0.219	0.213	0.261	0.083	0.101	0	0.395	0.157	0.132	0.116
9	0.26	0.326	0.353	0.44	0.06	0.06	0.126	0.185	0	0.059	0.067	0.2
10	0.252	0.245	0.319	0.359	0.144	0.057	0.119	0.105	0.189	0	0.037	0.15
11	0.216	0.222	0.272	0.336	0.166	0.061	0.08	0.082	0.211	0.055	0	0.119
12	0.234	0.163	0.207	0.232	0.27	0.122	0.104	0.057	0.298	0.108	0.058	0

Outgoing flux $fp(i) := \sum_{ii=1}^{12} q(i, ii)$ $fpp_i := fp(i)$

Incoming flux $fm(i) := \sum_{ii=1}^{12} q(ii, i)$ $fmm_i := fm(i)$

fpp =

	1
1	1.708
2	2.222
3	1.997
4	2.605
5	2.153
6	2.083
7	1.438
8	2.048
9	2.135
10	1.977
11	1.82
12	1.854

fmm =

	1
1	2.187
2	1.825
3	2.379
4	2.89
5	2.438
6	1.175
7	1.394
8	1.247
9	3.508
10	1.596
11	1.386
12	2.016

Net flux

$fd(i) := fp(i) - fm(i)$

Initial BransPROMETHEE II

$fdd_i := fd(i)$ fdd =

	1
1	−0.479
2	0.397
3	−0.381
4	−0.284
5	−0.285
6	0.908
7	0.043
8	0.801
9	−1.373
10	0.381
11	0.435
12	−0.162

Total preorder:

6 → 8 → 11 → 2 → 10 → 7 → 12 → 4 → 5 → 3 → 1 → 9

Alternative 6 is preferred

Figure 5 Results with Brans Initial PROMETHEE II methods for La Colacha.

environment variables, much (SED and ERO) and less (PRU and CAM). In economic variables the costs INV and MAN would increase much, ameliorating a little BEN through lesser losses of soil and water. In social criteria, EXT would be favorably reduced, the farmers would be against the change but the society would appreciate it ameliorating ACE criteria. Concerning LEG there is a law promoting this change, but that action depends on the will on land owners, and they have very few adhered to it.

4. The change from ACT to ACT + HM, affecting hydrological management maintaining actual use of lands, would require public investment in agro-infrastructure engineering, protection of streams, permanent or transitory, and rehabilitation of wetlands, mostly by microdams. That will ameliorate environmental criteria variables (SED, ERO, PRU, and CAM), the HM works being more efficient than the SC ones in reducing PRU and SED and less ERO and CAM. The HM requires severely higher INV and MAN than SC, and would have (if setting only microdams and no irrigation that is not evident here) no effect on BEN. In social values, EXT would increase more than with CS and also EMP at little values.
5. With both CS and HM effectuated, all the environmental values would increase, (SED, ERO, PRU, and CAM) at big costs, INV and MAN, increasing a bit BEN. That would cause problems with FIM and LEG criteria as the solution is complicated and with different acceptations ACE and requiring use of all natural resources of basin and mixed private and public action.

Election of Water Resources Management Entity

Introduction

In the twenty-first century, water resources (WR) are one of the top priorities worldwide. This is not only due to the need of this element for each one of the society sectors (agriculture, industry, residential use, etc.) but also due to its great variability in time and space. The consequences of the lack, as well as the excess can be dangerous, as the loss of productions by catastrophic floods and landslides. Besides, water pollution due to uncontrolled drainages carries out strong consequences for people's health, and also for the extinction of the natural habitat and the environmental risks.

In most countries, the worry for the knowledge of the existent WR and its integral dealing has recently started within four fields: (1) The transformation into irrigable land, of huge extensions of dry land, due to a bigger demand of agriculture products, (2) the usage of water for leisure and tourism purposes, as in large areas where water was not used, the population has increased strongly by a factor of 10, having installed golf courses, tourist, and residential areas, (3) bigger concerns

Initial Brans PROMETHEE I

pr(i,ii) :=
z← −1
z← 0 if (fp(i)=fp(ii)) · (fm(i)=fm(ii))
z← 1 if ((fp(i)>fp(ii)) · (fm(i) < fm(ii))) + ((fp(i) > fp(ii)) · (fm(i)=fm(ii))) + ((fp(i)=fp(ii)) · (fm(i) < fm(ii)))
z

prr =

	1	2	3	4	5	6	7	8	9	10	11	12
1	0	−1	−1	−1	−1	−1	−1	−1	−1	−1	−1	−1
2	1	0	1	−1	1	−1	−1	−1	1	−1	−1	1
3	−1	−1	0	−1	−1	−1	−1	−1	−1	−1	−1	−1
4	−1	−1	−1	0	−1	−1	−1	−1	1	−1	−1	−1
5	−1	−1	−1	−1	0	−1	−1	−1	1	−1	−1	−1
6	1	−1	1	−1	−1	0	1	1	−1	1	1	1
7	−1	−1	−1	−1	−1	−1	0	−1	−1	−1	−1	−1
8	1	−1	1	−1	−1	−1	1	0	−1	1	1	1
9	−1	−1	−1	−1	−1	−1	−1	−1	0	−1	−1	−1
10	1	−1	−1	−1	−1	−1	−1	−1	−1	0	−1	1
11	1	−1	−1	−1	−1	−1	1	−1	−1	−1	0	−1
12	1	−1	−1	−1	−1	−1	−1	−1	−1	−1	−1	0

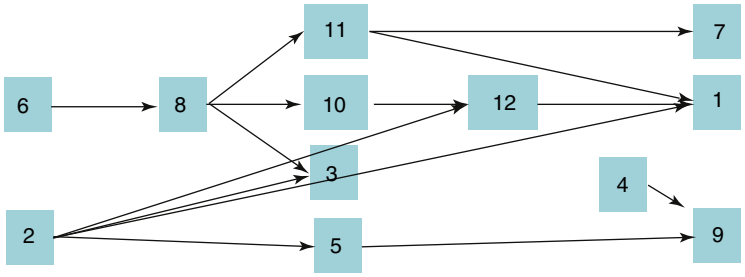


Figure 6 Results with Initial BransPROMETHEE I Methods for La Colacha.

about environmental issues, and (4) the mass-media pressure that derives from climate change.

For all that, new laws and rules for surface water and groundwater are coming up, as well as the creation of organism to watch, standardize, and manage the water resource use. However, there is a problem that it is not always easy to deal with, as the competences are spread and in many cases are confronted, being more important political and competence subjects than rational, technical, and economic.

In Valencia (Spain), 'El Tribunal de las Aguas' ('The Water Jury') exists for more than 500 years, functioning as a model that is unique in the world. This model cannot be exported to other parts of the world due to the international intercommunity relationships. In the limit one should have a special entity worldwide that could cope with all the competences and to delegate some of them to other national entities. The ideal is not reachable, but we must arrive as close as possible and we will minimize the distance. A model needs to be found that can be adapted to the characteristics of each area (see Grau, 2003; Romero, 1993).

The Salta Province covers 155 000 km^2 and has a population of 1 million. It is in the North West of Argentina (NOA), having latitudes around 25° S. It has rain from 400 to 800 mm $year^{-1}$ (with peaks of 1200 in high altitude places in SW) and great ranges of altitude (at NE are areas at 200 m and at NW a PUNA region with summits higher than 6000 m. It has a low density of population in small cities located in important long mountain valleys, and has low standards for roads and an environment that is 'deteriorating progressively.'

The Bermejo River is the most important fluvial artery in the area. The majority and the more important rivers flowing out of the Paraná drain through this region, such as Pilcomayo, San Francisco that flows into Bermejo, Juramento, or Salado. The Horcones and the rest like Itiyuro, Rio Seco, Dorado, Del Valle streams, etc., have less water but very important for the Province, end in marshlands, generating wet areas. The lack of water is a characteristic of the whole region. Rainfall is concentrated in the summer time. The rainfall presents a strong fall, from 1200 mm $year^{-1}$ in the east to 300 mm in the Southwest. In the Northeast it goes up to 1200 mm. The groundwater resources are poor in volume and quality (salty and with arsenic). It is possible to find good quality groundwater but at deep levels (100 m) with high operating costs.

Water is the most critical factor, as much for human and animal consumption, as for the production system in general. For that reason, it is so important to define an official entity for managing the WR, in order to consider all the aspects related with data control and water management since its capture till it is used, as well as those in relation to the social, cultural, and

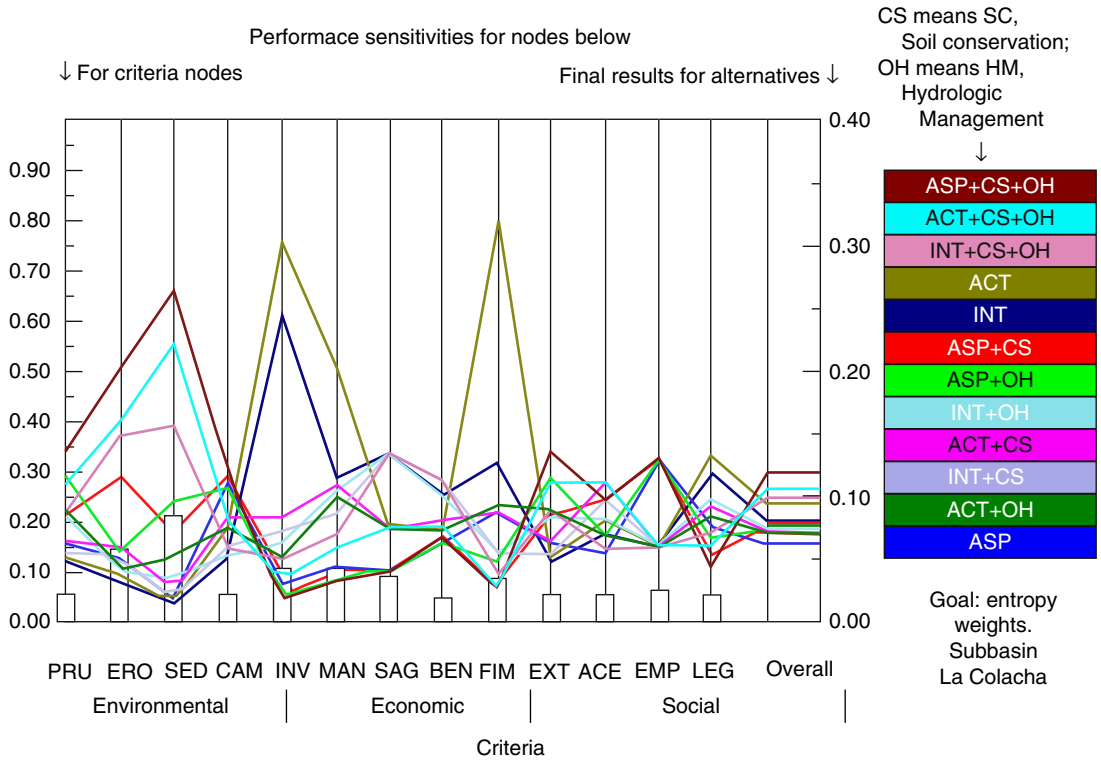


Figure 7 Results with Analytic Hierarchy Process using Expert Choice Software.

Table 3 Results with discrete multicriteria methods

		Systems of weights (Trends)		
		Environmental	*Social*	*Economic*
Discrete MCDM Methods	ELECTRE	Alternative 4 (ASP + SC + HM)	Alternative 4 (ASP + SC + HM)	Alternative 12 (INT + SC + HM)
	Initial PROMETHEE		Alternative 6 (ACT + SC)	
	Weighted PROMETHEE	Alternative 6 (ACT + SC)	Alternative 8 (ACT + SC + HM)	Alternative 10 (INT + SC)
	AHP	Alternative 4 (ASP + SC + HM)	Alternative 4 (ASP + SC + HM)	Alternative 12 (INT + SC + HM)

Abbreviations: ACT, actual soil use; AHP, analytic hierarchy process; ASP, agrosilvopastoral use; HM, river basin actions; INT, intensive agricultural use; MCDM, multicriteria decision making; SC, soil conservation practices.

economic substratum, where they must be applied. The management of water must include both the surface water and groundwater. An effort should be made in seeking the best way of extraction and usage in low cost and to implement good management and the best practices.

Multicriteria methods applied

Alternatives, criteria, and initial matrix

The data that were included in our IM were obtained from the conclusions of meetings held in Salta (Argentine) in 2004. Following those conclusions five alternatives were finally selected: Public Entity, Institute, Foundation, Cooperative, and Private Company. Besides, five criteria were considered relevant: Implementation Facility, Implementation Delay, Legislation in Force, Social Acceptance, and Flexibility. To fix the weights two expert commissions were created. The order of preferences given was different and more meetings were needed to fix them. In September 2007, the authors obtained the following weights and the filled decisional matrix is shown in **Table 4** (Antón *et al.*, 2003; Anton *et al.*, 2004; Jamshidi *et al.*, 2003; Keeney and Raiffa, 1976; Zeleny, 1982; Yu, 1985; Antón *et al.*, 2007; Munda, 1995). The criteria were rated on a 1–10 scale, according to local evaluations, and other methods of elicitation except implementation delay.

ELECTRE I method

In the first place, the ELECTRE I Method is applied with the MATHCAD program (see **Figures 8–10**). In these figures, the Decisional Matrix, standardized weights, indexes, concordance matrix, discordance matrix, concordance and discordance thresholds, and the aggregated dominance matrix are shown.

Table 4 Initial matrix

		Criteria				
		1 Implementation facility (qi.)	*2 Implementation delay (days)*	*3 Legislation in force (qi.)*	*4 Social acceptance (qi.)*	*5 Flexibility (qi.)*
Alternatives	1 Public entity	8	12	10	5	5
	2 Institute	7	18	8	6	6
	3 Foundation	6	18	7	7	7
	4 Cooperative	7	20	7	8	8
	5 Private company	6	15	5	4	9
Weights (adding 1)		0.30	0.10	0.15	0.20	0.25
Indexes		+1	−1	+1	+1	+1

Note: +1 is 'more is better' and −1 is 'more is worst'.

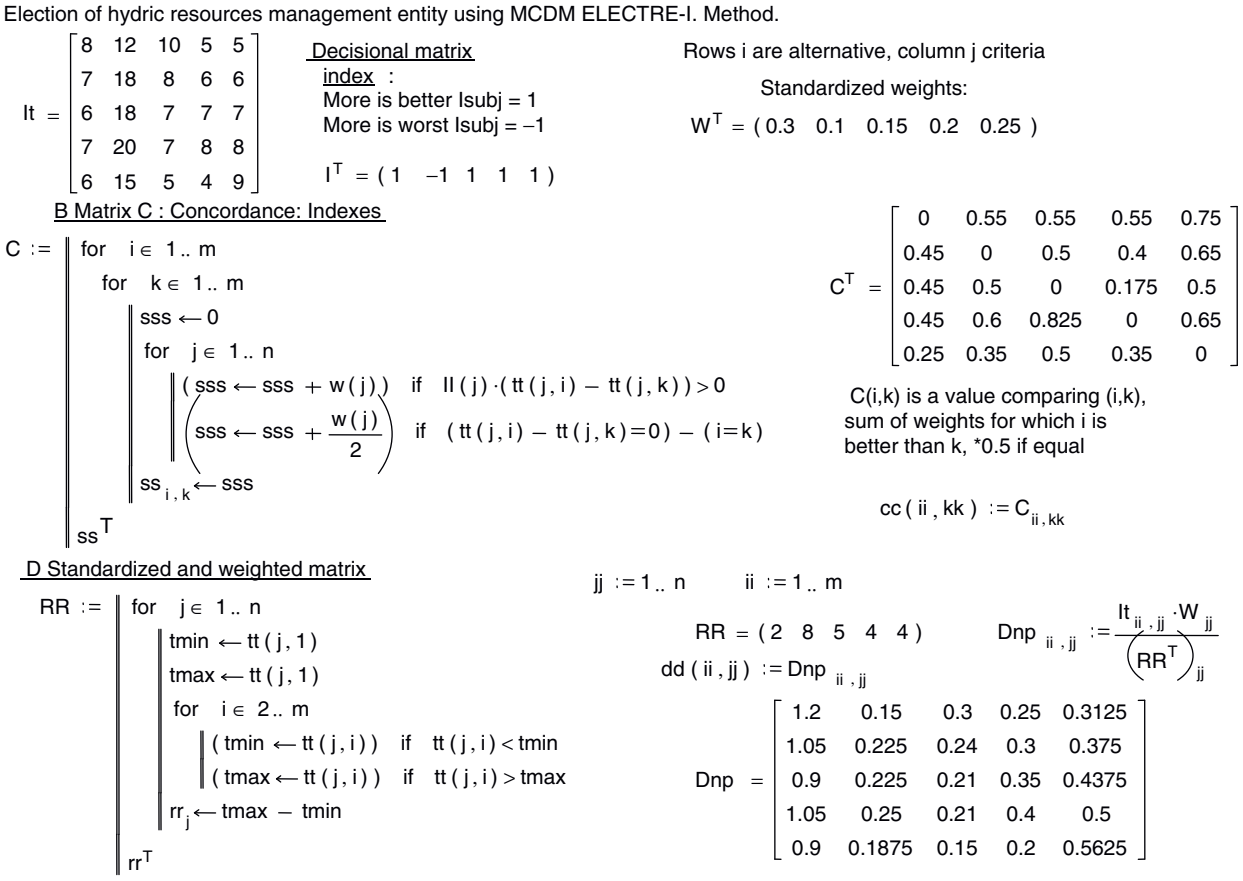


Figure 8 ELECTRE I with MATHCAD (part 1).

Finally, the Public Entity and the Cooperative are in the kernel. For that, both are preferred, but at the same level.

Analytic hierarchy process method

The results, obtained using the AHP Method, are shown in Table 5. It can be seen that the higher global weight is 0.2166903, i.e., the Cooperative is obtained as the first option.

PROMETHEE methods

Following Brans and Vincke (1985) the results in Table 6 are obtained. With PROMETHEE II the higher Phi (Net flux) corresponds to Cooperative, i.e., Cooperative Alternative is preferred. With PROMETHEE I Public Entity and Cooperative are incomparable.

Using the MATHCAD program, the results for weighted PROMETHEE in Figure 11 are obtained.

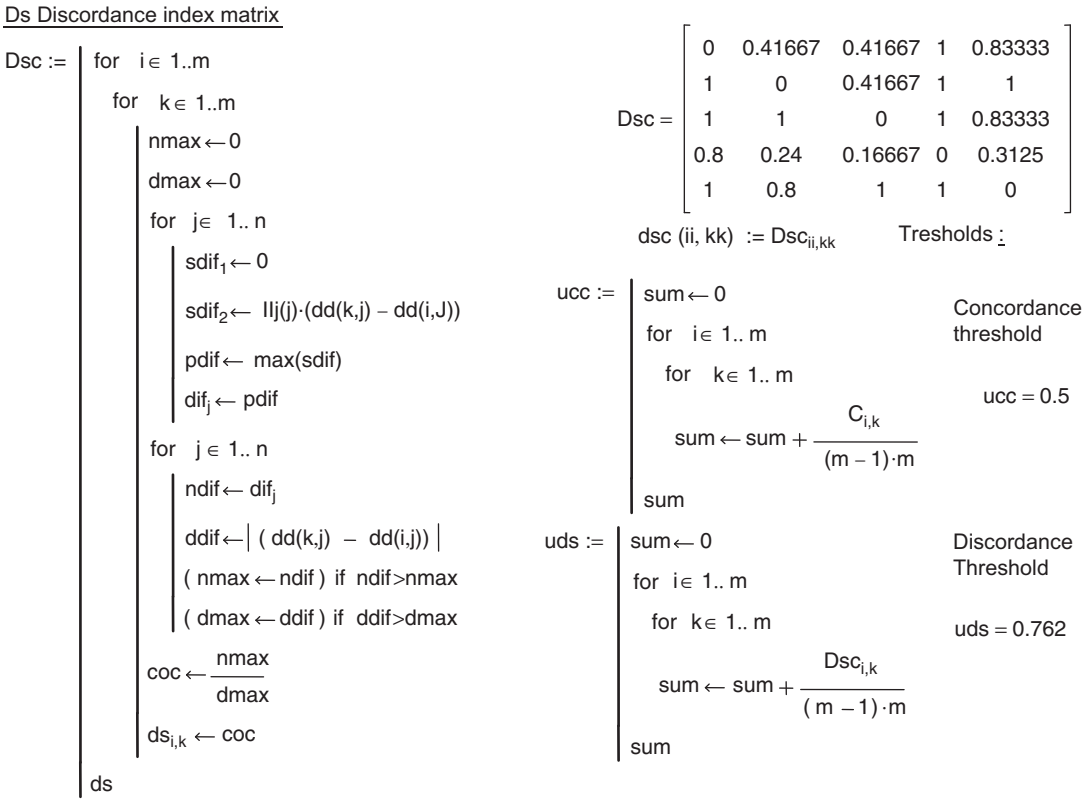


Figure 9 ELECTRE I with MATHCAD (part 2).

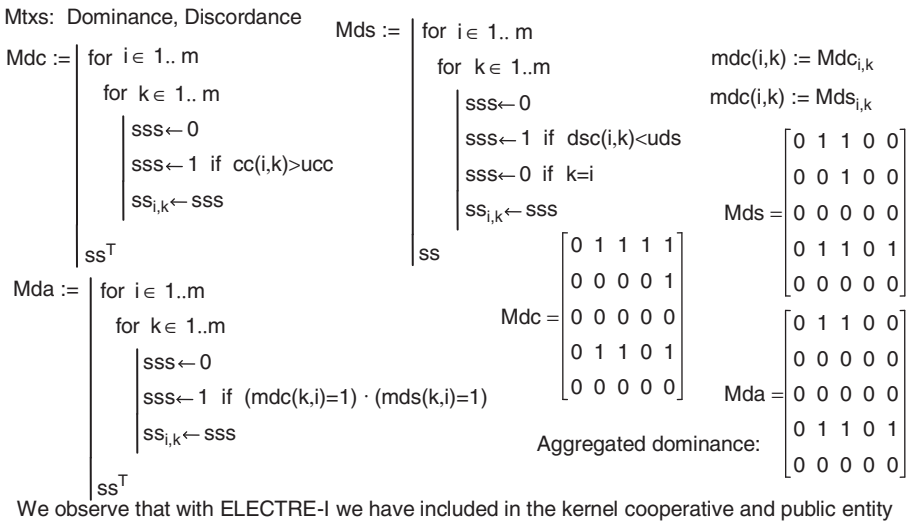


Figure 10 ELECTRE I with MATHCAD (part 3).

Considering the future situation

The authors now consider the result of the decision taken in the present situation (n) and that derived of the decision that should be taken in a fixed future step ($n+1$). It is started with initial decisional matrix (see Table 4). Normally, 25 years is taken as fix future step.

Probabilities

The probabilities associated with the change of the data indicated in the initial decisional matrix are shown in Table 7. The first number is the probability that the data is going up, the second if it is maintained, and the third one if it is going down.

Table 5 Results from analytic hierarchy process method

			Criteria					*Global weights*
			1 Implementation facility	*2 Implementation delay*	*3 Legislation in force*	*4 Social acceptance*	*5 Flexibility*	
Alternatives	1	Public entity	4/17	15/56	10/37	1/6	1/7	0.20696
	2	Institute	7/34	5/28	8/37	1/5	6/35	0.19491
	3	Foundation	3/17	5/28	7/37	7/30	1/5	0.19584
	4	Cooperative	7/34	9/56	7/37	4/15	8/35	0.21669
	5	Private Company	3/17	3/14	5/37	2/15	9/35	0.18559
Weights			0.30	0.10	0.15	0.20	0.25	

Table 6 Results with initial PROMETHEE I and PROMETHEE II

	Public entity	*Institute*	*Foundation*	*Cooperative*	*Private company*	*Phi +*
Public Entity	–	0.55	0.55	0.55	0.75	0.6
Institute	0.45	–	0.45	0.25	0.65	0.45
Foundation	0.45	0.45	–	0.10	0.35	0.337
Cooperative	0.45	0.45	0.75	–	0.65	0.575
Private company	0.25	0.35	0.35	0.35	–	0.325
Phi –	0.40	0.45	0.525	0.312	0.60	
Phi	0.20	– 0.00	– 0.187	0.262	– 0.275	

$$q(i,ii) := \frac{\sum_{j=1}^{5} P(i,ii,j)\cdot W_j}{1} \qquad qq = \begin{bmatrix} 0 & 0.55 & 0.55 & 0.55 & 0.75 \\ 0.45 & 0 & 0.45 & 0.25 & 0.65 \\ 0.45 & 0.45 & 0 & 0.1 & 0.35 \\ 0.45 & 0.45 & 0.75 & 0 & 0.65 \\ 0.25 & 0.35 & 0.35 & 0.35 & 0 \end{bmatrix}$$

Outgoing flows: $fp(i) := \sum_{ii=1}^{5} q(i,ii)$ $\quad fpp_i := fp(i)$ $\quad fpp = \begin{bmatrix} 2.4 \\ 1.8 \\ 1.35 \\ 2.3 \\ 1.3 \end{bmatrix}$ $\quad fmm = \begin{bmatrix} 1.6 \\ 1.8 \\ 2.1 \\ 1.25 \\ 2.4 \end{bmatrix}$

Incoming flows: $fm(i) := \sum_{ii=1}^{5} q(ii,i)$ $\quad fmm_i := fm(i)$

Net flows: fdd = fpp – fmm

$$prr = \begin{bmatrix} 0 & 1 & 1 & -1 & 1 \\ -1 & 0 & 1 & -1 & 1 \\ -1 & -1 & 0 & -1 & 1 \\ -1 & 1 & 1 & 0 & 1 \\ -1 & -1 & -1 & -1 & 0 \end{bmatrix} \qquad fdd = \begin{bmatrix} 0.8 \\ 0 \\ -0.75 \\ 1.05 \\ -1.1 \end{bmatrix}$$

Alternative 4 is preferred cooperative

Weighted PROMETHEE I

Weighted PROMETHEE II

Figure 11 Result using weighted PROMETHEE.

The probabilities associated with the change of weights are shown in Table 8.

The results of applying probabilities in $n+1$ to data are shown in Table 9.

Initial matrix

Applying the probabilities to Table 4, the decisional matrix in $n+1$ shown in Table 10 is obtained.

Table 7 Probabilities associated with change of data from n to $n+1$

	Legislation in force			*Social acceptance*			*Flexibility*		
	To go up	*To maintain*	*To go down*	*To go up*	*To maintain*	*To go down*	*To go up*	*To maintain*	*To go down*
Public entity	0	0.7	0.3	0.1	0.3	0.6	0.2	0.4	0.4
Institute	0	0.5	0.5	0.3	0.6	0.1	0.4	0.4	0.2
Foundation	0.2	0.5	0.3	0.2	0.5	0.3	0.3	0.5	0.2
Cooperative	0.6	0.4	0.2	0.6	0.3	0.1	0.6	0.3	0.1
Private company	0.2	0.5	0.3	0.2	0.4	0.4	0.5	0.3	0.2

Table 8 Probabilities associated with change of weights from n to $n+1$

Change of weights	*Current weight* (n)	*To go up*		*To maintain*		*To go down*	
		Probabilities	*Forecast weight* (n + 1)	*Probabilities*	*Forecast weight* (n + 1)	*Probabilities*	*Forecast weight* (n + 1)
Implementation facility	0.3	0	0.4	0.3	0.3	0.7	0.15
Implementation delay	0.1	0.3	0.15	0.6	0.1	0.1	0.09
Legislation in force	0.15	0.1	0.2	0.6	0.15	0.3	0.1
Social acceptance	0.2	0.7	0.3	0.2	0.2	0.1	0.15
Flexibility	0.25	0.7	0.3	0.2	0.25	0.1	0.2

Table 9 Results to apply probabilities associated with changes from n to $n+1$

	Current data (n)	*To go up*		*To maintain*		*To go down*	
		Probabilities	*Forecast data* (n + 1)	*Probabilities*	*Forecast data* (n + 1)	*Probabilities*	*Forecast data* (n + 1)
Legislation in force							
Public entity	10	0	–	0.7	10	0.3	9
Institute	8	0	9	0.5	8	0.5	7
Foundation	7	0.2	8	0.5	7	0.3	6
Cooperative	7	0.6	8	0.4	7	0	6
Private company	5	0.2	7	0.5	5	0.3	4
Social acceptance							
Public entity	5	0.1	6	0.3	5	0.6	4
Institute	6	0.3	7	0.6	6	0.1	5
Foundation	7	0.2	8	0.5	7	0.3	6
Cooperative	8	0.6	10	0.3	8	0.1	6
Private company	4	0.2	5	0.4	4	0.4	3
Flexibilty							
Public entity	5	0.2	7	0.4	5	0.4	4
Institute	6	0.4	7	0.4	6	0.2	5
Foundation	7	0.3	8	0.5	7	0.2	6
Cooperative	8	0.6	10	0.3	8	0.1	6
Private company	9	0.5	10	0.3	9	0.2	8

PROMETHEE methods applied

Applying initial PROMETHEE II method, the authors obtain in $n+1$, the results shown in Table 11.

Results

The results obtained with this method are summarized in Figures 12 and 13.

In all the figures it can be seen that Cooperative is preferred, at present, and in the future.

Conclusions

The results obtained with the proposed methods seem to be the best alternative to give the water management in the Salta Province to a Cooperative. This role could be played by the actual 'Asociación de Consorcios de Usuarios de Aguas Públicas de Salta' (Consortium Association) with the competences delegated from the 'Agencia de Recursos Hídricos' (WR Agency). The fundamental hydrology infrastructure works in the authors' opinion should be paid by the Province

Table 10 Decisional matrix in $n+1$

			Criteria				
			1 Implementation facility	*2 Implementation delay*	*3 Legislation in force*	*4 Social acceptance*	*5 Flexibility*
Alternatives	1	Public entity	8	12	9.7	4.5	5
	2	Institute	7	18	7.5	6.2	6.2
	3	Foundation	6	18	6.9	6.9	7.1
	4	Cooperative	7	20	7.6	9	9
	5	Private company	6	15	5.1	3.8	9.3
Weights			0.196	0.115	0.141	0.267	0.281
Indexes			+1	−1	+1	+1	+1

Table 11 Results with PROMETHEE

	Public entity	*Institute*	*Foundation*	*Cooperative*	*Private company*	*Phi +*
Public entity	–	0.452	0.452	0.4	0.719	0.519
Institute	0.548	–	0.337	0.115	0.604	0.401
Foundation	0.548	0.548	–	0.115	0.408	0.405
Cooperative	0.548	0.689	0.885	–	0.604	0.681
Private company	0.281	0.396	0.396	0.396	–	0.367
Phi –	0.481	0.521	0.518	0.269	0.584	
Phi	−0.038	−0.12	−0.113	0.412	−0.217	



Figure 12 Results with PROMETHEE II in n + 1.

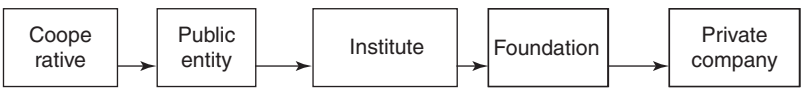


Figure 13 Results with PROMETHEE II in n.

Government with funds coming from The Federal Investment Council. The canon due to water use would be transferred to the Cooperative. This entity would be responsible for hydrologic information network, water distribution, maintenance task, and police actions.

This election is robust, due to the fact that the authors have demonstrated that with the changes foreseen in a medium-range level, the alternative elected does not change.

Erosion Control by Crop Management

Introduction

This case study is located in the Chaco Area (Salta Province of Argentina). It has a low density of population in small cities located in important long mountain valleys, and Indian places named '*puestos*' or '*colonias*' (see Figures 14 and 15).



Figure 14 'Puesto' Wichi in J. V. González.



Figure 15 Typical housing in La Unión.



Figure 16 Provincial road in Chaco.



Figure 17 Bermejo River.

It has poor quality roads and it has an environment that is 'deteriorating progressively' (see Figure 16).

As said before, the Bermejo River (see Figure 17) is the most important fluvial artery in the area. It presents a zone known as a meander digression and due to low slopes its course changes constantly forming meanders. That area during monsoon rainy period is transformed into an immense sheet of floodwater that completely isolates the communities living by the river along 5–10 km from the riverside. It produces constant erosion that makes a great lot of sediments settling down at the Paraná River generating an important cost in the continuous drainage.



Figure 18 Pasture as *modus vivendi*.

One of the most important problems is the erosion, progressive desertification, and environment degradation. Besides the water, other factors have an important influence in the erosion and progressive desertification of this region and environment degradation. Historically, human exploitation of natural forest to be used in the railway and other activities produced an environment degradation process. Later on, the indigenous population followed the irrational wood extraction and did an over pasture as '*modus vivendi*' contributing to make the situation worse (see Figure 18). Actually, the farms and big single-crop exploitations in some locations do not give solution to the desertification problem.

For the study of this area, the authors have divided it into six zones: Las Lajitas, La Estrella, Pichanal, Martin Hickmann, Rivadavia banda sur, and Joaquín V. Gonzalez (see Figure 19).

Only one integral plan considering all factors involved and the differences among subzones, it will be an initial point to change the direction of the desertification process.

Alternatives of desertification control

The following five alternatives have been selected (see Table 12; Figures 20–24).

Criteria

Eight criteria have been applied following field research, expert panels, social investigation, and personal interviews. The criteria were rated on a 1–10 scale, according to local evaluations and other methods of elicitation.

Criterion 1: Water erosion

Water erosion (WE) is very important because of the interaction between natural and socioeconomic conditions. The relative WE indexes figure in the IM. For that the authors have considered this criterion as of the 'more is worst' kind.

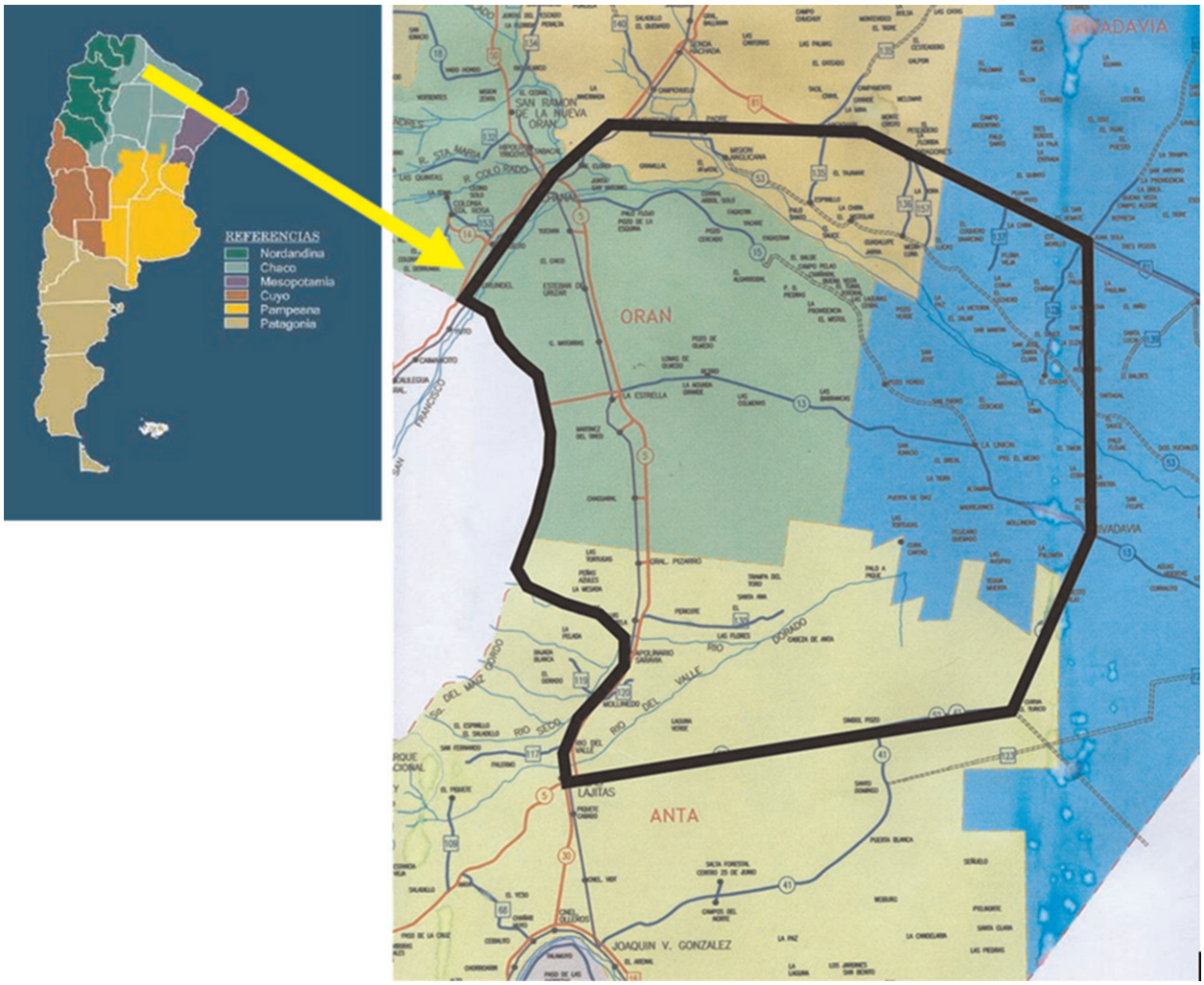


Figure 19 Study area.

Table 12 Five alternatives for 'Chaco'

No.	*Alternatives*	*Description*
1	Native forest	Trees like 'quebracho-blanco' and 'quebracho Colorado' (see **Figure 20**).
2	High value forest	Mainly teak, ebony, walnut tree, cherry tree, lignum vitae, eucalyptus, etc. (see **Figure 21**).
3	Traditional farms	Extensive agriculture and livestock mixed with native forest modified and several foraging plants (see **Figure 22**).
4	Erosion control crop with agriculture use	See **Figure 23**.
5	Erosion control crop with industrial use (biomass)	See **Figure 24**.

Criterion 2: Eolian erosion

Winds erosion, transport and deposit materials and are effective agents in several areas of this region. This criterion has been considered as of the 'more is worst' kind.

Criterion 3: Implementation facility

Have been established taking into account actors' opinions (Grau, 2003). This criterion is considered as 'more is better.'

Criterion 4: Water resources

By each alternative, the needs of WR have been considered. The relative results have been taken into the IM for this criterion. This criterion is considered as 'more is better.'

Criterion 5: Economical benefits

The relative economical benefits using each alternative in a period of 25 years have been obtained. This criterion is considered as 'more is better.'



Figure 20 Native forest in J. V. González.



Figure 21 High value forest in La Estrella.

Criterion 6: Hand power

The authors have considered that it would be satisfactory to give employment to the majority of the population. For that, they have considered this criterion as of the 'more is better' kind.

Criterion 7: Environmental impacts

They have been considered in each subzone. The environmental impacts (EI) have been calculated according to Gómez Orea (1999).

Criterion 8: Social acceptance

The figures included in this criterion have been obtained from the results of different forums and meetings with institutions, organizations, and native people (Grau, 2003).

Multicriteria methods applied

Initial matrix

In this article, the authors show the IM (see Table 13) and results using different discrete multicriteria decision methods for the subzone La Estrella. The recommendation for the total zone will be included in the conclusions.

ELECTRE method

From the IM using MATHCAD program the following graph and kernel (see Figure 25) are obtained.

Alternatives A and B are the preferred ones.

PROMETHEE method

From the IM using the pseudocriteria shown in Table 14 and weighted PROMETHEE II with Mathcad program, the results shown in Figure 26 are obtained.

The higher total flux is in relation to the preferred alternative. In this case, it is alternative B: High value forest.

Analytic hierarchy process method

From the IM (see Table 13) using Expert Choice Software, the following order (see Figure 27) is obtained:

Native forest, high value forest, traditional farms, erosion control crop with industrial use (biomass), and erosion control crop with agriculture use.

Conclusions

All the methods show consistency in the selection of the best alternative to control desertification in Chaco area (Salta Province of Argentina). The weighted PROMETHEE II method is a very useful tool to design an erosion control integral plan. It is robust as the authors have confirmed by changing, a little, the relative preferences. They recommend the use of weighted PROMETHEE II with the usual criterion and type III pseudocriterion.

Following the results obtained for the total zone, the authors recommend the following:

- Las Lajitas: Extensive farming and livestock. If it is only farming it could be with crop rotation. The livestock would be with natural forestry and foraging plants.
- La Estrella: Native and high value forestry can be combined.
- Pichanal: Similar to Las Lajitas.
- Martin Hickman: Native forestry.
- Rivadavia Banda Sur: Similar to La Estrella.
- Joaquin V. González: Similar to Las Lajitas combined, in some areas, with high value forestry.

Waste Management

Introduction

Worldwide, the management of urban solid waste (USW) of all types is a major problem and it is more virulent in areas that lack financial, technological, and cultural resources. It is difficult to convince the population to avoid casting waste into rivers or into open dumps. The domestic waste must not be disposed into the river or free air deposits. In general, this disposition affects not only the flora and small fauna destroying the biodiversity but also the health of people living in their margins. To avoid this situation, it is necessary to change the culture of the people. The means are limited, so it will be necessary to move resources from other public services.



Figure 22 Traditional farms. Extensive agriculture and livestock in J. V. González.



Figure 23 Winter crop in Las Lajitas.



Figure 24 'Cártamo' crop in Las Lajitas.

Table 13 Initial matrix for subzone 'La Estrella' for ELECTRE

			Criteria							
			1 WE	*2 EE*	*3 IF*	*4 WR*	*5 EB*	*6 HP*	*7 EI*	*8 SA*
Alternatives	1	A	7	6	1	8	5	2	8	6
	2	B	7	6	5	4	5	9	6	5
	3	C	3	3	6	4	8	9	3	9
	4	D	2	2	6	4	5	6	5	6
	5	E	3	2	8	5	8	6	4	8
Weights			0.15	0.15	0.15	0.1	0.15	0.1	0.1	0.1

Abbreviations: EB, economical benefits; EE, Eolian erosion; EI, environmental impacts; HP, hand power; IF, Implementation facility; SA, social acceptance; WE, Water erosion; WR, water resources.

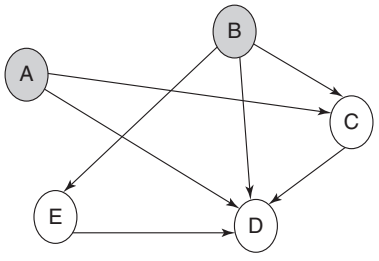


Figure 25 ELECTRE graph showing the kernel (subzone La Estrella).

This situation of USW currently involves the following consequences:

- The pollution of surface and groundwater that produces serious health problems and water-treatment costs, which are unaffordable in many cases by the municipal resources.

- Degradation of the soil by the presence of heavy metals and other pollutants. Soils are degraded, making them unproductive and potentially damaging to wildlife and citizens.
- Waste incineration produces air pollution.
- The gases produced by organic matter decomposition (carbon dioxide and methane) contribute to the greenhouse effect.
- The proliferation of disease vectors that directly or indirectly affects public health.
- The wind dispersal of many wastes, which also affects the environment and the countryside that are a propellent of wildland fire.
- A medium- and long-term factor of erosion, desertification, and climate change.

Table 14 Initial matrix for subzone 'La Estrella' for PROMETHEE

			Criteria							
			1 WE	*2 EE*	*3 IF*	*4 WR*	*5 EB*	*6 HP*	*7 EI*	*8 SA*
Alternatives	1	A	7	6	1	8	5	2	8	6
	2	B	7	6	5	4	5	9	6	5
	3	C	3	3	6	4	8	9	3	9
	4	D	2	2	6	4	5	6	5	6
	5	E	3	2	8	5	8	6	4	8
Weights			0.15	0.15	0.15	0.1	0.15	0.1	0.1	0.1
Pseudocriterion			III	III	III	I	I	III	III	III
Thresholds			2	4	4			6	6	2

Abbreviations: EB, economical benefits; EE, Eolian erosion; EI, environmental impacts; HP, hand power; IF, Implementation facility; SA, social acceptance; WE, Water erosion; WR, water resources.

The problem was considered first by Prof. J.B. Grau during the time of his association with universities and public organizations of Salta in 2003 and 2004 (Grau, 2003). From these previous studies an MCDM problem of election between three alternatives considering a set of criteria was stated in adapted formats of ELECTRE-1, PROMETHEE, and AHP methods. Some indecision peculiarities were detected and needed critical reasoning to obtain some of the results. Actually a project is being developed in municipalities of Córdoba province (Argentina).

This case study was located in one area of the Salta Province (Argentina). The selected Andean area is very rich in natural resources and has a low density of population in small cities located in important long mountain valleys, has low standards for roads, and has an environment that according to

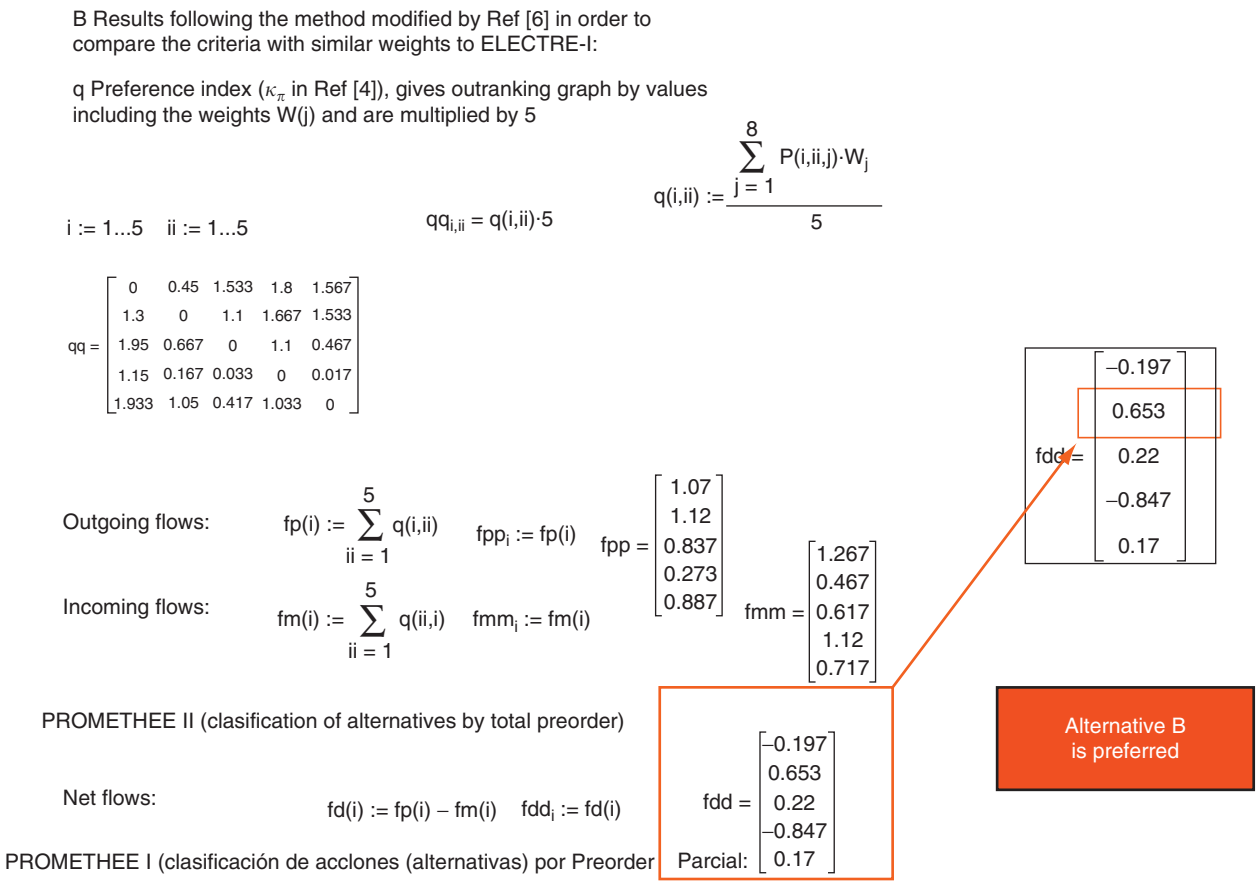


Figure 26 Result with weighted PROMETHEE II.

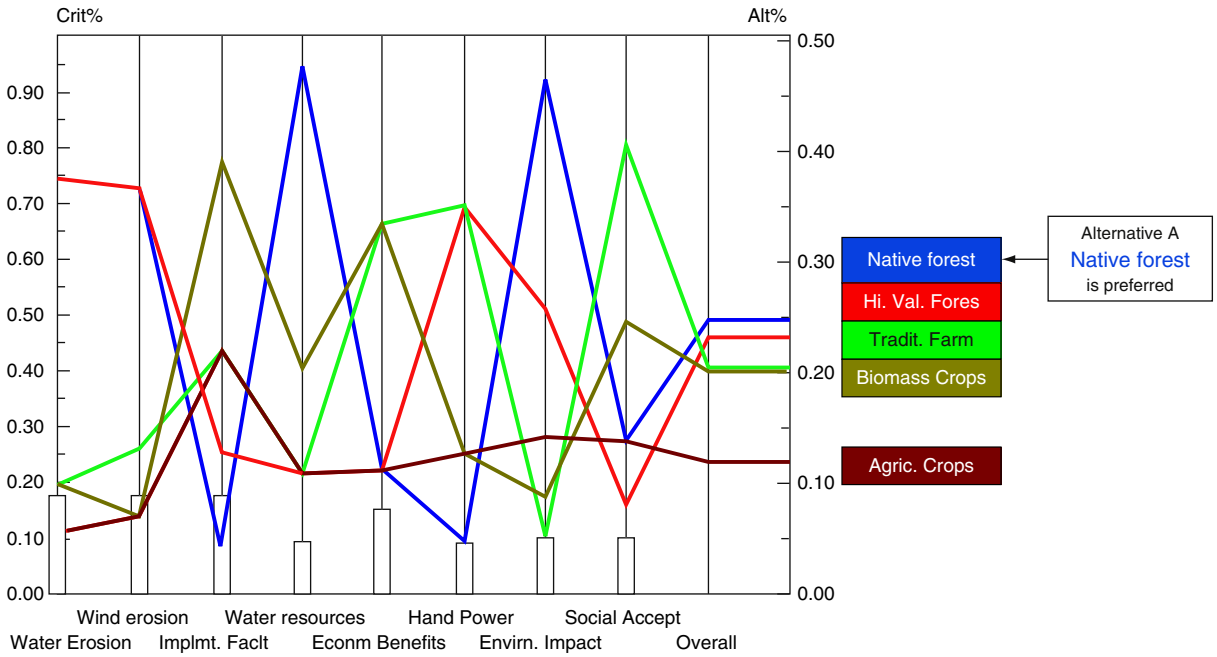


Figure 27 Analytic Hierarchy Process using Expert Choice software.

Table 15 Alternatives

No.	*Alternatives*	*Description*
1	Direct local sanitary filling	Disposal of residues in mass in such filling located in the source municipality.
2	Sanitary filling and compost Production	Disposal of inorganic residues in a direct local filling and compost production from organic residues in an adjacent plant.
3	Transport to external plants	The residues are carried to the nearest sanitary plant located out of the municipality.

Table 16 Criteria

No.	*Aspects*	*Criteria*	*Indexes (I_j)*	*Weights (W_j)*	
1	Technical aspects	(EIM)	Ease in management	−1	0.05
2	Environmental aspects	(LOC)	Location	+1	0.1
3		(LEI)	Local environmental impact	−1	0.15
4	Economic aspects	(ICO)	Installation costs[a]	−1	0.15
5		(OCV)	Operating costs net present value[a,b]	−1	0.15
6	Social aspects	(LDE)	Labor demand	+1	0.15
7		(CTP)	Compatibility with traditional practices	+1	0.05
8		(SAC)	Social acceptance	+1	0.15
9	Normative aspects	(CLR)	Compatibility with effective laws and rules	+1	0.05

[a]Costs are in thousands of pesos of Argentina (study in 2004), for a typical example municipality.
[b]Operating costs minus perceived incomes valued at start date as NPV; alternative 2 costs more initially but produces compost sales incomes that have been prudently estimated.
Note: Each criteria contains two data as (I_j; W_j); the I_j are indexes being 1 if the criterion is of the kind 'more is better' and −1 if it is of the kind 'more is worse'; the W_j are weights, having already 1 as sum in this example, as defined and used by ELECTRE and PROMETHEE methods later.

local opinion is 'deteriorating progressively.' White *et al.* (1995) and Chang *et al.* (1997) studied solid waste management, interesting for any human concentration; literature and pages for Latin America are easily found on the web, and Gallardo and Bordás (2001), Peñuelas *et al.* (2001) and Santos *et al.* (2001) are Spanish examples. The problem of urban residue management in that area was considered at this time by local officials and experts, and is contained in internal surveys considering the local aspects: territorial, socio-economic, and environmental. Discrete multicriteria decision methods were appropriated to reflect the criteria of different nature occurring in territorial studies, and three different

Table 17 Initial decision matrix It = (t_{ij}), weights w_j and indexes I_j

			Criteria								
			1 EIM	2 LOC	3 LEI	4 ICO	5 OCV	6 LDE	7 CTP	8 SAC	9 CLR
Alternatives	1	Direct local sanitary filling	2	2	3	50	30	2	2	1	1
	2	Sanitary filling and compost production	2	2	2	75	18	3	1	3	3
	3	Transport to external plants	1	1	1	48	42	1	2	2	2
		Weights (W_j)	0.05	0.1	0.15	0.15	0.15	0.15	0.05	0.15	0.05
		Indexes (I_j)	−1	+1	−1	−1	−1	+1	+1	+1	+1

Abbreviations: CTP, compatibility with traditional practices; CLR, compatibility with effective laws and rules; EIM, ease in management; LEI, local environmental impact; LOC, location; ICO, installation costs; OCV, operating costs net present value; LDE, labor demand; SAC, social acceptance.

$$D = \begin{bmatrix} 0.1 & 0.2 & 0.225 & 0.278 & 0.187 & 0.15 & 0.1 & 0.075 & 0.025 \\ 0.1 & 0.2 & 0.15 & 0.417 & 0.112 & 0.225 & 0.05 & 0.225 & 0.075 \\ 0.05 & 0.1 & 0.075 & 0.267 & 0.262 & 0.075 & 0.1 & 0.15 & 0.05 \end{bmatrix} \qquad V = \begin{bmatrix} -0.240278 \\ -0.004167 \\ -0.179167 \end{bmatrix}$$

j – criteria

Figure 28 Decisional Matrix (D) standardized and weighted, i-ELECTRE-values {V_i}.

$$C = \begin{bmatrix} 0 & 0.275 & 0.425 \\ 0.725 & 0 & 0.6 \\ 0.575 & 0.4 & 0 \end{bmatrix} \qquad Dsc = \begin{bmatrix} 0 & 1 & 1 \\ 0.926 & 0 & 1 \\ 0.667 & 1 & 0 \end{bmatrix}$$

average Thresholds,

Concordance: ucc = 0.5
Discordance: uds = 0.932

Figure 29 Concordance matrix C, discordance Matrix Dsc, average thresholds.

methods of disposal of these residues were adopted as alternatives.

Alternatives

The following three alternatives have been selected (see Table 15).

Criteria

These studies put in evidence for MCDAM nine criteria grouped into five aspects. These are shown in Table 16.

Multicriteria methods applied

ELECTRE-I method

Table 17 shows the initial decision matrix of data elements for the nine criteria and the three alternatives, as collected by J. Grau and D. Sánchez in Salta in 2004 for the rather transparent ELECTRE-I method. Some criteria were costs/benefits put in monetary values as said before, and other criteria received rather subjective indexes with values {1, 2 or 3} depending on the importance of the effect. As said an index I_j was assigned to each criterion, and a weight value W_j, already standardized, carefully chosen by the analysts.

From these data, following Roy (1985), the authors obtain the decisional matrix (D) standardized and weighted in Figure 28.

Figure 29 shows concordance and discordance matrixes, obtained with MATHCAD, and first values for thresholds *ucc* and *uds* that are the average of the six nondiagonal elements of matrixes C and Dsc. Finally, changing the thresholds and in spite of higher initial costs, alternative 2 may be considered preferable.

PROMETHEE methods

PROMETHEE methods were next considered following Brans and Mareschal conserving the precedent consensus election of criteria and tradeoffs by adopting the initial decision matrix, the indexes column I_j and the weights $w_j = \pi_j$ of Table 17, and by using 'type III, Criterion with Linear Preference Functions.' Figure 30 indicates one of the qualifying functions.

The results obtained with initial Brans PROMETHEE I and II are shown in Figure 31.

The results obtained with weighted PROMETHEE I and II are shown in Figures 32 and 33.

The higher Net flux is in relation to the preferred alternative. In this case, it is alternative 2: Sanitary Filling and Compost Production.

Analytic hierarchy process method

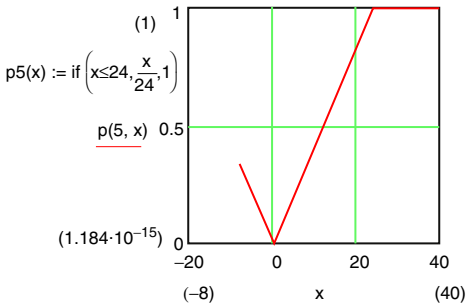
Using the AHP method, the second (sanitary filling + compost) alternative was preferred as before, followed by the first (direct filling) near the third (transport to external plants). The relative order of the first and the third has changed. The obtained performance sensitivity graph of Figure 34 contains some data and results, showing that environment impact had got a higher preference than for ELECTRE.

Pseudocriteria

- m = r–s
- j = 1 type III, s = 1, r = 2,
- j = 2 type III, s = 1, r = 2,
- j = 3 type III, s = 1, r = 3,
- j = 4 type III, s = 48, r = 75,
- j = 5 type III, s = 18, r = 42,
- j > 5 type III, s = 1, r = 3,

$$p(j, x) := \text{if}\left(x \le m_j, \frac{x}{m_j}, 1\right)$$

$p5(x) := \text{if}\left(x \le 24, \frac{x}{24}, 1\right)$



$p1(x) := \text{if}\left(x \le 1, \frac{x}{1}, 1\right)$ $p2(x) := \text{if}\left(x \le 1, \frac{x}{1}, 1\right)$ $p3(x) := \text{if}\left(x \le 2, \frac{x}{2}, 1\right)$

$p4(x) := \text{if}\left(x \le 27, \frac{x}{27}, 1\right)$

$p5(x) := \text{if}\left(x \le 24, \frac{x}{24}, 1\right)$

Figure 30 Qualifying function in PROMETHEE.

Initial PROMETHEE I and II

$$q(i, ii) := \frac{\sum_{j=1}^{9} P(i, ii, j)}{9}$$

$qq_{i,ii} := q(i,ii)$

$$qq = \begin{bmatrix} 0 & 0.214 & 0.222 \\ 0.389 & 0 & 0.444 \\ 0.342 & 0.389 & 0 \end{bmatrix}$$

Outgoing flux : $fp(i) := \sum_{ii=1}^{3} q(i, ii)$ $fpp_i := fp(i)$

$$fpp = \begin{bmatrix} 0.436 \\ 0.833 \\ 0.73 \end{bmatrix}$$

Incoming flux : $fm(i) := \sum_{ii=1}^{3} q(ii, i)$ $fmm_i := fm(i)$

$$fmm = \begin{bmatrix} 0.73 \\ 0.603 \\ 0.667 \end{bmatrix}$$

PROMETHEE I

$pr(i,ii) :=$ z←−1; z←0 if (fp(i)=fp(ii))·(fm(i)=fm(ii)); z←1 if ((fp(i)>fp(ii))·(fm(i) < fm(ii))) + ((fp(i) > fp(ii))·(fm(i)=fm(ii))) + ((fp(i)=fp(ii))·(fm(i) < fm(ii))); z

$$prr = \begin{bmatrix} 0 & -1 & -1 \\ 1 & 0 & 1 \\ 1 & -1 & 0 \end{bmatrix}$$

PROMETHEE II

Net flux: $fd(i) := fp(i) - fm(i)$ $fdd_i := fd(i)$

$$fdd = \begin{bmatrix} -0.294 \\ 0.23 \\ 0.064 \end{bmatrix}$$

With both methods: Order: 2,3,1

Figure 31 Results with initial PROMETHEE I and II.

Conclusions

In a global study the sanitary filling and compost alternative was preferred with the three methods. The direct filling and the transport out of the city alternatives were rather equivalent. For application in practice programming of actions would be required, actuations could be started progressively through independent initiatives by municipalities; a central agency could offer technical information and pilot plant experimentation,

$$P(i, ii, j) := \text{if}[l_j \cdot (t_{j,i} - t_{j,ii}) \le 0, 0, p(j, |t_{j,i} - t_{j,ii}|)]$$

$$qq = \begin{bmatrix} 0 & 0.189 & 0.25 \\ 0.425 & 0 & 0.5 \\ 0.311 & 0.325 & 0 \end{bmatrix} \qquad q(i, ii) := \frac{\sum_{j=1}^{9} P(i, ii, j) \cdot W_j}{9}$$

$i := 1...3 \quad ii := 1...3 \quad qq_{i,ii} := q(i, ii) \cdot 9$

Outgoing fluxes: $fp(i) := \sum_{ii=1}^{3} q(i, ii) \quad fpp_i := fp(i)$

$$fpp = \begin{bmatrix} 0.046 \\ 0.1028 \\ 0.0679 \end{bmatrix}$$

Incoming fluxes $fm(i) := \sum_{ii=1}^{3} q(ii, i) \quad fmm_i := fm(i)$

$$fmm = \begin{bmatrix} 0.0818 \\ 0.0515 \\ 0.0833 \end{bmatrix}$$

Figure 32 Result with weighted PROMETHEE I and II (part 1).

Weighted PROMETHEE I

$pr(i,ii) := |z \leftarrow -1$

$z \leftarrow 0 \text{ if } (fp(i)=fp(ii)) \cdot (fm(i)=fm(ii))$

$z \leftarrow 1 \text{ if } ((fp(i)>fp(ii)) \cdot (fm(i) < fm(ii))) + ((fp(i) > fp(ii)) \cdot (fm(i)=fm(ii))) + ((fp(i)=fp(ii)) \cdot (fm(i) < fm(ii)))$

$prr_{i,ii} := pr(i,ii)$

Where pr(i,ii) = 1 means that action i outranks action ii, pr(i,ii) =0 is equivalence, and pr(i,ii) = –1 indetermination maybe solved looking at pr(ii,i)

$$prr = \begin{bmatrix} 0 & -1 & -1 \\ 1 & 0 & 1 \\ -1 & -1 & 0 \end{bmatrix}$$

2 is better than 1 and 3 but 3 do not outrank to 1

Weighted PROMETHEE II

Net flux: $fd(i) := fp(i) - fm(i) \qquad fdd_i := fd(i)$

$$fdd = \begin{bmatrix} -0.0358 \\ 0.05123 \\ -0.01543 \end{bmatrix}$$

Order: 2,3,1

Alternative 2 is preferred

Figure 33 Result with weighted PROMETHEE I and II (part 2).

and investment subsidies. The selected MCDM methods have been suitable as aid for the planning of such practical and real problem. ELECTRE-I was clear as a first guide but required addenda of additive valuations for decision, AHP was more dependent on analysts that emphasized environmental aspects diminishing the influence of social aspects, and PROMETHEE was efficiently adapted by the use of linear preferences and weights as used with ELECTRE-I. This method is named weighted PROMETHEE and is actually used in many real cases.

Final General Model

With the experience obtained from the above four cases the authors have elaborated a model to apply to climate change.

In the first place, the following alternatives and criteria are adopted.

Alternatives

1. Industrial and agricultural activities reduction in first world: To prepare and to sign a Memorandum of Understanding (MoU), similar to Kyoto Protocol in order to reduce, step by step, the industrial and agricultural dangerous activities mainly in developed countries.
2. To maintain the activities in industrial countries transferring funds to improve environmental activities compatibles with sustainable progress in the third world: To prepare and to sign a protocol in order to establish a mechanism similar to 'green-bonus.'

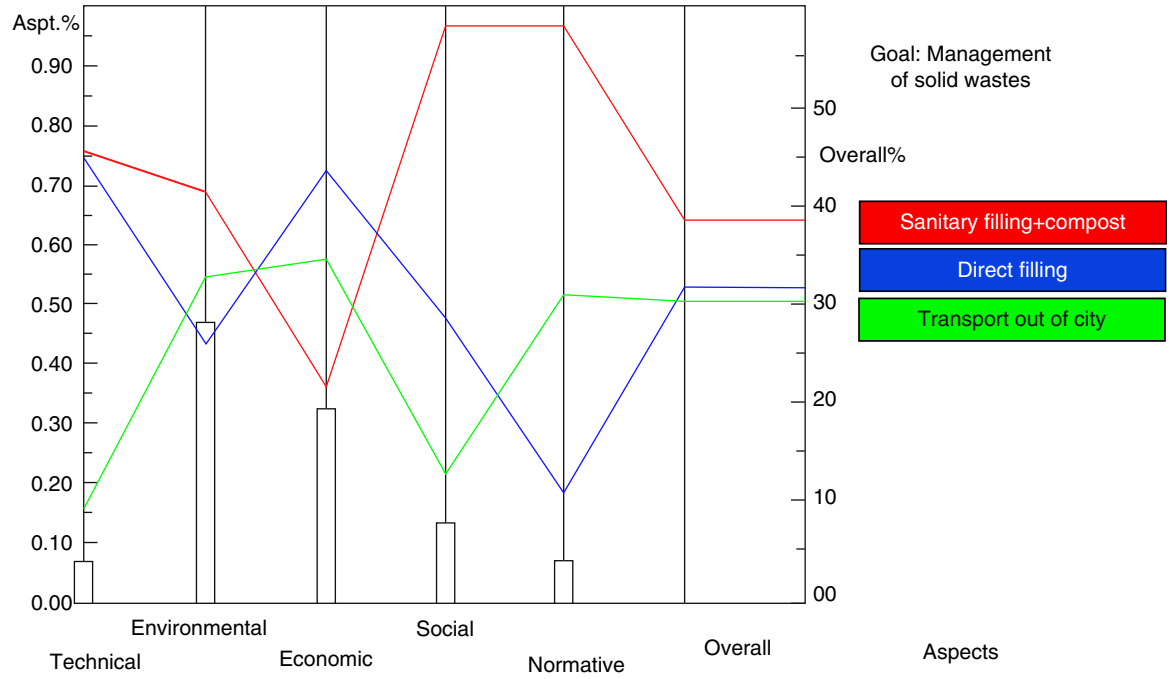


Figure 34 Results Analytic Hierarchy Process using Expert Choice software.

3. To Increase economic support to countries and activities aimed at improving the environment.
4. To give resources to research groups in order to study integral adaptation plans: To increase the subvention and funds from international entities like European Commission through the CALLS as CALL FP7 – ENV – 2012 "Strategies, costs and impacts of adaptation to climate change" in order to encourage the research groups to dedicate the efforts to this activity.
5. To help natural reactions: From the creation of the world the earth has been changing and the natural resources included the human people have been adapting to those changes. The human action would be to help the natural forces to adapt us to new situations.
6. To maintain actual policy: To follow with the studies, convention and action in the framework of International Organizations.

Criteria

Environmental criteria

- Peak runoff, of the kind 'more is worse.'
- Average annual erosion (ERO), of the kind 'more is worse.'
- Index of Environmental Quality (EQI), of the kind 'more is better.'

Economic criteria

- Investment (INV), of the kind 'more is worse.'
- Maintenance (MAN), of the kind 'more is worse.'
- Benefits (BEN), of the kind 'more is better.'

Social criteria

- Ease for implementation (FIM), of the kind 'more is worse.'
- Social acceptability (ACE), of the kind 'more is better.'
- Employment impact (EMP), considered of the kind 'more is better.'

Physical type

- Meteorological: Monthly pluviometry (mm) of rain in the last 50 years and maximum rain in 6 h month by month in the last 50 years. Overflows, earthquake, cyclone year by year during last 50 years. Some cases will be the kind 'more is better' and in others 'more is worse.'
- Soil (SOI): Classification following the method developed by Antón and Grau (2009). It is of the kind 'more is better.'
- Water resources (WR). It is of the kind 'more is better.'

The use of soil

In relation to the use of soil, several criteria must be considered:

- Agricultural use (AGR), livestock (LIV), forestry (FOR), mining (MIN), industrial (IND), urban (URB), and sport and tourism (TOU). Some cases will be of the kind 'more is better' and in others 'more is worse.'

Political Criteria

- Legislation in force (LEG), to be in accordance with it is positive for adopting the solutions in an alternative, and it was measured by a valuation (*qi.*) in the range (1–10) 'more is better' scale.
- Votes gained or lost (VOT).

Initial Matrix

With the preliminary studies and the database elaborates for the interdisciplinary research groups, the authors create the initial decisional matrix (see Table 18).

Multicriteria Methods Applied

The following discrete MCDM has been applied:

- ELECTRE – TRI, see Roy (1985, 1996), Roy and Bouyssou (1993), and Mousseau *et al.* (2000) and other versions.
- For initial PROMETHEE, see Brans and Vincke (1985), Brans *et al.* (1986); from it is derived the adopted weighted PROMETHEE that seems preferable to introduce indication of relative importance of criteria, see Brans and Mareschal (1994), Anton *et al.* (2006, 2010), and Grau *et al.* (2008, 2009).
- AHP, see Saaty (1980, 1996a,b).

For ELECTRE and PROMETHEE methods, MATHCAD® software was used, and for AHP method, EXPERT CHOICE® software (from EXPERT CHOICE Inc). These methods got successively varied extensions and also commercial software, but for the goals of this article the adopted versions were robust and reliable. These methods have been used by the authors formerly in other applications such as: 'Madrid-Valencia high-speed rail line: A route selection' (Anton *et al.*, 2004), 'Compromise Programming Calibration for financial analysis of firms of a common sector of business, case study for a set of Spanish banks in 1995' (Antón *et al.*, 2007), and 'Application of decision theory methods for a Community of Madrid soil classification' (Antón *et al.*, 2007).

Other Methods

Bayesian methods and statistical methods using time series will be used completing some aspects. These have been tested in the case study 4.2. For the DSS used here, the Bayesian views considering various states of future that may change, such as in climate or in human uses, as populations, products and markets, normally with elicited probabilities at decision time, and sometimes with elicited utility functions, and maybe with changes in opinion transferred perhaps into elicited weights. These points of views are also used with high initial spending, but that is not the case here unless great public works, as of hydraulic management, are indicated against climate change.

Advantages of the Proposed Solution

The advantages of the proposed solution are:

- The models that currently exist, analyzed individually the variables that are altered by climate change (water, CO_2, temperature, greenhouse gases, etc.) without considering it in an integrated way to understand how they can affect life on earth. However, this model allows us to see how the life on earth, including human people, can be affected by changes in all the variables analyzed. This can be

Table 18 Initial matrix

		Criteria																				
		Environmental			Economic			Social			Physical			Soil uses						Political		
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
		PRU	ERO	EQI	INV	MAN	BEN	FIM	EXT	ACE	EMP	MET	SOI	WR	AGR	LIV	FOR	MIN	IND	URB	TOU	LEG	VOT
Alternatives	1	IAR																					
	2	IAT																					
	3	SEI																					
	4	SRG																					
	5	HNR																					
	6	MAP																					
Weights																							
Indexes																							

Abbreviations: ACE, social acceptability; AGR, agricultural use; BEN, benefits; EMP, employment impact; ERO, average annual erosion; EXT, externalities; FIM, ease for implementation; FOR, forestry; HNR, help natural reactions; IAR, industrial and agricultural activities reduction; IAT, industrial countries transferring funds; IND, industrial; INV, investment; INT, intensive agricultural use; LEG, legislation in force; LIV, livestock; MAN, maintenance; MAP, maintain actual policy; MET, meterological; MIN, mining; PRU, peak runoff; SEI, activities with environmental improving; SOI, soil; SRG, resources to research groups; TOU, sport and tourism; URB, urban; WR, water resources.

considered as a next step to the final report of MCA4 climate initiative (see UNEP, 2011).

- It is a global solution applicable in every geographical area.
- It takes full advantage of the existing information and it makes the maximum use of efforts carried out by research groups, universities, and different institutions.
- The proposed model generates results that can be more easily borne by society in accepting the mitigation and adaptation plans to climate change.
- It generates a scientific base that can be analyzed, adapted, and presented at international decision forums.
- Many of the current models to foresee certain changes can serve as a basis and support to the proposed integrated model.
- The model will quantify the costs of actions derived from the implementation of the proposed alternatives.

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Relevant Websites

www.expertchoice.com
Expert Choice Inc.
www.mca4climate.info
UNEP.

Medicinal Crops

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Glossary

Biosynthesis Enzyme-catalyzed process in cells of living organisms by which substrates are converted to more complex products.

Good agricultural practices Specific methods applied to agriculture create food for consumers or further processing that is safe and wholesome.

Medicinal plants Plants used as natural medicines.

Plant endophytic fungi Fungi that spend the whole or part of their lifecycle colonizing intracellularly inside the healthy tissues of host plants, typically causing no apparent symptoms of disease.

Traditional Chinese medicines Medicines sharing common concepts which have been developed in China and are based on a tradition with a long time.

Introduction

Medicinal crops are designated as cultivated/semicultivated plants for prevention/treatment of human/animal diseases. They include cultivated medicinal fungi such as Chinese caterpillar fungus (*Cordyceps sinenesis*), *Coriolus versicolor*, *Ganoderma lucidum*, *Polyporus mylittae*, *Polyporus umbellatus*, *Poria cocos*, and *Lentinus edodes* (Philippoussis *et al.*, 2007); cultivated lichens such as *Thamnolia vermicularis*, *Umbilicaria esculenta*, and *Usnea diffracta*; cultivated mosses such as *Conocephalum conicum*, *Marchantia polymorpha*, and *Sphagnum palustre*; cultivated ferns such as *Huperzia serrtata*, *Lycopodium japonicum*, *Cibotium barometz*, *Alsophila spinulosa*, and *Dryopteris crassirhizoma*; and a large number of cultivated seed plants (higher plants) including gymnosperms and angiosperms.

An increasing number of new drugs with efficacy against some common diseases have been derived from medicinal plants. These include artemisinin from *Artemisia annua* for the treatment of malaria, Folium Ginkgo (*Ginkgo biloba* leaves) extract EGb 761 for age-related memory disease (Alzheimer's disease), and *Salvia miltiorrhiza* extract for cardiovascular disease. However, the increasing use of medicinal plants for healthcare and the plant medicine boom in recent years have imposed a great threat to the conservation of natural resources and endangered plant species (Zhou and Wu, 2006). Owing to overexploitation, wild medicinal plants have become rare (e.g., *Aconitum deinorrhizum*, *Panax* spp., *Paris polyphylla* var. *yunnanensis*, *Rheum emodi*), threatened (e.g., *Berberis artistata* and *Rauvolfia serpentina*), and endangered (e.g., *Dioscorea deltoidea*, *Sassurea lappa*, *Taxus* spp.). This has caused serious ecological damage and rapid genetic loss of medicinal plants, which have forced the need for cooperation and coordination to undertake programs for conservation of medicinal plants to ensure that adequate quantities are available for future generations. Cultivation of medicinal plants can meet the long-term use of medicinal plant resources. Furthermore, it gives scope to improve the quality of the drugs. Many medicinal crops are also used for cosmetic and aromatic purposes, and thus the definition medicinal, aromatic, and cosmetic plants would better describe such crops (Lubbe and Verpoorte, 2011). The medicinal crops discussed in this article are limited to cultivated seed plants.

Resources and Distribution

Medicinal plants are mainly distributed in the tropical and subtropical areas of the world. Accordingly, medicinal crops are also widely cultivated in these areas. They mainly belong to the families Araliaceae, Boraginaceae, Compositae, Dioscoreaceae, Gentianaceae, Lamiaceae, Leguminosae, Liliaceae, Papaveraceae, Rutaceae, Solanaceae, and Umbelliferae. Most of them are herbal plants. **Table 1** shows the main medicinal plants cultivated throughout the world.

Processing and Utilization

Processing of medicinal crops means to dry and then cut or powder the whole plant or just one part of the plant (i.e., flowers, roots, stems, leaves, and seeds). They can be treated with solutions (e.g., water or organic solvents) to obtain crude extracts, which will be further separated to obtain pure bioactive substances. Both crude extracts and pure substances can be used as medicines.

The isolated bioactive components of medicinal crops can be developed either as pharmaceuticals directly or as starting materials for the pharmaceutical industry to produce semisynthetic pharmaceuticals (e.g., cortisone and progesterone; Houghton, 2001). Examples of the former include antimalarial artemisinin from *A. annua*, antimicrobial berberine from *Coptis sinensis*, anticancer alkaloid paclitaxel (taxol) from yew trees (*Taxus* spp.), Sanchi saponins from *Panax notoginseng*, vinblasine from the Madagascar periwinkle (*Catharanthus roseus*), and digoxin from foxglove (*Digitalis lanata*). A good example of the latter is the use of plant steroids (e.g., diosgenin), such as those extracted from yams (*Dioscorea* spp.), to semisynthetically produce corticosteroids and oral contraceptives. Plant-derived components play an important role in the production of such 'single chemical entity' medicines. More than 25% of the pharmaceutical drugs used in the world today are derived from plant natural products (Farnsworth, 1979; Schmidt *et al.*, 2008). **Table 2** lists some examples of plant-derived drugs.

Medicines in the form of extracts, teas, tinctures, or capsules produced from medicinal plants are referred to as

Table 1 Examples of the main medicinal crops distributed throughout the world

Medicinal plant (family)	*Region (country)*
Acacia farnesiana (L.) Willd. (Leguminosae)	Africa
Adenanthera pavonina L. (Leguminosae)	Africa and South Asia
Aegle marmelos (L.) Correa. (Rutaceae)	South Asia (Malaysia and Thailand)
Aesculus hippocastanum L. (Sapindaceae)	Europe (Greece)
Aloe barbadensis Mill. (Liliaceae)	North Africa and South America
Alstonia boonei Wild. (Apocynaceae)	Africa
Alstonia constricta (Apocynaceae)	Australia
Ammi majus L. (Umbelliferae)	South Asia
Andrographis paniculata Nees. (Acanthaceae)	South Asia
Angelica sinensis (Oliv.) Diels (Umbelliferae)	Asia (China)
Annona squamosa L. (Annonaceae)	Australia, Asia (China), and Central America
Aquilaria agallocha (Lour.) Roxb.	Australia and Southeast Asia (China, Indonesia, Malaysia, and Vietnam)
Arctostaphylos uva-ursi (L.) Spreng. (Ericaceae)	Europe
Artemisia absinthium L. (Compositae)	Asia, Europe, and North America
Artemisia annua L. (Compositae)	East Asia (China)
Artemisia capillaries Thunb. (Compositae)	Asia (China)
Asclepias tuberosa L. (Asclepiadaceae)	North America
Astragalus membranaceus (Fisch.) Bunge (Leguminosae)	Asia (China)
Astragalus mongholicus Bunge (Leguminosae)	Asia (China)
Atractylodes macrocephala Koidz. (Compositae)	Asia (China)
Azadirachta indica A. Juss.(Meliaceae)	Asia (Burma, and India)
Cananga odorata (Lamk.) Hook. f. et Thoms. (Annonaceae)	South Asia and Africa
Carthamus tinctorius L. (Compositae)	Asia (China)
Centella asiatica (L.) Urban (Umbelliferae)	Africa, Asia, and Australia
Chondrodendron tomentosum (Menispermaceae)	Central America and South America
Cinchona ledgeriana (Howard) Moens et Trim (Rubiaceae)	South America and Africa
Cissus modecoides Planch. var. *subintegra* Gagn (Vitaceae)	Central America
Codonopsis pilosula (Franch.) Nannf. (Campanulaceae)	Asia (China)
Cola acuminata Schott et Endl. (Sterculiaceae)	South America (Brazil) and West Africa (Nigeria)
Coleus forskohlii (Willd.) Briq. (Lamiaceae)	Southeast Asia (Bhutan, China, India, and Nepal)
Coptis chinensis Franch. (Ranunculaceae)	Asia (China)
Curcuma longa L. (Zingiberaceae)	South Asia (India)
Datura stramonium L. (Solanaceae)	South Asia (Iran) and South America (Ecuador)
Digitalis purpurea L. (Scrophulariaceae)	Europe
Dioscorea opposita Thunb. (Dioscoreaceae)	Asia (China)
Dioscorea zingiberensis C. H. Wright (Dioscoreaceae)	Asia (China)
Dolomiaea souliei Shih (Compositae)	Asia (China)
Dracaena draco L. (Liliaceae)	South America (Brazil)
Echinacea purpurea Moench (Compositae)	Europe
Ephedra sinica Stapf. (Ephedraceae)	Asia (China)
Eschscholzia californica Cham. (Papaveraceae)	North America
Eucalyptus globulus Labill. (Myrtaceae)	Australia and Asia (China)
Eucommia ulmoidea Oliv. (Eucommiaceae)	Asia (China)
Fallopia multiflora (Thunb.) Harald. (Polygonaceae)	East Asia (China)
Fritillaria cirrhosa D. Don (Liliaceae)	East Asia (China)
Gastrodia elata Blume (Orchidaceae)	East Asia (China)
Gentiana scabra Bunge (Gentianaceae)	East Asia (China)
Ginkgo biloba L. (Ginkgonaceae)	East Asia (China)
Glycyrrhiza uralensis Fisch. (Leuguminosae)	East Asia (China)
Hamamelis virginiana (Hamamelidaceae)	North America
Hydrastis canadensis (Ranunculaceae)	North America (Canada and USA)
Hyoscyamus niger L. (Solanaceae)	South Asia
Hypericum perforatum L. (Guttiferae)	North America, Europe, and Asia
Hyssopus officinalis (Lamiaceae)	Europe and Asia (India and Iran)
Lavandula angustifolia L. (Lamiaceae)	Europe
Levisticum officinale Koch. (Umbelliferae)	Asia, Europe, and North America
Lonicera japonica Thunb. (Caprifoliaceae)	Asia (China and Japan)
Lycium chinense Miller (Solanaceae)	East Asia (China)
Magnolia officinalis Rehd. et Wils. (Magnoliaceae)	East Asia (China)
Marsdenia condurango Reich. (Asclepiadaceae)	South America
Melaleuca alternifolia (Myrtaceae)	Australia

(*Continued*)

Table 1 Continued

Medicinal plant (family)	*Region (country)*
Mosla chinensis Maxim. (Poaceae)	South Asia
Myristica fragrans Houtt. (Myristicaceae)	South Asia (Indonesia and Malaysia)
Myroxylon pereirae L. (Leguminosae)	South America
Nigella damascene L. (Ranunculaceae)	North America
Ocimum sanctum L. (Lamiaceae)	Asia (China, India, Malaysia, Indonesia, and Philippines) and Australia
Oenothera erythrosepala Borb. (Onagraceae)	Europe, North America, South America, and Asia (China)
Olea europaea L. (Oleaceae)	North Africa
Panax ginseng C. A. Mey. (Araliaceae)	East Asia (China, Japan, and Korea)
Panax notoginseng F. H. Chen (Araliaceae)	East Asia (China)
Panax quinquefolium L. (Araliaceae)	North America (Canada and USA)
Papaver somniferum L. (Papaveraceae)	South Asia (India and Turkey) and South America (Ecuador)
Peganum harmala L. (Zygophyllaceae)	South Asia
Phellodendron amurense Rupr. (Rutaceae)	Asia (China)
Phellodendron chinense Schneid. (Rutaceae)	Asia (China)
Physostigma venenosum Balf. (Leguminosae)	West Africa
Phytolacca Americana L. (Phytolaccaceae)	North America
Pinellia ternate (Thunb.) Breit. (Araceae)	Asia (China)
Piper longum L. (Piperaceae)	South Asia
Piper methysticum Forst. (Piperaceae)	Europe
Piper nigrum L. (Piperaceae)	South Asia
Platycodon grandiflorus (Jacq.) A. DC. (Campanulaceae)	Asia (China, Japan, and Korea)
Podophyllum hexandrum (Berberidaceae)	Asia (India)
Polygala tenuifolia Wild. (Polygalaceae)	Asia (China)
Pueraria lobata (Willd.) Ohwi. (Pedaliaceae)	South Africa
Quassia amara L. (Simaroubaceae)	South America
Ranunculus ternatus Thunb. (Ranunculaceae)	South America and Asia (China)
Rauvolfia womitoria Afzel. (Apocynaceae)	South America
Rehmannia glutinosa Libosch. (Scrophulariaceae)	Asia (China)
Rhodomyrtus tomentosa Hassk. (Myrtaceae)	South Asia (India)
Ricinus communis (*Euphorbiaceae*)	East Africa
Rosmarinus officinalis L. (Lamiaceae)	Europe, North America (USA), and South America (Ecuador)
Saussurea costa Lipsch. (Compositae)	Asia (China)
Schisandra chinensis (Tuecz.) Baill. (Magnoliaceae)	Asia (China)
Scutellaria baicalensis Georgi (Lamiaceae)	Asia (China, Japan, North Korea, and Mongolia)
Solanum nigrum L. (Solanaceae)	Africa, Asia, Europe, and America
Strychnos nuxvomica (Loganiaceae)	Africa and South Asia
Swertia chirayita (Roxb. ex Flemi) Karsten (Gentianaceae)	South Asia (India)
Syzygium jambos (L.) Alston. (Myrtaceae)	Australia and South Asia
Tabernaemontana orientalis (Apocynaceae)	Australia
Thymus mongolicus Ronn. (Lamiaceae)	South America (Ecuador)
Vaccinium myrtillus L. (Ericaceae)	Europe (Germany)
Valeriana officinalis L. (Valerianaceae)	Europe
Vanilla fragrans (Salisb.) Ames. (Orchidaceae)	Australia, Asia, and Africa
Vanilla planifolia Jacks. ex Andrews (Orchidaceae)	West Africa
Viburnum opulus L. (Adoxaceae)	North America and Europe
Withania kansuensis Kuang et A. M. Lu (Solanaceae)	South Africa, South Asia (India), and Mediterranean
Zanthoxylum americanum P. Mill. (Rutaceae)	North America
Zingiber officinale Rosc. (Zingiberaceae)	Southeast Asia (China and India) and Europe

phytopharmaceuticals, phytomedicines, herbal medicines, and botanical drugs. Medicines are produced to high standards and must undergo clinical evaluation of safety and efficacy (Schmidt *et al.*, 2008). Clinical trials have been performed for many phytomedicines and for the most part it is known which constituents are responsible for the medicinal effect (Houghton, 2001). Phytomedicines are standardized in terms of active constituents. Examples of popular phytomedicines are *G. biloba* extract to improve cognitive function (O'Hara *et al.*, 1998), ginseng (*Panax ginseng*) as a general tonic and cognitive enhancer (Attele *et al.*, 1999), ginger (*Zingiber officinale* Rosc.) against nausea and vomiting (Ernst and Pittler, 2000), and Saw palmetto (*Serenoa repens*) for the treatment of symptomatic benign prostatic hyperplasia (Boyle *et al.*, 2004). Further examples of popular phytomedicines are shown in **Table 3**.

Partial Medicinal Crops

The following are descriptions of some selected important medicinal crops including their taxonomy, distribution, pharmacology, and bioactive components.

Table 2 Examples of commonly used pharmaceutical components of plants

Component	*Chemical class*	*Medicinal plant*	*Therapeutic use*
Artemisinin	Sesquiterpene	*Artemisia annua*	Antimalarial
Atropine	Tropane alkaloid	*Atropa belladonna*, *Hyoscyamus* spp.	Antispasmodic and pupil dilator
Berberine	Isoquinoline alkaloid	*Coptis sinensis*	Antimicrobials
Camptothecin	Indole alkaloid	*Camptotheca acuminate*	Antineoplastic
Digoxin	Steroidal glycoside	*Digitalis lanata*	Heart disorders
Galanthamine	Isoquinoline alkaloid	Various members of *Amaryllidaceae*	Against mild Alzheimer's disease and dementia
Gastrodin	Phenolic glycoside	*Gastrodia elata*	Have a good sedative and hypnotic effect
Morphine and codeine	Alkaloid	*Papaver somniferum*	Analgesic and antitussive
Paclitaxel	Diterpene alkaloid	*Taxus* spp.	Anticancer (ovarian)
Podophyllotoxin	Lignan	*Podophyllum* spp.	Antiviral and antineoplastic
Tanshinones	Diterpenoid quinone	*Salvia miltiorrhiza*	Cardiovascular diseases
Quinine	Quinoline alkaloid	*Cinchona* spp.	Antimalarial
Sanchi total saponin	Triterpenoid glycoside	*Panax notoginseng*	Inhibiting platelet aggregation and increasing cerebral blood flow
Scopolamine	Tropane alkaloid	*A. belladonna*, *Hyoscyamus* spp.	Sedative, against mortion sickness
Sanchi saponin	Triterpenoid	*P. notoginseng*	Promoting blood circulation by removing blood stasis
Vinblastine and vincristine	Indole alkaloid	*Catharanthus roseus*	Anticancer (leukemia)

Table 3 Examples of commonly used phytomedicines

Medicinal plant	*Active component*	*Source*	*Therapeutic use*
Angelica	Coumarins, ferulic acid, and volatile oil	*Angelica sinensis*	Invigorating blood, relieving pain, and moistening the intestines
Milkvetch	Triterpene glycosides and polysaccharide	*Astragalus* spp.	Immune modulator and antimicrobial
Black cohosh	Triterpene glycosides	*Cimicifuga racemosa*	Premenstrual symptoms and dysmenorrhea
Echinacea	Alkylamides	*Echinacea purpurea*	Immune modulator
Ephedra	Alkaloid	*Ephedra sinica*	Congestion, stimulant, and appetite suppressant
Feverfew	Sesquiterpene lactones	*Tanacetum pathenium*	Migraines and inflammation
Garlic	Allicin	*Allium sativum*	High cholesterol, hypertension, and respiratory infections
Ginkgo	Ginkgolides and flavonol glycosides	*Ginkgo biloba*	Mental fatigue and cognitive decline
Ginseng	Ginsenosides and eleutherosides	*Panax ginseng*	Fatigue and stress
Kava kava	Kavalactones	*Piper methysticum*	Anxiolytic
Purple gromwell	Shikonin and its derivatives	*Lithospermum erythrorhizon*	Antimicrobial and antiinflammatory
Saw palmetto	Phytosterols and fatty acids	*Serenoa repens*	Benign prostatic hyperplasia
St. John's wort	Hyperforins	*Hypericum perforatum*	Mild depression
Valerian	Iridoid glycosides, terpenoids, valerianic, and isovaleric acid	*Valeriana officinalis*	Anxiolytic, sleep improvement

Angelica (*Angelica sinensis*)

Angelica sinensis (Oliv.) Diels (family Umbelliferae) is a fragrant and perennial herb native to China, Japan, and Korea. It has been widely cultivated in the southwest of China. Chinese herbalists have used the roots of *A. sinensis* for thousands of years to strengthen heart, lung, and liver meridians, as well as lubricate the bowel. It has been considered as a blood tonic, and has been used by generations of women for health concerns such as menstrual pain and regulating the menstrual cycle. The roots of *A. sinensis* contain 0.4–0.7% volatile oil, the key components of which are *n*-butylidenephthalide, LIG (3-butylidene-4,5-dihydrophthalide), *n*-butyl-phthalide, ferulic acid (4-hydroxy-3-methoxycinnamic acid), nicotinic acid, and succinic acid. The extracts of *A. sinensis* and its active components have wide-ranging pharmacological activities on cardio- and cerebrovascular systems, antiinflammatory effect, immune support and hematopoiesis, and so on. Clinically, *A. sinensis* is officially listed in the Chinese Pharmacopoeia. It is one of the most commonly used traditional Chinese medicines, and has been used in the treatment of menstrual disorders, menorrhagia, and rheumatalgia. It is also used in many tonic preparations and Chinese patent drugs. Angelica root is used to replenish blood, invigorate blood, stop pain, and moisten the intestines. In the USA, *A. sinensis* is used for relief of vasomotor symptoms associated with menopause, including hot flashes, skin flushing, perspiration, and chills (Fang *et al.*, 2012).

Sweet Wormwood (*Artemisia annua*)

Artemisia annua L. (family Compositae) is an annual herb native to China. It grows in many countries such as Australia, Argentina, Bulgaria, France, Hungary, Italy, Spain, and the USA. *Artemisia annua* is used for the crafting of aromatic wreaths, as a source of essential oils used in flavoring of vermouth, and also as a source of artemisinin, a potent antimalarial drug. This herb has been used for malaria therapy in China for over 1000 years (Dhingra *et al.*, 1999). Artemisinin has a peroxide bridge to which its antimalarial properties are attributed. It has a unique structure and lacks a nitrogen-containing heterocyclic ring, which is found in most antimalarial compounds. The isolation and characterization of artemisinin from *A. annua* is considered one of the most novel discoveries in recent medicinal plant research. Artemisinin was isolated from the plant *A. annua* in 1972, and its structure was determined by X-ray analysis in 1979 (Krishna *et al.*, 2008; Balint, 2001).

Periwinkle (*Catharanthus roseus*)

Cathranthus roseus (L.) G. Don (family Apocynaceae) has a pantropic distribution, naturalized in continental Africa, America, Asia, Australia, southern Europe, and on some islands of the Pacific Ocean. This medicinal plant is cultivated as an ornamental, used particularly for beddings, borders, and for mass effect. It blooms throughout the year and is propagated by seeds or cuttings. *Cathranthus roseus* has been studied extensively for its remarkable anticancer constituents of terpenoid-indole alkaloid class such as vincristine and vinblastine. Among other components, ajmalicine and serpentine are used in relieving hypertension and related cardiac disorders (Mujib *et al.*, 2012).

China Goldthread (*Coptis chinensis*)

Coptis chinensis Franch. (family Ranunculaceae) has been used for more than 2000 years in China for treatment of damp-heat syndromes. The major active component in *C. chinensis* is berberine, an isoquinoline alkaloid. There are a few species in genus *Coptis* such as *C. chinensis*, *C. deltoidea*, *C. teetoide* in China, *C. japonica* in Japan, and *C. trifolia* in North America. In China, *C. chinensis* has been extensively cultivated in eastern Sichuan Province and western Hubei Province under good agricultural practice (GAP) for Chinese Crude Drugs. Berberine constitutes the most abundant alkaloid in the dried herb *C. chinensis*. This medicinal plant has long been recognized in the treatment of intestinal infections including acute gastroenteritis, cholera, and bacillary dysentery, which can be linked to their antibacterial, antiviral, and antiinflammatory effects (Kyoko *et al.*, 2007; Tang *et al.*, 2009).

Peltate Yam (*Dioscorea zingiberensis*)

The rhizomes of several species of the genus *Dioscorea* (family Dioscoreaceae), known as yam, are a food staple for the populations of Asia, Africa, and tropical America. Most species contain steroid saponins and sapogenins, such as diosgenin, which is the starting material of industrial interest in the synthesis of many steroids that are on the market as anti-inflammatory, androgenic, estrogenic, and contraceptive drugs. Furthermore, these steroids are reported to possess cytotoxic, antitumor, antifungal, immunoregulatory, hypoglycemic, and cardiovascular properties (Sautour *et al.*, 2007). *Dioscorea zingiberensis* C. H. Wright is the dominant source for diosgenin production in China. The rhizomes have a high content of diosgenin, which is approximately 8% on dry basis (Li and Ni, 2011).

Gastrodia (*Gastrodia elata*)

Gastrodia elata Blume (family Orchidaceae) is well known as an important substance for Chinese medicine in Asian countries. It is broadly distributed in the temperate and boreal regions of China, Korea, and Japan. Cultivation of *G. elata* is associated with the infection of the fungus *Armillaria mellea* (Cha and Igarashi, 1995). *Gastrodia Elata* is used to treat headaches, dizziness, tetanus, epilepsy, infantile convulsions, and numbness of the limbs, providing evidence that *G. elata* has central nervous system-protecting effects. Gastrodin and vanillin derived from *G. elata* show sedative and anticonvulsive effects. The crude extract had an anticonvulsive effect on kainite-induced seizures and epilepsy in rats, and an inhibitory effect on glutamate-induced cell death in IMR-32 human neuroblastoma cells, supporting the central nervous system actions of *G. elata* (Tsai *et al.*, 2011).

Ural Licorice (*Glycyrrhiza uralensis*)

Glycyrrhiza uralensis Fisch. (family Leguminosae) is an important perennial medicinal herb and is mainly cultivated in arid and semiarid areas in China. It has a long history of medicinal use in Europe and Asia to treat peptic ulcer disease, constipation, and cough. There are a variety of components in *G. uralensis* such as flavonoids, triterpenoids, stilbenoids, coumarins, and polysaccharides that show antiinflammatory (e.g., β-glycyhrritinic acid), antimicrobial (e.g., flavonoids), antiviral (e.g., glycyrrhizic acid), antiprotozoal (e.g., lichochalcone A), antioxidative (e.g., licochalcones A, B, C, and D), hepatoprotective (e.g., glycyrrhetinic acid), and antitumor (e.g., glycyrrhetinic acid) activities (Asl and Hosseinzadeh, 2008).

Purple Gromwell (*Lithospermum erythrorhizon*)

Lithospermum erythrorhizon Sieb. et Zucc. (family Boraginaceae) has been used traditionally as medicine in China, and as a dye for staining fabrics and food colorants. It has been cultivated in China, Korea, and other Asian countries. Shikonin and its naphthoquinone derivatives have been proved to be the active components that possess a wide spectrum of wound-healing, antitumor, antifungal, antiHIV, antioxidant, and contraceptive activities (Han *et al.*, 2008). The successful production of shikonin derivatives on a large scale from the cell, tissue, and hairy root (transgenic root) cultures of *L. erythrorhizon* has been achieved (Papageorgiou *et al.*, 1999; Syklowska-Baranek *et al.*, 2012).

Table 4 Examples of the medicinal compounds produced by both endophytic fungi and their host plants

Medicinal compound	*Endophytic fungus*	*Host plant*	*References*
Camptothecin	*Fusarium solani* INFU/Ca/KF/3	*Camptotheca acuminata*	Kusari *et al.* (2009)
Diosgenin	*Paecilomyces* sp. 80	*Paris polyphylla* var. *yunnanensis*	Cao *et al.* (2007)
Huperzine A	*Shiraia* sp. Slf14	*Huperzia serrata*	Zhu *et al.* (2010)
Hypericin	*Chaetomium globosum*	*Hypericum perforatum*	Kusari *et al.* (2008)
α-Irone and β-irone	*Rhizopus oryzae* 94Y-01	*Iris germanica*	Zhang *et al.* (1999)
Paclitaxel (Taxol)	*Alternaria* sp. Ja-69	*Taxus cuspidata*	Strobel *et al.* (1996)
Podophyllotoxin	*Phialocephala fortinii* PPE5	*Podopyllum peltatum*	Eyberger *et al.* (2006)
Vinblastine	*Alternaria* sp. 97CG1	*Catharanthus roseus*	Guo *et al.* (1998)
Vincristine	*Fusarium oxysporium* 97CG3	*C. roseus*	Zhang *et al.* (2000)

Boxthorn (*Lycium chinense*)

Lycium chinense Miller (Solanaceae) is mainly distributed in northern China. It is now widely cultivated in temperate and subtropical countries such as Japan, Korea, and other southeast Asian and European countries. The fruits have been used as a tonic in traditional Chinese medicine, and have been reported to exhibit hypotensive, hypoglycemic and antipyretic activities and to prevent stress-induced ulceration in experimental animals. Scientists have concentrated their attention on elucidating the bioactive components in *L. chinense*, which include polysaccharides, alkaloids, glycopeptides, glycoprotein, peptides, tocopherols, and flavonoids. Other species in the genus *Lycium* include *L. barbarum*, *L. yunnanensis*, and *L. ruthenicum*, which have similar medicinal functions (Qian *et al.*, 2004).

Panax spp. (*Panax ginseng*, *Panax notoginseng*, *Panax quinquefolium*)

Asian ginseng (*P. ginseng* C. A. Mey.), sanchi ginseng (*P. notoginseng* F. H. Chen), and American ginseng (*Panax quinquefolium* L.) are three important cultivated medicinal species in the family Araliaceae. *Panax ginseng*, which is cultivated in northeast China, Japan, and Korea, has been used for over 2000 years as a tonic, stimulant, and fatigue-resistance medicine. *Panax notoginseng*, which is distributed in southwest China (i.e., Yunnan and Guangxi), has been used for more than 400 years in the treatment of trauma and bleeding due to internal and external injury (Guo *et al.*, 2010). *Panax quinquefolium* is native to the hardwood-forest regions of the Eastern part of North America, but it has been successfully cultivated in New Zealand, China, Australia, Holland, France, and Poland (Kolodziej *et al.*, 2006). The main bioactive components in *Panax* species have been proved to be triterpenoid saponins, flavonoids, polysaccharides, and acetylenic compounds.

Yunnan Manyleaf Paris (*Paris polyphylla* var. *yunnanensis*)

Paris polyphylla var. *yunnanensis* (Franch.) Hand.-Mazz. (family Trilliaceae) is a perennial plant native to Yunnan Province, in the southwest of China. Its rhizomes have been used in traditional Chinese medicine as hemostasis, antimicrobial, and antiinflammatory agents for hundreds of years (Zhou *et al.*, 2003a). Its principal bioactive components are thought to be steroids, oligosaccharides, and polysaccharides (Zhou *et al.*, 2003b; He *et al.*, 2006).

Danshen (*Salvia miltiorrhiza*)

Salvia miltiorrhiza Bunge (family Lamiaceae) is a perennial herb widely used in Chinese traditional medicine for treatment of diseases such as coronary heart disease, cerebrovascular disease, hepatitis, hepatocirrhosis, chronic renal failure, dysmenorrhea, and neuroasthenic insomnia (Lu and Foo, 2002). Biologically active components in *S. miltiorrhiza* are considered as phenolic compounds (e.g., rosmarinic acid), tanshinones (e.g., cryptotanshinone), and polysaccharides. The polysaccharide SMP-W1 from the roots of *S. miltiorrhiza* displayed efficient immunoregulatory and antitumor activities (Liu *et al.*, 2013). Other species in the genus *Salvia* include *S. przewalskii* Maxim and *S. verticillata* L., which have similar medicinal functions (Matkowski *et al.*, 2008).

Medicinal Plant-Derived Bioactive Compounds Produced by Endophytic Fungi

Plant endophytic fungi are defined as fungi that spend the whole or part of their lifecycle colonizing inter- or intracellularly inside the healthy tissues of host plants, typically causing no apparent symptoms of disease. They are important components of plant microecosystems (Rodriguez *et al.*, 2009). Plant endophytic fungi are rich and potential resources for producing bioactive compounds with their potential applications in the agriculture, medicine, and food industries (Strobel, 2003; Zhou *et al.*, 2010; Kharwar *et al.*, 2011). Many valuable bioactive compounds with antimicrobial, insecticidal, cytotoxic, and anticancer activities have been successfully discovered from endophytic fungi. During the long period of coevolution, a friendly relationship is formed between each endophyte and its host plant. Some endophytes have the ability to produce the same or similar bioactive compounds as those originated from their host plants (Zhao *et al.*, 2011). Table 4 lists some examples of the medicinal compounds produced by both endophytic fungi and their host plants. Bioactive compounds of the partial medicinal plants could be produced by endophytic fungi through fermentation on a large scale. This could be an important approach for plant resources protection as well as for ecological and environmental conservation.

Conclusions and Future Perspectives

Many wild medicinal plants have become rare, threatened, or endangered due to overexploitation (Chatterjee, 2002). To conserve wild medicinal plant resources and to use them sustainably, the intensive cultivation of medicinal plants is crucial. Countries such as China, India, Indonesia, and Brazil are famous for cultivation and utilization of medicinal crops. GAP for the production of medicinal crops has made great progress through planning and drafting, examination, promulgation, and enforcement since 1999 in China (Ding *et al.*, 2012). Furthermore, bioactive components of medicinal plants could be produced by means of biotechnology (Zhou and Wu, 2006). Biosynthesis of some medicinal compounds may be stimulated by the endophytes existing in medicinal plants, and some medicinal compounds may be produced by the endophytes (Zhao *et al.*, 2011). Thus, the coevolutions on medicinal component biosynthesis between medicinal plants and their endophytes should be studied in detail.

See also: Biotechnology: Plant Protection. Cloning: Plants – Micropropagation/Tissue Culture. Genomics: Plant Genetic Improvement. Root and Tuber Crops. Spices and Aromatics

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Mineral Nutrition and Suppression of Plant Disease

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Glossary

Oomycota A fungal-like chromistan that produces oospores; a water mold related to algae.
Pathogenesis-related proteins Groups of proteins with different chemical properties produced in a cell within minutes or hours following inoculation but all being more or less toxic to pathogens.
Phytoalexin A substance that inhibits the development of a fungus on hypersensitive tissue formed when host plant cells come in contact with the parasite.
Rhizosphere The soil near a living root.
Systemic acquired resistance Systemically activated resistance after primary infection with a necrotizing pathogen accompanied by increased levels of salicylic acid and pathogenesis-related proteins.

Introduction

One of the fundamental strategies for maintaining plant health is to manage the nutritional status of the plant (Datnoff *et al.*, 2007a). Nutrition can often govern the fine line between a crop's susceptibility and resistance to a plant disease. Complete and balanced nutrition should always be the first line of defense against the development of a plant disease. One major problem in providing proper nutrition is that many agronomic and horticultural crops vary in their nutritional requirements and those different nutrients may affect different diseases in different ways. Furthermore, the fertilization regimes necessary to maximize plant health when a plant pathogen is present can differ from optimal fertilization when the pathogen pressure is absent. This article provides an overview of the governing role of nutrition on crop health as related to resistance and susceptibility to disease.

In many cases, the amount of a nutrient needed to suppress a plant disease may far exceed a healthy plant's nutritional requirement for that nutrient, suggesting that many nutrients may participate in multiple mechanisms for plant disease suppression. Chemical interactions with the rooting medium, pH, and specific communities of microorganisms can, in turn, influence disease development. For example, the form of nitrogen (N) can have striking effects on plant disease through root-mediated changes in pH, microbial profile in the root zone, and alterations in the availability and function of micronutrients. Moreover, calcium (Ca) composes only approximately 0.5% of the dry weight of most plants, yet Ca is routinely applied in great quantities to container mixes to affect root medium pH and suppress certain plant diseases. These observations suggest that these inorganic elements are influencing disease directly through physiological mechanisms and indirectly through soil interactions that, in turn, affect the activity of plant pathogens.

Both essential and beneficial elements can affect disease defense mechanisms in plants. These nutrients play important roles in metabolic pathways that lead to the production of lignin, phenols, phytoalexins, and other defense-related molecules. Many of these pathways use enzymes that require the micronutrients manganese (Mn), copper (Cu), zinc (Zn), molybdenum (Mo), or boron (B) as cofactors or activators. Other elements such as potassium (K) and chlorine (Cl) influence osmotic relations, water cycling, and root exudation, which, in turn, influence beneficial microbes. Indirect mechanisms include effects on soil medium nitrification, rooting medium pH, and chemical transformation of micronutrients.

Below, each element's effect on plant disease is discussed, but caution must be exercised in that nutrition must be viewed holistically, because all nutrients affect the uptake and function of other elements and can ultimately increase or decrease plant susceptibility to disease.

Nitrogen

Nitrogen is the fourth most abundant element in plants and is an essential component of amino acids, enzymes, hormones, phenolics, phytoalexins, and proteins, all of which can have direct effects on disease development. The amount of N applied can have immediate effects on a plant disease, relative to the nutritional requirement of the plant (**Table 1**). The greatest responses are generally in the range from deficiency to physiological sufficiency. Nitrogen-deficient plants may not provide the nutrient environment necessary for obligate pathogens, whereas excess N may inhibit the production of defense responses to other pathogens (Huber, 1980; Huber and Watson, 1974).

The time of application can also have striking effects on disease development. Side-dressing nitrogen can compensate for early-season losses caused by leaching and denitrification but, more importantly, can avoid the early-season seedling diseases that accompany nitrogen application, such as damping-off caused by species of *Rhizoctonia* or *Pythium*. However, caution should be exercised as mechanical damage made to the roots from side dressing may increase root rots. Many times the choice as to when to apply nitrogen can be influenced by disease pressure. For example, delaying N application

Table 1 Influence of nitrogen form on plant disease

Disease or disorder	*Pathogen or causal agent*	*Host*	*NH_4*	*NO_3*
Aflatoxin	*Aspergillus flavus* group	Corn and peanut	D	–
Anthracnose	*Gnomonia leptostyla*	Black walnut	D	D
Black root rot	*Thielaviopsis basicola*	Tobacco	D	I
Black root rot	*Rhizoctonia fragariae*	Strawberry	D	I
Blast	*Magnaporthe grisea*	Rice	D	I
Blossom-end rot	Physiological disorder	Tomato	I	–
Brown patch	*Rhizoctonia solani*	Ryegrass	D	–
Club Root	*Plasmodiophora brassicae*	Cabbage	D	–
Corky root	*Pyrenochaeta lycopersici*	Tomato	I	I
Crown rot	*Rhizoctonia solani*	Beets	I	D
Crown and root rot	*Fusarium oxysporum*	Tomato	I	D
Eyespot	*Pseudocercosporella herpotrichoides*	Wheat	I	D
Leaf blight	*Erwinia chrysanthemi*	Chrysanthemum	I	I
Leaf spot	*Alternaria macrospora*	Cotton	D	–
Lesion nematode	*Pratylenchus penetrans*	Strawberry	D	I
Mummy berry	*Monilinia vaccinii-corymbosi*	Blueberry	D	–
Nematodes	*Criconemella* spp.	Turfgrass	–	I
Root rot	*Fusarium oxysporum* and *Fusarium proliferatum*	Asparagus	I	D
Root rot	*Phytophthora parasitica*	Tomato	–	I
Root rot	*Fusarium* spp.	Pea	I	D
Root rot	*Thielaviopsis basicola*	Pansy	D	I
Root and stem rots	*Sclerotium rolfsii*	Many plants	D	D

Abbreviations: D, decrease; I, increase; – no effect.

Source: Adapted from Huber, D.M., Thompson, I.A., 2007. Nitrogen and plant disease. In: Datnoff, L.E., Elmer, W.H., Huber, D.M. (Eds.), Mineral Nutrition and Plant Disease. St. Paul, MN: American Phytopathological Society, pp. 31–44.

in winter wheat until spring can result in early N deficiency and increase susceptibility of plants to take-all root rot caused by *Gaeumannomyces graminis* (Sacc.) Arx & D. Olivier var. *tritici* (J. Walker) (Huber and McCay-Buis, 1993). However, a fall application can impose excess N availability during cold, wet winter periods and increase susceptibility to *Rhizoctonia* root rot (Huber, 1989).

The rate of nitrogen also affects disease susceptibility. Excessive nitrogen is well documented to increase the severity of *Botrytis* blight on numerous greenhouse plants (Dik and Wubben, 2007; Yermiyahu *et al.*, 2006). Root diseases are similarly exacerbated under high nitrogen rates. Root rot of wheat caused by *Fusarium culmorum* (Papendick and Cook, 1974) and *Pythium* root of geraniums (Gladstone and Moorman, 1989) are more severe under high nitrogen regimes. Although growers pay close attention to rates of nitrogen applied, most do not recognize the role that form of nitrogen may play in enhancing or suppressing disease. Nitrogen is the only nutrient that is available as both a negatively charged ion, nitrate (NO_3^-) and a positively charged ion, ammonium (NH_4^+). Nitrate N and NH_4-N are metabolized differently in plants and can have opposite effects on diseases. In fact, many of the conflicting research reports regarding the role of nitrogen in plant disease may be due to a failure to recognize and report the form of nitrogen used in the experiments. Interestingly, the form of nitrogen can have striking effects on the effectiveness of biological control. Borrero *et al.* (2012) observed suppression of *Fusarium* wilt of tomato with *Trichoderma* spp. but only under increasing concentrations of NH_4-N. Suppression from *Trichoderma* spp. was minimal under the nitrate regime.

Many of the underlying mechanisms governing disease suppression with different nitrogen forms relate to soil pH (Smiley and Cook, 1973). Nitrate N increases the pH of the rooting medium and NH_4-N lowers pH, making both the bulk soil and rhizosphere more acidic. These effects occur through microbial and chemical reactions in the soil as well as root-mediated ion exchanges near the roots. Acidification of the root zone also solubilizes oxides of zinc, copper, manganese, and iron, which increases their availability for uptake. As discussed below, these micronutrients can play pivotal roles in disease suppression. When the nitrogen form is applied as nitrate, *Fusarium* wilts and root rots of asparagus, basil, beets, carnation, chrysanthemum, cyclamen, gladiolus, tobacco, tomatoes, and watermelon are reported less severe than when applied as NH_4-N (**Figure 1**; Elmer, 1997; Huber and Thompson, 2007). Our understanding of this phenomenon relates to the effect on rhizosphere pH, root exudation, and the availability of Fe to microbes (Jones and Woltz, 1970).

The opposite is true for diseases caused by *Gaeumannomyces* spp., *Thielaviopsis* spp., and *Verticillium* spp. where NH_4-N suppresses disease and NO_3-N favors it. Take-all root rot of wheat caused by *G. graminis* can be suppressed in the field by supplying nitrogen in the ammoniacal form, such as NH_3, $(NH_4)_2SO_4$, NH_4Cl, and $(NH_4)_2PO_4$ (Huber, 1989; Reis *et al.*, 1982). Ammonium sulfate suppressed take-all patch of turfgrass but was more effective when combined with other cultural practices for disease control (Dernoeden, 1987). The effects of NH_4-N occur through chemical reactions in the soil as well as root-mediated ion exchanges near the roots that, in turn, increase the availability and uptake of micronutrients and promote beneficial microbes in the rhizosphere.

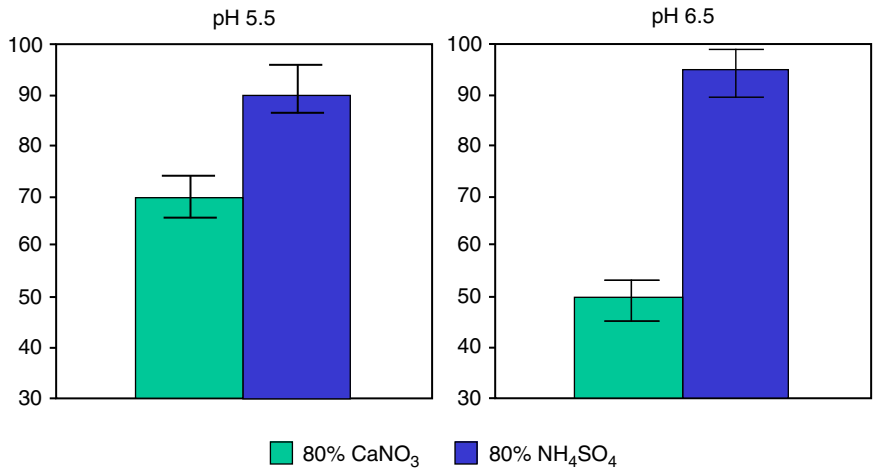


Figure 1 Effect of N form and soil pH on percentage of tomatoes with *Fusarium* wilt. Data from Jones, J.P., Woltz, J.P., 1970. *Fusarium* wilt of tomato: Interaction of soil liming and micronutrient amendments on disease development. Phytopathology 60, 812–813.

Managing soil acidity with NH_4-N has become an important strategy for managing black root rot caused by *Thielaviopsis basicola* on tobacco and ornamentals. On eggplant, *Verticillium* wilt was suppressed and yields were increased by 20% when NO_3-N was replaced with NH_4-N (Elmer and Ferrandino, 1994). In strawberry, the black root rot complex caused by *Rhizoctonia fragariae* and the lesion nematode, *Pratylenchus penetrans*, was reduced by the application of ammonium sulfate, but not with calcium nitrate fertilizer (Elmer and LaMondia, 1999a,b). Plants treated with ammonium sulfate had more yield, more leaf area, more runners, and higher tissue levels of K, S, Mn, and Zn than strawberries treated with calcium nitrate.

It is very common for N to interact with other nutrients. Potassium increases uptake of NO_3 and promotes the synthesis of organic N compounds, whereas phosphorus and chlorine decrease NO_3 uptake and enhance the uptake of NH_4. Ammonium and Cl increase the uptake of manganese (Mn). Manganese is required for NO_3 assimilation and protein synthesis. Molybdenum (Mo), magnesium (Mg), iron (Fe), ascorbic acid, and energy are required for the reduction of NO_3 to NH_4. Growers should also pay attention to the ion that accompanies the nitrogen salt.

Phosphorus

Phosphorus (P) is the second component listed in the analysis of fertilizers due to its vital role in cell division, energy transfers, and its regulatory role for transport of sugars within the plant. Although there are exceptions, most reports on P and plant disease suggest that increasing phosphorus above that necessary for proper growth may be associated with increased disease. In fact, those cases where P reduced disease may have been in situations where the element was deficient. Cases where the disease became worse following P application might have been in soils where excess P decreased the availability of other elements that, in turn, increased the plant's susceptibility. In acidic soils, P reacts with Fe, Al, and Mn to form insoluble products, making P less available. In alkaline soils, P reacts with Ca and reduces P availability. Therefore, maintenance of soil pH is very important to maximize availability of P and promote root health.

Another important consideration is the role of beneficial mycorrhizal fungi in P nutrition and disease development. These fungi form a symbiotic relationship with the plant's roots known as mycorrhizae that improve plant health and reduce disease damage. Many crops have mycorrhizal associations that are likely interrupted during propagation cycles. If mycorrhizae are present or have been established on roots, there may be a need to alter the P applications because mycorrhizal associations can be inhibited by increased P availability. Commercial applications of mycorrhizal fungi are available and may have value in management of soilborne disease. Their use may allow other nutrients to be more available as added P could lead to the precipitation of other elements.

Foliar applications of phosphorous acid (H_3PO_3), or its salts (also referred to as phosphonate, phosphate, and phosphonic acid), may inhibit plant pathogens from the fungal-like Oomycota, i.e., species of *Phytophthora* and *Pythium* (Brunings *et al.*, 2012). The inhibiting effect from phosphorous acid is probably due to either an inhibition of the metabolic activity of the pathogen or a direct toxic effect on the pathogen. Phosphorous acid has been demonstrated to control a number of plant diseases, including downy mildew, late blight of potato and tomato, foliar blights on peppers and cucurbits, root and stem rots, and damping off.

Potassium

Potassium (K) plays many essential roles in plant nutrition. Although K is not structurally bound in the plant, it increases root growth, improves water and nutrient uptake, increases cellulose and protein content, reduces lodging, enhances and regulates at least 60 different plant growth enzymes, and can affect the occurrence of a plant disease (Prabhu *et al.*, 2007).

Potassium alone or its combination with N, P, and other nutrients can alter the disease severity of many soilborne and

Table 2 Effect of potassium on plant disease development

Pathogen Group	*Number of articles showing the effect of potassium on disease*[a]			
	Decreased	*Increased*	*No effect*	*Total*
Fungal	89	33	8	130
Bacterial	19	5	*	24
Viruses	9	5	3	17
Nematodes	3	6	1	10

[a]Data adapted with permission from Huber, D.M., Arny, D.C., 1985. Interactions of potassium with plant diseases. In: Munson, R.D. (Ed.), Potassium in Agriculture. Madison, WI: American Society of Agronomy, pp. 467–488.
*Data not available.

foliar plant pathogens. These have been extensively reviewed before for a number of crops, diseases, and pathogens (Prabhu *et al.*, 2007; Huber, 1980). Even though no generalization can be made on the effect of K on disease development, this element is reported to decrease the intensity of many diseases caused by pathogenic fungi, bacteria, viruses, and nematodes (**Table 2**). Unfortunately, in many of these studies, investigators have failed to give adequate consideration to the companion anions, nutrient balance, and nutrient status in order to determine a definitive role of K (Prabhu *et al.*, 2007). Thus, there may be a greater response to K in deficient than fully sufficient plants or with an excess of K beyond that required for nutrient sufficiency. This suggests that K may affect host resistance more as opposed to a direct effect on the pathogen.

Some rice genotypes are more efficient than others in K uptake, and this may contribute to their increased disease resistance and higher grain yield (Fageria *et al.*, 1990). Several diseases increase with an increase in N and the effect of K can be directly correlated with the level of N. The critical factor affecting rice blast caused by *Pyricularia oryzae* is the N:K ratio in leaves. Blast severity is low when there is a high tissue K:N ratio, whereas a high N:K ratio increases blast. When the concentration of N is low, the addition of K suppresses rice blast. However, when the level of N is high, the addition of K increases blast. The K and N ratio greatly influences plant growth as well as disease development, and the ratio may change with growth of the plant.

Although the physiological function of K in disease resistance mechanisms is not well understood, nutritional factors favoring host plant resistance have been attributed to alterations in protein or amino acid availability, decreased cell permeability, or decreased susceptibility of tissue to maceration and penetration (Prabhu *et al.*, 2007). Arginine increases as the level of K increases and resistance of potato plants to late blight (*Phytophthora infestans)* increases as the levels of K increases due to the accumulation of fungistatic levels of arginine in leaves. Exudates of arginine inhibit germination of sporangia of *P. infestans* and exudation is lowest in the absence of K when N and P are high. The ability of various soil-applied or foliarly applied K salts, such as potassium phosphonate, K_2HPO_4, KH_2PO_4, and KNO_3, to stimulate systemic acquired resistance in susceptible plants against powdery mildews, anthracnose, rust, and several other pathogens suggests that fundamental changes in physiological pathways are probably important in disease resistance (Reuveni *et al.*, 2000; Becot *et al.*, 2000; Orober *et al.*, 2002). Anatomical changes affected by K nutrition may also play an important role in disease resistance. Enhanced silicification of cell walls by K is one explanation for increased disease resistance. A deficiency of K decreases Si accumulation in epidermal cells and increases the susceptibility of rice to leaf blast. Potassium, in combination with P, induces the development of thicker cuticles and cell walls that function as mechanical barriers to infection by several pathogens or limit the growth of some pathogens as a result of a higher proportion of sclerenchyma tissue (Huber, 1980).

Fertilizer sources of K include various salts from which the anion may also manifest an effect on disease in combination with or independent of the K ion. The more common sources of K fertilizers include the chloride (muriate) or sulfate salts; however, carbonate, nitrate, phosphate (mono- and dibasic), silicon, and various organic salts are also used. It is difficult to distinguish between the effect of the K and the anion in the fertilizer salt used for disease management unless many combinations are studied. It is well known that the Cl anion can affect various diseases independent of K (Elmer, 2007) and that K influences plant uptake of nitrate, Ca, and other mineral elements. Similar interactions are observed with phosphate salts of K (Lopez and Lucas, 2002). The level of K in plants depends on the availability of Mg and Ca. Calcium alters the Ca:K ratio and interacts with other elements. The function of K in cellular organization and permeability is complimented by large Ca reserves in mature plant tissue. Calcium enhances K availability in neutral soils, but not in acidic soils. An interaction between K and Mg was demonstrated on rice leaf blast; blast increased when K was applied alone but could be reduced by adding Mg.

Calcium

Calcium (Ca) is the third most abundant nutrient in most plant species. Calcium concentrations in plant tissues are usually twice that of magnesium. Because both nutrients are cations with a double positive charge, they often antagonize and interact with each other in nutrient management programs.

Calcium is extremely important in normal cell growth where it forms the glue between cell walls, i.e., Ca-polygalacturonates are needed for the middle lamella for cell wall stabilization. This element may act as a secondary messenger; consequently, it plays a role in many enzymatic reactions involved in early plant defense mechanisms (Huber *et al.*, 2012). Calcium is commonly applied as $CaCl_2$, $CaSO_4$, or $Ca(NO_3)_2$.

Many previous studies investigating the role of $Ca(NO_3)_2$ credited all of the plant disease suppression to the NO_3 component and failed to recognize the calcium ion. Unfortunately, most studies do not examine different sources of Ca and its companion anion to demonstrate the contribution of calcium to plant disease control. A study on roses found that foliar applications of $CaCl_2$ reduced the incidence of gray mold (*Botrytis cinerea)*. Calcium applications to carrot infected with *Sclerotium rolfsii* reduced damage and increased yield. Many times the influence of Ca on soil pH is more important than the actual concentration of Ca in soil. For example, a reduction in the incidence of cavity spot of carrot by *Pythium coloratum* was achieved with lime, whereas gypsum ($CaSO_4$), which does not affect pH, applied to the same soil at the same rate had no effect on the incidence of disease. The role of pH and Ca in suppressing clubroot of cabbage caused by *Plasmodiophora brassicae* was recognized in 1878, and liming of the soil for control of clubroot has been practiced for more than 200 years. The severity of *Fusarium* wilt of tomato caused by *Fusarium oxysporum* f. sp. *lycopersici* is also reduced with calcium applications. Greenhouse and field experiments in Florida showed that amending *Fusarium*-infested soil with gypsum ($CaSO_4$) did not increase the soil pH and did not reduce the occurrence of tomato *Fusarium* wilt, whereas the Ca content of tissues of plants grown in soil amended with hydrated lime ($Ca(OH)_2$) was increased and did reduce the occurrence of wilt.

Spraying calcium salts, such as $CaCl_2$ and $Ca(NO_3)_2$, on tomatoes reduced powdery mildew colonies. A study on roses found that foliar applications of $CaCl_2$ reduced the incidence of gray mold (*B. cinerea*). The same study found that increasing Ca concentrations in the soil improved the shelf life of the flower. Calcium may also influence the spread of *Phytophthora* spp. in water; vinca plants that were flood irrigated and then infected with *Phytophthora* spp. were healthier when the complete fertilizer solution was amended with $Ca(NO_3)_2$. Other studies demonstrated that calcium applied as either $CaCl_2$ or $Ca(NO_3)_2$ in water or in Ca-free soluble fertilizer solutions suppressed the release and the motility of the swimming spore. These results demonstrate the urgent need to understand more about how calcium amendments interfere with *Phytophthora* in recirculating irrigation systems.

Magnesium

Magnesium (Mg) is usually applied as $MgSO_4$ or $MgCl_2$ and has been associated with both increased disease and suppression of plant disease (Jones and Huber, 2007). Of 46 studies investigating the role of magnesium on plant disease, 22 found that this nutrient decreased disease, 18 found that it increased disease, and 6 found that there was little or no difference. As the data are so conflicting, no real patterns can be discerned. As a consequence, there is a paucity of information regarding the direct effects of Mg on plant pathogenesis. It may be that some of these studies corrected a magnesium deficiency and the result was a healthier plant with more vigor and disease resistance. When Mg was applied in excess of what is required for normal growth, a nutritional imbalance developed that promoted plant stress and more disease. The few examples on ornamentals may illustrate this point. The addition of extra magnesium to potting soil was associated with increased damping-off of calendula. However, when carnations were grown on calcareous soils, applications of Mg suppressed *Fusarium* wilt. The latter study was likely a result of the added magnesium correcting a deficiency due to the high Ca concentration.

Chlorine

Chlorine has been routinely applied to crops as chloride (Cl), which served as a companion ion for NH_4-N, K, and Ca fertilizers. Chloride was thought to have little value in improving plant growth because Cl was thought to be highly available in soils and not essential. Yet reports of chloride deficiency in more than 11 economic crops have been published (Engel *et al.*, 1997; Fixen, 1993; Gausman *et al.*, 1958). The role of Cl in plant disease management has also long been misunderstood (Elmer, 2007). The benefits of Cl are still mistakenly being ascribed to the accompanying cation. For example, although it is well documented that proper K nutrition will suppress some plant diseases, many subsequent studies that examined different forms of K found that the ameliorating effects on disease were restricted to KCl amendments, suggesting that Cl was the active ion.

Nutritionally, Cl is regarded as a micronutrient, yet, as in the case of Ca, benefits are achieved with rates that far exceed the plant's nutritional requirements. Monocots tend to be more tolerant of high amounts of chloride. High rates of Cl salts have marked effects on inhibiting soil nitrification, enhancing availability of Mn and other micronutrients, and on increasing beneficial microorganisms.

As an element, Cl^- is the only inorganic anion that is not structurally bound to a metabolite. Its major role is to serve as a charge-balancing ion. When a cell absorbs Cl^-, it accumulates in the cell vacuole and lowers the cell water potential below that of the medium surrounding the cell. Water then flows into the cell and increases hydrostatic cell pressure so that it maintains a pressure that exceeds the force exerted by the plasmalemma. The cells remain turgid and are able to grow even when drought conditions prevail. Theoretically, plants that get root diseases might be protected by supplying sufficient Cl so that they could still grow normally in soils with greater moisture deficits. Studies are needed to validate this theory. Chloride ions also alter the quantity and quality of organic solutes that are exuded into the rhizosphere, thus reducing the germination of and infection by root pathogens. Another major role of Cl in disease suppression comes from its effect on increasing the availability of Mn, which has direct effects on host resistance.

Most reports that demonstrate disease suppression with chloride fertilization have been conducted on monocots, but there are many notable studies where crop health was advanced on dicots (**Table 3**; Maas, 1986; Fixen, 1993). Plants such as asparagus, barley, beets, celery, and coconut evolved near coastlines (Bailey and Bailey, 1976) and acquired tolerance or even preference for chloride in their nutrition. It appears that chloride nutrition may have its greatest benefits to the host in providing tolerance to stresses such as drought and

Table 3 Host plants, diseases, and pathogens suppressed by chloride salts

Host plant	*Disease*	*Pathogen(s)*
Asparagus	*Fusarium* crown and root rot	*Fusarium oxysporum* *Fusarium proliferatum*
Barley	Common root rot	*Bipolaris sorokiniana Fusarium culmorum*
	Powdery Mildew	*Erysiphe graminis* f. sp. *hordei*
	Rust	*Puccinia hordei*
Beets	*Rhizoctonia* root and crown rot	*Rhizoctonia solani*
Celery	*Fusarium* yellows	*Fusarium oxysporum* f. sp. *apii*
Coconut	Leaf spot	*Bipolaris incurvata*
Corn	Stalk rot	*Gibberella zeae* *Gibberella fujikuroi*
Corn	Smut	*Ustilago maydis*
Cyclamen	*Fusarium* wilt	*Fusarium oxysporum* f. sp. *cyclaminis*
Date Palm	*Fusarium* wilt	*Fusarium oxysporum* f. sp. *albedinis*
Pearl Millet	Downy Mildew	*Sclerospora graminicola*
Sorghum	Stalk rots	*Gibberella thapsinum* *Gibberella zeae* and *Macrophomina phaseolina*
Soybeans	Soybean cyst nematode	*Heterodera glycines*
	Sudden death	*Fusarium solani* f. sp. *glycines*
Wheat	Take-all	*Gaeumannomyces graminis* var. *tritici*
	Root rot	*Fusarium culmorum* *Gibberella zeae* *Bipolaris sorokinian*
	Stripe (yellow) rust	*Puccinia striiformis*
	Leaf Rust	*Puccinia recondite* f. sp. *tritici*
	Powdery mildew	*Erysiphe graminis* f. sp. *tritici*
	Tanspot	*Pyrenophora tritici-repentis*
	Glume blotch	*Septoria tritici*
	Stagonospora blotch	*Phaeosphaeria avenaria*

Source: Adapted from Elmer, W.H., 2007. Chlorine and plant disease. In: Datnoff, L.E., Elmer, W.H., Huber, D.M. (Eds.), Mineral Nutrition and Plant Disease. St. Paul, MN: American Phytopathological Society, pp. 189–202.

disease. For asparagus, NaCl applications increased fern vigor and spear yields by 15–30% in plots affected by *F. oxysporum* f. sp. *asparagi* and *Fusarium proliferatum*, but there was no evidence that NaCl improved growth in healthy plantings (Reid *et al.*, 2001). Barley had less common root rot caused by *Bipolaris sorokiniana* (Goos *et al.*, 1989; Timm *et al.*, 1986) when plants were fertilized with chloride. Kettlewell *et al.* (1990) observed suppression of powdery mildew of wheat caused by *Erysiphe graminis* f. sp. *tritici* and brown rust of barley caused by *Puccinia hordei*, when plants were sprayed with KCl. As adequate K was found in the soil, it was concluded that a potassium deficiency was unlikely.

Elmer (1997) found that applications of NaCl, KCl, $CaCl_2$, and $MgCl_2$ were equal in suppressing *Rhizoctonia* root rot of table beets, caused by *Rhizoctonia solani*. Yields were increased in infested soil when NaCl (560 kg ha^{-1}) was applied in an NH_4-N regime, but not in an NO_3-N regime (Elmer, 1997). Alternatively, Schneider (1985) found that the effectiveness of chloride in suppressing *Fusarium* yellows of celery was enhanced in an NO_3-N regime and in the presence of adequate potassium. Both studies demonstrate the complexities of chloride nutrition and its interaction with other elements.

Chloride fertilization contributes to a range of physiological and soil chemical responses. Although Cl applied at high concentrations may have a minor toxic effect on the pathogen, most soilborne pathogens grew better in culture as the chloride concentration increased by 0.5–1.0% (Firdous and Shahzad, 2001; Suleman *et al.*, 2001). Other processes that act through the soil environment, host physiology, or microbial community are more probable mechanisms for disease suppression. Chloride affects nitrification (Christensen *et al.*, 1986), manganese availability (Krishnamurti and Huang, 1992), and osmoregulation (Kettlewell *et al.*, 2000; Schneider, 1990). It has also been associated with enhancing biological control (Amir *et al.*, 1996; Elmer, 1995). Scientists at Oregon State University suspected that chloride was affecting water relations in wheat (Christensen *et al.*, 1981; Powelson and Jackson, 1978). Using pressure chambers to measure leaf water potential (ψ leaf) and thermocouple psychrometry to measure osmotic potential (ψ osmotic) in cell sap, they observed lower leaf water potentials and lower osmotic potentials in leaves treated with NH_4Cl than in leaves fertilized with $(NH_4)_2SO_4$. Turgor potential (ψ pressure), calculated from the formula ψ leaf$=\psi$ osmotic$+\psi$ pressure, was often greater in Cl-treated plants. Elmer and LaMondia (1999a,b) similarly monitored the water potential of ferns of NaCl-treated asparagus plants and found that NaCl applications significantly lowered the predawn fern water potential and increased the estimated turgor potential. Kettlewell and colleagues (Kettlewell *et al.*, 2000; Mann *et al.*, 2004) also found that KCl applications reduced the osmotic potential of the wheat leaves and prevented the germination of spores of *E. graminis*. These studies implicated chloride in reducing the osmotic potential of cell sap. The optimal water potential for most

plant-infecting fungi is less than −0.5 mPa, and the growth rates of most of them are reduced by 50% when the water potential decreases to −3.0 mPa. There are exceptions. For example, *F. culmorum* prefers an osmotic potential of −0.8 to −1.2 mPa. Complete inhibition of many pathogens occurs at −5.0 to −10 mPa (Cook and Papendick, 1972). The reduced growth of the pathogen before the onset of pathogenesis would play an important role in reducing disease. Schneider (1990) advanced a theory that chloride ions are used by plants to tolerate the osmotic up-shocks that plant cells encounter when plant water potential is abruptly altered. In the absence of chloride ions, root cells manufacture organic ions, such as organic acids and amino acids, to maintain charge balance. Schneider (1990) argued that when plant water potential is altered by irrigation or changes in irradiation, organic solutes are quickly exported to the root apoplast to maintain a pressure potential within the root cells. These organic compounds would, in turn, act as nutrition for root pathogens before pathogenesis. When chloride was applied, plants would need to produce less organic and amino acids for charge balance. Roots would export chiefly chloride ions of low nutritional value in their exudates. The concept of altered root exudation, as proposed by Schneider (1990), may explain changes in microbial communities in the rhizosphere. The possible role of beneficial microbes in chloride-treated wheat plants was proposed by Halsey and Powelson (1980) and Christensen *et al.* (1981). Chloride fertilization of neutral soils has also been associated with changes in the microbial community (Amir *et al.*, 1996; Elmer, 1995, 2003). Elmer (1995) isolated bacteria from NaCl-treated asparagus plants and found greater densities of beneficial fluorescent pseudomonads. It is reasonable to assume that the effect of chloride in reducing osmotic potential also affects water cycling and root exudations. In later split root studies, Elmer (2003) reported that NaCl application to asparagus decreased root exudation of malic acid and amino acids, increased Cl ions, and increased fluorescent pseudomonads on the nontreated side of the root system. Thus, chloride had a root-mediated effect on the microbial community.

The ability to increase Mn also could increase host resistance by favoring the deposition of ligneous defense barriers following infection. The synthesis of these products requires many reactions in the shikimic acid pathway that contain enzymes activated by manganese.

Sulfur

Sulfur (S) is an essential element and a component of proteins and is the oldest recorded fungicide in use on vegetables and other crops. The fungicidal effect of elemental S was discovered in the early 1800s and has been widely used in agricultural production since the end of the nineteenth century (Hoy, 1987). Elemental S proved to be most efficient against rust and powdery mildew (Coleno, 1987; Cook, 1987; Hoy, 1987) but was also successfully used against other diseases, such as downy mildew in cereals (Hoy, 1987) and common scab of potato (Vlitos and Hooker, 1951). However, the significance of soil-applied S on plant disease only recently became evident when S deficiency symptoms were noted following the drastic decrease of SO_2 emissions from coal-burning facilities (Haneklaus *et al.*, 2007). Most growers do not consider S nutrition as a component in their fertility programs. However, it is frequently applied as $NH_4(SO_4)_2$, Ca_2SO_4, or $MgSO_4$. These salts are almost exclusively applied with the aim of supplying the cations N, Ca, or Mg. When manipulation of pH is the sole objective, elemental S and $AlSO_4$ are often used. On field crops, several studies have shown that proper sulfur nutrition can induce resistance to plant pathogens through its effect on the function and availability of S-containing amino acids. Under controlled conditions in a greenhouse experiment, Wang *et al.* (2003) found that disease severity of oilseed rape infected with *Sclerotinia sclerotiorum*, corn infected with *Bipolaris maydis*, and winter wheat infected with *Rhizoctonia cerealis* was significantly decreased when the S supply was increased to young plants. Under the conditions of S deficiency in field experimentation, soil-applied S fertilization significantly reduced the infection of oilseed rape with light leaf spot (*Pyrenopeziza brassicae*), of grapes with powdery mildew (*Uncinula necator*), and of potato with stem canker (*R. solani*; Schnug *et al.*, 1995; Klikocka *et al.*, 2003). Soil-applied S reduced the infection rate and disease severity of *R. solani* on potato tubers by 41% and 29%, respectively (Klikocka *et al.*, 2003).

Sulfur-induced resistance runs parallel to other defense mechanisms, which are activated after fungal attack so that a clear differentiation is difficult, particularly under field conditions. The S-containing amino acids cysteine, methionine, and glutathione play roles in protein synthesis of many defense products.

In addition, salicylic acid as well as H_2O_2 initiates and maintains systemic resistance, and the accumulation of salicylic acid is linked to S metabolism (Haneklaus *et al.*, 2007). As air quality improves and atmospheric S decreases further, growers will need to be more attentive to S nutrition.

Micronutrients

The metals iron, manganese, zinc, copper, molybdenum, boron, and nickel have diverse but essential roles in plants, functioning as cofactors or activators of enzyme systems, as previously mentioned in the section on Cl. Many of these enzyme systems play pivotal roles in disease resistance through the production of defense products, including key roles in phenol metabolism and lignin biosynthesis. In general, the concentrations that correct visual deficiency symptoms in plants are often far below the levels needed to ensure proper plant health and defense against a plant disease. Most micronutrients become less available as the pH rises so growers should be aware that although a crop species may favor alkaline soil and may not show deficiencies, it may be more susceptible to attack from plant pathogens. One quick method to correct aboveground deficiency symptoms and boost resistance to foliar diseases is to apply a foliar application of the needed micronutrient(s). However, as micronutrients are not translocated to the roots, this application would not suppress a root disease. Below is a more comprehensive discussion of each element's role in plant disease suppression.

Iron

Iron (Fe) nutrition not only boosts plant vigor and health, it indirectly affects disease development in the root zone where its unavailability may limit the growth of pathogens (Expert, 2007). One of the major roles where Fe influences plant disease is through siderophores, which are synthesized and excreted by certain microorganisms to acquire their iron and thereby rob other microorganisms of Fe in the rhizosphere (Buyer *et al.*, 1994; Crowley and Gries, 1994; Marschner, 1995). Siderophores are low molecular weight molecules (<1500 Da) that possess a high affinity for Fe^{3+}. They specifically capture Fe^{3+} ions and transport them back into the microorganism that produces them. However, the siderophores can also release their Fe^{3+} ions to iron-deficient plants. Therefore, it seems possible that microbial siderophores present in soils increase Fe availability on the root surface, depending on their different chemical, physical, and absorptive characteristics. Mechanisms involved in these processes have, however, been poorly defined.

In addition to exploitation of microbial siderophores by plant roots, there are other beneficial effects of siderophore-producing rhizobacteria on plant growth. Specific *Pseudomonas* strains called plant growth promoting rhizobacteria (PGPR) are able to enhance the growth of plants. Application of these microbes can result in significant yield increases and were attributed entirely or in part to competition for Fe with pathogenic microorganisms (Schroth and Hancock, 1982). In fact, several strains of *Pseudomonas fluorescens* are effective in biocontrol of plant diseases due to their ability to deny available Fe to pathogenic bacteria or fungi. However, siderophore-mediated biocontrol activity of rhizosphere *Pseudomonas* species is affected by the availability of Fe in the rhizosphere. The rhizosphere needs to be Fe limiting to maximize the biocontrol potential that, in turn, may limit its overall use in biocontrol. Another mechanism of biocontrol by rhizobacteria is induced systemic resistance (ISR). Siderophores produced by bacteria might induce ISR. Leeman *et al.* (1996) and Buysens *et al.* (1996) both found that ISR against plant disease was governed by determinants regulated by Fe availability.

Another critical aspect concerns the signaling role of Fe in plants and plant-associated microorganisms. The cellular and molecular regulatory mechanisms controlling the genes involved in Fe uptake, trafficking, and storage are still unclear. Elucidating these issues may eventually help to develop strategies in plant disease management. Nevertheless, it should be recognized that biotechnological approaches targeting isolated components within complicated metabolic pathways are limited in their application.

Manganese

A rich body of information exists on the role of manganese (Mn) nutrition in suppressing a plant disease (Thompson and Huber, 2007). Manganese in plants is absorbed in the reduced Mn^{2+} form and is poorly mobile in mature leaves but slightly mobile in root and stem tissue. However, the availability of Mn in soil is influenced most strongly by soil pH and microbial activity (Gilkes and McKenzie, 1988; Norvel, 1988). At soil pH below 5.2 or above 7.8, Mn becomes chemically available or unavailable, respectively. Its availability between these ranges is largely influenced by the Mn-transforming microbes. For this reason, soil microbes, especially bacteria and fungi, have a profound effect on the global cycling of Mn and its availability for plant uptake (Elmer, 1995; Erhlich, 1996; Ghiorse, 1988; Tebo *et al.*, 1997). It has been demonstrated, for example, that Mn-oxidizing microbes can decrease Mn availability by up to five orders of magnitude (Brouwers *et al.*, 2000; Tebo *et al.*, 1997).

It has long been noted that certain environmental conditions that affect Mn availability has the same effects on disease, such as pH, N form, organic matter, moisture status, soil temperature, and microbial activity (Huber and Wilhelm, 1988). One obstacle to increasing Mn levels in plants is its lack of mobility. Foliarly applied Mn is not basipetally translocated to roots. Furthermore, soil-applied Mn can be rapidly immobilized by oxidizing soil organisms. It is not always possible to override the biological and environmental factors affecting Mn availability and utilization (Graham and Webb, 1991).

Potential mechanisms of controlling disease with Mn have not been totally resolved. Manganese affects the production of many host defense products. Manganese functions primarily as an activator of enzymes, including dehydrogenases, tranferases, hydroxylases, and decarboxylases (Burnell, 1988). Fundamentally, Mn serves as an activator of several enzymes in the shikimic acid pathway for production of important secondary metabolites that lead to the production of phenolics, cyanogenic glycosides, and the deposition of ligneous defense barriers (Burnell, 1988). The role of Mn in carbohydrate, nitrogen, and secondary metabolism indirectly affects disease (Graham, 1983; Huber, 1989). More directly, Mn can reduce growth of the pathogen, which may explain why these organisms evolved mechanisms for oxidizing Mn to unavailable forms.

Zinc

Zinc (Zn) nutrition is associated with important plant defense pathways against fungal, bacterial, viral, and nematode pathogens (Siddiqui *et al.*, 2002). Zinc protects plant cells from toxic oxygen radicals and plays an important role in the production of disease resistance signaling proteins. Zinc has direct effects on fungal growth and secondary metabolism and indirect effects on host susceptibility. Zinc strictly modulates fungal accumulation of citric acid, stimulates glucose uptake, and pigment and antibiotic production by microbes (Duffy, 2007).

Zinc nutrition has pronounced effects on root diseases. Tomato diseases caused by *Macrophomina phaseolina*, *Fusarium solani*, and *R. solani* and charcoal rot of maize caused by *M. phaseolina* were all reduced by increasing soil concentrations of Zn (Siddiqui *et al.*, 2002; Pareek and Pareek, 1999). In-furrow treatment with a mixture of zinc oxide (ZnO) and zinc sulfate ($ZnSO_4$) reduced the incidence of powdery scab of potato, caused by *Spongospora subterranea* f. sp. *subterranea* (Falloon *et al.*, 1996). Zinc soil amendments reduced the severity of maize smut, caused by *Ustilago maydis*, and the effect was increased with nitrogen fertilizers (Kostandi *et al.*, 1997). Maize grain yields were correspondingly increased.

Zinc influences the biocontrol activity of many bacteria. Amendment of Zn soil amendments improved the activity of *Pseudomonas aeruginosa* against *M. phaseolina*, *F. solani*, and *Meloidogyne javanica* on tomato, even though they exhibited little direct effect on root disease or galling and zinc-deficient soils supported higher populations of *P. aeruginosa* (Siddiqui *et al.*, 2002). The role of Zn in microbial interactions involves biocontrol of *Fusarium* with *Pseudomonas*. Duffy and Défago (1997) showed that the biocontrol activity of *P. fluorescens* CHA0 against *Fusarium* root rot of tomatoes was enhanced in the presence of Zn with increased production of the antibiotic 2,4-diacetylphloroglucinol. The effect was mediated by a Zn-induced inhibition of fusaric acid by the pathogen that can, in turn, inhibit the antibiotic. Another example where Zn indirectly influences biological control is for pathogenic strains of *R. solani* that produce phenylacetic acid (Siddiqui and Shaukat, 2003, 2005). This metabolite can inhibit the production of nematicidal compounds by *P. fluorescens* when damaged by root knot nematode (*Meloidogyne incognita)* and is greater when *R. solani* is present. However, when sufficient Zn was present, phenylacetic acid production by *R. solani* was decreased, which relieved the repression of nematicidal compounds and resulted in enhanced biocontrol of the nematode.

Copper

The recognition of the inhibitory effect that copper (Cu) has on microorganisms has made it a common component of many pesticides, whereas its role in plant physiological and host defense reactions that influence disease resistance or susceptibility has received much less attention (Graham, 1983; Graham and Webb, 1991). The reduction of foliar diseases with soil-applied Cu and benefits from Cu applied at subbiocidal rates are evidence of increased plant resistance rather than a direct effect on the pathogen (Graham, 1983; Graham and Webb, 1991; Shabranskii *et al.*, 1984). Copper-activated physiological processes also increased the resistance of hops to downy mildew (Shabranskii *et al.*, 1984). The system where Cu nutrition has made the striking difference is in barley. Low levels or deficiency of Cu causes pollen sterility, which reduces yield and predisposes plants to ergot (Azouaou and Souvré, 1993; Graham, 1975) by causing the normally closed flowers of wheat and barley to open, exposing them to infection by *Claviceps purpurea* (Mantle and Swan, 1995).

Copper affects plant disease by three known mechanisms. Direct toxicity as a bactericide or fungicide is the most common one. However, the effects of Cu on plant resistance and pathogen virulence can also operate simultaneously. For example, Cu is an essential cofactor in various enzyme systems involved in plant defense against infection, the production of antimicrobial compounds, and general disease resistance (Graham, 1983; Graham and Nambiar, 1981; Graham and Webb, 1991; Lebeda *et al.*, 2001). Copper chloride induces the activity of chalcone synthase, a key enzyme in the biosynthesis of diverse flavonoids involved in plant disease resistance (Harker *et al.*, 1990). Amino oxidases involved in H_2O_2 production in cell walls in response to attack of pea by *Ascochyta rabiei* (Pass.) Labrousse required Cu (Laurenzi *et al.*, 2001).

Copper is an essential micronutrient for pathogens as well. Copper deficiencies in *Colletotrichum lindemuthianum* can result in the pathogen becoming avirulent to bean. Copper-containing laccases can be important virulence factors for many plant-pathogenic fungi, enabling them to degrade physical barriers and detoxify phytoalexins and tannins (Mayer and Staples, 2002). For example, *Heterobasidion annosum* declined in aggressiveness as laccase levels decreased (Johansson *et al.*, 1999). Integrated research involving Cu with other defense-stimulating approaches could enhance the effectiveness of many cultural management strategies for disease control.

Molybdenum

Molybdenum (Mo) is not associated with influencing plant disease like other elements. A few studies show an increase in disease, but an equal numbers show no effect (Graham and Stangoulis, 2007). Suppression of *Verticillium* wilt of tomato by treatment of roots with molybdenum has been reported (Dutta and Bremner, 1981) along with a study by de Jesus *et al.* (2004), who reported that application of Mo 25 days after sowing beans suppressed angular leaf spot, caused by *Phaeoisariopsis griseola*.

The best-known role of Mo involves nitrogen metabolism and its role in activating the nitrate reductase enzyme, which may then influence disease development. In addition, heavy metals like Mo are effective in deactivating viruses by denaturing protein coats (Verma and Verma, 1967), killing zoospores of *Phytophthora* sp. (Halsall, 1977) and inhibiting nematodes (Haque and Mukhopadhyaya, 1983). However, at this point, manipulating Mo nutrition has not been demonstrated to be an effective strategy for disease management.

Boron

The role of boron (B) nutrition in plant disease is through its wide ranging effects on structural and metabolic processes that control plant defense (Stangoulis and Grahm, 2007). In general, B deficiency leads to host susceptibility by compromising the plant's ability to manufacture lignin and phenolic compounds that are necessary for inhibiting pathogen invasion. When B fertilizers are used in these situations, plant health and disease suppression are increased. Much of the role of B in disease suppression is yet to be investigated.

Nickel

The role of nickel (Ni) as an essential mineral element for higher plants is a relatively recent discovery (Brown *et al.*, 1987). Its low requirement in plants qualifies it as a piconutrient rather than a micronutrient, yet deficiencies are observed on a wide variety of plants (Wood and Reilly, 2007). Nickel deficiency is increased when root knot nematodes are present. These observations indicated an adverse influence of nematodes on Ni nutrition of plants. Given that a wide range of physiological processes are disrupted by insufficient Ni nutrition, Ni may be a missing link in certain recalcitrant

disorders affecting several crop species that suffer from replant disorders associated with pathogenic nematodes or fungi.

Beneficial Elements (Silicon and Aluminum)

As stated above, not all elements are viewed as essential, but a growing body of research has shown that many nonessential elements can suppress a number of plant diseases. It is interesting that the ameliorating effects of these elements are frequently only realized when the plant is under a biotic stress, such as a plant disease that, once again, implicates their influence in host defense mechanisms.

Plants that accumulate silicon (Si) have shown enhanced resistance to a number of foliar and root diseases in both dicots and monocots (Datnoff *et al.*, 2007c). Silicon is absorbed by roots as monosilicic acid, $Si(OH)_4$, and most plants accumulate this element in great quantities (between 1% and 10% of their dry weight). The availability of silicon to plants varies depending on the soil. Tropical/subtropical soils highly weathered, low in base saturation, and acidic are known to be low in plant-available silicon. Organic and sandy soils also contain low levels of silicon. Further, soilless mixes are silicon deficient. Consequently, plants grown on these types of rooting media may benefit from a silicon application. Many agronomic and horticultural crop plants supplied with silicon may gain protection from pathogenic fungi, bacteria, nematodes, and viruses (**Table 4**). Silicon appears to affect a number of components of host plant resistance that includes delaying the incubation and latent period and reducing lesion expansion rates, lesion size, and lesion number (Seebold *et al.*, 2001). Subsequently, disease progress and final disease severity is dramatically reduced, and the resistance of susceptible cultivars is augmented to almost the same level as those with complete or partial resistance (Seebold *et al.*, 2000; Rodrigues *et al.*, 2001). Silicon may even suppress plant disease as effectively as a fungicide (Resende *et al.*, 2013; Seebold *et al.*, 2004). As the silicon concentration (insoluble or soluble) increases in plant tissue, plant disease suppression greatly improves.

The underlying mechanisms that govern disease protection are still not well understood; however, the effect of silicon on plant resistance to disease is considered to be due to either an accumulation of absorbed Si in the epidermal tissue or an expression of pathogenesis-mediated host defense responses (Datnoff *et al.*, 2007c). Accumulated monosilicic acid polymerizes into polysilicic acid and then transforms to amorphous silica, which forms a thickened Si cellulose membrane. By this means, a double-cuticular layer protects and mechanically strengthens plants. Silicon also might form complexes with organic compounds in the cell walls of epidermal cells, thus increasing their resistance to degradation by enzymes released by fungi.

Research also points to the role of silicon *in planta* as being active, and this suggests that the element might be a signal for mediating defense reactions to plant diseases (Belanger *et al.*, 2003; Rodrigues *et al.*, 2003). Silicon has been demonstrated to stimulate chitinase activity and rapid activation of peroxidases and polyphenoxidases after fungal infection. Glycosidically bound phenolics extracted from Si-amended plants when subjected to acid or β-glucosidase hydrolysis displayed strong fungistatic activity (Cherif *et al.*, 1994). More recently, flavonoids and momilactone phytoalexins, low molecular weight compounds that have antifungal properties, were found to be produced in both dicots and monocots, respectively, fertilized with Si and challenged inoculated by the pathogen in comparison with nonfertilized plants also challenged inoculated by the pathogen (Fawe *et al.*, 1998; Rodrigues *et al.*, 2004). These antifungal compounds appear to be playing an active role in plant disease suppression. In addition, an increase in superoxide (O^-) generation was observed in rice leaves of plants treated with silicon 15 min after inoculation with *Magnaporthe grisea* (Maekawa *et al.*, 2002). Rodrigues *et al.* (2005) showed that β 1–3 glucanase, peroxidase, and PR-1 proteins are associated with rice blast suppression. Both these studies suggest that other additional mechanisms may be involved in silicon-mediated resistance to plant diseases. Recently, genome-wide studies for tomato, rice, and wheat amended with silicon and compared with nonamended control plants have shown a differential expression of a large number of genes, and these genes are known to be involved in host plant defense mechanisms or metabolism (Brunings *et al.*, 2009; Chain *et al.*, 2009; Ghareeb *et al.*, 2010).

Given the low silicon content now being found in a number of soil types and its role in enhancing disease resistance, it seems prudent to consider soluble silicon supplementation as amendments as simple, inexpensive methods to reduce plant diseases.

Recent research has shown that aluminum (Al) is similarly taken up in plants at low levels and may be important to plant health (Shrew *et al.*, 2007). It has been a long-held practice to lower root medium pH with $AlSO_4$, which is often accompanied by reductions for many plant diseases caused by *Verticillium* and *Thielaviopsis*. However, evidence may suggest that the aluminum ion is partially responsible for suppression of disease through its effect on the germination of fungal spores in soil. Applications of different forms of Al to peat soils at pH 4 and 6 were followed by reductions in the population densities of *Phytophthora parasitica*. Strategies for incorporating Al in disease management need to be developed.

Summary

There is no question that proper nutrient management has marked effects on plant diseases. Nutrients influence the plant pathogen both directly and indirectly by controlling the pathogen's rate of germination, penetration, colonization, and reproduction; affecting the infection rate or the progress of disease; and having a toxic effect (Datnoff *et al.*, 2007b). In addition, nutrients promote plant vigor, aiding recovery from infection, and change the anatomical or physiological plant state by thickening the cuticle or changing biochemical reactions. Hence, these nutritional practices often serve as the first line of defense against the occurrence of plant disease. However, the strategy of using fertilization practices as a management strategy against disease needs to be developed for each crop species.

This article highlights a few examples where manipulating fertilization reduced disease. Another more important goal

Table 4 Host, disease, and plant pathogen response to silicon applications

Host	*Disease*	*Pathogen*	*Effect*[a]
Monocots			
Rice	Leaf and neck blast	*Magnaporthe grisea*	⊕
	Brown spot	*Cochliobolus miyabeanus*	⊕
	Sheath blight	*Thanathephorus cucumeris*	⊕
	Leaf scald	*Monographela albescens*	⊕
	Stem rot	*Magnaporthe salvinii*	⊕
	Grain discoloration	Many fungal species	⊕
	Bacterial leaf blight	*Xanthomonas oryzae pv. oryzae*	⊕
	Root knot nematode	*Meloidogyne* spp.	⊕
Wheat	Powdery mildew	*Blumeria graminis*	⊕
	Leaf blotch	*Septoria nodorum*	⊕
	Foot rot	*Fusarium* spp.	⊕
	Leaf spot	*Phaeosphaeria nodorum*	⊕
	Eye spot	*Oculimacula yallundae*	⊕
	Brown foot rot	*Fusarium culmorum*	∅
	Brown rust	*Puccinia recondita*	∅
	Sorghum Anthracnose	*Colletotrichum graminicola*	⊕
Barley	Black point	*Alternaria* spp.	⊕
	Powdery mildew	*Erysiphe graminis* f.sp. *hordei*	⊕
Rye	Powdery mildew	*Erysiphe graminis*	⊕
Sugarcane	Brown Rust	*Puccinia melanocephala*	∅
	Ring spot	*Leptosphaeria sacchari*	⊕
Zoysiagrass	Leaf blight	*Rhizoctonia solani*	⊕
Creeping bentgrass	Root rot	*Pythium aphanidermatum*	⊕
	Brown patch	*Rhizoctonia solani*	⊕
	Dollar spot	*Sclerotinia homoeocarpa*	⊕
Kentucky bluegrass	Powdery mildew	*Sphaerotheca fuliginea*	⊕
Bermudagrass	Leaf spot	*Bipolaris cynodontis*	⊕
St. Augustine-grass	Gray leaf spot	*Magnaporthe grisea*	⊕
Corn	Stalk rot	*Pythium aphanidermatum* and *Fusarium moniliforme*	⊕
	Corn smut	*Ustilago maydis*	⊕
Dicots			
Tomato	*Fusarium* wilt	*Fusarium oxysporum* f.sp. *lycopersici* (races 1 and 2)	∅
	Fusarium crown and root rot	*Fusarium oxysporum* f.sp. *radicis-lycopersici*	⊕/∅[b]
	Powdery mildew	*Oidiopsis sicula*	⊕/∅[b]
	Bacterial wilt	*Ralstonia solanacearum*	⊕
Cucumber	Powdery mildew	*Sphaerotheca xanthii*	⊕
	Anthracnose	*Colletotrichum orbiculare*	⊕
		Colletotrichum lagenarium	∅
	Leaf spot	*Corynespora citrullina*	⊕
	Crown and root rot	*Pythium ultimum* and *Pythium aphanidermatum*	⊕
	Gray mold rot	*Botrytis cinerea*	⊕
	Black rot	*Didymella bryoniae*	⊕
	Fusarium wilt	*Fusarium oxysporum* f.sp. *cucumerinum*	⊕
Lettuce	*Pythium* root rot	*Pythium* spp.	∅
Muskmelon	Powdery mildew	*Sphaerotheca xanthii*	⊕
Zucchini	Powdery mildew	*Erysiphe cichoracearum*	⊕
Pumpkin	Powdery mildew	*Sphaerotheca xanthii*	⊕
Rose	Powdery mildew	*Sphaerotheca pannosa*	⊕
	Black spot	*Diplocarpon rosae*	⊕
Morning glory	Anthracnose	*Colletotrichum gloeosporioides*	⊕
Pea	Leaf spot	*Mycosphaerella pinodes*	⊕
Paper daisies	Anthracnose	*Colletotrichum gloeosporioides*	⊕
Grape	Powdery mildew	*Uncinula necator*	⊕/∅[b]
Soybean	Stem canker	*Diaporthe phaseolorum* f.sp. *meridionalis*	⊕
	Rust	*Phakopsora pachyrhizi*	⊕[c]
Strawberry	Powdery mildew	*Sphaerotheca macularis* f.sp. *macularis*	⊕
Tobacco	BdMV	*Belladonna mottle virus*	⊗

[a]Silicon can decrease (⊕), increase (⊗), or has no effect (∅) on disease intensity.

[b]Silicon decreases disease intensity if sprayed onto the leaves but has no effect on disease if added to the nutrient solution.

[c]Lemes *et al*., 2011.

Source: Adapted from Datnoff, L.E., Rodrigues, F.A., Seebold, K.W., 2007c. Silicon and plant disease. In: Datnoff, L.E., Elmer, W.H., Huber, D.M. (Eds.), Mineral Nutrition and Plant Disease. St. Paul, MN: APS Press, pp. 233–246.

was to underscore how nutrient management could advance a major strategy for disease control and how that could have an immediate impact on agriculture and food systems. Unfortunately, the fractionation of the data has hindered development of a working plan for disease management. Most experimental studies tend to focus on one plant, one element, and one disease in isolation of other variables, so most research provides only 'snapshots' of information. The dearth of experimental data, combined with the gigantic number of agronomic and horticultural crop species whose fertility requirements differ widely from each other, makes the development of this strategy a daunting task.

Growers are encouraged to consider their fertility regimes and nutrient management plans against the aforementioned information and make adjustments first on a small scale, then expand as the results warrant. Researchers are encouraged to explore a crop's horticultural and disease response to a wide array of elements applied in many combinations. The role that each nutrient plays in disease must be viewed in the greater context of its numerous interactions with other elements, the host plant, root medium, and with beneficial and pathogenic microorganisms.

See also: Climate Change and Plant Disease. Emerging Plant Diseases. Food Safety: Emerging Pathogens. Food Security: Postharvest Losses. Organic Agricultural Production: Plants. Plant Disease and Resistance. Plant Health Management: Biological Control of Plant Pathogens

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Natural Capital, Ecological Infrastructure, and Ecosystem Services in Agroecosystems

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Glossary

Agroecosystem Ecosystem arbitrarily defined as a spatially and functionally coherent unit of agricultural activity, and includes the living and nonliving components involved in that unit as well as their interactions. The basic unit of study for an agroecologist.

Ecological infrastructure The way natural capital stocks are organized to produce ecosystem goods and services.

Ecosystem services The direct and indirect contributions of ecosystems to human well-being.

Natural capital The stocks of natural assets (e.g., soils, forests, and water bodies) that yield a flow of valuable ecosystem goods or services now and into the future.

Natural resource management The management of natural resources, including soils, land, water, animals and plants, for the production of goods to meet changing human needs, while simultaneously ensuring the long-term productive potential of these resources and the maintenance of their environmental functions.

Soil (1) The unconsolidated mineral or organic material on the immediate surface of the earth that serves as a natural medium for the growth of land plants. (2) The unconsolidated mineral or organic matter on the surface of the earth that has been subjected to and shows effects of genetic and environmental factors of: climate (including water and temperature effects), and macro- and microorganisms, conditioned by relief, acting on parent material over a period of time. A product soil differs from the material from which it is derived in many physical, chemical, biological, and morphological properties and characteristics.

Introduction

Population growth and the need to obtain energy and food from the planet's finite resources are intensifying pressures on natural ecosystems that are required for life support. This increasingly raises questions about the sustainability and viability of agricultural systems into the future, and one's ability to mitigate the impacts of ongoing production gains on the environment. Much of the current economic growth strategy is based on the false assumption that natural resources, such as land and water, are inexhaustible, which they are not, raising the question of the long-term viability of the current economic model (Munda *et al.*, 1994). A recent report to the United Nations "Building a Sustainable and Desirable Economy-in-Society-in-Nature" (Costanza *et al.*, 2012) stated that new economic models and agricultural systems are needed, "that respect planetary boundaries and recognize that the ultimate goal is sustainable human well-being and not growth of material consumption" (Rockström *et al.*, 2009).

In his latest book Brown (2012) argued that "food is the new oil and land is the new gold." He identifies major pressures on agroecosystems, which threaten food security globally. These include increasing soil erosion, desertification, salinity, and the expansion of urban areas over the best and most versatile soils. Despite the fact that land is continually being lost to urbanization, the total area under cultivation continues to rise, with new arable and pasture lands being created, often at the expense of forests. Demand for agricultural land continues to increase in line with population growth. This has resulted in the clearing of marginal land that is more susceptible to degradation.

The Millennium Ecosystem Assessment (MEA, 2005) was a wakeup call for the society, because it highlighted the link between ecosystems and human well-being (**Figure 1**), and elucidated the rapidity with which ecosystems are being degraded, as well as the associated social and economic impacts of environmental degradation. The MEA generated sufficient concern about the health of the natural ecosystems to lead many governments and international agencies to seek out a less destructive and more sustainable way forward. There is widespread agreement that if ecologically sustainable development is to be achieved, one must both protect some

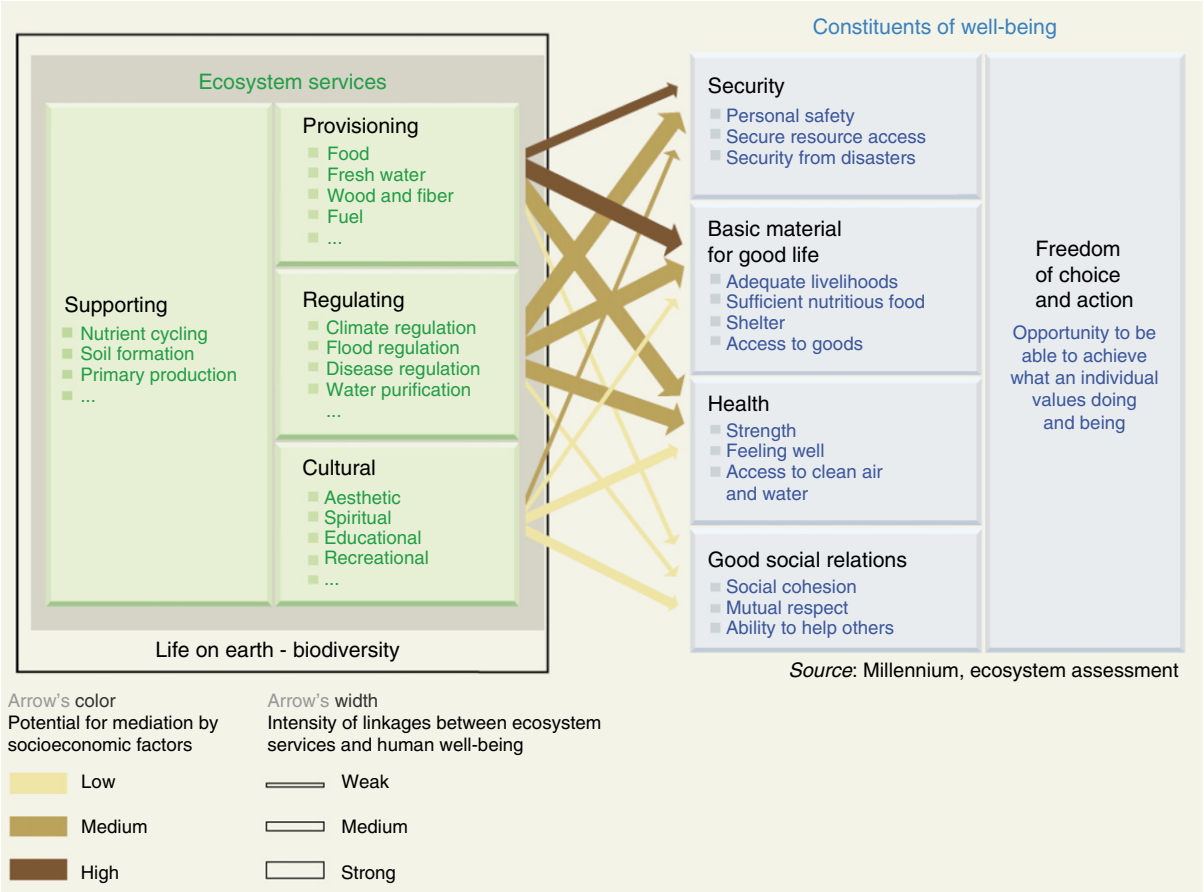


Figure 1 Millennium ecosystem assessment framework for ecosystem services. Reproduced from MEA, 2005. Millennium Ecosystem Assessment: Ecosystems and Human Well-being: Synthesis. Washington, DC: Island Press.

ecosystems from development, and find better ways of managing those one uses for production. The 'ecosystems approach' to natural resource management (NRM) focuses on how to better manage the natural resources (Convention on Biological Diversity (CBD) principles of the ecosystem approach). It accomplishes this by recognizing the wide range of benefits that one obtains from the harvested goods and ecosystem services they deliver through better representing the value of ecosystem services in decision-making frameworks and indicators of progress (Robinson *et al.*, 2013).

The major challenge for agroecosystems is to shift from management of a single function, namely production, to management that meets multifunctional goals of production and land stewardship. This challenge is becoming more widely recognized, for example, in the European Union Common Agricultural Policy (CAP), where reforms are slowly transitioning away from a focus on production only to a broader land stewardship and ecosystem service delivery approach to provide additional services, including clean water or increased biodiversity. Intensive use of agricultural land for food production can result in soil degradation and declining biodiversity, thus limiting the provision of ecosystem services. The challenge for future agricultural production is to limit and mitigate degradation processes, while maintaining and even increasing yields. The economies of nations worldwide rely on the sustainability of agroecosystems. As history has shown, entire civilizations can be lost if agroecosystems collapse (Diamond, 2005; Hillel, 1991; Montgomery, 2007).

To create more multifunctional agroecosystems, new frameworks and tools are needed to enable resource managers and policy makers to more holistically quantify the ecological value of natural resources, and thus enable more informed decisions on trade-offs. Research in agronomy, soil science, and the hydrological and environmental fields also needs to adapt to the changing policy landscape that the ecosystem services approach to sustainable development brings (Bouma, 2005; Daily, 1997; Robinson *et al.*, 2013).

The ecosystem services approach and associated discipline of Ecological Economics bring a new set of terminology to agriculture and agricultural systems, giving it a more economic feel. Ecosystems are conceptualized as 'natural capital,' as distinct from manufactured and human capital, and the functions of ecosystems that benefit society are termed 'ecosystem services.' These concepts have gained considerable traction in NRM research and policy making over the past decade. Resource management frameworks based on ecosystem services approaches are being adopted and promoted

by many international organizations including: the Conference of the Parties to the CBD, the Food and Agriculture Organization of the United Nations, The Organization for Economic Cooperation and Development, the United Nations Environment Programe (UNEP), and the United Nations Development Program (Robinson *et al.*, 2013). The concept of ecosystem services is the foundation for international initiatives, such as the Millennium Ecosystem Assessment (MEA, 2005), The Economics of Ecosystems and Biodiversity (TEEB, 2010) initiative, and the Intergovernmental Panel on Biodiversity and Ecosystem Services (Marris, 2010).

This article examines the concepts of natural capital, ecological infrastructure, and ecosystem services in the context of agroecosystems, with a focus on soil. The article provides a brief history of the origin of the concepts, their modern use, and how they are being adapted to agroecosystems. It then discusses some major challenges associated with the further development of these concepts for future research and use in NRM.

Origin of the Concepts

In the second half of the twentieth century, some environmentally aware economists (Schumacher, 1973) and ecologists (Westman, 1977) began to highlight the societal and economic benefits one obtains from ecosystems. The economists started to analyze environmental problems in economic terms in order to point out the dependence of human societies on natural ecosystems (de Groot, 1987, 1992). They stressed that the undervaluation of the contributions of ecosystems to public welfare and economic growth was due in part to the fact that many ecosystem services are public-owned and consequently not adequately quantified in terms comparable with economic indicators (Braat and de Groot, 2012; Costanza *et al.*, 1997). To ensure sustainability, they argue that the critical nonmarketed contributions of ecosystems underpinning human economies need to be explicitly incorporated in economic decision making.

An emerging discipline, ecological economics (Costanza, 1991; Costanza *et al.*, 2012), sees global economies as a subsystem of the larger finite global ecosystem. Economies exchange energy, materials, and waste flows with the social and ecological systems with which they coevolve (Braat and de Groot, 2012; Martinez-Alier, 2001). Ecological economists question the sustainability of the existing economy, because environmental impacts are not internalized and raw material and energy are not seen as finite resources (Martinez-Alier, 2001). One of the main focuses of ecological economics is to develop biophysical indicators and indices of sustainability (Costanza, 1991) and include the environment in macroeconomic accounting. Following the trend set by environmental economics, ecological economics uses concepts from conventional neoclassical, or welfare economics, and expands them to include environmental impacts, ecological limits, finite natural resources, and issues of equity and scale as necessary requirements for increasing the sustainability of human activities (Martinez-Alier, 2002). Ecological economics acknowledges the reality of entropy, and emphasizes the dependence of economic systems on social systems, and of social systems on ecological systems. Foundational concepts include natural capital, ecosystem services, and ecological infrastructure (see Sections Natural Capital, Ecological Infrastructure, and Ecosystem Services).

Natural Capital

Natural capital refers to the extension of the economic idea of manufactured capital to include environmental goods and services. The first documented usage of the term in this context can be traced back to at least as early as 1837 (Robinson *et al.*, 2012). In the twentieth century, William Vogt pioneered the idea of natural capital in his book, 'Road to Survival' (Vogt, 1948). In it he wrote, "By using up our real capital of natural resources, especially soil, we reduce the possibility of ever paying off the debt" (Mooney and Ehrlich, 1997, p. 44). Costanza and Daly (1992) went on to define natural capital as "stocks of natural assets (e.g., soils, forests, and water bodies) that yield a flow of valuable ecosystem goods or services into the future". This concept was brought into prominence by the landmark paper by Costanza *et al.* (1997) who defined it as 'the stock of materials or information contained within an ecosystem.' Natural capital, like all other forms of capital, is a stock as opposed to a flow, but the idea of information, connection, and organization of stocks (Robinson *et al.*, 2009) is being increasingly associated with the concept. Natural capital stocks can move around the earth-system and can be equated, for example, with the goods one harvests from nature, termed by Costanza *et al.* (2012) as 'stock-flows.' The interaction between stocks forms the basis of the flow of emergent ecosystem services that Costanza *et al.* (2012) termed 'fund-services,' because they arise from the fund of stocks. A major difference between neoclassical and ecological economists is that neoclassical environmental economists mostly embrace what is termed a 'weak sustainability' approach, which assumes substitutability between natural and manufactured capital, for example, substituting soil nutrients from mineral weathering with fertilizer, whereas ecological economists generally advocate the 'strong sustainability' approach, which maintains that natural capital and manufactured capital are complementary rather than substitutable (Costanza and Daly, 1992).

Ecological Infrastructure

Ecological systems are complex and interconnected. Interactions between organisms and their environment take place at multiple and nested scales. Amplifying feedbacks and counterbalancing loops occur within and between scales, and thresholds and tipping points separate alternative stable states of systems (Walker *et al.*, 2006). These many and varied interactions can be simply referred to as 'connectivity.' Connectivity in the ecological sense includes both quantity (number) and quality (strength, direction, and duration) of connections. This notion is recognized by some authors (Costanza *et al.*, 1997; Costanza *et al.*, 2012; Dominati *et al.*, 2010a,b; Robinson *et al.*, 2009) using the natural capital concept, but its importance cannot be overstated. A holistic

conception of nature links natural capital and ecosystem services within a framework that explicitly accounts for ecological connectivity. It must go beyond simple 'stocks and flows' and depict a supply chain that ultimately delivers ecosystem services required for human well-being.

The concept of 'infrastructure,' which is defined as 'the underlying foundation, or framework, of a system' (American Heritage Dictionary, 2009), is robustly applicable to both ecological and socioeconomic systems. The term 'ecological infrastructure' was introduced and elaborated in government policy reports in 1977 and 1981 in the Netherlands (Van Selm, 1988b). In this earliest usage, ecological infrastructure was related to the design of structures that would enable many species to move between the 'islands' of natural environments that were left remaining among the 'oceans' of agricultural land (Van Selm, 1988a). The term ecological infrastructure has continued to be used as a design concept for the incorporation of ecological features, such as 'corridors' and 'networks' into human infrastructure design (Morrish, 1995; Xuesong and Hui, 2008). However, some authors are now suggesting that ecological infrastructure can also be used to depict an underlying framework that supports the terrestrial and aquatic ecosystems producing clean air, clean water, and biodiversity that is critical to the resilience and regenerative capacity of natural and human systems alike (Quinn and Tyler, 2007; Postel, 2008).

The essential feature of the underlying framework of ecological infrastructure is connectivity (Arthington *et al.*, 2006; Soule *et al.*, 2004; Ward and Stanford, 1995). Maintaining ecological connectivity is the key to ecosystem health and integrity, and a certain level of ecological integrity is required for the continued production of ecosystem services that are essential for human well-being. The relationship between natural capital, ecological infrastructure, and ecosystem services can be conceptualized as 'Ecological infrastructure is how natural capital stocks are organized to produce ecosystem goods and services' (Bristow *et al.*, 2010; **Figure 2**). Being the source of ecosystem services, ecological infrastructure also provides the 'sink' for the wastes produced by socioeconomic systems (**Figure 2**).

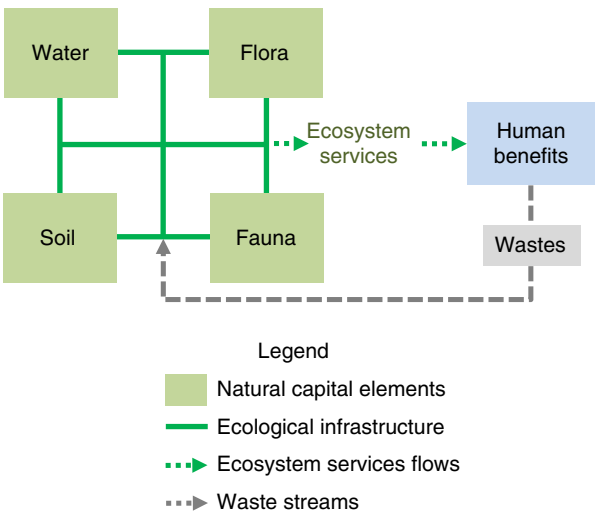


Figure 2 The relationship between natural capital, ecological infrastructure, and ecosystem services.

Ecosystem Services

The origin of the concept of ecosystem services is to be found within work from the 1970s (Braat and de Groot, 2012; Gomez-Baggethun *et al.*, 2010). Mooney and Ehrlich (1997) trace the first usage of 'Nature's services' to a report from 1970 entitled, 'Study of Critical Environmental Problems,' but the paper by Westman (1977) is strongly associated with the development of modern-day ecosystem service concepts. Proponents of the modern-day ecosystem services approach argue that the functions of ecosystems beneficial to society must be accounted for in economic decision making to increase the sustainability of human activities (Braat and de Groot, 2012). References to ecosystem services in the professional literature have grown exponentially since 1990 (Costanza and Daly, 1992; Daily, 1997; de Groot, 1992). In the late 1990s, much of the focus was on methods to estimate the economic value of ecosystem services (Costanza *et al.*, 1997; Hanley and Spash, 1993; Patterson, 1998).

The definition of ecosystem services continues to evolve from:

- The conditions and processes through which natural ecosystems, and the species that make them up, sustain, and fulfill human life (Daily, 1997).
- The benefits human populations derive, directly or indirectly, from ecosystem functions (Costanza *et al.*, 1997).
- The benefits people obtain from ecosystems (MEA, 2005).
- Components of nature, directly enjoyed, consumed, or used to yield human well-being (Boyd and Banzhaf, 2007).
- The aspects of ecosystems utilized (actively or passively) to produce human well-being (Fisher *et al.*, 2009).
- The direct and indirect contributions of ecosystems to human well-being (TEEB, 2010).
- To the final contributions that ecosystems make to human well-being – Common International Classification of Ecosystem Services (CICES, 2013).

The definition by the MEA (2005) is regarded by many as a simple and appropriate working definition of the concept. The increasing acceptance of the importance of ecosystem services in policy-making circles over the past two decades has resulted in the development of general typologies and classification systems, which characterize the diversity of roles played by ecosystems. De Groot's classification system (1992) was one of the first. It defined ecosystem functions as "the capacity of natural processes and components to provide goods and services that satisfy human needs, directly or indirectly" and grouped these functions into four primary categories:

- Regulation functions to regulate essential ecological processes and life support systems and the maintenance of ecosystem health,
- Habitat functions to provide refuge and reproduction habitat to wild plants and animals,

- Production functions for processes creating living biomass used for human consumption (food, raw materials, energy resources, and genetic material),
- Information functions to provide opportunities for reflection, spiritual enrichment, cognitive development, recreation, and esthetic experience.

The paper by Costanza *et al.* (1997) on the total value of global ecosystem services was a milestone in the mainstreaming of ecosystem services (Braat and de Groot, 2012). It detailed seventeen goods and services, including most of de Groot's (1992) functions. The monetary figures presented had a profound impact on both science and policy communities. The paper generated strong support as well as fervent criticism (Toman, 1998), and it marked the start of a notable increase in the development and use of monetary valuation concepts for NRM in parallel with the ongoing development of ecosystem services quantification.

Daily (1997) produced an ecosystem services framework including five services:

- Production of goods: Food, pharmaceuticals, durable materials, energy, industrial products, and genetic resources;
- Regeneration processes: Cycling and filtration processes and translocation processes;
- Stabilizing processes: Regulation of hydrological cycle, stabilization of climate, and coastal and river channel stability;
- Life-fulfilling functions: Esthetic beauty, cultural, intellectual, and spiritual inspiration;
- Preservation of options: Maintenance of the ecological components and systems needed for future.

De Groot *et al.* (2002) identified 23 functions in the four primary categories established in earlier work (de Groot, 1992) and detailed the corresponding processes and services, noting that "ecosystem processes and services do not always show a one-to-one correspondence" (de Groot *et al.*, 2002, p. 397). To the four categories, they later introduced a fifth, a carrier function and specified that the "regulation functions provide the necessary preconditions for all other functions" (de Groot, 2006, p. 177). Ekins *et al.* (2003) used a similar classification to argue that the principles of environmental sustainability must be based on the maintenance of the important life-support 'functions of nature' that form the basis on which the 'functions for people' are fundamentally dependent.

The novel idea that de Groot *et al.* (2002) and Ekins *et al.* (2003) advanced in their frameworks was that some ecosystem functions – or processes – support others. The Millennium Ecosystem Assessment (MEA, 2005) took up this idea in a 'framework of ecosystem services' (**Figure 1**). The MEA was conducted under the umbrella of the UNEP. It studied the state and relevance of ecological systems for society, and introduced the concept of ecosystem services to a global audience. The MEA assessed the consequences of ecosystem change for human well-being, and defined ecosystem services as "the benefits people obtain from ecosystems" (MEA, 2005, p. 40). The MEA framework classified ecosystem services into four categories:

- Provisioning services, the products obtained from ecosystems;
- Regulating services, the regulation of ecosystem processes;
- Cultural services, obtained from ecosystems through spiritual enrichment, cognitive development, reflection, recreation, and esthetic experiences;
- Supporting services, those that are necessary for the production of all other ecosystem services.

The first three categories of services directly affect people, whereas the supporting services maintain the other services and life support. The approach set out in the MEA has since been adopted and used widely (Barrios, 2007; Lavelle *et al.*, 2006; Sandhu *et al.*, 2008; Swinton *et al.*, 2007; Zhang *et al.*, 2007).

The MEA was followed by The Economics of Ecosystems and Biodiversity study (TEEB, 2010), which was also carried out under the UNEP umbrella. The TEEB study aimed at providing more comprehensive data and understanding of the economic significance of the loss of ecosystem services and the consequences of policy inaction. The TEEB study took a clear economic approach to facilitate the adoption of an ecosystem services approach in policy making. This was brought about by increasing research on the monetized value of ecosystem services, and the associated increasing interest of policy makers in designing market-based instruments (e.g., payments for ecosystem services and economic incentives for conservation) to affect change (Braat and de Groot, 2012). In the TEEB framework, an extension of the so-called cascade model (Haines-Young and Potschin, 2009) was presented (**Figure 3**). Here ecosystem services are placed between the natural and human systems. This framework also separates services from human benefits and their economic values. A benefit is not a service. It is the advantage one receives from a good or service.

A further refinement that has emerged from the development and discussion of these typologies is the differentiation between 'intermediate' processes (analogous to the MEA supporting services) and 'final' services (Boyd and Banzhaf, 2007; Fisher *et al.*, 2009). This refinement stems from the need to differentiate between intermediate products and final products in welfare economics accounting to avoid double counting. The United Kingdom's national ecosystem assessment (Watson and Albon, 2011) adopts this differentiation, focusing on the delivery of final services. Ecosystem services are undoubtedly becoming an increasingly influential tool, but adoption of the concept is constrained by the confusion surrounding the definition of terms and the limited number of practical examples of application. The quantitative relationships between ecosystem components and ecosystem processes, functions, and service delivery are still poorly understood in many areas, and conceptual frameworks continue to be refined.

An Ecosystem Approach for the Management of Agroecosystems

The CBD laid down 12 principles to guide an ecosystems approach (**Table 1**). These principles are highly anthropocentric, as they focus on management and decision making. The strong emphasis on management is of particular relevance to agroecosystems, as is the recognition of the need to manage

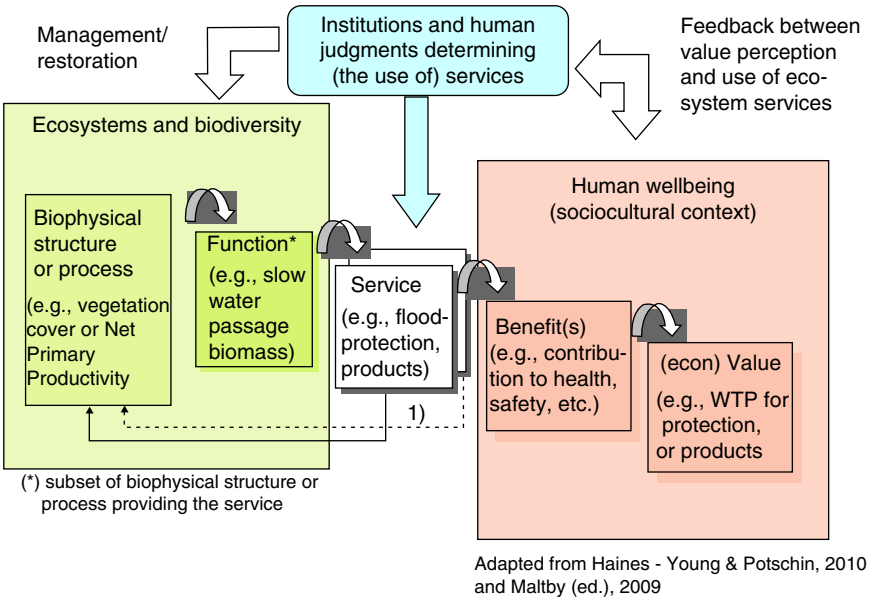


Figure 3 The Economics of Ecosystems and Biodiversity framework for ecosystem services: The pathway from ecosystem structure and processes to human well-being. WTP, Willingness to pay. Reproduced from Figure 1.4 in TEEB, 2010. The economics of ecosystems and biodiversity: Mainstreaming the economics of nature: A synthesis of the approach, conclusions and recommendations of TEEB. Available at: www.teebweb.org (accessed June 2013).

Table 1 Convention on biological diversity: Twelve principles of the ecosystem approach

Principle 1	The objectives of management of land, water, and living resources are a matter of societal choices
Principle 2	Management should be decentralized to the lowest appropriate level
Principle 3	Ecosystem managers should consider the effects (actual or potential) of their activities on adjacent and other ecosystems
Principle 4	Recognizing potential gains from management, there is usually a need to understand and manage the ecosystem in an economic context. Any such ecosystem-management program should: a. Reduce those market distortions that adversely affect biological diversity b. Align incentives to promote biodiversity conservation and sustainable use c. Internalize costs and benefits in the given ecosystem to the extent feasible
Principle 5	Conservation of ecosystem structure and functioning, in order to maintain ecosystem services, should be a priority target of the ecosystem approach
Principle 6	Ecosystems must be managed within the limits of their functioning
Principle 7	The ecosystem approach should be undertaken at the appropriate spatial and temporal scales
Principle 8	Recognizing the varying temporal scales and lag-effects that characterize ecosystem processes, objectives for ecosystem management should be set for the long term
Principle 9	Management must recognize that change is inevitable
Principle 10	The ecosystem approach should seek the appropriate balance between, and integration of, conservation and use of biological diversity
Principle 11	The ecosystem approach should consider all forms of relevant information, including scientific and indigenous and local knowledge, innovations, and practices
Principle 12	The ecosystem approach should involve all relevant sectors of society and scientific disciplines

Source: Reproduced from Convention on Biological Diversity: 12 Principles of the Ecosystems Approach. Available at: http://www.cbd.int/ecosystem/principles.shtml (accessed June 2013).

ecosystems in a socioeconomic context to maintain ecosystem services provision, via balancing the conservation of resources with their use (Robinson *et al.*, 2013). The power to choose the outcomes of ecosystem management, but not necessarily the means, rests with society. In addition, it is recognized that change is inevitable, which is a growing area of interest within Soil Science, with respect to understanding how human activity is causing soil change on anthropogenic time scales (Richter *et al.*, 2011).

International initiatives, such as The Economics of Ecosystems and Biodiversity, (TEEB, 2010) and the United Nations initiative 'The Economics of Land Degradation' (September 2011) have embraced an ecosystems approach, using the concepts of natural capital and ecosystem services as their framework for addressing sustainable land management. The ecosystems approach is also reflected in the European Union's strategy for land management in the CAP. In 2007, the European Commission published the Thematic Strategy for

Soil Protection, which identified a specific policy need to address the threats to soils, including the protection of the essential soil functions and ecosystem services that they provide. A number of international projects are now working on strategies to embed ecosystem services into decision making and policy frameworks for land and soil management (Soil Service, SoilTrEC, and EcoFinders). Defra in the UK has also adopted an ecosystem services approach to inform resource management: the 'ecosystem-based approach' (Beddington, 2010; Defra, 2007, 2013). The UK also released the 'UK National Ecosystem Assessment' (Watson and Albon, 2011), which advertizes new ways of estimating national wealth (Watson and Albon, 2011) and now has a Natural Capital Committee to advise Treasury. In Wales, the new Natural Resources Wales organization incorporates the Environment Agency, Forestry Commission, and Countryside Council for Wales into a single body, to be organized using an ecosystems approach. Thus both policy and the government bodies that monitor and manage the environment are being influenced by the ecosystem services approach.

In this section, recent developments in soil natural capital frameworks that are relevant for agroecosystems are reviewed. The linkages between these frameworks and soils information and soil change are also explored, along with recent progress in ecosystem services frameworks that attempt to synthesize these concepts. Finally, valuation approaches are examined to provide an insight into the different contextual settings where valuation of ecosystem services can be useful.

Agroecosystems and Soil Natural Capital

Soil natural capital is perhaps a more intuitive concept for soil science and agronomy because it focuses on soil stocks, which are routinely measured and inventoried in soil surveys. Soil stocks are the building blocks of the soil infrastructure, so maintaining and developing these stocks is key to delivering ecosystem services. Definitions of soil natural capital and what it includes have developed in recent years. Palm *et al.* (2007) defined soil natural capital as texture, mineralogy, and soil organic matter. Robinson *et al.* (2009) added 'matter, energy, and organization,' recognizing the importance of connections and organization as a stock. Dominati *et al.* (2010a,b) (**Figure 4**) took a more generic approach following Costanza and Daly (1992), defining it as a stock of natural assets yielding a flow of either natural resources or ecosystem services. Dominati *et al.* (2010a,b) (**Figure 4**) differentiated between inherent and manageable soil properties similar to the inherent and dynamic properties used by Robinson *et al.* (2009) (**Figure 5**). These concepts attempt to differentiate between stocks that change through pedological processes and

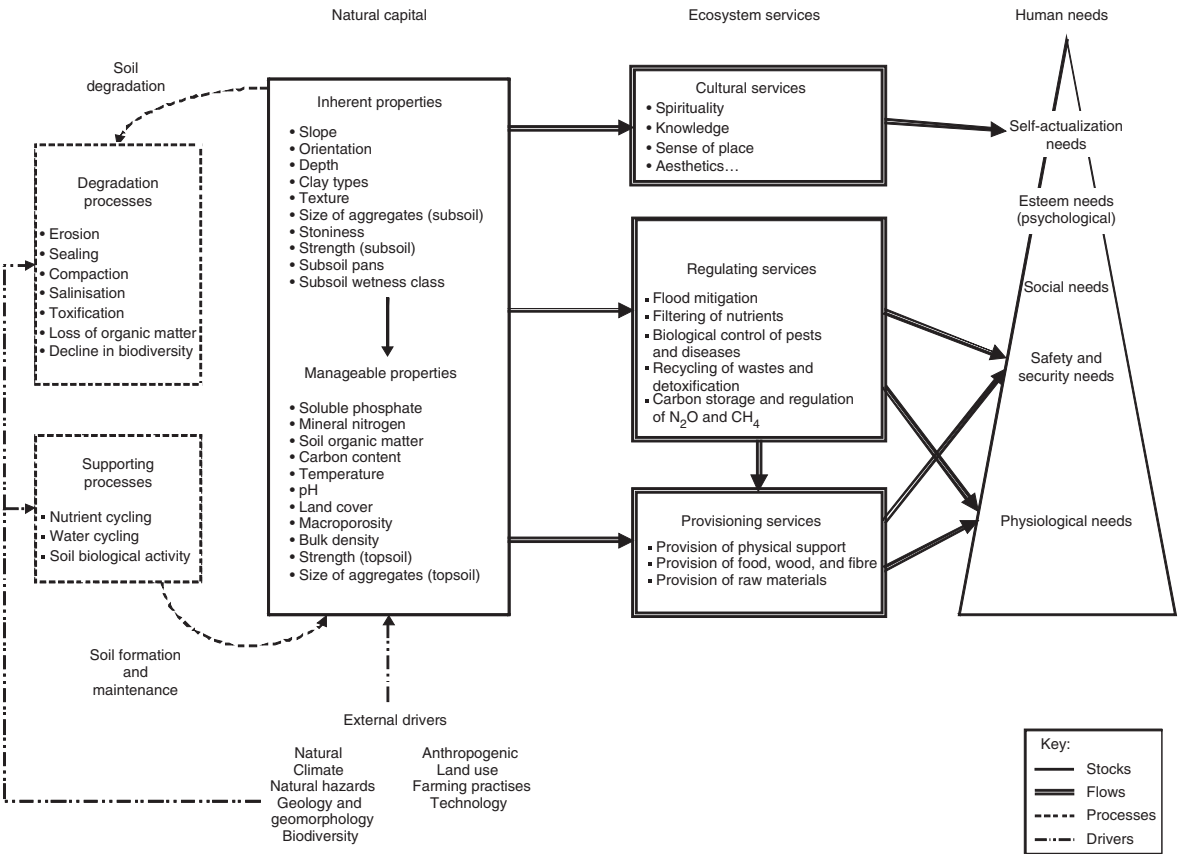


Figure 4 Conceptual framework linking soil natural capital and functioning with ecosystem services provision and human needs. Reproduced from Dominati, E.J., Patterson, M.G., Mackay, A.D., 2010a. A framework for classifying and quantifying the natural capital and ecosystem services of soils. Ecological Economics 69, 1858–1868.

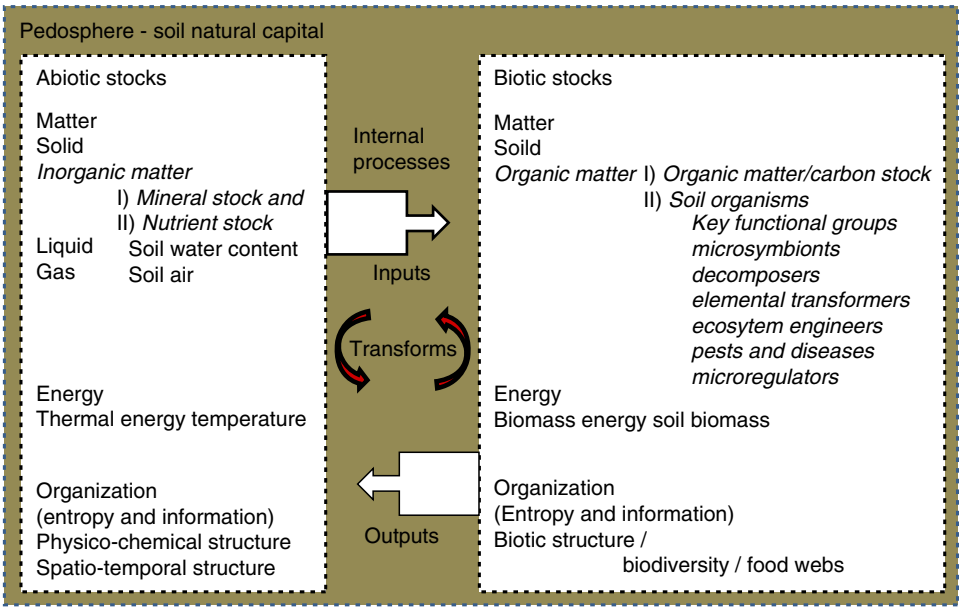


Figure 5 Soil natural capital stocks using a matter, energy, and organization framework (Robinson *et al.*, 2009) divided between abiotic and biotic components (Robinson *et al.*, 2012). Reproduced from Robinson, D.A., Hockley, N., Cooper, D., *et al.*, 2013. Natural capital and ecosystem services, developing an appropriate soils framework as a basis for valuation. Soil Biology and Biochemistry 57, 1023–1033.

those that can be changed by management. For example, inherent soil properties would typically include soil depth, texture, and mineralogy. They cannot readily be changed without significant modification of the soil or its environment (Dominati *et al.*, 2010a,b) (**Figure 4**). Manageable or dynamic soil properties typically include nutrients, organic matter, and soil moisture and structure, all of which can be influenced by land use. Robinson *et al.* (2013) synthesized these concepts, with some of the work done on soil biology (Barrios, 2007) by splitting the capital stocks into abiotic and biotic components (**Figure 5**), in order to recognize that there are constant fluxes and transformations of materials between the biotic and abiotic pools. It is these processes that contribute to soil formation, development or supporting processes in Dominati *et al.* (2010a,b) framework (**Figure 4**). The biological component of soil acts as a biogeochemical cycling engine. Key functional groups rather than particular species are of greatest interest in the delivery of ecosystem services (**Figure 4**).

Farmers understand and appreciate the value of their soil natural capital and continually explore ways to supplement stocks or compensate for a lack of it in different ways. Most commonly, the natural capital is supplemented with added capital or built capital, which is associated with technologies employed to replenish and lift the productive capacity of soils. As an example, fertilizers or animal wastes are used to substitute depleted nutrients and irrigation is used to overcome limited water supplies or water-holding capacity. Artificial drains can be used to improve soil drainage and compensate for a lack of macropores. Identifying where soil natural capital stocks are restricting and how they can be improved using added or built capital is critical for monitoring and the assessment of the sustainability of land uses (Dominati, 2011; Mackay, 2008). An important benefit of using an ecosystem approach with monetized valuation is that changes in stocks can be assessed and interventions valued, allowing the grower the opportunity to consider different options using a comparable value, for example, an economic value.

Agroecosystems and the Provision of Ecosystem Services

The literature addressing the provision of ecosystem services from agroecosystems has focused on two areas: the general provision of ecosystem services from agroecosystems, or more specifically the provision of services from soils. Most of the work done on ecosystem services from agroecosystems uses the MEA (2005) framework (Porter *et al.*, 2009; Sandhu *et al.*, 2010; Swinton *et al.*, 2007; Zhang *et al.*, 2007). The main ecosystem services addressed in relation to agroecosystems are generally the provision of food, feed, fuel, and fiber, the filtering of nutrients and contaminants, carbon storage, greenhouse gases regulation, and pollination and cultural services, including recreation and esthetics. Many of the other ecosystem services provided by agroecosystems (**Table 2**) have not been studied.

General ecosystem service frameworks tend to consign the soil system to 'supporting services' based on the MEA (2005). Although supporting services are vital for the provision of all other services, this classification can result in the role played by soils in the provision of other services being overlooked. For example, the TEEB initiative (TEEB, 2010) has removed supporting services from their framework, as they do not directly benefit society, and now refers to them as 'biophysical structure, processes, and functions' (**Figure 3**). As a consequence one may fail to recognize the large differences that exist between soils in their ability to provide services. For instance, the

Table 2 Goods and ecosystem services provided by agroecosystems and their soils

Service	*Definition*
Provisioning services	
Provision of food, feed, fuel, and fiber	Agroecosystems, first purpose is to produce food and grow crops for a diversity of purposes. Soils physically support plants and supply them with nutrients and water
Provision of raw materials	Soils and vegetation can be a source of raw materials, for example, topsoil, peat, turf, sand, clay minerals, biomedical and medicinal resources, genetic resources, and ornamental resources. However, the renewability of these stocks is sometimes questionable
Provision of support for human infrastructures and animals	Soils represent the physical base on which human infrastructures and animals (e.g., livestock) stand
Regulating services	
Flow regulation	Soils have the capacity to absorb and store water, thereby regulating water flows (fresh water levels) and mitigating flooding
Filtering of nutrients and contaminants	Soils can absorb and retain nutrients (N, P) and contaminants (*Escherichia coli*, pesticides) and avoid their release in water bodies
Carbon storage and greenhouse gases regulation	Soils have the ability to store C and regulate the production of greenhouse gases, such as nitrous oxide and methane
Detoxification and the recycling of wastes	Soils can absorb (physically) or destroy harmful compounds. Soil biota degrades and decomposes dead organic matter thereby recycling wastes
Regulation of pests and diseases populations	By providing habitat to beneficial species, soils and vegetation of agroecosystems can control the proliferation of pests (crops, animals, or humans) and harmful disease vectors (viruses and bacteria) and provide biological control
Pollination	Agroecosystems provided habitat for the regulation of beneficial insect populations, ensuring key biological processes, such as pollination of crops
Cultural services	
Recreation/ecotourism	Natural and managed landscapes can be used for pleasure and relaxation (walking, angling, and mountain biking)
Esthetics	Appreciation of the beauty of natural and managed landscapes (wildlife viewing and scenic driving)
Heritage values	Memories in the landscape from past cultural ties (landscape associated with an important event of regional or national significance)
Spiritual values	Sacred places
Cultural identity/inspiration	Natural and cultivated landscapes provide a sense of cultural identity. This establishes a strong cultural linkage between humans and their environment

Source: Adapted from Dominati, E.J., Patterson, M.G., Mackay, A.D., 2010a. A framework for classifying and quantifying the natural capital and ecosystem services of soils. Ecological Economics 69, 1858–1868; Dominati, E.J., Patterson, M.G., Mackay, A.D., 2010b. Response to Robinson and Lebron – Learning from complementary approaches to soil natural capital and ecosystem services. Ecological Economics 70, 139–140; MEA, 2005. Millennium Ecosystem Assessment: Ecosystems and Human Well-Being: Synthesis. Washington, DC: Island Press; TEEB, 2010. The economics of ecosystems and biodiversity: Mainstreaming the economics of nature: A synthesis of the approach, conclusions and recommendations of TEEB. Available at: www.teebweb.org (accessed June 2013); and CICES, 2013. Common International Classification of Ecosystem Services (CICES). Available at: http://www.cices.eu/ (accessed June 2013).

MEA mentions 'soil formation' as a supporting service and recognizes that 'many provisioning services depend on soil fertility' (MEA, 2005, p. 40). Further, the role of soils in the provision of regulating services like flood mitigation, filtering of nutrients, and waste treatment is mentioned, but the part played by soils in the provision of these services and more generally in the provision of services from above-ground ecosystems is not explicitly identified. General ecosystem services frameworks need to be extended to explicitly detail the relationships between soil stocks, soil processes, and soil services, as they contribute to the ecosystem service supply chain.

A major emphasis of ecosystem service frameworks is provisioning services, which include food, feed, fuel, and fiber. The current valuation of agricultural land is primarily based on its productive capacity. This is referred to as Ricardian land value (value in agricultural production) (Daly and Farley, 2010). Other components of land value, such as value for development (location, distance from urban centers, iconic coastal, and lake side, distance to services, such as roads and power lines), land value as a speculative investment, or as a hedge against risk are usually small, but can become significant.

However, soils provide other important functions that support ecosystem services delivery. This was articulated, for example, by Daily (1997), Andrews *et al.* (2004), and Wall *et al.* (2004), who described in detail the services soils provide to human society, from being a substrate for plant growth to buffering floods to recycling wastes. Daily (1997) noted that soils are a valuable asset that 'takes hundreds to hundreds of thousands of years to build and very few to be wasted away' (Daily, 1997, p. 113). Given the important role of soil biology in the functioning of soils, there has been an increasing interest in the contribution of the below-ground biota and microbial communities in supporting processes and thereby providing services (Barrios, 2007; Bell *et al.*, 2005; de Bello *et al.*, 2010; Gianinazzi *et al.*, 2010; Guimarães *et al.*, 2010; Hedlund and Harris, 2012; Keith and Robinson, 2012; Smukler *et al.*, 2010; van Eekeren *et al.*, 2010; Wall *et al.*, 2004; Wall, 2012). Dominati *et al.* (2010a,b) recognized that a

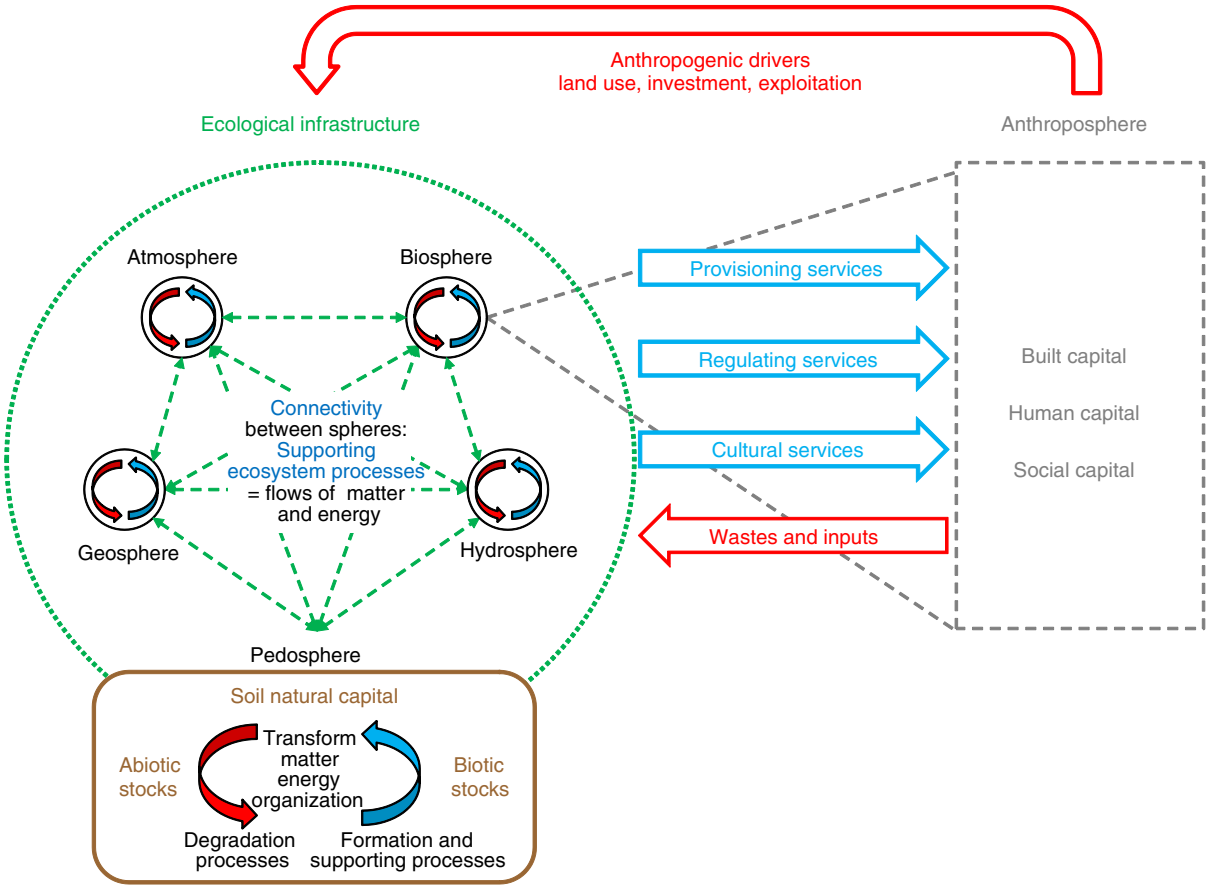


Figure 6 Combined framework for natural capital, ecological infrastructure, and ecosystem services.

combined natural capital and ecosystem service approach is needed for soils (Figure 5). They detailed each of the ecosystem services provided by soils and studied the properties and processes behind them (Dominati, 2011). Robinson *et al.* (2012) also proposed a holistic framework detailing goods and services from soils. Table 2 provides a summary of goods and ecosystem services provided by agroecosystems and their soils based on the latest literature.

Ecological Infrastructure and the Ecosystem Service Supply Chain

No matter how modified they may be, agroecosystems are inseparable from the ecological infrastructure that forms the basis for the provision of ecosystem services. This is because all living organisms require material, energy, and information inputs and produce waste and other outputs.

Recent work has recognized the importance of understanding the continuum along the ecosystem service supply chain (Mooney, 2010; Robinson *et al.*, 2012). Dominati *et al.* (2010a,b) were the first to bring all these concepts together in an overarching framework (Figure 5). In that framework, the ecological infrastructure component is identified on the left side and constitutes the soil natural capital, including the processes acting on and within soils. When put to use, these stocks contribute, along with built capital, toward the delivery of ecosystem services that fulfill human needs. Robinson *et al.* (2012) synthesized these ideas to fit within the stock-flow, fund-service framework used in ecological economics (Daly and Farley, 2010; Farley and Costanza, 2010; Georgescu-Roegen, 1971).

Figure 6 incorporates the concepts developed by Bristow *et al.* (2010), Dominati *et al.* (2010a,b), and Robinson *et al.* (2012) into a framework that goes beyond the pedosphere and considers the bio-, geo-, atmo-, hydro-, and anthropospheres and is applicable to agroecosystems.

On the left-hand side, the earth-system approach (Figure 6) recognizes all the Earth's resources. The major compartments, or 'spheres,' are the atmosphere; hydrosphere, including oceans, surface and ground water, and lakes; the biosphere with its plants and animals, including humans; the pedosphere, the thin skin of soil around the earth; and the geosphere, containing rocks and minerals. The pedosphere is expanded to give an example of the biotic and abiotic stocks that each compartment contains, in this case the soil natural capital stocks (Figure 6). Stocks and their condition within each sphere are tangible materials that can be stock piled and are relatively easy to quantify. The arrows within each sphere represent the processes that build up or degrade stocks. These processes result in the cycling and flow of materials and their transformation. Supporting and degradation processes are

influenced by external drivers, embodied by flows coming from and going to the other spheres. The connectivity among and within spheres, that is the flows of matter, energy, and information, maintain the integrity of the ecological infrastructure, and can also be referred to as supporting processes (Dominati *et al.*, 2010a,b; MEA, 2005; TEEB, 2010).

On the right-hand side of the framework is the anthroposphere. The anthroposphere is contained within the biosphere and includes various types of anthropocentric capital: built capital (transport, communications, water, energy, housing, and other infrastructure), human capital (health, education, and security capital), and social capital (equity, agency, leadership, institutions, and social networks) (**Figure 6**). Ecosystem services, classified here according to the Millennium Ecosystem Assessment typology (MEA, 2005), are the flows coming from the ecological infrastructure, directly useful to humans. Many of these services are intangible, so they cannot be stockpiled and in general can be measured as units per unit time. The processing of goods directly harvested from the various spheres, as well as the use of natural stocks, built capital and ecosystem services, results in wastes, or impacts on each of the earth system spheres. Anthropogenic drivers, such as land use and management, determine the levels of natural resource exploitation, changes to natural capital stocks and the provision of ecosystem services, and the nature, and quantity of wastes produced.

A sustained flow of ecosystem services depends on the integrity, and thus connectivity, of the ecological infrastructure. This means that the entire supply chain needs to be considered when identifying and determining the impacts of land management on agroecosystems. At present, the value of an agroecosystem is generally limited to its immediate economic productivity capacity, but agroecosystems provide a wide range of services, and are also valuable for maintaining the integrity of ecological infrastructure.

The ecosystem services approach has been very useful in highlighting the lack of consideration for the holistic and long-term value of agroecosystems. An important challenge is how best to deal with recognizing the value of the ecological infrastructure, along with the ecosystem services, beyond provisioning. Given the global level of environmental degradation, food security for growing populations can only be achieved via agroecosystems that serve a dual purpose. Along with producing socioeconomic goods, such as food, feed, fuel, and fiber, the farming enterprises must also contribute toward the integrity of the ecological infrastructure that underpins the continued provision of essential ecosystem services (Gliessman, 2007).

Approaches to Valuation

The economic value of commodities produced by agroecosystems is well understood. Agricultural products are gradually transformed as they progress along the 'production chain,' where economic value is often added at a number of stages. Agroecosystems are also closely linked to the economic value of land. The value of agricultural land is currently defined mostly by its productive capacity. The productive capacity of the land, plus its location, plus the value of the built infrastructure on the land determine the land's economic value. There are very few valuation systems that recognize or capture the other contributions land makes to the well-being beyond its economic contribution. To achieve land use sustainability, one needs to value the multifunctionality of this scarce resource and include it in decision making.

To convince financial institutes, economists, and others in society regarding the value of soils, the current approach to valuing land and agroecosystems needs to be extended to include all the ecosystem services provided. Approaches that have the capacity to quantify and value the ecosystem services supplied by agroecosystems would be a significant advance on the current method. Such approaches would provide a holistic representation of the sustainability of current land use, and the pivotal role the pedosphere plays in human well-being.

It has been widely argued that the undervaluation of the contributions of ecosystems to human welfare, including agroecosystems, can be partly explained by the fact that they are not adequately quantified in terms comparable with economic services and built capital (Braat and de Groot, 2012; Costanza *et al.*, 1997). In response, since the 1990s, an increasing number of studies have focused on the economic valuation of ecosystem services (Costanza *et al.*, 1997) including services from agroecosystems (Breure *et al.*, 2012; Porter *et al.*, 2009; Sandhu *et al.*, 2008). This is because framing ecological concern in economic terms has great appeal to decision makers (NZIER, 2013; Braat and de Groot, 2012; Robinson *et al.*, 2012).

There is an enormous scope to improve the provision of ecosystem services from agroecosystems, but first a more holistic value of land is needed to inform a number of contexts. Economic valuation of ecosystem services from agroecosystems can assist in (Defra, 2007; OECD, 2002):

- revising national accounting: fully accounting for the environmental impacts of economic activities in decision making, use indicators of change in natural capital stocks, contribution of agriculture to GDP/exports,
- land use decision making: priority setting, cost effectiveness of policy, comparing infrastructure developments/land uses/policy options using cost–benefit analysis including ecosystem services provision and costs of degradation,
- creating new insights for policy development,
- designing incentives, setting charges/taxes, creating markets for ecosystem services (policy around payments for ecosystem services), and
- communicating with the public and land managers about the value (e.g., moral, esthetic, economic, and ecological) of the environment and agroecosystems.

Value is often solely associated with price. Although price is a type of value (monetary value), the two are not synonymous, and any kind of commodity, including ecosystem services, can have many values associated with it. Valuation is about using a common measure to bring things into a frame of comparability (Robertson, 2012), and the common measure might or might not be of economic value.

Environmental management is, as a rule, associated with qualitative information in valuation problems. Thus, there is a clear need for methods that are able to take into account qualitative information, or information of a 'mixed' type (both qualitative and quantitative) (Munda *et al.*, 1994). Martinez-Alier *et al.* (1998) argued that incommensurability (the

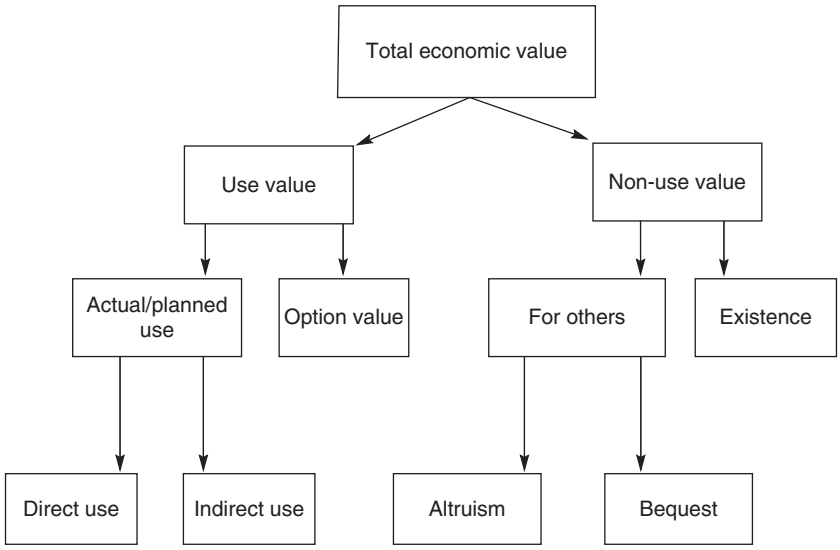


Figure 7 Total economic value. Adapted from Defra, 2007. An Introductory Guide to Valuing Ecosystem Services. London: Department for Environment, Food and Rural Affairs.

absence of a common unit of measurement across plural values) is the 'foundation stone for ecological economics' (Martinez-Alier *et al.*, 1998, p. 279), and that instead of complying with any type of physical reductionism (monetary, energy, or other), valuation should push toward multicriteria analysis and the use of weak comparability (comparing options without recourse to a single type of value) and which does not imply a hierarchy of values. Ecological economics investigates a range of theories of value including the neoclassical economic theory of value. These include:

- The embodied energy theory of value (EMERGY) (Hannon *et al.*, 1986; Patterson, 1998): EMERGY considers energy as the fundamental driver of ecological systems and thereby the economy.
- Ecological value: Ecological value is defined as the value of direct and indirect interactions of a component of an ecosystem, an ecological entity (species), or compartment, with the other components of the same ecosystem (Cordell *et al.*, 2005).
- Contributory value: Natural ecosystems make contributions to the value of final economic goods and services (Norton, 1986; Ulanowicz, 1991). Contributory value assigns value to environmental resources not due to their direct value to humans, but according to their indirect role in maintaining and accentuating the ecosystem processes that support these direct benefits (Costanza *et al.*, 1989, p. 338).

Even though a range of value theories exist, economic value is still getting the most traction in resource management. The rationale of neoclassical economic valuation of ecosystem services lies in the need to ensure that all the services are taken into account in decision making on the same basis as the conventional costs and benefit of conventional economic activity (Pearce and Barbier, 2000).

Neoclassical economics uses the concept of total economic value (TEV). TEV can be broken down into several components, which can then be used to describe the value of ecosystems (**Figure 7**). TEV can be broken down into use and nonuse values (Defra, 2007; Patterson, 1999; Pearce, 1995). Use values include direct and indirect use, and option values:

- Direct-use value: The value of all goods and services derived from the direct or planned use of ecosystems, consumptive use of resources (e.g., food, timber, and parks), or nonconsumptive use of services (e.g., recreation and landscape amenity). They are generally attributed to provisioning and cultural services.
- Indirect-use value: They are derived from the functioning of ecosystems underlying direct-use activities (Defra, 2007; Pearce, 1995). Indirect-use values correspond to supporting processes and regulating services.
- Option value: The value that people place on having the option to use, directly or indirectly, a resource or service in the future, even if not currently in use (Costanza *et al.*, 1989; Defra, 2007).

Nonuse value, also referred to as 'passive value,' is not related to the actual use of ecosystem goods and services, but is derived from the knowledge that ecosystems are maintained (Defra, 2007). They concern all types of services. Nonuse value can be further subdivided into three main components (**Figure 7**):

- Existence value: It relates to the existence of ecosystem goods and services even if an individual has no actual or planned use for it (Costanza *et al.*, 1989). Many people are willing to pay for the preservation of species (whales and rainforest insects) even if they know they might actually never be in contact with them.
- Altruistic value: The value individuals attach to the availability of the ecosystem resources or services to others in the current generation.
- Bequest value: The value that people place on knowing that ecosystem goods and services will be available for future

generations. Bequest value is sometimes regarded as part of existence value.

Some authors (e.g., Pearce, 1995) debate the merit, and hence application of this classification to neoclassical economic valuation, but the TEV framework is a useful tool to identify what type of value is being measured, based on the type of good or service concerned, thereby assisting the selection of an appropriate valuation method (Defra, 2007).

Neoclassical economic valuation is used to measure public and individual preferences for changes in ecosystem services provision. **Table 3** presents a number of valuation techniques currently used for the valuation of ecosystem services. Valuation techniques for valuing ecosystem services can be distinguished by the type of preferences they elicit: (1) revealed or (2) stated.

1. Revealed preference techniques obtain values by looking at individuals' preferences and willingness to pay (WTP) for a marketable good with environmental attributes. These techniques rely on conventional markets, actual markets in which the environmental goods and services are already traded (e.g., timber market or CO_2 market). Revealed preference techniques can also value nontradable goods and services indirectly through marketed goods and services that embody their values (e.g., air pollution affects the price of houses) (**Table 3**).
2. Stated preference techniques elicit individuals' preferences for a given change in a natural resource or service through structured questionnaires (Defra, 2007; Pearce and Barbier, 2000). Stated preference techniques use hypothetical markets, which are simulated markets, where individuals can express their WTP for a nontraded environmental good or service (Pearce and Turner, 1990; Pearce and Barbier, 2000). These techniques, including contingent valuation, choice modeling, and the more modern deliberative group valuation, are the only ones that can estimate nonuse values for some natural resources. In some cases, these nonuse values can be a significant component of the overall TEV (Defra, 2007, **Table 3**).

Valuing environmental goods and services provides additional information that can potentially be used in a benefit–cost analysis (BCA), if appropriate. BCA quantifies, in monetary terms, as many of the costs and benefits of a proposal as is feasible (Defra, 2007). It has been, and still is, extensively used for resource management and decision making. Failure to include ecosystem services in benefit–cost calculations implicitly assigns them a value of zero. To date this has been the norm, and it has contributed to the major depletion of natural capital stocks and increasing environmental issues (MEA, 2005). Valuing ecosystem goods and services for inclusion in BCA is one of the tools available to advance sustainable development by ensuring that policies completely account for the costs and benefits of development proposals on the natural environment (Defra, 2007). For policy making in the context of agroecosystems and resource management, the more relevant application of economic valuation is to compare management options, or assess an investment in either built (e.g., irrigation) or ecological (e.g., soil conservation) infrastructure.

A number of problems have been raised regarding the use and effectiveness of neoclassical economic valuation in assessing the value of ecosystem goods and services that, as yet, lack markets, and in taking these values into account in decision making. These include:

1. Imperfect knowledge or information: Some neoclassical valuation techniques that try to elicit individual's WTP for a nonmarket good are confronted by anomalies based on human beings having imperfect knowledge of ecological processes and functions (Patterson, 1998). This is particularly important when valuing ecosystem services as they are often abstract and the result of complex biophysical processes unknown to nonexperts. Even when using revealed preference methods, challenges arise from the complexity of the biophysical processes. Imperfect information about processes and the provision of ecosystem services is transferred to the quantification of the service and then the economic valuation. Data availability is also always a challenge because a great deal of information, both biophysical and economic, is needed for the quantification and valuation of ecosystem services.
2. Discounting: Another argument against neoclassical economic valuation is its nonequitable aspect when it comes to the intergenerational assignment of benefits and costs. Discounting is an important, but very controversial part of BCA. It is used to compare present and future costs/benefits (Gasparatos *et al.*, 2008). The greater the discount rate adopted, the greater the devaluation of future costs/benefits. Therefore, in projects with a long time horizon, for example, encompassing several generations, future impacts can count for little, or even nothing. This is contrary to the interests of future generations, because it amounts to a nonequitable distribution of costs and benefits. It has been suggested that low discount rates should be adopted for projects that will greatly affect future generations, since small discount rates capture long-term net benefits, whereas higher discount rates put more weight on short-term benefits.
3. Market failure: The exchange of some economic goods and services takes place in markets. However, markets can, and often do, fail. One of the most common areas of market failure is in the provision of public goods, such as ecosystem services. Either ecosystem services are lacking markets, or if markets exist, they can fail to reflect the entire value of the service. For example, there is a market for carbon. The multifunctional value associated with soil carbon includes not only carbon storage, but also the importance of organic matter for soil structure cohesion, and nutrient retention. These values are always very significant for soil functioning, whereas carbon prices fluctuate quickly and frequently. The use of stated-preference methods to determine the value of ecosystem services offers solutions to deal with market failure.
4. Validity of techniques: Whatever the technique used, there are always uncertainties associated with it. For example, where cost-based approaches are used to value services, sometimes the valuation is limited to the scale covered by the technique or the infrastructure element considered, for example, dam, road, or building, whereas the extent of the

Table 3 Economic valuation methods

Market type	*Method name*	*Method type*	*Type of value captured*	*Definition*	*Example*
Conventional market	Market price	Revealed preferences	Use values	Market prices can be used directly to capture the value of ecosystem goods and services already traded in markets	Market price of food, wood, or agricultural land
	Productivity change	Revealed preferences	Use values	Productivity change approach is not a valuation technique per se but can be used with diverse valuation techniques. It uses production functions to describe the relationship between a particular ecosystem service, the natural capital stocks behind it, and the production of a market good	Production function linking soil type, irrigation quantity, and air temperature to wheat yield (the traded commodity)
	Defensive expenditure	Revealed preferences	Use values	Defensive expenditure focuses on the price paid by individuals to mitigate against environmental impacts. The method uses the money spent by individuals to avoid exposure to degradation of the environment and a decrease in the provision of an ecosystem service as a proxy for the value of the service	The cost of mitigation techniques on farm to prevent nutrient and contaminant loss are used as a proxy for the value of the filtering of nutrients
	Replacement cost	Revealed preferences	Use values	The replacement cost approach uses the costs of replacing or restoring damaged ecosystem goods or services to their original state or productivity, using market goods, as a proxy for the value of the service	Cost of plowing to improve soil porosity as a proxy for the value of support, cost of drainage
	Provision cost	Revealed preferences	Use values	The provision cost approach is a variant of the replacement cost. It does not refer to the replacement or restoration of the ecosystem service *in situ*, but to actual costs of providing the damaged service through alternative means. This technique relies on the existence of human-made systems and techniques	Wetlands that provide flood protection may be valued through the cost of building human-made defences of equal function, e.g., dams or flood banks
	Hedonic pricing	Revealed preferences	Use values	Hedonic pricing seeks to find a relationship between environmental characteristics (view levels and air quality) and the price of properties (house and farm land). The value of the environmental component (good or service) can therefore be captured by modeling the impact of all possible factors influencing the price of the property	Influence of soil properties on farmland values
	Travel cost	Revealed preferences	Use values	The travel cost method is predominantly used in outdoor recreation modeling (fishing, hunting, boating, and forest visits). It is a survey-based technique that uses the cost of a trip taken by an individual to a recreation site (e.g., travel costs and entry fees) as a proxy for the value of the recreational service	Travel costs and entry fees are used as a proxy for the recreational value of, for example, a national park

(*Continued*)

Table 3 Continued

Market type	*Method name*	*Method type*	*Type of value captured*	*Definition*	*Example*
Hypothetical market	Contingent valuation	Stated preferences	Use and nonuse values	The contingent valuation method aims at obtaining an estimate of the economic value of a marginal change in the level of provision of an ecosystem good or service not traded in market by directly questioning a sample of the population concerned	Contingent valuation method uses questionnaires to obtain estimates of the social benefit from soil erosion reductions from programs to mitigate the off-site impacts of soil erosion for a watershed. Ask respondents their willingness to pay (WTP) for different scenarios to change erosion levels more than 20 years. Bids can be expressed as tax payments and used to suggest upper limits on per haectare payments for soil conservation programes (Colombo *et al.*, 2006)
	Choice modeling	Stated preferences	Use and nonuse values	Choice modeling is a family of survey-based methodologies for modeling preferences for goods, where goods are described in terms of their attributes and of the levels that these attributes take. Respondents are presented with several alternative descriptions of a good, differentiated by their attributes and levels, and are asked to rank the various alternatives, to rate them or to choose their most preferred. One of the attributes of the good is the price/cost, which is used to indirectly record people's WTP from their rankings, ratings, or choices	A lake may be described in terms of water quality, water clarity, number of fish species, catches per year, and entry fees. Participants are presented with different combinations of attributes and asked to choose their preferred combination or rank the alternative combinations. The results are then used to value an extra unit of, for example, water quality
	Group valuation	Stated preferences	Use values	Group valuation methods are based on principles of deliberative democracy and the assumption that decision making about public goods, such as ecosystem services, should not result from the aggregation of separately measured individual preferences, but from open public debate	Focus groups: aim to discover the positions of participants regarding an issue. In-depth groups: similar to focus groups, but less closely facilitated, and focus on how the group creates discourse on the topic. Citizens' juries: A sample of citizens considers evidence from experts and other stakeholders, hold group discussion on the issue, and give an informed opinion that is supposed to reflect public opinion. Deliberative forums: they spend time listening to the opinions of others (experts, stakeholders, or general public) with the aim of forming a collective view

service can be greater. In such a case, the price obtained will not be representative of the real value of the service. With stated preferences like contingent valuation or choice modeling, many biases, such as design bias, cognitive burden, strategic bias, or information bias are common when respondents state their WTP (Pearce *et al.*, 2006).

5. Sustainability concerns, such as rights, fairness, and intergenerational equity (Spash, 2007).

Because of the problems associated with economic valuation of ecosystem services, researchers are increasingly using several techniques simultaneously to compare results. Cost–benefit analysis is still frequently used because it is cheaper and quicker than other methods, and is well understood by decision makers. But methods, such as deliberative monetary valuation, a novel hybrid of economic and political processes to value environmental change, are now being used more often. This is because they are based on deliberative processes between stakeholder groups and therefore offer some answers concerning fairness and equity.

Application of the Concepts to Resource Management

Challenges of the Ecosystems Approach for Resource Management

Generally speaking, the ecosystems approach and the concepts of natural capital, ecological infrastructure, and ecosystem services are powerful tools for resource management as they contribute to a better understanding of the linkages between on-site changes and off-site impacts. With respect to agroecosystems and soil in particular, these concepts provide a holistic framework, which places agroecosystems within the greater ecological infrastructure.

A number of challenges must be overcome if the ecosystem services approach is to be used as an overarching framework for the management of agroecosystems. Robinson *et al.* (2012) identified four key research areas needing attention to further develop the soils' component of the ecosystems approach. Combining these specific research priorities for soils with general guidelines for application of the ecosystems approach (Braat and de Groot, 2012; Omuto *et al.*, 2012; TEEB, 2010) identifies the key challenges as:

- Framework development, to identify exactly how, where, and when soils and the other spheres are involved in the provision of ecosystem services.
- Quantifying changes to the natural capital stocks under the impact of natural and anthropogenic drivers. This can be achieved through monitoring and modeling of stocks, fluxes, and transformations, within and between spheres and identifying appropriate indicators that can be used in monitoring schemes. This requires enhancing the quantity and quality of information on the functioning of ecological infrastructure: data generation and collection, analysis, validation, reporting, monitoring, and integration with other disciplines.
- Better assessment of spatial and temporal dynamics of service provision, including threshold changes, alternative states, and irreversibilities, especially in relation to beneficiaries.
- Developing means to value ecosystem services and incorporating these values into decision making about alternative management options.
- Developing management strategies and decision-support tools including models and maps of natural resources.
- In the long-term harmonization of methods, measurements, and indicators for the sustainable management and protection of soil resources.

Investing in Ecological Infrastructure for Resource Management

The concept of ecological infrastructure provides a framework that locates ecosystem services within a holistic model of nature. Ecological infrastructure is also directly comparable to built infrastructure in terms of the need for public investment to maintain its integrity. In developing and developed countries alike, there are increasing demands for additional and improved public infrastructure. The global recognition of the need for built infrastructure investment can be used to exemplify and prioritize investment in ecological infrastructure.

Bristow *et al.* (2010) argued that although built infrastructure investment has been ever-increasing, one has not been investing sufficiently in the ecological infrastructure. Indeed, inadequate investment in ecological infrastructure has led to a worsening environmental crisis, in which critical ecosystem services have been and are being lost across the globe. For example, 60% of ecosystem services examined by the Millennium Ecosystem Assessment (MEA, 2005) was found to be degraded. This means that the underlying ecological infrastructure that provides these services is deteriorating, or has collapsed. When the current state of global ecological infrastructure is added to increasing population growth and resource consumption trends, the need for significant and ongoing investment in ecological infrastructure is undeniable.

Investing in ecological infrastructure involves three strategies that must be carried out concurrently:

1. Research and extension investment to improve and disseminate knowledge about ecological infrastructure and the ecosystem services it provides;
2. Restoration of degraded ecological infrastructure; and
3. Maintenance and enhancement of the capacity of relatively undisturbed ecological infrastructure to continue to produce ecosystem services.

Improving our knowledge about ecological infrastructure is necessary to ensure that 'returns' on ecological infrastructure investments are maximized. Although there are still many knowledge gaps, humans already possess a vast amount of information about how healthy catchments, forests, rivers, wetlands, soils, and coral reefs should look and function. The extent and depth of this knowledge is sufficient to begin investing in restoring, maintaining, and enhancing ecological infrastructure immediately (Karr, 1993; MEA, 2005). Sufficient investment in ecological infrastructure also obviates the various problems that arise from the use of neoclassical economic concepts to value ecosystem goods and services that are not amenable to market-based logics. Whether or not ecosystem

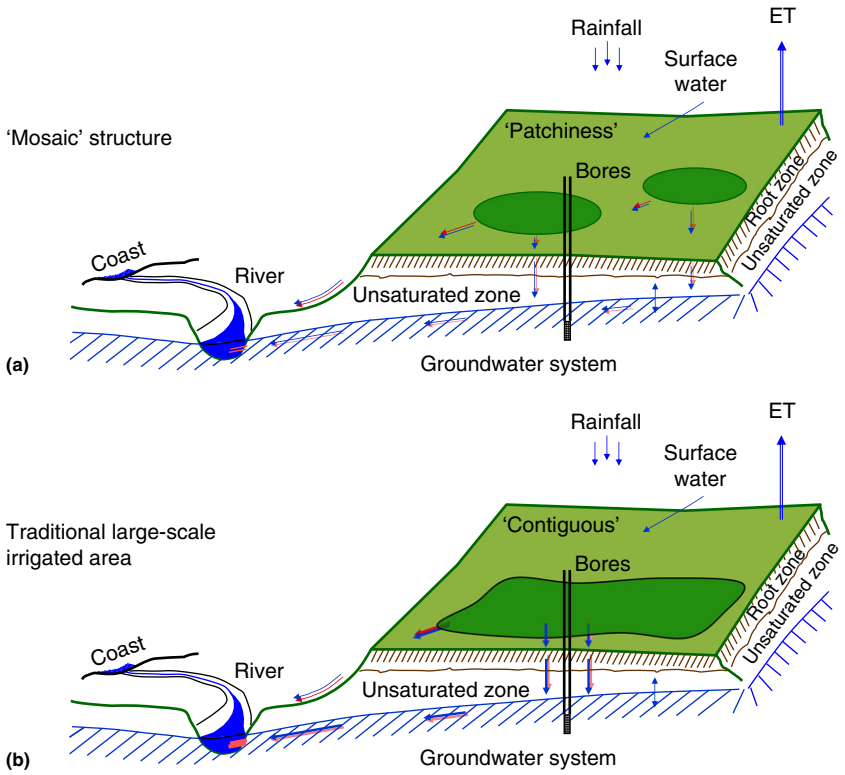


Figure 8 Schematic showing the basic features of irrigation mosaics compared to large contiguous irrigation developments. Reproduced from Paydar, Z., Cook, F.J., Xevi, E., Bristow, K.L., 2007. Review of the current understanding of irrigation mosaics. CRC for Irrigation Futures Technical Report No. 08/07. CSIRO Science Report 40/07. Available at: http://www.irrigationfutures.org.au/imagesDB/news/CRCIF-TR0807-web.pdf (accessed 06.01.10).

processes and functions are able to be traded in markets, if the integrity of the ecological infrastructure that produces ecosystem services is maintained, the services will continue to flow.

A key operational aspect of investing in ecological infrastructure is the development of newly built infrastructure and the reconfiguration of existing built infrastructure, so that these contribute toward ecological integrity. This is particularly important in the case of agroecosystems. One approach that can be used for both new and existing irrigation developments is based on the concept of mosaics (Figure 8). This approach, which involves developing smaller discrete patches of irrigated land dispersed across the landscape, may offer an alternative to large-scale contiguous irrigation systems (Paydar *et al.*, 2007). Zones of transition between adjacent ecological systems are important characteristics of natural mosaics and play a key role in energy and material fluxes (Paydar *et al.*, 2007). Irrigation mosaics could be used to create or enhance zones of transition in the agricultural landscape, leading to greater biodiversity and improved microclimates. Improved zones of transition also help to minimize erosion and absorb surplus nutrients, sediments, and solutes that flow from the surrounding crop fields, thus decreasing the discharge of irrigation 'waste' out of the irrigation area (Paydar *et al.*, 2007). Understanding the likely performance of irrigation mosaics can also help to identify how existing irrigation systems could be reconfigured for improved harmonization with natural systems (Figure 8) (Story *et al.*, 2008).

To sum up, one cannot escape the reality of a finite planet with limited resources, growing human populations, and increasing demands for ecosystem services. Unless the approaches to NRM include programs for restoring, maintaining, and enhancing ecological infrastructure, the world's ecosystems, including the agroecosystems, will continue to be fragmented and destroyed.

Use for Policy Making at the Regional Scale

In developed countries around the world, government bodies responsible for NRM are increasingly under pressure from the general public to deliver higher environmental standards when managing land for sustained use of resources. For example, in New Zealand over the past 50+ years, investment in soil conservation in agroecosystems has run into billions of dollars. Soil conservation policies aim to reduce the risk of soil erosion in vulnerable land (e.g., hill and steepland country), the downstream costs associated with nutrient losses and sediment loadings to waterways, and damage to productive farmland and towns. Current evaluation of soil conservation policy and justification for the associated expenditure is limited to an assessment of the reduction in the loss of productive capacity, soil loss, and sediment and downstream impacts on community of flooding and sedimentation. Until the full range of ecosystem services below and above ground is considered in the analysis, the true cost of erosion, beyond productivity loss, and full value of soil conservation is not available for informed land-use decision making.

In the case of soil conservation, an ecosystem services approach offers a methodology that can answer such questions, through the following steps:

- Quantify the provision of ecosystem services from the agroecosystems of interest (e.g., hill country sheep and beef farming) to assess the baseline flows of ecosystem services under current land use on uneroded soil, before implementation of a soil conservation programe, based on information from existing planning tools.
- Compare these baseline flows with an assessment of the provision of ecosystem services from a similar agroecosystem with well-developed soil conservation plan and practices, for example, wide-spaced poplars on steep hill for sheep and beef pastures, to see how the soil conservation policy impacts the provision of ecosystem services.
- Use the quantitative information for both systems in an economic valuation of the provision of ecosystem services from the two base-line scenarios.
- Quantify and value the provision of ecosystem services from eroded land to evaluate the loss of services compared to an undisturbed pedosphere and ecological infrastructure.
- Characterize and quantify the recovery profile of the provision of ecosystem services in the years following an erosion event (0–1000s years) based on soil recovery data to assess how the provision of ecosystem services recovers.
- Implement a cost–benefit analysis of investment in soil conservation on steep hill pasture prone to erosion compared with no conservation, using an ecosystems services approach, to assess the return on investment from the soil-conservation policy.
- Inform the 'full value of the soil-conservation policy,' enabling a more holistic assessment of flood and catchment management, by allowing, for example, a comparison of the value of a dollar spent on conservation practices (e.g., tree planting) with engineers' structures, such as stop banks.

Such studies address actual conservation issues and show how an ecosystem services approach can be used to advance existing governance frameworks to solve resource management challenges. Understanding how current investments in built capital and current and future investments in ecological infrastructure are likely to change the flow of ecosystem services from managed landscapes is critical to assess the efficiency, cost effectiveness, and sustainability of resource management policies, and for a more complete understanding of the socialecological value of our land.

Conclusion

The ecosystem services approach to NRM is undoubtedly an increasingly influential tool, which is very useful to highlight the holistic and long-term value of agroecosystems. Challenges remain for its implementation. Future NRM needs to focus concurrently on:

- Addressing dual purpose served by agroecosystems: producing socioeconomic goods, as well as underpinning the continued provision of essential ecosystem services.
- Restoring, maintaining, and enhancing the capacity of current ecological infrastructure to continue providing ecosystem services.
- If and when economic valuation of environmental change is needed, increasingly using valuation techniques that answer concerns about fairness and equity.
- Providing solutions based on sound science to minimize potential damage, on top of looking for solutions to overcome limitations.

The ecosystem services approach to NRM has a tremendous potential to help achieve goals, such as Green Growth and the sustainable use of finite natural resources, while enabling agroecosystems to be adaptable and more resilient to uncertainty, change, and shocks.

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See also: Agricultural Policy: A Global View. Agroforestry: Conservation Trees and Erosion Prevention. Biodiversity and Ecosystem Services in Agroecosystems. Economics of Natural Resources and Environment in Agriculture. International and Regional Institutions and Instruments for Agricultural Policy, Research, and Development. Land Use: Management for Biodiversity and Conservation. Market-Based Incentives for the Conservation of Ecosystem Services in Agricultural Landscapes: Examples from Coffee Cultivation in Latin America. Soil: Conservation Practices

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Organic Agricultural Production: Plants

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Glossary

Agroecosystem An agricultural system of interacting biological communities and environmental components.
Biodiversity The diversity of species and functional groups in a natural or agricultural ecosystem.
Compost Decomposed organic materials such as plant and animal matter, usually prepared in a controlled manner via mixing and aerating.
Conventional agriculture Typically chemical-intensive, short-rotation cropping systems designed for maximum yields, which rely on synthetic chemical inputs to control pests and maintain soil fertility.
Cover crop A nonharvested crop grown for the purpose of preventing soil loss, adding organic matter, fixing nitrogen (in the case of leguminous cover crops), or otherwise improving soil quality and health.
Crop rotation A planned sequence of a diversity of crops grown in succession over multiple years in the same field.
DDT A synthetic insecticide introduced in the 1940s, known technically as dichloro-diphenyl-trichloroethane.
Green manure A nonharvested crop grown for the purpose of adding organic matter, fixing nitrogen (in the case of leguminous cover crops), or otherwise improving soil quality and health.
Nutrients Elements that are necessary for organisms to live, including nitrogen, potassium, phosphorous, and a variety of other nutrients that are required only in very small quantities.
Organic farming The practice of farming that generally avoids the use of synthetic fertilizers, pesticides, and herbicides, and instead relies on biological interactions for agricultural functions.
Organic nutrients Nutrients that are in the form of organic matter or organic compounds.
Soil organic matter Refers to the living or dead plant and animal material in the soil, including crop residues, animal manure, microorganisms, and any other biological material in various stages of decomposition.
Soil quality The capacity of a soil to sustain biological activity, maintain environmental quality, and promote plant and animal health.
Sustainable agriculture For a farm to be sustainable, it must produce adequate amounts of high-quality food, conserve resources, and be environmentally safe, profitable, and socially responsible.
Synergy The condition of two or more interacting components resulting in a greater effect than any/either individual component alone.

Introduction

Sale of organic foods in the past two decades has been one of the fastest growing market segments within the global food industry (Willer *et al.*, 2009). As a result, more arable land, research funding, and research test sites are being devoted to organic farming worldwide. In addition, there has been an increase in published scientific studies of organic systems, with different types of studies evolving and more parameters being measured.

Organic farming systems have been shown to be energy-efficient, environmentally sound, productive, stable, and tending toward long-term sustainability (Lotter, 2003; Mäder *et al.*, 2002). Organic farming systems do not represent a return to the past. They use modern equipment, certified seed, soil and water conservation practices, improved crop varieties, and the latest innovations in feeding and handling livestock. Organic farming systems range from strict closed cycle systems that go beyond organic certification guidelines by limiting external inputs as much as possible, to more standard systems that simply follow organic certification guidelines.

Organic farming relies on the integration of a diversity of farm components, the cycling of nutrients and other resources, and stewardship of soil and environment. The result is a farming system that is more knowledge intensive than resource intensive. By minimizing or eliminating chemical inputs such as artificial fertilizers, synthetic pesticides, and antibiotics, and instead using composts and manures, organic farms aim to build soil, minimize pollution, and recycle nutrients.

This article aims to describe organic agriculture in its variety of forms. Organic agriculture is at once a set of ideological principles and a science-based agronomic practice. It is a

quickly expanding global market force as well as an alternative to conventional agriculture that seeks socioeconomic and environmental sustainability on local and global scales. This article discusses the global history of the organic movement and its international origins, the role of organic certification, global trends in sales and production of organic foods, the underlying principles of organic farming, examples of management practices, and current research on the production, economic, environmental, and social sustainability of organic farming.

History

Before the advent of chemical pesticides and synthetic fertilizers, farmers had to rely on organic materials for fertilizers and on physical methods of weed control. However, these historical farming systems were often unrelated to the organic farming practices of today. Often these historical farming systems relied on depleting the natural soil resources by not replacing harvested nutrients, not protecting the soil from erosion, and not sufficiently rotating crops. Organic farming is not a reversion to past practices, but rather, it is what Vogt (2007: p. 12) calls "an intensification of farming by biological and ecological means in contrast to chemical intensification by mineral fertilizers and synthetic pesticides."

Around the turn of the twentieth century, agriculture was quickly changing, with increased mechanization, the discovery of inorganic mineral fertilizers, and shipping of crops over larger distances (Conford, 2001). These rapid changes began to cause problems with soil compaction, uncontrollable pest and disease outbreaks, soil acidification, and declines in soil fertility. Additionally, the increasingly urban populations of many developed countries at the time led to changes in lifestyle and diet. Concern over these problems set the stage for organic agriculture movements to develop independently in Central and Western Europe, the US, and Japan.

In Germany, the early 1900s saw the rise of the life reform movement in reaction to increasingly unhealthy urban lifestyles and diets. The life reform movement sought a natural way of living, which consisted of leading a physically active agrarian-based life and a strictly vegetarian diet of locally and naturally produced food. Leaders of the movement encouraged composting, green manures, conservation tillage, and recycling municipal wastes on fields to replace lost nutrients. They saw the use of synthetic fertilizers as the cause for decreasing food quality. The Natural Farming and Back-to-the-Land Association was founded in 1927 and established early standards for organic farming, which were published in journals and through lectures and courses. Ewald Könemann's three-volume book entitled Biological Soil Culture and Manure Economy is an important culmination of the principles of the natural farming movement that was emerging from Germany (Vogt, 2007).

Complementing the life reform movement, in 1924 in Koberwitz, Germany (now Kobierzyce, Poland), an Austrian scientist Rudolph Steiner gave a series of eight lectures on agriculture later published under the title Spiritual Foundations for the Renewal of Agriculture (Paull, 2011). Founder of the Anthroposophy spiritual movement and the Waldorf educational philosophy, Steiner's agricultural lectures offered guidelines for organic farming practices, stressing the ideas of the farm as an organism, of on-farm nutrient cycling, and of the close integration of the various parts (or 'organs') of the farm (Vogt, 2007). A mix of scientific and astrological thinking, Steiner's lectures also laid the groundwork for biodynamic agriculture, popularized by Ehrenfried Pfeiffer's (1938) publication of Bio-Dynamic Farming and Gardening (Pfeiffer, 1938). In 1928, the first standards for biodynamically grown food were developed under the name Demeter, which is thought to be the first set of agricultural food standards (Schmid, 2007; Gomiero *et al.*, 2011).

In the early 1900s, a handful of American and British agricultural scientists also began to draw contrasts between their countries' increasingly industrialized farming and the farming practices that they observed in parts of Asia. Former Chief of the Division of Soil Management for the United States Department of Agriculture (USDA), Franklin H. King, left America in 1907 to study the farming practices of East Asia. He published his observations in a 1911 book entitled Farmers for Forty Centuries, in which he described the many lessons he thought American and European agriculturalists should learn from Chinese, Korean, and Japanese farmers, specifically their practices of composting and returning all waste products to farmland and their long-term view of maintaining and building soils with cover crops and organic amendments (King, 1911). "Man," King wrote, "is the most extravagant accelerator of waste the world has ever endured. His withering blight has fallen upon every living thing within his reach, himself not excepted; and his besom of destruction in the uncontrolled hands of a generation has swept into the sea soil-fertility which only centuries of life could accumulate – fertility which is the substratum of all that is living" (King, 1911: pp. 196–197).

During the same period, Sir Robert McCarrison, a British nutritionist, began remarking on the linkages between the excellent physical health, whole food diets, and healthy integrated farming systems of three tribes in India. Returning to England in 1935, he greatly influenced agricultural and health professionals, and inspired physician G.T. Wrench to write his book entitled The Wheel of Health (Wrench, 1938).

Often cited as the father of modern organic agriculture, Sir Albert Howard first traveled to India in 1905, and it was not until 1924 that he was given the bureaucratic freedom and leeway to pursue integrated interdisciplinary agricultural research in the state of Indore. Familiar with King's writings on composting and soil building, Howard adapted these practices to the local conditions of Indore, resulting in what became known as the Indore Process. Howard's (1931) book entitled The Waste Products of Agriculture quickly spread the concepts of the Indore composting process around the world (Howard, 1931). Just as McCarrison attributed a person's health and resistance to disease to their appropriate diet, activities, and surroundings, Howard saw healthy soils as the foundation for healthy plants and animals (Conford, 2001). In 1940, Howard wrote his most famous work, An Agricultural Testament, in which he writes:

"Insects and diseases are not the real cause of plant diseases but only attack unsuitable varieties or crops imperfectly grown. Their true role is that of censors for pointing out the crops that

are improperly nourished and so keeping our agriculture up to the mark. In other words, the pests must be looked upon as nature's professors of agriculture: as an integral portion of any rational system of farming [...] The policy of protecting crops from pests by means of sprays, powders, and so forth is unscientific and unsound as, even when successful, such procedure merely preserves the unit and obscures the real problem – how to grow healthy crops" (Howard, 1943: p. 159).

Inspired by the work of Howard, King, McCarrison, and others, Lady Eve Balfour established what is thought to be the first long-term comparison of organic and nonorganic production, called the Haughley experiment (Stinner, 2007). Informed by her research and experimentation, she wrote her influential work The Living Soil (Balfour, 1943), which highlighted the importance of soil biota in nutrient availability. She became an integral founder and first president of the Soil Association in Britain in 1946. Rooted in both scientific and Christian values, Balfour was a strong proponent not only of healthy soils and foods, but also of the important social aspects of healthy farming communities (Conford, 2001). Another follower of Howard's work, Lord Walter Northbourne wrote Look to the Land, in which he is the first to use the term 'organic farming' (Northbourne, 1940). He uses the term both to refer to the use of organic material as fertilizer and amendment and to the idea of the farm as an organism, much like the language used by Steiner (Scofield, 1986).

In Japan, Mokichi Okada and Masanobu Fukuoka separately began to practice forms of what they called 'natural farming,' both based on principles of using natural fertilization, prohibiting the use of chemicals, and mimicking natural processes on the farm (Kristiansen and Merfield, 2006). Fukuoka practiced what he called 'do-nothing farming,' which aimed to minimize human interference with agricultural ecosystems in order to maintain the natural vitality of the field. Fukuoka published The One Straw Revolution in 1975, in which he outlines five principles: (1) cultivating the soil and the use of powered machines are unnecessary; (2) prepared fertilizers and the making of compost are unnecessary; (3) weeding, both mechanical and chemical, is unnecessary; (4) use of pesticides is unnecessary; and (5) pruning fruit trees is unnecessary (Fukuoka, 1978). Both men saw prepared fertilizers as weakening the natural vitality of the crops, and central to both men's philosophy was a spiritual element that unified farming, diet, and human well-being (Kristiansen and Merfield, 2006).

Much of the work being done in Europe was quick to impact the US, most notably through a man named Jerome Rodale. Rodale's interest in health and agriculture was first ignited when he heard a talk given by McCarrison in Pittsburg in the 1920s, and was later elaborated on when, as a publisher, he began what would become a close friendship with Howard (Conford, 2001). In 1940, Rodale purchased a farm in Emmaus, Pennsylvania, still the site of the Rodale Institute today, to begin practicing Howard's farming practices. In 1942, he began publishing the *Organic Farming and Gardening* magazine, and in 1945 he wrote Pay Dirt, in which he communicates the ideas of Howard, Steiner, and others to an American audience (Rodale, 1945). In his book, he also offers early criticisms of using chemical pesticides such as the newly marketed DDT. The Rodale Institute began its Farming System Trial in 1981 to compare a conventional grain rotation with an organic manure-based rotation and an organic cover-crop-based rotation (Stinner, 2007). It is now the world's second-longest running experiment comparing organically and conventionally managed plots, and the Rodale Institute continues to be an important research institute for organic and alternative farming practices (**Figure 1**).



Figure 1 Rodale Institute's ongoing Farming Systems Trial began in 1981. Photo © 2012 Rodale Institute.

The 1960s and 1970s were a time of significant social change in many regards, and also proved to be a transformative time for the organic movement. Rachel Carson's book, Silent Spring, transformed the dialog about the use of pesticides and other toxins, ultimately leading to the federal ban on DDT in the US in 1972 (Carson, 1962). A new perspective was gaining the global stage through books such as the influential Limits to Growth (Meadows *et al.*, 1972), which explores the limits of economics and resources to support a growing human population, and the then president of the Soil Association E. F. Schumacher's Small is Beautiful: A Study of Economics as if People Mattered (Schumacher, 1974), which introduces alternatives to capitalistic growth with a focus on human and environmental well-being (Kristiansen and Merfield, 2006).

Influenced by the British and German work on organic farming, organic thinking spread to France under the name 'agriculture biologique' (Vogt, 2007). Claude Aubert, author of the popular book, *L'Agriculture Biologique* (Aubert, 1970), helped found the French association Nature et Progrès. This activism in France led to the foundation of the International Federation of Organic Agriculture Movements (IFOAM) in Versailles in 1972. With the aim of creating an exchange network between the now numerous organic associations throughout the world, the founding organizations were the Soil Association in the UK, the Soil Association of South Africa, the Swedish Biodynamic Association, and the French Nature et Progrès (Geier, 2007). From its small roots, IFOAM quickly grew to become an important global network, promoting organic farming practices around the world, and setting basic global standards for organic practices.

In 1973, the Research Institute of Organic Agriculture (known by its German initials FiBL) was founded, and continues today to be the world's largest organic agriculture research establishment

(Niggli, 2007). Founded in part to answer questions about the scientific basis and economic viability of organic agriculture, in 1978 FiBL established the DOK trial to compare side-by-side biodynamic (D), organic (O), and conventional (K) plots. The DOK trial is now the longest-running comparison of organically and conventionally managed land in the world, and its results regularly continue to be published (Mäder *et al.*, 2002).

In the early days of IFOAM and the long-term cropping experiments of FiBL and the Rodale Institute, organic agriculture was still seen as a radical movement in many parts of the world. The United States Department of Agriculture (USDA) did not acknowledge organic farming as a noteworthy form of agriculture until the controversial publication of the USDA's Report and Recommendations on Organic Farming in 1980 (USDA, 1980). Carried out in conjunction with a survey of Rodale Press publication The New Farm readers, the report found comparable yields to most conventional acreage and slightly lower economic returns on organic land than conventional. The report's conclusions included remarks that fundamentally changed the national dialog on organic farming, including "it may be economical for some farmers to produce certain crops and livestock organically rather than conventionally" (p. 46), and "much can be learned from organic farming to reduce soil erosion and nonpoint source pollution"(p. 84).

The ensuing decade brought a new wave of dialog about organic agriculture in the US. The 1981 national meeting of the American Society of Agronomy, Crop Science Society of America, and the Soil Science Society of America included a significant discussion on organic agriculture and was recorded in a 1984 proceedings report entitled Organic Farming: Current Technology and its Role in a Sustainable Agriculture (Bezdicek *et al.*, 1984). A 1989 National Research Council report entitled Alternative Agriculture asserted that wider adoption of alternative farming systems such as organic farms "would result in even greater economic benefits to farmers and environmental gains for the nation" (National Research Council, 1989: p. 6). The organic farming movement in the US received a further boost with the passage of the Organic Foods Production Act in 1990, requiring the Secretary of Agriculture to develop a national list of prohibited substances in organic production, and paving the way for the USDA's National Organic Program. The year 1990 also coincided with Nicolas Lampkin's publication of his influential book, Organic Farming (Lampkin, 1990).

This momentum, which began in the 1970s, continues to grow even today. Widely read books such as Eric Schlosser's Fast Food Nation and Michael Pollan's The Omnivores Dilemma have dramatically increased the public's awareness of issues surrounding food and agriculture (Schlosser, 2001; Pollan, 2006). Popular films such as Supersize Me and Food, Inc. have also increased awareness of processed foods and the industrial food system and have left people seeking alternatives (Spurlock, 2004; Kenner, 2008).

Markets and Trends

Markets

Throughout most of the twentieth century, organic food was a small fraction of total food markets, limited to environmentally minded individuals and health-food proponents. Organic food was either sold directly from farms, or through health food stores and small cooperatives, and up until the early 1980s, organic food had global market shares of less than 0.1% (Aschemann *et al.*, 2007). The social changes that began in the 1960s led to the development of many certification schemes in the 1970s, as well as the foundation of IFOAM in 1972. These new organic certification programs allowed for quality assurance in a larger, less personal marketplace, and allowed for broader distribution of organically produced foods. In Europe sales of organic foods grew rapidly, and began to outpace the ability of small cooperatives and health-food stores to supply the growing demand. For these two reasons, the 1980s saw the entry of large supermarket chains into the organic foods market in Europe. It was not until the 1990s that a similar shift took place in the US, Japan, and Oceania. In almost every case, national sales of organic foods began to increase and even accelerate when conventional supermarkets began selling organic products (Aschemann *et al.*, 2007). The trend has largely continued into the twenty-first century, with Europe and North America consistently dominating the global market (**Figure 2**).

In 2010, Switzerland and Denmark spent the most on average per capita on organic foods, with the US and Canada also in the top 10 (**Figure 3**). Most countries have seen a large increase in per capita spending since 2000, with the exception of Denmark whose spending has been high throughout. Japan is one of the largest consumers of organic foods outside of Europe and North America, with the market for organic foods growing from US$350 million in 2002 to US$750 million in 2007 (Sahota, 2004; Sahota, 2007).

Geography

Land area under organic management had been steadily increasing in Europe since the 1980s (Willer and Yussefi, 2000), and has been expanding worldwide since the 1990s (**Figure 4**). Growth in organic land area in North America has lagged behind that of Europe, and still remains significantly lower proportionally. Despite growing domestic production of organic food, these countries have been relying increasingly on imported organic foods. In 2003, Germany and the UK imported 50% and 65%, respectively, of their organic food (Sligh and Christmann, 2003).

Increasing demands and expanding supermarket involvement with organic foods in Europe and North America has created a demand for more types of organic food, including tropical and out-of-season foods, and opened the market for growing and exporting organic foods in Africa, Latin America, and Oceania (Aschemann *et al.*, 2007). Organically managed land area in Oceania and Latin America increased dramatically in the 1990s and early 2000s, with the majority of land being extensively cattle-grazed rangeland. In 2004, Oceania and Latin America contained 42% and 24.2%, respectively, of the world's organic land, followed by Europe, with 23% (Yussefi, 2004). Although expanding more slowly, organic production in Africa and Asia has continued to grow through the past decade.

The strong majority of organic foods produced in the countries of Africa, Asia, and Latin America are exported to the

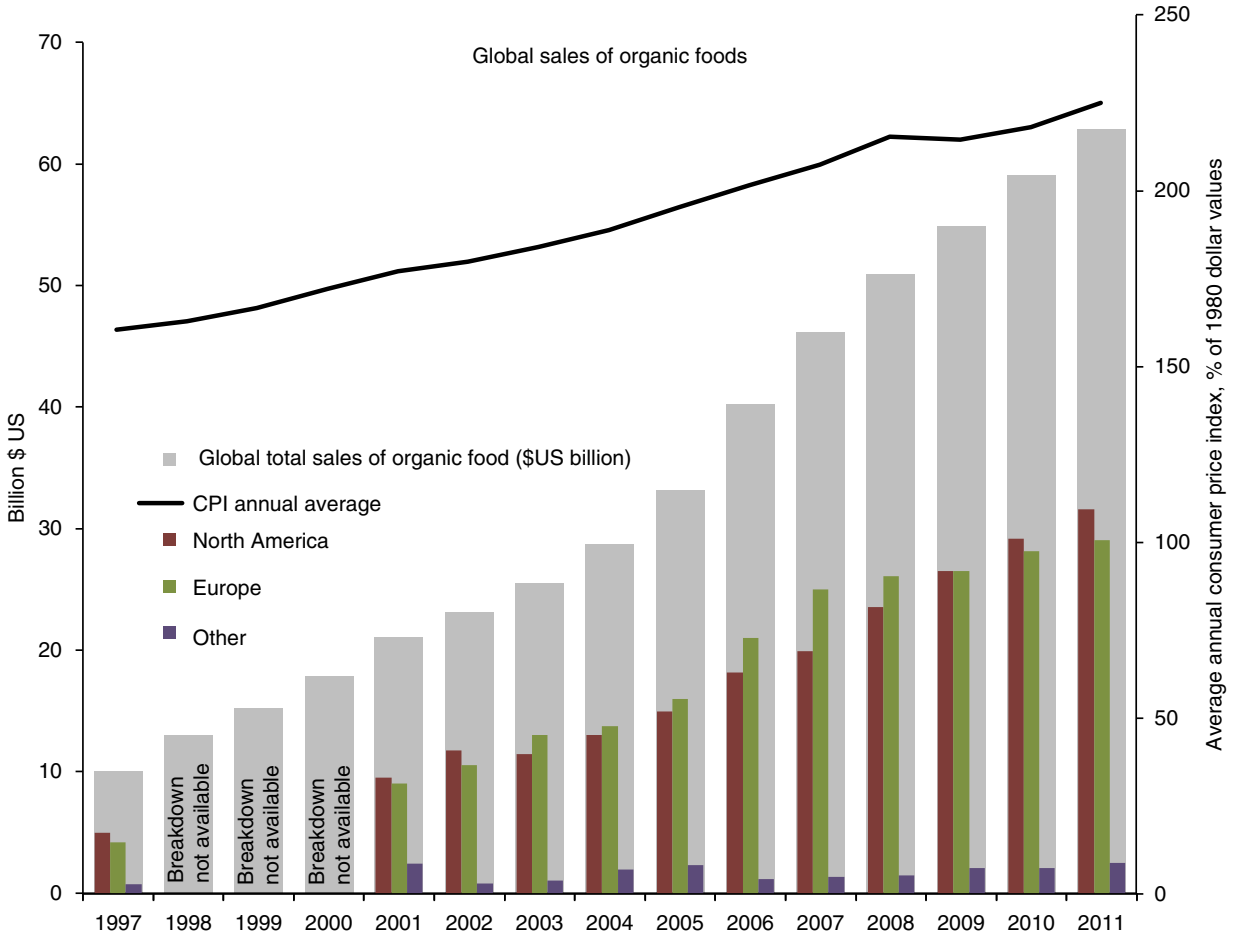


Figure 2 Annual global market for organic foods in billions of US dollars. The global total, shown in gray, is also broken down into three areas: Europe, North America, and all other countries. US Consumer Price Index (CPI) is displayed to show that the organic market is growing faster than inflation. Reproduced with permission from Willer, H., Yussefi, M., 2000. Organic Agriculture World-Wide: Statistics and Perspectives. Bad Dürkheim, Germany: Stiftung Ökologie und Landbau; Willer, H., Yussefi, M., 2001. Organic Agriculture Worldwide: Statistics and Future Prospects. Bad Dürkheim, Germany: Stiftung Ökologie und Landbau; Willer, H., Yussefi, M., 2004. The World of Organic Agriculture: Statistics and Emerging Trends 2004. Bonn, Germany: International Federation of Organic Agriculture Movements; Willer, H., Yussefi, M., 2005. The World of Organic Agriculture: Statistics and Emerging Trends 2005. Bonn and Frick: IFOAM and FiBL; Willer, H., Yussefi, M., 2006. The World of Organic Agriculture: Statistics and Emerging Trends 2006. Bonn and Frick: IFOAM and FiBL; Willer, H., Yussefi, M., 2007. The World of Organic Agriculture: Statistics and Emerging Trends 2007. Bonn and Frick: IFOAM and FiBL; Yussefi, M., Willer, H., 2002. Organic Agriculture Worldwide 2002 – Statistics and Future Prospects. Bad Dürkheim, Germany: Stiftung Ökologie und Landbau; Yussefi, M., Willer, H., 2003. The World of Organic Agriculture 2003 – Statistics and Future Prospects. Bonn, Germany: International Federation of Organic Agriculture Movements; Willer, H., Yussefi, M., Sorensen, N., 2008. The World of Organic Agriculture: Statistics and Emerging Trends 2008. Bonn and Frick: IFOAM and FiBL; Weidmann, G., Kilcher, L., Garibay, S., 2009. The World of Organic Agriculture: Statistics and Emerging Trends 2009. Bonn, Frick, and Geneva: IFOAM, FiBL, and ITC; Weidmann, G., Kilcher, L., Garibay, S., 2010. The World of Organic Agriculture: Statistics and Emerging Trends 2010. Bonn, Frick, and Geneva: IFOAM, FiBL, and ITC; Willer, H., Kilcher, L., 2011. The World of Organic Agriculture: Statistics and Emerging Trends 2011. Bonn and Frick: IFOAM and FiBL; Willer, H., Kilcher, L., 2012. The World of Organic Agriculture: Statistics and Emerging Trends 2012. Bonn and Frick: IFOAM and FiBL; Crawford, M., Church, J., Rippy, D., 2013. CPI Detailed Report. United States Department of Labor Bureau of Labor Statistics. Available at: http://www.bls.gov/cpi/ (accessed 08.08.13); and Willer, H., Lernoud, J., Kilcher, L., 2013. The World of Organic Agriculture: Statistics and Emerging Trends 2013. Frick and Bonn: FiBL and IFOAM.

countries in Europe and North America, as well as to Japan (Lockie *et al.*, 2006). In Latin America, 90% of organic production is exported to the Northern Hemisphere (Garibay and Ugas, 2010). Africa's organic exports are largely destined for Europe (Bouagnimbeck, 2010). Although domestic sales of organically certified foods in these developing countries remain small, organic markets are emerging in urban areas such as Buenos Aires, São Paulo, Kampala, Nairobi, Dubai, and Kuwait City (Sahota, 2007; Sahota, 2010). In 2008, domestic organic food sales in Uganda and Kenya were estimated to be US $712 771 and US$397 351, respectively (Bouagnimbeck, 2010).

Motivations

As global and domestic markets and production have changed, so too have the motivations behind farmers choosing to farm

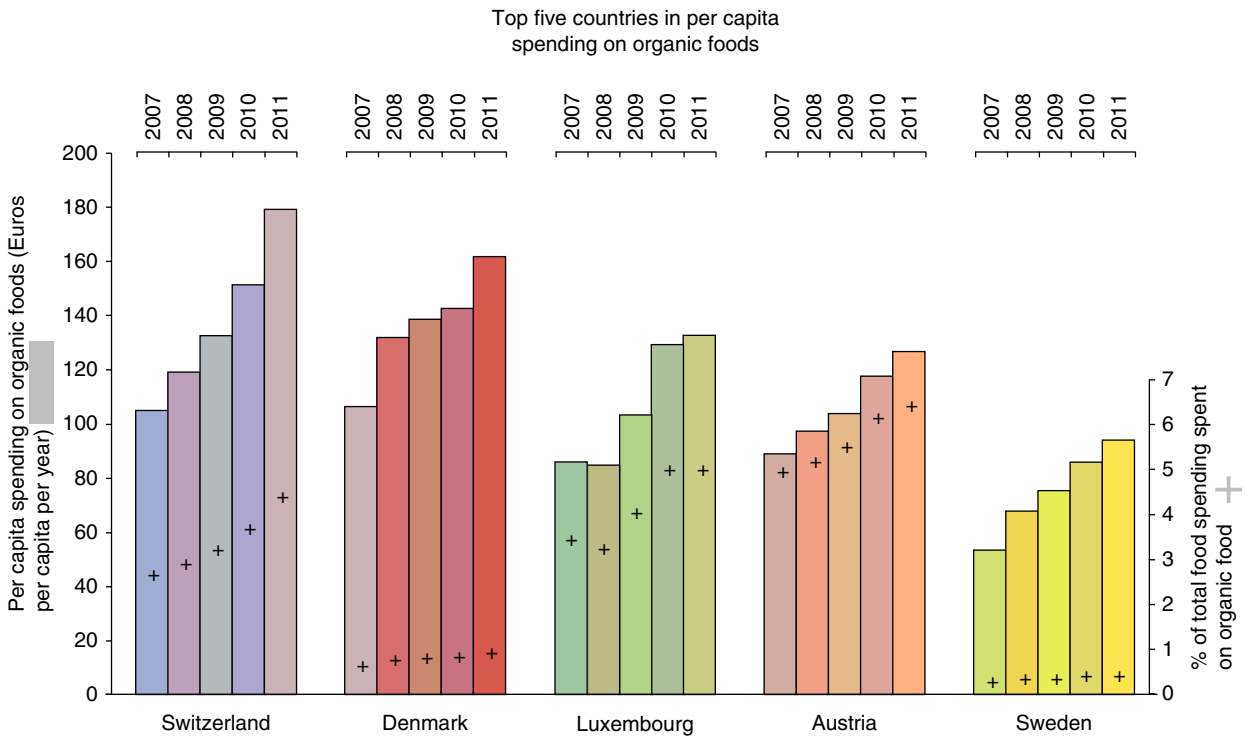


Figure 3 Top five countries for annual per capita spending on organic foods, in euros per person per year (bars), and percent of total food spending that is spent on organic foods in these countries (cross-hatches) for the years 2007–11. Reproduced with permission from Weidmann, G., Kilcher, L., Garibay, S., 2009. The World of Organic Agriculture: Statistics and Emerging Trends 2009. Bonn, Frick, and Geneva: IFOAM, FiBL, and ITC; Weidmann, G., Kilcher, L., Garibay, S., 2010. The World of Organic Agriculture: Statistics and Emerging Trends 2010. Bonn, Frick, and Geneva: IFOAM, FiBL, and ITC; Willer, H., Kilcher, L., 2011. The World of Organic Agriculture: Statistics and Emerging Trends 2011. Bonn and Frick: IFOAM and FiBL; Willer, H., Kilcher, L., 2012. The World of Organic Agriculture: Statistics and Emerging Trends 2012. Bonn and Frick: IFOAM and FiBL; Willer, H., Lernoud, J., Kilcher, L., 2013. The World of Organic Agriculture: Statistics and Emerging Trends 2013. Frick and Bonn: FiBL and IFOAM; and Eurostat, 2013. Eurostat Statistics Database. European Commission. Available at: http://epp.eurostat.ec.europa.eu/portal/page/portal/statistics/ (accessed 08.08.13).

organically. Surveys from the early 1990s and prior have found environmentally motivated decisions to be the primary factors in adopting organic practices (Lotter, 2003). In a later study, Guthman (2001) observed price premiums to be the most often-cited reasons for converting into organic practices, contrasting with the motivations found just 10 years prior. Often these farmers follow the minimum standards for organic certification and downplay the agroecological elements of organic farming (Lotter, 2003). Willer and Yussefi (2000) describe additional reasons for the growing interest in organic farming in Africa besides price premiums: first, the disappointments with Green Revolution technologies have made some farmers more receptive to organic practices and second, many organic farming practices are comparable to or compatible with indigenous farming practices.

With more trust in organic certification, increasing popularity of organic foods, and limited supply, price premiums on organic foods are an important part of the organic market. Organic premiums are highly variable; a 2003 study reports premiums of 20–30% in Austria; 10–50% in Germany; and 0–100% in the US (Sligh and Christmann, 2003). In Denmark, there was little difference between organic and conventional prices. Price premiums are the result of higher production costs, limited supply, and as a mechanism to compensate farmers for environmental stewardship.

The top reasons given for consuming organic foods include health, environment, taste, and animal welfare (Lockie *et al.*, 2006). Furthermore, in the absence of standalone requirements for labeling foods produced from genetically modified organisms (GMOs), many consumers choose organic foods because they exclude GMOs. Lockie *et al.* (2006) identify the top barriers to consumption of organic foods, from most important to least, as follows: high prices, limited availability, distrust of product claims, food appearance, not being aware of organic food, and being content with existing choices.

Organic Certification

In the early days of organic agriculture, organic foods were sold either directly to consumers or in small markets, in which a farmer's organic practices were taken on trust and relationship between the producer and the consumer. As the market for organic foods expanded into larger supermarkets, and as organic foods were distributed across larger distances, the need for organic standards, certifications, and labels became

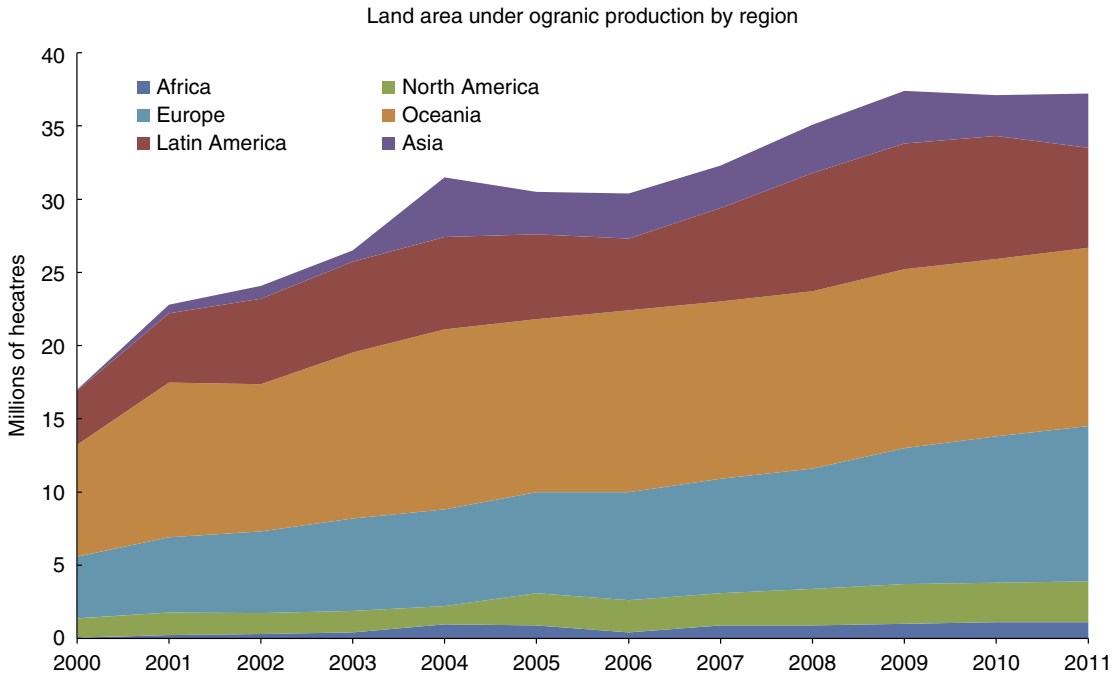


Figure 4 Millions of hectares under organic production by continent. Data from Willer, H., Yussefi, M., 2000. Organic Agriculture World-Wide: Statistics and Perspectives. Bad Dürkheim, Germany: Stiftung Ökologie und Landbau; Willer, H., Yussefi, M., 2001. Organic Agriculture Worldwide: Statistics and Future Prospects. Bad Dürkheim, Germany: Stiftung Ökologie und Landbau; Willer, H., Yussefi, M., 2004. The World of Organic Agriculture: Statistics and Emerging Trends 2004. Bonn, Germany: International Federation of Organic Agriculture Movements; Willer, H., Yussefi, M., 2005. The World of Organic Agriculture: Statistics and Emerging Trends 2005. Bonn and Frick: IFOAM and FiBL; Willer, H., Yussefi, M., 2006. The World of Organic Agriculture: Statistics and Emerging Trends 2006. Bonn and Frick: IFOAM and FiBL; Willer, H., Yussefi, M., 2007. The World of Organic Agriculture: Statistics and Emerging Trends 2007. Bonn and Frick: IFOAM and FiBL; Yussefi, M., Willer, H., 2002. Organic Agriculture Worldwide 2002 – Statistics and Future Prospects. Bad Dürkheim, Germany: Stiftung Ökologie und Landbau; Yussefi, M., Willer, H., 2003. The World of Organic Agriculture 2003 – Statistics and Future Prospects. Bonn, Germany: International Federation of Organic Agriculture Movements; Willer, H., Yussefi, M., Sorensen, N., 2008. The World of Organic Agriculture: Statistics and Emerging Trends 2008. Bonn and Frick: IFOAM and FiBL; Weidmann, G., Kilcher, L., Garibay, S., 2009. The World of Organic Agriculture: Statistics and Emerging Trends 2009. Bonn, Frick, and Geneva: IFOAM, FiBL, and ITC; Weidmann, G., Kilcher, L., Garibay, S., 2010. The World of Organic Agriculture: Statistics and Emerging Trends 2010. Bonn, Frick, and Geneva: IFOAM, FiBL, and ITC; Willer, H., Kilcher, L., 2011. The World of Organic Agriculture: Statistics and Emerging Trends 2011. Bonn and Frick: IFOAM and FiBL; Willer, H., Kilcher, L., 2012. The World of Organic Agriculture: Statistics and Emerging Trends 2012. Bonn and Frick: IFOAM and FiBL; and Willer, H., Lernoud, J., Kilcher, L., 2013. The World of Organic Agriculture: Statistics and Emerging Trends 2013. Frick and Bonn: FiBL and IFOAM.

necessary. Organic certification provides verification that products are indeed produced according to certain standards. For consumers who want to buy organic foods, the organic certification standards ensure that they can be confident in knowing what they are buying. For farmers, these standards create clear guidelines on how to take advantage of the expanding demand for organic products. For the organic products industry, these standards provide an important marketing tool to help boost trade in organic products.

'Certified organic' means that the agricultural products have been grown and processed according to the specific standards of various international, national, state, or private certification organizations. Certifying agents review applications from farmers and processors for certification eligibility, and qualified inspectors conduct annual onsite inspections of their operations. Inspectors talk with producers and observe their production or processing practices to determine if they are in compliance with organic standards. Organic certification standards detail the methods, practices, and substances that can be used in producing and handling organic crops and livestock, as well as processed products.

Certification is not without its critics. Some argue that organic standards shift the emphasis to specific inputs and farming methods, and away from the more holistic process-based philosophies that gave birth to the organic movement (Ikerd, 2006). Some see certification as encouraging the conventional paradigm of maximizing production, without being specific enough about long-term sustainability goals (Ikerd, 2006). Others argue that national and global certification schemes do not account for important local and regional differences in farming systems, and that the cost of certification gives favor to large farms over small operations (Schmid, 2007). Finally, some point to the potential for organic standards to be diluted over time due to political and business interests.

In 1980, the IFOAM developed its Basic Standards for Organic Agriculture, which have since been periodically revised (Courville, 2006). IFOAM later established the IFOAM



Figure 5 European Commission's label for certified organic foods (European Commission, 2012).

Accreditation Program to provide international equivalency of certification bodies worldwide, and in 2011 a new program was launched, the IFOAM Family of Standards, in an effort to simplify harmonization across international bodies. In 2011, 61 certification bodies were either members of or in the application stages for the Family of Standards (IFOAM, 2012a). The other major international overseer of organic standards is the Codex Alimentarius Commission, created in 1961 by the Food and Agriculture Organization of the United Nations and the World Health Organization; the Commission's guidelines for the production, processing, labeling, and marketing of organically produced foods became effective in 2001 (Courville, 2006). Both IFOAM and the Codex Alimentarius Commission serve as global standards for certification programs worldwide.

Although several countries in Europe had existing certification programs, such as France's Agriculture Biologique label and Germany's Bioland label, the European Union (EU) developed a regulatory framework to oversee organic practices across all of Europe, beginning with the EU Council Regulation 2092/91 in 1991 (Schmid, 2007). These standards prohibit the use of synthetic pesticides and fertilizers, the use of growth hormones and antibiotics in livestock (with some exceptions for the sake of humane treatment), and the use of GMOs. New regulations went into effect in 2009 to place greater emphasis on environmental protection, animal welfare, and preservation of biodiversity (European Commission, 2012). The new regulations allow organic products to contain 5% nonorganic ingredients, a limit of 0.9% of unintentionally present genetically modified materials, and require organically certified foods to use the EU organic label (**Figure 5**).

As in Europe, individual states in the US had existing organic certification, such as the California Certified Organic Farmers, founded in 1973, when Congress passed the Organic Foods Production Act in 1990, charging the USDA with developing national standards for organic production. The USDA National Organic Program standards went into effect in 2002, setting standards for all food, domestic and imported, that is labeled 'organic,' and specifically prohibiting the use of genetic engineering methods, ionizing radiation, and sewage sludge for fertilization. The USDA National Organic Program



Figure 6 USDA National Organic Program's label for certified organic foods (USDA, 2012).

was established, and requires organic foods to be certified by a USDA-accredited third-party certifier, marked by the USDA organic foods label (**Figure 6**).

A 2010 survey found 488 organic certifiers worldwide, with only 10 certifiers in Africa and 164 in Asia (Rundgren, 2010). Seventy-three countries worldwide reported having national organic standards, with an additional 16 countries in the process of drafting legislation (Huber *et al.*, 2010).

An alternative to governmental or third-party certification, called Participatory Guarantee Systems (PGS), has been growing in popularity. PGS is designed for small farms and short supply chains, in which stakeholders verify producers' practices and hold them to the standards of a chosen certifier. They are designed to be less expensive and more locally focused, in order to be more accessible to small farms in developing and developed countries alike (IFOAM, 2012b). PGS is furthermore seen as returning to the local quality assurance systems built around social networks and trust on which the organic movement was founded (Katto-Aandrighetto, 2010). A recent survey estimates there to be approximately 10 000 farmers involved in PGS worldwide, with the majority in developing countries, as well as more than 800 in the US and approximately 500 in France (Katto-Aandrighetto, 2010).

Principles of Organic Farming

At its core, organic agriculture treats farms as whole organisms. Instead of seeing many pieces that can be treated in isolation (e.g., spraying pesticide for an insect outbreak, using herbicides for a weed control, or applying fertilizers solely for plant growth), the organic farm seeks to understand all the components of the agroecosystem in the context of one another. Organic farms try to strengthen the interconnections between components to achieve a self-managing, integrated agroecosystem similar to an organism or a natural ecosystem (Kristiansen and Merfield, 2006). Organic agriculture also treats humans as an integral component of the agricultural system, but not dominant in their control of the system. Agroecological systems are understood to be extremely complex, not fully understood or predictable, and therefore not able to be fully controlled. Humans are at once animals in the system, consuming products of the agroecosystem and returning wastes, as well as acting as managers of the system, making decisions on crop rotations, grazing, and soil management.

Many descriptions and principles of organic agriculture have been published over the past century (DARCOF, 2000).

Table 1 IFOAM principles of organic agriculture through time

1980 IFOAM Basic Principles
To work as much as possible within a closed system, and draw on local resources
To maintain the long-term fertility of soils
To avoid all forms of pollution that may result from agricultural techniques
To produce foodstuffs of high nutritional quality and sufficient quantity
To reduce the use of fossil energy in agricultural practice to a minimum
To give livestock conditions of life that conforms to their physiological needs and to humanitarian principles
To make it possible for agricultural producers to earn a living through their work and develop their potentialities as human beings
Current IFOAM Principles of Organic Agriculture
Principle of Health
Organic agriculture should sustain and enhance the health of soil, plants, animals, and humans as one and indivisible
Principle of Ecology
Organic agriculture should be based on living ecological systems and cycles, work with them, emulate them, and help sustain them
Principle of Fairness
Organic agriculture should build on relationships that ensure fairness with regard to the common environment and life opportunities
Principle of Care
Organic agriculture should be managed in a precautionary and responsible manner to protect the health and well-being of current and future generations and the environment

Source: Reproduced from Kristiansen, P., Merfield, C., 2006. Overview of organic agriculture. In: Kristiansen, P., Taji, A., Reganold, J. (Eds.), Organic Agriculture: A Global Perspective. Ithaca, NY: Comstock Publishing Associates, pp. 1–23 and IFOAM, 2012c. The principles of organic agriculture. International Federation of Organic Agriculture Movements. Available at: http://www.ifoam.org/en/organic-landmarks/principles-organic-agriculture (accessed 08.08.13).

IFOAM first published a set of basic principles of organic agriculture in 1980, a list that has been updated periodically (**Table 1**). The original principles are particular about the need for organic agriculture to be site-specific, to produce adequate food, to limit its environmental impact, to be socially just, and to be humane. IFOAM's current revised list includes only four general principles, putting more of an emphasis on interconnections and on social well-being.

The IFOAM principle of health emphasizes that environmental health and human health cannot be separated. Health is meant not to just mean a lack of illness, but rather an intact and thriving whole, including the health of humans, soils, crops, livestock, and surrounding environment. Emergent properties of a healthy and integrated agroecosystem include the system and the ability of its components to self-regulate and to exhibit resilience in the face of disturbance. By this principle, the use of synthetic pesticides, fertilizers, antibiotics, and additives is virtually banned for risk of negative health effects (IFOAM, 2012c).

The IFOAM principle of ecology states that organic agriculture should function in the same way that the natural ecosystems function. Central to this goal is the maintenance of biodiversity through diverse crop and livestock rotations, hedgerows, and wild areas. Agricultural systems should operate as a closed and integrated web of energy flows, nutrients dynamics, and biological interactions, with minimal losses and inputs to the system. Through this diversity of interactions emerge feedback mechanisms and self-regulating populations. In an intact agroecosystem, disease and pest outbreaks will be minimized through ecological balance, without the need for human intervention. Furthermore, agroecosystems must be managed and adopted in relation to its specific environmental, climatic, and social conditions (IFOAM, 2012c).

The IFOAM principle of fairness emphasizes organic agriculture's role in fostering equity, respect, and justice in every step of the food market. Workers, distributors, processors, and marketers are all to be treated with respect and paid fair wages. Animals are to be treated humanely, allowing them to live under natural conditions and exhibit their natural behavior. Furthermore, organic agriculture must be practiced in a way that is fair to future generations; it must conserve resources, maintain healthy ecosystems, and make decisions with long-term forethought (IFOAM, 2012c).

Finally, the IFOAM principle of care follows that organic agriculture has a responsibility to avoid risk of causing harm. This principle emphasizes that agriculture is practiced in the context of its environment, and has potential to impact its surroundings. IFOAM asserts that the use of new technologies should be limited until they are proven to be safe. Furthermore, although scientific knowledge and modern cost–benefit analyses are critical in agricultural practice, this principle also emphasizes the importance of traditional and indigenous knowledge in farming practice and in decision-making (IFOAM, 2012c).

The recent IFOAM revision resulted from concerns over lists of organic principles becoming overburdened with detail and lacking consistency (Kristiansen and Merfield, 2006). Numerous discussions have led to more general principles, such as those of the national survey carried out by the Danish Research Center for Organic Farming (DARCOF, 2000). The following is a list of specific principles, drawing from numerous efforts from around the world (USDA, 1980; DARCOF, 2000; Lotter, 2003; Kristiansen and Merfield, 2006; Gomiero *et al.*, 2011). It is not an exhaustive list, but is intended to illuminate specific principles that fall under the four general IFOAM categories described above.

- *Farm with the future in mind*: One of the central goals of organic farming is to conserve resources, protect natural habitats, and build soils, so that agriculture can be

sustained into the future. Organic agriculture offers one alternative to conventional agriculture, which with current rates of soil degradation, energy use, and pollution cannot be sustained in its current form.

- *Adapt to local conditions*: Being a complex agroecosystem, an organic farm must be adapted to its specific environmental, climatic, and social conditions. Crops and varieties are chosen based on soil, surrounding environment, climate, and the needs of the farmer and clientele. Specific crop rotations are designed for the needs of the soil, as well as weed and pest conditions (und Niemsdorff and Kristiansen, 2006).
- *Build and maintain healthy soils*: A central aim of organic agriculture is to build and maintain soils with high organic matter, long-term fertility, active and diverse biology, and minimal environmental losses due to erosion and nutrient runoff (Gomiero *et al.*, 2011). In contrast to conventional systems in which fertility is based largely on inorganic fertilizer additions, organic farms depend on biologically mediated fertility resulting from diverse soil microbiology and large stores of soil organic matter (Welbaum *et al.*, 2004). This is achieved most importantly by using organic nutrient sources (i.e., nutrients contained in carbon-based compounds) and avoiding the sole addition of inorganic nutrients (i.e., nutrients not coupled with carbon). The use of organic (carbon-coupled) nutrient sources such as compost, manure, and plant residues builds soil organic matter, and depends on the gradual biologically mediated decomposition of this organic matter into more plant-accessible inorganic forms of nutrients (Drinkwater and Snapp, 2007). The use of organic amendments can furthermore promote an abundant and diverse soil microbial population, which may lead to competition against soil pathogens (Letourneau and van Bruggen, 2006).
- *Conserve or enhance biodiversity*: In its effort to mimic natural ecosystems, an organic farm encourages biodiversity in its design and its management. A diversity of crops and livestock utilize different resources, attract different pests, compete differently with weeds, and increase income diversity. The use of long and diverse crop rotations – often 3–years or longer – is central to increasing this diversity over time and space. Additionally, many farms keep hedgerows and other semiwild areas that serve as habitat for insects, larger animals, and soil biota (Letourneau and van Bruggen, 2006). Increasing biological diversity – in flora, fauna, and soil microbiology – may increase the stability of the system, reducing outbreaks of pests and diseases (Shennan, 2008).
- *Integrate all components of the farm and close the nutrient cycle*: As an ecosystem, the organic farm is an interconnected network of components, each utilizing different resources and producing different waste products that serve as inputs for other components (**Figure 7**). The goal is a tightly integrated agroecosystem that minimizes its input requirements by recycling all waste products back into the farm. Composting wastes and returning them to the field is a central practice in organic farming. Mixed crop and livestock operations are also common in organic agriculture (Lampkin, 1990). Livestock feed on unused crop residues, control weeds, perform work, and return nutrients to the soil. One principle listed by IFOAM in 2004 was "to create a harmonious balance between crop production and animal husbandry" (Kristiansen and Merfield, 2006). Components can be integrated within a single farm, such as keeping livestock and raising crops together, or can be integrated over multiple farms in a region, with manure from one farm being exchanged for feed from another (Pearson, 2007). Other examples of on-farm integration include

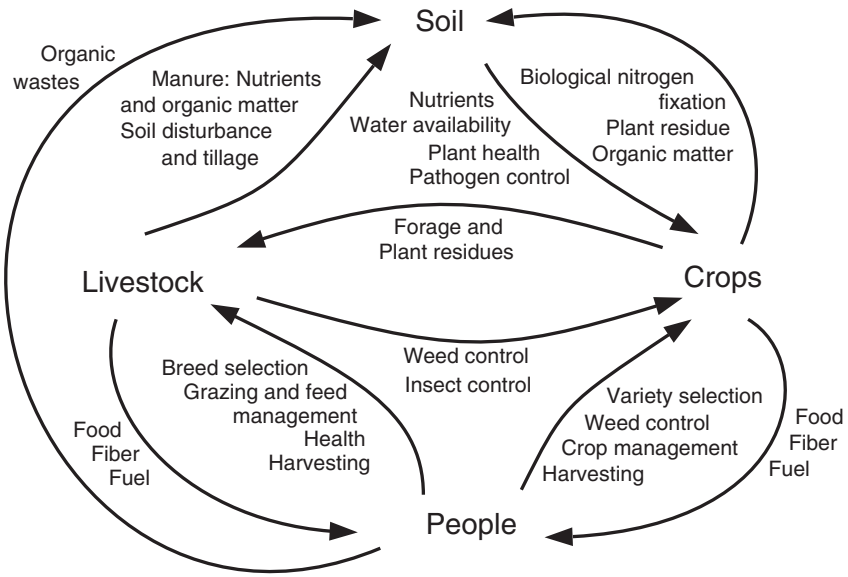


Figure 7 The integration and cycling of nutrients, energy, and materials through the components of an integrated organic farm. Adapted with permission from Stockdale, E.A., Lampkin, N.H., Hovi, M., *et al.*, 2001. Agronomic and environmental implications of organic farming systems. Advances in Agronomy 70, 261–327.

growing oil crops to use as fuel for tractors, and using methane biodigesters for power generation.

- *Reduce chemical and energy inputs and minimize losses*: Organic agriculture virtually prohibits the use of synthetic pesticides, herbicides, and fertilizers, seeks to minimize the use of fossil energy, and seeks to minimize nutrient losses and soil erosion. By integrating farm components and using long-term crop rotations, organic farms reduce weed, pest, and pathogen pressure, and thereby reduce the need for herbicides and pesticides. Natural controls, such as the use of diatomaceous earth for insects or the application of plant-based herbicides, are used occasionally as a last resort (Letourneau and van Bruggen, 2006). By recycling all materials and growing leguminous nitrogen-fixing crops and green manures, organic farms minimize the need for nutrient inputs. To replace nutrients lost with the export of crops, organic farms use biologically fixed nitrogen from green manures and cover crops supplemented with imported compost, animal manure, or rock minerals such as rock phosphate for phosphorous and greensand for potassium (und Niemsdorff and Kristiansen, 2006). Minimizing nutrient losses both keeps nutrients on the farm and limits atmospheric and surface water pollution. As previously discussed, the use of organic (carbon-coupled) nutrient sources such as compost, manure, and plant residues, plays a major role in reducing nutrient losses from organically managed farms (Drinkwater and Snapp, 2007). Nutrient losses are further minimized by planting perennial buffers to catch nutrient runoff and planting cover crops in fields to retain nutrients during wet periods of the year in which nutrient runoff is high (also called 'catch crops') (Lynch, 2009). The use of fossil fuel energy and its consequent greenhouse gas emissions are minimized on organic farms by avoiding the use of energy-intensive artificial nitrogen fertilizers, by selling locally and sourcing inputs locally, and occasionally using draft animal power instead of mechanical tractors.
- *Foster social well-being and animal welfare*: Organic agriculture aims to produce sufficient quantities of humanely raised, healthy food while treating and paying all workers fairly. Organic farms often produce foods for their community or region. Foods are produced without chemical additives or pesticides that may be unhealthy. Farmers should be able to support themselves and other workers with fair incomes, while maintaining safe and dignified working conditions. Furthermore, animals must be raised humanely under conditions that allow for the expression of their natural behaviors and needs. For example, USDA organic regulations require that livestock have access to the outdoors year round, that ruminants be raised on pasture, and that sick animals be treated as needed, even with the use of antibiotics if required (USDA, 2012).

Organic Farming Practices

Organic farms take maximum advantage of the synergistic interactions between their various farm enterprises. Instead of relying on prescriptive treatments for fertilization and crop protection, organic management practices depend on the complex interactions among soil fertility and biology, crop rotations, pest and weed populations, species diversity, and production (Figure 8). Diversified, location-specific crop rotations, often in combination with livestock grazing, are at the core of organic crop husbandry. The managerial goal of an organic farm is to use crop and livestock rotations to build soils and create an ecologically balanced community, such that the system is self-enriching, self-regulating, and requires a minimum of human intervention. The use of curative treatments, such as hand weeding or using natural pest deterrents, is often viewed as a secondary practice.

Soil and Fertility Management

Maintaining fertile and biologically active soils is at the core of managing an organic farm. Fertility in organic systems is derived predominantly from organic matter, such as compost,

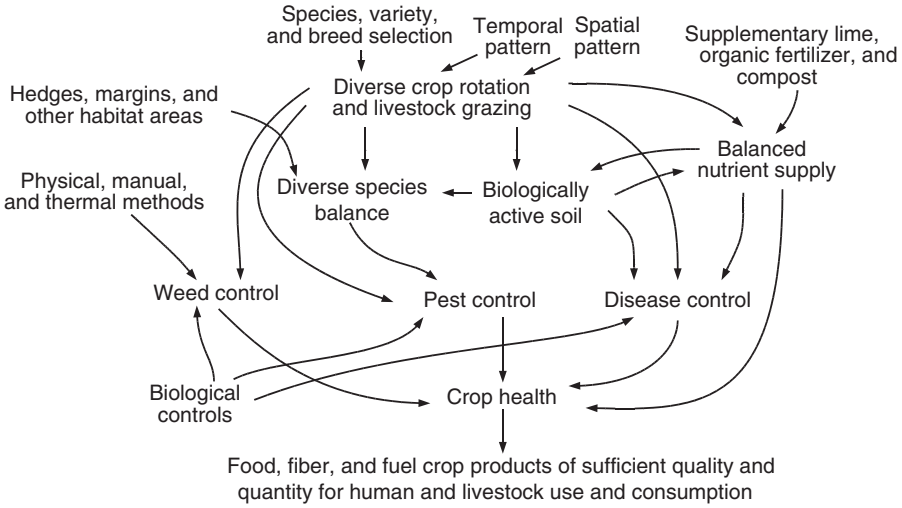


Figure 8 The integration of organic management practices. Adapted with permission from Stockdale, E.A., Lampkin, N.H., Hovi, M., *et al.*, 2001. Agronomic and environmental implications of organic farming systems. Advances in Agronomy 70, 261–327.

crop residues, manures, and other organic materials. Nutrients are made available slowly, as the soil biota mineralizes organic materials into smaller soluble compounds that can be taken up by plants. This biologically mediated gradual release of soluble nutrients can increase nutrient-use efficiency and reduce leaching losses (Drinkwater and Snapp, 2007). The addition of various organic materials may promote higher microbial abundance and enhance soil ecosystem processes (Shepherd *et al.*, 2002; Davis and Abbott, 2006). Furthermore, organic matter improves soil structure, increases its water storage capacity, and promotes tilth, or the physical condition, of the soil (Weil and Magdoff, 2004). The better the tilth, the more easily the soil can be tilled or direct-drilled with seed, and the easier it is for seedlings to emerge and for roots to extend downward. Water readily infiltrates soils with good tilth, thereby minimizing surface runoff and soil erosion.

Crop rotation – a sequence of different species of crop plants growing in the same field more than 2–4 or even more years – is critical in building soil organic matter and supporting a diverse soil biota. Crop rotations can be designed so that soil nutrient resources are used differently each season over the course of the rotation. Rotating crops for nutrient management may be especially important in organic systems in which nutrient availability is slow and biologically mediated. For example, crops that demand high levels of nitrogen might follow a leguminous crop that fixes nitrogen (und Niemsdorff and Kristiansen, 2006). Green manures and cover crops – plants grown solely to be returned to the soil – help to further diversify crop rotations, add large amounts of organic matter, and, in the case of leguminous crops, can fix nitrogen. Leguminous cover crops play an important role in supplying nitrogen through biological nitrogen fixation; some farms use on-farm biological nitrogen fixation to be self-sufficient in nitrogen (Reganold, 1988; Stockdale *et al.*, 2001). Cover crops are sometimes called 'catch-crops' when they are used to uptake and hold on to nutrients during periods of high leaching risk, such as winters with high precipitation. Nutrients are recycled throughout an organic farm wherever possible. Plant residues, processing wastes, and animal manure are composted and returned to fields.

Most farms rely on exporting crops and other products away from the farm, thereby exporting nutrients from the soil that must be replaced. Although a farm can fix its own nitrogen using leguminous green manures, other nutrients must be imported in the form of compost, manure, and other naturally occurring nutrient sources. Dried blood, bone meal, fish and seaweed extracts, and manures are common biological sources of macro- and micronutrients. Naturally formed rock minerals, such as limestone, gypsum, rock phosphate, elemental sulfur, and dolomite, are used as nutrient supplements and to adjust soil acidity. Limits and restrictions on the use of amendments are detailed in by individual certification programs.

Weed Management

Weed management is often cited as a primary challenge of organic farmers. Weeds can be especially challenging during periods of conversion to organic practices, during which weed populations are changing (Ngouajio and McGiffen, 2002).



Figure 9 Example of winter wheat intercropped with winter peas. Peas fix nitrogen and shade out weeds as the rows of wheat fill in and mature. Photo courtesy of Kristy Borrelli, Washington State University.

Crop rotations are designed to diversify resource competition against weeds, and to diversify timing and type of operations in which weeds can be controlled. Dense green manures, cover crops, and pasture phases of a rotation can compete against weeds, as well as providing a heavy mulch to physically suppress emergence (Bàrberi, 2002). Crops can be seeded with wide-row spacing to facilitate tillage and hand weeding between rows throughout the season; this practice is used especially with vegetable crops. Alternatively, higher planting densities can be more competitive against weeds and can limit their emergence, and are used for crops in which inter-row cultivation is difficult, such as with cereals (und Niemsdorff and Kristiansen, 2006). Other methods of increasing competition against weeds include intercropping, in which different crops are planted in an alternating manner, such that they maximize resource use and weed competition over space and time, and the use of a living mulch, in which a crop is undersown with a competitive cover crop (**Figure 9**). These crop layouts are designed to maximize the complementarity of resource use between the crops, minimize intercrop competition, and maximize interference with weeds, such as shading out emergent weeds and crowding out weed roots. Although these can be effective, challenges with decreased yields due to intercrop competition persist (Stockdale *et al.*, 2001).

In addition to these indirect weed management practices, which focus on diversifying crop rotation and improving crop-weed competition, organic farmers make use of numerous direct weed control practices. A variety of mulches, such as straw, cardboard, and plastic sheeting, are used to suppress weed emergence. Challenges of mulch include the high labor needs of applying the mulch, interference with crop growth and harvesting, nitrogen immobilization from carbon-rich mulches, and the heavy resource use of plastic mulch (und Niemsdorff and Kristiansen, 2006). After weeds have emerged, mechanical tillage is a common practice. Shallow cultivation, before planting or between rows, is common practice. Other cultivation methods are used under specific conditions and for specific crops, such as the use of harrows in postemergent cereal crops (Stockdale *et al.*, 2001). In mixed crop–livestock farms, animals are sometimes used to graze weeds instead

of cultivation. Thermal methods of weed control, such as flame- and steam-weeders, can effectively control emergent and preemergent weeds, but are energy intensive and can be expensive to operate. Solarization, heating the soil surface under clear plastic at temperatures high enough to kill weed seeds, is used in suitable climates, but can also be intensive in its use of materials and labor. Finally, an important method of weed control, especially on small farms, is hoeing and hand weeding. Although labor intensive, hand weeding has no capital cost and can be minimally invasive to crops.

Pest and Disease Management

As in any other agricultural system, basic best practices are critical to the success of an organic farm. These include the use of certified pathogen-free seed, selection of resistant crop varieties, effective crop rotations, residue management, and testing soils and plant tissues for pathogens (Cook, 2000). However, because organic farming focuses on whole system management and prohibits the use of synthetic insecticides, fungicides, and fumigants, organic management practices are largely preventative in nature, rather than reactive.

On a landscape scale, efforts are made to balance cropping land with noncropped and semiwild areas in order to maintain a diverse population of pests and their natural predators (Lampkin, 1990; Stockdale *et al.*, 2001). Field borders and hedgerows are often planted with flowering plants to attract a diversity of insects, and perennial species to attract larger insectivorous animals such as owls and bats. Efforts can be made to isolate fields of the same crop to limit the spread of crop-specific pests and diseases.

Niche diversity is also enhanced by crop rotations at a field scale. Intercropping, cover crops, and long diverse rotations are all used to disrupt pest life cycles and to support a diversity of pests and their natural predators. Certain pests and diseases can be avoided by planting crops at strategic times of the year to avoid pest and disease outbreaks in specific stages of plant growth (Letourneau and van Bruggen, 2006). Organic farmers can also select tillage methods, planting times, crop rotations, and plant-residue management practices to optimize the environment for beneficial insects that control pest species, or to deprive pests of a habitat or resources.

Plant root diseases are generally less severe in organic systems than in conventional systems (van Bruggen, 1995). This effect may be due to the functionally diverse soil biological communities found in organic systems (Stockdale *et al.*, 2001). Furthermore, the lack of excess nitrogen in organic systems, and the consequently low foliar nitrogen of crop plants, has been correlated with reduced disease and pest incidence in organic crops compared with conventional crops (Letourneau and van Bruggen, 2006).

Management practices on the scale of individual crops include selecting disease-resistant crop varieties, intercropping, and using biological controls. Severity of pests and diseases can sometimes be reduced with the higher within-field diversity of intercropping and living mulches (Letourneau and van Bruggen, 2006). Biological controls include introducing or promoting natural predators, parasites, or competitors that keep pest and pathogen populations below injurious levels. Specific soil treatments can be used to induce soils that are suppressive to pathogens. One such example is a recent research on the application of *Brassica napus* and *Brassica juncea* seed meal to control multiple pathogens responsible for apple replant disease (Mazzola and Brown, 2010).

Organically certified pesticides are typically used as a last resort to control insects and diseases, and are applied when pests are most vulnerable or when beneficial species and natural predators are least likely to be harmed. For example, diatomaceous earth is a powder made from crushed rock and is applied to the leaves of vegetables. Although harmless to humans, the edges of the particles lacerate the undersides of flea beetles and other insects. Another important fungal treatment on organic fruit farms is the use of sulfur sprays to control powdery mildew. Restrictions on the use of these natural fungicides and insecticides are detailed by individual certification programs.

Sustainability of Organic Farming Systems

A 2010 National Academy of Sciences report (National Research Council, 2010) defined four goals for a farming system to be sustainable: it must (1) supply abundant, affordable food, feed, fiber, and fuel, (2) be profitable, (3) enhance the natural resource base and environment, and (4) contribute to the well-being of farmers, farm workers, and rural communities. Just because a farm is organic does not mean that it is sustainable. For any farm to be sustainable, whether it is organic or conventional, it must meet all four sustainability goals. So, if an organic farm produces high yields of nutritious food and is environmentally friendly and energy efficient, but is not profitable, then it is not sustainable. Likewise, a conventional farm that meets all the sustainability criteria but pollutes a nearby river with sediment because of soil erosion is not sustainable. **Figure 10** illustrates the four sustainability goals and their overlapping areas representing the highest level of sustainability.

With the rise of organic farming worldwide, researchers are being presented with new opportunities to study organic

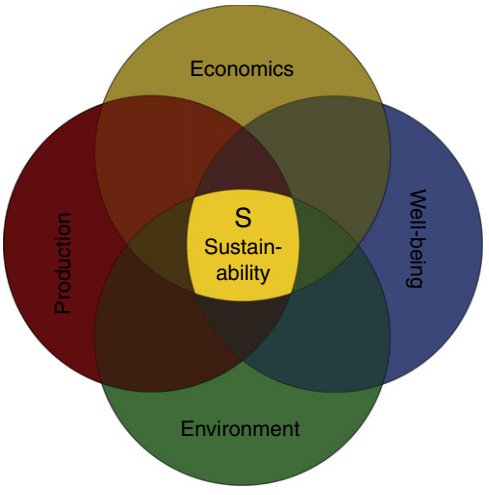


Figure 10 The four components of agricultural sustainability.

systems and also to compare them with their conventional counterparts. For example, organic farming systems provide an opportunity to link basic and applied ecology through research on biodiversity and ecosystem services (Letourneau and Bothwell, 2008). In addition, one can compare sustainability indicators, such as soil health, crop quality, and financial performance, of organic and conventional systems (Reganold, 2013). This section focuses on farming systems research comparing the sustainability of organic and conventional farming systems.

Examples of comparison studies that have helped shape farming systems research are the Corn Belt study (Lockeretz *et al.*, 1981), the Palouse erosion study (Reganold *et al.*, 1987), the South Dakota grain study (Smolik *et al.*, 1995), the Rodale Farming Systems Trial (Drinkwater *et al.*, 1998), the Washington State apple sustainability study (Reganold *et al.*, 2001), and the Swiss 'DOK' systems trial (Mäder *et al.*, 2002). To illustrate what is entailed in a multiple farming systems experiment measuring a large number of sustainability indicators, it is worth discussing the study by Reganold *et al.* (2001). In 1994, Reganold *et al.* (2001) established a 1.7-hectare replicated study of organic, conventional, and integrated apple production systems in a new commercial 'Golden Delicious' orchard in WA, USA. For six growing seasons (1994–99), five major sustainability indicators were measured: crop yield and quality, financial performance, soil quality, environmental impact of pesticides, and energy efficiency.

Although differences in annual apple yields were inconsistent among the systems, all three systems gave similar cumulative apple yields (**Figure 11(a)**). Organic apples were smaller, but sweeter and less tart, and as firm or firmer than were conventional and integrated apples. The organic system was more profitable based on breakeven points from enterprise budgets, followed by conventional and then integrated (**Figures 11(b)** and **(c)**). Receipts for integrated fruit were calculated using prices for conventional fruit. Receipts for organic fruit were estimated using prices for conventional fruit in 1995 and 1996 (the last year for transition to organic certification). Price premium to the grower for each grade of organic fruit (1997–99) averaged 50% above conventional prices. The breakeven point, when cumulative net returns equal cumulative costs, was 9, 15, and 17 years, respectively, for the organic, conventional, and integrated systems under actual fruit quality conditions (with significant apple russeting, a physiological skin disorder) (**Figure 11(b)**). When the economic analysis was adjusted by eliminating the effects of russeting, but maintaining the same size and grade and assuming a 15% cullage rate (average for Golden Delicious in Washington), the organic system was the most profitable in 1997 and 1998, and the breakeven points were much shorter (**Figure 11c**). For breakeven points of the organic and integrated systems to occur in the same year as the conventional system, price premiums of 12% for the organic system and 2% for the integrated system would be necessary under measured fruit quality conditions. Under nonrusseted fruit quality conditions, premiums of 14% for the organic system and 6% for the integrated system would be necessary to match the breakeven point of the conventional system.

Organic and integrated systems had higher soil quality than the conventional system (**Figure 11(d)**) mainly due to addition of compost and mulch in 1994 and 1995. Organic matter has a profound impact on soil quality, enhancing soil structure and fertility, and increasing water infiltration and storage. The conventional system ranked lowest because of a poorer ability to accommodate water entry and resist surface structure degradation. Compared with the organic system, the total potential negative environmental impact rating from the use of pesticides and fruit thinners was approximately 6× higher for the conventional system and 5× higher for the integrated system (**Figure 11(e)**). When a nonpheromone mating disruption conventional system was included for comparison, the conventional system was almost 8× higher than the organic. The organic system was 7% more energy efficient than the conventional system and 5% more efficient than the integrated system (**Figure 11(f)**). Major differences in energy inputs was higher weed control, insecticide, and fertilizer inputs for conventional and integrated systems, and higher fungicide and labor inputs for the organic system. On the basis of the results of all of these sustainability indicators, Reganold *et al.* (2001) concluded that the organic system ranked first in environmental and economic sustainability, the integrated system second, and the conventional system last. These results further suggest that integrated farming systems, which use a middle ground approach by blending organic and conventional practices, can achieve higher sustainability performance than conventional systems. For another example, Davis *et al.* (2012) found that two integrated maize/corn-based systems using small amounts of synthetic agrichemical inputs exceeded the overall sustainability performance of their less diverse conventional counterpart.

The results of the apple study (Reganold *et al.*, 2001) illustrate that, although crop yield and quality are important products of a farming system, the benefits of better soil and environmental quality provided by the organic and integrated production systems are equally valuable and usually overlooked in the marketplace. Such external benefits can come at a financial cost to growers. Currently, growers of more sustainable systems may be unable to maintain profitable enterprises without economic incentives, such as price premiums or subsidies for organic and integrated products that value these external benefits. Equally important, on incorporation of external costs into economic assessments of farming systems, it may be found that many currently profitable farming systems are uneconomical and therefore unsustainable. The challenge facing policymakers is to incorporate the value of ecosystem processes into the traditional marketplace, thereby supporting food producers in their attempts to employ sustainable practices.

What do other studies comparing organic and conventional farming tell us? Starting with the production goal of sustainability – that is, sufficient crop yields of high quality – yield differences between organic and conventional farming systems have been the topic of intensive debate. Although numerous individual studies have compared these yield differences, four have synthesized this information on a global scale. Stanhill (1990) was likely the first to conduct an extensive literature review of organic/conventional comparative yield data and found organic yields to be 9% lower than conventional yields in developed countries. Badgley *et al.* (2007) later found organic yields to be 8% lower in the developed world.

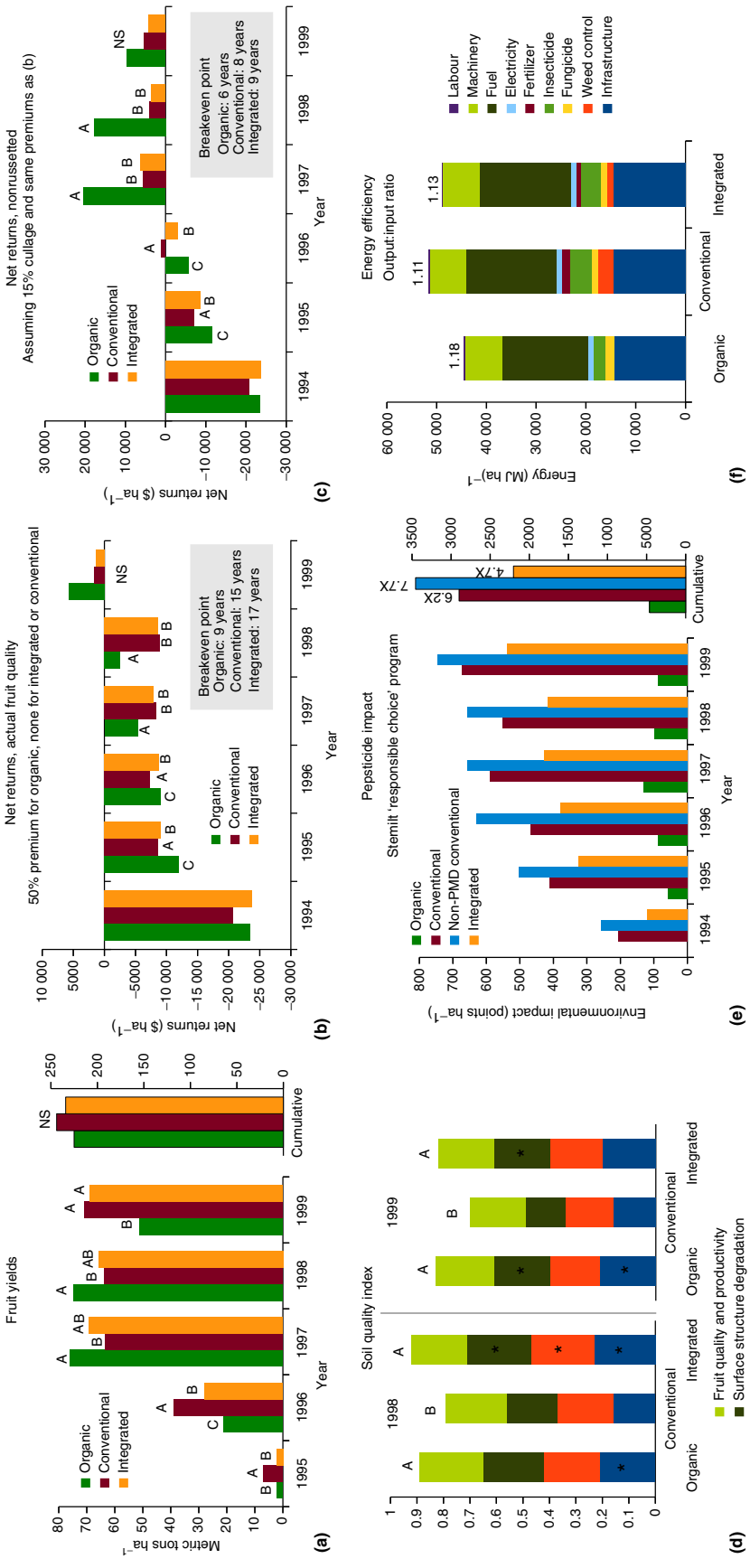


Figure 11 Sustainability indicators for the organic, conventional, and integrated apple treatments in the Reganold *et al.* (2001) study. (a) Shows annual and cumulative apple yields. (b) Shows annual net returns for actual fruit quality conditions, with breakeven points indicated. (c) Shows annual net returns for nonrusseted fruit quality conditions, with breakeven points indicated. (d) Shows soil quality index based on four equally weighted components: fruit quality and productivity, surface structure degradation, water movement and availability, and water infiltration. (e) Shows the potential negative environmental impact rating from the use of pesticides and fruit thinners using the Stemilt 'Responsible Choice Index,' (f) Shows energy efficiency (output/input ratios) based on energy accounting of output (yield) and all inputs.

In two recent metaanalysis studies of organic and conventional yield comparisons, de Ponti *et al.* (2012) found organic yields to be 21% lower in developed countries and 20% lower globally (362 yield comparisons), and Seufert *et al.* (2012) showed that organic farming systems had 20% lower yields in developed countries and 25% less when data from both developed and developing countries were combined (316 yield comparisons). However, these two studies also found that with certain crops, growing conditions and management practices, organic systems nearly matched conventional yields. For example, de Ponti *et al.* (2012) found that the best yielding organically grown crops are rice (6% lower than conventional), soybeans (8% lower), corn (11% lower), and grass-clover (11% lower). In comparison, the highest-yielding organic crops identified by Seufert *et al.* (2012) were organic fruits (3% lower yield than conventional), rain-fed legumes such as soybeans (5% lower), and oilseed crops (11% lower). One of the findings from the latter three studies (Badgley *et al.*, 2007; de Ponti *et al.*, 2012; Seufert *et al.*, 2012) is that most of the reliable, high-quality data are from developed countries, with there being a lack of solid quantitative data with appropriate scientific controls from developing countries.

Although metaanalysis is a great tool that can describe broad patterns not immediately visible in primary field research (Arnqvist and Wooster, 1995), it must also be treated with caution because no single farming system or practice works best everywhere (Reganold, 2012). Still, all four studies (Stanhill, 1990; Badgley *et al.*, 2007; de Ponti *et al.*, 2012; Seufert *et al.*, 2012) give strength to the argument that adoption of organic agriculture under agroecological conditions where it performs best may close the yield gap between organic and conventional systems. In addition, improvements in management techniques and crop varieties for organic systems may also close the yield gap between organic and conventional systems. For example, Murphy *et al.* (2007) found that direct selection of wheat cultivars in organic systems resulted in improved yields in organic systems when compared with indirect selection of wheat cultivars in conventional systems. In addition, as most agricultural research has historically been in support of conventional farming systems, more research directed at organic systems could show significant benefits in yields.

Crop quality can be divided into two parts: pesticide residues on foods and nutrition of foods. With the former, research has found that organic foods have significantly less pesticide residues (Baker *et al.*, 2002; Curl *et al.*, 2003; Lu *et al.*, 2006). For example, Baker *et al.* (2002) found that organically grown foods consistently had approximately one-third as many pesticide residues as conventionally grown foods, using data from three test programs: The Pesticide Data Program of the USDA; the Marketplace Surveillance Program of the California Department of Pesticide Regulation; and private tests by the Consumers Union, an independent testing organization.

With nutritional quality, although there is no universally accepted definition of what constitutes a nutritious food, recent scientific opinion has stressed that more nutritious foods are those that are more nutrient dense relative to their energy contents (Drewnowski, 2005). Although carbohydrates and fats are considered essential nutrients, the current concept of nutrient-dense foods, and hence more nutritious foods, places the emphasis on foods that contain more protein, fiber, vitamins, or minerals, as well as specific phytochemicals, such as the polyphenolic antioxidants found in fruits and vegetables (Scalbert *et al.*, 2005). In the past 12 years, at least 12 review studies (some being metaanalyses) of the scientific literature comparing the nutrition of organic and conventional foods have been published. Nine of these review studies (Soil Association, 2000; Brandt and Molgaard, 2001; Worthington, 2001; Williams, 2002; Magkos *et al.*, 2003; Rembialkowska, 2007; Benbrook *et al.*, 2008; Lairon, 2010; Brandt *et al.*, 2011) found some evidence of organic food being more nutritious, whereas three review articles (Bourn and Prescott, 2002; Dangour *et al.*, 2009; Smith-Spangler *et al.*, 2012) concluded that there were no consistent nutritional differences between organic and conventional foods.

Comparisons of foods from organic and conventional systems are often complicated by the interactive effects of farming practices, soil quality, plant varieties, and the time of harvest on nutritional quality. Hence, many of the comparative studies cited in some of the earlier reviews were not experimentally well designed to draw valid conclusions (Bourn and Prescott, 2002; Magkos *et al.*, 2003); for example, soils or crop varieties were not the same on each organic/conventional field pair. Nevertheless, studies, including recent reviews, have indicated that organic fruits and vegetables are generally more nutritious than their conventional counterparts, with the differences often being the higher antioxidant and vitamin C levels in the organic foods. The few studies that have compared organic and conventional foods for their organoleptic (sensory) properties have shown mixed results or used unreliable experimental designs (Bourn and Prescott, 2002; Rembialkowska, 2007).

There is growing evidence in the literature that adoption of organic farming systems produces financial benefits. However, transitioning to organic production (usually 3 years for crops) can be economically challenging and more information intensive. This transition period is generally, therefore, financially the most difficult time for organic farmers. After transition, the net return per hectare for organic compared with conventional farms is often equal or higher because of good yields and price premiums, as shown by numerous studies (e.g., Padel and Lampkin, 1994; Smolik *et al.*, 1995; Reganold *et al.*, 2001; Pimentel *et al.*, 2005; Cavigelli *et al.*, 2009). Net returns do not account for externalities, the importance of which is discussed previously. However, many European governments provide direct financial support for organic farmers in recognition of their farms' contribution to current policy objectives, including environmental protection, resource conservation, overproduction control, and reorientation of agriculture toward areas of market demand. Labor is higher with organic systems; it is often related to an increase in the diversity of enterprises on organic farms and sometimes to the development of new marketing and processing activities, rather than simply to increases in labor for specific crop or livestock enterprises (Padel and Lampkin, 1994).

For organic systems to be profitable, Zentner *et al.* (2011: 209–210) summarize that the main determinants "are the relative crop yields, extent of the cost savings due to the reduced reliance on nonrenewable resources and purchased inputs, the supply of unpaid family labor, the existence of price premiums for organic products and the magnitude and duration of

reduced income during the organic certification/transition period." MacRae *et al.* (2007) found that most organic farms in North America perform better financially under organic management compared with their previous tenure as conventional operations. They attribute this outcome to lower input costs, more diversified production and marketing channels, resilience in the face of variable market conditions, higher premiums, and a better capacity to adapt to weather extremes.

Research studies commonly support the general perception that organic farming systems are more environmentally friendly than conventional farming systems (Alföldi *et al.*, 2002; Kaspercyk and Knickel, 2006; Tuomisto *et al.*, 2012). Environmental benefits of organic agriculture include enhanced soil quality, which has been shown in numerous studies to be greater on organic than conventional farms or trials (Reganold *et al.*, 1993; Lotter, 2003; Gomiero *et al.*, 2011). For example, under organic management soil loss is greatly reduced (Reganold *et al.*, 1987; Gomiero *et al.*, 2011) and soil organic matter content increases (Mondelaers *et al.*, 2009; Gomiero *et al.*, 2011). Furthermore, organically managed soils generally have a higher water-holding capacity than conventionally managed soils, resulting in larger yields under conditions during drought periods (Lotter *et al.*, 2003; Gomiero *et al.*, 2011) (**Figure 12**). Soil biochemical and ecological characteristics are also improved (Mäder *et al.*, 2002; Lotter *et al.*, 2003; Gomiero *et al.*, 2011). For example, Reganold *et al.* (2010), in a comparison of numerous pairs of organic and conventional strawberry farms in California, not only found organically farmed soils to have better soil quality based on traditional soil characteristics, but also to exhibit greater numbers of endemic genes and greater functional gene abundance and diversity for several biogeochemical processes, such as nitrogen fixation and pesticide degradation; they were able to conclude that the higher quality soils on the organic strawberry farms may have a greater microbial functional capability and resilience to stress. Owing to these features, soils farmed organically are healthier than those farmed conventionally for passing on to future generations.



Figure 12 Plots in the Rodale Institute's Farming Systems Trial during a drought in 1995. Corn is planted in a legume-based treatment (left) and a conventional treatment (right). Photo © 2012 Rodale Institute.

In a metaanalysis of environmental quality parameters in organic and conventional farming comparison studies, Mondelaers *et al.* (2009) concluded organic farming contributes positively to agrobiodiversity (breeds used by the farmers) and natural biodiversity (wildlife). For example, Mäder *et al.* (2002) found organic systems to have higher below- and above-ground biodiversity than conventional systems in a long-term trial in Switzerland. Studies discussed in Kristiansen *et al.* (2006) showed that organic farms generally have more plant diversity (30–350% increase in floral species diversity in organic fields in Europe), greater faunal diversity (insects, soil fauna and microbes, and birds), and often more habitat and landscape diversity on organic farms.

As organic agriculture uses virtually no synthetic pesticides, there is no risk of synthetic pesticide pollution of ground and surface waters (Alföldi *et al.*, 2002). Concerning the impact of the organic farming system on nitrate and phosphorous leaching and greenhouse gas emissions, Mondelaers *et al.* (2009) found that organic farming systems score better than conventional farming for these items when expressed per production area; however, given the lower land-use efficiency of organic farming in developed countries, this positive effect is less pronounced or not present at all when expressed per unit product. In a summary of several nitrate leaching studies from organic and conventional farming comparisons in Germany and The Netherlands, Alföldi *et al.* (2002) found that nitrate leaching rates per hectare are significantly lower in organic farming systems. In the US, Kramer *et al.* (2006) found that annual nitrate leaching was 4.4–5.6 times higher in conventional apple orchard plots than in organic apple orchard plots. In a metaanalysis of environmental quality parameters in organic and conventional farming comparison studies, Tuomisto *et al.* (2012) found organic farms to have lower nitrate leaching, nitrous oxide emissions, and ammonia emissions per unit of field area but higher per product unit for the same three parameters.

Using a model of riverine nitrogen export for 18 Lake Michigan Basin watersheds based on nitrogen budgets at 5-year intervals from 1974 to 1992, Han *et al.* (2009) reported that if farmers choose organic practices and reduce fertilizer use, nitrogen export levels by rivers could decrease to below present-day levels. They projected future nitrogen fluxes under three land-use and two climate scenarios: (1) business as usual, (2) increased dependence on organic farming, (3) increased fertilizer use from corn-based ethanol production, (4) a 5% increase in rainfall, and (5) a 10% increase in rainfall. The study revealed that the combined effect of 10% more rainfall and more ethanol production would increase nitrogen levels in rivers by 24%. However, increased use of organic farming practices could reduce nitrogen levels in rivers by 7%, even if rainfall increased by 10% (Han *et al.*, 2009). Reducing nutrient and pesticide pollution to aquatic and marine systems – especially as there are more than 400 dead zones today – is an added environmental benefit of organic farming systems.

Organic systems have been shown to usually be more energy efficient (ratio of energy output or yield to input) than their conventional counterparts (Lockeretz *et al.*, 1981; Reganold *et al.*, 2001; Alföldi *et al.*, 2002; Kaspercyk and Knickel, 2006; Tuomisto *et al.*, 2012). For example, Alföldi *et al.* (2002) summarized numerous comparison studies on

energy consumption both per hectare and per unit of output (tons) for different crops from organic and conventional farming systems in Germany, Italy, Sweden, and Switzerland. On a per hectare scale, all organic farms had a significantly lower energy consumption than their conventional counterparts. For organic winter wheat (three studies), citrus (one study), olive (one study), and milk (two studies), energy consumption per output unit was lower relative to conventional production, but not for organic potatoes (in two out of three studies) and apples (one study), where energy consumption per output unit was higher (Alföldi *et al.*, 2002).

Comparison research studies comparing organic and conventional farming systems for the social aspects of agricultural sustainability are scarce despite their importance in providing farmers with knowledge to design systems that balance different social sustainability goals to improve overall sustainability (National Research Council, 2010). Studies on social sustainability are difficult to conduct and complicated because social dimensions are influenced by the behavior of farmers and consumers, values of community members, and market and policy conditions. Such studies are needed to discover how well organic, conventional, and other farming systems are doing in, for example, adequately compensating farm workers in an equitable way and contributing to building strong rural communities.

Are there significant differences in social sustainability indicators of organic and conventional farming systems? MacRae *et al.* (2007) found some evidence in North America that when a community has many sustainable (including organic) producers, there are positive shifts in community economic development and social interaction; the reasons appear to be related to the need to hire more labor, the increased demand for local goods and services, and a greater commitment to participate in civic institutions.

Future of Organic Farming

Organic farming offers one alternative to conventional agriculture at a time of increasing concern over global climate change, water scarcity, diminishing resources, water and air pollution, and issues of food quality and access. Organic farming systems offer many sustainability benefits in energy-efficiency, environmental viability, productivity, and stability. Reliance on recycled organic wastes such as compost and manure means these nutrients are kept out of the waste stream and used on the farm to build soil (Pearson, 2007). The use of these organic amendments increases water-holding capacity, which can lead to more robust yields under conditions of water scarcity, an important factor in a changing climate (Lotter *et al.*, 2003). Using organic fertilizers reduces nutrient leaching losses, while eliminating the high-energy requirements of producing synthetic fertilizers (Drinkwater and Snapp, 2007). Furthermore, organic farming principles value and integrate indigenous knowledge, diversify local food supplies, and advocate for fair worker conditions (Kristiansen *et al.*, 2006).

Concerns over the meaning and rigor of organic practices persist, however, as the organic food trade becomes increasingly global and corporate in nature. The expanding market for organic food may lead to increased specialization, a loss of crop diversity, and simplified crop rotations, all contrasting with commonly accepted best practices of organic agriculture (Ikerd, 2006). Long-distance trade of organic foods separates consumers from producers and processors, can lead to a lack of transparency and certifier oversight, and ruptures regional nutrient cycling. Some argue that concerns over ecological justice, land appropriation, resource rights, and worker compensation are not being adequately addressed by organic agricultural movements (Halberg *et al.*, 2007). Furthermore, certification requirements may not adequately address the need for organic farming systems to be highly catered to local ecological and social conditions. However, although challenges exist in implementing meaningful organic standards, the development of organic certification programs has played an important role in increasing sales and production of organic foods worldwide and continues to maintain minimum standards for organic practices (Aschemann *et al.*, 2007).

Significant barriers to farmers adopting organic practices remain. In parts of the world, some individuals and organizations hold strong cultural biases against the connotations of organic agriculture, which can limit the spread of organic practices (Wheeler, 2008). Many areas, especially rural regions and developing countries, have a lack of access to markets for organic foods or infrastructure for storage and distribution. Some governments and nongovernmental organizations are making efforts to eliminate these barriers, such as the international course recently developed by the United Nations Capacity Building Task Force on Trade, Environment, and Development called Successful Organic Production and Export (Naqvi and Kaukab, 2010). Certification costs imposed by certifying agencies can be an additional barrier, and the transition period into organic certification can be a risk to farmers, with little experience in organic management and rapidly changing weed and fertility conditions.

Policy can play an important role in encouraging organic farming practices. For example, policies can support the development of research and technology that is applicable to organic farms, governments can remove or change agricultural subsidies to support organic farms, and regulations can be developed to limit the overuse of fertilizers or synthetic pesticides (Kristiansen *et al.*, 2006; Reganold *et al.*, 2011).

Furthermore, organic farming is knowledge intensive and relies on an intimate understanding of ecological processes. Organic farming is biologically mediated, with nutrient supplies mediated by the mineralization of soil organic matter, and is therefore inherently complex and unpredictable (Drinkwater and Snapp, 2007). Kristiansen *et al.* (2006) emphasize the importance of creating knowledge networks and educational frameworks to help farmers in their transition to organic practices. Additionally, a relative dearth of research on organic systems over the past century compared with conventional systems has left organic agriculture at a disadvantage (Lotter, 2003).

Coordinated whole-system research comparing organically and conventionally managed farms in a variety of geographical locations is needed to better understand the impacts of different fertilization and pesticide regimes on biodiversity,

ecological functions, and nutrient dynamics. The factors affecting soil biota and their influence on ecological processes are not well understood, and are especially important in understanding soil fertility, crop productivity, and disease dynamics on organic farms (Reganold *et al.*, 2010). Furthermore, research is needed on the effects of climate – specifically of location-specific climate change scenarios – on soil organic matter, nutrient dynamics, and gas emissions from organic farming systems (Kaspercyk and Knickel, 2006). More research is needed in developing countries on ecosystem services and social impacts of organic farming (Halberg *et al.*, 2007). Finally, research on the role of organic agriculture in global food security, food access, and nutrition is in its early stages and must be developed further (Stockdale *et al.*, 2001).

If one wants to feed a growing world population, producing adequate yields is vital. However, as described earlier, sufficient productivity is only one of the four main goals that must be met for agriculture to be sustainable. Mainstream conventional farming systems have provided growing supplies of food and other products, but often at the expense of the other three sustainability goals – economic, environmental, and social. Although organic farming may generally have lower yields, a US National Research Council Report (2010) identified organic farming as one of the several innovative, more diverse systems that better integrate production, environmental, and socioeconomic objectives. Other innovative systems include agroforestry, integrated or hybrid organic/conventional, conservation agriculture, grass-fed livestock production, and mixed crop/livestock systems. No one agricultural system alone will safely feed the planet. Rather, a blend of these and other innovative farming systems will be needed for future global food and ecosystem security. Research studies discussed here indicate that organic farming can play a significant role in feeding the world. Yet, only approximately 1% of global agricultural land is now managed organically (Willer, 2011). Owing to the multiple sustainability benefits of organic agriculture, this percentage should be much larger in the future.

See also: Advances in Pesticide Risk Reduction. Agricultural Ethics and Social Justice. Agroforestry: Practices and Systems. Air: Greenhouse Gases from Agriculture. Biodiversity and Ecosystem Services in Agroecosystems. Biodiversity: Conserving Biodiversity in Agroecosystems. Climate Change: Agricultural Mitigation. Climate Change: Cropping System Changes and Adaptations. Climate Change, Society, and Agriculture: An Economic and Policy Perspective. Ecoagriculture: Integrated Landscape Management for People, Food, and Nature. Food Security: Development Strategies. Industrialized Farming and Its Relationship to Community Well-Being. Organic Livestock Production. Pathogen-Tested Planting Material. Plant Health Management: Biological Control of Insect Pests. Plant Health Management: Biological Control of Plant Pathogens. Plant Health Management: Pathogen Suppressive Soils. Regulatory Challenges to Commercializing the Products of Ag Biotech. Small Ruminants in Smallholder Integrated Production Systems. Social Justice: Preservation of Cultures in Traditional Agriculture. Soil: Conservation Practices. Soil Greenhouse Gas Emissions and Their Mitigation. Soil: Nutrient Cycling. Water: Water Quality and Challenges from Agriculture

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Washington State University's Organic Agriculture Program.

Organic Livestock Production

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Glossary

Agroecosystem Within a commercial farm system, basic ecological processes – competition, herbivory, and predation remain but are overlaid and regulated by agricultural processes of cultivation, subsidy, control, harvesting, and marketing. In contrast to ecosystems, processes are not self-regulatory but require stockmanship to steer and regulate the processes on the various scales.

Certification A determination made by a certifying agent that a production or handling operation is in compliance with the regulations in this part, which is documented by a certificate of organic operation.

Ecosystem An ecological community that consists of all the organisms in an area – plants, animals, and microbes – interacting with one another and with their physical environment.

Labeling All written, printed, or graphic materials accompanying an agricultural product at any time or written, printed, or graphic materials about the agricultural product displayed at retail stores.

Organic (1) Belonging to a superordinate whole (system) in which the single parts (subsystems) are closely related to one another.

Organic (2) A labeling term that refers to an agricultural product produced in accordance with the regulations in this part.

Production diseases Diseases that are multifactorial by origin and represent a negative side effect of livestock production primarily caused by an inappropriate farm management. Fertility disorders, infectious diseases such as mastitis and pneumonia, lameness, and metabolic disorders represent the main production diseases within dairy and pig production farming throughout the world.

Qualitative growth A process during which resource productivity increases but the resource use decreases. This is possible because knowledge and immaterial services are substituted for material resources and manual work.

Sustainability The ability of agroecosystems to maintain productivity when it is subject to a major disturbing force. It determines the persistence or durability of an agroecosystem's productivity under known or possible conditions and is a function of the intrinsic characteristics of the agroecosystem, of the nature and strength of the stresses or shocks to which it is subject, and of the human inputs that may be introduced to counter these stresses and shocks.

System approach A line of thought in the management field that stresses the interactive nature and interdependence of external and internal factors within a system. It integrates analytical and synergistic methods, encompassing both top–down and bottom–up approaches.

Introduction

Organic livestock production is an integrated and integrative part of organic agriculture. In comparison with other agricultural fields, it is a fairly new approach within agriculture and agricultural science. Thus, the availability of on-farm experiences as well as scientific knowledge, elaborated by various disciplines, is comparably low. Nevertheless, a review of numerous research works that have been conducted in the past might provide enough knowledge to risk at least some conclusions about what has been developed and achieved so far.

Organic livestock production is not practiced on an island but is surrounded and influenced in many different ways by the developments in conventional livestock production. Accordingly, there is a large area of intersection between both production methods, which might be even bigger than the differences between them. Although the development of organic livestock production occurs worldwide, the focus of this article is on the situation in Europe and the United States, where the longest experiences are available and most of the research work has been conducted.

To understand organic livestock farming, it is necessary to consider the initial conditions, how it has developed as an alternative to the predominant approach, and which driving forces have been involved to arouse the considerable increase in the number of organic farms. Further questions of interest address the differences between organic and conventional livestock farming with respect to their potentials and obstacles, regarding not only the performance capacity of the farm animals but also the qualitative outcomes in terms of product and process qualities from the different production methods. Furthermore, it is worth reflecting on this concept by introducing the leading ideas and the principles highlighted by the representative organizations and by assessing whether the practices of organic livestock farming correspond to the principles. Additionally, the constraints and the defaults where organic livestock production was not able to achieve its own claims so far have to be looked at.

Last but not least, the system approach is introduced as an access to the complexity that emerges from the interconnectedness between the various factors within the farm system. Following a different approach, organic livestock production not only is interesting in itself but also offers a point of view that enables the perception of mainstream agriculture from a distant position and at the same time promotes a critical debate between both approaches in an ongoing process of changing perspectives. As a result, the observer might gain additional knowledge that goes beyond conventional and organic agriculture.

Finally, the main question is what can be learnt from the different approaches of organic livestock production, what has proven to be of overall benefit and hence should be expanded, and what has failed to provide good solutions and therefore should no longer be emulated when facing an increasing necessity to put agriculture on the right track to sustainability.

Short Historical Retrospective

The beginnings of organic agriculture, reviewed among others by Schaumann (2002), Lockeretz (2007), and Youngberg and DeMuth (2013), can be associated with Arthur Young (1770), defining a 'well-proportioned farm,' followed among others by Justus von Liebig (1803–73), with his recommendations for a 'balanced crop rotation,' and Albert Howard (1873–1947), explaining an 'applied agricultural ecology.' Rudolf Steiner (1861–1925) and Hans Müller (1891–1988), who developed the concept of Biological Dynamic Agriculture and Organic Biological Agriculture, respectively, were further outstanding pioneers of the concept of Organic Agriculture. These pioneers and also the first private associations of organic agriculture, such as the Demeter Association and the Soil Association founded in 1924 in Germany and in 1946 in the United Kingdom, respectively, had their topical focus on soil biology and plant production, whereas farm animals played, if at all, only a marginal role, primarily as suppliers of organic manure.

Many pioneers of organic farming argued that soil quality is the key to long-term sustainable agriculture (Reganold *et al.*, 1990). They believed that synthetic chemical fertilizers and pesticides (and the monocultural cropping systems that these materials permit) disrupted the sensitive balance of organic matter, beneficial microbial and biological activity, and micro- and macronutrients, thus requiring ever-increasing applications of artificial compounds. There was also the widely held belief that food produced in artificially fertilized soils had less nutritive value and was likely to have toxic pesticide residues. Soil quality was the foundation that supported a number of additional core beliefs, such as the proper way to structure a farm enterprise so as to optimize soil health, the health of farm crops and animals, and the health of those families who lived on the farm or who consumed the food produced.

Guidelines have been a characteristic feature of organic farming since 1954 because trademark legislation in Germany required clear criteria to identify organically produced goods (Schaumann, 2002). As the variety of production sites and the resulting product properties did not allow their identification to be linked to products qualitatively in terms that could be described exactly and understood analytically, the production method itself became the identifying criterion for labeling organic food. This fundamental principle has been kept to the present day in private standards and meanwhile has been adopted by legislators in many countries of the world.

In the United States, the first-ever USDA-authorized investigation of organic agriculture was conducted by the USDA Study Team on Organic Farming (1980), elaborating the following definition:

"Organic farming is a production system which avoids or largely excludes the use of synthetically compounded fertilizers, pesticides, growth regulators, and livestock feed additives. To the maximum extent feasible, organic farming systems rely upon crop rotations, crop residues, animal manures, legumes, green manures, off-farm organic wastes, mechanical cultivation, mineral-bearing rocks, and aspects of biological pest control to maintain soil productivity and tilth, to supply plant nutrients, and to control insects, weeds, and other pests."

This definition helps to understand that organic farming in former times was nearly exclusively explained from the perspective of plant production while particular claims and requirements of farm animals were not considered. Also the founders of the International Federation of Organic Agriculture Movement (IFOAM) took this approach in 1982 when aiming to guide worldwide standard settings.

In early 1990, the Organic Foods Production Act (OFPA, 1990) was introduced, provided for establishing a USDA 'organically produced' label for products meeting a strict set of national standards and guidelines and counteracting against a misuse to the word as goods labeled organic often sell at premium prices, which increases the temptation. Ultimately, the OFPA became part of the 1990 Farm Bill. However, disputes between the organic industry and the USDA, and disagreements within the industry itself over the meaning of specific provisions of the bill, delayed its implementation until 2002 (Youngberg and DeMuth, 2013).

In the European Union, organic farming has been governed since 1991 by the EEC Regulation 2092/91 (EC, 1991) setting out the rules for labeling a food product as 'organic' or the equivalent terms 'biological' or 'ecological' in other languages. The Regulation was developed to harmonize the rules of organic crop production across member states, to protect the consumers from unjustified claims, to avoid unfair competition between those who label their products as organic, and to ensure equal conditions for all operators. The result was a legally enforceable and officially recognized common standard for crop production, certification, and labeling in the European Union, setting a minimum standard for all organic systems across EU member states although allowing the private sector to maintain stricter rules.

Although it was officially intended by the EU Commission to supplement production rules for organic livestock production shortly after those for crop production, it took the European member states 8 years to finally agree on rules for organic livestock production (EC, 1999), thus supplementing Regulation no. 2092/91 on organic production and becoming law in August 2000. The considerable delay reflects the challenges that the EU Commission had to deal with when trying to share a common idea of organic livestock production in the face of very complex and heterogeneous production processes and manifold areas of conflicting aims. An increasing awareness of the different stakeholders in the different European countries with regard to the possible advantages and disadvantages for the interests of national operators made it excessively difficult to agree on a common regulation.

Although the official implementations of organic standards can be seen as milestones of a long-lasting process, which to some degree summarized the corresponding stage of the process, they should not distract one from the fact that the on-farm practices developed quite confusingly and largely heterogeneously. Organic farming has never been and will

never be organized uniformly, neither with respect to the various objectives nor in the degree of their implementation. This heterogeneity is a common attribute with conventional farming. There have been and still are different perspectives on organic agriculture with different understandings of what it is and what it develops. Alroe and Noel (2008) identified protest (negation of certain aspects of modern mainstream agriculture), meaning, self-creating movement (entity or network with certain goals and principles), and market niche (based on standards) as the most significant perspectives on organic agriculture that cannot be merged into one but can be helpful in understanding its past and its future development.

It can be summarized that organic farming has its historical roots in efforts to establish alternatives to mainstream agriculture primarily in the fields of soil biology and plant production while livestock production played only a marginal role in the view of the organic pioneers.

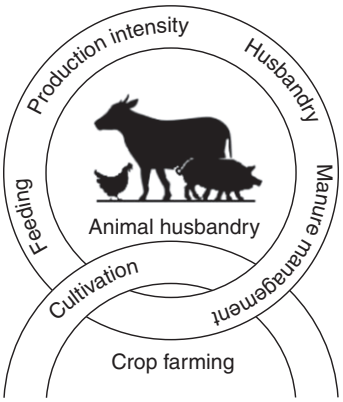


Figure 1 Need for reorganization of the farm system when striving for self-sufficiency.

Initiation of Organic Livestock Production

The Regulation (EEC) 1804/99 (EC, 1999) historically marks the beginning of organic livestock production in farm practice in Europe. In the time before this Regulation was put into force, only a few single aspects regarding the livestock issue have been formulated by private organic organizations, inspired by the basic norms of IFOAM. Even in 2000, only 3 from the 17 basic objectives of organic agriculture, defined by the general assembly of the IFOAM (2000), dealt more or less with the topic of organic livestock production: maintenance of biodiversity, freedom and access to possibilities for the execution of natural behavior, and balanced mix of crop and livestock production.

From a scientific perspective, a first definition of organic livestock production was provided by Sundrum (1998), addressing the need to focus not only on standards but also on general objectives to be envisaged by the production method: "Organic livestock production is based on the voluntary self-restriction in the use of specific means of production with the objectives to produce food of high quality in an animal appropriate and environmentally friendly manner within a nearly complete nutrient farm cycle."

Taking into account the standards in plant production, the emphasis of the considerations was placed on the need for an intensive adaptation process. For instance, the ban of mineral nitrogen fertilizer and the cultivation of legumes for nitrogen fixation require to adapt the crop rotation not only according to the demands of plants and soil biology but also according to the nutrient requirements of the farm animals in their various stages and depending on their performance levels when striving for a high level of self-sufficiency (**Figure 1**).

Correspondingly, conversion to organic farming demands a comprehensive reorganization within the farm structure where the needs of plant cultivation have to be balanced with the requirements of livestock production, whereas stocking density and animal performance have to be adapted to the nutrient potential of the homegrown feedstuffs. The need for restructuring the farm system is, among others, enforced by the ban of chemically synthesized feed (enclosing extracted soybean meal) and feed additives (e.g., synthetic amino acids and growth promoters).

The voluntary self-restriction in the use of external nutrients goes along with limitations with respect to the possible performance levels and the productivity on the average level of an animal while the farm management is encouraged to improve the productivity on the farm level and within the farm system by achieving the best possible efficiency in the use of homegrown resources.

From the very beginning, the low-input strategy of organic livestock production has to compete with the high-input strategy of conventional production; the latter striving for a decrease in production costs in the first place, mainly by increasing the stock and the stocking density as well as the performance level. Therefore, it should be comprehensible that a strategy based on self-restriction in the use of relevant external production tools, primarily intended to decrease production costs per product unit, cannot compete on the base of production costs. Necessarily, organic livestock production has to strive for alternatives to compensate for lower yields and higher production costs by focusing on quality instead of purely quantitative traits. Qualitative traits and added values are a precondition to gain and to justify premium prices that enable a reliable farmer's income. Consumers are asked to pay premium prices not only for a specific quality of the products of animals' origin but also for the production process itself defined and distinguished as different process qualities according to the expected outcome of the production process in terms of a high status of animal health and welfare and a high level of environmentally friendly production.

Correspondingly, potentials of the alternative strategy have to be balanced by the farm management toward various disadvantages. Potentials can be seen among others in the inherent incentive to increase the efficiency in the use of homegrown nutrient resources, being less dependent on external resources and their price developments, incentives to improve preventive strategies with respect to the occurrence of animal diseases because of restrictions in the use of medical remedies. Furthermore, lower performance levels are expected to reduce the risk for metabolic disorders and those diseases that develop from metabolic disorders, for example, due to an impaired immune competence. Overall, potentials lie in the

elaboration of synergetic effects when adapting processes to the local conditions and to natural processes for reasons of a more resilient system that is able to compensate for changing deficits, either in the availability of nutrients or in the case of changing market prices, thus developing strategies for qualitative growth. Instead of striving for general solutions, farm-specific optimization strategies have to be developed.

It is in the nature of the complex processes that the organic approach requires high management skills. The farm manager must be capable of gaining an overall picture of the complex interactions within a farming system. One has to make available the use of a comprehensive dataset of information about the internal processes on the various stages within the farm system, to reflect on the most relevant factors, to implement feedback mechanisms, and to guide the production process.

Further constraints are due to the fact that conflicting aims that occur when facing a limited availability of resources have to be solved within the farm system and cannot be easily outsourced by purchasing external input. Thus, organic farmers are more restricted by the local production conditions than is generally the case in conventional production. Above all, organic farmers are depending on the willingness of consumers to pay premium prices that are high enough to cover the expenditures and the farmers' income. Correspondingly, organic livestock production has to take into account the demands and perspectives of consumers to a high degree. As with conventional farmers, organic farmers share the concerns about inadequate low market prices.

According to the EC Regulation 1804/99, labeling food of animal origin as being 'organic' identifies the products as deriving from a production method defined by guidelines and minimum standards, intended to ensure quality production rather than maximizing production. The Regulation includes specifications for the conversion process, housing conditions, animal nutrition, care and breeding, disease prevention, and veterinary treatment, while creating frameworks for organic livestock production and product labeling, referring to the whole farm as the base of a comprehensive farm system. Since its introduction, various slight amendments to the regulation have been passed.

According to Padel *et al.* (2009), the EC Regulation 1804/99 defined organic livestock farming by the practices rather than the principles and ethical values. That is why the authors see a widespread concern that core organic values of organic agriculture are not well represented in standards and especially in governmental regulations that set only minimum standards for all organic producers.

In 2002, the US National Organic Program (NOP) Regulation was put into force, also encompassing among others numerous specifications about the handling, feeding, and treatment of farm animals. In the following years, other countries also followed the examples of the European Union and United States. However, organic livestock farming practices and certification requirements vary worldwide. All of these have in common that farm animals are fed organically produced feed that is cultivated without the use of mineral N-fertilizer, pesticides, and genetically modified organisms and their derivative (IFOAM, 2005). They are reared without the preventive use of antibiotics or growth hormones. They are provided outdoor access, direct sunlight, fresh air, and freedom of movement.

The US concept seems to be more consumer driven ('pure' food, produced without the use of antibiotics), whereas the European approach considers not only the health aspects of the food but also the animal welfare aspects as important issues. Detailed information on the differences between international organic standards is provided by Schmid *et al.* (2008).

Besides statutory minimum standards, organic farming, represented by the general assembly of the IFOAM, commits itself to a number of substantial values and thereby sets itself apart from conventional farming. During the assembly in the year 2006, the members of IFOAM adopted four principles: Health, Ecology, Fairness, and Care, which grew out of stakeholder consultations. According to the preamble, they represent a vision to improve agriculture in a global context. The value elements covered by these principles include the integrative values of sustainability, naturalness, and a system approach (IFOAM, 2005).

Summing up, organic livestock production follows a clearly different approach than mainstream of animal production when striving for a high level of self-sufficiency and a high level of product and process quality to justify premium prices, which are essential to cover higher production costs.

Framework Conditions of Organic Livestock Farming

Some of the most relevant standards in relation to livestock production are outlined below. If not separately highlighted, they are based on the Regulations, enforced in Europe (EC, 2007, 2008).

According to the Regulation, livestock production is fundamental to the organization of agricultural production on organic holdings in so far as it provides the necessary organic matter and nutrients for cultivated land and accordingly contributes toward soil improvement and the development of sustainable agriculture.

Animals should have, whenever possible, access to open air or grazing areas. Organic stock farming should respect high animal welfare standards and meet animal species-specific behavioral needs whereas animal health management should be based on disease prevention. Disease prevention shall be based on breed and strain selection, husbandry management practices, high quality feed and sufficiently opportunity to exercise, appropriate stocking density, and adequate housing maintained in hygienic conditions. Moreover, the choice of breeds should take account of their capacity to adapt to local conditions. Organic livestock shall be born and raised on organic holdings. Husbandry practices and housing conditions shall ensure that the developmental, physiological, and ethological needs of animals are met. It shall primarily obtain feed for livestock from the holding where the animals are kept or from other organic holdings in the same region. Livestock shall be fed with organic feed that meets the animal's nutritional requirements at the various stages of its development. Part of the ration may contain feed from holdings that are in conversion to organic farming. Further details with respect to housing, feeding, mutilation, and treatment are discussed in the following paragraphs.

Table 1 Comparison between the EC-Council Directives and the EC-Regulation on organic livestock farming (EC 1804/1999) in relation to minimum standards concerning the housing conditions

Farm animals	*EEC-Council Directives on protection of farm animals*	*EEC Regulation on organic livestock farming*
Dairy cows	No Council Directives	
Locomotion area[a]		6.0 m^2 indoors + 4.5 m^2 outdoors
Floor characteristics		Lying space with litter (bedding)
Husbandry practices		Keeping tethered is forbidden
Calves		
Locomotion area[a]	1.3 m^2	1.5 m^2 indoors + 1.1 m^2 outdoors
Floor characteristics	Dry litter bedding[c]	Dry litter bedding
Husbandry practices	Group penning after 8 weeks	Generally group penning
Sow with piglets		
Locomotion area[a]		7.5 m^2 indoors + 5.0 m^2 outdoors
Floor characteristics	Isolated and nonperforated floor	Dry litter bedding
Fattening pigs		
Locomotion area[a]	0.65 m^2[b]	1.3 m^2 indoors[b] + 1.0 m^2 outdoors
Floor characteristics	Safe floors	Dry litter bedding
Husbandry practices	Tools for occupation > 1 h	No tail docking and tooth clipping
Laying hens		
Locomotion area	450 cm^2	1660 cm^2 indoors + 4 m^2 outdoors

[a]Area per animal.
[b]Up to 110 kg live weight.
[c]For calves up to 2 weeks of age.

Housing

Specific housing conditions should serve a high level of animal welfare, which has priority in organic livestock farming and therefore may go beyond community welfare standards that apply to farming in general. Concerning the indoor area provided for livestock in organic farming, the EEC Regulation goes far beyond the current space allowance in conventional production with respect to different species. In addition, the indoor area is supplemented by an outdoor area that has to be at least 75% of the indoor area. Furthermore, organic livestock are not allowed to be kept tethered or in individual confinement housing. The comparison between the EC-Council Directives and the EC-Regulation on organic livestock farming (EC 1804/1999) in relation to minimum standards concerning the housing conditions is presented in Table 1.

Although beef cattle, pigs, and poultry in conventional systems are frequently housed in unbedded systems with partly or fully slatted floors, all farm animals in organic farming must be provided with litter. Completely slatted floors are forbidden. In addition to its role as a cushioned physical surface, the provision of straw is expected to reduce health and welfare hazards through its role as a behavioral substrate.

Piglets shall not be kept on flat decks or in piglet cages. Exercise areas shall permit dunging and rooting by porcine animals. For the purposes of rooting, different substrates can be used.

Organic husbandry practices should prevent poultry from being reared too quickly. Therefore, specific provisions to avoid intensive rearing methods should be laid down. In particular, poultry shall either be reared until they reach a minimum age or shall come from slow-growing poultry strains, so that in either case there is no incentive to use intensive rearing methods.

Feeding

Livestock should be fed on fodder produced in accordance with the rules of organic farming, preferably coming from the farmer's own holding, by taking into account their physiological needs. In the case of herbivores, at least 50% of the feed shall come from the farm unit itself or in case this is not feasible it should be produced in cooperation with other organic farms primarily in the same region.

All young mammals shall be fed on maternal milk in preference to natural milk, for a minimum period of 3 months for bovines, 45 days for sheep and goats, and 40 days for pigs.

At least 60% of the dry matter in daily rations of herbivores shall consist of roughage, fresh or dried fodder, or silage. A reduction to 50% for animals in dairy production for a maximum period of 3 months in early lactation is allowed. Roughage, fresh or dried fodder, or silage shall be added to the daily ration for pigs and poultry. Growth promoters and synthetic amino acids shall not be used. The feed is supposed to be free of genetically modified material.

Mutilation

In contrast to conventional livestock production, where several surgical mutilations are carried out as a matter of routine in farm animals, including castration, dehorning, tail docking, and beak trimming, mutilations are widely banned in organic livestock farming and are restricted to derogations that require separate permission by the certifying bodies. An exception is the castration of male pigs that is also practiced to a large extent in organic pig farming. However, from the beginning of the year 2012, castration of piglets has to be carried out with the application of anesthesia or analgesia

(EC, 2008), which differs from the current practices in conventional production.

Treatment

Where animals become sick or injured they shall be treated immediately, if necessary in isolation and in suitable housing. The preventive use of chemically synthesized allopathic medicinal products is not permitted. In organic farming, phytotherapeutic essences and homeopathic products shall be used in preference to chemically synthesized allopathic medicinal products or antibiotics, provided that their therapeutic effect is effective for the species of animal and the condition for which the treatment is intended. It is emphasized that if the use of the authorized substances and measures is not effective and if the treatment is essential to avoid suffering or distress, chemically synthesized products may be used with some limitations. With the exception of vaccinations, treatments for parasites and compulsory eradication schemes where an animal or group of animals receive more than three courses of treatment with chemically synthesized allopathic veterinary medicinal products or antibiotics within 12 months, or more than one course of treatment if their productive lifecycle is less than 1 year, the livestock concerned, or produce derived from them, may not be sold as organic products, and the livestock shall undergo the conversion periods.

The withdrawal period between the last administration of an allopathic veterinary medicinal product to an animal under normal conditions of use and the production of organically produced foodstuffs from such animals is to be twice the legal withdrawal period.

Although some overlap exists between European and US organic standards, there are some key differences. On organic livestock farms in the United States, animals or products from animals given NOP-prohibited substances may no longer be sold as organic, and these animals must then be removed from the herd. However, producers are prohibited from withholding necessary treatment from a sick or injured animal (USDA National Organic Program, 2011).

Practices of Organic Livestock Farming

As all organic farms are obliged to follow the same minimum standards, one might expect a high level of uniformity in the living conditions of farm animals, at least higher than in the nondefined conventional commercial farms, and a more homogeneous outcome with respect to traits of product and process quality (e.g., animal health status). Several aspects contradict with this expectation.

Production conditions of organic livestock farming in Europe vary from outdoor production to indoor production and encompass huge differences between countries and regions, not only in relation to environmental conditions and the genotype used but also in relation to the nutrient supply and the management measures (Vaarst *et al.*, 2006; Sundrum, 2010). Housing conditions encompass largely varying options with respect to space allowance, group size, climate and air conditions, etc., depending on the farm-specific and local conditions. Although most organic farmers make use of conventional breeds and genotypes, a large variation in the performance level and in the nutrient resources used is found. Although feeding rations should be based in the first place on homegrown feedstuffs, they provide a higher variability in ingredients and composition than is expected in the case of fodder from feed mills (Sundrum *et al.*, 2008).

In the United States, organic dairy production practices require access to pasture suitable to the stage of production, climate, and environment. Sato *et al.* (2005) reported that 76% of conventional herds included in his study had some access to pasture, whereas 50% of the organic herds utilized intensive rotational grazing, in contrast to only 7% of the neighboring conventional herds. In the United States, lactating cows in organic dairies in Michigan, Minnesota, New York, and Wisconsin were more likely to be housed in tie stalls, whereas most conventional dairies housed cows in free stalls and milked in a parlor (Zwald *et al.*, 2004). Compared with conventional farms, organic farms typically house their animals in older housing during the winter months (Ruegg, 2009). In general, conventional farms tend to be bigger, produce more milk, feed more grain, have longer calving intervals, and have younger cows than their organic counterparts (Zwald *et al.*, 2004; Stiglbauer *et al.*, 2013).

An epidemiological study based on 101 pig herds in 6 European countries revealed that farmers differed widely in their feeding regimes, in the implementation of disinfection measures, the use of clinical examination of the individual pigs, separation of diseased from healthy animals, presence of the farmer during farrowing, and with regard to routine measures such as castration, grinding teeth, and iron supply of piglets (Sundrum *et al.*, 2010).

Although the literature on organic dairy and pig production indicates a large heterogeneity of the living conditions of farm animals, the development of conventional livestock systems shows a clear trend to closely controlled environments. Living conditions have typically been adopted across regions and countries to maximize aspects of animal productivity, thereby increasing environmental homogeneity between farms and leading to the predominance of a small number of breeds and genotypes that are particularly productive under these specific conditions. Parallel to the increasing performance of livestock, nutrient demands have increased the call for the use of particularly energy- and protein-rich concentrate to meet the nutrient requirements of the animals at their various life stages. The equipment of indoor housing and the feeding ration is offered by specialized enterprises, becoming more and more standardized all over the world.

On organic farms the income is often provided by profits from the livestock sector. The majority of 550 farms surveyed in 11 EU countries generated their income mainly from one category of enterprise, such as grazing livestock (50%), arable crops (20%), permanent crops (7%), horticulture (3%), or intensive livestock (3%), whereas 17% are ruled as mixed farms (Nieberg *et al.*, 2005).

In the United States, organic dairy products comprise 15% of total organic sales, and organic fruits and vegetables account for 38% of total sales, making them the top 2 sectors of organic food (Organic Trade Association, 2010). From 2000 to 2008, the number of certified organic cows in the United States

increased from 38 196 to 249 766 (USDA Economic Research Service, 2008).

Summing up, the living conditions of farm animals in organic livestock farming are largely heterogeneous. Although common ideas and guidelines exist only on a meta-level, the concrete implementation in farm practice results in a large variety of stocking densities, performance levels, nutrient availabilities, housing conditions, and hygiene measures. Thus, low input and highly intensified farms mark the cornerstones of different objectives, various priorities, and diverse living conditions for farm animals in organic agriculture.

Consumers' Perspectives

In face of the heterogeneity, questions arise whether the outcome of the production processes meet the expectations of consumers. Consumers' concern over the quality and safety of conventional food has intensified in recent years and primarily drives the increasing demand for organically grown food, which is perceived as healthier and safer (Magkos *et al.*, 2006). Consumers express concern about possible hormone, antibiotic, pesticide, or chemical residues in animal products. A survey commissioned by an organic cooperative indicated that 70% of US consumers expressed at least moderate concern about health risks associated with use of pesticides and antibiotics in food production (Roper Public Affairs, 2004). Concern for human health and safety as a key factor influencing consumers' preference for organic food is consistent with observed deterioration in human health over time and therefore motivates consumers to buy organic food as insurance and investment in health (Yiridoe *et al.*, 2005). Organic products are marketed to lessen these concerns by requiring that farm animals are raised using a whole systems approach that includes the use of organic feeds (grown without use of pesticides or synthetic fertilizers), no usage of antibiotics or growth hormones, and emphasis on husbandry practices that limit stress and promote health.

However, as literature reviews revealed (Woese *et al.*, 1997; Yiridoe *et al.*, 2005), consumers purchase organic food for very different reasons. Aside from concerns about human health, this includes the effects of conventional farming practices on the environment and perceptions that organic foods are tastier than their conventional alternatives. Particularly in Europe, more and more consumers expect their food to be produced with greater respect for the needs of farm animals. Many consumers associate organic farming directly with enhanced animal health and welfare and conflate organic and animal-friendly products (Harper and Makatouni, 2002; McEachern and Willock, 2004). Thus, for many people, organic farming appears to be a superior alternative to conventional livestock production (Hughner *et al.*, 2007). Consumers' interests and expectations are linked to their willingness to pay premium prices on products (Zanoli, 2004). In contrast, consumers are less strongly motivated by the altruistic concerns of environmental protection and the support for rural society – the so-called public goods.

Even though organic farming covers only a small percentage of the food market, the expressed liking in the general public appears far greater than the market share. Interest in organic food has grown remarkably as consumers react to popular media about health effects and then have gradually evolved attitudes toward the origins and to the production process of food. For example, a change from confinement to grazing systems is one of the tools to evoke positive associations with the product. In this way, animal health and welfare have been turned into quality attributes of food.

However, not only the word 'health' but also the word 'organic' means many different things to different consumers. Correspondingly, consumers of organic foods are homogeneous neither in demographics nor in beliefs (Hughner *et al.*, 2007; Aertsens *et al.*, 2009; Martelli, 2009). They hold a huge variety of motivations, perceptions, and attitudes regarding organic foods and their consumption (Yiridoe *et al.*, 2005). Although consumers typically understand the broad issues about organic foods, many tend not to understand the complexities and niceties of organic farming practices and organic food quality attributes. Furthermore, there is a reason to assume that consumers delegate responsibility for ethical issues in food production to the retailer or the government as many consumers do not like to be reminded about issues connected with the animal when choosing products of animal origin (Skarstad *et al.*, 2007). Moreover, knowledge of production systems often appears of little importance for food market potentials as some consumer groups often freely remark that there is no link between the negative images of production methods and consumers' purchase behavior (Ngapo *et al.*, 2003). According to the authors, consumer groups are often confused and they mistrust the limited information available at the point of purchase, whereas price is an extremely visible attribute of products related to quality by the notion of value (McEachern and Schröder, 2002). Demand tends to depend more on the price differential with respect to conventionally grown products than on actual price. In contrast to sensitivity of demand to changes in price, income elasticity of demand for organic foods is generally small (Martelli, 2009).

Summing up, the decision-making process to buy organic food of animal origin is driven by many different factors, from which expectations regarding 'healthy' products show the highest priority. However, neither are consumers a uniform group covering common interests nor are they experts who can decide on how to evaluate product and process qualities and what is needed to provide framework conditions that are appropriate to ensure quality production.

Gap Between Theory and Practices

By following the practices set out in the standards, the farmers make a promise to the consumer to deliver added values, beyond the legal minimum standards for conventional agriculture and food (Padel *et al.*, 2009). The question arises to what degree organic livestock farms are capable to fulfill these demands. In the following, a preliminary assessment is given regarding the issues of animal behavior, animal health, product quality, and the use of antibiotics.

Animal Behavior

When considering demands of livestock in organic farming, possibilities to execute natural behavior patterns have been

one of the first objectives, implemented in private regulations asking for instance to provide access to pasture in the summer season for dairy cows. Minimum standards refined in legally binding regulations in relation to animal welfare are primarily focused on the locomotion area, floor characteristics, and husbandry practices. In Europe, dry litter as well as group penning is prescribed for all farm animals. Tethering of farm animals and completely slatted floors are forbidden. Comparing the organic standards with those in conventional production (minimal standards of the Council Directives) and private branded programs, Sundrum (1999) concluded that they reach a clearly higher level and enable the execution of behavioral patterns to a far higher degree. In addition, the regulations prescribe a regular check of the standards by independent certifiers, providing an additional advantage in comparison to conventional ordinances.

Close confinement of farm animals raise welfare concerns into both physical and behavioral issues. Physical concerns arise from the consequences of lack of exercise, such as leg weakness, skin lesions, and lameness (Ruis-Heutinck *et al.*, 2000; Buchwalder and Huber-Eicher, 2004). Enlarging the locomotion area and providing litter bedding is expected to provide substantial benefits for farm animals (Hindhede *et al.*, 1996; Guy *et al.*, 2002). In the case of pigs, the litter bedding can be eaten to provide gut fill and rooted to permit appropriate expression of foraging behavior. This generally prevents the development of stereotyped tail-biting behavior and reduces social aggression (Meunier-Salaün *et al.*, 2001). Furthermore, the prescription to provide roughage in the daily diet of pigs can reduce risk of constipation and gastric ulcers and increase satiety from increased feeding time and greater physical bulk in the gut (Stewart and Boyle, 2008).

Although raising the level of minimal standards is suited to improve the living conditions, a higher level of minimal standards cannot be treated as equivalent to appropriate livestock housing conditions and high welfare status for different reasons (Sundrum, 2000). However, minimum standards represent only a small section of the interrelationship between farm animals and their living conditions. Besides the housing conditions, the quality of stockmanship and management, the patterns of feeding, climatic factors, and the hygienic situation all have significant influences on animal health and welfare of farm animals. Owing to differences in genetic origin, age, sex, or in the experiences during ontogenesis, farm animals can vary widely in their requirements in relation to the housing conditions. Furthermore, it is well known that poor quality straw bedding can contain high levels of mycotoxins, which causes health and reproductive disorders. Moreover, increased use of straw, especially in deep litter systems, is a significant risk factor for endoparasites (Nansen and Roepstorff, 1999; Haugegaard, 2010). Keeping farm animals in outdoor systems potentially has both advantages and disadvantages. Greater space and environmental diversity permit expression of a wider range of behavior and health challenges may be reduced by the lower animal density and better air quality; however, there are also negative influences of reduced biosecurity, contact with wildlife disease reservoirs, and increased numbers of endoparasites, some of which can only be transmitted outdoors (Redbo *et al.*, 1996; Edwards, 2005; Van de Weerd *et al.*, 2009).

Summing up, the higher level of the minimum standards concerning the housing conditions in organic livestock farming and their regular check provide clearly improved preconditions for the behavior of farm animals compared with the conventional situation.

Animal Health Status

Most production diseases emerge from a multifactorial etiology, meaning that various factors contribute to the occurrence of disease. In addition to pathogens and animal-related conditions, other contributing factors (housing, feeding, hygiene, etc.) may be considered as stressors in the environment, disturbing homeostasis in the animal. Owing to the various interactions between health-influencing factors, the assessment of animal health status on the herd level faces a high level of complexity. In the literature, huge differences and intercountry variation exist in study designs and in definitions of diseases (LeBlanc *et al.*, 2006).

The status of animal health in organic livestock farming on the farm level has been described in various reviews, mainly addressing the European situation. In this context, animal health is primarily related to the occurrence of production diseases. The reviews cover different species (Cabaret, 2003; Hovi *et al.*, 2003; Thamsborg *et al.*, 2004), dairy cows (Vaarst *et al.*, 2008; Sundrum, 2012a), pigs (Sundrum *et al.*, 2010; Sundrum, 2012b), or poultry (Tuyttens *et al.*, 2008; Van de Weerd *et al.*, 2009). Available reviews concerning the health status in organic herds in the United States are narrowed down mainly to dairy production, focusing on mastitis in the first place (Sato *et al.*, 2005; Ruegg, 2009; Cicconi-Hogan *et al.*, 2013) or also include ketosis and pneumonia (Richert *et al.*, 2013a).

Studies that have compared health performance in conventional and organic farms have shown that disease problems tend to be similar to what is found under conventional conditions although the extent of these problems varies considerably among farms (Thamsborg *et al.*, 2004), and between countries (Vaarst *et al.*, 2008). As differences between farms appear to be greater than those between production methods, organic livestock farming defined by minimum standards does not provide a homogeneous outcome with respect to the animal health status (Sundrum *et al.*, 2006). The reviews clearly indicate that organic standards do not automatically lead to a high status of animal health that exceeds the level in conventional production.

Sources of variation in relation to animal health attributes are due to the numerous interactions between genotype, age, sex, nutrient supply, housing conditions, care, and their varying impacts on the dynamic nature of animal health status. Thus, it primarily depends on the management as to whether the potentials for a high level of animal health are fully realized. Differences in management practices, restrictions in the availability of resources (such as labor time and financial budget), and a lack of feedback and control mechanism within the farm system appear to be primary reasons for the substantial variation.

Fertility disorders, mastitis, lameness, and metabolic disorders represent the main production diseases within dairy

farming throughout the world (Rushton, 2009). These are multifactorial by origin and indicate an overstrained capacity of the farm animals to cope with the living conditions provided by the farm management (Gröhn *et al.*, 1998).

The level of production diseases in organic livestock production have been the issue of various studies. Brinkmann and March (2011) investigated the animal health status of 50 organic dairy farms in Germany in the years 2002–03 and with the same approach in 2005 on 43 farms. The mean incidence rates of mastitis were 33% (0–101%) in the first and 29% (2–81%) in the second study. Prevalence rates of lameness averaged 18% (2–53%) and 20% (4–53%) in the first and second study, respectively. The frequency of metabolic disorders showed a large variation between farms. Mean incidences rates of hypocalcemia showed 5.9% in the first and 10.2% in the second study. In contrast, the incidence rates of ketosis and acidosis were on average below 2% in both studies. Bennedsgard *et al.* (2010) found hypocalcemia in organic dairy farms to occur on an average level of 12%. 74 organic dairy farmers in Germany were asked for disease incidences on their farm (Hörning *et al.*, 2005). Those mentioned as regular or frequent were 44.6% for udder health problems, 31.1% for fertility disorders, and 36.4% for claw health problems. Somatic cell counts (SCC) in the bulk tank averaged to 223 000 cells ml^{-1} of milk. According to Roesch *et al.* (2007), cow-level prevalence of subclinical mastitis in dairy cows in Swiss organic production systems for visits at 31 days and 102 days postpartum were 39% and 40%, respectively. In a study on Swedish organic herds, the most common reason overall for culling was poor udder health followed by low fertility and leg problems (Ahlman *et al.*, 2011).

In the United States, mean SCC from previous 3 months in the bulk tank of organic farms were 221 000 cells ml^{-1} (Stiglbauer *et al.*, 2013). In a study by Cicconi-Hogan *et al.* (2013), the presence of *Staphylococcus aureus* in the bulk tank milk was higher on organic farms (61%) than on conventional farms (42%), confirming previous studies (Sato *et al.*, 2005; Pol and Ruegg, 2007). In this context, it is noteworthy that in a comprehensive study based on the analysis of 615,187 quarter foremilk samples, in 83% of all samples with SCC > 100 000 cells ml^{-1} mastitis pathogens were detected, indicating a case of mastitis (Schwarz *et al.*, 2010).

The results of slaughter animal and carcass inspection were evaluated by Machold *et al.* (2005) in the case of pigs and cattle reared in organic and conventional production systems, respectively. The most common pathological findings in pigs were liver diseases, condemned carcasses, and lesions of the tail tip. In cattle the most common pathological findings were claw and leg disorders; diseases of liver, kidney, and pleura; and parasitic infections. From cattle reared in organic systems, less carcasses, livers, and kidneys were discarded in comparison with conventional cattle. Pigs from organic systems showed similar incidence of 'milk spots' in the liver caused by *Ascaris suum*. There was no pronounced difference concerning the number of condemned carcasses and the incidence of tail tip lesions between pigs from organic and conventional farms.

Another study showed that in a lower proportion of the organic pigs, abnormalities were detected in the lungs, 53.0% versus 58.6% among conventional pigs, whereas 64% of the livers from organic pigs showed milk spots, whereas 43% of the conventional livers were affected (Sundrum and Ebke, 2004). A further study, 10 years later at the same abattoir, revealed that the situation concerning the pathological findings from organic pigs had not improved (Hoischen-Taubner and Sundrum, 2013).

Living conditions found in practice are so multiform and diverse that it is very difficult to identify factors that are influential in any actual combination of factors. To cope with production diseases, it is of high importance to consider the farm-specific conditions, the availability of resources for both farm animals and farm management, and the ongoing outcome of the interactions in various fields. It largely depends on the capability of the farm manager to think through the complexity of the processes on different process levels and to organize appropriate living conditions for farm animals although often facing severe limitations in the availability of relevant resources (labor time, investments, knowledge, etc.).

It can be summarized that in general the enhanced minimum standards fail to clearly improve the animal health status on the farm level in comparison with conventional production that is influenced in the first place by the farm management, being not covered by the regulation on organic livestock.

Product Quality

The milk quality of organic farms compared with their conventional counterparts is a topic of interest for many scientists as well as consumers in Europe and United States. The term 'quality' is documented very diversely in general language use and in the scientific literature. Although some understand something very sound and normal by this term, others consider it as rather something special and extraordinary. According to Mair-Waldburg (2002) quality includes both free of defects and inadequacies and the fulfillment of previously determined properties that exceed the usual. For a consumer-oriented product it is significant that quality includes a high degree of fulfillment of the consumer's expectation as far as the desired properties are concerned.

It is generally accepted that bulk milk SCC are the primary indicator of milk quality in dairy herds and are associated with management practices on the farm (Barkema *et al.*, 1998; Schukken *et al.*, 2003). Based on treatment data from the Norwegian Cattle Health Service, Hardeng and Edge (2001) did not find any significant difference in individual cow SCC between organic and conventional-farmed dairy herds. Other studies show varying results, including better udder health on organic farms (Garmo *et al.*, 2010), no difference (Fall *et al.*, 2008; Zwald *et al.*, 2004; Sato *et al.*, 2005), or even higher levels of mastitis on organic farms (O'Mahony *et al.*, 2006). Thus, the consumer perception that organic milk is of higher quality (Hill and Lynchehaun, 2002) is not supported by scientific studies.

Concerning the meat quality of organic pork and beef, a review revealed substantial variation in the quality of organic meat entering the marketplace (Sundrum, 2010). According to the available literature sources, quality of organic pork and beef provide inconsistent results and often fall short of expectations as it is often similar to that of conventionally

produced meat. Not only in conventional but also in organic meat production, the trade value of carcasses is determined by lean meat and cuts composition in the first place, whereas qualitative traits of meat (e.g., traits of the eating quality) are in general not taken into account. Neither does continuous recording of qualitative traits take place nor is an outstanding meat quality rewarded by higher prices. Of the various parameters, marbling and intramuscular fat, respectively, are highly related to palatability traits in both pork and beef and could be used to distinguish between different levels of eating quality (Sundrum *et al.*, 2011).

Summing up, the expectations of consumers toward a clearly higher level with respect to traits of product and eating quality of organic animal products are in general not met by organic producers, which bring a largely heterogeneous outcome of the production processes onto the market.

Use of Antibiotics

Intensive management practices are closely associated with frequent veterinary usage. For many consumers, and especially those who buy organic food from animal origin, the use of antibiotics in the production process is a matter of concern and a relevant issue of food safety. Indeed, the use of antibiotics includes a certain amount of risk regarding selection and transmission of resistant bacteria (Schwarz *et al.*, 2001) and can promote the development of resistance reservoirs. Therefore, the selection for resistant bacteria is an increasing public health problem. Research has shown increased resistance rates in pathogenic and commensal bacteria of animals related to antibiotic use (Harada and Asai, 2010).

However, antibiotics are a powerful tool to treat animals suffering from infectious bacterial diseases. Because animals should not suffer, allopathic antimicrobials are allowed in the EC Regulation for organic farming. The legislation, however, encourages avoidance of allopathic treatment in organic milk production if any alternative is available and prescribes to a doubling of the withdrawal time on milk and meat compared with conventional herds (EC, 1999). In contrast, the US regulations define any animal treated with antimicrobials as nonorganic for the rest of its life (USDA National Organic Program, 2011). Consequently, the use of antimicrobials has a severe impact on the fate of the treated animal in organic herds. Antimicrobials are therefore only rarely used in US organic herds (Zwald *et al.*, 2004; Pol and Ruegg, 2007). In a questionnaire, administered on site to selected dairy farmers located in Michigan, Minnesota, New York, and Wisconsin, most organic farmers (90.6%) reported no antibiotic treatments of milk cows, whereas 9.4% reported treating 1–10% of milk cows (Zwald *et al.*, 2004).

Information about medication in organic livestock production in Europe is scarce. In Denmark, in a study involving 27 organic and 57 conventional dairy herds, the percentage of cows treated for mastitis per month was 1.8–5.1 (25% and 75% percentiles) in organic herds and 3.3–6.7 in conventional herds (Vaarst and Bennedsgaard, 2002). A study in Switzerland revealed that bacteria in milk from organic dairy cows with mastitis exhibited antibiotic resistance at a comparable frequency as found previously in conventional farms (Busato *et al.*, 2000). In a Norwegian study on conventional and organic farms with respect to udder health and antibiotic resistance in udder pathogens, coagulase-negative staphylococci with penicillin resistance were isolated from subclinically infected quarters in 48.5% of the cases in conventional herds and 46.5% in organic herds (Garmo *et al.*, 2010).

An investigation of the use of antibiotics to fattening pigs in Denmark showed that the conventional herds consumed three times as much as the organic herds (Hegelund *et al.*, 2006). Based on a comprehensive review comparing the health effects of organic and conventional food, Smith-Spangler *et al.* (2012) concluded that the published literature lacks strong evidence that organic foods are significantly safer than conventional foods. According to the authors, consumption of organic foods may reduce exposure to antibiotic-resistant bacteria. Bacterial contamination of retail chicken and pork was common but unrelated to the farming method. However, the risk for isolating bacteria resistant to 3 or more antibiotics was higher in conventional than in organic chicken and pork.

It can be summarized that organic livestock producers use clearly less antibiotics than their conventional counterparts going along with a reduced risk for bacteria resistant to antibiotics.

Inconsistencies between Principles and Minimum Standards

Since 2000, a number of publications have specifically aimed at identifying ethical values or principles of organic farming that can guide practice. Niggli (2000) summarized the ethical values that the pioneers of organic farming referred to as follows: respecting and enhancing production processes in closed cycles; stimulating and enhancing self-regulatory processes through system or habitat diversity; using strictly naturally derived compounds, renewable resources, and physical methods for direct interventions and control; and considering the wider social, ethical, and ecological impacts of farming. Vogt (2000) summarized the main values as a biological understanding of soil fertility, the intensification and maintenance of the agroecosystem with 'biological' and 'ecological' tools, the production of high quality food for a healthy diet, and visions of alternative living and organizing society.

Principles have a normative aim stating what is a 'right' or 'good' organic system. This is comparable to deontological ethics, in which certain principles are formulated to assure respect for a range of fundamental values. Such ethical principles can function both as a source of inspiration and as boundaries for certain activities (Padel *et al.*, 2009). Of particular importance for organic agriculture are the four 'Principles of Organic Agriculture' of International Federation of Organic Agriculture Movements (IFOAM, 2005). The process of formulating core Principles of Organic Agriculture was based on expert and stakeholder consultation, resulting in the Principles of Health, Ecology, Fairness, and Care, democratically accepted by IFOAM's members in 2005. The process aimed to bridge the values from the pioneers of organic agriculture to the present time of globalization and to extended growth of the organic sector. As a result the principles are now considered worldwide as the basis from which organic

agriculture grows and develops. According to Luttikholt (2007), the four principles offer a perspective on how to deal with the challenges of globalization. A response to these challenges seems to be to extend and further detail the standards so that, for instance, externalities can be included. An ideal situation would be in which a balance between the principles and standards can be realized.

However, the previously cited literature reveals a considerable gap between objectives and practices in organic agriculture, particularly in organic livestock production. This gap is discussed below in the Section Principle of Health in relation to the four Principles of Organic Agriculture, providing some examples of inconsistencies without any claim to comprehensiveness.

Principle of Health

> Organic Agriculture should sustain and enhance the health of soil, plant, animal and human as one and indivisible.
>
> –IFOAM, 2005

Although maintaining and enhancing animal health and welfare of an individual animal and of the herd is stated to be an important goal in organic farming (Verhoog *et al.*, 2004), the organic farmers are still far from providing an outstanding health status in comparison with conventional farming. The formulation of a common principle of health, including animal health, has not been done in the past and cannot be expected to change the situation in the future. It could be even argued that such a principle prevents facing the obvious and the reality. Obstacles to reduce the gap are certainly manifold and are expected to vary considerably from farm to farm. As explained above, minimum standards fail to provide an appropriate tool to improve animal health status on the farm level. Thus, the main question is unavoidable, that is, who is to blame in the first place for the current unsatisfactory situation: the individual organic farmers, the standards, the organic associations, the market situations, the consumers, the animal scientists, or the politicians?

Some of the various discrepancies between claim and reality with respect to the handling of the animal health issue in organic and conventional livestock production and some of the conflicting areas provoked therewith have been previously addressed by Sundrum *et al.* (2011). According to his analysis, all stakeholders are involved in the current unsatisfying health status on organic farms and are more or less responsible. Producers and retailers claim to offer products that derive from healthy animals without providing transparency and evidence of the animal health status of farm animals. Retailers want to increase the turnover by offering organic food with comparably low prices at the expense of the possibilities of the farmers to investigate in substantial improvements of animal health. Producers who strive for a high status of animal health by using appropriate management concepts and encountering higher production costs are confronted with unfair competition when competing with their products on the same market as those who produce on a low-cost and low-quality base. A high percentage of consumers announce their special interest in the issue of animal health and their willingness to pay premium prices but hesitate to do so when corresponding food is offered and instead prefer purchasing cheaper food. Many consumers prefer to delegate responsibility for ethical issues when choosing animal products to the retailer or the government and are by their ignorance jointly responsible for the severe deficits in animal health within livestock production.

Owing to the complexity of the interactions of various factors on different scales, evidence cannot refer to some input variables, for example, minimum standards. The farm-specific animal health status is the result of the steering process of the farm management and hence the emergent property of the farm system. Correspondingly, to improve the animal health status, the farm management has to focus on the outcome of the production process. Appropriate reference points for an output orientation are, for instance, the prevalence rates of production diseases on the individual farm. Within a label program such as organic, quality assurance, and control programs for products labeled as deriving from healthy herds should rely on fixed levels regarding an acceptable prevalence rate of diseases.

Despite decades of research and an enormous increase in knowledge, the prevalence and incidence rates of production diseases remain high, independent of the production method (LeBlanc, 2013). The reasonable assumption that the situation might have been worse without the elaborated knowledge in animal science is not convincing. In fact, it is not known very much about the impacts of animal science on the status of animal health. It could also be argued that the problems are induced to some degree by specific disciplines of animal science whereas other disciplines fail to provide appropriate tools and knowledge to compensate for suboptimal living conditions in practice and for growing demands on the regulatory capacities of farm animals in connection with increasing performance levels.

The fact that there is an increasing gap between the availability of specific knowledge and a target-aimed implementation of knowledge into practice should no longer be masked. It can be partly explained economically by higher preventive costs in relation to failure costs in many farm situations (Hogeveen, 2012). However, the gap is also due to the fact that the implementation of measures often fails to be effective because the effectiveness depends to a high degree on the specific farm context, which is often not or only partly considered in research work. Farmers are often left alone in their need to decide which measures are likely to be effective and efficient in their specific farm situation.

In addition, the standards themselves are inconsistent and provoke conflicting aims. For instance, although diseased animals should be treated immediately when showing clinical signs to prevent suffering, the use of antibiotics and chemically synthesized remedies is restricted (in Europe) or totally banned (in the United States). The farmer is at risk to lose the premium for organic products when treating animals with chemically synthesized remedies, which they may try to avoid. Correspondingly, farmers often decide, not to treat diseased animals at all or shift to phytotherapeutic and homeopathic remedies. These remedies, however, often lack an effective therapeutic effect for the diseases and the condition for which the treatment is intended. For the certification bodies it is nearly impossible to verify that animals should have been

treated appropriately as long as the incidence and prevalence rates of production diseases are not a control point for the certification bodies. Thus, the high incidence and prevalence rates of production diseases in organic livestock production are not only the result of suboptimal living conditions and farm management but also the consequences of inappropriate and unsuccessful treatments.

Principle of Ecology

> Organic Agriculture should be based on living ecological systems and cycles, work with them, emulate them and help sustain them.
> –IFOAM, 2005

Ecosystems are defined as a community of living organisms (plants, animals, and microbes) in conjunction with the abiotic components of their environment, interacting as a system (Chapin *et al.*, 2002). Biotic and abiotic components are linked together through nutrient cycles and energy flows.

Producers (plants), primary (herbivores) and secondary (carnivores) consumers, and decomposers and detrivores are a maintaining part of dynamic equilibrium in the matter and energy cycle. The sustainability of matter and energy cycles in the ecosystems is based on self-regulatory processes. It is often emphasized by proponents of organic agriculture that organic farm systems should enhance production processes in nearly closed nutrient cycles while stimulating and enhancing self-regulatory processes. These considerations neglect that ecosystems in general produce a comparably low biomass and are not compatible with the goal to produce high amounts of biomass that is exported from the systems, this being the case in farm practice in terms of products.

In farm systems at least the nutrients that are lost due to the purchased products or due to emissions and the conversion losses have to be substituted by external sources. To minimize the need for nutrient inputs, the farm manager has to gain detailed knowledge on the input and output variables. According to Liebig's Law of the Minimum, valid for both plant and livestock production, growth processes are controlled not by the total amount of resources available but by the scarcest resource. When striving for an enhanced productivity in organic farming, the farmer should be aware of those first limiting factors to be able to substitute where necessary in order to increase the efficiency in the resources. Correspondingly, organic farms are not equivalent to a self-regulatory ecosystem. As an agroecosystem, organic farms require a stewardship, able to steer the nutrient flow through the various subsystems of the farm system and to deal among others with the restricted availability of resources (nutrients, labor, and investments).

Farm animals react very sensitively to a restricted availability of limiting nutrient factors. A suboptimal nutrient supply is often the cause, not only of metabolic disorders but also of infectious diseases deriving from a suppressed immune competence due to an imbalanced nutrient supply. To close the nutrient cycle of an organic farm in terms of minimizing the nutrient input should not be a goal in itself as it can contradict with the principle of animal health, which requires a balanced nutrient supply and a farm management that is capable of providing this in an appropriate manner for all farm animals in their various stages of life. On-farm assessments show that many farmers are not able to correspond to this demand (Sundrum *et al.*, 2008). In dairy production, farmers are challenged and have difficulties to provide an appropriate energy supply due to a lack in the availability of energy-rich forage, such as maize silage and fodder beets, as well as restrictions in the use of concentrate.

In the case of monogastric animals, the first limitation in exploiting the genetic potential of monogastric animals in organic farming is the supply of limited amino acids (Sundrum *et al.*, 2006; Høøk Presto *et al.*, 2007). As soybean meal from conventional processing and synthetic amino acids are banned as feed ingredients, grain legumes represent the main protein source. These are characterized by comparably low concentrations of limited amino acids. The preferred use of homegrown versus bought-in feedstuffs can cause a high variation in the nutrient content of feeding rations and this has consequences for the growth processes within the different stages of life, for the performance level, and the occurrence of imbalances and metabolic disturbances. Restrictions in the availability of ingredients do not necessarily give rise to specific nutrient deficiencies, provided that careful ingredient control, ration formulation, and mixing of feed are carried out.

A recent study on the level of nutrient efficiency in comparison between organic and conventional dairy cows revealed that the overall farm efficiency of N use (animal product N per N input) did not differ significantly between conventional and organic farms, neither in relation to the total farm nor with respect to defined subsystems but showed a large variability between farms (Sundrum and Suender, 2012). The results provided farm-specific pictures, indicating adjusting screws that suggest the most effective and efficient measures on how to increase N efficiency. Differences between farms and subsystems indicated considerable potentials for improvements without adverse effects on production. Thus, striving for nutrient efficiency provides options to balance ecological and economic goals. However, improvements cannot be expected by following general objectives or recommendations but require farm-specific assessments and regulation processes based on the availability of comprehensive data.

Principle of Fairness

> Organic Agriculture should build on relationships that ensure fairness with regard to the common environment and life opportunities.
> –IFOAM, 2005

Positive cost–benefit calculations of recommended measures are essential to convince the farmer into action. Neither the formulation of principles nor profound knowledge alone can be expected to provide progress and improvements if farmers do not gain any benefit and profit from the market to compensate for the additional efforts and resources needed to improve the farm management aiming at product and process qualities. Currently, producers are very much at the mercy of retailers and supermarkets in terms of price paid, for example, per liter of milk or kilogram of carcass meat. In the past, retailers had continuously tried to drop the prices to producers,

therewith widely ignoring the impacts on producers and farm animals. As a consequence, dairy farmers have been chronically underpaid in recent years and left alone by the market, which does not offer any monetary incentives to substantially improve traits of product and process qualities on the farms. Thus, the market fails in improving traits of product and process quality.

Although the labeling of organic products by regulations was introduced to prevent misuse and unfair competition, the current market conditions widely ignore the large variability in the quality traits and in the impacts on common goods, promoting unfair competition when enabling equal prices for very different performances in relation to product and process qualities. Farmers who gain economic benefits by selling products while providing only a low-quality level undermine any efforts of other farmers attempting to improve quality traits (Sundrum, 2007a). Producers who strive for product and process qualities by making use of appropriate management concepts and encountering higher production costs due to increased efforts and resources to be used are confronted with competitive disadvantage and unfair competition when competing with their products on the same markets and with the same prices as those who produce on a low-cost and low-quality base, while hazarding the consequences. Consequently, for example, dairy cows pay the gap between a continuous increase in productivity and milk yield and the restricted availability of various resources by the farm management among others with an increase in the prevalence rates of production diseases and with a decrease in longevity (Knaus, 2009).

Despite the fact that many consumers express their wishes for high milk or meat quality, the payment and marketing systems counteract all efforts to follow consumer demands and to enable a product offer with differentiated eating quality. It is concluded that only a direct assessment of qualitative traits and a payment systems that honors quality grades beyond average can contribute to improve the currently unsatisfactory situation. Without evidence-based progress and a system of financial penalties and bonus payments to promote top quality, organic livestock production faces the risk of losing consumers' confidence while being trapped between own demands, consumer expectations, and limited resources (Sundrum, 2008).

Principle of Care

> Organic Agriculture should be managed in a precautionary and responsible manner to protect the health and wellbeing of current and future generations and the environment.
>
> –IFOAM, 2005

Although organic agriculture and organic livestock production strives for self-sufficiency, at least for a low input farming, it makes considerably less use of external nonrenewable resources and in general can be expected to have less negative impacts on the environment. Therefore, it can be assumed as being more sustainable than comparable intensified conventional farm systems. However, the principle of care in its current description seems to be overambitious. It is not convincing to express some kind of responsibility for future human generations while in the current farm practices many organic farmers are not able to protect the health and wellbeing of the farm animals for which they are directly responsible. The high prevalence and incidence rates of production diseases in organic livestock farming indicate that farmers often fail to care and deal with the farm animals appropriately. Production diseases are multivariate responses to a complex set of interrelated causal factors and are often due to mistakes of the farmer, inadequate handling, and inappropriate housing conditions (Enevoldsen and Gröhn, 1996). In different studies, organic dairy producers were more likely to use less outside support from experts and advice from veterinarians for recommendations of treatment than conventional producers and were more likely to rely on advice from other farmers (Zwald *et al.*, 2004; Richert *et al.*, 2013b).

Furthermore, it is not in correspondence with a principle of care to sell organic products that derive from diseased farm animals. For instance, a high level of SCC in milk indicates that cows suffer from a clinical or subclinical mastitis. The threshold differentiating infected and noninfected mammary glands was found to be greater than 200,000 cells/ml on the animal level by the IDF (1999), whereas the majority of organic dairy farms exceed this threshold in the milk of the bulk tank containing a mixture of all lactating cows on the farm. Although milk with a high somatic cell count is not a direct issue of food safety, due to the fact that milk has to be pasteurized by which the pathogens are killed, the high SCC above the threshold found in milk from organic and conventional cows cannot pass through as an expression of care neither toward dairy cows nor toward consumers.

Conclusions

Although the options to execute species-specific behavior pattern are clearly improved for organic farm animals, the enhanced level of minimum standards in organic livestock production failed to entail a clearly improved animal health status and a higher product quality in comparison with conventional production. The reasons for these unsatisfying findings are manifold as are the influencing factors within and between individual farms. The large heterogeneity between organic farms in their structures, local conditions, availabilities of resources, living conditions for the farm animals, and last but not least skills of the farm management corresponds with the heterogeneity of the outcomes of the production processes in terms of product and process qualities.

A further enhancement of minimum standards cannot be expected to improve the situation due to the general inappropriateness of this approach in livestock production. In the current situation, organic agriculture is far from providing the best solutions for different regional, national, or global challenges. However, without the fact that organic livestock production was able so far to establish itself as an economically viable production method – although being only a niche production – and without being recognized by an increasing number of consumers and retailers, and hence by politicians and also finally by traditional agricultural scientists, the option to overlook the agricultural scenery and the ongoing developments from a different perspective would still be

missed, identifying possible benefits and progress but also being aware of constraints.

Not only organic but also conventional livestock farming fails to improve animal health status and traits of product quality. Both production methods should learn from the field experiment of organic farming – from their success in various fields as well as from their failures in achieving certain aims – and should try not to repeat misguiding tracks. However, when recognizing the current attempts of conventional farming to restore its spoilt image by initiatives with specific label programs based on minimum standards, there is little hope that this will happen in due time.

Retrospectively, it can be argued that it was a failure from the beginning of labeling organic products to make the production method an identifying criterion for labeling organic food. What might more or less work for organic plant products does not work for livestock production. Although organic agriculture has been developed and still is dominated by specialists with a focus on plant cultivation, the specific requirements of farm animals were not considered when the course of organic agriculture was set in the middle of the last century. It has proven to be a fundamental false estimation when transferring suppositions with respect to plants being primary producers within an agroecosystem to farm animals as primary consumers of plant biomass. Self-regulating processes within farm animals are far more complex than those in plants while at the same time huge differences exist between individual animals and their specific demands, requiring the necessity for the farm management to regulate the living conditions and provide a nutrient supply according to the individual requirements and needs of farm animals.

Although minimum standards do not have a resounding success on animal health status and the level of product quality, the situation is complicated by the fact that farmers face a severe limited availability of resources, such as high quality feed, labor time, or investments within the farm system and simultaneously a high pressure on the production costs. Not only conventional but also organic livestock production is characterized by a buyer's market where the retailers are pressing the producers for the lowest purchase price, therewith widely ignoring the internal and external effects of this strategy. Because the prices for conventional products are already on a low level, premiums for organic products are often not sufficient to cover the additional production costs so that organic farmers are liable to be trapped between aroused consumer expectations and limited resources.

Currently, organic agriculture cannot claim to promote a sustainable development, neither for the farm animals and organic farmers nor for the production method of organic agriculture. Lack of success in criteria of animal health and product quality being very important for the buying decisions of consumers calls for drastic changes and not only for slight modifications if the credibility of organic agriculture should be prevented from further erosions, depriving the production method of their commercial basis.

An essential precondition to improve the current situation is marketing conditions that honor the production of products with a high level of product and process quality instead of focusing alone on quantitative traits and low prices. Appropriate prices and monetary incentives for a qualitative production are the starting conditions for farmers to provide appropriate living conditions, intensive care, and adequate treatments so that diseased animals would occur as exceptions and not as the rule as it is nowadays. Only appropriate living conditions enable the farm animals to adapt and cope with their environment and ongoing changes and to keep themselves healthy.

The previous approach of minimum standards is doomed to fail, among others, because it provides a large variation of the outcome in terms of traits of product and process quality; it provokes unfair competition and therewith torpedoes any efforts to invest monetary and labor resources into improvements while allowing retailers to play their game in playing off the producers against one another.

In urgent need of more transparency, it is concluded that only a shift in the paradigm from a standard- and input-oriented to an output-oriented production process is able to overcome the inconsistencies regarding the current organic principles and the main constraints in organic livestock production. Verifiable information about the level of product and process qualities emerging from the production process within each farm system has to be provided by the producers. Simultaneously, a high level of product and process quality has to be honored by premium prices to cover the additional costs and efforts that are needed to improve quality production. The output-oriented approach has to be accompanied and supported by a systemic approach. It is beyond the scope of this article to explain this approach comprehensively. The potentials of this approach for livestock production are introduced elsewhere (Sundrum, 2007b; 2010; 2012b).

Although neoclassical economists and the majority of agricultural scientists pretend to have confidence in the ability of markets to drive technological and behavioral changes that will enable the capacity of the economy–environment system to satisfy the increasing needs, ecological scientists tend to believe that solving problems in relation to restrictions in the availability of resources cannot be left to technological developments and economic growth alone but will require different kinds of regulations in a top–down as well as a bottom–up approach.

See also: Animal Health: Global Antibiotic Issues. Animal Health: Mycotoxins. Animal Welfare: Stress, Global Issues, and Perspectives. Consumer-Oriented New Product Development. Detection and Causes of Bovine Mastitis with Emphasis on *Staphylococcus aureus*. Ecoagriculture: Integrated Landscape Management for People, Food, and Nature. Farm Management. Food Labeling. Food Marketing. Markets and Prices. Organic Agricultural Production: Plants. Production Economics

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Relevant Website

http://www.impro-dairy.eu
IMPRO.

P

Pathogen-Tested Planting Material

RR Martin, USDA-ARS, Corvallis, OR, USA
IE Tzanetakis, University of Arkansas, Fayetteville, AR, USA

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Glossary

Buffer zone An area surrounding or adjacent to an area for production of plants in a certification scheme designed to minimize the probability of spread of the target pathogens, pollen, or seed into or out of the block, to meet phytosanitary or other control measures as defined in a certification standard.

Certification standard Comprehensive process established and authorized by a regulatory entity for the production of plants free of regulated pathogens, with predefined trueness-to-type or genetic purity. These regulations also define plant production, plant identification and labeling, and quality assurance requirements.

Generation or G-level It indicates the relationship of plants in a certification scheme to the original pathogen-tested plant material at the top of the scheme. Regulations developed by certifying agencies specify the conditions under which each Generation (G) level must be maintained in order to meet the standard.

Heat therapy A method used to eliminate viruses in which plants are grown at 37–40 °C for 4–6 weeks. After this meristem tips (0.3–1.0 mm) are removed and used to regenerate plants. This results in the production of plants that are often free of targeted pathogens. Once grown in tissue culture, rooted and planted in soil, the plants are retested for the targeted pathogens to determine their health status.

Index Procedure to determine whether a given plant is infected by a targeted pathogen. It involves the transfer of a bud, scion, sap, etc. from one plant to one or more indicator plants sensitive to the virus.

International Standard for Phytosanitary Measures It is an international standard adopted by the Conference of the Food & Agriculture Organization(FAO) of the United Nations, the Interim Commission on Phytosanitary Measures, or the Commission on Phytosanitary Measures, established under the International Plant Protection Convention.

Meristem-tip (tissue) culture A pathogen-elimination technique whereby tissue pieces (cells) are separated from an organism and cultured in a sterile growth media apart from that organism. One of the preferred pathogen-elimination methods for plants is 'microshoot tip culture,' which is effective for eliminating most viral, bacterial, and fungal contaminants. In this technique a meristem tip of less than 0.3–1.0 mm is extracted from the shoot and placed in sterile tissue culture growth media; the meristem then grows to a complete plant.

Phytosanitary measure Any legislation, regulation, or official procedure with the purpose to prevent the introduction or spread of pests or diseases.

Quarantine Official confinement of regulated articles for observation and research or for further inspection, testing, and treatment.

Vegetative propagation Plants are reproduced using the following methods: cuttings, layering, division, grafting, budding, and tissue culture.

Introduction

Large-scale production and globalization of agriculture has resulted in a narrow germplasm base for all major food crops being grown over vast areas, which increases the risk of epidemics that could impact food security on a broad scale (Strange and Scott, 2005). In addition, the majority of the production of these crops is in areas far from their centers of origin and subjected to many plant pathogens that they did not coevolve with. Cassava is an excellent example of this, as its center of origin is in South America, but African cassava mosaic virus, which causes a devastating disease in Africa, is not present in South America (Fauquet and Fargette, 1990; Thresh *et al.*, 1998). Most of the production of these crops is isolated from new strains of pathogens as they evolve at centers of origin and are at risk of severe disease outbreaks should new strains of a pathogen be distributed with planting material. This is also true for most of the fruit, vegetable, and

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ornamental species that are grown commercially. Concomitant with the globalization of crop plants is an increased risk of globalization of plant pathogens that can lead to serious epidemics. The classic example of such movement of a pathogen is *Phytophthora infestans*, the causal agent of potato late blight in the mid-nineteenth century, where its impact on human suffering and migration is well documented (Schumann, 1991). Yet, 150 years later, new strains of this pathogen have emerged and continue to cause serious plant disease problems (Vleeshouwers *et al.*, 2011). There are examples of outbreaks of all types of pathogens (fungi, bacteria, nematodes, and viruses) that have resulted from movement of plant pathogens with the movement of plant propagation material.

To protect agricultural production from introduced pathogens, two types of phytosanitary systems have been employed. Plant quarantine is generally used at the national level to restrict introduction of plant pathogens that are not present in a country or have limited distribution and active programs to eradicate or delimit the pathogen. There are also domestic quarantines that restrict the movement of plant material within a country to address pests and pathogens that have limited distribution or may have been deregulated as a federal quarantine pest. Plum pox virus (PPV), Golden nematode, Light brown apple moth, *Ralstonia solanacearum* race 3 biovar 2, and *Phytophthora ramorum* are examples of quarantine pathogens and pests in the United States. Certification programs are national, state, or provincial programs used to produce planting materials, vegetative or seed, that are free of or have less than some predetermined threshold of various pathogens (Waterworth, 1998). These programs primarily target domestic pathogens for plants at the G1–G4 (**Figure 1**) level of certification programs. These programs aim to ensure that the planted crop has a pathogen(s) level low enough to minimize the risk of severe crop loss, increasing the chance of harvesting an acceptable crop. The pathogen tolerances allowed in certified plants depends on the pathogen, crop, and agroecosystem where the crop is grown. The primary goal of quarantine and certification programs is to facilitate movement of plants without increasing trade of plant pathogens. The objective of all plant certification programs is to provide a supply of healthy plants, which is accomplished through adherence to Best Management Practices (BMPs) that are science based together with a defined level of testing to monitor the effectiveness of the program. The application of BMPs to the production system combined with audit testing has proven to be a very useful means of producing plants of high health status. Certification programs should be reevaluated periodically to take into account new pathogens or vectors that have been reported in the region, or other changes that affect the pathogen, vector, host, or environment that may impact the integrity of a certification scheme.

BMPs require that a Hazard Analysis and Critical Control Points evaluation of the entire certification system be completed. This process is used to: (1) identify weak points and greatest risk factors to the system in terms of introduction of pathogens or pests, and (2) establish inspection, testing and mitigation procedures, and record-keeping requirements (Parke and Grünwald, 2012). Once the weak points are identified, management practices are designed to prevent intrusion of pests and pathogens. Mesh size on a screenhouse might be adjusted to account for the primary virus vectors in the region to protect a G1 block. For example, if pathogens in a region are vectored by aphids the screen size might be larger than in another region with pathogens vectored by thrips. Vector management in field blocks of certified plants will be adjusted based on the vectors and pathogens present in the region. Knowledge of the phenology of vectors is also important, because times of peak vector movement present the greatest risk of pathogen intrusion into the system; thus, vector control measures may well change during the year to take into account the risk of vector migration into a nursery. Knowing which of the targeted pathogens are most prevalent in a region and how they are vectored are important considerations when developing BMPs for a nursery (Martin and Tzanetakis, 2013).

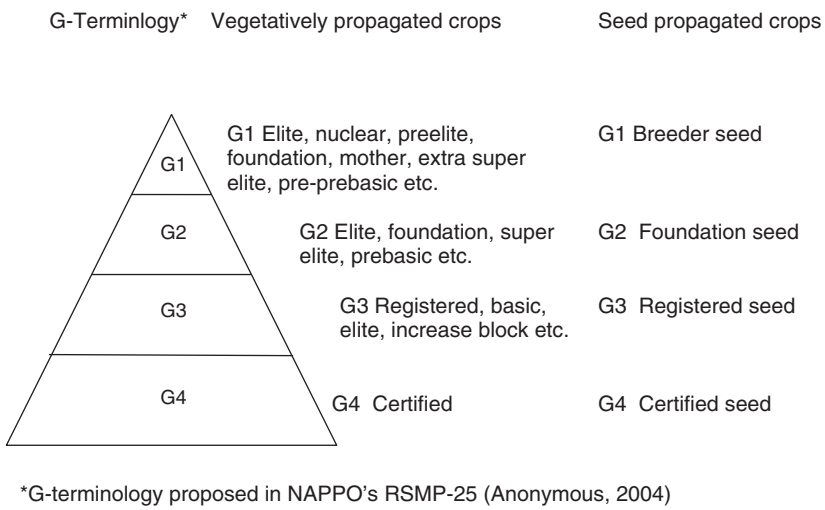


Figure 1 Simplicity of the G-terminology and the concept of G-levels for identifying the stages of plant propagation in certification programs for phytosanitary purposes.

Quarantine

In addition to certification programs that are designed for mass production of planting materials of high health status for plant, food, and fiber production, there are extensive quarantine programs that have been developed in many countries to reduce the risk of introduction of exotic pests. Though not the focus of this article, quarantine goes hand-in-hand with certification to provide an integrated system to protect agriculture and environment from plant pests and pathogens, thus its relation to certification will be touched on briefly. The rationale for a brief overview of quarantine is that many certification programs focus on domestic or endemic pathogens, with the assumption that quarantine pathogens are detected and eliminated at the stage where plants enter the country and need not be included in the domestic certification program. Quarantine programs are operated primarily at the national level and deal with pathogens that are not known to occur in the country or are present at a very restricted level and have active programs targeted to eradicate or prevent further spread of the pest or pathogen (Foster and Hadidi, 1998; Reed and Foster, 2011; Anonymous, 2006). As examples, plant material of berry crops, citrus, grape, potato, sweet potato, pome, and stone fruit, etc. coming into the United States under quarantine are tested for exotic pathogens before they are released for propagation, but they could be released if found to be infected only with viruses already endemic in the country. In some cases plants may be held in quarantine for 3–4 years while graft indexing on indicators is carried out.

To be effective, quarantine programs are dependent on the public understanding the risks associated with introducing exotic pathogens into natural and agricultural ecosystems. Public in this sense includes anyone who may wish to transport plant material from a foreign country to their homeland, including hobbyist interested in a new ornamental or food crop to add to their garden or plant collection, plant breeders interested in new potential germplasm, plant pathologists interested in adding to their pathogen collection for scientific study, germplasm curators attempting to broaden the diversity of their collections, or growers interested in getting a head start on a new cultivar developed in a foreign country. Also, an effective quarantine program needs to have an effective and efficient mechanism to introduce plant material into the country. This combination of an educated public that understands the risks of introducing foreign pathogens and pests, together with an efficient system to bring plant material through approved quarantine and testing facilities will reduce the temptation by individuals to do 'suitcase' imports that could threaten local environments and agriculture. The introduction of PPV into Pennsylvania highlights the benefits of quarantine systems to exclude exotic pathogens. Plum pox is a devastating disease first identified in the early 1900s in Bulgaria that has since spread through much of Europe and the Mediterranean countries, where it is the most serious disease of stone fruits. It was detected for the first time in the Western Hemisphere in Chile in 1994 (Herrera *et al.*, 1998) and is now considered to be widespread there and has since been detected in Argentina. PPV was detected in a localized area of Pennsylvania in the United States in 1998 (Levy *et al.*, 2000) and an eradication program was implemented immediately. After 14 years, the eradication effort was deemed successful, but the cost was in excess of $55 million US dollars to eliminate the pathogen from a relatively small geographic area (Welliver, 2012). Thus, quarantine programs can be an effective and economical way to reduce international movement of plant pathogens and pests to protect local agriculture and native flora.

The International Plant Protection Convention (IPPC) is an international agreement on plant health to which 181 countries are signatories. The Secretariat of the IPPC is provided by the Food and Agricultural Organization of the United Nations. The IPPC has the mission to protect cultivated and wild plants by preventing the introduction and spread of pests and pathogens. They develop standards (International Standards for Phytosanitary Measures (ISPMs)) that are recognized by participating countries and provide for science-based standards for the safe movement of plants and plant products. As an example, ISMP No. 28 (Anonymous, 2007b) provides recognized standard treatments to eliminate plant pathogens and pests, including fumigation, cold treatment, heat treatment, and irradiation; and ISMP No. 31 (Anonymous, 2008) provides agreed on sampling levels that participating countries use when shipping plants or plant products internationally to protect against movement of quarantine pests and pathogens. The IPPC develops standards for range of issues related to plant protection. Once the standards are approved by the IPPC member countries, they become an ISMP.

Certification

Certification programs have been developed for many vegetatively propagated food crops over the past 50 years (Hadidi *et al.*, 1998; Hadidi *et al.*, 2011). The first certification programs were developed in The Netherlands and Germany in the early 1900s for potato production when they realized that leaf crinkling, rolling, and mosaics were transmitted through the tubers to the next generation and that by selecting the most vigorous and healthy-looking plants for propagation, tuber production was improved greatly. They developed a program for plant inspection and production, which was adopted in the United States and other countries long before it was known that many of the diseases were caused by viruses. In the United States and Canada the first seed potato production programs were established in 1913 (Slack and Singh, 1998). Visual inspections still play a major part in seed potato certification programs with inspections carried out early and midlate in the growing season to observe foliar symptoms, at harvest for observing tubers symptoms, and a postharvest inspection of plants grown from tubers to look for late-season infections (Frost *et al.*, 2013). Visual inspections are part of all plant certification programs. Trained inspectors also watch for other problems, such as herbicide damage, cultivar mixtures or trueness-to-type issues, physiological disorders, etc. During visual inspections, thousands of plants can be observed in a relatively short time. In most programs there is also laboratory testing that is carried out on each tuber or 'seed' lot to identify viruses that may be present and to monitor for symptomless pathogens. As laboratory-based diagnostics are improved in terms of sensitivity, specificity, and costs, more programs are

incorporating their use to improve the quality of the program. Certification programs have been developed for a wide range of crops (Hadidi *et al.*, 1998). Testing methods including mechanical transmission to herbaceous hosts, immunological and molecular techniques (Enzyme-linked immunocapture assay (ELISA), Polymerase chain reaction (PCR), etc.), isolation of fungi or bacteria, etc. that are used for detection of various pathogens are similar in all programs. With woody crops there is often the need to do graft transmission onto indicator plants to test for uncharacterized graft-transmissible agents (Converse, 1987; Hadidi *et al.*, 2011).

There are many definitions for certification programs. North American Plant Protection Organization (NAPPO) defines a certification program as: "A domestic program consisting of maintenance, multiplication, distribution, and production of plant materials intended for release either domestically or for export, under an officially sponsored certificate attesting to the status of the material" (Lanterman *et al.*, 1996). Many certification programs are based on a published standard that defines site selection and preparation, isolation distances from plants of the same species and other vegetation, number of inspections, record keeping on plant traceability so that tracebacks or traceforwards can be done if a problem should arise, a pest and disease management plan, records of all pest management activities, the conditions and protocols to be followed during plant or seed production, and types and amount of testing that needs to be done at each level in the propagation cycle. The selection of plant material that is true-to-type is an essential first step. The selected plant(s) is then subjected to pathogen testing using a range of laboratory and biological indexing. If infected with any of the targeted pathogens listed in the standard, the plants are subjected to 'cleanup.' After 'cleanup' the plants are retested to ensure the pathogen(s) have been eliminated. Once determined to be free of targeted pathogens and true-to-type, this plant can be designated as a G1 (**Figure 1**) plant that enters into the certification program. In many cases these plants are maintained in protected culture (screenhouse) and become the source plants that are propagated in certification programs.

There is an effort in the United States to develop audit-based certification programs that rely on BMPs outlined in the Certification Standard (Thompson, 2011). An audit-based program relies on compliance monitoring and requires a reasonable level of trust between the regulatory agency (inspectors) and nursery managers for the certification systems to function. The audit or inspection assesses the degree of compliance of the nursery to the certification standard, so that plants can be certified to meet that standard. An auditor or inspector designated by the certifying agency is responsible for the audit process. All records of the nursery can be reviewed by the auditor (Thompson, 2011). With such a system in place, record keeping by the nursery becomes even more critical as the inspector's decision will be based on the records reviewed, visual inspection of the nursery, and some limited testing. The goal is to have a systems approach that uses science BMPs for nursery production of plant materials (Parke and Grünwald, 2012).

The use of pathogen-tested planting material is the first and arguably the most important step for the control of many systemic plant pathogens. Most effort in this area has focused on viruses, viroids, systemic bacteria, and phytoplasmas because there are no postinfection treatments that can be used in plant or food production systems to rid plants of these pathogens. Many important systemic pathogens are not transmitted through the seed or transmitted to less than 100% of the seedlings, or transmitted as seed coat contaminants that can be controlled with various seed treatment methods (Ling, 2010; Liu *et al.*, 2014). In this case, seedlings free of the targeted pathogen(s) can be identified and then grown in isolation to produce seed free of these pathogens or with an incidence below some predetermined threshold. With seed coat contaminants the seed can be treated to inactivate pathogens on the seed surface (Ling, 2010). In the case of vegetatively propagated crops it is often necessary to eliminate a specific pathogen, usually through thermal-, cryo-, or chemotherapy combined with meristem-tip culture to produce plants free of the targeted pathogens (Mink *et al.*, 1998; Laimer and Barba, 2011). The plants regenerated from such meristems are then thoroughly tested, and a single plant free of pathogens of interest is the starting point for massive vegetative propagation. In the case of seed or vegetatively propagated plants, the plants are propagated under a defined set of conditions described in a certification standard.

Certification standards often have tolerance levels of some small percentage of infection, defined requirements for the site where the crop (seed or vegetative) is grown, required field inspection(s) during the production cycle that include cleanliness in terms of weeds, other crops that may serve as contaminants in seed lots or as hosts for targeted pathogens and freedom from pathogen vectors. Tolerances for pathogens depend on the rate of pathogen spread for annual crops, but tolerances are much lower for perennial crops. Crops that are only grown for a single year or a few years in production fields, such as most seed crops and potatoes, strawberries, sweet potatoes etc., may have higher tolerances than most of the fruit and nut crops, such as citrus, tree fruits, grapevines, or berries, which are expected to be productive for many years or decades in the same field. To set tolerances for various pathogens requires sampling and testing, and a major concern is how many samples to test. The number of samples that need to be tested per lot to achieve a confidence level (i.e., 95% or 99%) that a pathogen is not present is outlined in ISPM No. 31 (Anonymous, 2008). In some countries, certification schemes are managed at the national level and in others at the state or provincial level.

Vegetatively Propagated Crops

Plant pathogens are recognized as major constraints to agriculture production worldwide. Most fruit and nut crops; major food crops such as potato, cassava, sweet potatoes; and many ornamentals are vegetatively propagated, using cuttings, tubers, or rhizomes. More recently, tissue culture propagation has become a major component of mass propagation for many of these crops. Elaborate protocols are used to eliminate targeted pathogens from one or a few infected plants to provide a source of plant material free of these pathogens (Mink *et al.*, 1998; Laimer and Barba, 2011). Plants entering a certification program are often advanced selections, cultivars, or varieties

developed in breeding programs. In some cases breeders work closely with the cleanup programs and get plants into the testing and cleanup phase before cultivar release, in an effort to have certified plants available at the time of release. Another source of material entering certification programs are 'heritage' cultivars – cultivars that have not been used for many years but are maintained at germplasm repositories. As requests for these cultivars have increased, there is a need to confirm that they meet current certification standards before commercial nurseries are willing to add them to their production systems. In the United States, there is an effort to have new cultivars coming into the country, as well as those developed in-country go through one of the 'clean plant centers' that have been developed over the past 50 years. Increased funding for these programs at the federal level since 2009 has provided for capacity building and the ability to process materials in a more timely manner to meet the needs for food production. These plants are tested for target pathogens before they enter into a G1 block, then a certification program and made available for production. In many cases, the G1 block is maintained by federal, provincial, or state government agencies, or some type of government/private entity, though recently private companies are maintaining their own proprietary G1 germplasm. These plants are tested on a predetermined schedule to monitor for reinfection, in addition, these blocks are retested if a new virus is discovered in the crop that may have been missed with the testing procedures used previously.

Producing G1 Plants

1. Candidate plant (advanced selections, heritage, new, or imported cultivars) arrive at clean plant center, (time = 0, T = 0).
2. Testing program to determine the health status of the plants with respect to targeted pathogens listed in the certification standard, grafting for many fruit and nut crops. This process can take up to three years for crops, such as grapevines or fruit trees, but less time for other crops (T = 0.2–3 years). If no grafting is required this can be completed in several weeks; this is the case for some crops, such as potatoes.
3. If negative for all targeted pathogens, the plant enters the G1 block. If infected, the plants are put through therapy treatment (2–6 months), meristem-tip cultured and whole plants regenerated (3–12 months).
4. These plants are then retested and, if 'clean,' enter the G1 block; but if still positive they go through the therapy again (T = 0.1–3 years). This is repeated until 'clean' plants are obtained. Each cycle of testing can take up to 3–4years for crops like grapevines or fruit trees, 1–2 years for strawberry or *Rubus*. In most cases protocols have been developed such that there is a reasonable likelihood of having 'clean' plants after the initial cycle of therapy. However, if three cycles of cleanup were needed to get plants free of targeted pathogens this can easily require 6–12 years, depending on the crop.

There is a misconception among many growers and researchers that 'tissue culture' propagated is synonymous with virus free. This is not the case. To eliminate viruses it is necessary to regenerate plants from meristematic tip, generally less than 0.5 mm and often in combination with some type of therapy (thermal, cryo, or chemo) before removing meristems (Mink *et al.*, 1998). Some viruses move into the meristematic tissue quite effectively, and a combination of thermal therapy or chemotherapy are required to get meristematic tissue free of the virus (Chen and Sherwood, 1991). In the past these were referred to as 'heat stable' viruses and were 'difficult' to eliminate using thermal therapy and meristem-tip culture, whereas 'heat labile' viruses were much easier to eliminate. One now know that many of the 'heat labile' viruses are phloem-associated viruses, such as luteoviruses and closteroviruses, and the reason they are 'heat labile' is that the phloem tissue is not differentiated in the meristematic dome. Thus, the virus does not move readily into the meristem. This is the case for the Grapevine leafroll-associated viruses, which are in the *Closteroviridae* family. In raspberry, Raspberry leaf mottle and Raspberry leaf spot were considered 'heat labile' as they were relatively easy to eliminate. These two diseases are caused by strains of Raspberry leaf mottle virus, which is a Closterovirus and phloem limited. Raspberry bushy dwarf virus (RBDV) was considered a 'heat stable' virus because it is difficult to eliminate using thermal therapy and meristem-tip culture. RBDV infects most cell types and is not restricted to phloem tissue, thus, it likely moves into the meristematic dome much sooner than phloem-restricted viruses. The ease of obtaining meristems free of a virus in combination with heat therapy is not related to the heat stability of the virus, but rather how rapidly or effectively it can invade the meristematic tissues.

The 'cleanedup' G1 plants are maintained under clearly defined conditions to minimize the risk of reinfection and should be free of all targeted pathogens outlined in the certification standard. In many cases the G1 plants are maintained in protected culture, such as in a screenhouse. The G1 plants are then sold to private nurseries for mass propagation under a set of conditions outlined in a certification program that is managed by a regulatory agency. The goal is to have a systems-based approach that addresses risks of reinfection and pathogen spread during plant propagation.

There are multiple cycles of plant increase for vegetatively propagated crops and unfortunately a wide range of terms have been used to identify each cycle (**Figure 1**). In 2004, the NAPPO (RSMP no. 25; Anonymous, 2004) suggested the use of a simple terminology for the cycles of vegetative propagation. G1 plants are the plants that have tested negative for all targeted pathogens outlined in the certification scheme. G1 plants propagated by tissue culture or by traditional vegetative propagation methods become G2 plants, and multiple cycles of tissue culture can be carried out and still retain G2 status. The use of tissue-culture propagation and the number of propagation cycles allowed in tissue culture should be defined in the certification standard and will vary depending on the crop and certifying agency. G3 plants are derived from G1 or G2 plants. G4 plants are grown as potted plants that are propagated from G1, G2, or G3 plants and grown at another location. Most existing programs use the various terminologies shown in **Figure 1**, but follow this basic scheme of scale up in stages 2–4 to produce plants that are sold to growers.

With the application of tissue culture in some propagation schemes, nurseries are able to sell G2 or G3 plants to growers, which should translate into higher health-status plants being

used by the industry. However, for many crops conventional vegetative propagation is still the primary means of plant multiplication that is used. There are several reasons for this: (1) costs for conventional propagation of crops, such as strawberry, where a 300–500 fold increase can be obtained in field production each year, is relatively inexpensive to produce millions of plants; (2) the agency that regulates the certification program may prohibit or limit the number of cycles of tissue culture as a means of propagation due to concerns about somatic mutations; (3) grafted plants may use a rootstock that is generated from seed, which is inexpensive. In such cases, the rootstock may be seed-propagated and the scions by tissue culture or by conventional vegetative propagation methods. During propagation it is important that care is taken to prevent contamination of tools with viruses that are readily mechanically transmitted. Tools are sterilized during tissue-culture propagation to maintain sterile conditions during transfers of tissue-culture plants. It is also necessary in conventional propagation to prevent spread of viruses during the cutting of tubers, rhizomes, taking cuttings, etc. (Lewandowski *et al.*, 2010). Contamination using cutting tools is much more likely in herbaceous crops, such as potatoes, than in woody crops like grapevines, tree fruits, nut crops, etc.

There are efforts among regional plant protection organizations (RPPOs) to harmonize quarantine standards between the member countries. There are nine RPPOs (Asian and Pacific PPO; Caribbean Plant Protection Commission; Comite de Sanidad Vegetal del Cono Sur; Comunidad Andina; European and Mediterranean PPO (EPPO); InterAfrican Phytosanitary Council; Near East PPO; North American PPO; Organismo Internacional Regional de Sanidad Agropecuaria and Pacific PPO (Roy, 2011)). There are also efforts at harmonizing certification standards across some of the RPPOs, such as for fruit trees and grapevines in NAPPO countries, and the EPPO countries have adopted certification schemes for 20 crops (Roy, 2011; EPPO website). These RPPO-developed standards are often a minimum standard that is required, but member countries can require a more stringent standard internally. Although this is happening at the international level, there are many cases where the harmonization of certification programs within countries has not happened. In countries where these programs are regulated at the province or state level, there are often significant differences between the certification standards. For example, in the United States some states require that the G1 plants for some crops be maintained within protected culture (screenhouse) to minimize vector transmission of pathogens, whereas other states do not require that same level of protection. Also, the type and level of testing required at each level in the certification scheme can vary between states. There is an effort underway to harmonize certification standards for some of the fruit crops across the United States. As these programs are developed, they are looking at certification schemes in other countries and RPPOs with the goal of harmonizing standards on a broader scale if possible.

Seed Propagated Crops

For seed propagated crops, seed is often increased in a country other than where the seed will be planted for food or fiber production. To speed up increase of seed for commercial production many companies grow seed in the northern and southern hemisphere to get two cycles of increase in a single year. As a result, seed is moved between countries on a frequent basis and are potentially exposed to quarantine or certification pests of concern in the country where the final crop is grown. Also, because seed has a long shelf life, it may be moved to several countries before it is planted, or a seed lot may be subdivided and shipped to multiple countries. Many countries have phytosanitary requirements for the movement of seed though requirements for field inspections, sampling, and testing can vary and cause problems if trying to move the seed internationally. The IPPC's ISPM No. 28 provides information on agreed on treatments for a range of regulated plants pathogens and pests (Anonymous, 2007a). The preparation of a phytosanitary certificate is done by the exporting country but must meet the requirements of the importing country.Thus, if a seed lot is being shipped to multiple countries the documentation can become very complicated. IPPC has also developed ISPM No. 12, which covers the reexport of the seed to a third country, where the phytosanitary requirements would have to be met by the original exporting country (Anonymous, 2011). For these reasons, harmonized standards could greatly facilitate seed trade to meet the needs of the increasing globalization of agriculture.

There are a number of agencies for seed testing and accreditation of certification schemes. The testing and accreditation by these agencies are recognized by various countries or groups of countries and provide a mechanism to harmonize seed certification standards for international movement of seed among a group of countries. The Association of Official Seed Analysts, Association of Official Seed Certifying Agencies, International Seed Trade Association (ISTA), National Seed Health System, OECD Seed Schemes (US), Society of Commercial Seed Technologists are all involved in seed testing and are recognized by multiple countries. ISTA testing and accreditation is recognized by more than 70 countries. NAPPO regional standards for phytosanitary measures No. 36 provides information on the movement of seed between countries in North America (Anonymous, 2013).

For seed production, the emphasis is on eliminating pathogens from the elite germplasm that can be transmitted through seed or contaminate the seed surface, including viruses, bacteria, and fungi. In many cases, elite germplasm of seed crops is produced and maintained by private companies. With seed certification, genetic purity is often as great a concern as pathogen contamination. There are multiple levels in certification programs for seed crops, similar to those used for vegetatively propagated crops. The seed crops would clearly fit under the G terminology shown in **Figure 1**, and in this case G would stand for generation in the true sense of the word. The four common levels in seed certification (AOSCA) include: Breeder Seed (seed controlled by the plant breeder, or the institution or company where the breeder works), Foundation Seed (propagated from Breeder Seed under conditions that retain genetic purity, identity, and health status), Registered Seed (propagated from Breeder or Foundation Seed under conditions that maintain genetic purity, identity, and health status), and Certified Seed (progeny of Breeder, Foundation or Registered Seed and grown under conditions that maintain

genetic purity, identity, and health status). In addition to genetic purity, identity, and health status, seed certification also requires information on percentage germination, date of germination test, and percentage contamination with other seed.

For pathogens that are transmitted internally in the seed, it is often possible to grow out seed and identify plants free of the pathogen because this type of transmission is rarely 100% efficient (Liu *et al.*, 2014; Mink, 1993). The exceptions to this are the cryptic viruses, which are seed transmitted at 100%. These viruses are not known to cause disease and are not considered in quarantine or certification programs. Heat treatments for eradication of embryo infection by virus have not been successful without a loss in seed viability (Maury *et al.*, 1998). For seed contaminants, various types of seed treatment have been used to eliminate or reduce pathogen level below set tolerances. Dry heat at 35°C for 24 h, followed by 50°C for 24 h, and finally 75°C for 72 h was very effective at controlling very stable viruses, such as tobamoviruses (Tobacco mosaic virus, Tomato mosaic virus, and Cucumber green mottle mosaic virus, Lee, 2004) and potexviruses (Pepino mosaic virus, Ling, 2010) as well as for a wide range of fungal and bacterial pathogens with little or no effect on seed germination (Lee, 2004). Soaking tomato seed for 30 min in a 1% sodium hypochlorite solution (dilution of commercial bleach, depends on the percentage active ingredient in the bleach product) containing 0.1% Triton-X-100 as a wetting agent completely inactivates potexviruses (Pepino mosaic virus; Ling, 2010) on the seed surface with little or no impact on seed germination. Hydrochloric acid or trisodium phosphate were not as effective as bleach in eliminating virus from seed coats (Ling, 2010).

Impact of Improvements in Pathogen Detection on Certification Programs

With woody plants that involve graft transmission assays for detection of viruses, grafted plants may need to be observed for two or more years for symptoms before the plant is determined to be free of the pathogen. These potentially long intervals for detection using biological indexing has prompted most quarantine facilities to adopt laboratory-based testing where possible (Rowhani *et al.*, 2005; Martin *et al.*, 2012; Martin *et al.*, 2013), including: electron microscopy, ELISA, immunospecific electron microscopy, nucleic-acid-based techniques such as PCR or reverse transcription –PCR (RT-PCR) combined with gel electrophoresis and sequencing of the any amplicons obtained, double-stranded ribonucleic acid (dsRNA) detection; and mechanical transmission to herbaceous hosts (Reed and Foster, 2011; Miller *et al.*, 2009). However, with widely used tests currently available, there is still a need for biological indexing onto woody indicators for some exotic pathogens. For many of the crops there are various laboratory tests available for the major pathogens of concern. Thus, in some cases, once all laboratory tests have been completed and found negative, plants are released to the importer on a provisional basis while the biological indexing is completed. This is done with an agreement that in case the tests are positive, the plant will be destroyed. This process allows the importer to begin multiplication of a new cultivar, which in some cases can reduce the time to get the materials to production fields by 2–3 years. The plants must be maintained and propagated under quarantine-approved conditions until all testing is completed.

The currently used assays for virus detection (ELISA, PCR, and q-PCR) are great for detecting a virus in a large number of samples, such as in surveys or ecological or epidemiology studies. However, for quarantine and certification programs a method that was capable of detecting all viruses in a single test would be ideal, rather than doing individual tests for each virus known to infect the host. In some crops, this means 40–60 tests per plant (berries or grapevines). Recent work with macroarrays has shown great promise for detecting the most common viruses in grapevine, with 38 viruses detected in a single test (Thompson *et al.*, 2014).

Potentially, within the next five years as 'Deep' or 'NexGen' sequencing becomes more widely adapted (Studholme *et al.*, 2011; Kreuze *et al.*, 2009), and universal plant microarrays are perfected (Hammond, 2011) they could replace indexing. This would require extensive validation of these technologies to ensure they are as good or better than current methods. The advantage of these technologies is that they have the potential to provide information on any virus in a plant without any *a priori* knowledge of the virus, in contrast to other laboratory techniques that detect known viruses (Kreuze *et al.*, 2009; Al Rwahnih *et al.*, 2009; Kashif *et al.*, 2012; Thekke-Veetil *et al.*, 2013; Seguin *et al.*, 2014; Hammond, 2011; Esteban *et al.*, 2010). Wang *et al.* (2002) demonstrated the feasibility and utility of the microarray technology to identify and characterize new viruses. They developed microarrays containing oligonucleotides that represented conserved sequences of all fully sequenced human respiratory viruses, which at the time represented a few hundred viruses. Using this array they identified a novel Coronavirus and showed that it caused severe acute respiratory syndrome, a newly emerging disease at the time (Wang *et al.*, 2003). NexGen sequencing has a huge impact on many aspects of biology and is used in virus discovery and is being investigated for virus diagnostics. Sequencing of total nucleic acids in plants has led to the identification of multiple viruses and viroids in single plants (Adams *et al.*, 2009; Al Rwahnih *et al.*, 2009, 2011; Kreuze *et al.*, 2009; Sequin *et al.*, 2014) and offers the potential to certify plants as virus-free rather than virus-tested. Obtaining the 'virome' of a plant provides much information on the range of viruses and their diversity within a single plant. However, work with grapevines has shown that many of the viruses were related to mycoviruses rather than plant viruses (Al Rwahnih *et al.*, 2011; Coetzee *et al.*, 2010). This leads to questions on the significance of these viruses in plant health. The new technology will allow for rapid discovery of many new viruses; unfortunately, characterizing the biological significance of these viruses will take much longer. Mycoviruses in grapevines may actually be modifying endophytes and indirectly impacting the health status of grapevines. Thus, eventually how viruses and other microorganisms impact the whole plant (understanding the microbiome) may be important in certification and quarantine, but we are not there yet. Although it is good to know what is in the plant, this technology is resulting in the identification of many new

viruses for which there is no biological information. For the next decade it is likely that the biological significance will lag behind the discovery of microorganisms in plants, and it is important that for certification and quarantine programs, any changes are made in response to the biology of these organisms rather than their presence. It seems reasonable that new plant viruses related to known plant pathogenic viruses should be considered as the highest priority for evaluating their biological significance and determining if they should be part of quarantine and certification regulations.

Certification standards vary widely among crops and regulatory authorities. The viruses included in a certification program can vary from country to country or state to state. An excellent example is grapevines where certification in Italy includes more viruses than programs in Germany or France; or grapevine certification in Washington State is different from California. Some of these differences are due to environmental considerations, where infection by a pathogen may cause severe disease in one setting, such as crown gall in grapevine in New York State, but be latent or symptomless under different environmental conditions, such as crown gall in grapevine in California. Attempts to harmonize certification schemes across boundaries to facilitate trade of plants without increasing trade in plant pathogens will require certification programs to account for disease expression by pathogens in areas where the certified plants may be sold, rather than only where the nursery stock is produced. In the United States, where certification programs are regulated by individual states, there are efforts underway in multiple crops (blueberry, grapevines, hops, *Rubus*, strawberry, and fruit trees) to develop a single certification standard that all states with programs for that crop would adopt. If successful, this in essence would provide a national program for certification of these crops. As this process is developing, there is an ongoing communication with trading partners to harmonize these standards as much as possible with their certification programs to facilitate international trade.

See also: Climate Change and Plant Disease. Emerging Plant Diseases. International Trade. Quarantine and Biosecurity. Regulatory Conventions and Institutions that Govern Global Agricultural Trade

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Plant Abiotic Stress: Salt

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Glossary

Electrical conductivity (EC) An indicator of the salinity in the water and is directly related to the salt concentration in the water. EC_e is the electrical conductivity of the saturated soil solution and EC_w is the electrical conductivity in the irrigation water.

Exchangeable sodium percentage The percentage of sodium (Na^+) occupying the total cation exchange sites on the soil.

Osmolytes Low molecular weight solutes (sugars, organic acids, amino acids, and other solutes) that are dissolved in solution lowering the osmotic potential of that solution. Organic osmolytes play an important role in osmotic adjustment.

Relative water content (RWC) The water content of a given amount of leaf relative to its fully hydrated or fully turgid state giving an indication the hydration state of the leaf. RWC = (fresh leaf wt. − dry wt.)/(turgid leaf wt. − dry wt.).

Salt overly sensitive (SOS) A coordinated signaling pathway comprised of SOS1, SOS2, and SOS3 transport proteins in the cell that some plants have as a means of maintaining ion homeostasis when exposed to salt stress.

Sodium adsorption ratio (SAR) A measure of the sodicity of the water. $SAR = Na^+/(Ca^{2+}+Mg^{2+})^{1/2}$ when units are in mmol l^{-1}.

Water potential The potential energy of water at any point within the soil–plant–water system. This energy potential is comprised collectively of osmotic, matric, elevation, and pressure components.

Introduction

The vast majority of crops grown in the world are glycophytes, or nonhalophytes. These plants are adversely affected in saline conditions unlike the halophytes, which thrive under these harsh environments. As a consequence, crops endure salt stress, a condition where the plant is unable to express its full genetic potential for growth, development, and reproduction, as the salinity in the soil exceeds critical levels (Läuchli and Epstein, 1990; Grieve *et al.*, 2012). However, there is no sharp distinction between salt stress and lack of stress. Rather, there is a gradual continuum from the absence of stress at low salinity to severe stress at high levels of salinity. In some plants, a beneficial response at low levels of salinity may even be observed (Kronzucker *et al.*, 2013; Shabala and Munns, 2012). Plants, however, vary widely in their tolerance to saline and sodic conditions as well as genotypes within a species even though there is no clear distinction between salt tolerance and salt sensitivity. A salt-stressed plant shows visual (e.g., leaf injury) or quantitative (e.g., reduced growth) signs of being adversely affected. This depends not only on the intensity of the salt stress but also on the chemical composition of the saline substrate and presence of other abiotic and biotic stresses such as temperature, water deficit, flooding, nutritional inadequacies, poor soil physical conditions, pests, and pathogens (Mittler, 2006). Thus, plants under field conditions often endure multiple stresses that show potential interactions, which can be both negative and positive (Läuchli and Grattan, 2007).

This article provides a general overview of plant responses and mechanisms to salinity and sodicity stress and focuses on agronomic crops and how the whole plant integrates these responses and mechanisms. Although this article does not focus much on biochemical and molecular mechanisms of salt tolerance or on genomics-type technologies, such emphasis can be found in a review by Munns and Tester (2008).

Salinity and Sodicity

Before plant response to salt stress can be addressed, it is important to address the chemical and physical edaphology of the saline environment. Soils and irrigation water sources contain mineral salts, but the concentration and composition of the dissolved salts vary from one location to another (Tanji and Wallender, 2012). In solution, these salts dissolve and form positively charged cations and negatively charged anions. The most common cations are calcium (Ca^{2+}), magnesium (Mg^{2+}), and sodium (Na^+), whereas the most abundant anions are chloride (Cl^-), sulfate (SO_4^{2-}), and bicarbonate (HCO_3^-). Potassium (K^+), carbonate (CO_3^{2-}), nitrate (NO_3^-), and trace elements also exist in water supplies and soil solutions but most often concentrations of these constituents are comparatively low. In addition, some ground water sources contain boron (B) at comparatively low concentrations but nevertheless at levels that may be detrimental to certain crops.

Saline and sodic environments are sometimes used interchangeably, which is incorrect. There is a clear distinction between salinity and sodicity; the former being related to salt concentration and the latter to salt composition. Salinity refers to the concentration of salts in the irrigation water or soil that is sufficiently high to adversely affect crop yields or crop quality. These adverse responses are caused by high concentrations of salts in the soil solution (i.e., osmotic effects) or by high concentrations of specific ions such as chloride or sodium that can cause specific injury to sensitive crops (i.e., specific-ion effects). Sodicity, however, is related to the proportion of

sodium in water, or adsorbed to the soil surface, relative to calcium and magnesium. Sodic water is synonymous with 'soft' water. Sodicity can contribute to the deterioration of physical properties of the soil, which can indirectly affect plants resulting in surface crusting, reduced water infiltration, and reduced aeration causing anoxic or hypoxic conditions for roots.

Sodicity has been described in different ways (Jurinak and Suarez, 1990). The sodicity of soil is characterized by the exchangeable sodium percentage (ESP). The ESP is the percentage of the soil's cation exchange capacity occupied by sodium (Na^+). The sodicity of water, however, is a measure of the sodium adsorption ratio (SAR), and is defined as

$$\mathrm{SAR} = \frac{\mathrm{Na}^+}{\sqrt{(\mathrm{Ca}^{2+} + \mathrm{Mg}^{2+})}} \quad [1]$$

where concentrations of the cations are in mmol l^{-1}. The ESP and SAR are related to one another and, for most practical purposes, are numerically equivalent in the range of 3–30 (Richards, 1954).

Sodic soils affect almost all crops because of the deterioration of soil physical conditions (Shainberg and Singer, 2012). Dispersion of soil aggregates in sodic soils decreases soil permeability to water and air, thereby reducing plant growth. However, the break down in soil structure is not related to SAR alone. The deterioration of physical conditions of the soil depends on the SAR and the electrical conductivity of water (EC_w). The electrical conductivity is an indicator of the salinity of water and is directly related to the ionic concentration of water. Figure 1 shows the relationship between the SAR and EC_w of the irrigation water. Irrigation water with both low salinity (e.g., low EC_w) and high SAR is particularly problematic (see the red zone). However, water with low SAR and high salinity has better infiltration (see the blue zone), even though the higher salt concentration could damage crops. Therefore, water infiltration rates decrease with decreasing soil salinity and with increasing exchangeable Na^+, or sodicity. Moreover, water very low in electrolytes, regardless of the SAR, can be damaging to the soil structure. Many river waters derived from snowmelt, such as California's Sierra Nevada mountains ($EC_w < 0.1$ dS m^{-1}), are notorious with this unique characteristic.

These deteriorating processes occur due to the combination of clay swelling and instability of soil aggregates (Shainberg and Singer, 2012). In addition, clay movement and deposition into soil pores reduces the fraction of large pores in the soil. Large pore size distribution is important for water movement, adequate drainage, and proper aeration. It is important to note that factors other than EC_w and SAR affect the physical properties of the soil. Factors, such as soil texture, mineralogy, organic matter, pH, and rates of soil wetting (Shainberg *et al.*, 2001; Shainberg and Singer, 2012), can have a large influence on the overall processes affecting soil deterioration.

Principal Responses of Plants to Salinity

Overall Plant Reponses

There are two properties of saline media that adversely affect crops. Salinity depresses the external water potential (osmotic effect) and particular ions in the solution may have chemical or specific-ion effects. Although these properties are often

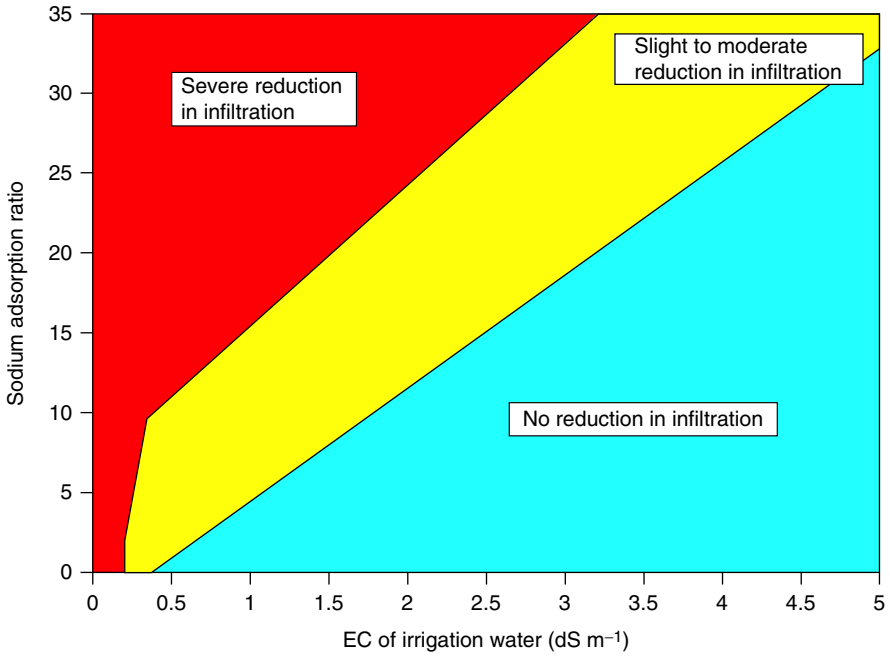


Figure 1 Relationship between salinity (EC) and sodicity (SAR) of irrigation water and its potential effects on water infiltration in the soil. Adapted from Ayers, R.S., Westcot, D.W., 1985. Water quality for agriculture. FAO Irrigation and Drainage Paper 29 Review 1, pp. 174. Rome: Food and Agriculture Organization of the United Nations.

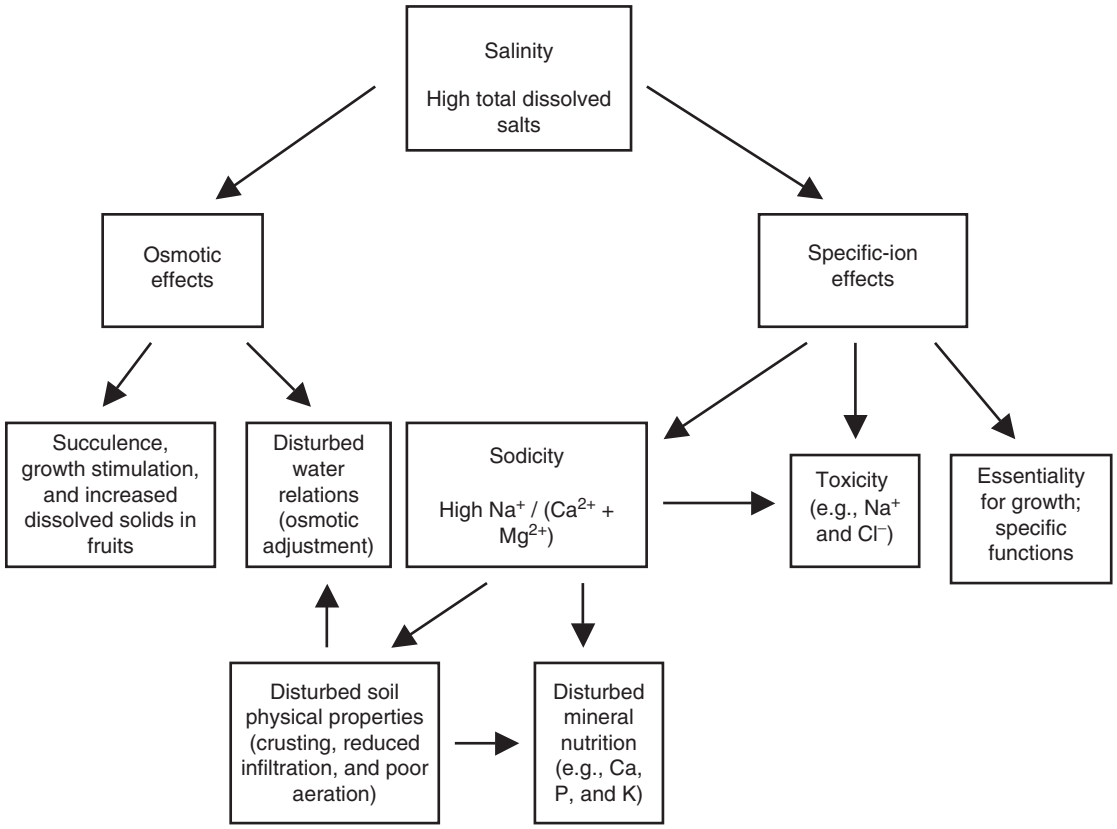


Figure 2 General effects of salinity and sodicity in plants. Reproduced from Läuchli, A., Grattan, S.R., 2012. Plant responses to saline and sodic conditions. In: Wallender, W.W., Tanji, K.K. (Eds.), Agricultural Salinity Assessment and Management. ASCE Manuals and Reports on Engineering Practice No. 71, pp. 169–205. New York, NY: American Society of Civil Engineers, with permission from ASCE.

discussed separately, usually both are implicated. A scheme that illustrates the effects of salinity on plants is shown in Figure 2. The left and right parts of Figure 2 suggest that some effects of salinity on plants are not deleterious. With few exceptions, however, saline conditions adversely affect crops.

Depression of the external osmotic potential by high salt concentrations tends to narrow the gap between the water potentials inside and outside the root cell. At high salinities, the external osmotic potential may be depressed below that of the cell water potential, resulting in osmotic desiccation. Even in less extreme situations, the water availability to the plant will at least initially tend to be lessened. The reduction in the osmotic potential of the medium is one of the primary causes of the adverse effects of salinity on plant growth. The plants exert considerable amounts of energy to transport, sequester, and exclude ions as well as synthesize and concentrate compatible solutes so that cells can osmotically adjust. This energy expenditure is at the expense of plant growth.

Salinity may also positively affect plant growth and crop quality. It may promote the growth of halophytes (Flowers and Colmer, 2008) or enhance quality of crops such as improved freezing tolerance of citrus (Syvertsen and Yelenosky, 1988), increased sugar content in carrots, increased soluble solids in tomatoes and melons, and improved grain quality in durum wheat (Grieve *et al.*, 2012).

As illustrated in Figure 2, these specific ion effects may be categorized under three headings. First, high concentrations of a given ion may cause mineral nutrition disorders. For example, high Na^+ concentrations, which create a sodic condition, may cause deficiencies of other elements, such as potassium or calcium. Second, certain ions, such as sodium or chloride, may have direct toxic effects, which may not always be clearly distinguishable from nutrient deficiencies. Third, there may be positive specific-ion effects that promote the growth or qualitative features of the plant such as succulence or pigment composition. These three types of specific-ion effects are not mutually exclusive but may manifest themselves on the plant at the same time to various degrees.

Sodicity is due to a high activity of Na^+ in the soil solution, relative to activities of Ca^{2+} and Mg^{2+}. Sodicity may, therefore, cause two of the effects discussed in connection with salinity; disturbances of mineral nutrition and toxicity; and there are indirect effects as well. Sodicity will not elicit strictly osmotic effects but, as described in the Section Salinity and Sodicity, can affect soil physical properties leading to crusting, reduced infiltration, and reduced aeration, which can also adversely affect plants (Shainberg and Singer, 2012).

Diversity of Plant Responses to Salinity

Plants show large diversity in their response to salinity (Grieve *et al.*, 2012; Shabala and Munns, 2012). Most crop plants are glycophytes and are relatively sensitive to salinity in

comparison to halophytes. Nevertheless, among crop plants there is considerable diversity in salt tolerance. Some crops like asparagus, barley, canola, sugar beet, and Swiss chard are tolerant of salinity whereas bean, carrot, onion, rice, and strawberry are sensitive to salinity. The salt tolerance of a crop can be described as a function of the percentage of yield decline across a range of salt concentrations relative to a nonsaline control (Grieve *et al.*, 2012). Although nonlinear models have been used to describe yield reduction with increased salinity, salt tolerance can be adequately described on the basis of two parameters. First is the 'threshold salinity,' which is the maximum salinity expressed as the electrical conductivity (EC_t) of the soil solution above which relative yields decline. Second is the slope of expected yield reduction per unit increase in salinity above the 'threshold' value. The yield potential (% yield) of this biphasic response can be expressed as

$$\text{Yield potential } (\%) = 100 - b(EC_e - a) \qquad [2]$$

where '*a*' and '*b*' are the 'threshold' and 'slope' values, respectively, specific for different crops. For example, Figure 3 illustrates the yield responses for alfalfa (lucerne), barley, corn (maize), rice, and wheat in relation to increased salinity. These response functions illustrate differences in salt tolerance mainly due to differences in osmotic effects among these important crops (Grieve *et al.*, 2012). These crops were salinized with a balanced mixture of salts and optimal nutrition minimizing specific ion effects. It is noted that rice and corn are considerably more sensitive to salinity than are wheat and barley. The tolerance of alfalfa, an important forage crop, falls between that of rice and wheat. Many horticultural fruit and nut crops such as almonds, apples, citrus, peaches, and plums tend to be sensitive to salinity. For a more complete list of crop tolerances and tables with specific '*a*' and '*b*' values, refer to Grieve *et al.* (2012). Using these '*a*' and '*b*' values and eqn [2], lines of other crops can be plotted similar to those selected in Figure 3.

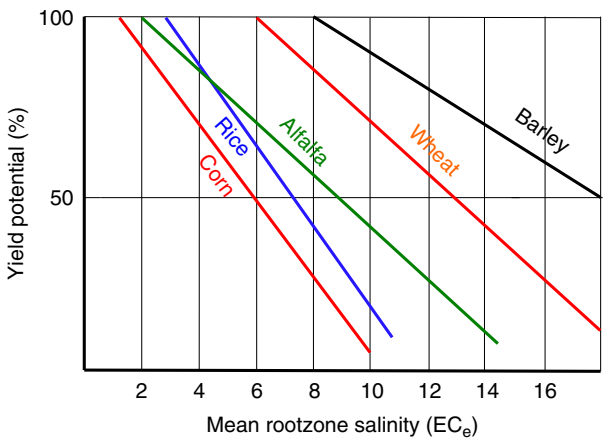


Figure 3 Relative yields of important world crops in relation to increased salinity (EC_e), where EC_e is the electrical conductivity of the saturated soil paste from soil samples collected in the active root zone. Reproduced from Grieve, C.M., Grattan, S.R., Maas, E.V., 2012. Plant salt tolerance. In: Wallender, W.W., Tanji, K.K. (Eds.), Agricultural Salinity Assessment and Management. ASCE Manuals and Reports on Engineering Practice No. 71, pp. 405–459. Reston, VA: American Society of Civil Engineers.

Unlike glycophytes, halophytes are the native flora of extremely saline soils and are distributed among several families of flowering plants, for example, pickleweed (*Salicornia* spp.), the salt bushes (*Atriplex* spp.), and mangroves (several genera) (Flowers and Colmer, 2008). Most halophytes only grow well in the presence of salt, and among the most salt-tolerant halophytes many can grow at salinities at or above seawater. A general physiological feature of halophytes is their capability to accumulate salt in specific compartments such as cell vacuoles, where it can be used for osmotic adjustment (see Section Osmotic Effects and Adjustment) whereas the relatively salt-tolerant glycophytes feature salt exclusion as a mechanism of tolerance. If response relationships of these halophytes were to be plotted in Figure 3, not only would there be a stimulatory effect with modest increases in salinity, but also the curves would fall further to the right of barley.

Physiological Mechanisms of Salinity Tolerance in Plants

Overall, salt tolerance in plants is determined by three distinct features: (1) osmotic tolerance, (2) ability to exclude Na^+ or Cl^-, and (3) ability of the tissue to tolerate high concentrations of Na^+ or Cl^- (Munns and Tester, 2008). Very often salt-tolerant plants will have one feature, but not the other. However, it is possible that salt-tolerant plants exhibit more than one of these features.

Osmotic Effects and Adjustment

Plant growth is inhibited by salinity through osmotic stress and a decrease in cell turgor. If the osmotic potential of the external medium were to immediately drop lower than that of the plant's cells, the cells would lose turgor and suffer osmotic desiccation. To maintain normal growth, plants must reduce their internal water potential to adjust to the drop in external osmotic potential. Osmotic adjustment can be achieved by (1) the absorption and accumulation of ions from the medium or (2) by synthesis and accumulation of organic solutes. Both processes occur but the extent by which one process dominates over the other is dependent on the type of plant and level of salinity.

Unlike glycophytes, halophytes are adapted to high saline environments by absorbing salt from the medium and using it as its major internal osmoticum (Flowers and Colmer, 2008). However, salt in plant cells can be toxic. A number of evidences indicate that high salt concentrations in the cytoplasm damage enzymes and organelles (Greenway and Munns, 1980). Salts absorbed from the soil solution apparently serves as an osmoticum in the vacuole, a membrane-bound compartment that occupies a large portion of the cell volume. In the cytoplasm, the function of osmotic adjustment is served mainly by organic solutes synthesized by the plant (Wyn Jones and Gorham, 2002). Thus, organic osmolytes are used to a large extent in only a small fraction of the total cell volume. The tonoplast (the membrane that separates the vacuole from the cytoplasm) must transport salt out of the cytoplasm and into the vacuole where it can concentrate while at the same

time prevents any substantial leakage of organic osmolytes from the cytoplasm into the vacuole.

Anatomical adaptation is a common feature among many halophytes as a means of tolerating highly saline environments (Shabala and Munns, 2012). Most of these adaptations are related to Na^+ sequestration or Na^+ secretion, but some other features are worth mentioning (Shabala and Munns, 2012). Leaf succulence describes leaf tissue thickening and is accompanied by increases in leaf sap volume causing an increase in cell size. This is particularly characteristic of mesophyll cells and hence their vacuoles are also larger. Larger vacuoles provide a more efficient means of Na^+ removal from the cytoplasm as there is more room for this toxic element to be sequestered. Salt glands and salt bladders are remarkable anatomical features on some halophytes that eliminate salt by literally expelling salts outside the plant or by sequestering excess salt from metabolically active tissues (Flowers and Colmer, 2008). A more detailed description of the anatomical effects caused by salinity and function of salt glands and salt bladders, is presented by Shabala and Munns (2012).

The glycophytes, unfortunately, are unable to cause the sharp asymmetrical intracellular compartmentation of inorganic and organic solutes that is central for the adaptation of salt-absorbing halophytes to their saline habitats. Exposed to moderate salinities, glycophytes tend to exclude Na^+ or Cl^- and to sequester what little salt they absorb in the roots and stems. Salt exclusion minimizes the exposure of the leaf cells, and hence the photosynthetic apparatus, to salt. Thus, the glycophytes regulate ion fluxes less effectively at the cellular level than do halophytes, but partition ions more effectively at the organ and tissue levels. Regardless, glycophytes do show differences in their ability to partition salt at the cellular level and this ability is related to salt tolerance. For example, Barley, a relatively salt-tolerant crop, can tolerate Na^+ concentrations up to 500 mmol l^{-1} in the leaf tissue primarily by sequestering this toxic ion in vacuoles; whereas the more salt-sensitive durum wheat are unable to partition Na^+ in vacuoles as effectively (Munns *et al.*, 2006).

To survive in saline conditions, overcoming their inability to absorb major quantities of external ions for osmotic adjustment, glycophytes must synthesize organic osmolytes called compatible solutes, by increasing their uptake, or by *de-novo* synthesis of such compatible solutes and concentrate them in the cytoplasm. Many such organic solutes have indeed been identified and are listed in **Table 1**. The term 'compatible solutes' is often applied to these organic compounds because of their compatibility with cytoplasmic entities and processes and do not interfere with cellular metabolism even at high concentrations (Bray *et al.*, 2000). Compatible solutes that commonly accumulate to high concentrations in plants are proline, glycine betaine, and sucrose (Munns and Tester, 2008). To function as compatible osmolytes, these solutes are highly compartmentalized in plant cells. The vacuoles accumulate charged ions and solutes that would otherwise perturb metabolism if accumulated in the cytoplasm. Compatible solutes in the cytoplasm, however, allow the cytosol to be osmotically balanced with the vacuole. As an example, very little glycine betaine (<1 mmol l^{-1}) is contained in the vacuoles of spinach leaves under salt stress, but its concentration in the cytosol and chloroplasts may reach 300 mmol l^{-1} (Bray *et al.*, 2000). At low concentrations, these organic solutes can function as 'osmoprotectants' (McNeil *et al.*, 1999).

Table 1 Compatible solutes (osmolytes) of higher plants

Class of compounds (1)	*Major compounds (2)*
Amino acid	Proline
Quaternary ammonium compounds	Glycine betaine
	Proline betaine
	β-Alaninebetaine
	Choline-O-sulfate
Polyhydric alcohols	D-Sorbitol
	D-Mannitol
Mono- and disaccharides	Sucrose and fructose
Cyclitols	D-Pinitol
	D-Ononitol
	L-quebrachitol
	Myo-inositol
	Trehalose
Tertiary sulfonium compounds	3-Dimethylsulphonio propionate

Source: Reproduced from Läuchli, A., Grattan, S.R., 2012. Plant responses to saline and sodic conditions. In: Wallender, W.W., Tanji, K.K. (Eds.), Agricultural Salinity Assessment and Management. ASCE Manuals and Reports on Engineering Practice No. 71, pp. 169–205. New York, NY: American Society of Civil Engineers, with permission from ASCE.

In addition to organic solutes, glycophytes can adjust osmotically by increasing the accumulation of inorganic ions such as K^+, Na^+, and Cl^-. Ion accumulation is the preferred method of adjustment because it is cheap energetically. However, the accumulation of inorganic solutes should not inhibit cell metabolism. K^+ ions can play this role, whereas Na^+ and Cl^- can only fulfill this role at low external concentration, as these ions are toxic to cell metabolism at higher concentration unless they are sequestered in cell vacuoles and away from metabolic activity as they are in halophytes.

The synthesis and transport of organic osmolytes, the transport of inorganic ions, and the compartmentation of organic and inorganic solutes, all require the expenditure of metabolic energy, that is, photosynthate (Epstein, 1980). Stavarek and Rains (1985) compared the performance of alfalfa cells selected for salt tolerance in cell culture with that of unselected (nontolerant) cells. At 170 mmol l^{-1} NaCl, the unselected cells grew very slowly. The selected (salt-tolerant) cells at the same salinity differed from those in the control treatment (no salt) only in having a lag period of a few days. Thereafter, their growth (i.e., gain in dry weight) paralleled that of the cells in the control treatment. Measurements of carbohydrate metabolism of the salt-tolerant selected cells showed maintenance costs to be relatively low when the cells grew under saline conditions. The maintenance costs of the unselected cells increased with salinity. Even selected cells, however, must divert energy to the processes of ion transport, synthesis of organic osmotica, and compartmentation. These costs result in diminished growth per unit of substrate (sugars) utilized (Stavarek and Rains, 1985; Yeo, 1983). Plants vary greatly in the adjustment of their energy economy to the presence of salt (Schwarz and Gale, 1981), which manifests into plants with different salt tolerances. Maintenance respiration rates usually increase at moderate salinities. The definition of 'moderate,' however, depends on the salt tolerance of

the plant. Raven (1985) concluded that the energy cost of the synthesis of compatible solutes leads to a potential growth penalty. The adenosine triphosphate (ATP) requirement for the synthesis or accumulation of solutes in leaf cells has been estimated by Raven (1985) to be approximately 3.5 mol for either Na^+ or Cl^-, 41 for proline, 50 for glycine betaine, and 52 for sucrose, respectively. ATP is the basic biochemical high-energy compound used in metabolic processes. Hence, the synthesis of organic, compatible solutes proceeds at the expense of growth, but it may allow the plant to survive (Munns and Tester, 2008).

Specific Ion Effects: Toxicity

In a number of instances, toxicity of specific ions is supported by evidence from two sources. One is that moderate concentrations of sodium, chloride, sulfate, or other ions reduce growth or cause specific injury. The other is that isosmotic solutions of different compositions may elicit different responses. As might be expected, genotypes may differ in these responses even within a species.

Toxicities due to even moderate concentrations of some ions in salt-affected soils are most common in woody plants, particularly tree crops and vines. Color photographs, depicting various degrees of leaf injury due to sodium and chloride toxicity in several fruit crops, are shown in a publication by Bernstein (1965). These woody crops have little ability to exclude sodium or chloride from their leaves and the plants are long-lived; hence, they often suffer toxicities at even moderate soil salinities.

Ion toxicities are not exclusive to woody crops. An example from experiments with wheat shows the usefulness of isosmotic solutions of different ionic composition, as well as the importance of the genotype. Kingsbury and Epstein (1986) found that the growth of a salt-sensitive line of wheat was adversely affected by nutrient solutions containing high concentrations of Na^+ (>100 mmol l^{-1}), but not by isosmotic solutions without Na^+ at elevated concentrations. The growth of a line selected for salt tolerance was unimpaired by any of the solutions used. Termaat and Munns (1986) also used isosmotic solutions to investigate osmotic versus specific ion effects.

Specific Ion Effects: Nutrition

The presence of high concentrations of sodium and chloride is a common feature in many salt-affected soils. The ratios of these ions to other nutrient ions in the soil solution may be quite high and may cause specific nutrient deficiencies in the plant (Läuchli and Epstein, 1990). Thus, plant performance may be adversely affected by salinity-induced nutritional disorders, resulting from salinity effects on nutrient availability, competitive uptake, transport, or partitioning within the plant (Grattan and Grieve, 1999). For example, in the saline environments in which sodium predominates over potassium, the plant's paramount nutritional requirement is acquiring potassium in adequate amounts (Rains and Epstein, 1967).

Saline conditions may inhibit the absorption of nitrate. Thus, in short-term experiments (up to 12 h) with barley seedlings, Aslam *et al.* (1984) found that SO_4^{2-} and, to a greater extent, Cl^- diminish the rate of NO_3^- absorption, the degree of inhibition being 83% at 200 mmol l^{-1} Cl. Chloride's effect on NO_3^- absorption was apparent within 1 min and the identity of the accompanying cation (Na^+ or K^+) had little effect on this inhibition. Salt did not affect subsequent NO_3^- reduction by the plant.

Sodium ions have been shown to cause disturbances in calcium and potassium nutrition. Excess sodium in the soil solution has been found to reduce both of these nutrient cations (Grattan and Grieve, 1999). Nutritional disorders involving other elements may be linked to the effects of salinity on the uptake, transport, and metabolism of calcium. High Ca^{2+} concentrations in the soil substrate may mitigate the effects of salinity. High ratios of sodium to calcium in the medium tend to be deleterious. Inadequate concentrations of Ca^{2+} may adversely affect membrane function and growth even within minutes of salt application (Läuchli and Grattan, 2012; Shabala and Munns, 2012). More details on sodium-induced calcium deficiencies are found in the Section 'Integrating the Whole-Plant Response.'

Integrating the Whole-Plant Response

Response to Salinity Stress during Plant Development

It has long been recognized that a crop's sensitivity to salinity varies from one developmental growth stage to the next (Bernstein and Hayward, 1958). The majority of the research indicates that most annual crops are tolerant at germination but are sensitive during emergence and early vegetative development (Läuchli and Epstein, 1990; Grieve *et al.*, 2012). As plants mature, they become progressively more tolerant to salinity, particularly at later stages of development. Salinity affects both vegetative and reproductive developmental processes in the plant. This is particularly important depending on whether the harvested organ of the crop is a stem, leaf, root, shoot, fruit, fiber, or grain (Läuchli and Grattan, 2007).

Germination and seedling emergence

Although there are exceptions such as sugar beet (Läuchli and Epstein, 1990), most plants are tolerant during germination and can germinate under high salinity conditions including many that are rated as sensitive to salinity such as corn, kenaf, *Limonium*, and tomato (Läuchli and Grattan, 2012). However, salinity stress delays germination even though the final percentage of germinated seeds will eventually be the same among moderate salinity treatments (Maas and Poss, 1989). However, further increases in salinity will eventually reduce the percentage of germinated seeds as well (Kent and Läuchli, 1985).

Unlike germination, many crops are less tolerant to salinity during emergence and as a result stand establishment is reduced (Maas and Grattan, 1999). For example, cotton, a crop classified as 'salt tolerant,' is particularly sensitive to salinity after germination and plant densities have been substantially reduced in fields previously irrigated with saline–sodic drainage water (Grattan *et al.*, 2013). Interestingly, stand establishment of more salt-sensitive crops including safflower and

tomato was not nearly as affected as cotton. Emergence studies have been conducted using different root media under various environmental conditions, making it difficult to interpret results and compare studies. For example, sodic waters, particularly those where NaCl was the sole salinizing salt, can cause deterioration of soil physical conditions thus reducing oxygen diffusion rates and increasing soil strength (Grattan and Oster, 2003). This condition inadvertently adds additional abiotic stresses to the emerging seedlings as compared with other salinity studies under saline and nonsodic conditions.

Vegetative growth

Most of the literature indicates that crops are particularly susceptible to salinity during the seedling and early vegetative growth stage, as compared with germination. Why is the seedling and early vegetative development so susceptible to salinity? It is well known that salinity even with an adequate supply of calcium reduces shoot growth, particularly leaf area, more than root growth (Läuchli and Epstein, 1990). However, inadequate calcium supply under saline conditions (i.e., saline–sodic conditions) can adversely affect membrane function and growth of the root within minutes (Läuchli and Epstein, 1970; Cramer *et al.*, 1988). When the calcium concentration was increased from 0.4 to 10 mmol l^{-1} in a medium salinized with NaCl, root length of cotton seedlings was substantially increased, particularly at the higher salinity levels (Cramer *et al.*, 1986). Moreover, root length at this increased level of Ca^{2+} was maintained over a wide range of salinities. However, shoot growth remained salt sensitive (Kent and Läuchli, 1985). These calcium additions favor cell elongation of cotton roots at the expense of radial cell growth and cell production rates were maintained (Kurth *et al.*, 1986). Additional studies conclude that supplemental Ca^{2+} alleviates the inhibitory effect of salt on cotton root growth by maintaining plasma membrane selectivity of K^+ over Na^+ (Läuchli, 1990, 1999; Zhong and Läuchli, 1994).

The effect of salt stress on shoot growth in many species can also be partly alleviated by supplemental Ca^{2+} (Läuchli and Epstein, 1990; Cramer, 2002), particularly those exposed to high Na/Ca ratios where Ca deficiency in developing leaves may occur (Maas and Grieve, 1987). The calcium status of the growing region of leaves is particularly sensitive to salt stress (Läuchli, 1990). The importance of supplemental Ca^{2+} in alleviating salt stress effects in the shoot has been emphasized by Cramer (2002), and Munns (2002b) recommended adding at least 5–10 mmol l^{-1} Ca^{2+} to the medium for salinities of 100–150 mmol l^{-1} NaCl, to counteract the inhibitory effect of high Na^+ concentrations on growth.

Reduction in shoot growth by salinity is characterized by stunted shoots with reduced leaf area, but the final leaf size depends on both cell division and cell elongation (Läuchli and Epstein, 1990). Although salinity can reduce cell numbers (Munns and Termaat, 1986), leaf extension, controlled by cell elongation, has been found to be an extremely salt-sensitive process (Papp *et al.*, 1983).

Cell expansion is controlled by processes related to cell-wall extension and cellular water uptake (Cramer and Bowman, 1993); the latter depends on the cell osmotic potential (Ψ_s). Hu and Schmidhalter (2004) concluded that the reduction of leaf elongation by salinity may either be related to decreases in cell wall extensibility or increases in yield threshold. In most plants, when leaf elongation partly recovered after the initial rapid drop in the elongation rate upon salinization of the medium, osmotic adjustment occurred with the solute content in the leaf cells becoming higher under saline than nonsaline conditions.

Although leaf expansion is highly responsive to salt stress by reductions in cell elongation, the leaf initiation rate appears less affected. Kriedemann (1986) observed that the rate of leaf expansion in sugar beet decreased linearly with increased salinity whereas the rate of leaf initiation was unaffected.

The relationship between salt sensitivity of leaf growth to the overall salt sensitivity of the plant was hypothesized by Munns and Termaat (1986) using the following model. When NaCl stress is added, the rate of leaf expansion slows down. At the same time, ions begin to accumulate in the leaves in a linear fashion until they reach a maximum concentration beyond which concentrations become lethal and the leaf dies. This first occurs in older leaves, then sequentially in younger leaves as salt stress continues. Eventually, the rate at which leaves die is faster than the rate of leaf expansion, whereby the carbohydrate reserve in the plant is eventually depleted. Leaves no longer expand once the carbohydrate reserves drop to the bare minimum required for further growth. As carbohydrate reserves are depleted yet further, the whole plant eventually dies. The time scale of this process will vary depending on the plant type or genotype and the level of salt stress. The more salt sensitive the plant and more severe the stress, the shorter the time scale. For the plant to survive salt stress, a salt balance in the leaves must be achieved and some minimum fraction of the total leaf area of the plant must remain healthy to continue photosynthesis and carbohydrate production.

The control of sodium acquisition and allocation in plants on the one hand, and carbon allocation and use, on the other, to be critical components of salt tolerance was considered by Cheeseman (1988). A substantial amount of research indicates that photosynthesis per se does not appear to determine plant growth under salt stress for many agronomic crops (Läuchli and Grattan, 2012). Although stomatal conductance is often reduced when plants are exposed to saline conditions, the rates of photosynthesis per leaf area are mostly unaffected (Munns and Tester, 2008) because the chloroplast density per unit leaf area in these salt-stressed plants is higher. However, photosynthesis expressed on a unit of chlorophyll is usually reduced. Overall, photosynthesis measured on a per plant basis is reduced by salinity due to the reduction in total leaf area of the plant (Munns and Tester, 2008). Salt accumulation in the chloroplasts of leaf cells could have a direct toxic effect on photosynthesis, or else salt could reach high enough concentrations in the cytoplasm of leaf cells to inhibit enzymes related to carbohydrate metabolism.

It was suggested among stress physiologists that water deficit in the leaves could limit shoot growth following salinization. Termaat *et al.* (1985) tested this hypothesis to determine whether leaf turgor limits shoot growth in salt-stressed plants by growing plants in a saline soil within a pressure chamber and applying a pressure to the soil media that raised the shoot water potential by the same amount as the pressure applied to the root. Experiments using barley,

wheat, Egyptian clover, white clover, and white lupin indicated that increased leaf water potential did not improve growth under saline conditions (Munns and Termaat, 1986). These results indicate that leaf water deficit does not limit shoot growth in nonhalophytes grown under saline conditions.

The possible role of cell turgor in the response of leaf elongation is unclear. Thiel *et al.* (1988) determined turgor in leaves of salinized barley seedlings by using the micro-pressure probe method and correlated the turgor values with leaf elongation rates. Adding NaCl to the medium caused the leaf elongation rate to immediately decline, followed by gradual recovery, the extent of which depended on the NaCl concentration. Salt stress reduced cellular turgor in expanding and expanded leaf tissue. The turgor of expanding tissue recovered quickly, but decreased turgor persisted in expanded tissue. These researchers suggested that salinity reduced leaf elongation through osmotic effects on turgor in the short term, but the sustained component of reduction in leaf elongation was not caused by leaf water deficit in the long term. The latter part of this conclusion is in agreement with Munns and Termaat (1986). In contrast to the results of Thiel *et al.* (1988), Yeo *et al.* (1991) observed that leaf elongation in rice grown under salinity declined without a change of turgor in the growing zone. Therefore, it appears that the long-term reduction in leaf growth due to salinity is not caused by a leaf water deficit (Munns *et al.*, 2006). Researchers used isopiestic psychrometry on wheat and barley and confirmed that tugor was unchanged when plants were exposed to a range of saline solutions. However, the relative water content (RWC), a widely used method of measuring plant water status, decreased under salinity. Earlier, James *et al.* (2002) and Rivelli *et al.* (2002) showed turgor (calculated from the difference between total water potential and osmotic potential in durum wheat) remained unchanged by salinity whereas RWC decreased. However, RWC, when measured with the conventional method of detaching leaves and rehydrating on deionized water, cannot be used on salt-exposed plants because of osmotic adjustment as a consequence of higher solute content of the cells in a saline medium than in the absence of salinity. The increased cell solute content in the salt-exposed plants leads to a higher uptake of water than in control leaves, resulting in an apparent low RWC in the salinity treatment. Thus, the conventionally used method of determining RWC is not an indicator of turgor in plants that are undergoing osmotic adjustment in response to saline exposure (Läuchli and Grattan, 2012). Additional evidence reviewed recently in detail by Läuchli and Grattan (2007) also indicates no direct role of turgor in the response of leaf elongation to salinity. Indirectly, the evidence supports the conclusion of Munns *et al.* (2006) that hormonal signals are controlling shoot growth and that control of shoot growth under salinity is not mediated by leaf water deficit or ion toxicity.

Reproductive growth

After the salt-sensitive, early-vegetative growth stage, the bulk of the research suggests that most crops become progressively more tolerant as the plants grow older (Läuchli and Grattan, 2007). In experiments with wheat, sorghum, and cowpea conducted at the USDA/ARS Salinity Laboratory (reviewed by Läuchli and Grattan, 2012), when the duration of salinity stress was held constant but the period of salt-stress imposition varied from one developmental stage to the next, investigators found that these crops were most sensitive during vegetative and early reproductive stages, less sensitive during flowering, and least sensitive during the seed filling stage. In all these studies, seed weight was the yield component of interest but similar conclusions regarding growth stage sensitivity were obtained with both determinate crops (the grain crops) and indeterminate (cowpea) crops.

Wheat and rice are not only two of the most important grain crops in the world but they have been the most intensively studied agronomic crops regarding salt sensitivity at different growth stages. These leading grain crops are of particular interest not only because they vary so widely in salt tolerance but also because salinity affects the reproductive processes differently (Läuchli and Grattan, 2007). Studies on wheat and rice were conducted in a variety of conditions including the field, greenhouse, and laboratory to better understand detailed changes in developmental processes, as the plants endure various degrees of salt stress at different growth stages.

Wheat

A mature wheat plant is a consequence of sequential developmental processes that are characterized by changes in shoot apex morphology. The yield components such as tillers per plant, number of spikelets per spike, and individual grain weights are developed sequentially as the crop develops. It has long been known that salinity reduces the growth rate of the entire wheat plant and its specific organs, but it also affects plant development (Hu *et al.*, 2005).

The duration of plant development is also affected by salinity. Salt stress retarded leaf development and tillering but hastened plant maturity (Maas and Poss, 1989). Salt stress, imposed while the shoot apex is in vegetative stage, can adversely affect spike development and decrease yields of wheat (Maas and Grieve, 1990). When wheat was salt-stressed during spike differentiation, reproductive development was stimulated, but the number of spikelets was reduced. Investigators found that salt stress accelerated the development of the shoot apex on the main stem and decreased the number of spikelet primordia. Salt stress decreased the yield potential mostly by reducing the number of spike-bearing tillers. Therefore, Maas and Grieve (1990) concluded that salinity stress needs to be avoided before and during spikelet development on all tiller spikes if full yield potential is to be achieved.

Rice

As one of the most important food crops in the world, both economically and nutritionally, rice ranks among those that are sensitive to salinity (Maas and Grattan, 1999). Not only is rice considerably less tolerant to salinity than wheat but salinity affects its reproductive development quite differently.

Rice sensitivity to salinity varies considerably from one growth stage to the next. In terms of grain yield, rice is tolerant during germination (Heenan *et al.*, 1988), sensitive to salinity during emergence and early seedling growth, becomes more tolerant later on in vegetative development, and then becomes sensitive again during reproductive growth (Flowers and Yeo, 1981; Khatun and Flowers, 1995; Abdullah *et al.*, 2001). The

vegetative shoot biomass of rice, however, is often affected much less than reproductive growth (except for young seedlings) (Khatun and Flowers, 1995; Munns *et al.*, 2002). Field and greenhouse studies have shown that salinity had a negative impact on stand establishment and adversely affected a number of yield components and even delayed heading (Grattan *et al.*, 2002). In one study, investigators found linear decreases in several yield components with increased salinity including the percentage of sterile florets, tillers per plant, and spikelets per panicle, which translated into larger reductions in grain weight per plant at a given salinity (Zeng and Shannon, 2000). However, these investigators suggested that seedling emergence and early seedling growth stages were most sensitive to salinity.

It has long been recognized that salinity can cause sterility in rice, particularly if imposed during pollination and fertilization but some cultivars are more susceptible than others (Akbar and Yabuno, 1977). The effect of salinity on rice has resulted in delayed flowering, a decrease in the number of productive tillers and fertile florets per panicle, and a reduction in individual grain weight (Lutts *et al.*, 1995; Zeng and Shannon, 2000).

The reduction in the number of spike-bearing tillers by salt stress during the vegetative and early reproductive development in most cereal crops appears to have a greater negative impact on grain yield than any other yield component. The time from planting to maturity in most cereal crops typically decreases with increased salinity (Grieve *et al.*, 1993), but salinity has just the opposite effect on rice (Lutts *et al.*, 1995). When salinity was applied to wheat from seedling emergence, it had a profound influence on reproductive development (Grieve *et al.*, 1993). Leaf initiation rate decreased even though the time of flag leaf initiation was unchanged, indicating salinity had no influence on the timing of the transition from vegetative to reproductive development, but greatly reduced the number of tillers and overall grain yield. Salt stress in rice can reduce seedling emergence and, when imposed at early vegetative stages, reduces tillers and grain-bearing panicles leading to low yields. However unlike wheat, certain rice cultivars can develop sterile spikelets, by a mechanism that appears to be genetically controlled, leading to further grain yield losses.

Regulations of Salt Balance in Leaves

Cellular uptake of sodium

Sodium levels in roots increase rapidly after plants have been exposed to salt stress. This is the result of several transport processes, including Na^+ uptake, Na^+ efflux to the apoplast and vacuole, and Na^+ transport to the shoot (Maathuis, 2007). These Na^+ transport processes require the activity of several membrane transporters that are important outputs for signaling pathways. A recent model of signaling pathways for both cellular Na^+ and Ca^{2+} during salt stress illustrates that these transporters may also have sensing functions. Plant roots respond specifically to external Na^+ almost instantaneously, yet the mechanism of Na^+ sensing is still unknown. One proposed hypothesis is that a plasma-membrane protein may function as the extracellular Na^+ sensor (Munns and Tester, 2008). The first response to an increase in salt stress around the roots is an elevated Ca^{2+} activity in the cytosol (Ca^{2+}_{cyt}) of root cells brought about by a flux of Ca^{2+} across the plasma membrane and the tonoplast (Munns and Tester, 2008). The increase in Ca^{2+}_{cyt} in response to salt is a central component of the SOS (salt overly sensitive) pathway. The SOS signaling pathway is composed of SOS1, SOS2, and SOS3 components and has been proposed as a mechanism to mediate cellular signaling under salt stress in order to maintain ion homeostasis at the cellular and whole-plant level (Hongtao *et al.*, 2013). The proposed regulations of these pathways are described in detail in reviews by Hongtao *et al.* (2013), Maathuis (2007), and Qiu *et al.* (2002).

The maintenance of an adequate K^+ concentration in the cytoplasm by favorable K:Na ratios under salt stress is an important feature of salt tolerance in plants. This feature is usually called K^+ homeostasis and is important for maintaining cellular metabolism (Zhu, 2003). A negative correlation between Na^+-induced net K^+ efflux and salinity tolerance in barley plants have been found and it was concluded that the cytosolic K^+/Na^+ ratio is an important determinant of salinity tolerance (Chen *et al.*, 2007), but its significance is probably located mainly in the root, because no strong relationship between leaf K^+ concentrations and salt tolerance has been found so far (Munns and Tester, 2008).

Calcium signaling in response to salt stress

As explained in Section Cellular uptake of sodium, the cytosolic Ca^{2+} activity is involved in the regulation of Na^+ concentration in the cytosol by functioning as a component of Ca^{2+}-signaling network (Hirschi, 2004; **Figure 4**). In the absence of salt stress, the cytosolic Ca^{2+} activity ('resting Ca^{2+}') is low, remaining at approximately 0.1–0.2 μM (Hirschi, 2004). A stimulus such as an increase in external Na^+ concentration elicits Ca^{2+} mobilizing signals. These mobilizing signals trigger a flow of Ca^{2+} into the cytoplasm, which generates the ON events. One of these ON events is the activation of the Na^+/H^+ antiporters at the plasma membrane and tonoplast, which lowers the elevated cytoplasmic Na^+ concentration following exposure to salinity, to low and nontoxic levels. The HIGH Ca^{2+}_{cyt} activates Ca^{2+}-sensitive processes, which are mediated by proteins such as calmodulin. The final step mediated by OFF mechanisms (e.g., transporters and binding proteins) removes Ca^{2+} from the cytosol and restores the Ca^{2+} activity at the resting state. This Ca^{2+}-signaling network is the cellular/subcellular basis for the important role that Ca^{2+} plays in mediating a component of salt tolerance in plants.

Salt exclusion

Regulation of salt balance in the leaves is significant for the salt tolerance of the whole plant. Flowers and Yeo (1986) concluded that for salt-sensitive species, such as rice, sodium supply to the expanding leaves exceeds the demand for osmotic adjustment at high salt stress, leading to excessive sodium concentrations in the leaves and ion toxicity. It is also well established that salt concentrations are highest in the oldest leaves of nonhalophytes (Greenway and Munns, 1980). Yeo and Flowers (1982) suggested that lower salt concentrations in younger leaves may be partly due to exclusion of specific ions

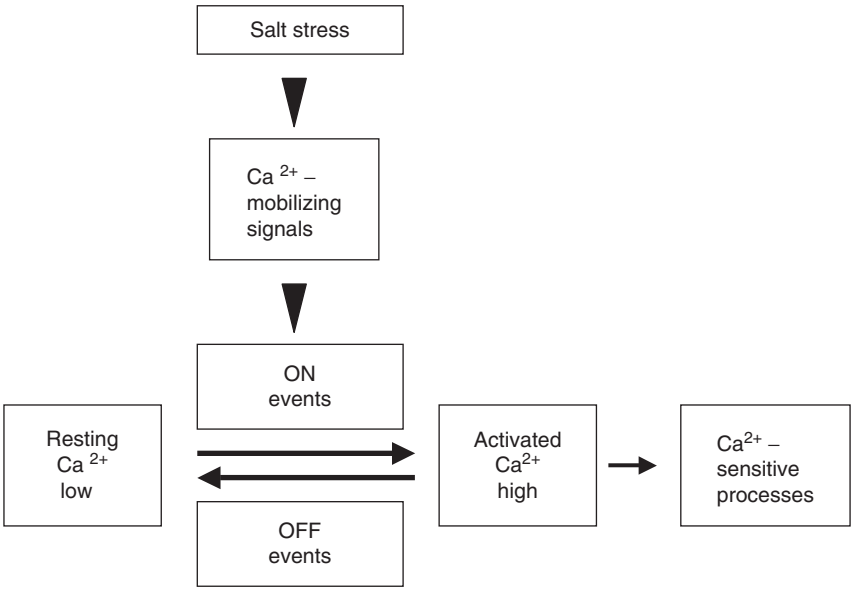


Figure 4 Ca^{2+}-signaling network in response to a stimulus such as salinity stress. Modified from Läuchli, A., Grattan, S.R., 2012. Plant responses to saline and sodic conditions. In: Wallender, W.W., Tanji, K.K. (Eds.), Agricultural Salinity Assessment and Management. ASCE Manuals and Reports on Engineering Practice No. 71, pp. 169–205. New York, NY: American Society of Civil Engineers and Hirschi, K.D., 2004. The calcium conundrum: Both versatile nutrient and specific signal. Plant Physiology 136, 2438–2442, with permission from the ASCE.

from the xylem vessels that supply them. In rice, the evidence clearly indicates that, on salinization, sodium moves first to the older leaves, which in effect protects the younger leaves. This partial exclusion of sodium from the young leaves appears to correlate positively with the salt tolerance of some rice cultivars relative to the germplasm base (Yeo and Flowers, 1986).

As illustrated by Davenport *et al.* (2007), Na^+ accumulation in the shoot is the result of several different transport processes in the root and the shoot (**Figure 5**). Under conditions of high salinity, Na^+ is transported passively into the root cytosol, probably by nonselective cation channels (1). Antiporters such as SOS1 (2) pump Na^+ back from the outer region of the root to the soil solution or sequester Na^+ in the root cell vacuoles by NHX transporters (3). Na^+ can also leak passively from the vacuole to the cytosol (4). The transport processes 1–4 are located in root cortical cells. Transport of Na^+ to the shoot is still poorly understood (Davenport *et al.*, 2007). In the stele of the root, Na^+ is loaded into the xylem, either passively (5) or possibly actively by SOS1 (6). Transport steps 5 and 6 occur in the mature part of the root or at low transpiration. Na^+ retrieval from the xylem, which can take place in the mature region of the root, base of the stem, and along the veins of the leaves, may also occur via the transport processes 5 and 6. Unloading of Na^+ into the leaf cells probably proceeds passively (7). Na^+ can also be recirculated from the leaves to the roots in the phloem (8, 9). The transport steps involved in the net delivery of Na^+ to the xylem have been described in detail by Tester and Davenport (2003). Recently, the thermodynamics of the transport processes and their possible molecular mechanisms have been assessed and summarized by Munns and Tester (2008).

Each of the transport processes that contribute to the net accumulation of Na^+ in the shoot requires their control by specific cell types in specific locations of the plant, thus

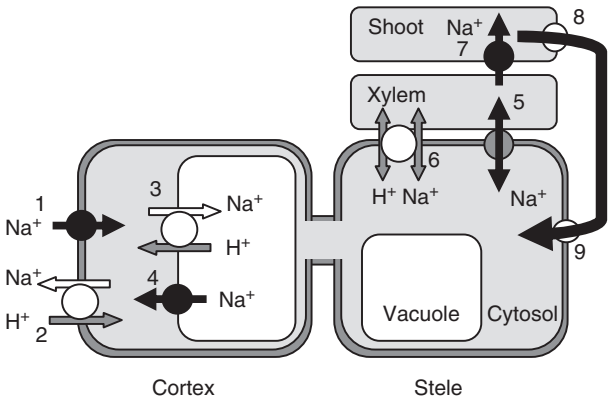


Figure 5 Involvement of different Na^+ transport processes of the root and the shoot in net Na^+ accumulation in the shoot. The numbered processes refer to (1) passive Na^+ transport (nonselective cation channels); (2) SOS1 antiporter; (3) NHX transporter; (4) passive Na^+ transport; (5) passive Na^+ loading in xylem; (6) active Na^+ loading in xylem (SOS1); (7) passive unloading of Na^+; and (8 and 9) recirculation of Na^+ via pholem. Reproduced from Davenport, R.J., Muñoz-Mayor, A., Jha, D., Essah, P.A., Rus, A., Tester, M., 2007. The Na^+ transporter AtHKT1 controls xylem retrieval of Na^+ in Arabidopsis. Plant, Cell and Environment 30, 497–507, with permission from John Wiley and Sons.

facilitating Na^+ transport in a coordinated manner (Tester and Davenport, 2003; Munns and Tester, 2008). A recent experimental example of elucidating the involvement of specific cell types in governing the major control points that limit Na^+ loading of the xylem is given by Läuchli *et al.* (2008) (see also Munns and Tester, 2008). This study indicated that the highest concentration of Na^+ in the cells of a relatively salt-tolerant

durum wheat genotype was found in the pericycle and therefore the pericycle may be the transport control point in the radial transport of Na^+, perhaps limiting xylem loading of Na^+ in the root (Läuchli *et al.*, 2008).

The question arises as to how significant salt exclusion from the shoot is as a mechanism of salt tolerance in non-halophytes. There is a strong correlation between salt exclusion and salt tolerance in many species (see reviews by Läuchli, 1984; Flowers and Yeo, 1986; Munns *et al.*, 2006). In species that retain Na^+ in the woody roots and stems, a strong correlation exists between Cl^- exclusion from the leaves and salt tolerance, especially trees and vines such as citrus, stone fruits, and grapes (Grieve *et al.*, 2012). In durum wheat genotypes, a negative correlation has been found between leaf Na^+ concentration and salt tolerance measured as shoot dry matter production (Munns and James, 2003). In the salt-tolerant wheat genotype, the transport of Na^+ to the leaf blades was maintained at low rates and controlled by xylem loading in the root and sequestration of Na^+ in the leaf sheath. In a recent review, Munns *et al.* (2006) convincingly argued that all plants must exclude most of the Na^+ and Cl^- in the soil solution or the salt concentration in the leaves becomes so high that the leaves are killed. The salt concentration in the soil solution, percentage of salt taken up by the roots, and percentage of water retained in the leaves is given by

$$[NaCl]_{shoot} = [NaCl]_{soil} \times (\%NaCl \text{ taken up}/\%water \text{ retained}) \quad [3]$$

Plants take up approximately 50 times more water from the soil than they retain in the shoot; thus they retain only approximately 2% of the cumulative water absorbed by roots. The vast majority of the water absorbed by roots is transpired by leaves. To prevent the shoot salt concentration exceeding that in the soil, only 2% of the salt should be allowed to move into the shoot; that is, 98% should be excluded (Munns *et al.*, 2006). In fact, most plants exclude approximately 98% of the salt in the soil solution and only 2% is transported in the xylem to the shoots. **Table 2** shows some examples of Na^+ and Cl^- concentrations in the xylem and % Na^+ and Cl^- exclusion from the xylem in plants grown in the presence of 50 mmol l^{-1} NaCl for 2 weeks (see Gregory, 2006; Table 5.9; data from R. Munns, personal communication). The data in **Table 2** show that bread wheat excludes Na^+ more effectively than durum wheat, rice, and barley. Although barley is a relatively poor Na^+ excluder, it is quite salt tolerant because it shows a high degree of 'tissue tolerance' to Na^+. The Cl^- exclusion data in **Table 2** do not correlate with salt tolerance as well as those for Na^+ exclusion, but the relatively salt-tolerant citrus genotype Rangpur lime shows the highest percentage of Cl exclusion. The use of wild relatives to improve salt tolerance of the corresponding crop species has recently been shown to have potential. For example, Teakle *et al.* (2007) compared two Lotus species (perennial forage legumes), *Lotus tenuis* (relatively salt tolerant) and *Lotus corniculatus* (less salt tolerant). *Lotus corniculatus* showed much higher Cl^- concentrations in the xylem and shoot than did *L. tenuis*; thus a higher salt tolerance in *L. tenuis* was correlated with a higher degree of Cl^- exclusion.

Does export of Na^+ and Cl^- from leaves through the phloem effectively help maintain a salt balance in the leaves of a salinized plant? Läuchli (1984) and Flowers and Yeo (1986) concluded that little evidence exists to support this. Munns *et al.* (1986) confirmed this conclusion with an experiment that involved salinized barley. They found phloem export of Na^+ and Cl^- from leaves to be only approximately 10% of the xylem import of those ions. In a more recent study on two genotypes of durum wheat that differ in rates of Na^+ accumulation in the leaves, Na^+ export from the shoot to the root via the phloem was very small (Davenport *et al.*, 2005). Nevertheless, Na^+ recirculation via the phloem may be of some importance in salt tolerance of halophytes (Tester and Davenport, 2003).

Hormonal regulation of salt tolerance

The integration of salt tolerance processes in the plant and their regulation is clearly dependent on the involvement of signaling pathways and plant hormones. This integrated control is a highly specialized field and is beyond the scope of this article. The interested reader is referred to recent reviews such as those prepared by Hasegawa *et al.* (2000), Munns (2002b), Zhu (2002), and Xiong (2007).

Table 2 Salt concentrations in the xylem and % Na and Cl exclusion from the xylem of plants grown in the presence of 50 mmol l^{-1} NaCl for 2 weeks

Species	*Genotype*	*Na^+*		*Cl^-*	
		Xylem exclusion		*Xylem exclusion*	
		Na^+ (mmol l^{-1})	*(%)*	*Cl^- (mmol l^{-1})*	*(%)*
Bread wheat	Janz	0.3	99	3.9	92
	Chinese spring	1.1	98	–	–
Durum wheat	Wollaroi	2.0	96	3.4	93
	Tamaroi	2.7	95	2.7	95
Rice	IR 36	2.8	94	–	–
Barley	Clipper	3.2	94	4.7	91
Citrus	Rangpur lime	2.4	95	1.5	97
	Rough lemon	3.3	93	2.6	95

Source: Reproduced from Läuchli, A., Grattan, S.R., 2012. Plant responses to saline and sodic conditions. In: Wallender, W.W., Tanji, K.K. (Eds.), Agricultural Salinity Assessment and Management. ASCE Manuals and Reports on Engineering Practice No. 71, pp. 169–205. New York, NY: American Society of Civil Engineers and Gregory, P.J., 2006. Plant Roots: Growth, Activity and Interaction with Soils. Oxford, UK: Blackwell Publishing, with permission from ASCE.

Crop Response to Saline Field Conditions: Interactive Abiotic and Biotic stresses

Most research that studies the effect of salinity on crops has been conducted in controlled laboratory and greenhouse environments, allowing scientists to better understand detailed responses and determine possible mechanisms the plant uses to cope with this stress. However, such experimental conditions do not reflect the natural conditions the plant encounters in salt-affected areas. There are a number of additional abiotic and biotic stresses that plants often endure under field conditions such as extreme temperatures, water deficits, flooding, nutritional inadequacies, poor physical conditions of soil, pathogens, and pests (Mittler, 2006; Läuchli and Grattan, 2007). Moreover, these stresses are not constant, but vary both spatially and temporally. Therefore, geneticists must be aware that genetically altered plants with higher salt tolerance must also thrive under field conditions with numerous additional interactive stresses for this improved plant to be commercially successful.

In the field, salt-affected crops must also contend with too much or too little water. Therefore, actual crop performance during the growing season is related to how the plant responds to both salinity and fluctuating soil–water conditions, either excessive or deficit.

Flooding

The combined effects of salinity and flooding are common in saline areas, particularly where shallow saline water tables exist or where soils are also sodic, reducing water infiltration and causing water to pond on the soil surface (Barrett-Lennard, 2003). In flooded or poorly drained soils, diffusion of oxygen to roots is reduced, thereby limiting root respiration and plant growth. In addition, important nutrients such as nitrate, sulfate, iron, and manganese can be chemically reduced, decreasing their availability to the plant (Kozlowski, 1997) and selective ion transport processes are disrupted (Drew *et al.*, 1988). Such hypoxic conditions adversely affect crop growth and developmental processes, influence morphological and anatomical adaptations, and cause many physiological dysfunctions in plants. When combined with salinity stress, Na and Cl concentrations increase in the shoot further decreasing plant growth and survival (Barrett-Lennard, 2003).

Water deficit

Plant stress from salinity and water deficit have much in common (Munns, 2002a), but how the plant responds to the combination of stresses remains unresolved (Homaee *et al.*, 2002). Under field conditions, water deficit is practically unavoidable as the soil water content varies temporally and spatially throughout the season. Therefore, some degree of both stresses can be occurring at different times and places in the root zone (Homaee *et al.*, 2002). For example, stress from water deficit may predominate in the upper portion of the root zone whereas salt stress may predominate in the lower portion.

Are the effects of salinity and water stress equivalent? Many evidences suggest that water deficit can be more damaging than an equivalent salt stress (Shani and Dudley, 2001; Shalhevet and Hsiao, 1986). For example, studies have shown that bean, pepper, and cotton were affected more by water stress than by salinity at equivalent reductions in soil water potential (see review by Maas and Grattan, 1999). Although matric and osmotic components are additive from a thermodynamic perspective, there are kinetic factors (i.e., water uptake and transpiration) that must be considered as well (Maas and Grattan, 1999). For example, the rate by which water is supplied to the root by the soil depends on soil water transport properties and evaporative demand. That is, plant response to these stresses under conditions of low evaporative demand is likely to be different than that observed under high evaporative demand as the matric and not the osmotic potential controls water flow to the roots from the surrounding soil. As the soil dries, the matric potential decreases, but increases the resistance of water flow to the roots in a nonlinear fashion (Homaee *et al.*, 2002). However, increases in soil salinity, at a given water content, reduces the osmotic potential but does not reduce water flow to the root. Moreover, the root cortical cells can osmotically adjust to some extent allowing water to readily move into the root. Clearly, the combination of stresses is more damaging than either one alone, but quantifying the growth-limiting contribution of each is difficult and can vary depending on the environmental conditions.

Plant pathogens

Salinity can affect the soil microbe populations in the rhizospere and their interaction with roots. For example, *Rhizobium* spp., which are integral to legume production, seem more salt tolerant than their host plants, but evidence indicates that nodulation and N_2 fixation by some crops are impaired by salinity (Läuchli, 1984). Other investigators have suggested that mycorrhizal symbioses improve the ability of some crops to tolerate salt by improving phosphorus nutrition (see review by Läuchli and Grattan, 2007).

Salt-stressed plants may be predisposed to infection by soil pathogens. Salinity has been reported to increase the incidence of phytophthora root rot in chrysanthemum (MacDonald, 1982) and tomato (Snapp *et al.*, 1991). The combined effects significantly reduced fruit size and yield of tomatoes (Snapp *et al.*, 1991), but wetter soil under salt-stunted plants, due to less evapotranspiration than nonsaline control plants, may contribute to increased susceptibility to fungal diseases. Research on salinity–pathogen interactions is rather limited despite its potential economic impact in salt-affected areas many of which are also prone to waterlogging. Therefore further research is warranted in this area.

Climate

It has long been known that climatic conditions have a profound influence on plant response to salinity. Crops are more sensitive to salinity in hot, dry climates than they are under cooler and more humid environments. The combined effects of salinity and conditions of high evaporative demand, whether caused by high temperature, low humidity, or increased wind are more stressful than salinity stress alone. Numerous crops including alfalfa, bean, beet, carrot, cotton, onion, squash, strawberry, clover, saltgrass, and tomato were found to be more sensitive to salinity at higher temperatures than

they are at lower temperatures whereas at high humidity many crops (e.g., barley, bean, corn, cotton, onion, and radish) were found to be more tolerant to salinity (see review by Läuchli and Grattan, 2007). As climate dramatically affects plant response to salinity, the time of year and location salt-tolerance experiments conducted will likely affect the results.

Soil physical conditions

Poor physical conditions of the soil can also contribute additional stresses in salt-affected areas (Grattan *et al.*, 2013). For example, soils with poor structure or impermeable layers could restrict root growth as well as influence water and salt distribution in the soil. Crusting at the soil surface acts as a physical barrier for emerging seedlings and can lead to poor stand establishment particularly if the young seedlings are already weakened by salt stress. Although there has been a considerable amount of research conducted on salinity and sodicity's effect on soil physical conditions, more research is needed to evaluate how these changes affect crop performance.

Composition of the salts in soil solution

Agricultural soils and irrigation waters around the world vary not only in salinity but also in the composition of salts, which is often characteristic of the geochemical properties of the area (Tanji and Wallender, 2012). In particular, the ratio of sodium to calcium varies dramatically. Gibbs (1970) analyzed the chemical constituents of global waters and found an interesting relationship between salinity and the ratio of Na/(Ca + Na), expressed in mg l^{-1}. Only in very pristine (< 10 mg l^{-1}) or extremely saline (> 10 000 mg l^{-1}) waters were the Na/(Ca + Na) ratio greater than 0.8. The ratio of Na/(Ca + Na) in most water sources used for agricultural production (100–1200 mg l^{-1}) is between 0.05 and 0.6, indicating that calcium is an important salinizing constituent. However, as salts in these waters concentrate due to evapotranspiration and reuse, these ratios increase due to precipitation of calcite and other divalent ion minerals in comparison to sodium (Tanji and Wallender, 2012).

Regardless of the fact that irrigation waters and agricultural soil solutions comprise multiple combinations of cations and anions, the vast majority of salinity experiments on plants use NaCl as the sole salinizing salt. Lazof and Bernstein (1999) discussed the shortcomings of research where not only NaCl was used as the sole salinizing salt but also those studies where nonsaline control treatments contained unrealistic trace amounts of Na and Cl. These investigators emphasize that the trace levels of NaCl in control treatments are problematic in light of observed stimulatory effects from small additions of NaCl up to 5 mmol l^{-1} in many glycophytes. Extremely high Na/Ca ratios, however, lead to nutritional disorders and secondary stresses due to adverse affects on soil conditions.

Not only is NaCl uncharacteristic of agriculturally saline environments, but experiments that use this as the sole salinizing salt create extreme ratios of Na/Ca, Na/K, Ca/Mg, and Cl/NO_3 in the root media (Läuchli and Epstein, 1990). These extreme ratios can adversely affect the mineral-nutrient relationship within the crop than would occur otherwise under normal saline environments (Grattan and Grieve, 1999). Nutrient imbalances in the crop may result from several factors including the effect of salinity on nutrient ion activity and availability, the uptake or distribution of a nutrient within the plant, or increasing the internal plant requirement for a nutrient element resulting from physiological inactivation.

The importance of calcium and its protective role for plants in saline environments has been known for over a century (Kearney and Harter, 1907). Calcium preserves the structural and functional integrity of cell walls and membranes and regulates ion transport and selectivity (Läuchli and Epstein, 1990; Cramer, 2002). Sodium-induced Ca^{2+} deficiency has been observed by numerous investigators when the Na^{+}/Ca^{2+} ratio in the solution, at a given salinity level for a particular plant, increases above a critical level. Crops in the grass family such as barley, corn, rice, sorghum, and wheat are particularly prone to this effect and large differences have been observed among species and cultivars (see review by Läuchli and Grattan, 2007.

Not all salt-affected soils are dominated by chloride salinity (Läuchli and Grattan, 2007). Many salt-affected soils are sulfate dominated such as those found in the Canadian prairie, California's San Joaquin Valley, and parts of Egypt and India. This article found that sulfate was less deleterious to growth than chloride at moderate salinity in alfalfa, pepper, and sorghum whereas at higher salinity levels, sorghum was more sensitive to sulfate salinity than it was to chloride salinity.

Interactions between salinity and boron toxicity

Boron is essential for cell wall structure and plays an important role in membrane processes and metabolic pathways (Brown *et al.*, 2002). However, there is a small range where concentrations in the soil solution are optimal (Gupta *et al.*, 1985). Above this range, boron becomes toxic and below it, boron is deficient. Toxicity can occur in crops when boron concentrations increase in young developing tissue or margins of mature leaves to lethal levels, but plant-tissue analyses can only be used as general guidelines for assessing the risk of B-toxicity (Nable *et al.*, 1997).

It has been known for decades that boron mobility is affected by climatic conditions and that it varies among species (Eaton, 1944). He found that after boron enters the leaf, it remains immobile in most plant species whereas in others, particularly in stone fruits, it can remobilize to fruits and other parts of the plant. More recent evidence has shown that boron can form complexes with polyols in some species allowing it to be phloem mobile (Brown and Shelp, 1997). In other species where these simple sugars exist in small amounts, boron remains immobile. This sheds light on why B-toxicity symptoms occur on margins of older leaves of some plants ('boron immobile') whereas toxicity symptoms appear on younger, developing tissue (i.e., tip dieback) in others ('boron mobile'). In those plants where boron is phloem immobile, boron concentrations in growing tips and reproductive tissue is much lower than concentrations in mature leaves. In boron mobile plants, just the opposite is found.

High boron, like salinity, is an important abiotic stress that adversely affects sensitive crops in many arid and semiarid climates. There are many agricultural areas around the world where both high salinity and high boron occur together (Tanji and Wallender, 2012). The question has recently been raised, are the effects of salinity and boron on crops additive,

synergistic, or antagonistic? From a review of the limited number of studies that addressed the combined effects of salinity and boron on the plant, it appears that the results are contradictory. In some cases salinity may enhance boron sensitivity whereas in others, it may reduce its sensitivity or have no effect. For example, investigators found that salinity enhanced B-sensitivity in wheat (Grieve and Poss, 2000; Wimmer *et al.*, 2001; Wimmer *et al.*, 2003), tomato, and cucumber (Alpaslan and Gunes, 2001) whereas other investigators found that salinity reduced boron's toxic effect in numerous vegetable crops, eucalyptus, and *Prunus* rootstocks (see review by Läuchli and Grattan, 2012). Regardless of these studies, tissue boron concentration was a poor indicator of toxicity. Therefore, it is unclear why crops vary in response to these combined stresses, but salinity can affect the boron distribution in plants and can affect the B-soluble fractions within the shoot (Wimmer *et al.*, 2001; Wimmer *et al.*, 2003). These investigators suggest that the soluble-B fraction in cells is an indicator of B-toxicity in wheat.

Moreover, recent research has shown the pH can have a profound influence on salinity–B interactions (see review by Läuchli and Grattan, 2012). In a controlled sand tank experiment at the USDA/ARS Salinity Laboratory with cucumber, increased salinity, boron, and pH (from 6 to 8) decreased the fruit yield but investigators did not find any significant salinity–boron interaction. However in slightly acidic conditions, regardless of salinity, increased boron was more detrimental than it was in slightly basic conditions. When the experiment was repeated with broccoli, investigators found different results (Smith *et al.*, 2013). They found that an increase in soil–water boron from 1 to 21 mg l^{-1} at pH 6 did not significantly reduce the head yields of broccoli at any salinity level. However at pH 8, as boron increased from 1 to 21 mg l^{-1}, head yields at both low (EC 2 dS m^{-1}) and high (EC 14 dS m^{-1}) were reduced by more than 85%. Interestingly at moderate salinities (EC 5–11 dS m^{-1}), increased boron had very little detrimental effect.

Much has been learned over the past decade regarding salinity–boron interactions but many questions remain unresolved. More research is needed to (1) understand the relationship between visual injury symptoms, tissue boron concentrations, soluble boron fractions, the role pH plays, and how these all interact affecting crop yield and (2) the influence of salinity on the soluble fractions of boron, boron mobility, and distribution within the plant and how these relate to visual injury.

In summary, plants under field conditions often endure multiple stresses during their development. However, the vast majority of research has focused on individual stresses in the absence of others. Plant response to combined stresses cannot be readily extrapolated based on their response to individual stresses (Mittler, 2006).

The potential interactions among several agricultural stress combinations are illustrated in **Figure 6** (Läuchli and Grattan,

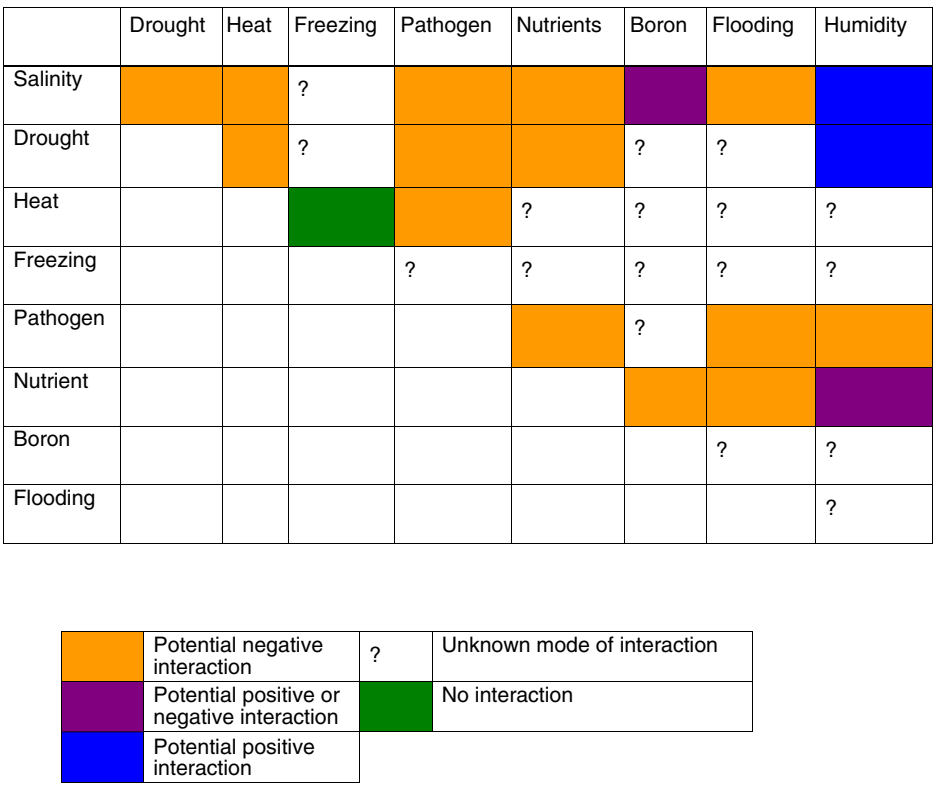


Figure 6 Agriculturally important environmental factors and their potential interactions. Reproduced from Läuchli, A., Grattan, S.R., 2007. Plant growth and development under salinity stress. In: Jenks, M.A., Hasegawa, P.A., Jain, S.M. (Eds.), Advances in Molecular-Breeding Towards Salinity and Drought Tolerance. New York, NY: Springer-Verlag, pp. 1–31 and Mittler, R., 2006. Abiotic stress, the field environment and stress combination. Trends in Plant Science 11, 15–19, with permission from Springer Science and Business Media.

2007). Some stress combinations show negative interactions whereas others exhibit positive interactions. For some stress combinations, there are no or unknown mode of interactions. Therefore, Mittler (2006) suggested that tolerance to a combination of stresses should be the focus of future research, particularly those where the goal is to develop transgenic crops with enhanced tolerance to natural adverse field conditions. Only by considering these additional stresses that plants endure under field conditions can true advancements be made in salinity tolerance research.

See also: Plant Abiotic Stress: Water. Water Use: Recycling and Desalination for Agriculture. Water: Water Quality and Challenges from Agriculture. World Water Supply and Use: Challenges for the Future

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Plant Abiotic Stress: Temperature Extremes

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Glossary

Anther dehiscence Splitting of anther pores (apical and basal) to allow pollen shedding on stigma during anthesis.
Anthesis Spikelets open with external protrusion of anthers.
Critical threshold The physiological limit beyond which there is significant loss in plant fitness.
Microsporogenesis The formation of microspores (male gametes) inside the microsporangia (or pollen sacs) of seed plants.
Ontogenetic development Origin and development of an organism from embryo to adult stage.

Introduction

World population is expected to reach 9.2 billion until 2050 (FAO, 2009). To feed this steadily growing population, it is estimated that world food production has to be increased by 70%, with demand for staple cereals, including rice, to increase by 43%. On the contrary, the annual yield increase has steadily declined from 3.2% per annum in 1960 to 1.5% in 2000 as a result of limited genetic biodiversity and changing climate (Powell *et al.*, 2012). Further, global climate models predict with >90% probability that increasing levels of CO_2 and other greenhouse gases may raise global mean air temperature by approximately 1.4–4.5 °C by 2100 (IPCC, 2007). With the increase in daily mean temperature, it is observed that the minimum nighttime temperature is increasing at a faster rate than daily maximum temperature both globally (Vose *et al.*, 2005) and regionally (Peng *et al.*, 2004).

The growth and productivity of rice could be negatively affected by temperature extremes depending on the developmental stage of the crop, and the intensity and duration of stress exposure. Most of the tropical and subtropical rice-growing areas are already close to the documented day temperature threshold of 33 °C (Nakagawa *et al.*, 2002, Teixeira *et al.*, 2011). Any further increase in temperatures coinciding with the sensitive stages such as anthesis and microsporogenesis will reduce spikelet fertility and grain yield (Shah *et al.*, 2011). Furthermore, high temperature affects grain-filling processes by reducing the substrate supply time, substrate translocation, and deposition in the grains (Fitzgerald and Resurreccion, 2009). However, mean seasonal night temperature above 23 °C recorded a 10% decline in yield and biomass for each 1 °C rise (Peng *et al.*, 2004). Likewise, a decline in yield across south and southeast Asian rice-producing regions was recently documented with average monthly night temperatures exceeding 24 °C (Welch *et al.*, 2010).

On the other extreme, cold-temperature stress adversely affects rice at the seedling stage in the subtropics (Ranawake and Nakamura, 2011) and at all growth stages in the temperate regions where it is grown as a summer crop. The critical threshold below which rice plants start to show a negative response is documented to be ≤15 °C (Zhang *et al.*, 2005). In some subtropical regions such as Brazil (comprising approximately 1 million ha of rice), cold stress at the vegetative stage accounts for up to a 20% yield loss (Cruz *et al.*, 2010).

Plants often have a strong adaptive mechanism to cope with unfavorable changes in the environment. However, tolerance of an abiotic stress such as temperature stress is a complex quantitative trait and considerable genetic variability is recorded among genotypes under different environments or within a similar environment. In this article, the authors have summarized the response of rice to extreme temperatures (heat and cold) and the basic mechanisms for adaptation, i.e., avoidance, escape and tolerance, particularly during the sensitive flowering and grain-filling stages. Using rice as a case study, the authors have shown the systematic approaches followed at the International Rice Research Institute, Philippines (IRRI), in an attempt to adapt rice to extreme heat stress and the extended impact of temperature interactions with other environmental factors. The word 'extreme' in this article is used in the context of temperatures above (heat stress) and below (cold stress) the critical thresholds identified for rice.

Response of Rice to Temperature Stress

Vegetative Growth

For most cereals, including rice, the vegetative stage is generally considered to be more tolerant of temperature extremes than other stages. However, tolerance of either cold or heat stress at the vegetative stage does not automatically translate into tolerance at the reproductive stage (Ranawake and Nakamura, 2011). High day temperatures during the seedling stage lead to poor establishment, reduced height, and reduced tillering potential (Shah *et al.*, 2011). Kanno *et al.* (2009) reported that high night temperature under controlled environments promoted vegetative growth and biomass in rice, whereas contrasting results were obtained with a 10% decline in biomass under field conditions (Peng *et al.*, 2004), indicating a knowledge gap with rice response to high night temperature. Conversely, for rice grown in early spring in temperate or subtropical environments, low-temperature effects on seedlings

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can be manifested as poor germination, slow growth, leaf discoloration or yellowing, withering, reduced tillering, and stunted growth (Andaya and Mackill, 2003).

Reproductive Development

The reproductive phase of the rice crop is known to be highly sensitive to exposure to both temperature extremes (Zinn *et al.*, 2010). High tissue temperature ≥33.7 °C (ambient air temperature of 35 °C) for even less than 1 h coinciding with anthesis is sufficient to induce sterility in rice (Jagadish *et al.*, 2007). The reproductive stage of rice encompasses several processes that are equally sensitive to high temperatures, namely, (1) microsporogenesis and early microspore development, (2) dehiscence of the anther, (3) shedding of pollen, (4) germination of pollen grains on stigma, and (5) pollen tube growth and fertilization (Rang *et al.*, 2011; Jagadish *et al.*, 2012). In the same way for high temperature, the young microspore stage of male gametophyte development is reported to be sensitive for cold stress in rice, resulting in pollen sterility and large yield reductions, a phenomenon that is characteristic of temperate rice-growing regions (Oliver *et al.*, 2007). Pollen sterility triggered by cold stress causes repression of the apoplastic sugar transport pathway in the tapetum, resulting in a disruption of sugar transport in anthers (Oliver *et al.*, 2007). Additionally, high night temperatures negatively affect pollen germination, which subsequently reduces spikelet fertility (Mohammad and Tarpley, 2009). Response of the female reproductive organ to adverse temperature stress is less understood.

Grain Filling and Development

The early phase of grain filling in rice is sensitive to extreme heat, and cumulative heat stress from the reproductive stage to grain filling drastically reduces grain endosperm size, the rate of development, grain number, and grain size (Morita *et al.*, 2005).

At the process level, exposure to high temperature during the grain-filling stage is associated with down-regulation of starch-synthesizing genes, whereas the level of starch-consuming enzymes and heat shock proteins gets up-regulated, ultimately resulting in reduced grain weight (Yamakawa *et al.*, 2007; Yamakawa and Hakata, 2010). Increased temperatures (both daytime and nighttime) accelerate ontogenetic development, so that maturity is reached earlier and the grain-filling duration is shortened. This reduces the time span for translocation of stored assimilates from the vegetative tissue, i.e., stem and leaf sheath, to the grains, leading to increased partially filled grains. Extremely high night temperature may result in increased respiratory losses and cause an insufficient supply of photosynthates to the grain. Similarly, cold stress can potentially reduce the grain development and filling by increased spikelet sterility and reducing photosynthesis and carbohydrate supply. However, information on the direct effect of cold temperature on sink strength and endosperm development in rice is still limited.

Grain Quality

Rice grain quality is characterized by traits grouped under physical appearance and cooking, sensory and nutritive properties (Fitzgerald *et al.*, 2009); of these, grain appearance and eating quality are the major factors that influence cultivar selection by farmers. High temperature greatly increases chalkiness in rice, and reduces gel consistency and amylose content, etc. Among these factors, chalk content is the principal determinant of market revenue. Temperature stress during the early grain-filling stage results in an increase in white core chalk, which determines the proportion of broken (<3/4 the size of a whole kernel) and the head rice (≥3/4 the size of the whole kernel) recovery, and, the greater the broken, the lower the market price (Counce *et al.*, 2005). High temperatures during the later grain-filling period result in white belly (peripheral part of the endosperm) chalk, which does not contribute toward grain breakage but decreases the quality of the visual appearance and hence entails a penalty in the market price. At the same time, some varieties have high assimilate translocation efficiency to compensate for the reduced grain-filling duration in response to increased temperatures, so they can potentially overcome or reduce chalk formation (Kobata and Uemuki, 2004). Furthermore, a rise in mean temperature (~31 °C) can result in a sharp decline in amylose content, resulting in changes in starch composition, which in turn increases the stickiness in cooked rice and reduces the degree of aroma (Nagarajan *et al.*, 2010). Effect of cold stress on rice quality traits is, however, poorly understood.

Temperature Stress Adaptation Mechanisms

Plants have adapted to a range of survival mechanisms under adverse environmental conditions. Rice in response to extreme heat stress exposure during the day can use its avoidance, escape, or true tolerance strategy and ensure normal reproductive success and grain yield.

Heat Avoidance

Changing leaf orientation, transpiration cooling, a reduction in nonphotosynthetic energy intercepted by the canopy and reflection of solar radiation are some ways by which crops avoid heat stress, of which transpiration cooling is perceived to be a dominant mechanism. High day temperatures in association with low humidity allow efficient use of transpiration cooling as long as the water supply is sufficient. High transpiration rates on rice plants are decisive features in hot environments such as in Pakistan, Iran, and Senegal as well as in the highly productive rice-growing regions of Punjab in India with temperatures of ≥38 to 40 °C during the heat-sensitive stages. The low moisture content in the air stimulates plant transpiration, thereby cooling the plant's immediate micro climate by up to 8 °C or more (Wassmann *et al.*, 2009). In the long run, however, with greater pressure on freshwater availability and erratic precipitation patterns, these productive regions are under intense risk with future warming climates. Moreover, the trend toward newer technologies to grow rice under less water, i.e., dry-seeded rice and aerobic rice, may further deteriorate yield potentials in high-temperature regions as these technologies are inherently more sensitive to increasing temperatures.

Heat Escape

As heat stress leads to immediate yield losses, farmers have intuitively adjusted cropping calendars to avoid high temperatures at the sensitive flowering stage. However, the time windows for sowing/transplanting are often restricted by other factors such as seasonal availability of rainfall and optimum radiation patterns to achieve high yields. In turn, adaptation at a micro level, i.e., the time of day of flowering, can be seen as a more promising option given that some rice types are observed to flower even at night. Wild rice (*Oryza officinalis*) flowers in the early morning at 06.00, a trait that will allow the sensitive flowering period to escape the high temperatures during late morning and early afternoon (Sheehy *et al.*, 2007). Recently, the genetic source of variation has been exploited and the chromosomal fragment inducing this change has been identified and introgressed into cultivated japonica and indica entries. This introgression has altered peak flowering to occur up to 2 h earlier in cultivated varieties such as Koshihikari (Ishimaru *et al.*, 2010). Because the actual physiological processes during anthesis, including pollination and pollen germination, are completed during the cooler hours of the morning and with high temperatures having no significant impact on fertility immediately after flowering (Yoshida *et al.*, 1981), early-morning rice accessions maintain good seed-set. This strategy can provide some respite for the immediate concern of extreme heat-induced spikelet sterility but the effect on different developmental stages, particularly microsporogenesis or grain filling, cannot be addressed through this approach and hence would require true heat tolerance or a combination of strategies.

True Heat Tolerance

Heat avoidance is useful in specific regions of high water availability and low relative humidity. However, heat escape depends on the stability of the trait in interaction with other environmental conditions, so that 'true' heat tolerance remains as the more sturdy solution across a wide range of vulnerable rice-growing regions. Incorporating heat tolerance in widely adapted rice varieties would allow reducing heat-induced losses not just at the flowering stage but also at microsporogenesis and other key developmental stages. This approach would require identifying rice entries with the ability to tolerate a higher degree of heat stress (irrespective of their yield or agronomic characteristics), which would translate into normal microsporogenesis and maintain pollen viability, thus allowing fertilization and seed-set to progress. A rice cultivar N22 was consistently identified as the most heat-tolerant accession in response to high day temperatures, and it was also reconfirmed at IRRI as the best performing entry dealing with microsporogenesis and under high night temperature. Although it has poor agronomic traits and low yield potential, its heat tolerance trait is being used in breeding programs at IRRI. Genetic progress at IRRI has resulted in the identification and reconfirmation of the most heat-tolerant accessions of N22, and the chromosomal regions (QTLs) inducing this heat tolerance have been identified (Ye *et al.*, 2012). Additionally, using molecular approaches, three candidate heat shock proteins, possibly having an active role in pollen viability and pollen germination under heat stress, have been identified (Jagadish *et al.*, 2010, 2011) and are being functionally validated through a transgenic approach. This genetic and molecular progress in combination with molecular marker technology will allow transferring heat tolerance into rice mega-varieties.

Acquired tolerance/acclimation involves modification of the crop's structure and function in response to mild stress such that the impact of severe stress is reduced compared to the crop's response in the absence of this modification. After a short exposure to stress or heat shock (<2 h), the plants respond with a cascade of signaling. This cascade starts with key signaling molecules (e.g., calcium, salicylic acid, hydrogen peroxide, etc.) and ultimately results in enhancing antioxidant defense machinery and up-regulating heat shock proteins that induce acquired thermo tolerance (Sung *et al.*, 2003). This temporal expression of defense genes acclimatizes the plant for a definite period and provides tolerance at the susceptible stage exposed to damaging levels of stress.

Cold Escape and Tolerance

Cold temperature ($\leq$10 °C) can seriously hamper seed germination or seedling establishment in rice and likewise low night temperatures are more damaging at reproductive development. Some management practices such as deep standing water at the panicle initiation stage, low nitrogen supply (to expose minimum biomass to cold nights), and adjusting sowing time (early sowing) are being adopted for cold escape. The adoption of new cultivars with traits such as more spikelets per panicle and more panicles and tillers with erect plant type even under low soil nitrogen seems to be effective to minimize yield loss in temperate regions (Anzoua *et al.*, 2010).

At low temperature, the tolerance mechanism employed to ensure survival includes the generation of reactive oxygen scavengers to minimize the effect of increased production of reactive oxygen species, and the accumulation of sucrose and other simple sugars in the apoplastic space to prevent intercellular ice from forming adhesions with cell walls and membranes that cause the cell to rupture (Sanghera *et al.*, 2011). Screening diverse germplasm for cold tolerance traits (e.g., coleoptile length, coleoptile regrowth, spikelet fertility, etc.) and using it in breeding programs can be deemed a promising approach to sustain rice production in temperate regions. Apart from conventional breeding methods, cold acclimation and incorporation of cold tolerance genes through gene pyramiding provide a new avenue for rice production, especially under extreme environments. Rice transgenics with genes such as *OSISAP1* (Mukhopadhyay *et al.*, 2004), *OsMYB3R-2* (Ma *et al.*, 2009), and many others for membrane stability (FAD1-7) and cryoprotectants are reported to be tolerant for cold and other abiotic stresses.

Adapting Rice to High-Temperature Stress – Prospects and Constraints

Adjusting agronomic practices to improve the outcome of crop response to extreme temperature involves many players and

differs from place to place, which makes adaptation an uneasy venture. Adaptation will have to be suited to the local climatic conditions. Some practices followed under high-temperature conditions are growing more tolerant crops, altering planting time to avoid reproductive damage, increasing the use of climate forecasting information to reduce risks and also using resilient agricultural systems (Howden *et al.*, 2007). But, many rice-producing regions (tropical and subtropical) are now at or slightly above the optimum temperature thresholds for rice production, which requires greater interventions under future extreme climatic events.

Some difficulties are associated with adaptation options such as altering planting dates and using short-duration varieties. Although altered planting time is considered and is partly being followed as an option to overcome heat stress, the major concern with extreme heat is the variability of heat spikes more than the rise in mean temperature, which is difficult to predict. Hence, altered planting is a 'hit or miss' option because the heat spikes could occur at any stage of the rice growth cycle. Short-duration rice varieties could be another option in areas with reduced water availability but, in cases where water is sufficient, it is hard to convince farmers to use a shorter duration variety that would invariably have a yield penalty, at times accompanied by undesirable quality parameters. Other problems can also be encountered, for example, delayed rice planting to avoid cold stress during the dry season in the Sahel savanna of west Africa led to serious yield losses mainly due to unexpected early rains. Moreover, long-established cultures and traditions in many rice-producing areas of Asia and Africa do not favor changes in farming practices. Hence, our current research prioritizes the identification of genetic variation for traits such as early-morning flowering or heat tolerance, for example, from landraces and using molecular marker technology to introduce the trait of interest into a farmer-preferred variety. By doing so, farmers still have their preferred variety with no change in yield or grain quality but with the target trait, for example, early-morning flowering or higher temperature tolerance, to overcome heat stress.

Conclusions

To overcome the rapidly increasing temperature effects, efforts have been intensified to identify heat-avoiding rice accessions, incorporating the early-morning flowering from *Oryza officinalis* and the QTLs and genes inducing true heat tolerance into farmer-preferred varieties. Using information from GIS mapping, hot spots for screening early and advanced generation breeding lines have been selected in India and Bangladesh. These hot spots have been grouped into hot-dry (where heat avoidance is an effective trait) and hot-humid (where either early-morning flowering or heat tolerance is more effective). Advances in molecular technology, particularly high-throughput genotyping and molecular marker-assisted backcrossing, are being employed to fast-track the developing rice varieties to withstand rapidly increasing temperatures. Similar approaches to enhance cold tolerance are under way.

See also: Food Security: Yield Gap. Plant Abiotic Stress: Water

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Plant Abiotic Stress: Water

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Glossary

Gene expression A process by which genes on DNA are transcribed into ribonucleic acid (RNA), which then translates into proteins or functional products.

Gene ontology A major bioinformatics initiative with the aim of standardizing the representation of gene and gene product attributes across species and databases. The project provides a controlled vocabulary of terms for describing gene product characteristics and gene product annotation data from GO Consortium members as well as tools to access and process these data.

Genetic linkage map A map of genes that are located proximally to each other on a chromosome to be inherited together during meiosis.

Microarray A collection of microscopic DNA spots attached to a solid surface. Scientists use DNA microarrays to measure the expression levels of large numbers of genes simultaneously or to genotype multiple regions of a genome.

MicroRNA (miRNA) These are usually not expressed to directly produce proteins, but their presence can affect the expression from other genes that typically do lead to the production of proteins. The small miRNAs sequences target messenger RNAs (mRNAs) to induce cleavage of the mRNAs and repress their translation into proteins.

RNA sequencing A technology that uses the capabilities of next-generation sequencing to reveal a snapshot of RNA presence and quantity from a genome at a given moment in time.

Introduction

Water is the most abundant compound on the earth's surface, covering nearly 70% of the planet. However, only 2.5% of total water on the earth's surface is fresh water (Table 1), i.e., if the earth's total water is equivalent to a gallon then fresh water is 20 teaspoons in volume. Most of the fresh water on the earth is locked up in glaciers as ice and only a small fraction is available in rivers and lakes (Table 1). Owing to the population explosion and economic growth, the majority of fresh water in rivers and lakes is being consumed by urban and industrial users leaving a small fraction for agriculture, with a recent prediction indicating that by 2030, nearly 47% of world population will be living in areas of high water stress (UN-Water). Although excess water can also create stress on plants, these data indicate that fresh water is increasingly becoming a scarce resource on the earth and stress caused by lack of water – commonly referred to as drought stress – is becoming an even more significant factor in limiting food production than it was previously. For the remainder of this article, the authors have referred to the stress of having inadequate water as water stress.

Agriculture depends on rainfall in many regions of the world. Global rainfall pattern is highly variable on a spatial scale and severe droughts have occurred many times in each of the major agricultural regions of the world, including Central United States, Southeastern China, India, Central Europe, Eastern Australia, and Southern Africa, during 1900–93 (Dai *et al.*, 1997). More recently, global drought severity index data captured during 2000–11 indicated that drought has occurred globally at high frequency and intensity (Mu *et al.*, 2013). Notable are the long-term droughts in South and Southeast Asia, Western United States, Central and Southern Africa, and Southern and Eastern Australia (Mu *et al.*, 2013). The duration and intensity of droughts have generally increased globally (Food and Agriculture Organization (FAO) facts). Since 1900, more than 11 million people have died due to drought and more than 2 billion people have been affected by drought (FAO facts). Extensive economic losses (in billion US dollars) have occurred due to drought in the United States, China, Australia, Spain, and other countries (Statista, 2013). The 2011 and 2012 extreme droughts in the United States caused an estimated loss of 20 and 8 billion dollars, respectively (Statista, 2013). Therefore, it is needless to say that water stress has profound effects on the global economy and human society.

Given its importance among abiotic stresses, a modest attempt is made here to summarize several concepts related to water stress in agricultural crops. The purpose of this article is not to provide an in-depth discussion on concepts related to crop water stress. Instead, the article is a summary of concepts that provides enough background to a novice reader while providing an updated review to an experienced reader. The following are discussed in the article: (1) water uptake and loss in crops; (2) water stress effects at the molecular, metabolic, and physiological levels in crops; (3) reducing yield loss under water stress; and (4) industry efforts to develop drought-resistant hybrids/varieties.

Water Uptake and Loss in Crops

Plants experience water stress when water extraction from the roots is less than that lost from the plants (usually from the aerial leaves and stems) determined by the evaporative demand of the atmosphere (Hall, 1993). It is ironic that, in spite of fundamental importance of water on plant metabolism, plant water uptake and loss are controlled largely by the environment and to a lesser extent by the plant. Therefore, to fully appreciate the concept of water stress it is important to understand how water moves from the soil to the plant, inside the plant, and evaporates to the atmosphere from the plant. This path of water movement into, through, and out of a plant

Table 1 Earth water resources

Observation	*Actual*	*%Total water*	*%Fresh water*
Total volume of water	1.4 billion km^3	100	n.a.
Volume of fresh water	35 million km^3	2.5	100
Volume of fresh water in glaciers	24 million km^3	1.7	70
Volume of fresh water stored underground	9.95 million km^3	0.72	27
Volume of fresh water in rivers and lakes	1.05 million km^3	0.08	3
Volume of water in the atmosphere	13 000 km^3	0.000 9	0.04
Volume of fresh water for the ecosystem and humans	200 000 km^3	0.014	0.6

Source: UN Water (UNWater.org).

is called the 'soil–plant–atmosphere continuum (SPAC)' and happens due to the gradient in 'water potential' along the path between soil–root, root–stem, stem–leaf, and leaf–atmosphere.

Water potential (denoted as Ψ) is the potential energy per unit volume (or pressure) of water in a system (e.g., soil) relative to that of the pure water at the reference pressure, temperature, and elevation. The water potential of pure water is arbitrarily set at zero; therefore, water potential of any (soil/plant/atmosphere) system is negative. In plant physiology, water potential has units of pressure (Pa for 'pascal') and water moves from a region of high pressure to low pressure. Water potential is influenced mainly by three components viz., gravitational potential (pressure of gravity on the mass of water), pressure potential (physical pressure of water on surfaces), and osmotic potential (pressure due to bonding of water to charged ions, which is related to what is dissolved in the water). The pressure potential is positive when saturated (e.g., water pressure on top of the soil after irrigation or turgor pressure on cell walls) or negative when unsaturated (e.g., matric pressure in the soil or xylem pressure). Gravitational potential is always positive, whereas osmotic potential is always negative.

The major driving force for water movement in the SPAC (pathway from soil through plants to the atmosphere) is the gradient in water potential generated by 'transpiration pull' caused by water evaporating through the process of transpiration from the plant. Water in the plant forms a continuous network of liquid columns from absorbing surfaces of roots to the evaporating surfaces in leaves. Water moves from the regions of high water potential to that of low water potential. The water potential of the atmosphere is very low (at 30 °C and 50% RH, the water potential of the atmosphere is approximately -97 MPa). Because the water potential of the leaf is higher than that of the atmosphere, water evaporates from the leaf to the atmosphere. This lowers the water potential of the adjoining regions of the evaporative surfaces in the leaf and the process continues into the xylem and to the roots, thus establishing a gradient in water potential in the plant that further moves water from the soil into roots to the aerial parts of the plant.

An illustration of gradient in water potential that exists under irrigated or water stress conditions is shown in **Figure 1**. Under irrigated conditions (**Figure 1**), leaf water potential of approximately -1.0 MPa, root water potential of approximately -0.4 MPa, and soil water potential of approximately -0.01 MPa were observed for maize seedlings (Adeoye and Rawlins, 1981). As the soils dried down during water stress (**Figure 1**), soil water potential decreased from approximately -0.01 to -0.6 MPa (moderate drought stress) and root and leaf water potentials further decreased from approximately -0.4 to -1.2 and approximately -1.0 to -1.6 MPa, respectively, in maize seedlings (Adeoye and Rawlins, 1981). Under field conditions, leaf water potentials in the range of -0.5 to -2.5 MPa are commonly seen for crop species (Cary and Wright, 1971). Leaf water potential can change significantly during the day, with maximum values in the morning and minimum values during the afternoon (Cary and Wright, 1971; Acevedo *et al.*, 1979). As the soil dry-down progresses during the drought stress, it becomes increasingly difficult to maintain the water potential gradient and extraction of water from the soil. Generally, a soil water potential of -1.5 MPa is considered the 'permanent wilting point' for crops (Taiz and Zeiger, 2010). At this point, no soil water is available for extraction by roots. Water is held by the soil particles at a pressure equivalent to approximately 15 times greater than the standard atmospheric pressure at permanent wilting point.

Water Stress Effects at the Molecular, Metabolic, and Physiological Level

When plants are exposed to water stress, a large number of molecular, metabolic, and physiological changes occur that, in turn, result in phenotypic changes that enable plants to mitigate the effects of the stress. Stress mitigation is seen as a reduced loss of yield at the field or agronomic scale.

The first step in plant response to water stress is to perceive the stress signal or 'signal perception' (**Figure 2**). The stress signal is perceived by receptors located on the cell surface (e.g., receptors like kinases and ion channel-linked receptors) or stress sensors inside cells (e.g., abscisic acid (ABA) sensor, hexokinases, and reactive oxygen species (Bhargava and Sawant, 2013)). The stress signal perceived by the receptors or sensors is transferred to the nucleus to activate the expression of genes needed to effect change in the plant by a process called 'signal transduction' (**Figure 2**). Some examples of messengers that enable this signal transduction are mitogen-activated protein kinases, calmodulin-binding proteins, and phosphoinositides (Bhargava and Sawant, 2013).

The arrival of stress signals at the cell nucleus results in either up- or downregulation (differential gene expression) of stress-specific genes. Changes in the expression of genes that code for osmolyte synthesis, late embryogenesis abundant

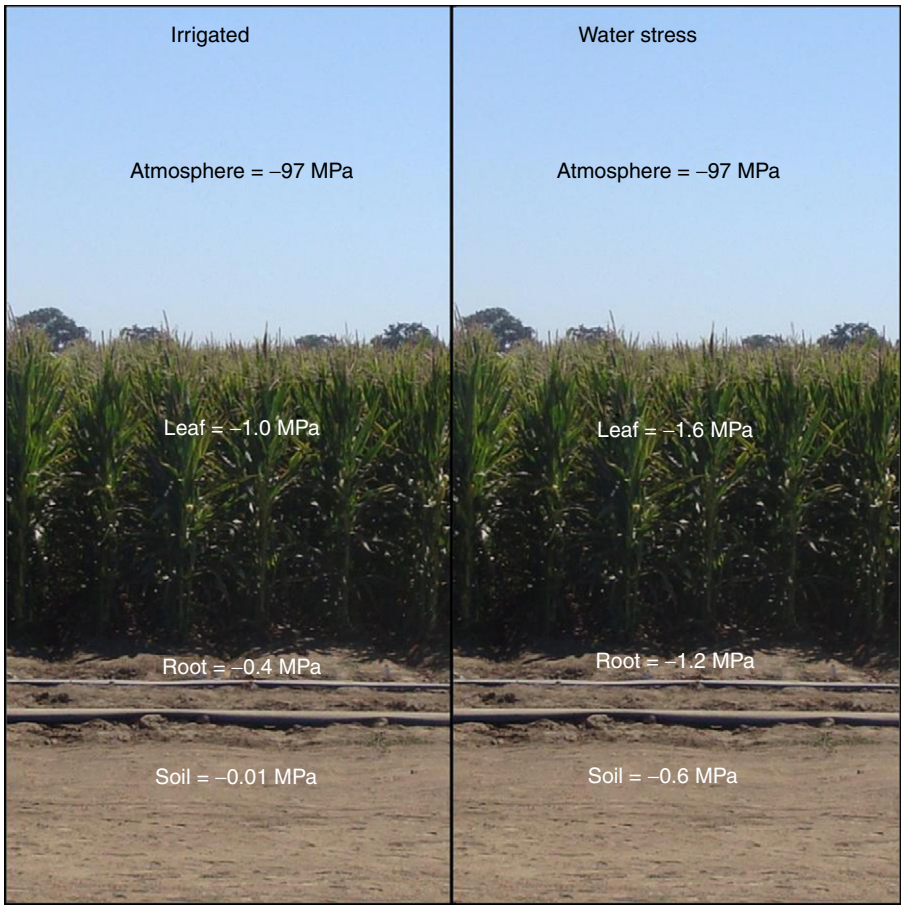


Figure 1 Differences in water potential in the soil-plant-atmosphere continuum under irrigated and water stress conditions in a field.

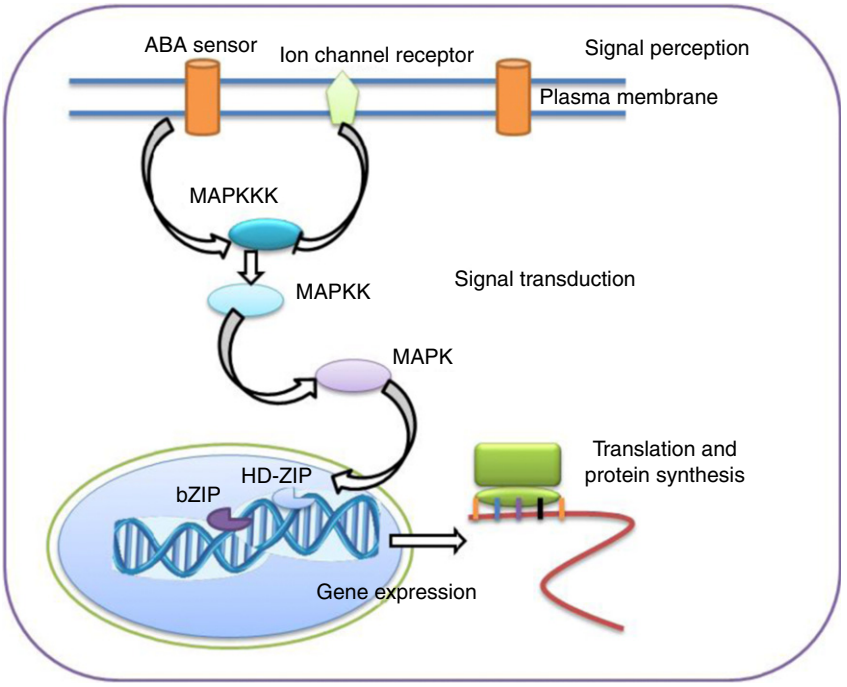


Figure 2 Signal perception, signal transduction, gene expression, and translation in plants.

(LEA) proteins, aquaporins, signaling molecules, and transcription factors (regulate expression of multiple genes) have commonly been detected in plants under drought stress (Bhargava and Sawant, 2013). Transcription factors that bind to the promoter region of other stress-response genes and regulate their expression can be produced (**Figure 2**). Several families of transcription factors, such as bZIP, AP2/ERF, HD-ZIP, MYB, NF-Y, and ZPT2, are known to regulate drought-specific gene expression (Bhargava and Sawant, 2013).

What changes do these genes produce in the plant? In response to stress signal transduction, several genes are differentially expressed, resulting in changes in stress-related metabolic pathways. Global gene expression is typically studied using microarrays (using complementary deoxyribonucleic acid (c-DNA) copies of messenger ribonucleic acid (mRNA) as a target for DNA probes) or more recently using RNA-sequencing (RNA-seq) analysis. Gene-expression changes under water stress in maize using RNA-seq analysis have indicated that more changes are generally seen in reproductive tissue than in vegetative tissue (Kakumanu *et al.*, 2012). This agrees with the observations that reproductive tissues are more sensitive to drought stress than vegetative tissue in maize. Downregulation of starch and sucrose biosynthesis genes and a host of genes encoding cell cycle progression and upregulation of genes encoding ABA biosynthetic pathway have been observed in maize (Kakumanu *et al.*, 2012). In response to water stress, gene-expression changes affect several stress-related metabolic pathways that result in changes in metabolites in different tissues. When metabolite changes were measured under water stress and well-watered conditions in maize hybrids, amino acids, sugars, and intermediates of the tricarboxylic acid cycle (TCA) cycle were increased under water stress conditions relative to well-watered conditions (Witt *et al.*, 2012). Changes in the amino acids, including proline, histidine, asparagines, tryptophan, and phenylalanine, were increased in all major tissues (Witt *et al.*, 2012).

In soybeans, microarray analysis of soybean leaves under water stress indicated that both transcription factors (DREB, NAC, and ZAT/STZ) and functional proteins (LEA proteins, glycosyltransferases, glycoside hydrolases, defensins, and glyoxalase I family proteins) were upregulated, whereas genes related to hormone pathways and photosynthesis-related genes were downregulated (Le *et al.*, 2012). Metabolite analysis of soybean plants under water stress indicated that accumulation of pinitol, a common osmolyte in legumes, was observed. In addition, accumulation of proline was observed under flowering stage; several changes in the intermediates of the TCA cycle were observed and nitrogenase activity was not altered (Silvente *et al.*, 2012). In rice, the majority of differentially expressed genes under water stress were identified in the leaf tissue at panicle-initiation stage (Wang *et al.*, 2011). Gene ontology revealed that several genes related to the photosynthetic pathway, cell membrane biogenesis, and cell wall modification were downregulated under water stress in rice (Wang *et al.*, 2011). Also in rice, photorespiratory metabolism increased, whereas no changes in Calvin cycle metabolism were noticed under water stress (Lakshmanan *et al.*, 2013).

At the physiological level, water stress can result in both short-term and long-term (acclimation) responses. Short-term responses to water stress include root signaling, changes in xylem conductivity, ABA-mediated stomatal closure, and inhibition of growth (Chaves *et al.*, 2003). Acclimation changes to water stress include osmotic adjustment, reduced leaf area, changes in carbon metabolism (lower photosynthesis and respiration), and changes in source–sink relationships and partitioning (more root or reproductive tissue growth over leaf growth) (Chaves *et al.*, 2003).

Considering the vast extent of research done in the area of water stress-induced physiological changes in plants, the article focuses on changes that affect crop yields. For field crops, timing of water stress is crucial. Maize is most sensitive at flowering stage (Claassen and Shaw, 1970; Boyer and Westgate, 2004; Campos *et al.*, 2006), whereas soybean is most sensitive to water stress between pod formation and pod-filling stages (Manavalan *et al.*, 2009). Rice is most sensitive to water stress during panicle initiation and flowering (Wopereis *et al.*, 1996; Lafitte *et al.*, 2007). The effect of water stress on physiological changes affecting crop yield can be understood from the equation $\text{Yield} = \text{WUE} \times \text{E} \times \text{HI}$ (Passioura, 1996; Blum, 2009), where WUE is water-use efficiency calculated as ratio of biomass produced to transpiration, E is transpiration, and HI is harvest index, calculated as ratio of grain yield to total biomass production.

WUE is affected by processes that affect both biomass production and transpiration in plants (**Figure 3**). Owing to an efficient photosynthetic pathway coupled with lower stomatal conductance in C4 plants, WUE of C4 species is higher than that of C3 species. For example, WUE of maize (C4 plant) is nearly 3–5 times higher than that of soybean and 2 times higher than that of rice (Sadras *et al.*, 2007, FAO report), both C3 plants. WUE of sorghum (C4 plant) is higher than that of soybean due to higher assimilation and lower transpiration rates (lower leaf area and stomatal conductance) in sorghum (Teare *et al.*, 1973). Generally, WUE is higher under water stress than irrigated conditions. Expression of the *Arabidopsis HARDY* gene in rice caused an increase in WUE, more under water stress than well-watered conditions (Karaba *et al.*, 2007). Water stress can affect biomass production, thereby WUE, reductions in green leaf area (Borrell *et al.*, 2000), light capture and radiation-use efficiency (Earl and Davis, 2003), photosynthesis (Shou *et al.*, 2004), and respiration (McCree, 1986). However, water stress can affect transpiration by causing a reduction in total leaf area (Sionit and Kramer, 1977; Sharp and Davies, 1979), stomatal conductance (Davies and Zhang, 1991), and root growth (Sharp and Davies, 1979).

Reduction in transpiration happens due to changes at both leaf (short term) and canopy (long term) levels (**Figure 3**). At the leaf level, reduction in transpiration is mainly brought about by stomatal closure. The hormonal ABA mediation of stomatal closure under water stress is well documented. Water stress is first sensed by roots, with ABA acting as a long-distance chemical carrier to transport the signal of water stress to the leaves (Davies and Zhang, 1991; Comstock, 2002) in plants. The hormone ABA also regulates Ca^{2+} concentration in the cytoplasm of guard cells, which further activates anion channels that efflux K^+ and other anions from guard cells (Mori *et al.*, 2006; Pandey *et al.*, 2007). This results in loss of turgor in guard cells and subsequent stomatal closure.

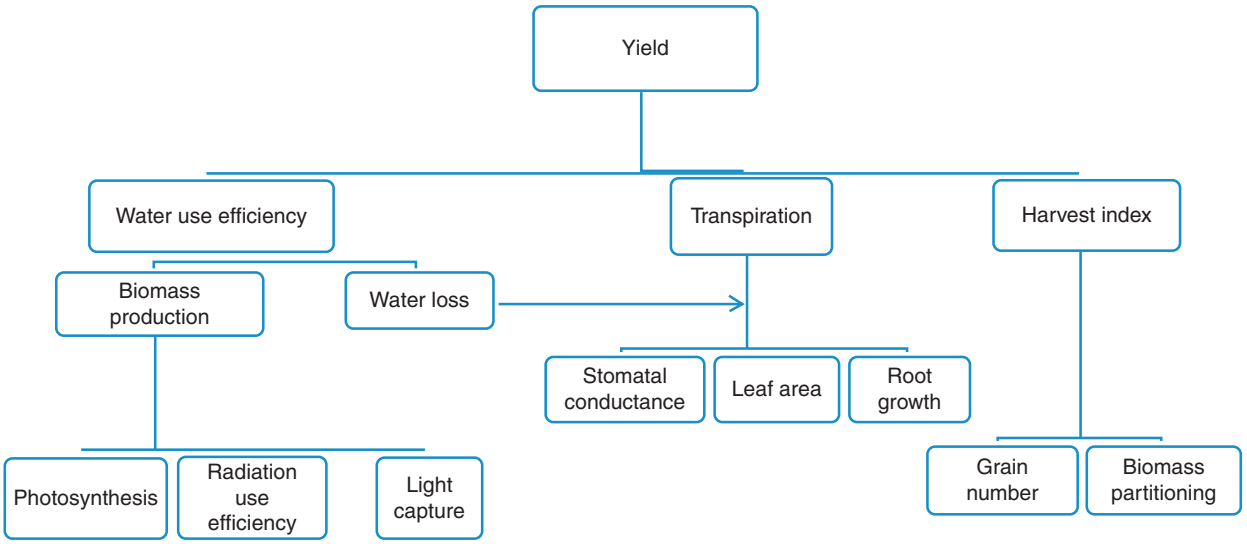


Figure 3 Effect of drought stress on physiological responses related to yield components that affect yield under water stress.

As ABA movement can be a slow process, the signal may take a very long time to reach leaves in tall trees. A different mechanism, namely a drop in hydraulic conductance, was proposed as a nonchemical and relatively rapid signal of water stress in tree species (Saliendra *et al.*, 1995; Comstock, 2002). As described before, long-term responses that result in reductions in transpiration include lowering leaf growth (Boyer, 1970; Sionit and Kramer, 1977; Sharp and Davies, 1979). The primary reason for lower leaf growth under water stress, in spite of increased sugar concentration, appears to be driven mainly by lower turgor in plants (Muller *et al.*, 2011).

Water stress can reduce the harvest index of plants (e.g., maize) likely due to the relatively higher sensitivity of reproductive growth than vegetative growth to water stress. A comparison of old and new tropical maize hybrids, where water stress is common, indicated that harvest index is less stable in the older, less developed hybrids due to lower kernel set (Echarte *et al.*, 2003). Thus, water stress can reduce harvest index by affecting the seed number set by the plant (**Figure 3**). In maize, the setting of the kernel number is affected by the amount of dry matter partitioned to the ear during the critical time – period that brackets silking (Echarte *et al.*, 2004; Tollenaar and Lee, 2006). Selection for drought resistance by imposing water stress during this critical period resulted in hybrids with increased harvest index due to improvement in the amount of assimilates partitioned to the ear (Edmeades *et al.*, 1999). Soybean appears more flexible than maize to responding to water stress, with a close coupling between reproductive and vegetative growth making the harvest index stable under both water stress and irrigated conditions (Spaeth *et al.*, 1984). In contrast, water stress during the grain-fill period increased harvest index in rice by increasing the remobilization of reserves into grain (Yang and Zhang, 2010).

Recently, research is being increasingly focused on the regulation of gene expression by microRNA (miRNA) gene silencing that can affect the pattern of growth in plants as a response to the stress. miRNAs are usually not expressed to directly produce proteins, but their presence can affect the expression from other genes that typically do lead to the production of proteins. The small miRNA sequences target mRNAs to induce cleavage of the mRNAs and repress their translation into proteins. An example is miRNA393, which is involved in lateral root growth development (Chen *et al.*, 2012). Root growth tends to be less lateral and more vertical under drought conditions to enable roots to reach deeper zones for water. The response is mediated by the plant growth hormone ABA in antagonism with auxins. Recent studies indicated that miRNA393 was involved in gene silencing of two auxin receptors, TIR1 and AFB2, required for the inhibition of lateral root growth by ABA (Chen *et al.*, 2012). Another example is miRNA159, which silences several MYB transcriptional factors that positively regulate ABA responses and miR398 which, in turn, targets genes that play a role in scavenging potentially damaging superoxide radicals generated during drought (Bhargava and Sawant, 2013).

So far, the effects of water stress on crops at molecular, metabolic, and physiological scales have been discussed. Luckily, plants have evolved mechanisms to cope with water stress. There are primarily two mechanisms for resisting water stress in crops, viz., dehydration avoidance and dehydration tolerance. Of these two, dehydration avoidance is the main mechanism for drought resistance in the major row crop plants (Blum, 2005). Dehydration avoidance is the capacity of plant to maintain high water status or cellular hydration when exposed to low soil water potentials. In other words, plants avoid exposure to drought or water stress when subjected to low soil water potential. The mechanisms that render dehydration avoidance include lower water loss from crops (via decreased stomatal conductance, leaf rolling, and decreased leaf area), increased water uptake by crops (via deeper root system), and maintenance of water uptake by crops at low soil water potential (osmotic adjustment). However, dehydration tolerance refers to the capacity of plant to function in spite of low water status or cellular dehydration. Dehydration

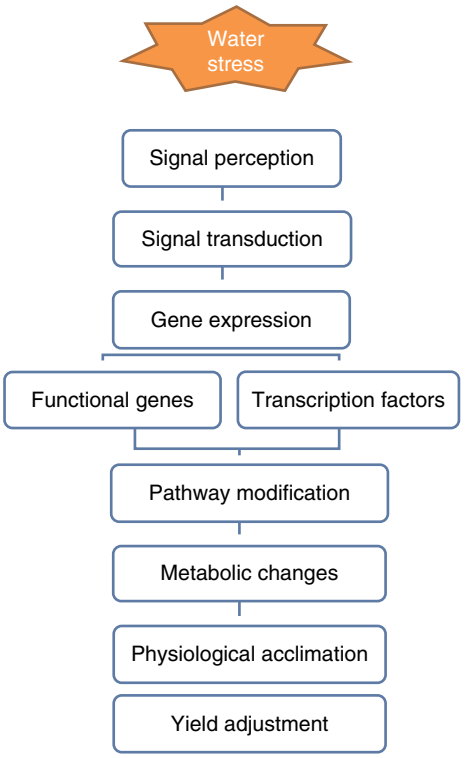


Figure 4 Cascade of responses at the molecular, metabolite, physiological, and agronomic scales in response to water stress in crops.

tolerance is rare in crop plants. It is observed in most seeds, but after germination the trait is normally lost in crops. Dehydration tolerance requires that plants undergo dormant conditions (Blum, 2005).

Starting from the signal perception stage until physiological changes in plants, water stress affects various processes in plants and the cascade of changes results in the final phenotype in which the plant is acclimated to the water stress (Figure 4). These phenotypic changes might help a crop to survive the drought but can affect crop yields. To cope with water stress, crop plants have mechanisms to reduce water loss, maintain transpiration, or continue uptake of water.

Reducing Yield Loss under Water Stress

In this section, three components – WUE, E, and HI and their effect on reducing yield loss under water stress conditions – are examined. An increase in any of the three components can have a positive impact on yield, if the net effect of other components does not change. Increases in WUE without a change in E can arise only if total biomass production or more specifically the rate of photosynthesis increases. Within a crop species, improvement in WUE is mostly due to factors that reduce transpiration (E) because increases in the rate of photosynthesis have not yet been genetically improved through breeding (Earl, 2002; Blum, 2005). If higher WUE due to lower E is a constitutive trait, then the crop may have lower yield when growing conditions provide plenty of water (Condon *et al.*, 2004; Blum, 2009). This is mainly because of the tight link between E and total biomass production under all environmental conditions (Blum, 2009). The penalty under well-watered or irrigated conditions for crops with high WUE can be minimized if high WUE can be triggered selectively under stress. A different term 'effective use of water' was proposed to emphasize the importance of improvement in yield due to increase in transpiration under water stress conditions (Blum, 2009). Maintenance of E under water stress requires either osmotic adjustment and increased root growth or a shift in partitioning of growth from shoot to root. The increase in investment in osmotic adjustment, or deeper root system, can be of no use under well-watered conditions or when water stress is alleviated. In tropical maize improvement, where water stress affects crop production, yield improvement was associated with the improvement in harvest index (Edmeades *et al.*, 1999; Echarte *et al.*, 2004; Tollenaar and Lee, 2006). A combination of higher WUE, lower E, and higher HI has been shown to increase crop yields in rice. When water stress was imposed during grain-fill stage in rice production, WUE increased along with HI, which increased due to an increase in mobilization of reserves to grain (Yang and Zhang, 2010). Thus, responses that improve water uptake or reduce water loss (in combination with improved remobilization of sugars) can result in lower yield losses under water stress conditions.

Industry Efforts to Develop Drought-Resistant Hybrids/Varieties

In the last decade, molecular breeding and biotechnology techniques have been used by industry to develop hybrids with increased resistance to water stress. Molecular breeding involves identifying regions of the genome (e.g., quantitative trait loci (QTLs)) that are related to favorable traits under water stress and then pooling genes together to develop new hybrids or varieties. A genetic linkage map of chromosomes showing the location of favorable genes (QTLs) is developed and, based on the map information, markers (short DNA sequences) that are closest to the gene are identified. Several QTLs are combined by traditional breeding and crossing techniques and markers are used to quickly identify the best combination of QTLs (genes). As markers can be identified from any tissue (seeds or seedlings) and are not influenced by environment, the process of selection can be efficient and rapid. Therefore, new hybrids or varieties can be developed in a shorter period of time than by traditional breeding methods. The limitation of this method is that only traits that are present in a species genome that can be crossed with commercial varieties or inbreds can be introduced into the new hybrids or varieties. However, biotechnology or genetic engineering can aid in introducing new and favorable genes from theoretically any organism or designed synthetically, thus broadening the diversity of source genes. The process involves combining appropriate genes with appropriate gene expression elements and using a variety of processes (including the bacterium *Agrobacterium tumefaciens* transfection or microparticle bombardment) to introduce the engineered DNA into plant cell genomes.



Figure 5 Ears of non-genetically modified organism (GMO) hybrid (top) and Monsanto DroughtGard hybrid (bottom) tested in Kansas, US, where water stress is common.

Since 2011, three drought-tolerant maize hybrids were released by industry using traditional breeding, molecular breeding, or biotechnology. These include Agrisure Artesian™ from Syngenta, Optimum® AQUAmax® from Pioneer, and Genuity® DroughtGard™ from Monsanto (Figure 5). Drought-tolerant hybrids were developed by Syngenta and Pioneer using traditional and molecular breeding technology, whereas the Monsanto drought-tolerant hybrid was developed by combining a biotechnology-derived drought-tolerant trait (Castiglioni *et al.*, 2008) and the best plant germplasm selected through advanced breeding. In regard to the use of biotech traits to manage drought stress, it is important to realize that the earlier developed biotech traits that protected plants against root-eating insects and weeds provided a degree of protection against drought stress by preventing insects or weeds from interrupting root access to the available soil moisture. Thus, these traits can be stacked with drought tolerance traits and germplasm to obtain an additive effect. Moreover, it is recognized that the use of optimal agronomic practices (including conservation tillage practices and appropriate crop rotation) in addition to the best germplasm (including the molecule breeding mentioned above) along with a multitude of biotech traits is required to have the most desired effect.

In conclusion, water stress is a major factor affecting food production due to insufficient rainfall and competition for fresh water from population and industry growth in several regions of the world. When crop plants are exposed to water stress, a series of molecular, metabolic, and physiological changes happen that lead to a desired phenotype that further aids in limiting crop loss. Several years of scientific advancement in the knowledge on crop water stress coupled with the importance of combating water stress in agriculture has enabled the seed industry to develop drought-tolerant hybrids or varieties to aid farmers. Future technologies include combining the optimal agronomic practices, use of best germplasm, and a multitude of biotechnology-derived traits to combat water stress.

See also: Biotechnology Crop Adoption: Potential and Challenges of Genetically Improved Crops. Breeding: Plants, Modern. Climate Change: Cropping System Changes and Adaptations. Genebanks: Past, Present, and Optimistic Future. Plant Abiotic Stress: Salt. Precision Agriculture: Irrigation. Soil: Conservation Practices. Water: Advanced Irrigation Technologies. Water Use: Recycling and Desalination for Agriculture. Water: Water Quality and Challenges from Agriculture. World Water Supply and Use: Challenges for the Future

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Plant Biotic Stress: Weeds

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Glossary

Crop mimicry The physical resemblance of the weed to the crop at some growth stage, which allows the weed to avoid eradication.
Dormancy The ability of a seed to not germinate even though suitable environmental conditions are available.
Herbicide resistance The inherited ability of a plant to survive and reproduce following exposure to a dose of herbicide normally lethal to the wild type.
Herbicide-tolerant crop Crop that has been bred, through conventional or genetic engineering, to have resistance to a herbicide that would normally harm the crop.
Lay-by herbicide application Residual herbicide applied to soil after the crop has established to control further weed germination.
Nonselective herbicide Herbicide that will control most plant species.
Postemergent herbicide Herbicide applied to the target weed after it has emerged.
Preemergent herbicide Herbicide applied before germination of the target weed.
Residual herbicide Herbicide that remains active in the soil for some time after application.
Seed destructor Equipment attached to the back of a harvester that destroys weed seed exiting the harvester.
Selective herbicide Herbicide that can be applied to both crop and weed without harming the crop.
Solarization The use of plastic sheeting to heat the soil surface using sunlight in order to kill weed seeds.
Weed biocontrol The introduction into the environment of a natural enemy of a weed species in order to control the population of the weed.

Introduction

Weeds are one of many biotic stresses on plants in agriculture. The move toward more managed agricultural systems with greater mechanization over the past two centuries has increased the importance of weeds as a constraint on agricultural production. Weeds can have a substantial impact on agricultural production. For example, Pimentel *et al.* (2001) estimated weeds caused losses of more than US$100 billion to agriculture production in just six countries.

Weeds – A Definition

There are many definitions for a weed. The one most often used is 'a plant out of place' or 'an unwanted plant.' From an agricultural perspective, a weed may be more narrowly defined as a plant that has an impact on agricultural production.

Although all plant species may be undesirable in specific locations, some plant species are more likely to occur as troublesome weeds than others. Baker (1974) provided a list of traits that were frequently associated with weedy species in agriculture. These traits are listed in **Table 1**, reorganized by the stage of the plant life cycle. There has been much discussion since about these characteristics and whether other characteristics should be included. There have also been attempts to predict weed species from functional groups (Reichard and Hamilton, 1997).

Many agricultural weeds tend to be r-selected species (Sutherland, 2004). These are species that produce numerous seeds with little maternal investment in each individual seed, rather than fewer, larger seeds. This allows populations to increase rapidly under suitable conditions. In general, weeds of annual crops tend to be annual species, whereas there are far more perennial species that are weeds of pastures and grazing lands (Maillet and Lopez-Garcia, 2000).

Crop mimicry is a trait common to several major weeds of agriculture. Crop mimicry is normally defined as physical resemblance of the weed to the crop at some growth stage, which allows the weed to avoid eradication. It is likely crop mimics originally evolved in response to selection pressure from hand weeding. A broader definition of crop mimicry includes similarity in life-history traits that allow the weed to germinate and produce seed at about the same time as the crop. For example, in *Echinochloa crus-galli* var. *oryzicola* in California crop mimicry results in the weed seed contaminating crop seed used for seeding subsequent crops of rice. This has allowed the weed to rapidly spread through the rice producing areas of California (Barrett, 1983).

Major weed species are typically well adapted for dispersal. Seed of some weed species, such as *Conyza canadensis*, are dispersed across locations by wind (Dauer *et al.*, 2007). However, other weed species have adaptations that allow them to be dispersed to other agricultural sites. These include the ability to pass intact through livestock, attaching to the outside of livestock or being of similar size to the harvested grain. The frequently disturbed nature of most agricultural ecosystems aids dispersal of weeds by providing numerous sites for germination.

Seed dormancy, the ability of seed to remain alive in the soil, but not germinate, can be an important characteristic for weed species. Seed dormancy allows weed species to survive through unfavorable conditions and to germinate when conditions are suitable. It also allows weed species to survive control actions. Seeds may have after-ripening dormancy, which inhibits germination for a period after the seed is first mature. Other forms of dormancy involve pods or hard seed coats that inhibit access of water into the seed. These will have

Table 1 Characteristics frequently associated with weedy species by stage of plant life cycle

Component of life cycle	*Characteristic*
Germination	Ability to germinate in many environments Discontinuous germination and seed longevity
Growth	Short juvenile phase Ability to compete through growth patterns or chemicals
Reproduction	Self-pollinated, or where cross-pollinated wind or nonspecialized pollinators are used Continuous seed production as long as conditions permit High seed production under favorable conditions Produces some seed under a wide variety of conditions For perennials, ability to reproduce from fragments Has adaptations for short- and long-distance dispersal

Source: Adapted from Baker, H.G., 1974. The evolution of weeds. Annual Review of Ecology and Systematics 5, 1–24.

to be breached before the seed can germinate. Seeds may also contain chemical germination inhibitors that need to be leached from the seed before it is able to germinate. Burial of seeds can induce secondary dormancy, which will persist until the seed is exposed to light or the seed dies. Not all weed species rely on dormancy to aid their persistence (Finch-Savage and Leubner-Metzger, 2006). Some species have short-lived seed banks and rely on continued invasion of wind-borne seed.

Few widespread weed species have specialized pollinators. Specialized pollinators restrict the geographical extent of the plant species. Many weed species are able to self-pollinate. This allows a new infestation to start from a single seed germinating. However, self-pollination restricts the genetic diversity within populations. Weeds that outcross often use wind as a means of dispersing pollen. Wind can disperse pollen to large distances and allows ready mixing of alleles within and between populations. A small number of weed species rely on bees as a vector of pollen. These weeds are particularly common in agricultural landscapes where the honey bee is used to pollinate crops.

Weed Impacts in Agricultural Systems

Weed species can have a variety of impacts in agricultural systems. The most obvious is loss of yield caused by weed competition for space, light, and nutrients. In annual crops, the amount of yield loss varies widely. Yield loss is impacted by the density of the weed population and the competitive ability of the crop. Yield loss is also impacted by the relative emergence times of the crop and weed species, with weeds emerging with the crop, or shortly afterwards, being the most competitive (Zimdahl, 2004).

In pasture and rangeland systems, weeds occupy space that could otherwise be occupied by more valuable pasture species. In this way, weeds reduce pasture productivity. Weeds may also have allelopathic impacts, whereby the weed either secretes chemicals into the soil through the roots, or chemicals are leached from dead leaf tissue into the soil, thus inhibiting the growth of nearby plant species (Qasem and Foy, 2001). In permanent plantings, weeds typically reduce productivity by competing for water and nutrients. This is particularly important in dryland crops. With short crop species, weeds may also grow taller than and shade out the crop.

In addition to yield loss, weeds may also result in reductions in quality of the end product. Such reductions in quality can come about due to contamination of the harvested product. For example, canola (oilseed rape) has low erucic acid and low glucosinolate content. Contaminating weed seeds from Brassica species, such as *Raphanus raphanistrum*, that have high erucic acid and glucosinolate content in the grain harvest may make the grain unsuitable for use (Blackshaw *et al.*, 2002). Likewise, contamination of weeds that are poisonous to stock in hay may make the hay unsalable. The presence of spiny weed seeds in dried grape production will downgrade the end product.

Apart from direct contamination of weed material in the end product, weeds can reduce the end quality of produce through taint. For example, dairy cattle grazing on certain species may result in undesirable compounds in milk, which alter the flavor or smell of the end product. Likewise, cattle grazing on *Allium ursinum* will accumulate compounds in their milk that results in unwanted flavors (Naylor and Lutman, 2002).

A third way that weeds impact agricultural activities is through reduction in access to grazing. In addition to utilizing space and resources that could be otherwise used by valuable pasture plants, weeds may inhibit stock from accessing pasture. Typically spiny plants, such as thistles or spiny shrubs, like *Ulex europaeus*, can reduce access of stock to valuable pasture growing around the weed species.

Another weed impact in grazing systems is where weed species cause direct damage to the stock. Poisonous species growing in pasture may kill stock or harm their health, reducing growth and longevity (DïTomaso, 2000). There are many examples of poisonous weeds. Some species are more poisonous to certain stock, for example *Echium plantagineum* can be grazed by sheep, but not by horses. Other species have sharp spines or seeds that can cause damage by sticking in the mouth, nose, or eyes of stock. In addition to the damage such spines do directly, they can be sites of infection. Weeds that have spiny seed, such as *Bromus* spp., *Hordeum* spp., and *Erodium* spp. can also puncture the skin of grazing animals causing damage to the pelt, or become entangled in wool causing vegetable fault (Bourdôt *et al.*, 2007).

Lastly, weeds may interfere with farm activities. Climbing weeds in orchards or vineyards may reduce access to fruit and slow picking of the product. Weeds with spines can cause damage to workers hand picking fruit and vegetables, slowing harvesting operations. Weeds can also interfere with mechanical field operations. For example, viney weeds present at sowing of the crop can entangle in the seeding equipment, slowing the seeding process. Weeds that grow as thickets, such as *U. europaeus*, may impede access to certain parts of the farm, reducing the ability to effectively manage the land (Clements *et al.*, 2001).

Weeds can also harbor pests and diseases and make management of these pests more difficult. For example, many broadleaf weed species are alternative hosts for polyphagous insect pests of crops and can maintain populations of the insect pest when the crop is not present (Norris and Kogan, 2005). In permanent plantings, broadleaf weeds hosting insect pests can result in increased populations of the pest during the early part of the season resulting in increased insect damage and more difficulty managing the pest. Many weeds that are related to crops, and some that are not, are alternative hosts for plant pathogens. For example, grass weeds are hosts to many cereal root diseases, as well as leaf diseases, such as rusts. *Berberis vulgaris* is an alternate host for the wheat stem rust, allowing sexual recombination that does not occur on wheat. The presence of these species in the environment increases the size of the pathogen population and can have the undesirable effect of increasing the risk of recombination within the pathogen to generate isolates with broader virulence toward existing resistant cultivars (Kolmer, 2005).

Weed Management Practices

Weed management typically aims to reduce the incidence of weeds in the crop or pasture to the point where they cause no or minimal damage. Often there has to be a compromise between the cost of weed management and the amount of damage caused, so that weeds are rarely eradicated from agricultural land. There are numerous practices that are used for weed management and implementation of these practices is influenced by their effectiveness, cost, time, availability of equipment, and technical knowledge of the manager.

In early agriculture, weed management was mainly through hand weeding. As time went on, mechanical weed management practices were developed, initially using animal power that replaced hand weeding. With better understanding of the biology of weed species, cultural practices were employed. The advent of the industrial revolutions saw the first chemical weed control practices, which have grown rapidly in importance since World War II. In the twentieth century, biological control was targeted for weed management.

In recent times, chemical weed control has become increasingly used as the main weed management practice in crop production in both developing and developing countries. However, nonchemical practices are still widely used in developing countries and are becoming adopted again in developed nations following problems with chemical control practices.

Mechanical weed controls include cultivation, hand rouging, mowing, mulch, and recently developed mechanical seed removal practices. The latter typically use powered equipment to destroy weeds or reduce their impact on production.

Weed management by cultivation involves the disturbance of soil with a mechanical implement that uproots the weed or severs the roots from the tops. There are numerous types of cultivation equipment and the amount of soil disturbance of the equipment used varies. As a general principle, the more soil disturbance by the equipment, the greater the amount of weed control that will result. Aggressive cultivation implements, such as rotary hoes, tend to pulverize the soil, and destroy any plants present. Moldboard and disc plows fully or partially invert the soil and bury the weeds and any seeds present on the soil surface. Blade plows are used to cut the roots from the tops to kill weeds.

Cultivation is used to control weed growth before seeding an annual or perennial crop, so the crop seed is planted into a seed bed free of weeds. After the primary cultivation event, there may need to be secondary cultivation to break up clods and provide an appropriate seed bed for seeding the crop. Shallow working cultivation equipment, such as harrows, can also be used to lightly bury seed and stimulate germination. Many broadleaf weed seeds are stimulated to germinate by light and so are promoted by cultivation (Juroszek and Gerhards, 2004). Cultivating at night can reduce their emergence. Cultivation may also be used between the rows of crops to reduce weed growth once the crop has established. Cultivation causes damage to soil, resulting in soil erosion, compaction and other problems. For this reason, and as a result of increased costs, the amount of cultivation in many agricultural systems has declined in recent decades and cultivation has been replaced by other practices (Chauhan *et al.*, 2006).

Hand rouging is the selective removal of weeds by hand during the crop growing phase. Hand rouging can involve the use of simple tools like the hoe and is most effective when there are few weeds present in the crop. It is still used widely in developing countries and occasionally in developed nations, particularly in organic production systems. The increasing cost and lack of availability of farm labor has seen a decline in hand rouging.

Mowing and slashing are typically used to reduce weed height rather than to remove weeds. They are effective practices, if timed correctly, in reducing weed seed set in pasture systems. Hay production is also used as part of a rotational strategy to reduce grass weed numbers in annual crop rotations. To be effective, mowing or slashing needs to be conducted after the weeds have flowered, but before any seed is set. To be effective as a weed management strategy, a follow up treatment is often required (Donald, 2006).

Mulch is the application of material to soil in order to stop weed seeds from germinating. Mulch may be organic material or made from plastic. Mulches prevent light from reaching the seed and may also provide a physical barrier to the movement of water to the seed. Where mulches are made from allelopathic material, such as rye straw, chemicals leached from the mulch may aid in weed management (Teasdale and Mohler, 2000). Mulches lose their utility as they break down and require frequent replacement. A variation on mulch is solarization, where plastic sheeting is spread on the soil surface.

Sun passing through the sheet heats the soil surface and kills weed seeds (Horowitz *et al.*, 1983).

Recently in Australia seed destruction practices have been employed to destroy weed seed that is present at harvest. These practices include the chaff cart that is towed behind the harvester and collects the fine or chaff fraction of the crop residue exiting the harvester. This fraction contains some of the weed seed that enters the harvester front, but would otherwise be returned to the field. The chaff can then be removed from the farm or burnt to destroy weed seed. Another device is the seed destructor. This device again collects the chaff fraction, but in this case pulverizes the material destroying any weed seed and spreading the material back on the field. Other devices concentrate the crop residue into rows that can be burnt later to destroy weed seeds (Walsh *et al.*, 2013).

Cultural weed management practices include crop rotations, competition, water management, and grazing. Weeds that are related to the crop frequently have an advantage when that crop is grown. This is because control tactics are less successful in controlling close relatives. Examples include grass weeds in cereals where crop mimicry allows grass weeds to survive many practices that control broadleaf weeds. Rotating between cereal and broadleaf crops can change the selection for crop mimics and help reduce their impact (Sosnoskie *et al.*, 2006). Likewise, perennial weed species often infest pastures, but are less common in annual crops as a result of the continual disturbance in the latter. Rotation between pasture and crop production can change the conditions favoring perennial species, reducing their numbers.

Competition aids weed management by reducing the growth and seed production of weed species. Competition for space is widely used in pasture management and it is well known that many weed species germinate in gaps in pasture stands (DiTomaso, 2000). Growing vigorous pasture stands will reduce the ability of weed species to germinate and establish in the pasture. Likewise, crop competition can be used in annual crops to reduce the impact of weeds, either through growing more competitive crop species or increasing the crop seeding rate where that can be an effective practice (Vandeleur and Gill, 2004).

Crops, pasture species, and weeds all require water to grow. In irrigated farming systems, it is possible to change the way water is delivered to favor the crop species. For example, in perennial plantings a change from flood irrigation to drip irrigation targets the water more effectively to the crop. This changes the area over which weeds can compete for water from the whole field to the area under the drippers. An alternative use of water is in rice production. Rice is tolerant to flooding and this can be used to control weeds that are not tolerant of flooding. When and for how long paddy fields are flooded can greatly alter weed infestations (Rao *et al.*, 2007).

Grazing is frequently used as a practice to manage weeds. Grazing is most effective for weed management when used in conjunction with other weed management practices. Grazers rarely consume unwanted plants only, so relying on them to just consume weeds is unlikely to be effective. Short periods of heavy grazing can be used to reduce the competitiveness of weeds in pasture situations, which, if followed by periods where the pasture species are allowed to recover from grazing, can be used to reduce the biomass of weeds (Rook *et al.*, 2004). Grazing can also be used in situations where crops are grown, so long as the crop plants are less attractive to the grazing animals than are the weeds. Grazing to reduce grass growth in vineyards or orchards is an example.

Biological control, or biocontrol, is the deployment of biological organisms to control weeds. Biocontrol may be the only cost-effective management option for widespread weeds in permanent plantings, pastures or grasslands that are difficult to otherwise control. Biocontrol is predicated on most weeds being alien species and separated from their natural enemies that would normally keep weed populations in check. The practice involves the use of a specific natural enemy or enemies of the weed species, typically an insect or a pathogen, that affects growth and seed production of the weed species. It is important that the agent does not cause local extinction of the weed species, because then the agent will also become extinct. Biocontrol is typically less effective in highly disturbed systems, such as annual crops, because the disturbance reduces the population of the agents. Biocontrol has been employed against many weed species, the most famous case being the control of *Opuntia* spp. in Australia by *Cactoblastis cactorum*. The benefit of biocontrol is that once the agent has been released and has established, little additional management is required. The agent will, over time, reduce the population of the weed to a low level (McFadyen, 1998).

Chemicals, called herbicides, are a very common way of controlling weeds in agricultural systems. Herbicides are used widely in annual crops and in vineyards and orchards. Herbicides are also used in pastures as a weed control method, but typically there is less herbicide use in pastures than in crops. Herbicides may be natural compounds, but most often they are synthetic compounds specifically chosen because of the weed spectrum they control and their safe use in crops (Cobb and Kirkwood, 2000).

Herbicides can be applied to bare soil to inhibit weeds germinating. These are known as preemergent herbicides. Preemergent herbicides are often applied just before or just after crop seeding to reduce the number of weeds that may emerge and compete with the crop. They can also be used in some circumstances after the crop has established and in perennial crops as lay-by applications. Preemergent herbicides have residual activity in the soil persisting for some period after application and may control weed germination for weeks or months. For this reason, they are also called residual herbicides.

Postemergent herbicides are applied after the weed species have germinated. These herbicides may or may not have residual activity in the soil. Postemergent herbicides are more flexible in use than preemergent herbicides. This is because they do not have to be used unless the weed is present.

Some herbicides are able to be used in certain crops without damage to the crop. These are known as selective herbicides. Typically, the herbicide is selective because the crop species is able to rapidly degrade the herbicide before the herbicide damages the crop. This often means that weed species that are related to the crop species are unable to be controlled by the herbicide.

A smaller number of herbicides kill, or damage, almost all plant species. These are called nonselective herbicides. These herbicides cannot be used over the crop and are used before

sowing the crop or between the crop rows. Nonselective herbicides are useful because they control most unwanted vegetation, but are less versatile than selective herbicides. This is because they can only be applied when the crop is not present or where the crop can be physically protected from the herbicide through use of a shroud.

The majority of herbicides inhibit a single enzymatic process within the plants that causes the plant to die. This is known as the herbicide target site. Inhibition of this enzyme may lead directly to death of the plant, or the plant may die from secondary reactions that occur as result of inhibiting that enzyme. It is possible to place herbicides into groups based on how they kill plants. This is known as the mode of action for that herbicide. The international herbicide resistance action committee describes 19 different herbicide modes of action as well as a small number of herbicides where the mode of action is not known (Menne and Köcher, 2012).

In the past two decades there has been the development of herbicide-tolerant crops. These are crops that have been bred to be tolerant of herbicides that would normally damage that crop species. Herbicide-tolerant crops can be useful in the control of weed species that would otherwise not be controlled. Several approaches have been used to develop herbicide-tolerant crops. These have included mutagenesis to create resistant target enzymes, crossing with species that have resistance to the herbicide or through genetic engineering to introduce new genes that provide resistance to the herbicide (Green, 2011).

In certain cropping systems, there has been widespread adoption of herbicide-tolerant crops. Examples include canola production in North America and Australia, soybean and corn production in North and South America, and cotton production in North America and Australia. The main reasons for adoption of herbicide-tolerant crops are to manage otherwise difficult to control weeds and to simplify the production system (Green, 2012).

Evolution of Avoidance of Weed Management

One of the consequences of adopting weed management tactics is that avoidance of the management tactic will arise. Such changes can occur because all of the weed species that are easily controlled by the management practice are removed, leaving the more tolerant weed species behind. An example would be selective grazing by animals removing the palatable species, but leaving behind the unpalatable ones to increase in number (Popay and Field, 1996). The more effective the weed management measure, the more rapidly the change will take place.

An example of avoidance in weed management is weed species shifts that have occurred as the result of adoption of herbicides. For example, from 1950s to the 1960s there was an increase in importance in grass weeds in UK cereal production (Fryer and Chancellor, 1970). The likely reason was the widespread use of herbicides that controlled broadleaf weeds in cereals during the 1950s and 1960s. The control of broadleaf weeds provided an opportunity for grass weeds to invade. Species shifts can occur more than once if weed control practices change. In the UK, the advent of effective grass herbicides in the 1970s has seen a decline in grass weed abundance in cereal crops since that time (Potts *et al.*, 2010). A weed species shift has been observed over a shorter time period in the United States with the rapid adoption of glyphosate-resistant crops (Webster and Nichols, 2012).

Another form of avoidance is where a species becomes resistant to the control method. One example is the evolution of biotypes of *Poa annua* and *Plantago vulgaris* for resistance to mowing. Continual mowing of grass swards over a long period has selected for more prostrate individuals with shorter inflorescences (Warwick and Briggs, 1979). Another example has been the selection of early maturity in *Hordeum glaucum* in Tasmanian alfalfa fields. A long period of continuous alfalfa mown every year resulted in the evolution of a population that matured early and shed seed before the mowing operation (Purba *et al.*, 1996).

The most well-known example of weed resistance is resistance to herbicides. For herbicides, resistance is defined as "the inherited ability of a plant to survive and reproduce following exposure to a dose of herbicide normally lethal to the wild type" (WSSA, 1998). Weed resistance to herbicides was first documented in 1953; however, the first example to have significant consequences was resistance to the triazine herbicides in corn production, starting in the 1980s. Resistance has evolved in at least one weed species to herbicides from 16 of the 19 different modes of action (Powles and Yu, 2010).

Herbicide resistance evolves because herbicide use selects individuals within the population that carry rare alleles that allow them to survive the herbicide application. At the same time the vast majority of the population is killed by the herbicide. If the surviving plants are allowed to reproduce, the frequency of individuals within the population carrying resistance alleles increases. Continual use of the same herbicide or of herbicides with the same mode of action selects for a population with a high frequency of individuals with resistance to the herbicide resulting in failure of the herbicide to control the population.

Herbicide resistance is at its worst in developed countries, with USA, Canada, and Australia having the greatest number of weed species with resistance. This is because weed management in agriculture in developed nations is more dependent on herbicides. However, herbicide resistance also occurs in developing countries and by 2013 resistance was reported to 217 weed species in 61 countries (Heap, 2013). Often weeds evolve resistance to a single herbicide mode of action; however, recently, more weeds with resistance to multiple herbicide modes of action are being reported. For example, one population of *Lolium rigidum* in Australia is resistant to seven herbicide modes of action (Heap, 2013).

The widespread adoption of glyphosate-tolerant crops in North and South America has led to the evolution of glyphosate-resistant weeds over large areas of these cropping systems. In these areas, the adoption of crop rotations entirely dependent on glyphosate for weed control has led to the rapid selection of glyphosate-resistant weeds (Green and Owen, 2010).

In several agricultural systems, such as wheat production in Australia and cotton production in the United States, the evolution of widespread herbicide resistant weeds has led to a reconsideration of weed management strategies based solely

on chemical control. In Australian wheat production, a number of alternative practices for control of major weeds are being adopted (Walsh *et al.*, 2013). In US cotton production, the reintroduction of tillage and increased hand rouging of weeds is taking place (Culpepper *et al.*, 2010).

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Plant Cloning: Macropropagation

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Glossary

Phase change The transition in plants from a juvenile vegetative state to the sexually reproductive state.
Physiological aging Aging attributable to the loss of vigor and a decline in physiological activity. This is one of the three forms of aging seen in trees.
Plagiotropic Nonvertical plant growth.
Plasmodesmata Microscopic channels for transport and communication between cells in plant tissues.
Scion A piece of stem with buds from a large mature plant, which is grafted to the shoot of a young plant with its own roots.

Introduction

Cloning is a process by which individual organisms are multiplied asexually – a process of vegetative regeneration or reproduction (Longman, 1993). Consequently, the individual plants forming a clone are genetically identical. Cloning can be both a natural and an artificial process. The natural process embraces the lateral spread of creeping plants by their shoots or roots, and the production of new plantlets from dispersed, separated, or fragmented plant parts. Vegetative regeneration is a common characteristic of undesirable and invasive weeds. It is often associated with organs that have evolved as part of a perennial life form involving specialized storage organs (e.g., tubers, bulbs, rhizomes, etc.). However, vegetative regeneration also has advantages in agriculture: first, some of the specialist storage organs are good sources of carbohydrates for human food and so become crops – potatoes, yams, cassava, onions, etc. In addition, the capacity to regenerate asexually can be used to multiply these crops without the alteration of their genetic characteristics during the segregation phase of sexual reproduction. This also applies to many trees and other plants which can be artificially regenerated by stem cuttings, grafting, budding, or marcotting (air layering).

The development of clonal crops producing specialist storage organs will not be considered further here as the process just involves the selection of the best individuals from natural populations or from the progeny of breeding programs. Instead, it will be examined as to how the artificial process of vegetative regeneration is used by agriculturalists, horticulturalists, and foresters in domestication programs to capture and multiply individual genotypes, and hence to produce cultivars and clones of crops that would not normally be multiplied clonally. This is especially important in trees as less progress has been made in tree crop domestication because of: their relatively long generation times (approximately 3–20 years); irregularity in flowering and fruiting due to climate and physiological rhythms; predominantly outbreed nature with low heritability in many traits, and high genetic diversity of base populations.

In this Encyclopedia two articles examine the processes of vegetative regeneration. One involves the relatively new processes of micropropagation which have arisen from the development of modern biotechnology, and the other, this article, which involves the more traditional techniques of macropropagation.

The Use of Macropropagation

The use of cloning is not a new concept associated with the advent of biotechnology. It has been used mainly in perennial crops for thousands of years by agriculturalists and horticulturalists, and used by foresters for at least 800 years (Hartmann *et al.*, 2010; Chapter 40). This is because there are many instances when multiplication by vegetative means is a more appropriate strategy than multiplication by seed (Mudge and Brennan, 1999). It is the capacity to rapidly develop cultivars by clonal selection and propagation that is especially important in the domestication of food and nonfood crops from trees, shrubs, and woody vines (Leakey, 2012). However, the techniques are not exclusively used to multiply woody plants, as many ornamental herbaceous plants are also propagated vegetatively because the techniques are simple, inexpensive, and result in high rates of multiplication. This article focuses on woody perennials as they are the most challenging subjects for vegetative propagation.

Vegetative propagation has the advantage that it captures nonadditive as well as additive gene effects, but it should be noted that vegetative propagation only replicates existing genetic traits within newly formed plantlets and does not in itself improve the genetic quality of the material being propagated.

There are a number of important practical issues that need to be resolved when making the decision to use vegetative propagation (**Table 1**). These are associated with the use of appropriate technologies, techniques, and plant tissues (**Table 2**) to ensure the efficient and wise use of clones for improved and sustainable production (Longman, 1993; Leakey and Simons, 2000), as part of a wise strategy for tree domestication (Leakey and Akinnifesi, 2008) for the delivery of agroforestry and multifunctional agriculture.

Techniques of Macropropagation

All techniques of macropropagation are dependent on the capacity of undifferentiated meristematic cells to divide and differentiate to form new shoots or roots (Hartmann *et al.*, 2010). Although it is sometimes possible to develop new shoots from root tissues, it is generally easier to develop new roots from shoot tissues.

Table 1 When to use vegetative propagation as a tool in tree domestication

When elite trees have a rare combination of a few inherited traits.
When there are many desirable traits for simultaneous selection.
When high uniformity is needed to ensure profitability and to meet market specifications.
When the products have a high value that can justify the extra expense.
When the trees to be propagated are 'shy' seeders and the material for propagation is scarce.
When the timescale required does not allow progress through the slower and less efficient process of breeding.
When seeds have a low level or short period of viability.
When the knowledge of proven traits is acquired through long-term experiments or the traditional knowledge of local people.

Source: Modified from Leakey, R.R.B., Simons, A.J., 2000. When does vegetative propagation provide a viable alternative to propagation by seed in forestry and agroforestry in the tropics and sub-tropics? In: Wolf, H., Arbrecht, J. (Eds.), Problem of Forestry in Tropical and Sub-tropical Countries – The Procurement of Forestry Seed – The Example of Kenya. Ulmer Verlag: Germany, pp. 67–81.

Table 2 Strategic opportunities to consider when to use vegetative propagation to domesticate trees

What is the most appropriate level of technology to use?
Which tissues are most appropriate – juvenile or mature?
When using juvenile tissues, which is the best source?
When using mature tissues, what are the best methods to use?
How can an easy, sustainable, and cost-effective approach be ensured?
How can the best individuals for propagation be selected from broad and diverse wild populations?
What are the opportunities for introducing new variation?
How can clones be wisely used and deployed?
How can a wide genetic base be maintained in clonal populations?

Source: Modified from Leakey, R.R.B., Simons, A.J., 2000. When does vegetative propagation provide a viable alternative to propagation by seed in forestry and agroforestry in the tropics and sub-tropics? In: Wolf, H., Arbrecht, J. (Eds.), Problem of Forestry in Tropical and Sub-tropical Countries – The Procurement of Forestry Seed – The Example of Kenya. Ulmer Verlag: Germany, pp. 67–81.

Grafting and Budding

Grafting and budding techniques are especially important in the vegetative propagation of woody plants that have a long period (3–20 years) of juvenile vegetative growth before becoming sexually mature and capable of flowering and fruiting. This is because mature tissues of trees seem to be very difficult to propagate by the formation of roots at the base of a piece of stem (a stem cutting). Consequently grafting and budding techniques are used in this situation as they do not involve root formation. Instead, they are dependent on the fusion of tissues from two different shoots (Hartmann *et al.*, 2010). In this way, grafting and budding form multiple copies of large mature tree on seedling rootstocks. Grafting and budding techniques involve the placement of a severed piece of shoot (a scion), or an axillary bud, from the chosen tree in immediate contact with similar tissues on the stump or rootstock of an unselected tree, such that the tissues grow together, fuse, and the buds on the attached scion grow out to form a copy of the chosen tree. A number of well-known techniques have been used and practiced for thousands of years – known as cleft grafts, approach grafts, whip/tongue grafts, and side veneer grafts (Hartmann *et al.*, 2010).

The success of all these techniques depends on the juxtaposed cambial cells producing callus to form a functional and strong graft union. The ability to achieve this is thought to be dependent on a combination of environmental, anatomical, physiological, and genetic factors.

Genetically, grafting is most successful when the scion and rootstock are closely related – ideally, that is, scions of a mother plant grafted on her own seedling progeny. Successful grafts between species and between genera are less common. Even if a union is formed between these poorly related plants there is the likelihood that there will be tissue rejection at a later date – even many years later – which results in the breakage of the union. Often this tissue incompatability is seen as a differential in the growth rate between the rootstock and scion, with one having a larger diameter than the other.

Graft incompatibility is thought to be biochemically mediated and to depend on recognition events between juxtaposed cells through their plasmodesmatal connections. One suggestion is that it involves differences in peroxidase activity across the union, which may regulate lignification processes. A difference in the peroxidase banding patterns in both the scion and rootstock is thought to predict graft incompatibility and hence weak graft unions (Gulen *et al.*, 2002). However, despite considerable recent experimentation the mechanisms remain elusive and general principles are hard to elucidate.

Environmentally, probably the main causes of graft failure are nonoptimal temperature for cell division, loss of cell turgidity, movement at the scion/rootstock interface, and disease (Hartmann *et al.*, 2010). Consequently, grafting should be done during the growing season and with proper protection from water stress and movement. However, almost nothing is known about the importance of the preseverance irradiance, the quality of light, and the nutrient status of the severed shoot. These environmental conditions are important for the successful rooting of cuttings. Likewise, not much is known about the best pregrafting environment for rootstocks.

Physiologically, the need for vigorous growth is widely recognized. However, in temperate trees success is often greatest when dormant scions that have been held in chilled storage are grafted to rootstocks that are already in active growth. This may reflect the reduced chance of water stress in the scion, although it may be associated with changes in the gibberellin and abscisic acid content of plant tissues.

One problem that can arise with grafting is that the scion dies, whereas the rootstock sprouts. If good observations are not made regularly, it can be difficult to know whether the shoots of a grafted plant are of the selected scion clone, or of the unselected rootstock seedling. Of course, if the latter occurs the grafting exercise will be a waste of time, effort, and money.

Marcotting or Air Layering

Layering, the stimulation of roots on intact stems in contact with the ground, is a natural feature of many plants, including some trees. This has been modified as an artificial process of vegetative propagation in two main ways – stooling and air layering (or marcotting). In the former, soil mounds are built around the shoots emerging from coppiced stumps and then the rooted shoots are severed from the stump and planted. This typically captures the juvenile characteristics of the tree associated with the base of the tree trunk.

Air layering is usually applied to mature (capable of flowering and fruiting) branches within the tree crown, usually a long way from the ground (Tchoundjeu *et al.*, 2010). In this case, a ring of bark is removed to promote the accumulation of photosynthates. Then the exposed cambium is typically treated with an auxin rooting powder to promote rooting. It is then wrapped in black polythene enclosing damp compost, peat, or other rooting medium and left for some weeks or months to form roots (**Figure 1**). This treated part of the branch should be close to the main stem. Once rooted the branch is severely pruned and detached from the tree and potted in a nursery.

Typically, air layered shoots form roots on the underside of the stem, which means that when subsequently planted out the tree does not have a radially orientating root system, and hence is prone to fall over as the tree gets bigger. To avoid this it is preferable to air layer vertical shoots, such as those formed after pollarding a tree. Alternatively, if a nonvertical branch is used, it can be potted and managed as a stockplant from which to regularly harvest cuttings for subsequent repropagation.

Rigorous studies are needed to determine the best environmental or physiological conditions for successful air layering, although it is affected by branch diameter/age and by season.

Stem Cuttings

The vegetative propagation of plants by rooting stem cuttings is relatively easy in annual herbaceous species, but becomes progressively more difficult as the subject becomes larger and more long-lived. Consequently, large trees provide the nursery manager with the ultimate test of skill, knowledge, and understanding. For this reason, this section focuses on some principles developed for the propagation of tree species.

A wide range of physical facilities are available for the propagation of stem cuttings. These range from sophisticated, electronically controlled glasshouses with fogging equipment, through mist propagation benches to nonmist, polypropagators that are cheap and simple to build and use. The polypropagators are very effective and appropriate for use in remote locations without access to capital and reliable water or electricity services. All these facilities are designed to reduce the postseverance physiological stress (wilting and leaf abscission) resulting from water loss through transpiration by keeping the cuttings cool, moist, and turgid.



Figure 1 A marcott set on a vertical shoot from a decapitated branch of *Dacryodes edulis*. Courtesy of Roger Leakey.

Stem cuttings can come in many forms, but the two major groups are leafy softwood cuttings from relatively unlignified, young shoots, which are dependent of current photosynthates for rooting, and leafless hardwood cuttings from older and more lignified shoots, which depend on the mobilization of carbohydrate reserves stored within the stem tissues. The former are typically a short piece of stem – perhaps a single node with its bud and leaf and the internode immediately below it (**Figure 2**), whereas the latter is often a longer piece of stem with 2–10 nodes and internodes. It is leafless as it has already shed its leaves due to the onset of winter or a dry season. Typically, these large leafless cuttings are taken toward the end of the dormant season.

Although widely practiced for hundreds of years, much of the literature on the rooting of cuttings has been anecdotal



Figure 2 A single-node rooted cutting of *Triplochiton scleroxylon*. Courtesy of Roger Leakey.

based on the experience of individuals who have neither used standardized conditions nor adequately described their protocols. This has left a confused literature with many contradictory statements about what determines success (Leakey, 2004). It is only in the past few decades that research has examined many of the factors influencing the rooting process under standardized conditions with the intention of identifying some key principles that ensure success. Furthermore, although much research has been focused on postseverance factors, such as the use of auxin 'rooting hormones' and the physical environment of the propagation system, much less, indeed very little, research has examined the effects of the preseverance environment of shoots on their stockplants or the effects of stockplant environment. Likewise, very little was known about the interactions between pre- and postseverance factors.

This rest of this section examines five key sets of factors that play a crucial role in determining whether or not leafy cuttings rapidly form a good root system, and hence determine the success of macropropagation for the development of clonal approaches to agricultural production.

The propagation environment

The act of severing a cutting from its stockplant creates a physiological shock. To ensure good rooting, the duration and severity of this shock has to be minimized (Mesén *et al.*, 1997). Thus, the most important aspect of the propagation environment is that it minimizes the physiological stresses arising from: (1) the loss of water from the tissues due to transpiration; and (2) the loss of carbohydrate reserves due to tissue respiration. In addition, the propagation environment should encourage photosynthesis in leafy cuttings, and promote meristematic activity (mitosis and cell differentiation) in the stem. These processes are linked to the need to transport assimilates and nutrients from the leaf to the base of the stem, and water from the base of the stem to the leaf.

To minimize these stresses the basic principles are to keep the cuttings well supplied with water at the cutting base, while also maintaining the leaves in an environment with high humidity (low vapor pressure deficit (VPD)). The aerial environment in the propagation area is kept cool by shading, and the leaves themselves are cooled by the evaporation of moisture from the leaf surfaces. It is important that the level of shading does not restrict photosynthesis in the leaves (i.e., typically above 400 μmol m^{-2} s^{-1}).

Comparative studies have identified that one of the major advantages of the environment in nonmist polypropagators (**Figure 3**) is their greater uniformity in both the moisture content of the rooting medium and the VPD across the beds; resulting in overall lower air and leaf temperatures (Newton and Jones, 1993). Mist systems have lower uniformity as a result of both the temporal and spatial distribution of moisture disbursed by intermittent bursts of pressurized mist from jets typically 0.5–1.0 m apart. In addition, peaks of VPD are associated with peaks in irradiance. Species vary in their sensitivity to VPD. This is a result of differences in leaf morphology which affect stomatal conductance, and is often associated with evolutionary adaptations to the physical environment found in the natural range of the species (e.g., rain forest vs. woody savannah).

The predominant use of mist and fogging systems by research teams has resulted in few studies on the relationship between photosynthesis and the rooting process due to the difficulty of measuring gas exchange in cuttings with wet leaves. However, studies of gas exchange during propagation have been made in nonmist polypropagators and these have illustrated the importance of photosynthesis for good rooting success, speed of rooting, and the number of roots produced per cutting (Hoad and Leakey, 1994, 1996).

There is a general assumption that the successful rooting of cuttings is associated with a positive carbon balance (i.e., assimilate production > losses through respiration) and a concentration gradient within a cutting which enhances the transport of assimilates from the leaves toward the cutting base. However, little is known about the relationships between respiration losses and cutting origin, leaf area, stem length/diameter, or the rooting environment.

In addition to the aerial environment of the propagator, the environment of the rooting medium is also important. However, the choice of medium is often based on availability of the materials or personal experience. Nevertheless, studies suggest that the medium should hold the cutting firm with its leaf held above the surface of the medium. In addition to providing moisture at the cutting base the medium should allow respiration from the tissues and prevent anoxia which encourages



Figure 3 Left: Nonmist propagator with its lid open. Right: A cross-section showing the different layers of gravel and medium. The arrow marks the top of the water. Courtesy of Roger Leakey.

rotting and cutting mortality. To prevent this, the medium should have an air:water ratio that optimizes the oxygen diffusion rate vis-à-vis the needs of tissue respiration. In practice, this involves the use of variously sized particles (sand and gravel) and a water-holding medium (compost, perlite, vermiculite, peat, coir, or other organic products) alone or in various mixtures. As in the relationship between leaf morphology and the aerial environment, there is some evidence that morphological and physiological adaptations to different environments may affect the optimum porespace.

Root development and growth is generally enhanced by the cutting base being warmer (artificially enhanced by providing 'bottom heat') than the leaves. This promotes meristematic activity at the cutting base, while the leaves remain cool and free from stress. The converse differential tends to promote the growth of buds creating competition for assimilates.

Postseverance treatments

Auxin applications

The application of auxin is considered to promote rooting by stimulation of cell differentiation, the promotion of starch hydrolysis, and the attraction of sugars and nutrients to the cutting base, but a better understanding is needed of the mechanisms regulating auxin concentrations and pathways (Atangana *et al.*, 2011). Indole-3-butyric acid (IBA) is typically the most effective auxin. However, auxins are not a 'cure-all' treatment and exogenous applications of auxin do not promote rooting in cuttings that are morphologically or physiologically dysfunctional. Thus, for auxins to have their stimulatory effects the cuttings should have been taken from shoots that are preconditioned by stockplant management to be physiologically active when in the propagator, free from water and respiratory stresses, and with the capacity to mobilize stored or current assimilates.

A point of practical importance is that the stems of some species are hairy, whereas others are waxy. This affects the retention of applied auxin. In addition, uptake is affected by the cross-sectional area of the cutting base (i.e., stem diameter).

Leaf area

The rooting of softwood cuttings is typically dependent on the presence of a leaf. Studies using infrared gas analyzers to measure the rates of photosynthesis in nonmist polypropagators during the propagation process found that rooting ability was maximized in photosynthetically active cuttings. However, a large photosynthetically active leaf is also actively losing water by transpiration and can suffer water stress – hence closing its stomata or shedding its leaf. This then prevents further photosynthesis. Conversely, small-leaved cuttings with inadequate assimilate production rapidly decline in their carbohydrate (sugars and starch) content due to respiration losses and hence cannot support root development.

Successful rooting, therefore, requires an optimal leaf area which balances the positive effects of photosynthesis and the negative effects of transpiration (Leakey, 2004). The leaf area associated with this balance varies depending on the adaptations in leaf morphology of different species to different environments. Such variation is also determined by leaf age (node position) and the position of a shoot with the stockplant.

In addition to leaf area, the correct balance between photosynthesis and transpiration will also be determined by the photosynthetic efficiency of the leaf due to the light environment of the propagator (level of irradiance) and the cutting's water relations (affected by the aerial environment of the propagator and the air:water ratio of the medium). Studies of these important aspects of propagation have found a. relationship between rooting ability and the content of reflux-extracted soluble carbohydrates, which confirm the importance of assimilate production throughout the rooting process.

The determination of the optimum leaf area is, therefore, a very important aspect of developing a successful propagation protocol, especially in difficult-to-root species.

In general, rooting experiments focus on the factors enhancing rooting success. However, to learn more about the processes affecting rooting, there is much that could be learnt from paying more attention to the causes of rooting failure. For example, more information is needed about how and when cutting death can be attributed to: water and heat stress, leaf abscission, photoinhibition, negative carbon balance, etc. In addition, some cuttings neither die nor root.

Other related reasons for the failure of cuttings to root can be the death of the leaf due to microbial infection, anoxia and rotting, necrosis, bleaching, or leaf abscission. These problems can arise due to the use of old shoots with senescent or photosynthetically inactive leaves that are past their compensation point (photosynthetic activity vis-à-vis senescence); water stressed or starch filled. The most common

symptoms are leaf shedding, leaf rot, and stem rot. Gaining an understanding of these causes of cutting death and hence the failure of the propagation process can be as important as determining how to achieve good rooting.

Despite the importance of photosynthesis for the rooting of leafy softwood cuttings, there is some evidence that some species are also able to mobilize and use stored reserves of carbohydrates to contribute to the rooting process. This may reflect differences in stem anatomy and perhaps also adaptations to seasonally harsh environments.

Cutting length

The stem length of a cutting is another important variable affecting rooting success (Leakey, 2004). It is important in two ways. First, it affects the depth of insertion into the rooting medium, as well as the height of the leaf above the surface of the rooting medium; and second, it inherently affects the capacity of the cutting to root. This is something that will be investigated later. Both the depth of insertion and the height of the leaves above the medium can be important in terms of providing uniform conditions for water uptake and preventing competition between cuttings for light. It is also desirable to prevent the leaves from touching the medium and getting saturated by water droplets.

Cuttings can be cut to a constant length (these may vary in the number of nodes and leaves present), or can be cut to the length determined by a chosen number of nodes. The simplest cutting is a single-node cutting. It has one internode and generally has one leaf and one bud. In this case, the internode will generally vary in length depending on its position within the stem (**Figure 4**). As a general rule, basal internodes are shorter than more apical ones, reflecting the vigor of growth at the time the node was formed in the terminal bud. This within-stem variability will be examined later. For practical purposes it is probably best to use a constant length close to the optimum, although this may not result in the availability of greatest number of cuttings.



Figure 4 The node-to-node variation in the length of the internode and the petiole in cuttings from the top two shoots of a *T. scleroxylon* stockplant (uppermost nodes on the left). Courtesy of Roger Leakey.

Stockplant factors: Cutting origin and environment

There are two major sources of variation attributable to the stockplant, which are: (1) within-shoot factors; and (2) between-shoot factors. Both of these are subject to the stockplant environment and hence can be influenced by stockplant management.

Within-shoot factors

It has been shown earlier that single-node cuttings vary in their internode length (**Figure 4**). This variation is associated with gradients in numerous other variables which basically run from the bottom to the top of the stem in parallel with chronological age, such as: leaf size, leaf water potential, leaf carbon balance, leaf senescence, internode diameter, stem lignification, nutrient and stem carbohydrate content, and respiration (Leakey, 2004). Thus, no two cuttings are identical and, as a consequence, no two cuttings have the same rooting ability (**Figure 5**). This is because all these variables affect the physiological processes in the cutting. A number of studies have used this node by node variation as an experimental variable to examine some of the key factors affecting rooting ability. For example, a comparison of the normal gradient in cutting length with an inverse gradient showed the importance of cutting length, whereas a comparison with standard length cuttings showed the importance of cutting diameter/volume. It seems that the stem volume of the cutting determines the storage capacity of the cutting for current assimilates. In this connection, there are interactions between stem volume and leaf area. The stockplant environment and/or stockplant management also interact with node position in ways that help to elucidate the effects of different treatments. Studies of this sort have shed light on the relative importance of carbohydrates and nutrients in the rooting process.

Between-shoot factors

As plants grow and increase in size they branch and become more complex. This creates competition between shoots for assimilates and nutrients; as well as causing mutual shading between leaves. This competition is made more complex by the processes of correlative inhibition and the development of dominance between shoots, which are mediated by growth regulators as well as by the plant's environment: especially light and nutrients (Leakey, 2004).

To maintain stockplants in a good condition for easy rooting they need to be pruned back hard to leave a short stump of approximately 20 cm. So the simplest form of stockplant is that which has just been cut back once and which then sprouts from its uppermost remaining buds. A comparison of the rooting ability of these different shoots has found that cuttings from the uppermost shoot roots best and those from lower shoots root progressively less well. However, if such stockplants are cut back to different heights (say between 20 and 100 cm) then usually the taller stockplants produce more shoots. In this case, the rooting ability of cuttings from the top shoot declines with increasing height and a relationship is found between the number of shoots and the percentage of cuttings rooted (**Figure 6**). This implies that competition between the shoots reduces rooting ability and the removal of the lower shoots increases the rooting ability of cuttings from upper shoots.

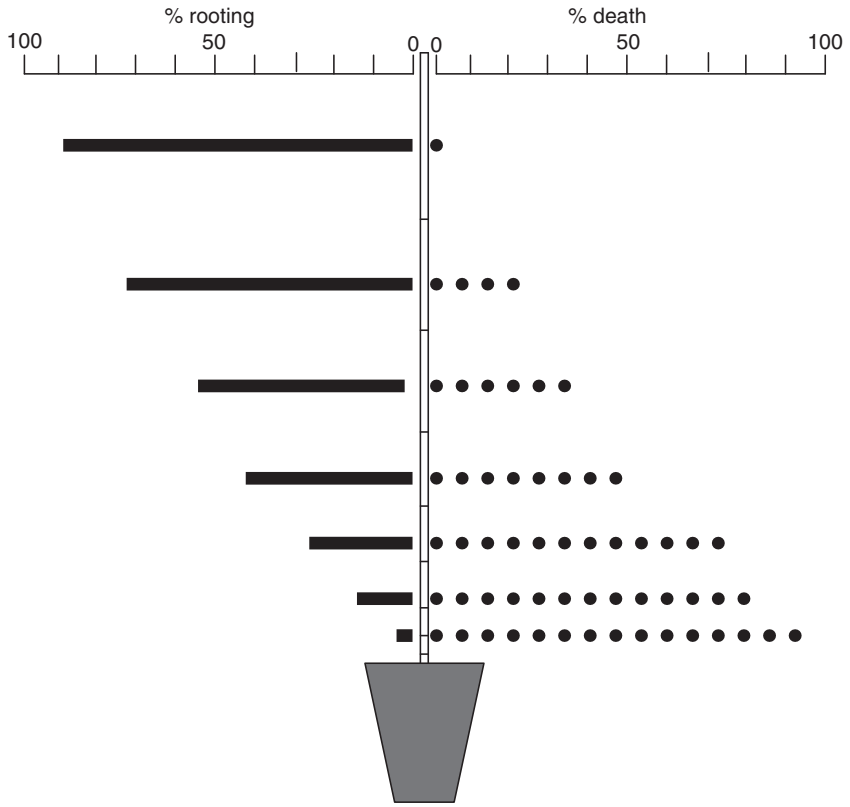


Figure 5 The gradient of variation in rooting ability within a shoot; the long uppermost cuttings root best, whereas short basal cuttings die.

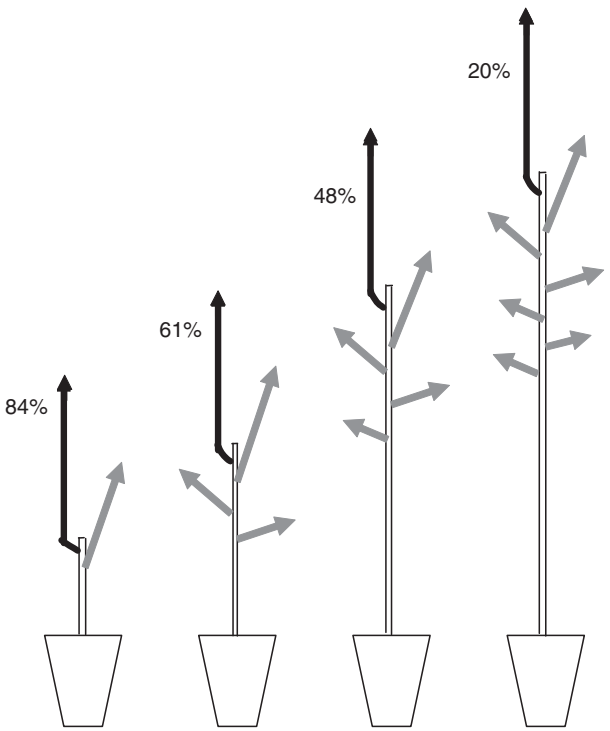


Figure 6 Effects on the rooting success of cuttings from the top shoot of stockplants pruned to different heights. Cuttings from short stockplants with few shoots root best.

Further studies to test the competition hypothesis in plants of the same height have found that other factors also seem to be involved. For example, the lower shaded shoots can root very much better than less shaded shoots, especially under conditions of high soil nitrogen. Additionally, reorienting the stockplant so that its stem is not vertical (e.g., 45° or 90° from the vertical) alters the location of vigorous growth and the fast-growing lower basal shoots become the most easily rooted. Thus, in addition to competition there are effects of shoot position and of stockplant environment.

When studies tried to elucidate these interactions between-shoot position and intershoot competition in two-shoot stockplants of the same height, it was found that basal shaded shoots had a higher rooting ability than upper shoots. However, if these basal and upper shoots were under conditions with the same light environment (irradiance) the differences between-shoot positions were eliminated (**Figure 7**). This finding led to experiments in controlled environment growth chambers to investigate the role of light (Hoad and Leakey, 1994, 1996).

Stockplant environment

As seen above, both nutrients and shade seem to affect the rooting ability of cuttings from shoots on relatively simple stockplants, but these complex preconditioning processes are poorly understood. It is clear that both the amount of light (irradiance) and the spectral quality of light (red:far-red ratio) – both features of shade – are important and independently

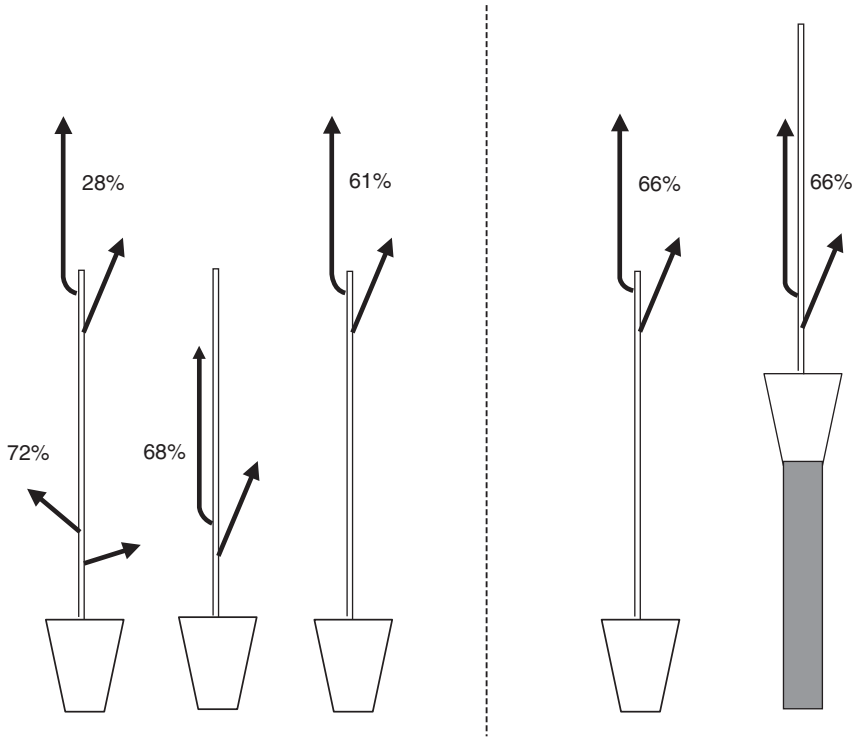


Figure 7 Effects of shoot position on the rooting success of cuttings from stockplants with apical and/or basal shoots. The effects of shade were examined by adjusting the height of the pots.

affect the rooting ability of cuttings. Shade light is also commonly associated with shoot etiolation, and hence with long internodes and with large thin leaves. These effects are then further complicated by an interaction with soil nutrients which promote shoot growth (Leakey and Storeton-West, 1992). The light/nutrient interaction affects photosynthetic processes. The most dramatic of these interactions seems to be the combination of high irradiance and low nutrients which results in short starch-filled stems, the inhibition of photosynthesis, and very poor rooting (**Figure 8**). At the other extreme, low irradiance and high nutrients is associated with active photosynthesis, low starch, and good rooting.

These preconditioning effects of irradiance, light quality, and nutrients on morphology are also associated with physiological differences in the stems and leaves of the shoot preseverance (Hoad and Leakey, 1994, 1996). Physiologically, shade reduces the tendency of the top shoot to dominate and reduce the growth of other shoots (i.e., promotes codominance), lowers the rates of preseverance net photosynthesis, lowers leaf chlorophyll concentration, but stimulates higher rates of net photosynthesis per unit of chlorophyll. Preseverance conditioning thus actively promotes postseverance photosynthesis during the rooting process. Such shoots are therefore said to be physiological 'young,' whereas shoots with low vigor and inhibited photosynthesis are physiologically 'old.'

A mechanistic model of carbohydrate dynamics during the rooting process can be used to gain further insights into the rooting process (Dick and Dewar, 1992) and to define key principles for the development of robust rooting protocols.

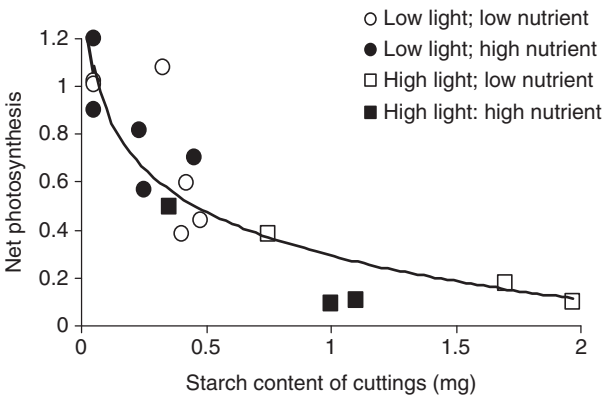


Figure 8 The effects of growing stockplants at two levels of light (low and high irradiance) and two levels of nutrients (low and high). This affects the rates of photosynthesis and the starch content of cuttings. Starch-filled cuttings with low rates of photosynthesis rooted very poorly. Modified from Leakey, R.R.B., Storeton-West, R., 1992. The rooting ability of *Triplochiton scleroxylon* K. Schum. cuttings: The interactions between stockplant irradiance, light quality and nutrients. Forest Ecology and Management 49, 133–150.

Stockplant Management

The major importance of all of the above morphological and physiological stockplant factors makes it clear that stockplant management (a combination of regular pruning, fertilizer use, and light management) should be a key component of any macropropagation protocol. To retain physiological youth,

Table 3 The importance of stockplant management for successful vegetative propagation. Note the lack of relationship between rooting percentage and the numbers of plants established, which reflects the understanding of the importance of stockplant management (which shoots to use and the role of stockplant environment)

	Standard hedged stockplant No knowledge of stockplant management	*Standard hedged stockplant Knowledge that rooting is best from upper shoots*	*Preconditioned (far-red light and fertilizers) hedged stockplant Knowledge that preconditioning improves physiological activity and rooting capacity*
No. of cuttings harvested	31	16	45
No. of cuttings rooted	16	16	40
Percentage of cuttings rooted	52	100	89
No. of plants established	16	16	40

Source: Modified from Leakey, R.R.B., 2004. Physiology of vegetative reproduction. In: Burley, J., Evans, J., Youngquist, J.A. (Eds.), Encyclopedia of Forest Sciences. London: Academic Press, pp. 1655–1668.

stockplants are often managed as hedges. Using nitrogen-fixing tree/shrub species to shade these hedges then maximizes the rooting success by provision of desirable light and soil nutrient environments.

One of the issues that has created much of the confusion in the scientific literature of vegetative propagation is the very common (even ubiquitous) use of percentage of rooting as the measure of success. Rooting percentage is, however, affected by the standards of stockplant management and use of the best shoots (the shoots with optimal morphology and highest physiological activity; **Table 3**). Contradictory results arise in the literature when authors do not provide the relevant information in the description of their experimental protocols.

Phase Change

The vegetative propagation literature has numerous references to what is called 'Phase Change' or ontogenetic aging. This literature basically attributes the loss of rooting ability as perennial plants age and get larger to their gradual transition from the juvenile phase of vegetative growth to a phase of sexual maturity. The propagation of mature tissues is one of the major constraints to many tree improvement programs focusing on cultivar development through macropropagation. This loss of rooting ability with increasing size and structural complexity is perhaps not surprising given the already mentioned effects of stockplant factors in even small and simple stockplants. Nevertheless, the importance of phase change vis-à-vis rooting ability is an unresolved aspect of vegetative propagation (Leakey, 2004).

The phase change hypothesis assumes that plants (and trees in particular) gradually progress from juvenility (sexually immature and easy to root) to maturity (sexually mature and capable of flowering and fruiting associated with low rooting ability) over time. In trees, maturity may not be achieved for 3–20 years. It is generally recognized that the best way to return a tree to the juvenile state is to cut it down and to allow coppice shoots to grow from the stump. These coppice shoots are young and vigorous and cuttings from them can usually be rooted easily. Studies have suggested, however, that there is a decline in rooting ability with the increasing diameter of the stump. It is not known whether this is due to some aspect of the aging process or to stockplant factors like those mentioned for seedlings above. For example, large stumps generally produce more shoots than smaller stumps. This loss of rooting ability could, therefore, be due to increased intershoot competition.

There are some inconsistencies between the concept of 'phase change' and observation. Originally the hypothesis was based on the work on ivy (*Hedera helix*) which has various leaf shapes. It was assumed that the normal palmate leaves of climbing ivy vines were characteristic of the juvenile easy-rooting phase, whereas the ovate leaves of flowering shoots were assumed to be characteristic of the difficult-to-root mature phase. Observation of large ivy plants suggests a different interpretation as palmate leaves can be seen to be associated with main stems (the climbing vine), whereas ovate leaves are associated with free-standing branches on which flowers are formed. The association of flowering with branches is common in many woody plants, and it is not unusual for branches and main stems to differ in the arrangement of their leaves and buds. Certainly, in ivy, it is common to see old and large vines climbing a cliff or dead tree with palmate leaves tens of meters above the ground, and flowering branches with ovate leaves all the way up the vine.

A second way in which the hypothesis is not supported is the evidence that ontogenetically mature plants (with the capacity to flower and form fruits) propagated by cuttings, grafts, or marcotts can be easily repropagated by cuttings when they are used as small managed stockplants. Although often plagiotropic, such stockplants have the vigor of juvenile seedlings and coppice shoots. This suggests that the poor rooting ability of 'mature' shoots can be attributed to 'physiological aging' rather than to 'ontogenetic aging.' In other words, the difficulty in rooting crown shoots in large mature trees is due to a severe case of the combination of undesirable morphological and physiological factors resulting from within and between stockplant factors and their interaction with the stockplant environment (Dick and Leakey, 2006). A start has been made to examine this experimentally within the crown of mature trees (Pauku *et al.*, 2010).

Genetic Variation in Rooting Ability

Early in this article, it was shown that there are genetic differences in the ease of propagation between species and even between provenances and clones within species. In severe cases, this has led to the conclusion that some species are 'impossible to root.' It has also been seen that species vary in

Table 4 The analogy between athletic ability and rooting ability in the vegetative propagation of tree stem cuttings

Sporting ability	*Rooting ability*
Young	Juvenile
Physiologically fit – lean, well-prepared, strong	Physiologically young – high rates of photosynthesis – long internodes, large leaf area, chronologically young node position
Genetic morphology – muscles, body build, etc.	Genetic morphology – stem and leaf anatomy
Preparation in gym – physiologically fit and full of energy	Preconditioning by stockplant management – physiologically active
Highly competitive and ready for action	Preconditioned to contain low starch–high soluble sugars and free from competing shoots
Use of performance-enhancing drugs	Use of auxins as rooting hormone
Stress-free Olympic village	Stress-free propagation environment
Different sports – refine training regime	Different species – refine propagation regime

Source: Modified from Leakey, R.R.B., 2012. Living with the Trees of Life – Towards the Transformation of Tropical Agriculture. Wallingford: CAB International, 200 pp.

the leaf and stem morphology, and in their adaptations and responses to environmental factors. There is now good evidence that species previously thought to be 'impossible to root' can now be preconditioned to be easier to root by good stockplant management based on an understanding of the morphological and physiological factors affecting rooting ability. Thus, the apparent genetic differences in rooting ability can instead be attributed to genetic differences in the growth and development of shoots.

The concept that inherent genetic differences in rooting ability are not critically important is also supported by the use of stepwise regression in the analysis of experimental data from rooting studies. Such analysis commonly finds that the factors explaining much of the variance are cutting length, leaf abscission, leaf area, etc., rather than clone or provenance (Dick *et al.*, 1999).

Contrary to the above, some studies to detect quantitative trait loci affecting vegetative propagation have, however, reported that phenotypic variation has a meaningful genetic component.

Conclusion

There are many facets to developing a robust approach to macropropagating plants, especially by the rooting of stem cuttings. Over the past 15–20 years much progress has been made to gain a good understanding of the numerous interacting factors (stockplant environment × stockplant management × topophytic variables × node position × nursery management × postseverance treatments × propagation environment) by studying them in tree species. This understanding now provides some general principles that can be applied to the propagation of new species, and especially those considered to be difficult to propagate.

Leakey (2012) has likened many of the factors that determine the success of propagation by stem cuttings to those that determine the success of an athlete competing in the Olympic Games (**Table 4**). This analogy has been found to help people to understand the key principles.

The greatest challenge remaining is to improve the design and reporting of experiments so that the quality of the literature is improved by researchers adequately describing the material they used, as well as the pre- and postseverance environments. This should remove the contradictory results in the literature created by people not using comparable material in terms of the physiology and morphology of the tissues used. There is then a need for more extensive studies of the importance of stockplant management and the stockplant environment across a wider range of species.

See also: Agroforestry: Practices and Systems. Agroforestry: Participatory Domestication of Trees. Cloning: Plants – Micropropagation/Tissue Culture. Domestication of Plants

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Relevant Website

www.worldagroforestry.org/Units/training/downloads/tree_domestication
ICRAF.

Plant Disease and Resistance

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Glossary

Disease The continuous abnormal functioning of an organism; a disruption in the health of the organism.
Effectors Pathogen proteins and small molecules that alter host–cell structure and function.
Effector-triggered immunity Direct or indirect recognition of pathogen effectors by plant resistance (R) proteins that leads to the activation of plant defense responses.
Evolutionary arms race Evolutionary struggle between competing sets of coevolving genes that develop adaptations and counteradaptations against each other.
PAMP-triggered immunity First active defense response of plants, also referred to as activation of basal defenses, after perception of PAMPs by plant PRRs.
Pathogen A disease-producing organism or biotic agent.
Pathogen-associated molecular patterns Highly conserved molecules associated with groups of microbes that are recognized by pattern recognition receptors (PRRs) on plant cell surfaces to activate the innate immune system.
Plant immunity The inherent or induced capacity of plants to withstand or ward off biological attack by pathogens.

Plants Get Sick Too!

The earth accommodates a staggering number of microbes, estimated to be as high as 10^{30} (Kallmeyer *et al.*, 2012). Among these microbes are as many as 5.1 million different species of fungi (Blackwell, 2011), more than 8000 of which cause disease on plants. Given the huge variety of plant pathogenic microorganisms, which also include viruses, bacteria, oomycetes, and nematodes, why are there so few diseased plants in nature? The reasons are many. Most microbes do not have the capacity to cause disease in plants, and those that do range from very efficient to very weak pathogens. Some microbes are even beneficial to plants, facilitating their growth in nutrient-limiting or adverse environments. Even closely related plants may vary greatly in their exposure or susceptibility to pathogens, ranging from highly susceptible to completely immune (resistant). Furthermore, environmental conditions including temperature, humidity, and availability of nutrients can influence whether the plant–pathogen interactions lead to disease or resistance. The interactions of susceptible host, virulent pathogen, and conducive environment can be conceptualized as a disease triangle (Figure 1).

Agriculturists who are interested in producing healthy crops frequently focus on the plant side of the arms race, determining which adaptations make the plant resistant to disease. However, given the complicated relationship between pathogen virulence and plant immunity, the most effective approach to designing a successful disease control strategy is one that considers both the partners. This article explores attributes of plant pathogenic microbes that enable them to access host nutrients and cause disease. Mechanisms by which the plant resists invasion by pathogens, and how the intimate interactions between microbes and plants have driven their coevolution are also discussed. Finally, how knowledge of these interactions influences disease control strategies in the field is explored. Although many common themes are found among the interactions between pathogens and plants, there is also huge diversity; thus, examples used are meant to provide context to this discussion, and are not meant to be comprehensive. Furthermore, given the breadth of the topic and limited space, we rely on citation of excellent reviews, where available, and provide primary references for recent examples.

A Conceptual Basis for the Evolution of Plant–Microbe Interactions

Plant pathogens form intimate relationships with plants to gain access to host resources needed to survive, grow, and reproduce. This process, which involves infection, colonization, and pathogen reproduction, is called pathogenesis. To cause disease, plant pathogenic microbes must (1) find and

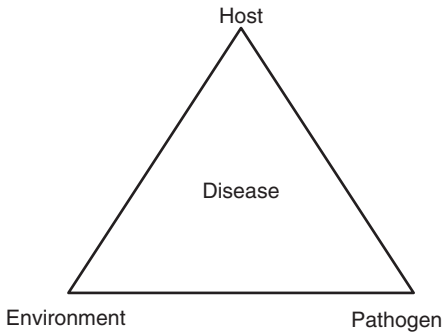


Figure 1 The plant disease triangle shows the three components necessary for disease to occur: (1) the pathogenic microbe must be virulent on a particular species and cultivar of plant; (2) the plant host must be susceptible to a particular strain/isolate/biotype of a pathogen; and (3) environmental conditions including temperature, humidity, and availability of nutrients must be suitable for the interactions that lead to disease. If a pathogen requires an insect vector for dissemination or inoculation then a fourth dimension is added (a plant disease pyramid).

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gain access to the host plant; (2) avoid, suppress, or overcome the plant's resistance repertoire; and (3) coerce the plant to provide nutrients or replication machinery to enable growth and multiplication. However, to avoid disease, the plant must (1) recognize the presence of potential pathogens and (2) mount a defense response that has sufficient strength to restrict pathogenic attack without being too detrimental to the plant's own physiology. The variation in virulence on the part of the pathogen and susceptibility or resistance on the part of the plant are the result of a coevolutionary arms race (Anderson *et al.*, 2010). Increased virulence of a pathogen places a strong selective pressure on the plant host to increase resistance; in response, the pathogen is under selective pressure to overcome resistance. A simple 'zigzag model' (**Figure 2**) was proposed to illustrate our current understanding of plant–pathogen interactions in an evolutionary context (Jones and Dangl, 2006). In this article, a step-by-step walk will be taken through the zigzag model to frame the discussion of the processes in pathogen–plant interactions that culminate in disease or resistance.

How do Pathogens Find and Enter the Plant?

For a microbe to cause disease, it needs to come into direct contact with its host plant, and often with a specific host plant tissue. Microbes are passively distributed from plant to plant by wind, splashing rains, or insect vectors (**Figure 3**). However, nonpathogenic microbes, once deposited, do not have the capacity to find wounds or natural openings on the plant surface, or to penetrate preformed surface barriers such as a waxy cuticle and thick cell walls. Pathogens, however, have evolved diverse mechanisms to find and enter plants to establish the disease.

Once they reach the host plant, a pathogenic microbe may land on the part of the plant suitable for infection, called the infection court. In other cases, pathogens need to expend energy to move or grow toward the infection court. Elegant work in the 1970s–1980s demonstrated that mycelia of some fungi exhibits directional growth toward the infection court of their host, in this case the stomata (for a review, see Tucker and Talbot, 2001; Mendgen *et al.*, 1996). For example, mycelial growth of *Uromyces appendiculatus*, the causal agent of bean rust, is oriented perpendicular to the ridges surrounding the stomata, a process known as thigmotropism (**Figure 4**) (Hoch *et al.*, 1987). Stomatal ridges of a height specific to bean signal the fungus to form specialized infection structures that penetrate the stomatal opening, a process called thigmodifferentiation.

Some pathogens orient themselves toward an infection court by sensing electrical fields (electrotaxis) or chemical signals (chemotaxis). Swimming spores of the oomycete *Pythium aphanidermatum*, which infects roots through wounds, are attracted to the negative charges associated with wounds along the root surface; *Phytophthora palmivora* zoospores, which can directly penetrate undamaged roots, are attracted to positive charges (van West, 2002). Access to wounds or natural openings by plant pathogenic bacteria such as *Agrobacterium* spp. *tumefaciens* (crown gall of most dicots), *Erwinia amylovora* (fireblight of apple and pear), *Pseudomonas syringae* pv. *glycinea* (bacterial blight of soybean), and *Pseudomonas lachrymans* (angular leaf spot of cucumber) is facilitated by chemotaxis toward simple plant chemicals such as sugars or phenolics.

Once the pathogen reaches the infection court, it needs to enter the plant (**Figure 3**). Unless the pathogen can enter the plant through indirect penetration of wounds or natural openings or is vectored by an insect, it must create an opening to enter the plant through direct penetration. Plant surfaces are barriers to pathogens, and surface structure varies widely among plants and among tissues on the same plant. Woody stems present a very different set of barriers to pathogens than leaves or flowers do. A typical leaf surface presents a tough outer cuticle that is composed of an insoluble polyester, cutin, embedded in a complex mixture of waxes. The thickness of the cuticle varies among species, organs, developmental stages, and environmental conditions. Many pathogens have evolved elaborate mechanisms for breaking through this barrier, which are usually only employed during the penetration phase of the life cycle. Fungi can penetrate the cuticle by chemical or enzymatic degradation or by force. *Magnaporthe oryzae*, a fungal pathogen causing rice blast disease, uses both the mechanisms. After the fungal spores germinate on the plant surface, the mycelia form specialized penetration structures called appressoria. Each appressorium is held in place on the leaf surface by a fungal-produced mucilage that is so sticky that it sticks to Teflon (Hamer *et al.*, 1988). The appressoria secrete cutinase, an enzyme that degrades and weakens the cuticle (Skamnioti and Gurr, 2007). Then, after building up enormous levels of turgor pressure, the appressorium forces an appendage called the penetration peg through the cuticle and the cell wall (Howard and Valent, 1996).

PAMP-Triggered Immunity: The First Line of Active Defense

For those microbes that get beyond the preformed structural barriers, the zigzag model proposes that the first line of active plant defense is PAMP-triggered immunity (PTI). PTI, the set of general defense responses of plants to diverse microbes, is a process by which plants actively recognize 'nonself' from 'self' via surface receptor molecules called pattern recognition receptors (PRRs). PRRs are membrane-spanning proteins with extracellular receptor domains. The receptor domains of PRRs recognize highly conserved pathogen molecules called pathogen-associated molecular patterns (PAMPs, also called microbe-associated molecular patterns or MAMPs) activating a signal transduction cascade that culminates in the induction of a suite of defense responses. PTI-associated defenses may include the production of reactive oxygen species, increases in intracellular calcium concentration, callose deposition in cell wall, activation of mitogen-activated protein kinases (MAPKs), production of antimicrobial compounds called phytoalexins, and a complex transcriptional response (Schwessinger and Zipfel, 2008). Together, these PTI-activated defense responses are the chief means by which microbes that get past plant structural barriers.

Plant-derived peptides or cell wall fragments that are released by pathogen degradation, called damage-associated molecular patterns (DAMPs), can also be recognized by PRR and activate signaling of PTI (reviewed by Monaghan and

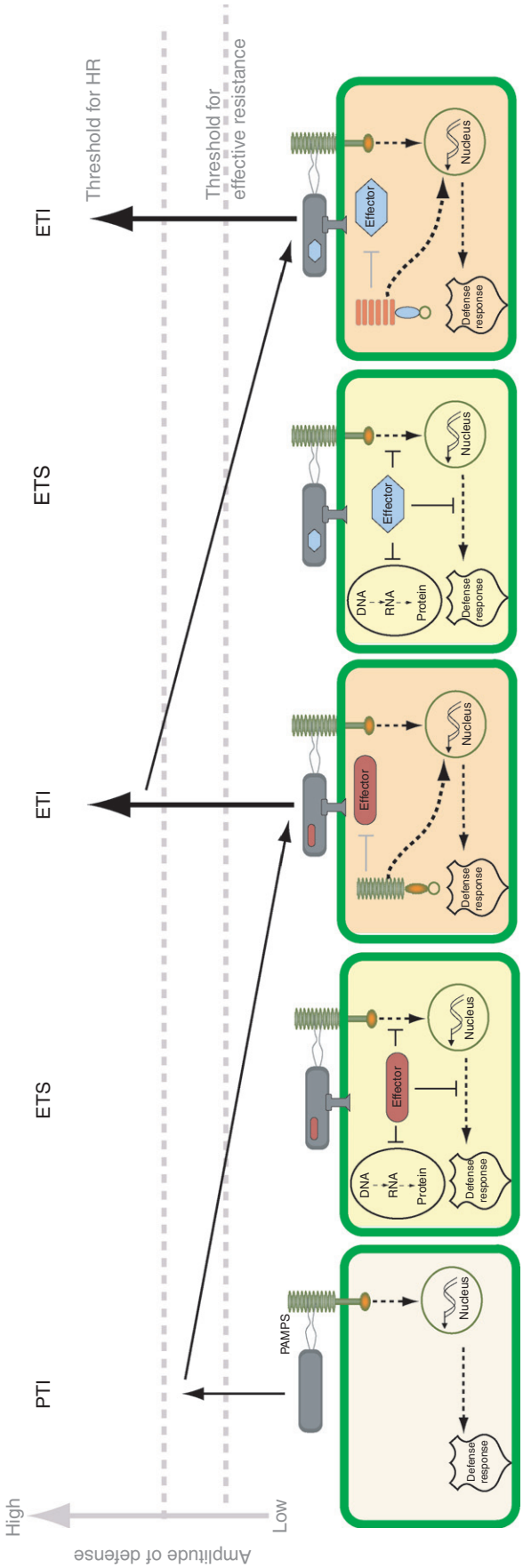


Figure 2 The zigzag model to illustrate the coevolution of the plant immune system and pathogen virulence effectors. Plants detect pathogen-associated molecular patterns (PAMPs) via pattern recognition receptors (PRRs) to trigger PAMP-triggered immunity (PTI). Pathogens evolve effectors that interfere with PTI or other host processes to result in effector-triggered susceptibility (ETS). In response, plants evolved NB-LRR proteins to detect effectors and to activate effector-triggered immunity (ETI). ETI has a higher amplitude (stronger and longer lasting response) than the PTI. Within the pathogen populations, pathogen isolates are selected that have lost the recognized effector, leading to suppression of ETI and restored ETS. Finally, new plant NB-LRR alleles are selected that can recognize a new effector, restoring ETI. Hypersensitive response (HR). Image drawn by Samuel Vazquez III adapted from Jones, J.D., Dangl, J.L., 2006. The plant immune system. Nature 444 (7117), 323–329, and Chisholm, S.T., Coaker, G., Day, B., Staskawicz, B.J., 2006. Host-microbe interactions: Shaping the evolution of the plant immune response. Cell 124 (4), 803–814.

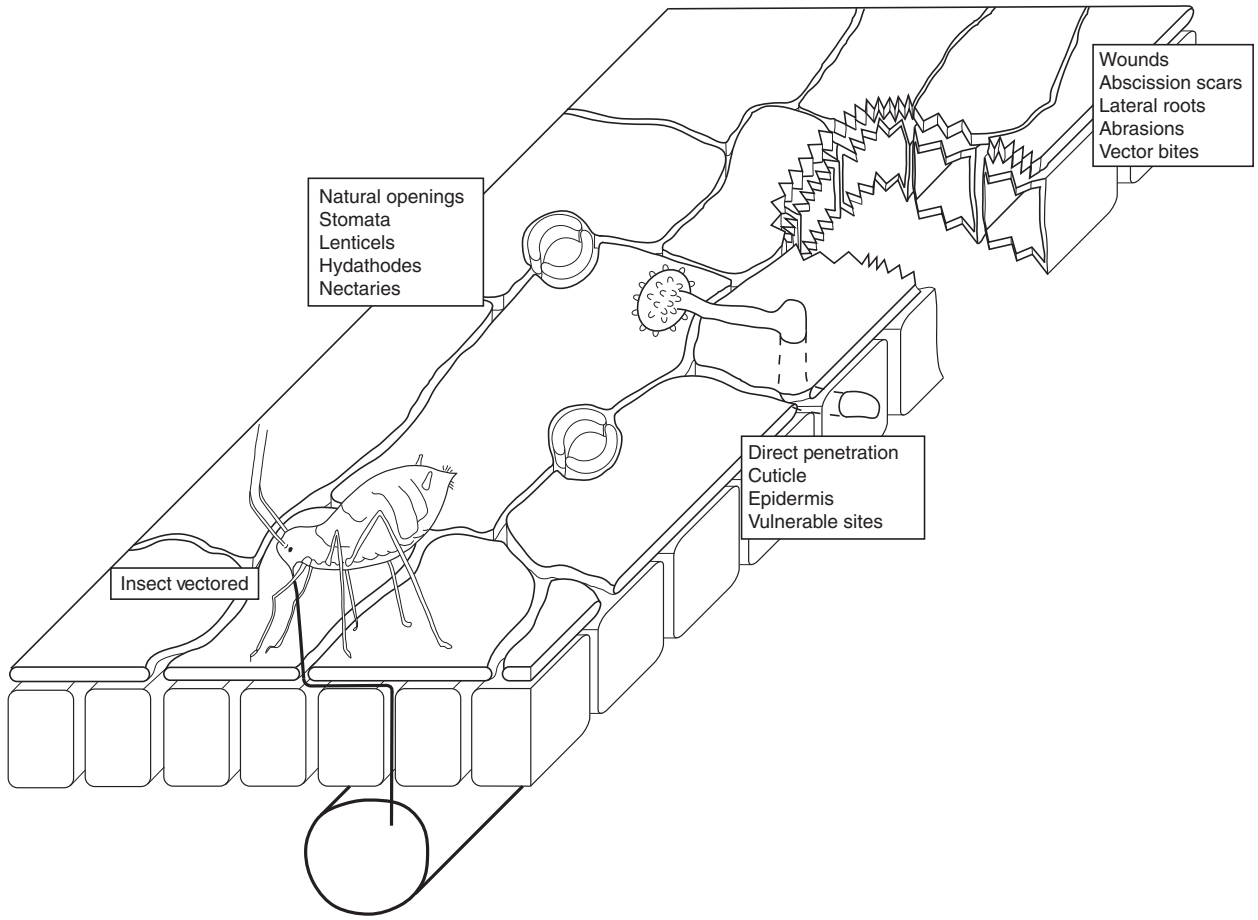


Figure 3 Methods of penetration and invasion by plant pathogens. Pathogens can enter through wounds (e.g., Tobacco Mosaic Virus, *Agrobacterium* spp. *tumefaciens*, and soft rot fungi) or natural openings such as stomata (rust fungi and *Pseudomonas syringae*), lenticels (*Pectobacterium carotovorum*), or hydathodes (*Xanthomonas oryzae* pv. *oryzae*). Fungi that can directly penetrate are powdery mildews, downy mildews, or *Magnaporthe oryzae*. Pathogens that are delivered by insect vectors include *Xylella fastidiosa*, Cauliflower Mosaic Virus. Image drawn by Samuel Vazquez III and Tony Campillo.

Zipfel, 2012). In one example, plants produce proteins that inhibit the activity of fungal-produced cell wall degrading enzymes called endopolygalacturonases. The plant-produced inhibitors reduce the activity of the endopolygalacturonases, leading to the accumulation of long-chain oligogalacturonides that function as DAMPs and trigger PTI (D'Ovidio *et al.*, 2004).

PAMPs tend to be highly conserved, essential components of the pathogen, so any mutation that affects their function is likely to be detrimental to the pathogen. Some PAMPS conserved among multiple microbes can be recognized by a single plant receptor, allowing a high degree of efficiency in the deployment of plant resources. For these reasons, PAMP receptors can confer resistance that is stable and broad spectrum, or effective against diverse pathogens. Not surprisingly, pathogens have evolved adaptations to overcome PTI. This may occur through the rare evolution of a PAMP to avoid recognition, or, more commonly, through the production of virulence effectors that enable the pathogen to overcome or avoid PTI and cause disease (reviewed by Pel and Pieterse 2013).

Effector-Triggered Susceptibility: The Pathogen Retaliates

Bacteria, fungi, oomycetes, and nematodes produce a suite of virulence effectors that are broadly defined as pathogen-produced proteins or metabolites that directly interact with the host and enhance virulence (Hogenhout *et al.*, 2009). Effectors are used by the pathogen to access nutrients, adversely affect host physiology, or to block PTI; the zigzag model describes this as effector-triggered susceptibility (ETS) (Jones and Dangl, 2006).

Collectively, effectors contribute to diverse pathogen lifestyles ranging from necrotrophy to biotrophy. Necrotrophic pathogens kill plant cells by producing effectors such as toxins or tissue-degrading enzymes; these effectors induce cell necrosis and cause leakage of nutrients that are used as substrates by the pathogen. Necrotrophic pathogens include the bacterial soft rot pathogen *Pectobacterium carotovorum* subsp. *carotovorum*, the fungal gray mold pathogen, *Botrytis cinerea*, and the oomycete root rot pathogen *P. aphanidermatum*. Biotrophic pathogens require living plant cells, and use complex

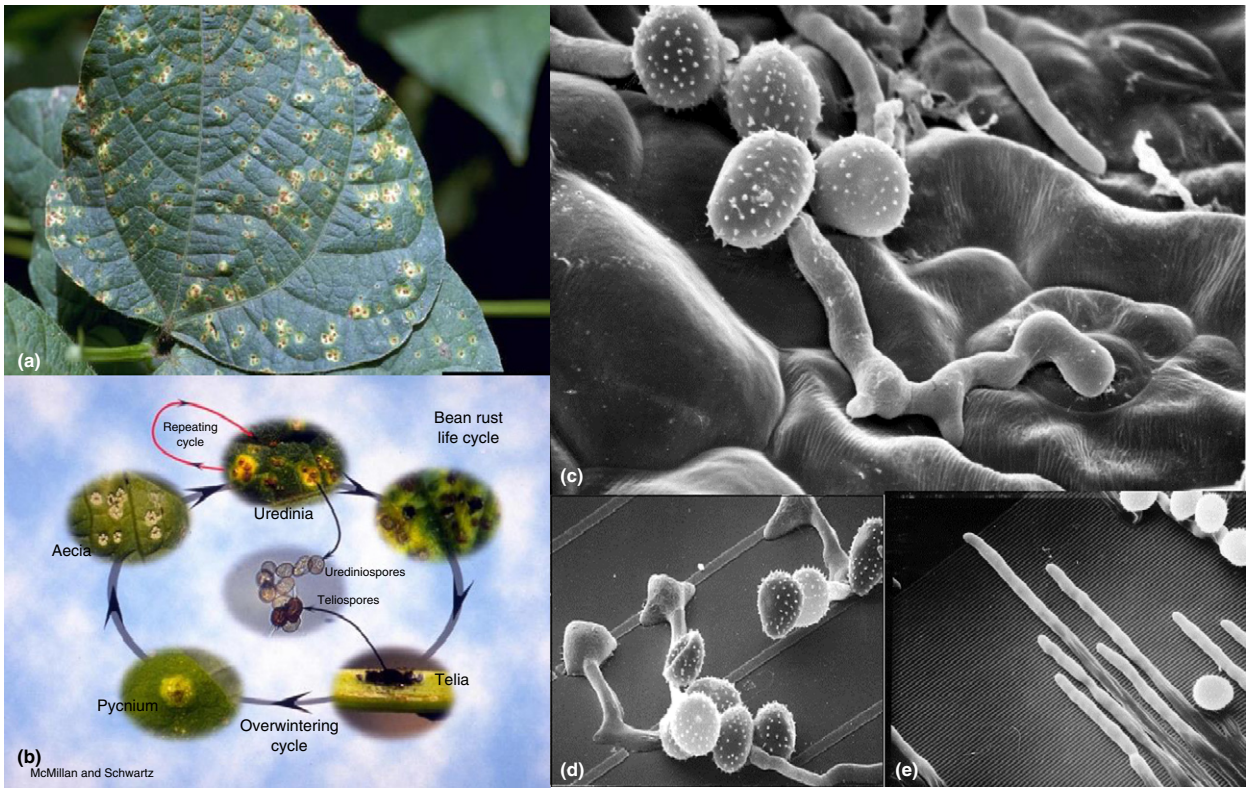


Figure 4 *Uromyces appendiculatus*, the bean rust pathogen, exhibits growth and differentiation directed by contact stimuli (thigmotropism and thigmodifferentiation, respectively). (a) Symptoms of bean rust. (b) Life cycle of *U. appendiculatus* on bean (*Phaseolus vulgaris*) showing the stage at which urediniospores are important. (c) Urediniospore germlings on the leaf surface of a bean leaf. The germling grew oriented to the stomata, and then differentiated into an appressorium (infection structure) over the stomate. (d) Polystyrene replica with 0.5 μm high ridges that are highly inductive for appressorium differentiation. (e) Polystyrene replica with 0.1 μm high ridges that do not induce appressorium formation. (a) and (b) from Howard F. Schwartz. Available at: http://www.bugwood.org/ (accessed 09.09.13); (c) and (d) adapted from Hoch, H.C., Staples, R.C., Whitehead, B., Comeau, J., Wolf, E.D., 1987. Signaling for growth orientation and cell differentiation by surface topography in uromyces. Science 235 (4796), 1659–1662; and (e) photo provided by Harvey Hoch.

mechanisms to derive nutrients from the live host. Biotrophs include fungi that cause powdery mildew (*Blumeria graminis* f. sp. *hordei*) and downy mildew (*Plasmopara viticola*), and *Xanthomonas oryzae* pv. *oryzae*, the bacterial blight pathogen of rice. Hemibiotrophic pathogens exhibit both biotrophic and necrotrophic life stages, keeping the plant cells alive in the early stages of infection, and killing them at later stages. These include the rice blast pathogen *M. oryzae* and the anthracnose pathogen *Colletotrichum lindemuthianum*. Although these three broad infection mechanisms (biotrophy, necrotrophy, and hemibiotrophy) provide a useful way to classify pathogens, there is no consistent agreement on what common features are relevant to support inclusion of a pathogen within a group. For example, *Phytophthora infestans*, the important oomycete pathogen that causes late blight of potato, has been classified as by various authors as a biotroph, hemibiotroph, and even a necrotroph (Oliver and Ipcho, 2004).

How do Pathogens Deliver Virulence Effectors?

Pathogens may secrete effectors into the plant apoplast (the space outside of the plasma membrane) or directly into the plant cell. Although effector secretion is a common strategy among bacteria, fungi, and nematodes, different pathogens have evolved diverse and elaborate secretion mechanisms. Multiple effectors are delivered by one secretion system, and mutations in secretion systems that block effector transfer can severely reduce or eliminate pathogenicity.

To get outside of a gram-negative bacterial cell, an effector must cross the inner plasma membrane, the periplasmic space, and the outer lipopolysaccharide membrane. Plant pathogenic bacteria have evolved at least seven types of secretion systems to accomplish this, most of which have structural and functional counterparts among bacteria pathogenic to plants, humans, and animals (Tseng *et al.*, 2009). Secretion systems vary widely in their structural complexity, but are grouped as either one-step systems, which move proteins directly through the bacterial cell envelope (type I, III, IV, and VI systems), or two-step systems, which deliver the protein first across the plasma membrane to the periplasm and then, in a second step, across the outer membrane (type III, IV, and VI) (for a review, see Records, 2011). The simplest of these is the type I secretion system (T1SS), which spans the inner membrane, periplasmic space, and the outer membrane, and transports proteins from the bacterial cytosol directly to the outside of the bacterium. Bacteria that cause soft rot diseases use this system to deliver proteases and lipases to the apoplast of plant cells.

Type III, IV, and VI pathways have complex structures that move effectors across the bacterial envelope and can deliver the effectors directly into the host plant cytoplasm. Type IV (TT4S) pathway is notable because it is the only pathway described so far to transport both protein and nucleic acid substrates; *A. tumefaciens* uses the TT4S to deliver plant-transforming DNA, called T-DNA (transferred DNA), along with proteins into the host cytoplasm.

Type III (T3SS) pathway is structurally complex, with more than 25 proteins, and has evolutionary similarities to bacterial flagella. This system delivers effectors from the bacterial cytoplasm directly to the host plant cytoplasm using a syringe-like structure that crosses the plant cell wall. Once at the plant membrane, secreted proteins form a pore in the host membrane enabling translocation of the effector proteins into the host cell (Galan and Wolf-Watz, 2006). On the basis of analyses of sequenced genomes and subsequent functional analyses, plant pathogenic bacteria in the species of *Pseudomonas* and *Ralstonia* secrete large numbers of T3SS effectors, in some cases, more than 40. The T3SS is essential for these pathogens to cause disease.

Large numbers of proteins are secreted from bacteria via the two-step type II (T2SS) and V (T5SS) secretion systems. In these systems, the first step of protein transfer requires an amino terminal signal peptide, which is removed as the protein crosses from the bacterial cytoplasm to the periplasmic space. The effector is then transported through the outer membrane by a second complex secreton structure. Many plant cell-wall degrading enzymes (CWDEs), such as pectin lyases, polygalacturonases, and cellulases, are secreted from *Xanthomonas* and *Erwinia*-type pathogens through the T2SS pathway. *Dickeya dadantii* (*Erwinia chrysanthemii*) secretes adhesins via the T5SS pathway.

For biotrophic and hemibiotrophic fungi and oomycetes, the process of delivering effectors is less well understood. Effectors secreted to the extracellular environment are likely transported by the eukaryotic (type II) secretory pathway, a process involving exocytosis of Golgi-derived secretory vesicles. Effectors moving through this pathway carry a canonical N-terminal type II secretion signal, allowing sequence-based identification of putative effectors that function in the apoplast. The hemibiotrophic fungal rice blast pathogen *M. oryzae* delivers apoplastic effectors using type II Golgi-dependent secretory pathway (Giraldo *et al.*, 2013).

For most fungi and oomycete pathogens, the pathway for effector transfer into the plant cell cytoplasm is just becoming known. The hyphae typically differentiate into a haustorium after penetration of the host cell. As the haustorium develops, a specialized interface forms around it; this interface consists of the plasma membranes of the pathogen and the host separated by a modified pathogen cell wall. The interface allows for a two-way movement; nutrients move from the host cell to the pathogen, and effectors are delivered from the pathogen to the host. Secretion and delivery of effectors from these haustorium-forming pathogens requires N-terminal motifs (RxLR) (Tyler *et al.*, 2013). It is believed that RxLR effectors move into the host cell independent of specialized structures from the pathogens, and possibly by exploiting the plant endocytic pathway (for a review, see Panstruga and Dodds, 2009). Not all fungi use haustoria, however; *M. oryzae* effectors targeted to the host cytoplasm are delivered from invasive hyphae (the hyphae that invade inside the plant cells) into host cells via a novel plant membrane-rich structure (Giraldo *et al.*, 2013).

Nematodes deliver effector proteins into plant cells through a stylet that pierces the host cell wall. Fluids from glands that contain effectors are then secreted into the host cytoplasm through an orifice at the tip of the stylet (reviewed by Haegeman *et al.*, 2012; Torto-Alalibo *et al.*, 2009).

Effectors that are Delivered to the Plant Apoplast

Effectors that are delivered to the apoplast were the focus of early studies of host–pathogen interactions because they could often be isolated from microbes grown *in vitro*. Apoplastic effectors, including CWDEs, toxins, hormones, and cysteine-rich peptides, are considered more important for necrotrophic pathogens than for biotrophic or hemibiotrophic pathogens. CWDEs facilitate penetration of plant tissues and release nutrients from the wall polymers. Bacteria that cause soft rot diseases produce a wide range of CWDEs, including pectinases, cellulases, proteases, and xylanases. Mutagenesis studies determined the relative contribution of CWDE-encoding genes for disease, showing that pectinase genes are especially important for tissue maceration (Beaulieu *et al.*, 1993; Walton, 1994). An analysis of the mutants revealed that producing a combination of different enzyme activities allows pathogens to efficiently degrade cell walls and feed on the byproducts. Some pathogens produce multiple CWDEs with the same type of activity; *D. dadantii* produce up to nine different endopectate lyase genes that vary in activity level, optimum pH, substrate preference, and length of product. The evolution and retention of multiple CWDEs provides the pathogen with flexibility to attack different host plants under diverse conditions, such as when the pH of the tissues being degraded changes during the infection process. The redundancy of these enzymes and the genes encoding them may also be important for the survival of the pathogen as a saprophyte outside of the host plant.

In addition to making use of redundancy in CWDEs, necrotrophic pathogens usually rely on the collective contribution of different types of effectors to promote plant cell death and nutrient acquisition. For example, the arsenal of *B. cinerea*, the causal agent of gray mold, includes both CWDEs and toxic low molecular weight metabolites (Choquer *et al.*, 2007). Many fungal and oomycete pathogens secrete small, cysteine-rich proteins that protect the pathogen by inhibiting the activity of plant-produced hydrolytic enzymes (proteases, glucanases, and chitinases). Avr2, an effector produced by the tomato pathogen *Cladosporium fulvum*, inhibits the activity of tomato apoplastic cysteine proteases. *P. infestans* secretes a suite of protein inhibitors of plant cysteine proteases, subtilisin-like serine proteases, and an endo-β-1,3 glucanase.

Phytotoxins, microbial products that are poisonous to plants, are produced by many necrotrophic bacteria and fungi resulting in chlorosis and necrosis of the affected host tissues. Phytotoxins are grouped into host-selective toxins (HSTs) and general toxins. HSTs, the essential components of pathogenicity, are toxic only to susceptible plants. These toxins produce visible disease symptoms of the resulting disease; that is, treatment with HST extracts alone induces the same symptoms as pathogen infection. HSTs were critical virulence factors

contributing to two devastating crop epidemics. The Southern corn leaf blight epidemic of 1970, caused by the pathogen *Cochliobolus carbonum* destroyed approximately 15% of the US maize crop. Symptoms on susceptible maize result from the production of a cyclic tetrapeptide called HC-toxin. The Victoria blight epidemic of oats in the mid-1940s was caused by *Cochliobolus victoriae*, which elicits symptoms caused by the cyclized peptide phytotoxin victorin.

Although most described HSTs are secondary metabolites, a few are proteins, such as ToxA, produced by *Pyrenophora tritici-repentis*, during the development of tan spot disease of wheat (Tomas *et al.*, 1990; Ciuffetti *et al.*, 1997). Although the pathogen secretes the toxin into the plant apoplast, ToxA must be internalized into susceptible wheat cells to have its toxic effect (Ciuffetti *et al.*, 2010). Resistant wheat cultivars do not internalize the toxin. Internalization is directed by a specific motif in ToxA that comprises Arg-Gly-Asp (RGD); this motif is predicted to interact with a plant membrane receptor that helps translocate the ToxA into the plant cell (Ciuffetti *et al.*, 2010).

General toxins, or nonhost selective toxins, are toxic to most plants, and have a broader host range than the producing pathogen. Often general toxins affect organisms beyond plants, including bacteria or yeast, a feature that has been exploited to study these toxins in systems simpler than plants. General toxins are not essential virulence factors; mutation of genes involved in the biosynthesis of these toxins does not render the pathogen avirulent. The mutant pathogen can still cause disease, but may be less aggressive. Coronatine, phaseolotoxin, and tabtoxin are three general toxins produced by the bacterial species in the *Pseudomonas* genus.

Some virulence effectors work as plant growth regulators, also called phytohormones. Phytohormones are molecules that regulate plant growth, at extremely low concentrations. Pathogen-produced auxins and cytokinins can induce developmental and morphological changes that can result in galls, epinasty, or a number of other grotesque shapes in the plant. The gram-positive bacterium *Rhodococcus fascians* synthesizes and secretes cytokinins that are taken up by the plant cells surrounding the infection site. These cytokinins activate a set of plant genes that keep the cells in a juvenile state, contributing to disease symptoms such as serrated leaves, stunting, and abnormal flowers (reviewed by Busch and Benfey, 2010). Besides inducing chlorosis and other disease symptoms, the general toxin coronatine produced by *Pseudomonas* spp. structurally and functionally mimics the plant hormone jasmonic acid isoleucine. In this role, coronotine promotes the opening of plant stomata, allowing the bacteria to enter the plant and access the apoplast (Melotto *et al.*, 2006; Thilmony *et al.*, 2006).

Effectors that are delivered to the inside of plant cells

Genome searches for signature signal domains has led to the discovery of large numbers of genes encoding effectors that could be translocated into the plant cytoplasm. For most of these putative effectors, the exact molecular target or role in the infection process is not known. The widely studied bacterial effectors delivered by the TTSS provide examples of the broad range of host pathways and functions that are targeted. Some TTSS effectors, such as the *P. syringae* effectors AvrRpt2 and AvrB, alter the hormone content of plant cells. AvrRpt2, a cysteine protease, stimulates turnover of proteins that negatively regulate auxin signaling to promote pathogenicity (Cui *et al.*, 2013). AvrB activates mitogen-activated protein kinase MAP kinase 4 (MPK4), which upregulates the expression of jasmonic acid response, a hormone perturbation that enhances plant susceptibility (Cui *et al.*, 2010).

Some microbial effectors function to actively suppress PTI, and thereby enhance susceptibility. One mechanism, employed by the *P. syringae* effector AvrPto, is to bind to and block the kinase activity of the PTI receptors (PRRs) that recognize several PAMPs. A second *P. syringae* effector AvrPtoB binds to and targets PRRs for degradation. Other effectors indirectly affect PRR signaling. Virulence effectors produced by some fungal pathogens, such as Sip1 produced by *M. oryzae*, bind the fungal PAMP chitin, thereby reducing the availability of the chitin for binding to the plant PRR, and inhibiting activation of PTI.

Still other effectors directly alter gene expression. The unique transcription activator-like (TAL) effectors produced and delivered to plant cells by *Xanthomonas* spp. enhance pathogen virulence by directly activating promoters of target plant genes associated with disease or susceptibility. These protein effectors contain a central repeat domain comprising 34–35 amino acid modules that are repeated in tandem; each repeat contains two hypervariable amino acid residues (for a review, see Scholze and Boch, 2011). The C-terminus carries signal sequences that direct the effector into the nucleus (nuclear localization signals; NLSs) and an acidic activation domain (AAD) characteristic of transcription factors. Once in the host cell, TAL effectors are targeted to the plant nucleus by the NLS. In the nucleus, the TAL effectors bind specifically to sequences in target plant gene promoters and induce expression of these plant genes. The DNA-binding specificity of TALs is determined by central hypervariable amino acid residues. Although the discovery and validation of the function of plant genes targeted by TAL effectors is in its infancy, some are known to activate expression of genes that enhance susceptibility. The *X. campestris* pv. *vesicatoria* effector AvrBs3 induces the expression of auxin-responsive genes in susceptible pepper plants; the resulting increase in auxin causes changes in cell division, cell enlargement, and hypertrophy, which may facilitate release of bacteria to the leaf surface and into the environment (Marois *et al.*, 2002; Kay and Bonas, 2009). AvrXa7 and PthXo1 produced by *Xanthomonas oryzae* pv. *oryzae* induce the expression of sugar transporters OsSWEET14 and OsSWEET11, respectively. The increased expression of these genes is predicted to enhance transport of sugar outside of the plant cell for bacterial consumption and thereby increasing the risk of disease (Chen *et al.*, 2010).

The few examples above demonstrate that pathogen effectors target a wide variety of plant functions to cause disease or increase pathogen fitness. However, functions are known for only a few effectors, mainly because the study of effector function is complicated by the large numbers of diverse effectors that any one pathogen secretes. *P. syringae* secretes more than 40 effectors (Chang *et al.*, 2005). Although some effectors are major contributors to pathogen virulence, most effectors likely function in concert to cause disease, with inactivation of multiple effectors needed to observe any change in virulence function (Cunnac *et al.*, 2009). As a better understanding of the effector function could reveal new strategies for disease control, effector biology remains a major research area.

Effector-Triggered Immunity: Evolution of Plants to Evade ETS

In response to the suppression or evasion of PTI by effectors, plants evolved a second line of defense called effector-triggered immunity (ETI). In ETI, plants use intracellular immune receptors that are the products of resistance (R) genes to monitor effectors or their activity and activate strong defense responses. ETI-associated defense responses frequently, but not always, are characterized by a rapid, localized programmed cell death (PCD) of the host cells called hypersensitive response (HR). Other localized host responses activated by ETI can include the production of reactive oxygen species, enhancement of cell walls, accumulation of toxic metabolites or proteins, and altered hormone regulation. In some cases, ETI results in a systemic activation of resistance, called systemic acquired resistance (SAR) or priming for a more efficient activation of defense mechanisms in response to a secondary pathogen attack (Conrath, 2011).

Flor (1971) first conceptualized the 'Gene for Gene Hypothesis' positing that R genes direct the recognition of pathogen avirulence genes (now called virulence effectors) to culminate in resistance. Many R genes and effector gene combinations have since been characterized, supporting the hypothesis. How the R proteins actually confer recognition, though, is still being discovered and debated (Zipfel and Robatzek, 2010). Most, but not all, R proteins contain nucleotide-binding (NB) and leucine-rich repeat (LRR) domains. There are two subclasses of these NB-LRR proteins; one with a coiled-coil (CC) domain and the other with a toll, interleukin-1 receptor, resistance protein domain (TIR) at the N-terminus (Bernoux *et al.*, 2011). Initially, R proteins were predicted to interact directly with their target effectors to activate defense in a ligand–receptor manner (Keen, 1990). Indeed, direct, physical interactions have been shown for some R/effector gene combinations. R proteins in rice (Pi-ta, Pik, and RGA4/RGA5) and flax (L-locus NB-LRR proteins) directly bind to translocated effectors produced by the fungal pathogens *M. oryzae* and *Melampsora lini*, respectively, to activate resistance (Jia *et al.*, 2000; Dodds *et al.*, 2006; Ellis *et al.*, 2007; Kanzaki *et al.*, 2012). For many R/effector gene combinations, however, direct interactions could not be detected.

With the realization that R gene partners were pathogen virulence effectors, and with the identification of plant virulence targets for several effectors, a new model was proposed. This 'Guard Model,' predicts that R proteins act by monitoring (guarding) the effector target (guardee), and that modification of this target by the effector results in the activation of the R protein, triggering disease resistance in the host (Jones and Dangl, 2006). An evolutionary assumption in this model is that the effector/guardee modification enhances the pathogen's fitness. Supporting the Guard Model, the *Arabidopsis* R-protein RPM1 directly interacts with and responds to the status of a plant membrane-associated protein RIN4. RIN4 is the target of multiple bacterial effectors, including the *P. syringae* effector AvrB, and AvrB-mediated phosphorylation of RIN4 activates signaling by RPM1 (reviewed by Chisholm *et al.*, 2006; Jones and Dangl, 2006). Thus, RPM1 (the guard) monitors the status of RIN4, and the change in RIN4 (the guardee) by pathogen effector activity triggers the defense response pathway.

Not all R/effector gene interactions fit the Guard Model, because fitness benefits could not be found for R-gene interactors. Therefore, a second model, the Decoy Model, was proposed (Zipfel and Robatzek, 2010). The Decoy Model predicts that the effector target monitored by the R protein is a decoy that mimics the effector target, but *only* functions in perception of pathogen effectors without contributing to pathogen fitness. An example of an interaction fitting this model is AvrPto, a TTSS effector produced by *P. syringae*. AvrPto is a kinase inhibitor that binds to the cytoplasmic Ser/Thr kinase domain of a PAMP receptor, blocking PTI and enhancing virulence of the pathogen. AvrPto also binds to the tomato R protein Pto. Pto confers resistance to *P. syringae* strains harboring *avrPto*, but only if the plant contains Prf, a protein that physically interacts with Pto. Binding of AvrPto to Pto is detected by Prf, and ETI is triggered. Thus, Pto is a decoy that binds AvrPto, and the interaction of Pto with AvrPto is detected by Prf for signaling of ETI.

Defense Response Pathways are Shared between PTI and ETI

Although the categorization of immunity into PTI and ETI may imply that these are totally distinct responses, in reality, there is a great deal of overlap in the molecular events induced by both PTI and ETI (Tsuda and Katagiri, 2010), and a continuum in the two categories is observed (Thomma *et al.*, 2011). For example, the downstream signaling machinery used and the defense genes activated by ETI and PTI overlap extensively, although the strengths of the responses and their duration vary considerably. ETI-activated responses are more prolonged and robust than those activated by PTI, and an interesting current hypothesis is that ETI is a faster and more robust reactivation of PTI (Tsuda and Katagiri, 2010). This is shown by the amplitude of the responses in the zigzag model (**Figure 2**).

How Does the Environment Impact Disease in the Context of Climate Change?

Crop production, with its wide geographical range and intensity, is clearly affected by climate change (Lobell and Gourdji, 2012). Climate change may cause unpredictable changes on pathogen populations in varying effects depending on the specific pathosystem (Newton *et al.*, 2012; Chakraborty *et al.*, 2000). Increased temperature results in more rust disease in wheat and oats, whereas forage species become more resistant to certain fungi. Temperature effects on disease levels can result from temperature-induced changes in the host, pathogen, or the host–pathogen interactions (Garrett *et al.*, 2006; Newton *et al.*, 2012). Host plant changes might include (1) the alteration of plant architecture to create more suitable microclimates for pathogen colonization, (2) changes in the effectiveness of plant disease resistance, and (3) the increase of stress on plants, all of which would affect disease development. Higher temperatures are predicted to accelerate the breakdown of plant disease resistance in many host–pathogen systems by increasing disease pressure and/or altering *R* gene efficacy (Garrett *et al.*, 2006; Coakley *et al.*, 1999; Webb *et al.*, 2010).

It has been documented that an increasingly warmer weather provides a first glimpse of the impact on disease distribution and changes in severity. A simple scenario is that warm temperatures will reduce the impact of cool season diseases. However, this assumes that the pathogen remains static. *Puccinia striiformis* causes stripe rust of wheat and barley, and is, in general, a cool season pathogen that does well in the Pacific Northwest of the USA (Chen, 2005; Hovmoller *et al.*, 2011). The pathogen was not a problem in the wheat belt of the US Great Plains before 2001, because the fungus could not thrive in the warmer weather of this region. Unfortunately, a variant of the pathogen that is more adapted to higher temperatures appeared in the Great Plains in the early 2000s, and stripe rust is now a serious problem in this region.

Applying Knowledge of Plant–Microbe Interactions to Disease Control Strategies

What is out There?

Diverse groups of organisms are capable of causing plant diseases, and many management strategies to control these pathogens vary according to the specific pathogen. Thus, a first step in controlling plant disease is to accurately identify the cause. Diagnosis is based on the presence of symptoms and signs in the diseased plant. Symptoms are phenotypic expressions of disease in a plant in response to activities of the pathogen, including pathogen effectors. The symptoms may be localized to specific plant tissues, or systemic, as in the case of diseases caused by viruses and vascular wilt pathogens. Symptoms include those that cause plant death or necrosis (e.g., lesions, cankers, and rots), or those that result in hypertrophy and hyperplasia of tissues as in the case of galls and witches' brooms (Figure 5). Although symptoms are often helpful in field diagnosis, they may be misleading because completely unrelated pathogens can cause nearly identical symptoms. Furthermore, the interaction phenotype resulting from infection may vary depending on environmental conditions or the age and genetic background of the plant. Thus, diagnosticians often rely on signs, or visual confirmation of the pathogen in host tissue, for disease identification. Some signs, including bacterial ooze or fungal hyphae and fruiting structures (Figure 5) may be readily seen in the field. However, most pathogen signs are visible only by using a hand lens or microscope. In some cases, pathogens must be cultured or identified by serological and molecular detection methods.

Pathogens Function as Populations

While in the laboratory, the focus of the researchers was on characterizing how single 'model' pathogen strains cause disease; disease at the field level is not caused by a single pathogen genotype. To cause disease, the pathogen functions



Figure 5 Signs and symptoms of plant disease. (a) *Botrytis* blight of juniper; mycelium (sign) of *Botrytis cinerea* showing brown decay (symptoms). (b) Symptoms of late blight of potato. (c) and (d) Fruiting structures (sporangia) and mycelium of *Plasmopara viticola*, causing downy mildew of grape. Photos provided by Ned Tisserat.

as a population that is made up of multiple genotypes or strains with unique genetic and pathogenic attributes. The pathogenic attributes of the entire pathogen population collectively determine the ability to cause disease, the amount of disease on a plant and in a plant population, and the epidemiological consequence on the plant population. The primary evolutionary forces that shape a pathogen population include mutation, population size, gene/genotype flow, reproduction system (asexual vs. sexual), and selection imposed on the pathogen by the host and environmental factors (McDonald and Linde, 2002). The interactions of these evolutionary forces shape the genetic structure of the pathogen population.

Pathogens with high mutation rates, large population size, mostly asexually reproducing but with occasional sexual recombination, high dispersal over distance (gene flow), and under strong directional selection by the host are considered to have the highest risk potential. In contrast, pathogens with low mutation rate, relatively small population size, short dispersal, limited recombination, or gene flow present lesser risk in an agroecosystem. This broad characterization of pathogen populations provides a useful framework for disease resistance breeding and disease management. However, ability to effectively manage a pathogen requires detailed and specific knowledge of the pathosystem, and the strategies employed must be flexible to adjust to changing agricultural production systems and physical environments.

Use of Disease Resistance Gene for Pathogen Control

Genetic resistance has been the mainstay of disease control for many crop species. The two broad categories of host resistance are major gene resistance and quantitative resistance. As discussed earlier, major gene resistance is primarily involved in ETI whereas quantitative resistance involves basal defenses triggered by PTI, recognizing that there are considerable overlaps in the mechanisms triggered by ETI and PTI. Under strong directional selection, as in the case of major gene resistance, one or a few adapted pathogen strains will predominate the pathogen population, leading to severe epidemics. However, selection imposed by quantitative resistance is predicted to be less, reducing the pressure on pathogen population to evolve toward high aggressiveness. In agronomic terms, major gene resistance provides a 'clean' crop but with uncertainty about its stability. Quantitative resistance, however, allows some level of disease development but offers stability. Unlike major R genes that can be dramatically overcome by simple mutations of major genes in the pathogen, quantitative resistance is predicted to be 'eroded' over time through gradual changes of pathogenicity genes to counteract the defense mechanisms imposed by the host (McDonald and Linde, 2002; Lannou, 2012). Finding the right combination of major and quantitative resistance to provide effective and potentially durable resistance is the goal of many plant breeding programs.

Pathogen Fitness Penalty as a Predictor of R Gene Durability

More than 50 years ago, Vanderplank (1963) proposed that a pathogen with unnecessary virulence has lower parasitic fitness on the host without the corresponding resistance. Intuitively, accumulation of mutations in avirulence effector genes to avoid recognition by major resistance genes would reach a point to reduce the overall fitness of the pathogen population. The fitness penalty concept is useful in that it suggests practical applications. In a simple case, if an avirulence gene codes for a product with important functions other than being a target of recognition by the host, a loss-of-function mutation would be disadvantageous to the pathogen. It follows that measuring the fitness penalty of mutation from avirulence to virulence can provide a predictor of the effectiveness of the corresponding R genes, which collectively (as in a gene pyramid) result in durability of resistance (Leach *et al.*, 2001). Although there are pathosystems that seem to follow this general 'rule,' for example, bacterial blight of rice (Vera Cruz *et al.*, 2000), there are cases where a pathogen carrying unnecessary virulence does not exhibit lower parasitic fitness. For example, Chen (2005) studied the virulence spectrum of *Puccinia striiformis* f. sp. *tritici* and *Puccinia striiformis* f. sp. *hordei*, two closely related pathogens, and noted that races of *P. striiformis* f. sp. *tritici* with wide virulence still dominated the population. In contrast, *P. striiformis* f. sp. *hordei* races with narrow virulence tended to predominate, as predicted by the fitness penalty hypothesis.

The long history of coevolution between the pathogen and host would guarantee that the pathogen has evolved multiple mechanisms to compensate the fitness penalty caused by mutation of a single avirulence effector gene. One scenario is that the pathogen can have multiple copies of related effector genes that provide the necessary functions. Secondary mutations at different loci may compensate for the primary function of the first mutated gene. Thus, understanding the biology of changes from avirulence to virulence is essential to effectively apply the fitness penalty concept in managing diseases.

With advances in knowledge of the genetic and molecular basis of avirulence effector genes (Win *et al.*, 2012), there are now more tools to test the fitness hypothesis. For example, in the blast fungus *M. oryzae*, 15 Avr genes have been identified and isolated (reviewed by Liu *et al.*, 2013). By genome sequencing, a further 851 genes in *M. oryzae* are predicted to produce effector proteins (Chen *et al.*, 2013). Similarly, with large repertoires of confirmed and predicted effector genes, it is now possible to genetically inactivate avirulence effector genes individually or in combinations and measure whether their fitness attributes, such as reproductive rate (fungal spore production, bacterial multiplication), latent periods, and infection efficiency under laboratory or greenhouse settings. A caveat of this approach is that these standard fitness attributes may not be the only ones that are important in the natural environment where the pathogen has to survive and compete in the presence of the host and under harsh environments.

An alternative and complementary approach would be to conduct field survey studies to test the association of avirulence effector genes in natural populations. For known effector genes, it is possible to test if avirulence gene combinations exist in random or significantly deviate from random in the natural populations. If some combinations occur much less frequently than expected, it would suggest that the corresponding R gene combinations are more effective. By

monitoring the frequency of avirulence gene combinations, it may be possible to reveal the R gene combinations that are more effective.

The approach of testing gene associations for the whole pathogen genome, including genes for effectors as well as quantitative pathogenicity in the pathogen, can be generalized by applying genome sequencing to characterize pathogen populations. By combining sequence and pathogenic attributes, genome-wide association studies (GWAS) can be done comparable to what has been practiced in humans, animals, and plants. Several pathosystems, such as cereal rusts, rice blast and bacterial blight, and potato late blight are particularly amenable for applying GWAS, considering their global importance. The alarming spread of the stem rust strain Ug99 since its detection in 1999 in Uganda (Singh *et al.*, 2011) would present an interesting case to examine genome-wide changes of the new strains spreading over a broad geographic region.

Combining Major R Genes and QTL

Despite the concerns of 'breakdown' and 'erosion' of disease resistance, there are examples where a combination of major R genes and QTL provide stability of resistance in a farmer's field. Liu *et al.* (2009) dissected the genetic basis of resistance in a rice variety Shan-Huang-Zhan number 2 (SHZ-2) that has a reputation of exhibiting durable resistance to rice blast in South China. SHZ-2 has multiple major R genes and QTL. Some of the R genes are in clusters rich in NBS-LRR genes (Liu *et al.*, 2013). SHZ-2-derived lines have been tested in disease hot spots and continue to show stable resistance for more than 10 cropping seasons (Manosalva *et al.*, 2009). Owing to its performance and the known underlying genetics, SHZ-2 has been used as a donor of blast resistance in breeding programs in Southeast Asia.

There are also examples of atypical R genes providing effective disease control. A classic example is the recessive gene *mlo* for barley resistance against powdery mildew (*B. graminis* f. sp. *hordei* (Jørgensen, 1992). The wild-type *Mlo* locus encodes a seven-transmembrane protein, which functions as a negative regulator of resistance to powdery mildew and could have a broad role in regulating resistance to biotic and abiotic stress (Piffanelli *et al.*, 2002). Since 1979, barley varieties carrying *mlo* resistance have been shown to be effective over large areas, satisfying the criteria of 'durable resistance' (Lyngkjær and Ostrergård, 1998). More recently, a recessive gene conferring blast resistance in rice was isolated and characterized. In contrast to the majority of blast resistance genes (*Pi* genes), which encode NB-LRR proteins, *pi21* encodes a proline-rich protein (Fukuoka *et al.*, 2009). The *pi21* recessive mutation is associated with durable resistance to blast in the upland rice grown in Japan. However, the area planted to varieties carrying *pi21* is relatively small. The effectiveness of *pi21* needs to be tested in varieties planted widely in intensive production system. Regardless, *pi21* is a welcome addition to the pool of resistance genes that are not NB-LRR types.

Another successful case of achieving durable resistance is the use of high-temperature adult plant (HTAP) resistance to manage stripe rust of wheat (Xu *et al.*, 2013). The effectiveness of this type of resistance depends on the age of the plant and high temperatures. Although used to control stripe rust for more than 60 years in the US, the genetic mechanisms of HTAP resistance were recently revealed through the characterization of the HTAP gene *Yr36* (Fu *et al.*, 2009). *Yr36* is upregulated by high temperature, explaining the phenotypic expression. In contrast to most NB-LRR genes for strong ETI-type resistance, HTAP resistance provides partial but stable resistance against stripe rust over time.

Plant Diversity to Manage Disease

The benefits of using plant diversity to manage diseases or enhance crop performance are generally recognized. However, there is much debate in the approaches of how to effectively deploy genetic diversity in modern agricultural systems. Diversity can be deployed at a single genotype level, or diversity could be used at the population level in a plant community.

Many major crop breeding programs have introduced more genetic diversity into the crops. For example, the 'Green Revolution' for rice production began with the release of the first semidwarf rice variety IR8 in the mid-1960s. IR8 has only three landraces in its pedigree. Though breeding efforts have focused on improving disease and pest resistance and grain quality, diversity was systematically incorporated into modern rice varieties derived from IR8 (Peng *et al.*, 2008). In contrast to IR8, the pedigree of the modern variety IR64, released in the mid-1980s, includes 20 landraces. IR64 is grown over millions of hectares in tropical Asia, partly because it has shown good resistance to rice blast for more than two decades since its release. The accumulation of diverse genes contributes to the stability of disease resistance observed in IR64. Thus, using a broad genetic base and practicing appropriate selection can play a key role in developing disease-resistant varieties.

Multilines and varietal mixtures

Besides combining diverse genes in a single genotype, individual genes can be used separately in time and space. The basic principle of having different host genotypes in a field is to reduce the selection pressure toward more virulence in the pathogen populations. Multilines carrying up to 10 individual resistance genes are being used for controlling crown rust in oats, and are currently being used to manage rice blast in some areas of Japan (Abe, 2004). In practical breeding, multilines fit a specific niche where resistance genes are added to a single genetic background to control disease. A main limitation of the multiline strategy is that much time and effort is needed to produce near-isogenic lines with individual resistance genes. Very often, by the time near-isogenic lines are produced, their other agronomic attributes are surpassed by other improved varieties. Wolfe (1985) advocated the use of varietal mixtures, a strategy that uses a mixture of varieties that are agronomically homogeneous but genetically diverse with respect to disease-resistance genes. The system is expected to stabilize the selection on the pathogen population. This strategy alleviates the need to produce isogenic lines and captures the complementary agronomic attributes provided by multiple varieties.

Interplanting

Interplanting resistant and susceptible varieties in different ratios is another strategy that capitalizes on diversity to control

disease. This strategy was deployed to control rice blast disease in a large-scale experiment in the Yunnan province of China (Zhu *et al.*, 2000). Disease was reduced by 94% in the interplanted plots compared with the monoculture plots. In this experiment, the susceptible was glutinous rice, which is 20 cm taller than the resistant variety (**Figure 6(a)**). The height difference may alter the microclimate of the canopy to become less conducive to disease development. Owing to the success of the interplanting experiment, and because glutinous rice has a high market value, the interplanting strategy was adopted in more than a million hectares of rice production (**Figure 6(b)**). Although interplanting may not be applicable to all crops and cropping systems, its success raised awareness of the importance of plant diversity for managing diseases.

Other Disease Control Strategies

Plant diseases cannot always be controlled by resistance. Resistance genes to a specific pathogen may not be available in certain plants, or the suite of quantitative resistance genes in some plants may not provide a sufficient level of control. In other cases, resistance genes may be difficult to incorporate (as in many woody perennials) or they may be linked to agronomically unsuitable traits. Therefore, other management strategies are needed to suppress pathogen populations and disease development, sometimes even where resistance is the primary means of controlling disease. Some diseases can be avoided by growing crops in regions that are not conducive to disease development. For example, many vegetable crops grown for seed are produced in arid regions of the western US, where low rainfall and a lack of extended leaf wetness necessary for infection inhibits foliar and seed pathogens. Plant pathogens may be excluded during a growing season by using pathogen-free seed or propagative parts. Heat treatment and meristem tip culturing are used to rid plants of viruses and hot water treatments can disinfest seeds of surface contaminating bacterial pathogens.

Once introduced into an area, pathogens (other than biotrophs) can rarely be eradicated, but their populations can be reduced by certain cultural practices. Crop rotation is an excellent method of reducing inoculum levels of some pathogens that exhibit host specificity. Plowing pathogen-infested plant residue into the soil at the end of the season hastens its decomposition and may reduce populations of pathogens that are not good soil inhabitants. Although the practice of reduced tillage has been widely adopted by farmers to prevent soil erosion and to conserve soil moisture, it may have the undesirable consequence of enhancing pathogen survival in crop debris. Goss's wilt, a bacterial disease of corn, has recently increased in severity in the Great Plains of the US in part because of widespread adoption of reduced tillage practices and a lack of crop rotation.

Many bacterial, fungal, and oomycete diseases are managed by chemical applications. Copper-based products, and to a much lesser extent antibiotics (streptomycin sulfate and tetracycline), are used for bacterial diseases whereas a broad array of fungicides with varying modes of biochemical action control oomycetes and fungi (see http://www.frac.info/publication/publication.htm). Fungicides are generally classified as protectants (also called contacts) or systemics. Protectants are not absorbed and redistributed but instead form a protective barrier on the plant surface. They, for the most part, affect multiple biochemical pathways in pathogens and are not prone to resistance problems. Some systemic fungicides are absorbed and move only in the leaf on which they were applied; others move acropetally in the xylem. Only the phosphonate fungicides are capable of acropetal and basipetal movement. Most systemic fungicides target specific enzymes in fungal or oomycete biochemical pathways and are therefore at a higher risk for fungicide resistance due to selection pressure in the pathogens. For example, there are numerous cases where mutations in the demethylase gene of fungal pathogens render them less sensitive to demethylation-inhibiting fungicides. Fungicide resistance is a major concern, and strategies such as avoiding multiple

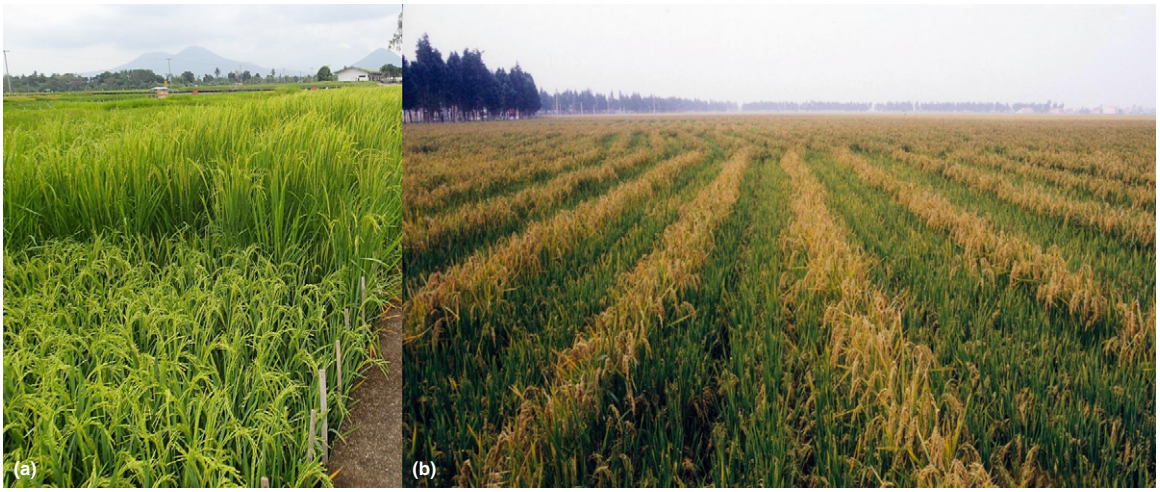


Figure 6 Interplanting of glutinous and hybrid rice to avoid rice blast disease in Yunnan, China. (a) Blast-susceptible glutinous rice (foreground) is 20 cm shorter than the blast-resistant hybrid rice (back). (b) Alteration of four rows of glutinous (short) rice with one row of the hybrid (tall) rice was very effective at reducing blast disease on the glutinous rice. Photos courtesy of the International Rice Research Institute.

applications of the same fungicide during the growing season or mixing or rotating different classes of fungicides have been recommended.

Concluding Perspectives

Much progress has been made in understanding the molecular evolution of plants and pathogens, and the integration of this information into crop improvement programs or for disease management is ensuring sustainable crop production for the immediate future. Still, the functions for very few pathogen effectors are known, and often these are only in model systems. Our knowledge is limited on how plant defense responses are differentially regulated or modulated in the spectrum from PTI to ETI, and how this regulation can be manipulated for better disease control. As an example, the relevance of epigenetic controls on plant disease and immunity is only just beginning to be addressed (Alvarez *et al.*, 2010).

Most of our knowledge has been gained by studying plant–microbe interactions in growth chambers and greenhouses, and rarely, in fields under conditions typical for a given disease. As a result, little is known about the interactions of environment with disease development, PTI, or ETI. The trend toward systems approaches to study how plant and pathogen genomes, metabolomes, and physiology are affected by interactions with each other and with environmental changes is a promising start, but frequently they are limited to growth chamber or greenhouse studies. The design of proactive disease management strategies for globally important diseases will require new experimental strategies. One possibility is to establish 'biostations' where disease can be assessed using a common set of genetic materials over different geographic areas with a range of climate scenarios.

Evolving new, improved, or cheaper technologies, such as genomics, proteomics, metabolomics, and high throughput phenotyping capacity at the field level, will provide deeper insights into plant disease and resistance. The integration of the molecular, organismal, and systems-level information gained from using these approaches will ultimately allow improvement of disease management strategies to include broad-spectrum and durable disease resistance.

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See also: Biodiversity: Conserving Biodiversity in Agroecosystems. Biotechnology: Plant Protection. Breeding: Plants, Modern. Climate Change and Plant Disease. Emerging Plant Diseases. Emerging Zoonoses in Domesticated Livestock of Southeast Asia. Genomics: Plant Genetic Improvement

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Plant Health Management: Biological Control of Insect Pests

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Glossary

Allee effect An effect in low-density populations where average per capita fitness increases with population density through increased efficiency of mating, food acquisition, or natural enemy escape.

Arthropod Any animal in the phylum Arthropoda that includes insects, mites, and other invertebrate taxa that are characterized by a chitinous exoskeleton, segmented body, and jointed limbs.

Ecosystem service Products and processes provided by natural ecosystems that are critical for human well-being.

Entomopathogen A bacterium, virus, protozoan, or fungus that causes disease in insects.

Epizootic An outbreak of disease in a population of the same animal species.

Hyperparasitism Occurs when a parasitoid species uses another parasitoid species as the host for its own larval development.

Irreplaceable mortality The mortality that would not occur if a specific mortality factor was removed, taking into account the compensating action of other mortality factors.

Parasitoid An insect with a parasitic larval stage that develops by feeding in or on the body of a single insect or other arthropod host.

Introduction

Biological control is a valuable ecosystem service that describes the suppression of an insect pest population by one or more living organisms that are known as natural enemies. Insect pests are broadly considered to include all populations that cause harm to humans and their agricultural resources, whereas natural enemies are more narrowly restricted to living predators, parasitoids, competitors, and entomopathogens (including nonliving, but replicating viruses). A number of other biological approaches to the management of insect pests have at times been considered to be biological control tactics, and these include host plant resistance, transgenic insecticidal crops, insect growth regulators (IGRs), botanical insecticides, pheromone disruption techniques, and sterile insect techniques. Although these valuable control tactics play an important role in insect pest management, they are distinct from biological control covered in this article in that they are not based on the ecological interactions between agricultural resources, target pests, and natural enemies.

The suppression of an insect pest population by natural enemies can occur naturally and unaided by humans, or can be facilitated by human intervention. It is the dynamics of the underlying ecological interactions that characterize biological control, and the traits of the species involved and the favorability of the abiotic and biotic environment that influence the strength of the interactions and consequently the degree of insect pest suppression that can be achieved. Thus, biological control involves both direct and indirect interactions (Moon *et al.*, 2012) between insect pests, natural enemies, and agricultural resources with humans playing an important role in both reaping the benefits and facilitating the other interactions (**Figure 1**). The direct interactions are those that occur between two species via various forms of consumption, such as predation, parasitism, or infection by the natural enemy, herbivory by the insect pest, and the contribution of agricultural resources to human welfare. The indirect interactions are more subtle and necessarily involve a third species, such as the indirect benefits of natural enemies for both humans and agricultural resources via suppression of insect pests, and the indirect control of an insect pest by a nondamaging competitor acting as a natural enemy via induced crop resistance to the insect pest. Although natural enemies seldom act as indirect suppressors of insect pests, it is a common mode of action for natural enemies (such as microbial antagonists) used in the suppression of plant diseases. Some notable exceptions, however, include the introduction of dung beetles for the suppression of bush fly populations in Australia, which compete for the removal of dung from cattle ranches (Tyndale-Biscoe and Vogt, 1996), and the induction of plant resistance by early season Willamette mites in vineyards in California to suppress populations of the later-season, more damaging, Pacific mites (Karban *et al.*, 1997). In addition, biological control can involve even more complex interactions, such as the mutualistic interactions between grasses and their endophytic fungi, *Neotyphodium* species (Hartley and Gange, 2009). By production of toxic alkaloids the endophytes can either deter, or reduce the performance of, insect herbivores as an example of a direct antagonistic interaction. In some cases, however, the endophytes may also cause an indirect negative effect on the performance of predators and parasitoids due to a reduction in the nutritional quality of the insect herbivores. The net effect of this mutualism is often beneficial in terms of the biological control of insect pests of pasture grasses, but can also depend on fungal and grass genotype, fungal, grass and insect species, and environmental conditions.

The application of biological control for the suppression of insect pests dates back some 3000 years in documented records, when weaver ant nests were collected from mountain forests and established on trees in citrus groves in China (Olkowski and Zhang, 1998). Weaver ants are effective predators of a number of citrus pests, and these and similar ant species continue to play a very important role in the suppression of insect pests in citrus production in many parts of

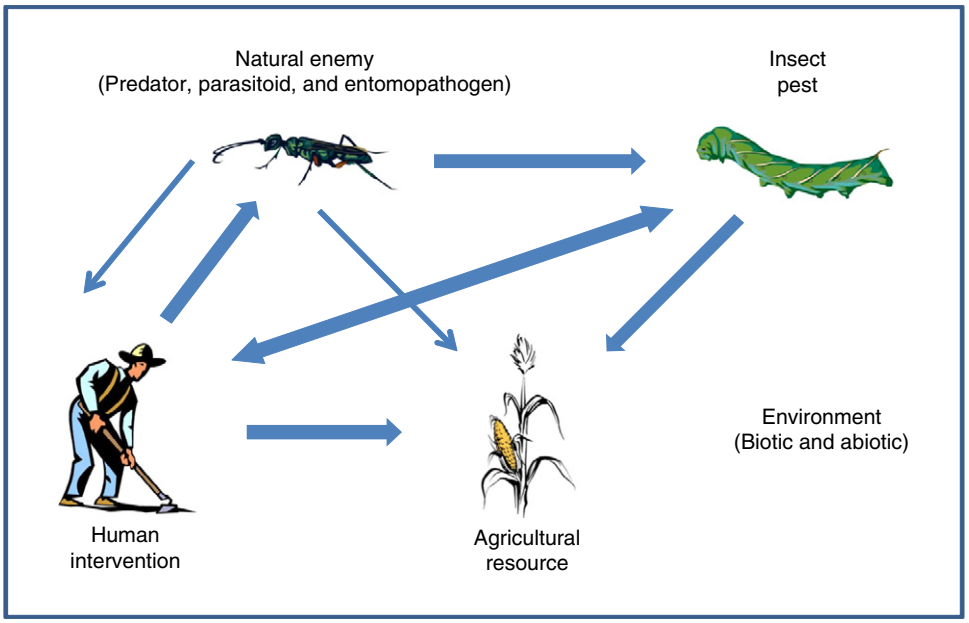


Figure 1 A diagram of the ecological relationships that characterize biological control. Direct interactions are shown by thick lines (direct trophic interactions with arrows pointing to the resource, direct competitive interaction with arrows at both ends), and indirect interactions by thin lines (with arrows pointing to the beneficiary).

the world. The original success of the weaver ants in citrus groves in China was further facilitated by surrounding the base of the citrus trees with moats to prevent ants from leaving the tree canopies, and by providing bamboo bridges between trees to encourage the spread of their foraging activity. This early record of the use of ants as natural enemies for the suppression of citrus pests is an example of augmentative biological control, one of four approaches to biological control that have since become recognized in insect pest management. The four approaches are (1) natural biological control, i.e., the natural suppression of potential insect pests by resident natural enemies that requires no human facilitation, (2) importation biological control, i.e., the deliberate importation and establishment of specialized natural enemies from the region of origin of an exotic invasive insect pest to provide long-term suppression over broad geographic regions, (3) conservation biological control, i.e., the localized manipulation of the crop environment to protect or enhance the activity of resident natural enemies for short-to longer-term suppression of insect pests, and (4) augmentative biological control, i.e., the mass production and localized release of resident natural enemies to augment their abundance for either immediate (inundation) or season-long (inoculation) suppression of insect pests.

Natural Biological Control

It is well known that only a minority of insect species ever achieve the status of an agricultural pest, in part because many of them do not live on cultivated plants but, more importantly, because the abiotic and biotic environment is often not favorable for their population growth. Environmental favorability is influenced by abiotic factors that can affect a potential insect pest either directly via tolerance of physical, chemical, or climatic conditions, or indirectly through their influence on the nutritional quality of cultivated plants. For example, heavy rains not only lead to direct mortality of plant-feeding insects, but can also lead to improved host plant quality through the stimulation of plant growth. Similarly, environmental favorability is influenced by biotic factors that, in addition to host plant quality, include host plant abundance, activity of competitors and natural enemies, and disturbance from human intervention. Given the broad range of factors that contribute to environmental favorability, what evidence do we have that natural biological control ever plays a pivotal role in the suppression of potential agricultural pests?

The best evidence for natural biological control comes from unintended consequences of the use of synthetic pesticides. Populations of natural enemies tend to be impacted to a greater extent by pesticide use than populations of insect pests due to the loss of their food supply and perhaps also to an increased level of exposure (from a combination of greater mobility on plant surfaces and their smaller size and consequently greater surface area to volume ratio) and reduced level of general detoxification mechanisms (mixed function oxidases used by plant-feeding insects to breakdown chemical plant defenses). One experimental approach used to verify the role of natural enemies in the suppression of arthropod pests is referred to as the 'insecticidal check method' and was used, for example, by Morris *et al.* (1999) to demonstrate the effectiveness of the mite predator, *Neoseiulus fallacis*, in suppressing the abundance of the twospotted spider mite, *Tetranychus urticae*, in mint fields in central Oregon. Similarly, several studies have highlighted the importance of surface-dwelling predators in the biological control of planthoppers in tropical irrigated rice fields. Settle *et al.* (1996) demonstrated this very effectively in an experimental field study in Indonesia, where one half of the replicated plots were treated with a

combination of carbamate and organophosphate insecticides and the other half not treated (Figure 2). Rice brown planthopper, *Nilaparvata lugens*, showed a classic pattern of late-season resurgence in population abundance due to reductions in the abundance of surface and aquatic predators.

Even more impressive as a demonstration of the significance of natural enemies in the suppression of potential insect pests is the disruption of natural biological control in seminatural habitats. Repeated applications of malathion bait as part of an eradication program for Mediterranean fruit fly, *Ceratitis capitata*, caused disruption of the natural biological control of an endemic gall midge, *Rhopalomyia californica*, in the southern part of the San Francisco Bay Area of California (Ehler *et al.*, 1984). The gall midge produces multichambered galls on the terminal shoots of an indigenous coastal shrub, *Baccharis pilularis*, and its resident natural enemies consist of seven solitary parasitoid species that attack the juvenile stages of the gall midge. Total parasitism in galls was severely impacted by the eradication sprays that took place in 1981–82, and gall midge populations, released from parasitism, rapidly increased in abundance from less than 20 larvae per 100 terminals to nearly 800 larvae per 100 terminals. Ehler and Kinsey (1991) note that it was not until 7 years after the eradication program that the abundance of gall midges returned to normal and that parasitism was comparable in both sprayed and unsprayed areas. This example provides an excellent illustration of the pivotal role played by natural enemies in seminatural ecosystems and a perfect recipe for transforming the status of an indigenous plant-feeding insect from an innocuous curiosity to a major, albeit temporary, pest.

These case studies provide powerful examples of the potential of natural biological control to contribute to the unfavorability of an environment for plant-feeding insects and, consequently, to prevent them from achieving pest status. But how general are these patterns, and what do we know about the broader importance of natural biological control relative to other factors that influence the favorability of an environment in suppressing the vast majority of plant-feeding insects to nondamaging levels of abundance? From an analysis of life table data collected from 79 different plant-feeding insects, Cornell *et al.* (1998) found that natural enemies were responsible for a greater level of mortality than any other mortality source and that their impacts were generally greater in agricultural than in natural habitats. Although this does not mean that natural enemies act alone in suppressing the abundance of plant-feeding insects, it does suggest that natural

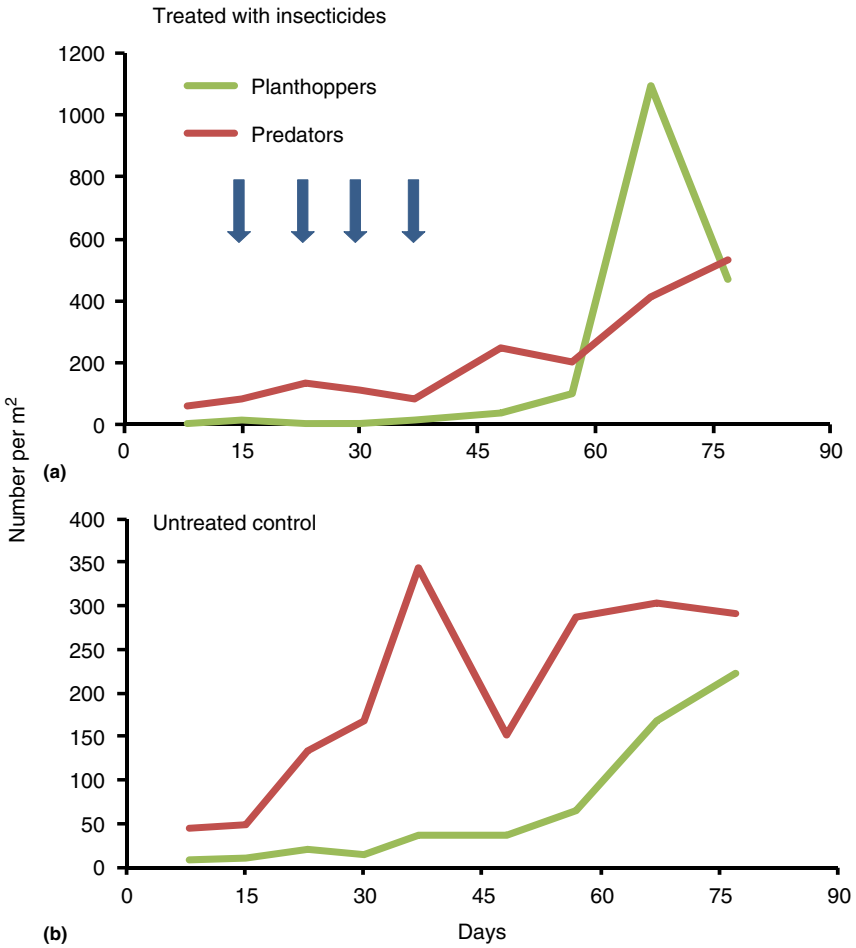


Figure 2 The abundance of brown planthoppers and their predators in rice fields in Java that were either treated with insecticides or left untreated as a control. Blue arrows indicate timing of insecticide treatments. Redrawn from Settle, W.H., Ariawan, H., Astuti, E.T., *et al.*, 1996. Managing tropical rice pests through conservation of generalist natural enemies and alternative prey. Ecology 77, 1975–1988

biological control may be more widespread in both cultivated and natural habitats than is generally appreciated.

Whenever resident natural enemies have the ability to suppress the abundance and activity of insect pests, their action is referred to as natural biological control. However, there can be many reasons why resident natural enemies may fail to provide sufficient suppression of insect pests in agricultural habitats. One clear reason is that the majority of our food and fiber crops are exotic to the geographic regions in which they are currently grown and are inevitably vulnerable to accidental invasions of exotic insect pests that are associated with these plants in their ancestral region. In general, resident natural enemies are poorly adapted to exotic insect pests and, consequently, are unable to suppress their abundance. In addition, modern conventional cropping systems are characterized by high-yielding varieties and intensified use of fertilizers, irrigation, pesticides and mechanization, and each one of these facets of modern agriculture can be responsible for disruption of the balance between insect pests and their natural biological controls. For example, crop domestication and the selection of high-yielding varieties have altered plant morphological traits that can act as barriers for natural enemies and provide direct benefits to insect pests, such as the olive fruit fly, *Bactrocera oleae*. Commercial olive varieties have greater pulp thickness than wild olives, which not only allows a greater number of individual larvae to develop per fruit, but also allows larvae to burrow to greater depths in the pulp where they experience less parasitism from specialized parasitoids, such as *Psyttalia lounsburyi*, due to short ovipositor lengths (Wang *et al.*, 2009). In addition to morphology, a suite of other plant traits, such as the herbivore-induced plant volatiles that are used by natural enemies as cues for host location, can also be influenced by crop domestication and crop variety with the potential to disrupt natural biological control (Gols *et al.*, 2011). Similarly, intensified use of fertilizers and irrigation typically improve the nutritional quality of crop plants and increase their susceptibility to insect pests, whereas pesticides, as noted above, can be particularly detrimental to natural enemies. Under these circumstances it may be possible to improve the biological control of insect pests through deliberate human intervention and the restoration of natural enemy populations.

Importation Biological Control

Importation biological control is an approach that focuses on the importation and establishment of specialized natural enemies from the region of origin of exotic insect pests. This approach is also referred to as classical biological control or biological control introduction. Exotic insects typically arrive in a new geographic region without their coevolved natural enemies, and resident natural enemies are unable to adapt to these novel hosts rapidly enough to provide effective biological control. Consequently, in being released from natural biological control, exotic insects often increase in abundance and expand their geographic range to become invasive and damaging pests, particularly in agricultural crops. The approach of importation biological control is for humans to deliberately import and establish specialized natural enemies from the region of origin of an exotic pest in an attempt to restore the ecological interactions that provide the natural biological control in the ancestral range of the pest.

One of the earliest and best known examples of importation biological control is the complete suppression of cottony cushion scale, *Icerya purchasi*, in citrus groves in California through the importation and establishment of the vedalia beetle, *Rodolia cardinalis*, from Australia in 1889 (Caltagirone and Doutt, 1989). The success of this ladybird beetle as a predator of the scale can be attributed, in part, to its specialization on the scale insect pest, and to its efficiency in responding to the volatile cues associated with its prey (Quezada and DeBach, 1973). More importantly, however, it has a shorter generation time than its prey, completing 10 generations per year in comparison to the three generations per year of the cottony cushion scale. Despite the greater per capita fecundity (325–450 eggs) of the cottony cushion scale compared to the vedalia beetle (150–190 eggs), and its hermaphroditic reproduction, the generation time ratio provides the vedalia beetle with a strong numerical advantage that is sufficient to drive the dynamics of the predator–prey interaction (Kindlmann and Dixon, 1999).

There were two important spin offs from this early success in the biological control of cottony cushion scale in California. One was that the success was repeatable, such that cottony cushion scale has subsequently been successfully controlled through importation of the vedalia beetle in most other citrus growing regions of the world. This repeatability, together with occasional observations of resurgence of cottony cushion-scale populations due to disruption of vedalia beetle populations by insecticide use in citrus, provides unquestionable proof of the potential for specialized natural enemies to provide effective and sustainable suppression of insect pests. A second spin off was that the dramatic success led to a brief worldwide infatuation with ladybird beetle species as effective natural enemies for importation biological control. Although this infatuation failed to result in other examples of success, it did generate the valuable insight that the probability of success of a biological control importation is not so easy to predict. As a result, we can now explain why the importation of the vedalia beetle proved to be so successful (Quezada and DeBach, 1973; Kindlmann and Dixon, 1999), and we have a much better appreciation of the importance of life history traits and foraging efficiency in determining the dynamics of the ecological interactions that form the basis for importation biological control (Mills, 2006; Murdoch *et al.*, 2006).

From a global perspective, there have been numerous programs developed in almost all parts of the world to manage invasive insect pests through importation biological control, and this has been the most extensively practiced of any of the approaches to biological control (Mills, 2000, 2006). There have been many other notable successes and, in general, parasitoids have been imported more frequently than predators, whereas entomopathogens have been used only rarely albeit with surprising success in the case of viruses. The majority of successes have been associated with sap-sucking pests (Hemiptera: Sternorrhyncha) and with tree crops to a greater extent than row crops. Thus it seems likely that both life history traits of the insect pests and frequency of disturbance of the agricultural habitat could be responsible for such patterns.

One of the largest scale projects ever conducted for importation biological control was the successful control of the cassava mealybug, *Phenacoccus manihoti*, an accidental introduction to the continent of Africa in the early 1970s from its ancestral home in Paraguay and Brazil (Herren and Neuenschwander, 1991). It spread from its initial points of introduction in Zaire and Congo at a rate of up to 300 km per year, and by 1990 it had covered most of the 10 million hectares of cassava production across the central belt of Africa, a region that is larger than the United States and India combined. Numerous national and international organizations collaborated in this program, which began with extensive foreign exploration for natural enemies in Central and South America. Following the discovery of the specialized parasitoid *Anagrus lopezi* in Paraguay, it was imported and established throughout the cassava-growing region through an extensive rearing and release program carried out in Benin by the International Institute of Tropical Agriculture. The parasitoid proved to be a tremendous success in suppressing the devastating damage caused by the cassava mealybug, and consequently it restored the exotic yet staple food supply of more than 200 million people across the central African belt (**Figure 3**). The significance of the project was recognized in 1995 by the award of the World Food Prize to Dr Hans Herren who had initiated and coordinated the project from the Biological Control Center for Africa in Cotonou, Benin. The success of the project was again due to the strength of the ecological interaction between *A. lopezi* and its host. In this regard, *A. lopezi* shares a number of traits in common with the vedalia beetle, namely specialization on the target pest, efficient host search through response to volatile chemical cues released from mealybug-infested cassava plants, a numerical advantage from a shorter generation time than its host, and the combination of a predatory adult life stage with a parasitic juvenile life stage (Herren and Neuenschwander, 1991; Nadel and van Alphen, 1987; Neuenschwander, 2001). In this case, however, the success of *A. lopezi* may also have been linked to its ability to produce female offspring from earlier instars of its mealybug host than was the case for other indigenous and exotic parasitoids (Gutierrez *et al.*, 1993). It also proved to be able to drive the dynamics of the underlying host-parasitoid interaction despite heavy levels of hyperparasitism (Neuenschwander, 2001), a trait that was also evident in the successful control of the walnut aphid, *Chromaphis juglandis*, in California through the importation of a parasitoid *Trioxys pallidus* from Iran in 1969 (van den Bosch *et al.*, 1979).

As noted earlier, viruses have been particularly successful in importation biological control, and this is well exemplified by the suppression of the rhinoceros beetle, *Oryctes rhinoceros*, a pest of coconut, oil and other palm trees in the tropical Asia/Pacific region. Adults are the damaging life-stage of the rhinoceros beetle and feed in the crown of palms causing wedge-shaped cuts in the unfurled foliage and even death of the

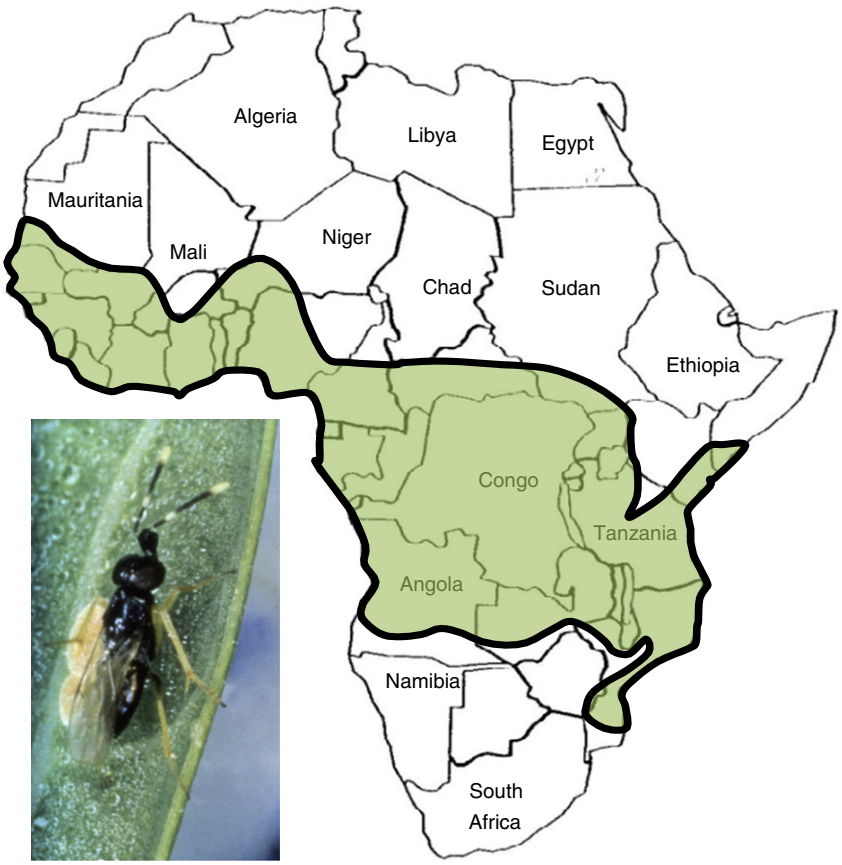


Figure 3 The extent of the cassava belt in Africa (shown green) with the cassava mealybug, *P. manihoti*, and its parasitoid *A. lopezi* inset.

palm. In contrast, the larval stage is not damaging and develops in compost or in the rotting trunks of dead palms. Following the discovery of the *Oryctes* nonoccluded virus in Malaysia in 1963, the first importation for biological control of rhinoceros beetle was made in Western Samoa in 1967. The result was a dramatic collapse of rhinoceros beetle populations due to effective horizontal spread of the virus across the Samoan islands by infected adult beetles (Huger, 2005). The success of this initial release led to an additional 17 importations throughout the Pacific islands, and in India and Tanzania, with establishment and significant suppression of the pest occurring each time (Hajek *et al.*, 2007; Huger, 2005). Life-history traits of entomopathogens that are linked with success are (1) a high level of specialization and virulence; (2) effective horizontal transmission, either by vectors or through possession of resistant stages that are able to persist for long periods in the environment; and (3) a very short replication time relative to the host generation time that allows them to cause high levels of host mortality (Hajek *et al.*, 2007; Shapiro-Ilan *et al.*, 2012).

Not all importation biological control programs against insect pests have proved to be successful; in many cases the imported natural enemies fail to establish, and those that do establish can also fail to provide the desired extent of suppression of the target insect pest. The BIOCAT database of importation biological control programs for insect pests, developed at the CABI UK Centre, lists more than 4700 releases of exotic parasitoids and predators (Greathead and Greathead, 1992; see also Clausen (1977) for further details), whereas Hajek *et al.* (2005) document 131 releases of exotic entomopathogens for the control of invasive insect and mite pests. From this documentation, on a global scale, the probability of establishment of a natural enemy following release has been greater for entomopathogens than for predators and parasitoids (**Table 1**), suggesting that, in small founder populations, predators and parasitoids may be more prone to allee effects than entomopathogens. The success of mate finding at low population densities can be an important constraint in the establishment of predators and parasitoids (Fauvergue, 2013) but does not limit the establishment of entomopathogens. Similarly, the probability of established natural enemies having a significant impact on the target pest has been greater for entomopathogens than for predators and parasitoids (**Table 1**). In this case, the greater success of entomopathogens is primarily due to the impacts of established viruses. Although the short replication time of viruses is considered to be of importance in generating high levels of host mortality, as noted above, viruses that are faster acting in killing their hosts may also limit the extent of horizontal transmission and consequently the propagation of viral epizootics (Sun *et al.*, 2006).

The variable success of importation biological control programs against insect pests over the past 100+ years clearly indicates that a more rigorous approach is needed in order to improve our understanding of the underlying ecological relationships that are central to importation biological control. Gurr *et al.* (2000) characterized the first half of this period of biological control importations as pursuing a 'shotgun' approach. It was anticipated that the extensive analyses of consumer-resource models by theoretical ecologists during the latter part of this period would provide a more informative framework for predicting success. Owing to a focus on stability and persistence (Briggs, 2009) rather than host suppression (Mills, 2000), however, these theoretical developments failed to lead to useful practical guidelines for importation biological control. One valuable pattern that did emerge from the historical record is that hemipteran pests are more likely to be suitable targets for successful population suppression than lepidopteran hosts, and there is some evidence that the explanation is linked to the numerical advantage of either a shorter generation time or gregarious development as a trait of the natural enemies involved (Mills, 2006).

There will always be a risk of unintended effects of deliberately imported exotic natural enemies on nontarget resident organisms occurring in the same geographic range as the target pest, and considerable attention has been paid to the identification and management of such risks in recent years. In addition to the potential for exotic natural enemies to directly impact nontarget organisms through trophic interactions, they could also cause indirect effects by disrupting other members of resident food webs in regions where they become established. A few historical importations, such as the misguided use of cane toads, *Rhinella marinus*, for the control of beetles in sugarcane fields and of the small Indian mongoose, *Herpestes auropunctatus*, for the control of rats, have played an inordinate role in fueling concerns about the irreversible and negative consequences of importation biological control. In recognizing the possibility for nontarget effects of imported natural enemies, most national plant protection organizations currently imposed regulatory requirements on the importation of exotic natural enemies, and procedures for minimizing the risk of direct effects on nontarget organisms are continually being improved (Barratt *et al.*, 2010). The Convention on Biological Diversity has also recently introduced some principles that govern access to genetic resources and the sharing of benefits arising from them (Cock *et al.*, 2010). The application of these

Table 1 The success of natural enemies used in importation biological control of insect pests

Natural enemy group	*Rate of establishment (n)*	*Rate of impact (n)*	*Overall rate of success (n)*
Predators and parasitoids	35.0% (2112)	41.4% (739)	14.5% (2112)
Entomopathogens	65.2% (69)	91.1% (45)	59.4% (69)

Notes: As estimated by the single best outcome approach to the bias caused by repeat introductions of the same natural enemy species in different geographic locations (see Mills (1994) for details).

Source: Data from Greathead, D., Greathead, A.H., 1992. Biological control of insect pests by parasitoids and predators: The BIOCAT database. Biocontrol News and Information 13, 61N–68N and Hajek, A.E., McManus, M.L., Delalibera, I., 2005. Catalogue of introductions of pathogens and nematodes for classical biological control of insects and mites. United States Department of Agriculture, Forestry Service FHTET-2005-05. Washington, DC: USDA, 59 pp.

principles has led to complex regulations that have already made the export of natural enemies from a number of countries almost impossible, and a more centralized regulatory framework will need to be developed if importation biological control is to be valued as a component of the future security of food production systems (Coutinot *et al.*, 2013).

Conservation Biological Control

In situations where natural biological control fails to provide sufficient suppression of an insect pest, the activity of resident natural enemies (indigenous or deliberately established) can be enhanced by human interventions that are known as conservation biological control. These interventions are based on the simple concept that, if the favorability of the environment for the resident natural enemies can be improved, it will lead to more effective suppression of the pest. However, as environmental favorability can be influenced by a wide variety of factors, discovering and manipulating the key limitation for the resident natural enemies in a particular agricultural environment can be challenging. Two more general aspects of conservation biological control that have shown promise more broadly in agricultural environments are habitat manipulation to favor natural enemies over insect pests and the protection of natural enemies from the harmful effects of pesticides.

Although habitat manipulation for conservation biological control has become the most extensively discussed topic in biological control (Bianchi *et al.*, 2006), it remains one of the least well understood and has yet to be widely adopted. The general concept is that local habitat manipulation to increase vegetation diversity through use of polycultures, cover crops, or the planting of noncrop habitats adjacent to crop fields can help to restore the limiting resources that predators and parasitoids experience in a crop monoculture, a concept that is deeply seated as one of the central tenets of agroecology (Altieri, 1999). Vegetation diversity influences predators and parasitoids by providing them with essential resources such as shelter and overwintering sites, alternative prey or hosts, and nectar and pollen as adult food sources. Cover crops can provide shelter and alternative prey for generalist predators, whereas mixed plantings of adjacent noncrop vegetation can provide valuable overwintering sites to facilitate rapid recolonization of fields in spring. Adjacent noncrop vegetation can also provide access to sources of alternative prey and hosts, and of floral resources to promote biological control during the cropping season (Landis *et al.*, 2012). The plant species to be used for habitat manipulation must be selected very carefully to ensure that they support natural enemies rather than insect pests or other antagonists. Native plants are favored over exotics as a result of their local adaptation and potential to contribute simultaneously to multiple ecosystem services. In addition, as the surrounding landscape is the source of natural enemies that can respond to local habitat manipulation, it also has an important influence on conservation biological control (Tscharntke *et al.*, 2005). The value of local habitat manipulation is expected to be greatest in landscapes of intermediate complexity, because complex landscapes should already provide a large community of natural enemies and supporting resources, whereas highly disturbed and simplified landscapes are unlikely to have a sufficient pool of natural enemies to be able to respond. Although there is some evidence that specialist natural enemies are more likely to respond to local habitat manipulation than generalists, the interplay between landscape complexity and local habitat manipulation seems likely to be system-specific and to depend on the biology and dispersal capabilities of different taxa of natural enemies.

One of the best examples of local habitat manipulation for the conservation of biological control in agriculture involves the planting of strips of floral resources in lettuce fields in California to enhance the abundance and activity of syrphid predators for suppression of the lettuce aphid, *Nasonovia ribisnigri*, an exotic insect pest first discovered in the state in 1998 (Tillman *et al.*, 2012). The lettuce aphid can form dense colonies on inner leaves of head lettuce where they are well protected from contact insecticides and many of the predators and parasitoids that are frequently associated with other aphid species. However, syrphid larvae were found to be the most important natural enemies of lettuce aphid in the Central Coast region where approximately 60% of the lettuce consumed in the United States is grown. This led organic lettuce growers to plant strips of sweet alyssum, *Lobularia maritima*, at intervals throughout their fields to provide a consistent supply of both nectar and pollen to a group of resident syrphid species that included *Allograpta obliqua*, *Platycheirus stegnus*, *Sphaerophoria sulphuripes*, and *Toxomerus marginatus*. Successful management of an invasive insect pest by a group of indigenous natural enemies is unusual, but the lettuce aphid provides an excellent example of local habitat manipulation that targeted the resource limitation of a specific taxon of natural enemies in a landscape of intermediate complexity. More generally, however, attempts to use floral strips to enhance biological control in agricultural crops have met with mixed results, indicating that it is not a universally applicable tactic for conservation biological control. Other examples of local habitat manipulation include the use of beetle banks, raised berms of tussock grass that provide suitable overwintering habitat-islands for generalist predators such as Carabidae, Staphlinidae, and Linyphiidae, within cereal fields in the UK (Tillman *et al.*, 2012), and the use of perimeter plantings that support alternative and overwintering hosts of insect parasitoids of leafrollers in fruit orchards in Washington (Unruh *et al.*, 2012). More generally, however, levels of adoption of strip or perimeter plantings to enhance biological control have been much lower than among organic lettuce growers in California, suggesting a need to better understand and predict when local habitat manipulation can be effective in conservation biological control.

Ever since the initial discovery of the insecticidal properties of dichlorodiphenyltrichloroethane in 1939 and the subsequent development of a broad range of synthetic insecticides as universal tools for the management of insect pests, the potential for disruption of natural biological control has been widely appreciated (Dutcher, 2007). The resurgence of target insect pests, and the replacement of initial targets by secondary insect pests as phenomena that result from the release of insect pests from natural biological control, have long been observed even when newer classes of reduced-risk pesticides such as neonicotinoids and spinosyns are used. Avoidance of pesticide-induced insect outbreaks can be achieved through

either physiological or ecological selectivity of the pesticides used in agricultural production. Physiological selectivity results from the differential susceptibility of insect species to a pesticide and can be greatly influenced by the mode of action of the pesticide. For example, the mode of action of many of the older classes of insecticides, such as organophosphates, carbamates, and pyrethroids, confers broad-spectrum activity such that they have lethal effects on a wide range of predators and parasitoids. For the newer classes of pesticides, the effects on natural enemies may still be lethal in some cases, but sublethal effects that reduce life-history performance are both more frequent and equally disruptive (Desneux *et al.*, 2007). In this regard, the International Organisation for Biological and Integrated Control Working Group on Pesticides and Beneficial Organisms has documented the selectivity of approximately 140 pesticides (acaricides, fungicides, herbicides, and insecticides) for a consistent set of 13 predator and parasitoid species using standardized bioassay methods (Jansen and Vogt, 2013). In contrast to physiological selectivity, ecological selectivity results from the differential exposure of insect species to pesticides (Hull and Beers, 1985). The most obvious approach to reducing the exposure of natural enemies to pesticides is through a reduction in the frequency or dose of pesticide applications. Lower dosages of pesticides frequently provide adequate levels of insect pest suppression, but unfortunately there is little evidence as to whether this typically results from conservation of natural enemies or from the lower dosages being as effective as higher dosages against the insect pests. Another approach to ecological selectivity is to choose pesticides with shorter persistence intervals, such that the natural enemies that are killed by a local application can be replaced more rapidly through recolonization from the surrounding landscape. More complex approaches include modification of either the timing or spatial placement of a pesticide application to ensure that natural enemies experience a refuge from exposure. For example, timing applications to avoid flight periods of adult predators and parasitoids, and either spot spraying or treatment of alternate rows or strips within a field, can provide suitable refuges for the persistence of natural enemies within an agricultural crop.

An extensive study of the management of sweet potato whitefly, *Bemisia tabaci*, in cotton in Arizona provides an interesting example of selective pesticide use and the conservation of biological control (Naranjo and Ellsworth, 2009a). An outbreak of the invasive B-biotype of *B. tabaci* in Arizona in 1992 devastated the cotton industry in the region and led to intensified use of broad-spectrum insecticides that included pyrethroids together with endosulfan and carbamates. However, between 1992 and 2007 Arizona cotton growers were able to reduce the number of foliar sprays from more than eight to just over one per year. There were three significant changes to the pest-management program over this period: (1) the introduction of two IGRs (pyriproxyfen and buprofezin) to replace pyrethroids for the suppression of *B. tabaci* in the mid-1990s; (2) the widespread adoption of transgenic Bt cotton for control of pink bollworm, *Pectinophora gossypiella*, by 2006; and (3) the introduction of flonicamid (with a new selective mode of action) to replace acephate for control of lygus bugs, *Lygus hesperus*, in 2007. Through a series of carefully designed field experiments, Naranjo *et al.* (2004) demonstrated the selectivity of the IGRs in comparison to conventional rotations of broad-spectrum insecticides in conserving the predatory arthropod community and in maintaining a greater ratio of predator to prey abundance (a measure of biological control potential) in cotton fields. In addition, using demographic life tables to analyze mortality in field populations of *B. tabaci* exposed to a series of different insecticide treatments (**Figure 4**; Naranjo and Ellsworth, 2009b) subsequently showed that insecticides typically replace the mortality caused by predation in the short term, and that the selectivity of the insecticides differentially influences the conservation of predation in the longer term.

Augmentative Biological Control

Augmentation is an approach to biological control when there are not enough resident natural enemies present in a specific local area, such as an agricultural field, to be able to suppress the abundance of an insect pest. The notion is that by deliberately releasing mass-reared individuals of one or more species of natural enemy, adequate suppression of the pest can be achieved either in the short term or for the whole growing season. A more rapid effect requires the release of large numbers of natural enemies to inundate the local area and suppress the abundance of an insect pest within a single generation. Thus inundation represents the use of natural enemies as biological insecticides without any expectation of longer-term effects from the turnover of natural enemy generations. In contrast, a season-long effect can result from the inoculation of smaller numbers early in the season with the subsequent turnover of natural enemy generations providing sufficient insect pest suppression throughout the cropping season. In reality, inoculation and inundation represent the two extremes of a continuum of augmentative biological control with intermediate scenarios occurring in many cases. One key assumption of augmentative biological control is that insect pest suppression is limited only by a lack of abundance of natural enemies in the target crop. This may not always be the case, however, as mass-reared generalist natural enemies may be unable to suppress populations of insect pests that are either less preferred components of their diet or that occur in habitats or microclimates to which they are poorly adapted. Similarly, augmentative releases of natural enemies may not be effective in domesticated crops that provide either spatial or structural refuges from natural enemy attack as in the case of the olive fruit fly discussed above.

For augmentation to be a commercially-viable approach to biological control, firstly, it is necessary to have a sufficient supply of mass-reared natural enemies available for use at specific, yet limited, times during the growing season. Secondly, the natural enemies must be of consistent high quality to ensure effectiveness, they must be easy to use to encourage adoption, and they must be produced at a cost that is attractive to the end user. The mass-rearing of natural enemies for augmentative biological control is conducted by state-funded and commercial natural-enemy producers who sell a range of different species for use in the management of insect pests. van Lenteren (2012) lists 230 species of predators and parasitoids, and Kabaluk *et al.* (2010) document the broad range of

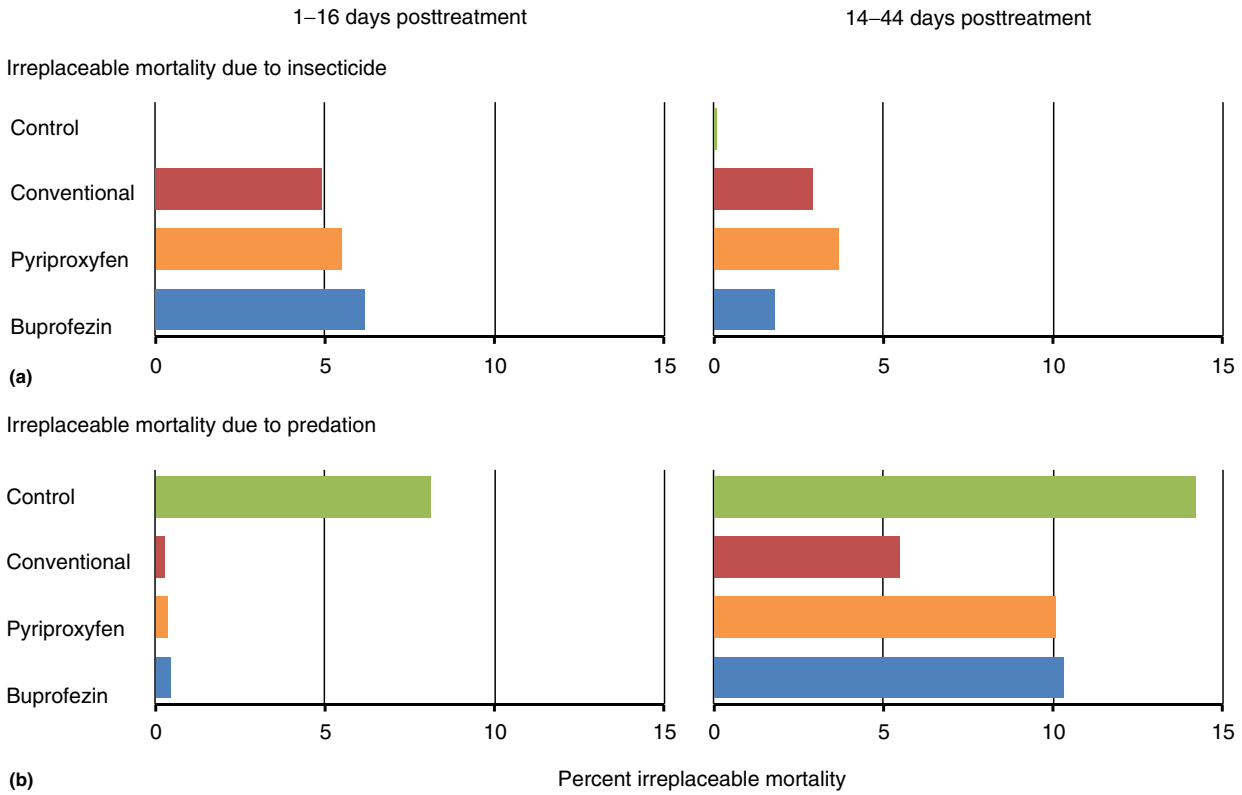


Figure 4 The irreplaceable mortality of *B. tabaci* in Arizona cotton fields. Whitefly mortality from predation was higher (8%) in the untreated control than from any of the insecticides (5–6%) in the treated plots immediately after insecticide applications (days 1–16). Two to six weeks later, mortality from the insecticides was low (2–4%) in the treated plots, and mortality from predation was high (14%) in the untreated control , but was also higher (10%) in the IGR-treated plots than in the conventionally treated plots (5%). Redrawn from Naranjo, S.E., Ellsworth, P.C., Hagler, J.R., 2004. Conservation of natural enemies in cotton: Role of insect growth regulators in management of *Bemisia tabaci*. Biological Control 30, 52–72.

microbial pesticides that are used globally for the augmentative biological control of arthropod pests.

Owing to a greater potential for reducing costs through improved methods of production, storage, and application, entomopathogens have been used more frequently than predators and parasitoids for inundative biological control (Shapiro-Ilan *et al.*, 2012). The narrow host-range of many entomopathogens reduces the potential risk of microbial insecticides to human health and to nontarget organisms, and their mass production is facilitated by culturing in liquid or solid fermentation. An interesting example of inundative biological control with an entomopathogen is the use of a host-specific nucleopolyhedrovirus (AgMNPV) for management of the velvetbean caterpillar, *Anticarsia gemmatalis*, in soybean production for more than 20 years in Brazil. The baculovirus was first isolated in the 1970s, and a small pilot program from 1980–82 demonstrated the tremendous potential of a viral insecticide for the management of velvetbean caterpillar in farmer's fields. The success of the pilot program led to a rapid increase in implementation from 2000 ha in 1982/83 to nearly 1.4 million ha or 10% of the total area of soybean production by 1998/99 (**Figure 5**). Production of the virus was initially based on harvesting diseased velvetbean caterpillars from virus-treated soybean fields, which were used initially as a crude solution and from 1986 as a wettable powder formulation. Commercialization of field production of the virus by private companies resulted in a peak harvest of approximately 45 tons of AgMNPV-infected caterpillars in 2003/04, sufficient to treat 2 million ha of soybean. However, the intensification of field production was associated with a reduction in the quality of the viral insecticide, and commercial laboratory production of a higher-quality product COOPERVIRUS PM began in 2004. Despite these successive improvements in virus production, the large-scale adoption of no-tillage planting and multiple cropping systems has led to significant changes in the insect pest complex associated with soybean production in Brazil and to the replacement of the viral insecticide program with renewed use of low-cost conventional insecticides (Panizzi, 2013). Nonetheless, the development of AgMNPV for inundative biological control of velvetbean caterpillar in soybean fields in Brazil represents a uniquely successful program, and one that involved the most extensive use of an entomopathogen for the biological control of an insect pest in a single crop. Its success can be attributed to a combination of high virulence and effective horizontal transmission of the virus, substantial tolerance of soybean to defoliation, lack of resistance in the velvetbean caterpillar, and efficient field-production of the virus by farmer cooperatives at low cost. Other viral insecticide programs, such as that for codling moth, *Cydia pomonella*, have

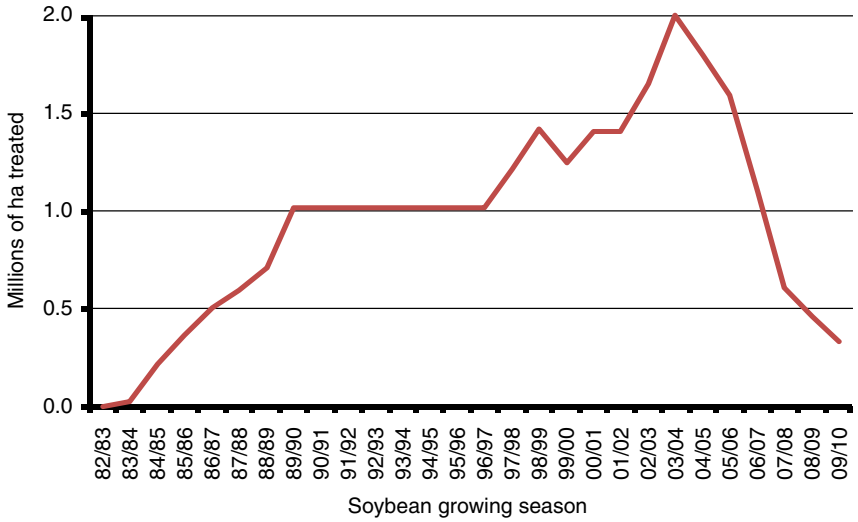


Figure 5 The number of hectares of soybean treated with viral insecticide for suppression of velvetbean caterpillar in Brazilian soybean fields. Redrawn from Moscardi, F., 1999. Assessment of the application of baculoviruses for control of Lepidoptera. Annual Review of Entomology 44, 257–289 and Moscardi, F., de Souza, M.L., de Castro, M.E.B., Moscardi, M.L., Szewczyk, B., 2011. Baculovirus pesticides: Present state and future perspectives. In: Ahmad, I., Ahmad, F., Pichtel, J. (Eds.), Microbes and Microbial Technology: Agricultural and Environmental Applications. New York, NY: Springer Science, pp. 415–445.

also been successful, although the development of resistance to the host-specific granulovirus CpGV after more than 20 years of use may pose a severe limitation to its continued use in Western Europe (Shapiro-Ilan *et al.*, 2012).

In contrast to inundative biological control, predators and parasitoids have been used more frequently than entomopathogens for inoculative biological control. Inoculation is very similar to importation as an approach to biological control, although it does not require the persistence of the natural enemy between cropping seasons. Nonetheless, the natural enemy must have a greater population growth rate than the target insect pest, must be well adapted to the habitat and microclimate in which it is used, and must be released into the crop early in the season to provide a sufficient ratio of natural enemy to insect pest individuals to ensure effective season-long suppression. Inoculative biological control has been used with greater success in enclosed greenhouse crops than in open field crops, with control of the greenhouse whitefly, *Trialeurodes vaporariorum*, by inoculative releases of the parasitoid *Encarsia formosa* being the best-known example (Hoddle *et al.*, 1998). This parasitoid was first mass produced for use in glasshouses in England in 1927 and has since become widely used for biological control of greenhouse whiteflies in tomatoes and cucumbers in many parts of the world. The parasitoid is typically mass produced by parasitizing whitefly nymphs on tobacco plants, and successful inoculative releases of parasitized nymphs early in the cropping season have been achieved using one of three methods. The pest-in-first method requires the deliberate release of whiteflies first, before release of *E. formosa*, to ensure that hosts are present in the crop for the parasitoids to colonize. The dribble method is based on regular releases of a low rate of parasitoids from the date of planting until parasitized nymphs are first found in the crop, and the banker plant method requires the introduction of previously grown plants that support breeding colonies of whiteflies and parasitoids. The effectiveness of greenhouse whitefly suppression is often monitored from levels of contamination of the crop by honeydew produced by the whiteflies and the sooty molds that grow on the honeydew. The success of inoculative biological control by *E. formosa* can be compromised if the quality of the host plants for greenhouse whitefly is too high, as in the case of beef versus round tomatoes, or if greenhouse temperatures fall much below 18 °C. For vegetable crops other than tomato and cucumber, and for greenhouse ornamentals, inoculative releases of *E. formosa* are generally not sufficient to provide season-long suppression of greenhouse whitefly, although control may still be achieved through inundative releases of *E. formosa* throughout the cropping season.

Future Directions

Reducing crop losses from insect pests is becoming of increasing importance as we seek solutions to the challenge of meeting the food security needs of a growing world population. For biological control to play a more pivotal role in the sustainable management of insect pests in agricultural production in the future, two developments will be needed.

First, one needs to become more effective in predicting when and where biological control can be most successfully implemented. As noted earlier, not every insect pest problem will have an available biological control solution. Better recognition of this limitation, and greater focus on problems where biological control is most likely to succeed would help to elevate the status of biological control in the minds of farmers and pest control practitioners. A variety of new research tools and directions are now available that provide valuable opportunities for future improvement in the success of implementing biological control solutions for insect pests

(Gurr and Kvedaras, 2010; Mills and Kean, 2010; Shapiro-Ilan *et al.*, 2012).

The globalization of trade and travel will continue to provide suitable pathways for the accidental introduction of exotic insect pests to areas of agricultural production in all parts of the world. Thus we can expect an ever-increasing need to consider importation biological control as a low risk option for the sustainable management of what could otherwise become a devastating problem that could threaten the stability of food production systems on a large geographic scale as occurred when the cassava mealybug was first discovered in Africa in the early 1970s. To be well prepared for such events, it will be necessary to resolve the constraints currently imposed by the Convention on Biological Diversity, and to be better able to predict and to improve on the probability for future successes. New research tools and approaches that have been developed in recent years offer exciting new directions for the improvement of successes in importation biological control. For example, prioritizing exotic insect pests for importation biological control and selecting effective natural enemies could be improved through greater use of molecular tools that allow a more rigorous approach for the identification of genetically distinct populations of invasive insect pests and their natural enemies, and for tracing the geographic origins of exotic invasions (Roderick and Navajas, 2003). In addition, the combined use of environmental niche models to facilitate climatic matching between regions of origin and invasion for imported natural enemies (Ulrichs and Hopper, 2008) and demographic models to facilitate the selection of effective natural enemies (Mills, 2005) could also lead to more predictable outcomes for importation biological control.

Current estimates of the extent of use of mass-produced natural enemies suggest that they may represent up to 5% of the global synthetic pesticide market (Jaronski, 2012; van Lenteren, 2012), with arthropod natural enemies being almost totally confined to use in greenhouse crops, and microbial pesticides being used in all cropping environments. The single most important factor limiting the more widespread adoption of augmentative biological control is cost effectiveness. The technical effectiveness of these natural enemy products is seldom in question, as was very clear to soybean farmers in Brazil when the viral insecticide for velvetbean caterpillar was first introduced (Moscardi, 1999); but the cost, if greater than the market can bear, could continue to be a limitation. Thus, the greater potential to reduce the costs of production of microbial versus arthropod products provides a clear opportunity and direction for the future expansion of augmentative biological control.

Second, and of equal importance, is the need for a greater emphasis on improved awareness of the value and potential of biological control. Whereas the successful outcome of a deliberate importation of an exotic natural enemy or an application of a microbial insecticide can provide a dramatic visual illustration of the tremendous value of natural enemies in the management of insect pests, it is far less easy to appreciate and value the contributions of natural enemies that result from either natural or conservation biological control. These contributions are much more difficult for farmers and pest control practitioners to visualize and can even be challenging to document from a research perspective. As noted in the Millenium Ecosystem Assessment (Sarukhán and Whyte, 2005) "In many agricultural areas, pest control provided by natural enemies has been replaced by pesticides." The reversal of this paradigm also provides one of the best opportunities to increase adoption of conservation biological control, as evidenced by the very successful program for insect pest management developed for rice production in Asia (Gallagher *et al.*, 2005). An important component of this particular program was the introduction of farmer field schools as a means to increase the awareness of farmers about the advantages of biological control (van den Berg and Jiggins, 2007). Other forms of complementary education and extension of information may be more appropriate for other crops and regions., It is clear, however, that a greater level of adoption of conservation biological control is unlikely to occur until its value can be elevated in the decision making of farmers and pest-control practitioners. In some cases, this may require strategies to incentivize farmers to change from the current market-driven model for decision making to one that considers the longer-term stewardship of agricultural resources and the environmental benefits experienced by the broader community.

See also: Biodiversity and Ecosystem Services in Agroecosystems. Climate Change and Plant Disease. Organic Agricultural Production: Plants. Plant Health Management: Biological Control of Plant Pathogens. Plant Health Management: Pathogen Suppressive Soils. Quarantine and Biosecurity

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Plant Health Management: Biological Control of Plant Pathogens

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Glossary

Antagonist The relationship between two species of organisms in which one individual adversely affects the other, as in competition; the inhibition of the growth of one type of organism by a different type that is competing for the same ecological niche.

Biocides A chemical or biological agent, such as a pesticide or herbicide, that is capable of destroying living organisms.

Biological control (biocontrol) Control of pests or pathogens by disrupting their ecological status, by the release of organisms that are natural predators or parasites.

Competitive exclusion An ecological principle that predicts that species that compete for the same resources cannot coexist when all factors are constant.

Disease suppressive A soil where the incidence of disease that develops on plants grown in that soil is less than that which develops on plants grown in other soils under similar conditions.

Endophyte Organisms that live within a plant for at least part of its life without causing apparent disease.

Inoculant Agricultural amendments that use beneficial, living microbes to promote plant health.

Pathogen A disease-causing organism or entity such as a bacterium, fungus, protozoan, or virus.

Pest An organism deemed detrimental to human concerns.

Pesticides Substances intended for preventing, destroying, repelling, or mitigating any pest.

Phytoalexins Antimicrobial substances that are synthesized *de novo* by plants and that accumulate rapidly at sites of pathogen infection. They tend to be broad-spectrum antibiotics that are key mechanisms in plant disease resistance.

Phytoanticipins These are antibiotic compounds similar to phytoalexins but they are always present in the plants. In many cases, they are stored as nontoxic compounds which on infection become activated by either the pathogen or the plant into the antibiotic structural state.

Rhizosphere The narrow region of soil that is directly influenced by root secretions and associated soil microorganisms.

Transgenic plant A plant whose DNA has been modified by adding a gene or genes from another individual or species, using advanced biotechnological techniques. The aim is usually to introduce a trait into the species, which is not normally there.

Concepts of Biocontrol Are Driven by an Ecological Balance

Biological control (BC) is an integral function of every ecological system that exists on this planet. Development and maintenance of an ecosystem requires mechanisms that regulate the balance between a host and its pest/pathogen populations. Any disruption in the system imperils the survival of both the host and pests/pathogens. Human attempts to rebalance an ecosystem by introducing living agents, their genes, or biochemical products to shift the balance in favor of the host are called BC. In its earliest phases of development BC focused on managing animals, insects, and weed species that became pests in ecological or agricultural systems (Howarth, 1991). In Australia, exploding populations of invasive species, such as rabbits and the prickly pear cactus, were successfully controlled by introducing pests from their native habitats. Control using such natural enemies is termed classical BC and it remains a major component of pest management on a global scale. Van Driesche *et al.* (2010) reviewed 70 cases of classical BC, which targeted 21 insect pests and 49 invasive plants. All projects proved to be successful in controlling the target pests and all benefitted biodiversity, protection of the products being damaged, and the ecosystem. Today, the concepts derived from classical BC are applied globally to protect greenhouse crops from insect pests. Classical BC of insect pests mostly involved finding an insect from its native habitat that could act as a control agent. Classical control for plant diseases, which are mostly caused by microorganisms, would require finding control agents that are also microorganisms (or their genes or gene products). This approach, however, has not been very successful, except perhaps for mycoparasites. A major reason is that in most countries the regulatory agencies automatically classify a microbe intended for pest control as a pesticide and their importation and deployment would be subject to approval under all pesticide laws. Until now insects intended or used for BC have not been regulated as pesticides but this may also change.

The United Nations estimates a world population of approximately 9 billion by 2050; an increase of almost 25% at the time of writing this article. To feed this population 70–100% more food will be needed. Meanwhile, preharvest losses due to pathogens, pests, and weeds account for anywhere from 20% to 40% of the world's agricultural productivity. Reducing such losses to plant diseases and pests would help meet the increased food production targets. However, this will require an increased use of pesticides at a time when society already demands reductions in agrochemical contamination of food, water, and the ecosystem. Societal pressures are boosting markets for biopesticides and transgenic crops. Drogui and Lafrance (2012) suggest that the rapid uptake of genetically modified crops carrying resistance to insects by virtue of

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proteins derived from *Bacillus thuringiensis* (Bt) can be viewed as the pivotal step in the development of modern agriculture as it induced a fundamental change in the use of pesticides. Although this has allowed a paradigm shift in the administration of pest control, it can also be viewed as a form of breeding for disease resistance which is certainly not a new agricultural concept. Studies on benefits derived from the implementation of Bt cotton in China from 1990 to 2010 show that the reductions in the use of chemical insecticides resulted in marked increases in arthropod predators that provided additional biocontrol services. These not only benefitted cotton but also the neighboring crops, such as maize, peanut, and soybean. It is expected that similar data from other ecosystems where ecological agricultural is practiced will greatly favor the growth in biocontrol technologies.

The evolution of commercial biological products and factors that contribute to the successes or failures of companies dealing with such products are complex (Ravensberg, 2011). Despite great turbulences in the market, the prospects for the growth of biocontrol products are universally predicted to increase at a rate of approximately 7% per year. In part, this is because the costs to get a biological product to market are less than US$10 million dollars, whereas development costs for chemical pesticides are closer to US$200 million. Currently, biological insect control products dominate the market and sales of control products for plant pathogens are less advanced. This is expected to change as pathogen management become a target for multinational companies. In 2012, Bayer Crop Science, one of the largest producers of chemical pesticides purchased AgraQuest, a world leader in BC products. The entrance of companies such as Bayer into the biocontrol business will provide a more stable platform for financial and human resources which ensures that products are widely marketed and supported, a factor that has been greatly missing in the field of BC.

Benefits and Limitations of Biocontrol

One of the major highlights of using biocontrol in agriculture is its specificity for a particular species or taxonomic group; also considered by some to be a limitation as growers are accustomed to pesticides that control a wide spectrum of pathogens. The narrow spectrum of activity makes biocontrol ideal for integrated pest management systems where other beneficial agents are being utilized. BC is ideal for organic production systems and is compatible with pollinators (bees primarily) which are very sensitive to pesticides. Biocontrol products do not leave harmful residues so agricultural produce can be marketed within a short time after treatment. The products are considered safe for applicators and reentry to treated sites is either not limited or can be as short as a few hours. Biocontrol agents are considered to be more resilient to the development of pest resistance than traditional chemical control. The major weakness of biocontrol is that efficacy is greatly influenced by environmental factors, and they are rarely as effective as chemical pesticides because of this. Control activity is not as rapid as with chemicals. Considerably more knowledge is required in the manufacture and use of these products and formulations than with traditional chemical pesticides, with shelf-life and storage conditions significantly affecting the utility of the product.

The list of BC agents and their products that are registered for use commercially is expanding at a tremendous rate. The references and web sites where products available to growers can be located are provided. Information is also available from specific publications that detail the biocontrol products currently marketed (McSpadden Gardener and Fravel, 2002; Fravel, 2005; Kabaluk *et al.*, 2010; Ravensberg, 2011; Glare *et al.*, 2012; Rana, 2012).

A Biological Control Model in Natural Systems: Endophytes

Endophytic microorganisms, primarily bacteria and fungi, are found inhabiting the interior of plants where they can contribute to the host's growth without causing disease. Endophytes are increasingly being recognized as organisms with enormous potential for use in management of plant health as they can overcome the major limitation in effective BC: biologically relevant delivery and robust establishment due to niche adaptation and shelter from microbial competition and environmental influences. These microbes are protected from the outside environment as they exist in the internal tissues of the plant where they form a diversity of relationships ranging from symbiotic to almost pathogenic (Ryan *et al.*, 2008). Although many endophytes are likely transmitted from generation to generation through seeds or vegetative organs, it is possible to introduce new endophytes to plants through wounds or through seed inoculation, where they can create systemic infection and persist for the lifespan of the plant. Endophytic microorganisms have been shown to control numerous plant pathogens, insects, and nematodes and to exert growth-promoting functions that make plants less prone to infections.

The potential of endophytes to impact plant health and productivity, as well as ecosystem integrity, is best illustrated by the relationship between perennial ryegrass and its fungal endophytes (Kuldau and Bacon, 2008). Perennial ryegrass is grown worldwide as feed for livestock and is an integral component of most pastures. Ryegrass is usually infected with the fungal endophyte *Neotyphodium lolii* formerly known as *Acremonium lolii*. The fungus depends on the plant for its survival and spread and; in turn, it confers numerous benefits to the plant that include increased growth, photosynthetic capability, nitrogen assimilation, and mineral uptake. Infected plants are taller, are more vigorous, have a greater capacity to resist harsh environmental conditions, such as drought, nutrient deficiencies, soil acidity, etc. Often they completely displace noninfected plants and eventually the ecosystem contains only plants with endophytes. Not all grasses tolerate colonization in an equal manner.

Most importantly the fungus confers host resistance to insect and animal herbivores by virtue of its ability to produce a number of toxic alkaloid metabolites generally known as tremallogens (Kuldau and Bacon, 2008). Of the many known and unknown compounds produced, several act synergistically to provide broad-spectrum protection to multiple pests. These compounds have antifeeding activity but, if ingested, they make the animals sick with a disease known as ryegrass

staggers. Similar alkaloids can be found in grain infected by *Claviceps* fungi (of which *N. lolii* is a member) that induce a human disease known as ergotism or St Anthony's Fire which caused hundreds of thousands of deaths in the Middle Ages. *Neotyphodium* endophytes confer resistance to some 45 species of insects (Kuldau and Bacon, 2008) and at least two plant-parasitic nematodes. The fungus also stimulates the accumulation of the phytoalexin resveratrol which has potent antifungal activity. This phytochemical may account for some of the resistance seen with infected grasses against *Pythium* disease, dollar spot, some rust and leaf spot diseases. There is also suggestion that the presence of the endophyte induces a systemic acquired resistance (SAR) mechanism, allowing plants to respond more quickly to parasitic attack from a diverse group of plant pathogens (Kuldau and Bacon, 2008).

Endophyte-infested grasses were previously sold for lawn use as a means of reducing insect damage and watering but they did not come into widespread use because of the accumulation of toxins. Since then, isolates that lack the capacity to produce toxins harmful to animals but still retain other desirable traits associated with disease suppression and plant growth promotion were identified and patented (USA patent 6,111,170) and are sold in New Zealand, Australia, USA, and South America as AR1TM and AR37TM in ryegrass and MaxQ in tall fescue. It is envisaged that not only will this benefit pasture maintenance, but once such seeds become widely planted populations of fungi that produce harmful toxins will be significantly reduced in the environment by competitive exclusion.

This example of improved endophyte delivery shows how seed transmission of beneficial microbes could become a very powerful technology. Such processes are likely ongoing in nature. Surface-sterilized husked seeds of rice have been found to contain 5 000 000 colony forming units of bacteria per gram (Ruiza *et al.*, 2011). Some of these seedborne bacteria fix nitrogen and protect against infection by the fungus *Curvularia* spp. Two isolates of these bacteria were potent root colonizers during seed germination, suggesting how they might colonize other parts of the plant. In a metagenomic analysis of the endophytic bacterial community that reside inside roots of field-grown rice, Sessitsch *et al.* (2012) found that the endophytes might be involved in the entire nitrogen cycle, including N_2-fixation, denitrification, and nitrification. The endophyte community comprised functions involved in plant growth promotion, improvement of plant stress resistance, biocontrol against pathogens, and bioremediation.

An example of the huge impact that endophytes could have in wide-scale agriculture is found in the implementation of sugarcane as a biofuel crop in Brazil. The success of the bioethanol industry is due to the development of production systems that allow this crop to be grown with minimum expense and little environmental impact. From inception, cultivars of sugarcane were selected and bred for minimum requirements of pesticides or fertilizers (Baldani *et al.*, 2002). Cultivars that performed well under such conditions were found to be harboring numerous bacterial species such as *Azospirillum*, *Herbaspirillum*, *Acetobacter*, *Klebsiella*, *Burkholderia*, and others. These bacteria not only helped to supply nutrients required for growth, but also provided protection to the roots from plant disease-causing agents. These beneficial plant–microbe relationships allow Brazilian sugarcane growers to use 70% less nitrogen fertilizer than sugarcane growers in the USA. The bacterial endophytes dramatically aid the plant's mineral nutrition, as well the plant's defense against pathogens. *Azospirillum* isolates improve growth of crops other than grasses including oilseed rape, tomato, pepper, etc. and significantly reduce disease symptoms or incidence of damping-off in chili caused by *Pythium*, or wilt pathogens such as *Verticillium dahliae* and *Fusarium oxysporum f.* sp. *lycopersici* and the bacterial pathogens *Clavibacter michiganensis* subsp. *michiganensis* (bacterial canker), *Xanthomonas campestris* pv. *vesicatoria* (bacterial spot), and *Pseudomonas syringae* pv. tomato.

Endophytes can be used as delivery vectors for genes from other biocontrol agents that provide plant protection. The *Bt* gene conferring CRY toxin production was cloned into several bacterial endophytes, such as *Xylaria*, in the hopes that it could help kill root worms. However, the biocontrol that resulted was not sufficiently effective due to the limited number of bacteria in the root environment. The endophytic nitrogen-fixing bacteria *Acetobacter* and *Herbaspirillum* were also used as potential models for gene delivery but as yet commercial products are not available. In another example, the antifungal endophytic fungus *Chaetomium globosum* has been genetically modified to express insecticidal lectins within rape, thus producing plants with both disease and aphid control capabilities (Qi *et al.*, 2011).

Management of Soilborne Pathogens Using Organic Amendments and Crop Rotations

Control of soilborne plant pathogens has been the most difficult aspect of plant protection. The most successful method of control available relies on plant resistance to a specific pathogen. When resistance is not available, fumigation with broad-spectrum biocides is usually employed but many such products are being removed from the market place. Adding pesticides to soil is difficult as a hectare of soil weighs approximately 2 million kg to a 15 cm depth and this requires adding large volumes of chemicals to reach toxic concentrations. Furthermore, due to the diversity of soil microorganisms chemicals are often rapidly degraded. The disease control strategy that has gained the most momentum is to alter both the microbial composition of bulk soil and the soil surrounding the root system known as the rhizosphere. Peter *et al.* (2009) characterize some of the processes being developed to manipulate the root-associated microbiome to improve plant health and productivity as 'rhizosphere engineering and management.' They detail case studies whereby plants or the microorganisms are genetically altered to enhance interactions that lead to expression of factors that bring about BC or improved root health. It is enticing to consider all soil treatment processes leading to either higher or lower disease incidences as a form of rhizosphere engineering and management.

Soils naturally resistant to the development of specific soilborne disease are termed 'disease suppressive.' Two classical types of suppressiveness have been identified and they will be dealt within another article. With 'general suppression,' the main factor altering disease outcomes is likely derived

from competition between the total soil microbiota and the pathogen for resources. This is not a transferable function between soils. 'Specific suppression,' however, is associated with specific antagonistic microorganisms, such as the fluorescent pseudomonads which interact with individual or select groups of pathogens. Suppressiveness can act either by keeping pathogen inoculum concentrations very low or, more commonly, keeping disease incidence low even though pathogens may be present at high levels. By adding suppressive soil to disease-conducive soils, suppressive traits can be transferred as the activity resides in microorganisms (Cook, 2007).

The most successful example of the creation of disease-suppressive soils known is actually a strategy where rotation is not used but is replaced with continuous cropping of a monoculture. The development of this technology is described in this book by Cook . Repeated cropping of wheat was shown to increase the populations of antibiotic producing fluorescent *Pseudomonads* on the roots resulting in significant reductions in the severity of take-all root disease of wheat and barley caused by the fungus *Gaeumannomyces graminis* var. *tritici*. Specific strains of *P. fluorescens* have subsequently been shown to be widely involved in suppression of other soilborne root diseases. Fluorescent pseudomonads have also been shown to suppress damping-off diseases caused by widespread and generalist pathogens such as *Pythium ultimum* (an Oomycete) or *Rhizoctonia solani* (a fungus) (Ligon *et al.*, 2000). Suppressive conditions in soils and substrates have been reported for a wide diversity of pathogens that cause wilts and root rots, including *Fusarium* spp., *Phytophthora* spp., *Thievilopsis*, *Plasmidophora*, *Streptomyces scabies* as well as for plant-parasitic nematodes. Identification of the biological properties contributing to disease-suppressive conditions have proven to be elusive for most systems except for the take-all disease of wheat. This model ecosystem can be considered a major breakthrough toward developing an ecologically based management technology for soilborne plant disease control. Establishing suppressive conditions provides a safe, effective, environmentally benign and cost-effective approach to managing crop diseases. Once the suppressive agents or their biological activities are known, DNA technologies based on polymerase chain reaction can be used to detect the trait and develop crop management technologies to keep suppressiveness in place or even improve its impact. Molecular technologies are now being applied to unravel factors and microbial communities impacting soils and crop health.

Traditional crop rotations were designed to withhold crops that are susceptible to a specific pathogen from agroecosystems for a sufficient time during which the pathogen populations decline to below crop loss disease thresholds. Cook (personnel communication) suggests that crop rotations of 2–3 years or longer provide sufficient time for the soil microbiota to reduce populations of a crop-specific soilborne pathogen to a level that is below the crop loss threshold, as long as the crop grown in rotation is unrelated to the primary crop. For some diseases, such as *Verticillium* wilt, this does not work well as resting structure of the fungus can survive for decades and they have the capacity to reproduce on a wide host range that includes weeds. The practice, however, does work for short-lived pathogens (Cook, 1988). For long-lived soilborne pathogens growing resistant cultivars induces the resting structures to germinate but infections do not lead the production of new inoculum and over a period of time the resting structures become depleted. Incorporating the residues of rotation crops induces the growth of a wide spectrum of microorganisms that have been shown to damage the resting structures of plant pathogenic fungal agents by numerous mechanisms (Bailey and Lazarovits, 2003). Application of organic amendments to soil has been shown to result in important changes in soil microbial communities which can reduce the impact of soilborne plant pathogens. Amendments may include animal and green manures (green crops plowed down), composts, agricultural by-products derived from food processing, such as molasses, meat and bone, soy meal, canola meal, fish and shrimp waste, etc. Applying organic amendments has been an integral part of agriculture since its inception, but now one is starting to understand how these treatments may alter populations of soilborne pathogens and their antagonists. Changes brought about by organic amendments can be considered as BC as the changes in the pathogen populations occur only after the products are metabolized by soil microorganisms. Accumulations of high levels of metabolic products such as ammonia, nitrous acid, volatile fatty acids including formic acid and acetic acid (vinegar), cyanide, etc. can be toxic to many pathogens and pests. Many of these products have been used for food preservation for millennia and are considered very safe. Whereas plant pathogens are often damaged or killed, most soil microorganisms increase in population by several log units. Some microorganisms known to be enriched include *Bacillus*, *Pseudomonas*, and *Trichoderma*, and they are known BC agents. The limitations for use of such technologies are the inherent variability of control achieved, high cost, limited quantities, and a lack of understanding of the processes that lead to disease control.

Numerous preplant strategies for the control of soilborne pathogens in various crop production systems have been shown to be effective. Mustard seed meal amendments were found to reduce pathogen populations and to even create disease-suppressive soils for a wide spectrum of root pathogens, including *Fusarium*, *Pythium*, *Rhizoctonia*, *Verticillium*, various plant-parasitic nematodes, and complex disease such as apple replant. Materials utilizing *Brassica* species or their seeds were commonly viewed as yielding disease control through the process of 'biofumigation,' i.e., the release of toxic products such as cyanide during residue decomposition. It is now known that specific elements of the soil biological community also contribute to disease or weed control. The modes of action likely vary from pathogen to pathogen and the source of the product can also modulate disease control efficacy.

Adding large quantities of organic matter to soil, wetting the soil, covering it with plastic and letting the microorganisms degrade the organic matter has been found to result in the formation of anaerobic conditions that reduce populations of a broad spectrum of soilborne plant pathogens and nematode pests. This control method, termed anaerobic soil disinfestation (ASD), is widely used in Japan where production sites are fairly small. The process is considered to act by numerous mechanisms including withdrawal of oxygen and production of volatile fatty acids. ASD has been consistently effective at suppressing a broad spectrum of soilborne plant pathogens

and has been used to control wilt and root diseases of high-value horticultural crops.

Nematode Control

Crop losses caused by plant-parasitic nematodes are estimated to exceed US$100 billion worldwide. The primary means of control has been the use of chemical fumigants but exciting new biocontrol technologies are being developed. *Pasteuria penetrans*, a bacterial parasite of nematodes, was discovered to be able to eradicate a wide spectrum of plant-parasitic nematodes and to bring about disease-suppressive conditions for such pests. The bacterium's spore has the appearance of a flying saucer and attaches itself to the nematodes' cuticle, penetrating through it on germination. Once inside, the bacterium divides rapidly until it fills the entire nematode cavity. The bacteria then start to produce spores that are released to infect other nematodes. *Pasteuria* is a biotroph, i.e., requires living tissues to grow. The discovery that these bacteria can be grown in nematode cell culture has allowed for large-scale production of the organism and their commercialization for agriculture. Pasteuria Bioscience, Inc., is commercializing this biological nematicide under the trade name Econem, which is currently registered for protection of turf. They are developing products to control all important nematode pests such as root-knot, soybean cyst nematode, and the reniform nematode. A patent has been granted for use of *Pasteuria* spores as a seed treatment. Syngenta acquired Pasteuria Bioscience Inc., in 2012 and intends to develop and commercialize this biocontrol products for nematodes worldwide. The first major product, a seed treatment for soybean cyst nematode, is expected to be launched in the USA in 2014. Along similar lines, MeloCon Biological Nematicide contains a naturally occurring fungus, *Paecilomyces lilacinus*, a highly effective parasite of all stages of development of common plant-parasitic nematodes, especially the eggs and infectious juveniles.

Induced Resistance

A plant's natural resistance to pest and pathogens will always be the best strategy for plant protection in agriculture. Plants have evolved many genes for disease resistance that negate the function of the pathogen's virulence factors. Pathogens, in turn, have evolved methods to overcome plant resistance genes, giving rise to new races that can cause disease. Introduction of new disease-resistant genes into crops by conventional breeding practices can take up to a decade, and in many cases genes for specific pathogens are not readily available. Although plants may become susceptible to new races of pathogen, they retain their resistance mechanisms. If one can activate these genes before attack then they confer resistance to the pathogen. Many of the mechanisms associated with the major plant disease defense response, called SAR, have been characterized. SAR has been shown to be activated in response to various biotic or abiotic triggers, including rhizobacteria, fungi, their products, and a number of chemical compounds. SAR activation can be measured by the expression of pathogenesis-related genes, production of defense-related enzymes, and accumulation of phytoalexins and phytoanticipins.

Biochemicals such as salicylic acid, methyl jasmonate, benzothiadiazole, or acibenzolar-*S*-methyl are potent activators of plant defense responses against certain pathogens and insects. For example, foliar application of methyl jasmonate (a volatile compound released from flowers and leaves) can trigger a plant's jasmonic acid pathway that, in *Arabidopsis*, significantly reduces disease development by necrotrophic fungi such as *Botrytis cinerea*, *Alternaria brassicicola*, and *Plectosphaerella cucumerina* (Pozo *et al.*, 2005). An extract from the giant knotweed *Reynoutria sachalinensis* has been commercialized under the trade name Regalia by Marone Bioinnovations. Regalia controls many important fungal and bacterial diseases, including powdery mildew, downy mildew, *Botrytis* gray mold, early blight, late blight, citrus canker, brown rot, bacterial leaf spot, target spot, gummy stem blight, and others. It is registered for use against soilborne pathogens such as *Pythium*, *Fusarium*, *Rhizoctonia*, and *Phytophthora* and was shown to improve root development and plant growth response with tomatoes, peppers, potatoes, strawberries, and others (http://www.marronebioinnovations.com/products/regalia/). A synthetically produced compound, acibenzolar-*S*-methyl, is sold by Syngenta Crop Protection as Actigard® or Blockade® and is registered with the US government's Environmental Protection Agency (EPA) as a plant defense activator. It is meant to be dissolved in water and applied as a foliar spray to preventatively control disease by triggering SAR.

Plants produce over 1000 volatile compounds naturally, some specifically in response to infection and pest attack. Many of these compounds activate plant defences not only in plants under attack but also in the neighboring plants. Interestingly, these volatiles can also function as signal molecules to predatory or parasitoid arthropods, informing them that prey may be present in large numbers. For example, methyl salicylates released by soybeans in response to aphid infestation act as strong attractants to lady beetles. Synthetic methyl salicylates have been successfully used for attracting beneficial insects to the field and constitute the active ingredient for PredaLure (AgBio, http://www.agbio-inc.com/predalure.html) a natural enemy attractant marketed for use in pest management. Kaplan (2012) details the complexities of using such mechanisms for insect control and the potential for wide-scale applications.

Transgenic Plants

The first commercially grown transgenic plants were virus-resistant tobacco and tomato grown in the early 1990s in China, followed in the USA by Calgene in 1996 with their delayed ripening Flavr Savr tomato (Collinge *et al.*, 2010). Since then, the total area planted to transgenic crops (in 2010) has grown to 365 million acres in 29 countries, planted by 15.4 million farmers; (http://www.isaaa.org/kc/cropbiotechupdate/pressrelease/2012/default.asp) an obvious case of commercial success. Interestingly, almost all of these commercially planted transgenic crops bear traits for herbicide tolerance for weed control and Bt resistance for insect control; very few were made for improved disease resistance. Indeed, with the exception of some virus-resistant transgenic plants, there are currently no commercially released transgenic plants

on the market for plant disease control; a situation that will likely change in time, as 2000 of the almost 16 000 field trials in the USA in the past 20 years are for disease resistance traits, suggesting there are crops either in the pipeline or on the shelf due to the high cost required for meeting regulatory approval (Collinge *et al.*, 2010). The restrictive regulations required to meet approval for products intended for export markets by all countries that may import the product has also acted as a constraint in the development of novel transgenic crops. Approval of the importation of virus-resistant papayas from Hawaii to Japan took in excess of 10 years.

Traditionally, classical breeding is used to enhance resistance by selecting optimal combinations of the plant's own genes. With transgenic techniques, also known as molecular breeding, selection of resistance genes can involve mutating or overexpressing alleles within the species, or it can additionally allow transfer of homologous genes from an unrelated plant species. Thus, research into the genetics and biochemistry of plant-pathogen signaling and resistance will increase the tool box for both the species being researched and other plant varieties as well.

Arabidopsis is the best understood plant species at the biochemical and genetic level. Although it has no agronomic value, it has proven to be a valuable resource for identifying genes and the mechanisms they control. For example, the entire biosynthetic pathway for benzylglucosinolate (a secondary metabolite involved in defense against generalist insects and pathogens) has been transferred from *Arabidopsis* to tobacco (Collinge *et al.*, 2010), with further work in potato expected to bestow resistance to *Phytophthora infestans* (late blight). The defense-signaling gene *NPR1* (nonexpressor of pathogen-resistance genes), which is necessary for induction of plant SAR in *Arabidopsis*, was stably transferred and overexpressed in tomato, wheat, carrots, and tobacco where it has increased the crop's ability to respond to and resist pathogen attack, without showing signs of compromised growth (Wally and Punja, 2010).

A divergent approach called pathogen-derived resistance transfers a pathogen's gene(s) into the plant genome to achieve disease immunity. This approach has resulted in the only commercially successful transgenic disease-resistant plants, which are immune to virus attack by virtue of their overexpression of genes for viral coat proteins (so the target virus cannot successfully unpack its nucleic acids and infect the plant) or gene constructs mimicking viral gene sequences, which trigger the plant's own gene-silencing mechanisms (RNA interferance (RNAi)). Transgenic virus-resistant plants have been grown commercially for over a decade in the USA, and even longer in China. The most famous commercially available example of this approach was showcased by the Hawaiian papaya industry, which was nearly wiped out by the papaya ringspot virus. In response to this catastrophic disease, the transgenic varieties SunUp and Rainbow were developed from the parent variety Sunset, by transferring the virus's own coat-protein gene to the plant's genome where it was overexpressed, thus blocking the virus's ability to undress and have its genes transcribed. These varieties of transgenic papaya currently enjoy over 70% of the acreage in Hawaii and are credited with saving the entire industry.

Additional attempts to protect plants from pathogens using transgenic technology include transfer of antimicrobial proteins from diverse sources, antibodies from animals (which are then termed 'plantibodies'), and mechanisms to interfere with pathogen virulence factors and communication. For example, transgenic expression of the antimicrobial peptide dermaseptin B1 from the South American tree frog *Phyllomedusa bicolor* has been shown to increase resistance to bacterial and fungal diseases, including late blight, dry rot, and pink rot, in addition to significantly extending the shelf-life of tubers (Osusky *et al.*, 2005). Plantibodies might be useful to tag particular pathogens for further antimicrobial targeting; this approach has been used successfully to deliver antifungal chitinase and defensin proteins specifically to *Fusarium* cell walls by generating antibody: antimicrobial gene fusions inserted into the genomes of *Arabidopsis* (which was then resistant to nine different species of *Fusarium*) and wheat (which was then resistant to *Fusarium* head blight) (Wally and Punja, 2010). Plants expressing large amounts of pectinase-inhibitory proteins dramatically inhibit the virulence of necrotrophic pathogens like *B. cinerea*, which secrete pectinases as a way to digest plant tissues and liberate nutrients for their absorption (Wally and Punja, 2010). Likewise, transgenic plants expressing enzymes that degrade bacterial communication signals (quorum sensing) can have enhanced resistance to pathogens, although this has not found commercial application yet.

Biological Amendments

Bacteria

Bacteria are among the most frequently used biocontrol agents to protect plants from diseases. Although bacterial agents have been used for several decades, it is generally thought that their potential is vastly underexplored. Bacteria reside on all plant parts in abundance and have direct and indirect plant growth-promoting capabilities. There are 10–100 times more bacteria living on the plant root than living in the soil mass. Bacteria live inside plant tissues and can be transmitted vertically through seed to the next generation. The search for bacterial biocontrol agents is in its infancy, however, with many labs developing screening criteria to use in high-throughput approaches for new agent isolation. Bacterial biocontrol agents are most frequently isolated from the root zone, but they can arise from any plant-associated environment, including the endosphere (inside the plant), phyllosphere (the surface of the leaf), and spermosphere (inside and around the germinating seed).

The most commonly proposed mechanisms by which bacteria control pathogens are niche competition with pathogens, production of inhibitory allelochemicals, and induction of plant resistance pathways (Compant *et al.*, 2005). To provide protection to crops, beneficial bacteria need to competitively colonize the plant tissue they are to protect. Bacteria use different mechanisms to effectively colonize the plant, including flagellar-driven motility, chemotaxis, and efficient utilization of nutrients in the environment. Common allelochemicals produced by biocontrol bacteria include antibiotics that directly inhibit pathogens, iron-capturing molecules that sequester this limiting nutrient, and secreted enzymes that lyse pathogenic cells.

Globally, bacteria represent 75% of the 3.5% of the agrichemical market that is represented by biocontrol (Glare *et al.*, 2012). In North America, the list of available bacterial biocontrol agents is growing continually as they are used more widely. That the majority of biocontrol agents are comprised of Gram-positive bacteria can perhaps be explained because these form spores which are more resistant to stress and are easier to store than are Gram-negative bacteria. Two widely used examples are Serenade (Bayer CropScience – Monheim, Germany), *B. subtilis*, and Sonata (Bayer CropScience – Monheim, Germany), *B. pumilus*. Both products protect a variety of crops from downy and powdery mildew, early and late blight, and brown rot. In addition to the dried *B. subtilis* spores found in Serenade, the fermentation conditions have been optimized to produce a profile of lipopeptides which improve biocontrol performance in the field and increase the spectrum of pathogens targeted.

Another important group of biocontrol bacteria are *Pseudomonas* species, which are robust plant colonizers, produce a variety of antibiotics, and are easy to culture (four are registered with the US EPA). Additionally, it is being recognized that combinations of bacteria may provide better crop outcomes than single strains. An example of this is the Biostacked soybean inoculant (Becker, Underwood – Ames, Iowa, USA), which contains the nodulating *Bradyrhizobium japonicum* and *B. subtilis* for growth promotion due to phytohormone production and disease suppression, primarily *Rhizoctonia* and *Fusarium*.

One of the earliest biocontrol products utilizing bacteria was *Agrobacterium radiobacter* K84 for control of the closely related bacterium *A. tumefaciens*, causative agent of crown gall in woody plants. By simply dipping the roots of plants in a cell suspension of *A. radiobacter* K84 before planting in an infested field, the crown gall is controlled. The biocontrol strain produces Agrocin-84, a molecule that mimics agrocinopine A, a nutrient source for bacteria inside galls. Agrocin-84 is imported into the pathogen cell by the same transporters used for agrocinopine A, whereupon it inhibits DNA replication and cell growth of the pathogen. For Agrocin-84 to work, the pathogen must require agrocinopine A for its growth. Thus, strains that do not utilize this opine during infection are insensitive to Agrocin-84. Many products containing *A. radiobacter* strains are commercially available for crown gall control. Members of the family Rhizobiaceae, containing the genera of *Rhizobium* and *Agrobacterium*, are common inoculants of legume plants. However, this genus is ubiquitous in soil and on nonlegume plants. There are some reports that Rhizobium spp. can act as biocontrol agents against soilborne pathogens and nematode pests, but they have not been seriously examined as potential biocontrol agents likely because they are viewed only as nitrogen fixers.

Although biocontrol bacteria need to be able to compete for colonization on the plant with native flora and pathogens, implicit in the name biopesticide is the need for reapplication as the biocontrol bacteria are not able to reside in the soil in large enough populations to provide disease control for years. Although improved fermentation conditions had led to increased product efficacy, genetic manipulation of the organisms provides a means to optimize activity and environmental survival. Owing to strict regulations and public perceptions of genetically modified organisms, no commercially available product is genetically modified. However, directed evolution of biocontrol bacteria is allowing for strain optimization without the genetically modified label. As effective delivery and establishment of bacteria onto the plants is difficult, current research is exploring the use of endophytes as their residence in the plant helps overcome delivery and survival difficulties. There is still room for improvements to formulation and of stress tolerance of the bacteria to extend shelf-life and improve field survival.

QuickRoots (http://www.tjtechnologiesinc.com/) markets a combination of a bacterium *B. amyloliquefaciens* and a fungus *Trichoderma virens* as a seed inoculant for enhancing plant health via increased root vigor and size and ability to take up nutrients. No claims for the product are made for BC activity. As both organisms have multiple plant growth-promoting mechanisms, including plant hormone production, enhancement of nutrient uptake, etc., BC traits are often not claimed. It is much simpler and cheaper to register a product as a fertilizer than as a pesticide.

Fungi

It is estimated by the FAO that 14% of global crop production is lost to plant diseases, with fungi accounting for 42% and bacteria accounting for 27% (Khan and Anwer, 2011). Ironically, fungi are also important for biocontrol of plant diseases, being responsible for 5% of the value of the biocontrol market (Glare *et al.*, 2012). Like bacteria, fungi are able to control plant diseases via several mechanisms, including antibiosis, competition, exclusion, parasitism/predation, and stimulation of plant defences. Unlike bacteria, fungi actively colonize their environment via hyphal growth, allowing them to better occupy the niches into which they are introduced. The first fungus registered as a biocontrol agent of plant disease with the US EPA was *T. harzianum* ATCC 20476 in 1989. Since then, 18 others have been registered including *Ampelomyces quisqualis* (mycoparasite of powdery mildew), two strains of *Aspergillus flavus* (competitive exclusion of toxin-producing strains of *A. flavus*), *Candida oleophila* (reduces rot caused by *Penicillium* spp.), *Coniothyrium minitans* (mycoparasite of *Schlerotinia*), two species of *Gliocladium*, *Muscodor albus* (a biofumigant of soil), *Pseudozyma flocculosa* (antagonist of powdery mildew), *P. oligandrum* (competition with *P. ultimum*), *Ulocladium oudemansii* (competition with *B. cinerea* on necrotic grape tissues), *V. alboatrum* (induces defense responses in trees, elevating resistance to Dutch elm disease), and six strains of *Trichoderma* (Fravel, 2005). Globally, well over 100 different fungus-based biocontrol products for plant diseases currently exist, sometimes sold as mixtures of different species or strains, and including additional fungi such as *C. verrucaria*, *Phlebia gigantean*, *Metschnikowia fructicola*, *A. niger*, *C. globosum*, *Fomes fomentarius*, *Ophiostoma piliferum*, *V. lecanii*, and nonpathogenic *F. oxysporum* (Whipps and Lumsden, 2001; Kabaluk *et al.*, 2010; Khan and Anwer, 2011). Although species of mycorrhizal fungi may form protective sheaths around plant roots and otherwise aid in plant nutrition and growth, they are not directly involved in controlling plant disease and are sold as biofertilizers, not as biocontrol products.

Trichoderma spp. are common rhizosphere and soil inhabitants found all over the world, and are often the most

prevalent culturable fungi when soil is studied *in vitro*. There are 89 species of *Trichoderma*, all saprophytic and possessing of a number of mechanisms that make them effective biocontrol agents of plant pathogens such as their high reproductive rate, their ability to colonize plant surfaces and interiors, their ability to survive under very unfavorable conditions, a strong mycoparasitism toward a broad range of pathogenic fungi, secretion of a large range of antibiotics and cell wall-degrading enzymes, and their ability to promote plant growth and defense responses. Of the many described strains, *T. asperellum*, *T. gamsii*, *T. virens*, *T. viride*, and especially *T. harzianum* are the most commercially important with many products developed to control soil and seedborne pathogens, including *Pythium*, *Rhizoctonia*, and *Fusarium* spp., and in some cases also *Botrytis*, *Macrophomina*, and *Phytophthera*. Although there is much commercial interest in manufacturing *Trichoderma* products, the fungus also lends itself conveniently to on-farm growth and application in small fermentors directly connected to irrigation systems. In many countries, particularly in South and Central America, such as Costa Rica, growers manufacture their own products for use in various production systems such as rose cultivation (Figure 1). Binab T is the name of the first fungal biocontrol registration to the US EPA, and is made by BINAB Bioinovation of Sweden for control of wood wound diseases of trees by a strain of *T. harzianum*. Another EPA-registered *T. harzianum* product, Root Shield® made by Bioworks Inc. (Victor, NY, USA) protects roots by quickly colonizing plant surfaces and parasitizing soil-transmitted plant pathogens such as *Pythium*, *Rhizoctionia*, *Fusarium*, *Thielaviopsis*, and *Cylindrocladium*. Over 100 *Trichoderma* products can be found such as Trichodermil SC in Brazil (*T. harzianum*), Trichosav in Cuba (*T. harzianum*), Tenet in New Zealand (*T. atroviride*), and Trichotech in Kenya (*T. asperellum*). *Trichoderma* is used for biocontrol in over 60 countries, with the greatest use in the USA, Brazil, and China (Kabaluk *et al.*, 2010).

Next to *Trichoderma*, *Gliocladium* spp. are the most common fungi used in biocontrol of plant pathogens and share similar ecological niches, also being cosmopolitan soil saprophytes. *Gliocladium virens*, which may actually be *T. virens*, has been formulated into products such as Gliogard™ and Soilgard 12 G™ that protect against root rot caused by *Pythium* and *Rhizoctonia* by parasitizing them, producing antibiotics, and excluding them from the root niche. *Gliocladium catenulatum* parasitizes *Pythium, Rhizoctonia, Botrytis, and Fusarium* spp., attacking these pathogens through aggressive hyphal



Figure 1 Utilization of *Trichoderma* for control of foliar and soilborne diseases of roses in Costa Rica. (a) *Trichoderma* is cultured on boiled rice. (b) Rice is suspended in a bucket of water and the dispersed spores sprayed onto foliage. (c) Remaining rice from bucket is spread on soil surface where sporulation occurs again in 24 h. (d) Disease-free rose production – low cost, safe, effective.

puncturing of cell walls. *Gliocladium catenulatum* is registered and is sold as Primastop® by Kemira Agro Oy of Finland, who recommends its application to soils, roots, and foliage to reduce the incidence of damping-off in the greenhouse. Another formulation, sold as Prestop® in Canada and Europe, protects against damping-off, foliar diseases, gummy stem blight, gray mold, root rot, seed rot, stem rot, storage diseases, and wilt.

Viruses

As a biocontrol measure, viruses are attractive ways to combat plant pathogens as they are nontoxic to eukaryotes, are specific to certain microbial species or strains, and are easy and inexpensive to isolate, produce, and store. Currently at the global level, viruses represent approximately 3% of the value of the biocontrol market, although this is mostly due to the popularity of baculoviruses for insect control (Glare *et al.*, 2012). Most plant diseases are caused by fungi, then bacteria, both of which have a large diversity of attendant viruses which might find use as biocontrol agents in the future.

Fungal viruses (mycoviruses) were first discovered as the causal agent of a serious disease of cultivated mushrooms (*Agaricus bisporus*) in the USA in 1962 (Ghabrial and Suzuki, 2009) and since have been found in every major group of fungi. Interestingly, fungal viruses are not known to have natural vectors and thus are transmitted intracellularly by hyphal fusion between vegetatively compatible individuals and from generation to generation via spores. In searching for a means of biocontrol in maize of the biotrophic fungus *Ustilago maydis*, Allen *et al.* (2011) discovered a strong antifungal protein transferred from a mycovirus to its fungal host. The killer protein, KP4, kills all noninfected strains of *Ustilago*, clearing the way for the virus-infected fungus to colonize the inside of the plant. This is likely the product of coevolution between fungus and a virus, which depends completely on survival of its host for transmission and its own survival. Transgenic expression of the protein was found to result in very high levels of antifungal activity against corn smut throughout the plant.

Although most fungal viruses cause no obvious phenotypic changes to their host, a small proportion do, stimulating changes in growth rate, color, morphology, fertility, and reproductive behavior, sometimes leading to a reduction in virulence to plants (hypovirulence) or an increase in virulence (hypervirulence). For use in biocontrol, it is the capacity of a mycovirus to stimulate hypovirulence in plant pathogenic fungi that has attracted the most attention. An important example of mycovirus-induced hypovirulence is with *Cryphonectria parasitica* by the Hypoviridae viruses. *Cryphonectria parasitica* was introduced into North America and Europe from Asia in the early twentieth century and it has killed billions of mature American and European chestnut trees. Hypovirulent strains of *C. parasitica* discovered in Italy in 1950 were employed by the French Ministry of Agriculture in large biocontrol programs starting in the 1960s with the belief that they would competitively exclude virulent strains of *C. parasitica* from infection sites in the chestnut tree. Such biocontrol programs are still used in Europe to control the spread and severity of chestnut blight. The high diversity of vegetative compatibility groups in North American populations of *C. parasitica* has limited the usefulness of this approach.

Bacterial viruses, called bacteriophage, are fundamentally different from mycoviruses in that they can infect bacteria from an environmental source (such as soil or a foliar spray), and thus show more promise for the development of bacterial biocontrol agents. The first plant bacterial pathogen-infecting viruses were discovered in 1924 by Mallman and Hemstreet who showed that the filtered liquid collected from decomposed cabbage was able to inhibit the growth of *X. campestris* pv. *campestris* on cabbage. The cause of bacterial growth inhibition was found to be lytic bacteriophage. Similar experiments with carrots, potatoes, cotton, and corn infected with species of *Erwinia*, *Xanthomonas*, and *Pantoea* suggested that these bacteriophages could play a role in biocontrol of bacterial plant pathogens in agriculture. Bacteriophages are strain-specific, requiring blends of phages to properly target pathogenic microbes. For control of fire blight on apple blossoms caused by *Erwinia amylovora*, three types of phages were combined and significant (37%) disease reduction was obtained. The use of phages for biocontrol of bacterial wilt of tobacco, citrus canker, citrus bacterial spot, bacterial blight on geranium, bacterial blotch of mushroom, and *Xanthomonas* blight of onion are being tested (Jones *et al.*, 2007).

The efficacy of bacteriophage treatments can be improved through coapplication with adjuvants such as traditional antibacterial treatments of copper and streptomycin, and live forms of bacterial and fungal treatments such as Blossom Bless (*Pantoea agglomerans* P10c; Gro-Chem NZ Ltd), and Superzyme (*B. subtilis*, *Trichoderma*, and *Pseudomonasputida*; JH Biotech Inc.). Though typical bacteriophage research focuses on direct killing of the pathogenic bacteria, research with the φRSM3 virus of *Ralstonia solanacearum* (a temperate filamentous virus which does not kill its host but changes it physiology and promotes continuous leakage of viral particles) has shown that inoculation of plants with infected bacteria can prime the plant's own induced defences and protect against bacterial wilt (Frampton *et al.*, 2012). Another line of research is taking endolysin genes from bacteriophage of *C. michiganensis* and overexpressing them transgenically in tomato xylem to kill the invading bacteria that cause bacterial wilt and canker (Frampton *et al.*, 2012). The first commercially available bacteriophage therapy for plant disease protection only recently became available, made by Omnilytics of Salt Lake City, Utah. The product is called Agriphage, and controls *X. campestris*, cause of bacterial spot in tomato and peppers, and *P. syringae* pv. *tomato*, the causative agent of bacterial speck on tomatoes (Frampton *et al.*, 2012). Agriphage is registered with the EPA (Registration no. 67986-1) for control of bacterial spot in Florida as part of an officially recommended integrated management program. A weakened form of zucchini mosaic virus was also registered for use in viral cross-protection (similar to vaccination) of small cucurbit plants against virulent forms of the virus.

Postharvest Control

It is estimated that 20–25% of harvested fruits and vegetables succumb to decay (Sharma *et al.*, 2009). Many aspects of crop storage lend themselves well to biocontrol measures: the crop is usually stored in a defined environment (temperature and

humidity), the agent is applied directly to the target, and the target has high value. In contrast to biocontrol of foliar and soilborne diseases, postharvest disease control involves applying the biocontrol agents directly to the harvested product. In many cases, the biocontrol agent is applied immediately before harvest to prevent any wounds generated during harvest from being colonized by pathogens. This protects a crop that has a latent infection from manifesting during postharvest storage. Organically grown fruit, a growing market, represents an ideal target sector as synthetic chemical fungicides are prohibited.

Most pathogens causing postharvest losses are necrotrophs, that is, they kill host cells and consume the dead tissues. For this reason, competitive exclusion by aggressive nutrient-consuming biocontrol agents is a commonly reported mechanism of protection against these diseases. For a postharvest biocontrol agent to work well, it is critical that it grows well in the storage conditions. Other proposed mechanisms of postharvest biocontrol include antibiotic production and direct parasitism of the pathogen. Whereas first-generation postharvest biocontrol measures were not widely used due to poor control compared to chemical means and lack of economic incentives, second-generation biocontrol agents have made improvements. These new products contain live cells with salts to stabilize the organisms, and lytic enzymes (chitosan or lysozyme) as adjuvants to improve control. In addition, new products are targeted to be combined with chemical and physical methods to increase the efficacy while still using lower quantities of chemicals than conventional control methods.

Commercially, several biocontrol products are available to control postharvest diseases. One of the most successful examples is the use of atoxigenic strains of *A. flavus* to control aflatoxin-producing strains of the same species. Atoxigenic strains compete for the same niche and interact with toxin-producing strains to decrease their population and the amount of aflatoxin produced in cotton seed meal. Aflatoxin has been implicated as a carcinogen in several animal models, and grain with this toxin at low levels cannot be used to feed livestock, nor can any product contaminated with aflatoxin be used for human consumption. Use of competitive, atoxigenic *Aspergillus* strains on peanuts has reduced aflatoxin production by up to 98%. A commercial product, Aflaguard (Syngenta) has been developed for use on a wide variety of crops to effectively reduce aflatoxin contamination.

Another example of postharvest control is interference of pathogen signaling mechanisms. This mechanism has been demonstrated to work on soft rot of vegetables caused by *Pectobacterium carotovora*. This organism requires a critical cell density to express virulence genes, including pectinases which degrade vegetables in storage. The cells sense their density by producing signaling molecules called *N*-acyl-homoserine lactones (AHLs). Naturally occurring bacteria have been identified which degrade AHLs. When vegetables are coinoculated with both the AHL-degrading strain and *P. carotovora*, the rotting is less than with *P. carotovora* alone. Although no commercial products are currently available, this mode of action provides great promise.

Using a novel culturing method, researchers isolated several antagonists of postharvest rotting. The traditional method to identify antagonists was to screen for antibiotic production on agar media in Petri plates. Instead, fruit was washed and this washing fluid was used to inoculate wounds infected with the rot pathogen (Wisniewski *et al.*, 2007). Organisms were isolated from those wounds that failed to rot. This yielded strains of *Candida* that parasitized hyphae of pathogens and produced lytic enzymes.

Several products are available commercially for postharvest BC. Fungal products include Aspire (Ecogen), which is *Candida oleophila*, and YieldPlus (Lallemand), which is *Cryptococcus albidus*. Bacterial products include Serenade (Agro Quess), a *B. subtilis*, and BioSave (Jet Harvest Solutions) which is *P. syringae*.

Biocontrol agents are used sparsely in postharvest control disease measures. This represents an area underexplored and an untapped market as consumers demand less or no pesticides on the produce they consume.

Future Directions

The concepts of BC will continue to expand as molecular technologies accelerate the understanding of the mechanisms by which biological pest control is achieved. It is likely that instead of using biocontrol organisms directly their genes or gene products are increasingly used for management of pathogens. This has already been achieved with Bt. By having the plant produce the toxin, only those insects that feed on the host plant are impacted while the impact on nontarget insects is minimized. This minimizes factors associated with variable efficacy such as formulation, storage, application, and environmental factors. Moreover, the biocontrol product is produced only where it is needed. Sources for such genes will expand and will provide plant breeders with virtually unlimited capacity to create disease resistance in crop plants.

Instead of biocontrol products using single organisms with only one mode of action, one can expect to see more consortia of many types of bacteria, fungi, and viruses that interact with each other and their host. For this to happen one should be able to identify microorganisms that can exist in an ecosystem together and that can promote increased expression of genes having a role in biocontrol. Such communities may already be present in or on plants (as found with sugarcane) and in soils. It is very likely that the agricultural practices, such as plowing, has impoverished soil microbial populations. It is also possible that by breeding for stress tolerance and yield only, many beneficial plant–microbe associations are eliminated. Model systems are now examining how bacteria producing varied compounds including auxin, acetoin, and phenazines influence the efficacy of BC (Kim *et al.*, 2011). Future research will lead to integration of complex and diverse traits into plant genomes and to more effective strategies of microbially mediated biocontrol of plant diseases.

The delivery and establishment of microorganisms that reside on the external parts of plants will continuingly be improved. More focus will be about microbial establishment on seeds and seedlings as they represent a convenient and efficient way to disseminate the microbes, while allowing for rapid and early colonization of the developing plant. The most important criteria for a biocontrol agent is that the application be compatible with growers' practices in the field.

It is very likely that many new species of BC agents will be discovered. Only 1% of soil bacteria have thus far been isolated in culture. Sequencing experiments routinely show that most of microbes in an environmental sample are unknown. For example, the study of the rhizosphere from potato roots by 454 sequencing of the chaperonin Cpn60 gene marker showed that when the 10 most common bacteria expected are isolated, greater than 40% of the isolates turned out to be new species. Similar phylogenetic studies of the microbiology of roots and soil are now coming out at a furious speed and will eventually be accompanied by isolation and characterization of these unidentified organisms and their role on/in the life and health of the plant. Just as plant breeders had no way to identify the presence of microbial associations (other than rhizobia) in their crosses, it is likely that the crop plants of today have lost important associations required for productivity in systems where environmental stresses are the norm. These associations, however, may still be present in their wild parents. It would not be a surprise to find that the next iteration of agriculture looks to insert beneficial plant–microbe associations as new traits into the development of more environmentally sustainable agricultural practices.

See also: Biotechnology: Plant Protection. Plant Health Management: Pathogen Suppressive Soils. Plant Virus Control by Post-Transcriptional Gene Silencing

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Plant Health Management: Crop Protection with Nematicides

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Glossary

Anhydrobiosis State of reversible dormancy induced by desiccation.
Chemigation Application of a pesticide through irrigation systems.
Detritus Nonliving organic particles.
Geographic information system (GIS) Geographic information system refers to information system that integrates, analyzes, and displays geographical data.
Global positioning system (GPS) A satellite-based navigation system that provides free location and time information anywhere on earth and in any weather conditions.
Metazoan Taxonomic group comprising the multicellular animals.
Phylum Taxonomic category between kingdom and class.
Vector An organism that transmits disease-causing to another host.

Introduction

Nematodes are commonly known as roundworms. They are the most abundant metazoans on earth with an estimated 80% of all animals belonging to the phylum nematoda. The number of species has been estimated between 500 000 and 10 million. They inhabit nearly every location on earth that contains at least some water periodically. They have digestive, nervous, excretory, and reproductive systems but respiratory and circulatory systems are absent. Internal turgor and longitudinally oriented muscles allow for snake-like movement (lateral undulation) in water films. The body is covered with a cuticle that is primarily composed of the fibrous protein collagen. Most of these unsegmented worm-shaped organisms live unnoticed by the general public because of their typically microscopic size, transparent, colorless body, hidden habitat and a diet of microorganisms or detritus. Although the vast majority of nematode species are considered beneficial because of their function in the food web and their nutrient cycling ability, the ones that parasitize humans, animals, and plants can cause considerable physical and economical hardship. Consequently for nearly one and a half centuries people have tried many techniques and products, including the use of natural and synthetic chemicals to protect themselves and their livelihood against these pests. While medications against mammalian-parasitic nematodes are termed anthelminthics, plant protection products against plant-parasitic nematodes are referred to as nematicides. Botanical or microbial extracts are often further distinguished as bionematicides. The term nematicide refers to chemical compounds that kill, inhibit, or repel nematodes or manipulate their behavior to mitigated crop damage. In general, the use of nematicides might be considered when other methods of crop protection against plant-parasitic nematodes are not feasible or are economically prohibitive. Alternatives to nematicides may include physical, biological, and cultural practices. Another important guideline is the economic damage threshold. This is expressed as the nematode population density that is predicted to cause economic loss exceeding the cost for the treatment. It is more a practical rule than a precise one, as it is influenced by various parameters such as virulence of the nematodes, host physiology, soil type, and temperature. In some cases, the nematode management choices are very limited. For example, certain countries may require nematicide treatments as a sanitary condition for allowing imports of specific produce.

Nematode-caused damages occur in almost any crop worldwide. Diagnosis of nematode-related damage is often difficult because of the lack of specific symptoms. In dense field plantings, oval-shaped areas of pale yellow, stunted, and wilted plants indicate potential root disease problems which might be related to plant-parasitic nematodes or other soilborne pathogens. With increasing spread of the nematode this often becomes less obvious as the whole field suffers under chronic disease pressure, lacking the comparison to healthy plants (Figure 1). Below-ground roots may be short, stunted, discolored, or in unusual abundance, all unspecific symptoms that may be related to other biotic or abiotic causes. An exception is the root galling induced by root-knot nematodes (*Meloidogyne* spp.), which is sufficiently distinct from similar symptoms to be diagnostic. In fruit, nuts, and vine orchards significant nematode parasitic activity might occur for years



Figure 1 Preseason soil treatment (left) with a nonfumigant nematicide revealed chronic lesion nematode (*Pratylenchus* spp.)-caused disease in wheat in the nontreated part of the field (right).

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before unthrifty growth and yield and/or quality decline alert the grower to a problem. Mixed populations of two or more parasitic species and interactions with soilborne microorganisms increase the difficulty of proper diagnosis. Consequently, correct identification of nematode species and population density is the first step in determining potential pest management strategies, including the use of nematicides.

Plant parasitic nematodes feed exclusively on living tissues, either on the outside (ectoparasitic) or inside of plants (endoparasitic). Their protrusible, hollow mouth stylet enables them to puncture plant cells and inject metabolites that may alter host physiology and morphology as well as ease the feeding process. A muscular thorax pump (metacarpus) provides the force for feeding on the cell contents. Depending on the nematode and plant species, the host–parasite relationship might be very complex with a series of recognition and response events. The details of these processes are still largely unknown but of importance for future nematicide development as they might reveal potential key targets for novel approaches.

The life cycle of plant parasitic nematodes includes distinct stages with four molts: egg, four juvenile, and adult. With endoparasitic nematodes the second-stage juvenile (J2) is often the infective stage. Both sexes are present in most species but mating is not always necessary for fertile offspring. Sex attraction guided by specific female metabolites (pheromones) has been shown with various species. The economically most important root-knot nematodes can produce hundreds of eggs that are contained in a gel-sack, deposited mainly on the outside of the host roots. The gel gives the eggs some protection against desiccation and microbial attack. Other nematodes often survive years in a dormant stage. For example with cyst nematodes, the egg-containing body of the dead adult female (cyst) provides some protection against biotic and abiotic factors. In other species, nematodes in a state of anhydrobiosis have not only a better chance to survive severe drought conditions but also are less susceptible to nematicides.

Nearly all plant parasitic nematodes dwell at least part of their life in soil while the economically most important species eventually become sedentary in roots. A few species occur in above ground parts such as bulbs, leaves, or seeds. The rate of nematode development is species-specific and primarily temperature dependent. For example, in warm climates, endoparasitic root-knot nematodes may go through their life cycle in less than 4 weeks and generate more than one generation on a single susceptible crop. In contrast, in temperate climates eggs of cyst nematodes remain dormant through the winter resulting in the completion of only one generation. This affects not only crop damage but is also important in considering nematicide application scheduling, efficacy, and cost/benefit ratio of nematicides. With multiple nematode generations, even efficient control at the beginning of a cropping season typically does not reduce nematode population density at harvest. In fact, the early protection often leads to a larger, healthy root system, and an increase in potential nematode feeding sites. This may result in more females and increased egg production. However, seedlings are typically more susceptible and damage-prone than older plants. The early nematicide protection might, therefore, sufficiently mitigate nematode damage to justify the cost of the treatment even though there is no difference in population densities at the end of the season. For some plant parasitic nematodes, temperature sum models have been developed to determine the approximate timing of the appearance of the next generation. These predictions can be useful to optimize crop management practices such as split or multiple nematicide applications to coincide with hatching when infective juveniles are most susceptible. Endoparasitic stages are better shielded against nematicides than soil-dwelling stages. In addition to the physical protection, nematicides in plant tissues are likely to be diluted and metabolized. After orchard removal, remaining larger roots often stay alive in soil for months or even years. They continue to provide endoparasitic nematodes and other plant pathogens with nutrition and protection. This reservoir is extremely difficult to eliminate even by some soil fumigants, and contact nematicides are ineffective.

Plant parasitic nematodes are capable of causing plant diseases and significant crop damage. A few nematode species in the family Longidoridae and Trichodoridae function as vectors of important plant viruses. Other nematode species predispose host plants to fungal or bacterial diseases. Nematicides have played an important role to demonstrate such interaction and to mitigate the resulting disease. In addition, many plant health problems are frequently the result of complex and poorly understood interrelationships with plant parasitic nematodes, soilborne fungal and bacterial plant pathogens or deleterious microorganisms, and abiotic stress. The etiology may be further modulated by mycorrhizal and rhizobial symbionts and other rhizosphere or endophytic microorganisms. Thus, nematicide use needs to be viewed not only in regard to the target organisms but also the ecosystem as a whole. For further information of the biology, ecology, and damage potential of plant parasitic nematodes, the interested reader is referred to several reference books (Barker *et al.*,1998; Chen *et al.*, 2004; Perry and Moens, 2006).

Historic Synopsis

The history of nematicides is fairly short but rich in lore from serendipitous discoveries to systematic high-throughput industrial screening; from scientific triumphs to technological disasters. The discovery of *Heterodera schachtii* in 1859 by botanist Hermann Schacht was one of the earliest reports of a plant parasitic nematode and the first of major agricultural and economic significance. Nearly half a century earlier, after Napoleon Bonaparte banned British ships from entering ports on the European continent, the British Empire imposed a sea blockade on his ships from the West Indies. The lack of cane sugar on the European continent accelerated the adoption of the new sugar beet crop that had been developed by German scientists at the end of the eighteenth century. The beets grew well in fertile soils in central Europe and traditional wide rotation schemes were abandoned in favor of more profitable narrow rotations or monoculture. But by the middle of the nineteenth century the consequences of such poor agronomic stewardship became obvious, particularly in declining sugar beet production fields in the Prussian Province of Saxony

where sugar beet cyst nematodes had built up to economically damaging populations.

Subsequent research by Kühn during the 1870s focused primarily on various management strategies against *H. schachtii* that included the search for chemical solutions to this problem. Phenol and carbon disulfide were among the first compounds tested because they had been previously used against soil-dwelling Phylloxera (*Daktulosphaira vitifoliae*), a tiny aphid-like insect that feeds on certain grape roots. Although the efficacy of these compounds against *H. schachtii* was generally poor at economically feasible rates, it stimulated further search for volatile compounds against all soil pests. It took about another half century before the first major breakthrough in chemical control of plant parasitic nematodes occurred. Obsolete inventory of the tear gas chloropicrin from World War I was experimentally tested against soilborne fungi and nematodes with great success in England and California.

Another major agronomic crisis brought on by monoculture promoted the commercial use of chloropicrin as a soil fumigant. This time the pineapple production fields on Hawaii suffered from a build-up of soilborne pathogens including root-knot nematodes. In the late 1920s, scientists of the Pineapple Research Institute found that there was a good dose–response relation between chloropicrin application rates and a reduction in nematode damage as well as a remarkable increase in pineapple weight in response to the treatments. The use of chloropicrin for preplant soil treatment became standard practice in production as the Hawaiian pineapple companies secured the cheap US military surplus. However, when the supplies dwindled the search for alternatives intensified as the production costs for newly synthesized chloropicrin became prohibitively expensive. In the early 1940s, methyl bromide was discovered as a fumigant with broad-spectrum biocidal activity against fungal pathogens, nematodes, weeds, and insects. With the development of a mechanical fumigant-injection and trapping equipment by Storkan in the 1960s, it became practical to fumigate large acreages accurately, safely, and economically feasible for high-value cash crops.

A key development for establishing Nematology as an important crop protection discipline was the accidental discovery by entomologist Carter of the nematicidal activity of D–D, a mixture of 1,3-dichloropropene and 1,2-dichloropropane while searching for an insecticide against pineapple mealybugs (*Dysmicoccus* sp.). Following decades of further product development and regulatory restrictions, it became 1,3-D or Telone II. Moreover, the discovery gave rise to other effective halogenated hydrocarbons, in particular ethylene dibromide (EDB) in 1944 and approximately a decade later 1,2-dibromo-3-chloropropane (DBCP). In contrast to methy bromide, 1,3-D, EDB, and DBCP had little effect on microbial plant pathogens and thereby left no doubt about nematodes causing plant diseases. They convincingly demonstrate the pathogenic potential of nematodes on crop health and production. DBCP with its low vapor pressure, small application rate and low acute toxicity was safe for perennial crops and allowed use in established orchards and vines. In 1956, metam sodium (sodium *N*-methyl dithiocarbamate dihydrate) came to the market, the first of the so-called methyl isothiocyanate-releasing compounds. It not only controlled plant parasitic nematodes but also had good activity against a wide spectrum of soilborne microorganisms and weeds.

In the 1960s and 1970s, several nonfumigant nematicides were developed that originated as insecticides and allowed postplanting use. Furthermore, some of those compounds were taken up by the plants systemically and potentially affected plant parasitic nematodes within the plant tissues. The nonfumigant nematicides all belonged to the chemical classes of carbamates or organophosphates and acted despite their high acute toxicity at labeled field rates primarily as nemastatic neurotoxins. They prevent the enzymatic breakdown of the neurotransmitter acetylcholine in the synapse, resulting in uncontrolled stimulation of the nervous system. As a consequence, the nematicides stunted nematode movement, feeding, and delayed development for several weeks. But nematodes typically recovered once the concentration of the compounds dwindled to ineffective levels via dilution or degradation. Remarkably, in contrast to insects, resistance of field populations of plant parasitic nematodes to these nematicides has never been demonstrated. However, frequent use favored accelerated biodegradation that shortened the useful residual longevity of the products. However, some persistent compounds were found as pollutants in ground water. Awareness of environmental pollution risk increased correspondingly with improvements in detection methods. One of the most acutely toxic pesticides registered by the US Environmental Protection Agency (EPA), aldicarb, was detected in groundwater in more than half the US states. Various regulatory actions restricted application techniques and nematicide-use rates to increasingly fewer crops and areas. Consequently many products were removed from the US market as their profitability was challenged.

EDB and DBCP were banned in the US in the late 1970s. Lack of proper worker protection in DBCP production facilities resulted in cases of male sterility and suspected carcinogenesis. But it was the detection of the compounds in groundwater that led finally to their cancellation by the US federal EPA. This development was fueled in part by a change in the attitude of the general public toward technology and environment protection.

In the beginning of the 1990s, methyl bromide was included in the Montreal Protocol, an international treaty to reduce the production and consumption of stratospheric ozone depleting substances. Ratified worldwide by nearly 200 countries, it scheduled the gradual phase-out of those compounds. This had tremendous repercussions for high-value annual crops, replanting of fruit and nut trees as well as for nurseries. It is safe to say, the consequences for agriculture will not be fully understood until years from now.

Another legislative act in the US had even more impact on the availability and use of nematicides. Alarmed by a National Academy of Science report on pesticides in the diets of infants and children, the US Congress unanimously decided with the 1996 Food Quality Protection Act to overhaul of the US's pesticide and food safety laws. It included stricter safety standards, in particular for infants and young children, and a periodic reevaluation of existing pesticide tolerances. Both carbamates and organophosphates, and therefore nearly all nonfumigant nematicides, belong among the EPA's first priority group. This was a group of closely related pesticides with

a common mechanism that required cumulative risk assessment. Risk mitigation measures resulted in use restrictions that limited the profit margin of many products, some of which were consequently withdrawn from the market. While most western companies stopped screening for carbamate and organophosphate nematicides in the early 1990s, two of the latest organophosphate nematicides fosthiazate (1992) and imicyafos (2010) were developed in Japan.

As the need for safe solutions to the nematode problems grew, it attracted development of the so-called bionematicides. DiTera, a sterilized fungal fermentation product received US EPA registration in 1996. Since then many botanical-derived products have been developed, targeting primarily specialty markets such tree and vine crops as well as turf. In 2006, the nematicidal seed treatment Avicta was registered in the US on cotton and subsequently on several other crops. The active ingredient abamectin, a mixture of complex microbial metabolites, has long been known for its potent nematicidal activity and has been used as an anthelmintic in animal health.

More recently, the nematicide R&D activities among the remaining agrochemical businesses has considerably increased. At least half a dozen new development products are in near-market testing that supposedly show better environmental compatibility and less acute toxicity with similar target efficacy as the previous generation of contact nematicides.

Delivery of Nematicides

During the past two decades, new plant protection products have been generally more environmentally benign than in previous times, particularly in terms of target specificity and nontarget toxicity. Furthermore, despite substantial reduction in application rates, many newer insecticides and fungicides have similar if not better efficacy than products of previous decades. In contrast, application rates of nematicides have stayed relatively similar with typically 1–9 kg ha^{-1} active ingredients per season for contact nematicides and approximately 120–750 kg ha^{-1} for fumigants. Use changes occurred primarily in response to regulatory restrictions, not so much because of new product or technology development. The reason for this is in part due to a consequence of the consolidation of the agrochemical industry.

One of the main technical problems of using nematicides lies in efficiently delivering the active ingredient to the target site. The majority of plant parasitic nematodes spend at least part of their lives in soil, the rhizosphere, roots, or other subterranean plant parts. Although the growth or mobility range of other plant pathogens is typically very limited, plant parasitic nematodes may occur anywhere from the surface to more than one meter deep in the soil. Therefore part of the target population is quite likely outside the effective treatment zone. They might reinvade the previously nematicide-treated zone by their own mobility after the concentration drops below an effective level. Nematodes are often guided to their host by a gradient of attraction signals. Under favorable conditions, nematicides with a high volatility that move through soil pores achieve a better distribution than low-volatile compounds. The latter require mechanical soil incorporation or movement with water to reach their target. Such resource-intensive applications are often compromised, negatively impacting treatment efficacy. Dissemination inside the treated soil depends on a variety of factors such as compound chemistry, soil type, temperature, water, organic matter content, and pore space. Treatment efficacy is typically better in soils with larger pore space than in heavier clay soils where small pore spaces limit movement of volatile compounds and extensive particle surface provides abundant adsorption sites. Organic matter also diminishes the treatment efficacy by adsorption. Similar limitations must be considered for the use of contact nematicides. In particular the organophosphates are known to lose their efficacy in soils with high organic content. The activity of the carbamate oxamyl, however, diminishes quickly in moist, warm and alkaline soils.

Nonvolatile nematicides are often available in different formulations such as as liquids and granuales. They are typically incorporated into the top 12–15 cm of soil and remain inhibitory to nematodes for a few weeks. To reduce nematicide use and reduce cost, band-application aims to treat primarily the root zone to provide temporary protection against plant parasitic nematodes. Application through low volume irrigation systems (drip systems) takes advantage of water-restricted root systems that are then flushed with a nematicide solution. Although usually by the end of the growing season root damage (galling) and nematode population density are often as large as under nontreated crops, the early protection against invading nematodes and secondary microorganisms may provide sufficiently beneficial effects.

Several carbamate and organophosphate nematicides are acropetally systemic, i.e., they can move from the root to the top of plants, and may affect endoparasitic nematodes after infection although the primary action occurs in soil. Foliarly applied nematicides must be taken up through the epidermis and transported downwards (basipetal, phloem transport). Adjuvants may aid in the uptake of foliar sprays, thereby increasing the efficacy. Currently, only a couple of nematicides have the ability of significant basipetal movement and their efficacy is variable. The paucity of such compounds might be related to the more time-consuming screening and testing for such additional properties compared to a simple dose–response assay.

After the development of contact nematicides, there was a brief interest in their potential use as seed treatments. Although useful activity in protecting the germinating seed and developing seedling was demonstrated, the better and longer lasting efficacy by high rate soil-applications stifled further development. Moreover, the loading rates to achieve significant seedling protection were a delicate balancing act between phytotoxicity and efficacy. As long as high rates of relatively inexpensive soil nematicides were permitted, seed treatments could not compete with their typically short-term protection capability. There was also the concern of bird and other wildlife feeding on seeds treated with highly acute toxic compounds. Perhaps most important, there was little incentive for the agrochemical industry to replace high volume soil applications with low volume seed treatments.

With the advent of high price hybrid or genetically modified seed and the market removal of many old soil pesticides, as well as merger of seed and agrochemical companies, a new marketing model emerged. It set out to provide the grower with 'complete' solutions against a variety of pest and disease

problems by offering quality seed coated with a combination of several pesticides (fungicides, insecticides, nematicides, etc.) for seedling protection. Such portfolio packaging has been controversial as it may reduce competition and limit grower's choices. However, it likely increases safety with respect to pesticide use and handling. It also reduces other operational inputs such as machinery use, fuel, and labor for pesticide applications replaced by seed treatments. Since the recent registration of combination products with the nematicidal components, seed-delivered nematicides have become a new development target. As such products are expected to protect developing seedlings for only a few weeks, this technology would benefit from a combination with additional protection modules.

Nematicidal Compounds

The most commonly known nematicides are listed in Table 1. This listing is neither complete nor does it indicate the current regulatory status for use. There are many more compounds, which at one time or another have been used for the purpose of mitigating the influence of plant parasitic nematodes. The following brief overview will discuss some of those compounds and products that are currently registered or under development in some parts of North America, Southern Europe, or East Asia.

Among the fumigants, 1,3-dichloropropene (1,3-D, Telone II) is considered the only one with primarily nematicidal activity at labeled rates. It is applied either as a volatile liquid that, injected into the soil, converts to gas, or as an emulsified compound for chemigation. It has excellent efficacy as a preplant nematicide. For decades, it was the primary tool for nematode control in many crop production systems. The detection of elevated levels of 1,3-D in the ambient air in a California county led to its suspension. It was reinstated again a few years later with reduced application rates and various other restrictions to address air quality concerns. Further label changes were implemented to reduce volatilization and safety. In combination with chloropicrin, it is considered to be the

Table 1 Products for plant protection use against plant parasitic nematodes[a]

Common name	*Active ingredient(s)*	*Chemical class/organisms*
Terr-O-Gas, Tri-Con, and Brom-O-Gas	Methyl bromide	Halogenated hydrocarbon
Cloropicrin 100 Fumigant and Metapicrin	Chloropicrin	Halogenated hydrocarbon
Telone II and Telone EC	1,3-Dichloropropene (1,3-D)	Halogenated hydrocarbon
Telone C-17, C-35, and InLine	1,3-D plus chloropicrin	Halogenated hydrocarbon
Midas	Methyl iodide	Halogenated hydrocarbon
Enzone	Sodium tetrathiocarbonate	Thiocarbonate
Paladin	Dimethyl disulfide	Organosulfur
Temik and Meymik	Aldicarb	Carbamate
Vydate	Oxamyl	Carbamate
Metam, Vapam, and Sectagon 42	Metam sodium[b]	Dithiocarbamate
K-Pam HL and Sectagon K54	Potassium sodium[b]	Dithiocarbamate
Basamid	Dazomet[b]	Dithiocarbamate
Counter	Terbufos	Organophosphate
Nemacur	Fenamiphos	Organophosphate
Nemathorin and Eclahra	Fosthiazate	Organophosphate
Nemakick	Imicyafos	Organophosphate
Mocap	Ethoprop	Organophosphate
Rugby and Apache	Cadusaphos	Organophosphate
Admire Pro	Imidacloprid	Neonicotinoid
Movento	Spirotetramat	Tetramic acid
Nimitz	Fluensulfone	Fluoroalkenyl (-thioether)
Avicta and Tervigo	Abamectin	Macrocyclic lactones, metabolites of *Streptomyces avermectinius* (syn. *S. avermitilis*)
DiTera	Killed, dried fermentation product	Solids and solubles of *Myrothecium verrucaria* strain AARC-0255
Ecozin Plus 1.2% ME	Azadirachtin derived from Neem	Botanical, extract from *Azadirachta indica*
MultiGuard Protect and Crop Guard	Furfural derived from sugarcane bagasse	Heterocyclic aldehyde, produced from various agricultural byproducts
Nema-Q	Extract derived from soap bark tree	Botanical, extract from *Quillaja saponaria*
Sesamin EC and NeMaX	Sesame oil derived from sesame seeds	Botanical, extract from *Sesamum indicum*
BioNem, BioSafe; VOTiVO, and Nortica	Live microorganisms	*Bacillus firmus* strain I-1582
Clariva	Live microorganisms	*Pasteuria nishizawae*
Klamic	Live microorganisms	*Pochonia chlamydosporia*
MeloCon and BioAct	Live microorganisms	*Paecilomyces lilacinus* strain 251

[a]This list is for general information only. Active ingrediants are often sold under various brand names and many more products claim nematicidal activity. Inclusion on this list does not constitute an endorsement by the author, nor is disapproval implied of products that are not mentioned.
[b]Methyl isothiocyanate releaser (MITC).

preferred alternative to replace methyl bromide for soilborne disease control.

Nonvolatile nematicides belonging to either the chemical class of the carbamates or the organophosphates are acetyl cholinesterase inhibitors that interfere with nerve transmission processes; a process used by many other animals, including humans. These compounds have a higher acute mammalian toxicity than halogenated fumigants but are relatively safe for plants, which allows postplant applications. Their application rates are considerably lower than soil fumigants. Although they do not compare in efficacy to soil fumigants, they usually remain active for several weeks before diluted or degraded. Repeated applications in 2- to 3-week intervals often improve efficacy but increase the risk of enhanced microbial degradation that has been documented for nearly all of these compounds. In cold soils, longer residual time increases the risk of ending up in ground water and wells. Efficacy is very much reduced in heavy-textured and organic-rich soils. Overall carbamate nematicides have dominated the nonvolatile nematicide market.

Aldicarb (Temik) is one of the oldest nonvolatile nematicides with excellent activity against plant parasitic nematodes, insects, and mites. This carbamate is extremely acutely toxic and systemically mobile in plants. These characteristics led to one of the most notorious foodborne pesticide poisoning cases in North America. Nearly 2000 people in California and Oregon fell ill after consuming watermelons illegally treated with Temik. It has been misused like no other pesticide for killing undesirable wild life. The nickname 'Two Step' cynically indicates the acute toxicity and fast lethal action.

There is a rich literature on plant-derived compounds that show some nematicidal or nematistatic activity *in vitro* or in pot tests. Seed extracts of the Neem tree (*Azadirachta indica*) have been insecticidal and nematicidal, primarily attributed to the complex secondary metabolite azadirachtin. Nema-Q is based on extracts of the Chilenean soap bark tree (*Quillaja saponaria*) that contains saponins, tannins, and other potentially active ingredients. The active ingredient in MultiGuard is furfurol, a heterocyclic aldehyde derived from sugar cane extracts. Other plant-derived products contain various essential oils, compounds with detergent-like characteristics or glucosinolates. Chitwood (2002) addressed such compounds in a comprehensive review. However, the active ingredients of botanical extracts are often not known. In most cases, the activity at realistic field application rates is at best marginal and highly variable. Composition of plant metabolites and their activity may vary with source, age, storage conditions, and extraction process, which make quality control of each production batch a critical issue. Some products are promoted by unsubstantiated producer claims and user testimonials that lack scientific evaluation. The increasing number of such products is helped by the lack of efficacy requirement for federal EPA registration.

Among the group of biological-derived compounds, the avermectins stand out as important pharmaceutical and agricultural products. Avermectins were discovered in a collaborative project between the Kitasato Institute in Japan and the Merck, Sharpe and Dohme (MSD) research laboratories in the US. After isolation of various Actinobacteria from soil near a Japanese golf course, one of them tested highly anthelmintic in mice that served at MSD as a model for human helminth infections. It was a chance discovery as later attempts to reisolate the organism *Streptomyces avermectinius* failed. This was the first commercial nematicide that was discovered in a nematode screen before its insecticidal and acaricidal properties were shown. Exposure to abamectin results in fast and permanent inactivation of the nematode's movement and feeding ability. This is due to binding to glutamate- and gamma-aminobutyric acid-gated chloride channels in nematode nerve cells that keeps the channels open. The unregulated influx of chloride ions causes irreversible paralysis. After years of use as an anthelmintic and in foliar sprays against insects and mites, recently abamectin has been developed in various crops as a seed coating to protect seedlings against plant parasitic nematodes.

Combination of Nematicides with Other Techniques

The use of nematicides with other plant protection agents is most often seen in combinations of 1,3-D with other soil fumigants that have little or insufficient activity against plant parasitic nematodes. The combination with chloropicrin expands the spectrum of activity and frequently results in synergistic activity that increases the efficacy against various pathogens. Recently, pesticide combinations in seed coatings showed considerable benefits for seedling growth and health. This was related to the effects plant parasitic nematodes exert on young seedlings. Apart from the feeding damage, nematodes can significantly change the plant's morphology and physiology. For example, in cotton *M. incognita*-infested roots became more susceptible to seedling disease and wilt. The soilborne fungus *Rhizoctonia solani* was attracted to the weakend host tissues and caused severe seedling damping-off. Protection against the nematodes and the fungus by a seed coat combination of several fungicides and the nematicide abamectin reduced the incidence of damping-off more than with a seed coating of only fungicides. Similarly, the cotton cultivar Pima S-7 is resistant to *Fusarium oxysporum* f. sp. *vasinfectum* race 1, but parasitism by *M. incognita* race 3 renders the cultivar susceptible to the wilt. Seed coating with abamectin and a fungicide/insecticide combination provided good protection against the nematodes during the critical seedling stage. In the presence of both the root-knot nematodes and the fungus, seedlings grown from abamectin plus fungicides/insecticide-coated seeds of Pima S-7 did not show any disease symptoms such as stunting, chorosis, and vascular discoloration that were typical for seedlings grown from seeds coated with only the fungicides/insecticide.

The combination of nematicides with biological control agents has not received much practical attention. One of the difficulties most soil-applied pesticides share is that protection demands an extended residence time in soil, which might then lead to potential environmental pollution. Consequently, the effective protection period is limited to a few weeks. In contrast, biological control organisms of endoparasitic nematodes are typically not very effective against the mobile juvenile stages that cause the initial seedling damage. Parasites of sedentary stages, however, can substantially reduce nematode population growth by castration or destruction of the adult

females. As nonvolatile nematicides have been found compatible with most fungi and bacterial biological control organisms, a combination of both strategies should limit their weakness and extend the protection period.

Although genetic host resistance is generally considered the most important nematode management tool, it might not be effective to prevent damage to a young seedling or a tree if planted in a field highly infested with plant parasitic nematodes. Nematicide treatments are recommended to achieve protection during the time the young plants are most susceptible. In tree and vine crops, such treatments can prevent damage that may affect the tree health for decades. For example, the grapevine fanleaf virus is transmitted by the dagger nematode *Xiphinema index*. Without effective soil fumigation, it will take more than a decade to safely replant an old vineyard site with a previous infestation. Proper use of nematicides may also lower the risk of developing resistance-breaking races of plant parasitic nematodes or to extend the useful life of a resistant cultivar. Nematicides can be an important part of crop rotation when there are no suitable nonhost or resistant cultivars to at least temporarily protect a susceptible host against nematode damage. This is often the case in warmer climates where the wide host range of root-knot nematodes make it difficult to devise an economically feasible rotation.

New Approaches

Regulatory restrictions on nematicides are often viewed negatively by growers and commodities as they initially limit the available tools and strategies to combat a serious foe. But in the long run, similar challenges to other pesticides have been met with the development of superior compounds and innovative technologies. The search for alternatives to soil fumigants and nematicides has already resulted in some remarkable developments, such as emulsified 1,3-D formulations for chemigation, combination of products with increased efficacy (1,3-D/choropicrin combinations) and improved tarpaulin covers that reduce treatment rate or increase efficacy while mitgating emissions (Yates *et al.*, 2011). Other innovations in preliminary stages of development will be briefly noted in the following paragraphs.

Seed treatments with contact nematicides developed in the 1970s have never been widely adopted. Low loading rates to avoid phytotoxicity and short persistence of the seed-delivered nematicide did not compete well in efficacy with the permitted high rates of soil-applied nematicides. Seed companies concentrated on genetic traits, not on pesticide coatings. To compete with other seed providers, the least expensive fungicide treatment was sufficient. This changed when agrochemical industries acquired biotechnology and seed companies. Superior hybrids and genetically modified crops were developed that increased the value and price of their seed. Consolidation of the various agrobusinesses resulted in development of product bundles that include hybrid seed with various seed-delivered plant protection products. After years of optimizing the treatments for microbial pathogen and insect protection, this product branding has now expanded the focus to protection against plant parasitic nematodes. Small amounts of nematicides, tens of grams active ingredient (a.i.) per hectare



Figure 2 Cucumber seed coated with the nematicide abamectin (0.3 mg a.i./seed) (right) mitigated early season attack of root knot nematodes (*Meloidogyne incognita*) compared to the nontreated control (left).

in the case of abamectin, protect crop seedlings against nematode attack during the most critical time of plant development (Figure 2). This compares favorably to several kilograms a.i. per hectare with soil-applied nematicides. Perhaps most exciting, there are now opportunities for additional modules to support and extend the protection period, for example with foliar nematicide sprays that are taken up by the plant and transported downward to the roots, and/or with biological control agents that interfere with nematode reproduction.

Nematicides are typically uniformly applied throughout a field, although distribution and population density of plant parasitic nematodes are far from uniform. A population density map would allow concentration of nematicide applications only to those areas where nematodes are expected to be present in significant number or to adjust the rate according to the predicted population density. Obtaining this information from nematode enumeration of extracted soil samples is cost-prohibitive for even a very low resolution map. However, soil texture can be a relatively good predictor of potential nematode population densities as most plant parasitic nematodes prefer coarse-textured, sandy soils. Electrical conductivity of soil is strongly correlated to soil particle size and texture; it increases from sand to silt to clay. Global positioning system/Geographic information system guided soil electrical conductivity systems can quickly and inexpensively produce field maps that predict potential nematode population levels. Limited soil sampling is performed to confirm population density predictions. Nematicide application guided by georeferenced soil electrical conductivity maps provides a promising techology for site-specific, variable-rate treatment of plant parasitic nematode-infested fields. A consortium of researchers in the southeast US that developed this technology found reduction in nematicide use by 30–50% in large-scale tests whereas yields remained unchanged or increased (Mueller *et al.*, 2010).

Planting site-specific application of soil nematicides is another development that attempts to reduce application rates, cost, and nontarget effects while retaining effective protection

against plant parasitic nematodes. This idea goes back to a time when tree and vine planting sites were treated with fumigant injections from a hand-held device. But advances in global positioning technology make this formerly hazardous and time-consuming method safe, effective, and economically feasible. Key elements are real-time kinematic satellite navigation and virtual reference stations that provide real-time corrections, allowing the application of soil fumigants/nematicides with pinpoint precision and at an economically feasible cost.

Nematicidal compounds might affect a range of processes in nematodes that are highly specific and therefore less likely to interfere with nontargets. The discovery and development of novel nematicides typically involves a number of approaches to find molecules with significant activity against nematodes. Sources may include inhouse produced or externally purchased synthetic compounds, microbial or botanical metabolites, and patent- or literature-guided synthesis. Agrochemical companies formerly screened several thousand synthetic and natural compounds per year against particular target sets of plant pathogens and pests, including plant parasitic nematodes. With advances in molecular biology and bioinformatics, chemogenomic screening systems now analyze huge molecule libraries with use-specific efficacy information to identify new metabolic targets and biologically active compounds. For optimization of lead molecules in efficacy, specificity or persistence, computational approaches are utilized to find molecular similarities related to nematicidal activity. Bioinformatic-supported chemists rely on large molecule databases and utilize quantitative structure-activity relationship models. Structural chemical scaffolds, the essential parts of a molecule thought to posess nematicidal activity, are then manipulated by computer-aided modeling and design tools. High-throughput screening assays evaluate the new generation of compounds with the previous leads. It is expected that such development effort will result in novel compounds with high nematode-specific activity but low acute mammalian toxicity and overall better environmental compatibility than currently used nematicides.

Outlook

For the past 70 years, nematicides have been important plant protection tools that improved agricultural production by ensuring yield quantity and quality under high disease pressure from plant parasitic nematodes. This was especially true where traditional diversified farming gave way to large-scale production relying on narrow rotations or monoculture. In most developed countries, plant parasitic nematodes may be responsible for an average of 5% reduction in attainable crop yield, whereas it is at least 15–20% in many other countries. In subtropical and tropical areas, crop damage caused by root diseases is more common and severe as most plant parasitic nematodes and their associated secondary pathogens thrive in warmer climates. Nematode-caused problems are likely to increase in the future due to global climate change and economic production constraints. But the success of chemical nematode control has been questioned, as real and perceived problems have emerged related to environmental pollution, hazardous manufacturing risks, nontarget exposure to highly toxic chemistry, and poor product stewardship. Ironically, the attempts by growers, commodities, and third-party distributors to hold on to old nematicidal products is counterproductive to the replacement with safer and even more effective compounds. The relatively small market compared to other classes of pesticides and the generally high cost for developing pesticides has left nematicide R&D to a dwindling number of agrochemical companies. Although the scientific discovery process has continued to advance, new products need to justify the development cost that is currently estimated at approximately US$200 million. With an estimated US$1 billion in sales, nematicides make up only 2.5% of the worldwide pesticide market. This appears to be small in contrast to the annual damage by plant parasitic nematode that is estimated at approximately US$130 billion worldwide and US$11 billion for the US. An even more realistic estimate would consider crop damage caused by interactions between plant parasitic nematodes and other soilborne pathogens or by including reduced grower's returns due to adjusting to less susceptible but also less profitable rotation crops. With the development of economically effective and ecologically acceptable nematicides, their global market could easily double or triple. In the future, plant protection against plant parasitic nematodes will increasingly rely on a combination of integrated nematode management tactics that require long-term planning to implement multiple nematode population reduction strategies, including the use of nematicides.

See also: Plant Health Management: Soil Fumigation

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Plant Health Management: Fungicides and Antibiotics

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Glossary

Antibiotic Any of a large group of chemical substances, as penicillin and streptomycin, that are produced by various microorganisms and fungi, have the capacity in dilute solutions to inhibit the growth of or to destroy bacteria and other microorganisms, and are used in the treatment of infectious diseases.

Fungicides Resistance Action Committee (FRAC) An industry technical committee dedicated to the management of fungicide resistance.

Fungicide resistance The naturally occurring, inheritable adjustment in the ability of individuals in a population to survive a plant-protection product treatment that would normally give effective control.

Fungicides Fungicides are biocidal chemical compounds or biological organisms used to kill or inhibit fungi or fungal spores.

Plant pathology (phytopathology) The scientific study of plant diseases caused by pathogens (infectious organisms).

Introduction

It is a well-known and often-published fact that the world population is growing, especially in the less developed countries of the world. Statistics from the United Nations (UNFPA) predict the world population will grow from the current seven billion to more than nine billion by 2050, with clear consequences on the quantity of food that will need to be produced to avoid widespread hunger. Sixty years ago, farmers had to feed two people from every hectare. Their grandchildren now have to feed more than twice as many. In addition, the pressure on land continues to grow. Some new land will come into agricultural production in the coming years, but other areas will be lost to urbanization and erosion. Worldwide, there are now more people living in cities than in the countryside. Outdated farming practices, deforestation, and other man-made factors also continue to cause erosion.

In addition to the effects of this increase in the number of people, it is clear that diets are changing and will continue to do so. In Asia in particular, increasing wealth has led to a preference for more variety in the diet, and more meat and poultry are now being eaten. As a consequence of the lower energy efficiency of a meat-based diet compared with the direct consumption of grain (rice, wheat, maize, etc.), this dietary change will continue to drive further increases in the global demand for grain crops. Finally, the quite recent demand for biofuels, although today quite small with regard to the use of cereals, is predicted to grow and will also add to the global requirement for grain. Of course, the increasing demand for food has an impact much beyond grain crops, and demand will increase for all major crops including legumes, vegetables, and fruits.

All of the above is happening at a time when the world stocks of crop commodities are at their lowest levels for many years and, as a consequence, the world price level of many commodities such as rice and wheat have risen dramatically with very significant consequences in the affordability of food to many millions of people. Put together, it is clear that the world is leading toward an ever-greater scarcity of food, which has even been referred to as a world food crisis.

The available statistics all add up to a clear situation, with clear consequences for the future – the world needs to grow more food from the available land and with the available water in a sustainable manner. The area of agriculturally productive land is likely to stay stable at approximately 1.5 billion hectares; the population is likely to increase by approximately 80 million per year. Among the many threats to crop production on a worldwide basis is the damage to these crops caused by pests (including fungal pathogens, insects, and weeds). Crop losses due to such pests have been calculated to be substantial and crop-protection techniques and products have been developed to reduce these losses and make crop productivity as high as possible.

Economic Impact of Plant Diseases and the Need to Control Them

Plant diseases are known from times preceding the earliest writings. Fossil evidence indicates that plants were affected by disease 250 million years ago. The Bible and other early writings mention diseases, such as rusts, mildews, blights, and blast, that caused famine and drastic changes in the economy of nations since the dawn of recorded history. Other plant disease outbreaks with similar far-reaching effects in more recent times include late blight of potato in Ireland (1845–60); powdery and downy mildews of grape in France (1851 and 1878); coffee rust in Ceylon (starting in the 1870s); Fusarium wilts of cotton and flax; southern bacterial wilt of tobacco (early 1900s); Sigatoka leaf spot and Panama disease of banana in Central America (1900–65); black stem rust of wheat (1916, 1935, 1953–54); and southern corn leaf blight (1970) in the United States.

Estimates of actual losses in crop production worldwide have been published by Cramer (1967) and Oercke *et al.* (1994) and recently updated for major food and cash crops for the period 2001–03 (Oercke, 2006). Although weeds are overall the most important pest group in crop production worldwide, the incidence and impact of pathogens is also substantial (Table 1). The actual losses shown in this table comprise the crop losses sustained despite the crop

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Table 1 Estimated loss potential from pathogens and actual losses in six major crops worldwide in 2001–03

Crop	*Attainable production (Mt)*	*Crop losses (%)*[a] *due to*			
		Pathogens		*Total crop pests*	
		Potential	*Actual*	*Potential*	*Actual*
Wheat	785	15.6 (12–20)	10.2 (5–14)	49.8 (44–54)	28.2 (14–40)
Rice	933	13.5 (10–15)	10.8 (7–16)	77.0 (64–80)	37.4 (22–51)
Maize	891	9.4 (8–13)	8.5 (4–14)	68.5 (58–75)	31.2 (18–58)
Potatoes	518	21.2 (20–23)	14.5 (7–24)	74.9 (73–80)	40.3 (24–59)
Soybeans	245	11.0 (7–16)	8.9 (3–16)	60.0 (49–69)	26.3 (11–49)
Cotton	79[b]	8.5 (7–10)	7.2 (5–13)	82.0 (76–85)	28.8 (12–48)

[a]Figures in parentheses indicate variation among 19 regions.

[b]Seed cotton.

Source: Reproduced from Oercke, E.-C., 2006. Crop losses to pests. Journal of Agricultural Science 144, 31–43.

protection practices employed. Absolute losses vary among crops depending on their ability to compensate for the effects of pathogen attack, and tend to be higher under conditions of high productivity and where climatic conditions are favorable to the pathogen.

Oercke *et al.* (1994) estimated losses due to plant diseases in the four major crops (rice, wheat, potato, and maize) to be 10–16% of potential production which translated into approximately US$64 billion in the years 1988–90. The losses increased to US$84 billion when the top eight crops were included. This is not including the recent uprising of Asian rust of soybean, where losses are reported to be up to 80%, and the projected losses in the main growing regions of Brazil are 2.2 million tons (US$487.3 million at 2004 crop prices) (Yorinori *et al.*, 2005). Since these figures were published, the prices of agricultural commodities have increased significantly (in some crops such as soybeans and wheat they have doubled) and, therefore, the financial impact of crop losses due to diseases in 2011 was considerably greater. In addition to yield losses caused by diseases, also to be considered are postharvest quality losses and the possible accumulation of toxins during and after the cropping season. Although food security is a critical issue in the developing world, food safety has become a dominant concern in the developed world; however, the critical importance of food safety is now recognized, at last, in the developing world as well (e.g., Wild and Gong, 2010).

In the case of potato late blight caused by *Phytophthora infestans*, crop losses can be complete. Indeed, potato late blight was famously the cause of the Irish potato famine, a period of mass starvation, disease, and emigration between 1845 and 1852. During the famine, approximately one million people died and a million more emigrated from Ireland. Use of crop protection measures, which include chemical fungicides, obviously has not completely prevented crop losses, but they have significantly contributed to productivity and quality of produce worldwide. In many regions, crop protection measures have enabled farmers to increase crop productivity considerably without losing an uneconomically unacceptable proportion of the crop to pests. Crop yields would be approximately half their current levels if no crop protection measures were implemented. However, even with crop protection, approximately a third of crop yields are still lost to weeds, diseases, and insects. These data show that there are still significant advances in crop protection practices, including chemical disease control, which need to be made in order to maximize worldwide crop production and avoid unnecessary losses. Crop yields will probably have to increase by approximately 50% on a global level by 2030 to ensure food security. This implies a higher annual rate of yield gain than has been achieved in the major grain crops in recent years and has led to calls for a 'second green revolution.'

A benefits study carried out for USA agriculture in 2005 quantified the economic impact of the use of fungicides to US crop production (Gianessi and Reigner, 2005). This study covered 50 crops and concluded that, for the 231 diseases considered, fungicides are the primary means of defense from fungi. As a result of fungicide application, yields of most fruit and vegetable crops in the USA are increased by 50–95%. Growers gain US$12.8 billion (44 000 metric tons of crop yield at 2005 crop commodity prices) in increased production value from the control of plant diseases caused by fungi. The yield gains attributable to the use of fungicides range from 20% to 100%, with the greatest gains tending to be achieved in fruit and vegetable crops. Furthermore, the authors conclude that the benefit of fungicide use in US agriculture is a significant increase in the production of fruit and vegetables, which are so important for the healthy diets of Americans. They even went as far as stating that because fungicides are so important in United States food production, it is worth asking whether there should be policies adopted to assure that American growers have the fungicides that they need for the foreseeable future.

In Europe, the economic impact of plant diseases has recently become a more important consideration for several reasons. These include the general food security and safety issues already described, plus assessments of the impact of the withdrawal from sale of various fungicides alongside other plant-protection products due to new legislation in Europe. The potential impact of a reduction in availability of fungicides on the market in Europe would include the possibility that growers are unable to control some diseases in crops due to the unavailability of effective solutions. In addition, there could be a longer term effect on the sustainability of the remaining fungicides due to an increased likelihood of resistance issues. Such an impact assessment has been carried out for the wheat crop in Europe (NOMISMA, 2012). The

conclusions of this study are that, with no fungicides available at all, yield losses in European countries range from 7% in Denmark to 25% in France. For durum wheat grown in Italy, this yield loss is estimated at 28%. If no triazole fungicides were available due to the European legislation, the immediate impact on conventional wheat yields is calculated to be 5–9% with a longer term impact of 10–15% yield loss due to resistance arising to other classes of fungicides due to a reduction of numbers of modes of action. It can clearly be understood from these examples that the global economic impact of plant diseases is very high and, therefore, the use of interventional measures such as fungicides to prevent losses in quantity and quality is essential. Comprehensive, up-to-date yield and economic loss data due to plant pathogens are surprisingly few and difficult to find; in these times of increased concerns over food security and safety, there is a need to evaluate these losses more carefully in order to help the setting of priorities in research and development (R&D), and in actions at field level (Savary *et al.*, 2012).

The Control of Plant Pathogens

To protect crops from diseases, there are several crop production and protection options. Conventional and organic farming use good agronomic practices to reduce the incidence of damaging diseases, for example, the choice of crop cultivars resistant or tolerant to diseases, crop rotations to minimize the carryover of pathogens, soil cultivations to bury infested crop residues, among others. Organic crop production relies largely on these practices alone and, although sustainable, yields in organic crop production are in general significantly lower than under conventional management. However, these yield differences vary between crops and, to a certain extent, also between countries and regions analyzed. Cereal yields in organic production are typically 60–70% of those under conventional management although vegetable yields are often just as high as under conventional management (Offermann and Nieberg, 2000). Few data are available on pasture and grassland yields in organic farming; reported values lie in the range of 70–100% of conventional yields, depending on the intensity of use. Taking organic cereal yields at 60% of conventional systems, this equates to a requirement of 67% more area to produce the same yield. When faced with a growing world population, the need to feed them, and growing urbanization, this land is unlikely to be available. On the contrary, an increase in intensity of crop production is most likely to be required.

Resistance or tolerance to crop diseases through natural traits or genetically modified crops (GMO) is an area under intensive scientific study. Plant breeding for disease tolerance, using classical or marker-assisted selection approaches, is a very important tool in disease management programs and the use of varieties of plants resistant to particular diseases has proved to be very effective, for example, stem rust of wheat, rust of dry bean, and *Rhizoctonia* root rot of sugar beet. It must be realized, however, that the product development time for successful new varieties is similar to that of a new chemical and, in cereals, advances take 12 years to bring benefits to the market (AEBC, 2005). The introduction of genetically modified (GM) crops has, however, been difficult in several other areas of the world (especially Europe) because of consumer and environmental concerns. Examples of tolerance to important crop pathogens achieved by GM have been few, however, and, to the author's current knowledge, except for control of papaya ring spot virus of papaya in Hawaii and watermelon mosaic virus of cucurbits in the eastern USA, none have been commercially introduced. Whether disease tolerance is brought about by naturally occurring traits or genetic modification, there is always the doubt about the durability of the disease resistance – plant pathogens have an established history of being able to overcome the host resistance of plants. It is probable that even if disease tolerance becomes successfully implemented in major economic crops such as cereals, potatoes, or soybeans, these traits will themselves require protection through the integrated approach of using chemical fungicides in programs to manage the diseases and avoid the tolerance breaking down.

Biological control methods have been proven to be very effective in certain situations, most notably in the control of several insect pests with natural predators, or with 'biopesticides' such as *Bacillus thuringiensis*. Biological control approaches do exist against plant pathogens, based on organisms such as *Coniotherium minitans*, *Bacillus subtilis*, and others, and under the right conditions can be very successful. Biological control of plant diseases in major agricultural crops has, so far, only met with limited success; such disease control agents are covered in another article in this encyclopedia.

The control of crop diseases with chemical fungicides has had a successful history for more than a century. They are integral to the production of crops in many countries of the world, resulting in increased yields and farmer income. Economic benefit studies show conclusively that, without fungicides for control of plant pathogens, production of some crops would be impossible in parts of the world (Gianessi and Reigner, 2005; Cook and Jenkins, 1988; Cuthbertson and Murchie, 2003). Fungicides have been responsible for ensuring the production of many crops over many years, such as protection of the potato crop against late blight as already mentioned or security of banana production in Central America. Cooke (1992) wrote that 'without the use of fungicides, large scale commercial potato production in Ireland would be impossible.'

Modern fungicides can be applied to crops using a range of technologies depending on the characteristics of the chemical and also according to the most effective way to target the disease in question. The majority of fungicide use today is applied using conventional spraying techniques to the foliage of plants. This technology has the advantage of being practical and convenient (growers have on-farm spray equipment that can be used for a wide range of crop protection products including herbicides and insecticides), as well as being a very good way to target predominantly foliar diseases with a range of fungicides that may have contact or systemic activity. There may, however, be some limitation of this technology, for example, in the requirement for quite high water volumes to ensure distribution of some fungicides, or the potential for spray drift; and it may not be the most appropriate time in the life cycle of the pathogen to target.

Application of a fungicide to soil has proved to be very effective for some soilborne pathogens. Examples of such use include soil applications of phenylamide fungicides such as mefenoxam to control *Pythium* spp. and soilborne *Phytophthora* spp. as well as the control of *Rhizoctonia* spp. by strobilurin and other fungicides. Further targeted application can be achieved through treatment of seeds with fungicides, a technology also used for insecticides. Seed treatment is clearly the most targeted application for fungicides against seedborne diseases such as bunts, smuts, leaf stripe of barley, seedling damping-off diseases, *Fusarium* spp., and many others. It is also a highly valuable technology for the control of pathogens that infect the crop systemically, either from a seedborne inoculum or from soilborne infections. Examples of such diseases include downy mildews of corn and peas (*Peronosclerospora* spp. and *Perenospora viciae*), against which conventional foliar sprays are much less effective than a targeted seed treatment. Seed treatment can also be effective against other soilborne pathogens, such as *Pythium* spp., *Rhizoctonia* spp., and *Fusarium* spp. Soil or seed treatment application are particularly effective delivery technologies for fungicides that are systemic in nature and thus have the ability to move into the plant and protect actively growing areas of stems, leaves, and roots. Owing to the long duration of disease control that can be conferred by such treatment methods, they are considered to be risky in terms of resistance management of foliar diseases. For this reason, soil and seed treatment applications of fungicides against foliar diseases have been discouraged by the Fungicide Resistance Action Committee (FRAC, www.frac.info).

Plant pathogenic bacteria cause many serious diseases of plants throughout the world (Vidhyasekaran, 2002), but fewer than fungi or viruses, and they cause relatively less damage and economic cost (Kennedy and Alcorn, 1980). The most important diseases caused by bacteria in plants include fire blight (*Erwinia amylovora*), bacterial blights in a range of vegetable crops caused by *Pseudomonas* spp. and *Xanthomonas* spp., bacterial leaf blight in rice caused by *Xanthomonas oryzicola*, and a range of bacterial soft rots and cankers. Many of these diseases can be devastating when environmental conditions are favorable, for example, fire blight, which can destroy whole production orchards of apple and pear trees. Many plants, both economic and wild, have innate immunity or resistance to many pathogens and the first line of control of plant pathogenic bacteria is through host-plant resistance. In addition, seed certification schemes are essential in some crops such as potatoes to control, for example, blackleg. Good agricultural practice, cultivations, and crop rotation are essential tools to minimize the effects of bacteria in commercial crops. However, these measures do not result in complete success and it is a fact that bacterial diseases in crops are difficult to control. Chemical control measures are few and tend to have only a moderate level of success – key products include copper and antibiotics. Some success has been achieved with the use of biological control agents. Some success has also been achieved with the resistance-inducing compounds such as acibenzolar-*S*-methyl, which are able to activate the plant's natural defense mechanisms including those against fungal and bacterial plant pathogens.

Challenges for Developing Chemical Agents for Plant Disease Control

According to industry studies (McDougall, 2010), a new crop protection product takes approximately 10 years and approximately US$250 million to be developed (from discovery to first sales). On average approximately 25%, and as much as 40%, of this cost is invested in researching toxicological risks, environmental fate, and impacts. The achievement of identifying a new active ingredient is only the start of the R&D process. For every active ingredient tested in early laboratory screening, only one in tens or hundreds of thousands actually makes it to the market. This is because there are a number of different obstacles that need to be overcome before a crop protection product is ready to go to market. According to market analysis, on average, the 15 leading crop protection companies spend approximately 7.5% of sales on R&D, amounting to a R&D expenditure in 2011 of more than US$6 billion (agrochemical and crops/traits combined – agrochemical investment was US$2.6 billion in 2011) (McDougall, 2012). This ratio places the plant science industry among the most R&D-intensive business sectors.

Fungicides, as is the case for all crop protection chemicals, must be targeted to meet the needs of farmers and growers, to solve the problems that regularly limit the productivity (yields) and quality of produce. They must answer these 'biological crop needs' and, at the same time, must be cost-effective to make their use worthwhile. At the same time, the target markets need to be viable to the company inventing and producing the products to justify the large investment of money and resources required to fully develop the products, bring them to the market, and support them in the market place. In addition to these requirements, products must meet modern-day requirements for human and environmental safety, and be compatible with other crop protection practices, avoiding undesired effects on, for example, beneficial organisms. Fungicide markets change and so do the market potential of crop/disease combinations. For example, while the worldwide market for the control of powdery mildews has traditionally been targeted by most agrochemical companies for new products, it has become apparent that, on its own, this market has become critical in terms of a cost–benefit ratio for industry. In other words, the high level of investment required to bring a new, powdery mildew-specific fungicide to the market is becoming difficult to justify against the rather crowded and limited market. Indeed, there are very few 'single disease,' targets that are financially viable for the development of a new chemical fungicide. Exceptions to this may be Septoria leaf blotch (*Mycosphaerella graminicola*) in Europe, and Asian Soybean Rust (ASR) (*Phakopsora pachyrhizii*) in Latin America. Increasingly, however, a broad-spectrum fungicide that is used to control a wide range of plant diseases across crops and regions is required to pass the economic hurdles of R&D.

Changes in the biology of plant diseases also have an impact on disease control and therefore on the targeting strategies of fungicide discovery in the R&D companies. Resistance of plant pathogens to fungicides is an important factor leading to the constant search for fungicides with new modes of action that are, on the one hand, not cross-resistant with other

fungicides on the market that may have problems with resistance, and ideally themselves having a novel mode of action that is of low risk of resistance arising. These two requirements are particularly challenging – it is difficult to invent a completely new mode of action by design with no scientific lead at all (which is why fungicide researchers look to other, existing fungicides in crop protection as well as human medicine for inspiration). At the same time, the prediction of the risk of resistance arising to the new mode of action is a great challenge requiring intensive studies and knowledge in each case. Ideally, the fungicide would have multiple modes of action to confer a low resistance risk, but these so-called multisite fungicides can have their own difficulties in passing registration hurdles due to the generally nonspecific modes of action involved. However, it is possible to discover such fungicides, as shown by the success of chlorothalonil and mancozeb. New needs and opportunities can also open up for the control of plant diseases such as the spread of ASR in soybeans in Latin America (a fungicide market estimated at more than US$1 billion), which is today an important target for new fungicides. Forecasting these biology and market changes is particularly difficult and challenging, considering the long timelines required to bring a new fungicide product to market and, therefore, is another factor in the complexity of new product invention and development.

Therefore, it will be realized that the search for the 'ideal' fungicide is complex and difficult. This is because there is a wide combination of properties of the fungicide that need to be considered and met. These include:

Biologically efficient:
- high selectivity (on target),
- fast impact (action),
- optimal residual effect,
- good plant tolerance, and
- low risk of resistance development.

User friendly:
- low acute toxicity,
- low chronic toxicity,
- good formulation characteristics,
- safe packaging,
- easy application method, and
- long storage stability.

Environmentally sound:
- low toxicity for nontarget organisms,
- fast degradation in the environment,
- low mobility in soil,
- no relevant residues in food and fodder, and
- low application rate.

Economically viable:
- good cost/profit ratio for the farmer,
- broad use,
- applicability in Integrated Crop and Pest Management,
- innovative product characteristics,
- competitive, and
- Patentable.

To meet all these needs and successfully bring a new active substance to the market is a real challenge to industry. To achieve a high level of potency (activity) against a target pathogen while having minimal or no effect on the crop, on beneficial organisms, and on humans and other mammals is extremely difficult. There has been a large effort by academia and industry in recent years to use target-site modeling in order to produce 'designer molecules' to selectively inhibit fungi at specific target sites and in that way find new modes of action for products although avoiding target sites known to be problematic in terms of mammalian toxicology. However, this has proved to be extremely difficult in practice and there have been, to the author's knowledge, no product successfully discovered and developed using these techniques. It also appears that the trend that started a number of years ago of the so-called 'high throughput screening' and combinatorial chemistry, where a huge number of randomly selected chemicals are screened for biological activity against a number of key target diseases, has proved no more successful than other approaches. The concept is that, according to the laws of averages, the greater the number of chemicals that are screened, the greater the chance of finding interesting biological activity that can then be further optimized. This approach, however, has proved to be somewhat too untargeted and has been largely abandoned.

The current approach in industry is still very much around optimization in known chemical classes and modes of action, although at the same time much research goes into the area of discovering new classes of fungicidally active chemistry and, hopefully, new modes of action. All companies have their own key 'search targets,' that is a clearly defined research strategy defining what they want a new product to look like, what its characteristics should be, and, therefore, what the market potential will be. These search targets include elements such as a completely new mode of action against the key diseases, and may be also multiple sites of action (multisite) or at least a very low risk of resistance. These requirements are easy to define and state – but success in discovering such solutions remains a real challenge. As a consequence, it is a fact that many of the novel fungicides brought to the market recently, as well as several due to be introduced to the market over the next few years, are site-specific fungicides, acting against the pathogens at a single binding site in a biochemical pathway. From a product safety point of view, this tends to be a good thing, especially if the target pathway is one that does not exist in mammals. However, from the consideration of resistance risk, and consequently the long-term sustainability of the product in the market, this might not be so favorable, depending on the nature of the mode of action, the pathogen and the consequences to the pathogen of the genetic changes needed to adapt to the fungicide.

History of Fungicides

The first chemical means for controlling plant disease in a practical way was discovered by B. Prévost in 1807. Bunts and smuts of cereals had been a key limitation to cereal cultivation for centuries, appearing unexpectedly on healthy-looking plants that should have been producing grain. Prévost was the first to observe that spores, which grew into tiny germinating 'plants,' caused wheat bunt. He then made the discovery that a weak copper solution (generated when he held the spore

suspension in a copper vessel) prevented their growth. Through experimentation, he showed that farmers could control bunt by wetting wheat kernels with a copper sulfate solution. Copper-based seed treatments remained popular in some countries, including France, through the end of the twentieth century. It was in the latter half of the nineteenth century that chemical disease control really started to develop. Sulfur had long been known to have therapeutic properties. In 1824, a recommendation was made for it to be used to control powdery mildew of peaches (Robertson, 1824), and, in 1848, sulfur dust was recommended for control of vine powdery mildew (*Uncinula necator*) and other powdery mildews. Lime sulfur, prepared by boiling lime and sulfur together, seems to have been first mentioned in 1833 by Kenrick as a means of controlling vine powdery mildew. Copper sulfate was tried as a foliar spray for various diseases but was found to be phytotoxic on some crops. Sometime before 1862, lime was added to the copper sulfate to reduce its damaging properties, initially to reduce damage to wheat seed. Lime sulfur did not control downy mildew of vines (*Plasmopara viticola*), but, in 1882, Millardet noticed that, where a liquid made from lime and copper sulfate had been applied to vines near roadways in order to discourage thieves from stealing the grapes, there was far less downy mildew. One of the best known fungicides, Bordeaux mixture, was thus announced in 1885. Fungicidal preparations based on the active ingredients of sulfur, lime, and copper sulfate dominated chemical disease control into the early twentieth century.

The major products used from 1940 up to the present day are listed in **Table 2**. Early chemical disease control was largely aimed at horticultural crops (fruits and vegetables) as well as seed treatments. Concerns for the products' impact on the environment were largely nonexistent, as were concerns for the applicator. Most users prepared their own fungicides from basic recipes. Proprietary products were available at this time for those who did not want to take the time and trouble to make their own. Before the introduction of the dithiocarbamates, the testing of which was described by McCallan of Cornell University in 1930, most of the products used as fungicides were applied at high rates, for example, 10–20 kg a.i./ha for sulfur against powdery mildew on grapes. The products did not always give good control, could be phytotoxic, and had to be applied frequently. The current use rates of well below 100 g ha^{-a} for many triazole fungicides against the same pathogens that these high-rate older fungicides were used against is a 200-fold reduction. From 1940 to 1970, there were a number of new chemistry classes introduced as fungicides. Among these, the dithiocarbamates, the phthalimides, and the benzimidazoles represented major innovations and improvements over the previously used inorganic fungicides, being significantly more effective at lower use rates and less phytotoxic. The lower use-rates of these fungicides made them easier for the grower to use and gain successful disease control. The decade from 1960 to 1970 saw a rapid expansion of R&D together with a rapid growth of the fungicide markets. In this decade, the most widely used protectant fungicides, mancozeb and chlorothalonil, were introduced. The decade also gave us the first broad-spectrum foliar systemic, thiabendazole, and the systemic seed treatment carboxin.

From 1970 to 1980, the rate of innovation in the fungicide industry continued to increase with approximately 30 new fungicides being introduced. Agriculture was booming in Western Europe and the Americas at this time, government-funded research into crop protection was increasing, the importance of crop diseases and their control was increasingly understood, and, as a consequence, industry stepped up their invention processes to discover totally new chemical classes and modes of action. Key introductions to the market during this time included carbendazim, the first major triazole fungicides (triadimefon and propiconazole), key novel

Table 2 Key fungicide introductions from 1940 to the present day

Year	*Fungicides*	*Number*
1940–60	Thiram, zineb, nabam, biphenyl, oxine copper, tecnazene, captan, folpet, fentin acetate, fentin hydroxide, anilazine, blasticidin S, maneb, dodine, dicloran	13
1961–70	Mancozeb, captafol, dithianon, propineb, thiabendazole, chlorothalonil, dichlofluanid, dodemorph, kasugamycin, polyoxins, pyrazophos, ditalimfos, carboxin, oxycarboxin, drazoxolon, tolyfluanide, difenphos, benomyl, fuberidazole, guazatine, dimethirimol, ethirimol, triforine, tridemorph	24
1971–80	Iprobenfos, thiophanate, thiophanate-methyl, validamycin, benodanil, triadimefon, imazalil, iprodione, bupirimate, fenarimol, nuarimol, buthiobate, vinclozolin, carbendazim, procymidone, cymoxanil, fosetyl-Al, metalaxyl, furalaxyl, triadimenol, prochloraz, ofurace, propamocarb, bitertanol, diclobutrazol, etaconazole, propiconazole, tolclofos-methy, fenpropimorph	29
1981–2000	Benalaxyl, flutolanil, mepronil, pencycuron, cyprofuram, triflumizole, flutriafol, penconazole, flusilazole, diniconazole, oxadixyl, fenpropidin, hexaconazole, cyproconazole, myclobutanil, tebuconazole, pyrifenox, difenoconazole, tetraconazole, fenbuconazole, dimethomorph, fenpiclonil, fludioxonil, epoxiconazole, bromuconazole, pyrimethanil, metconazole, fluquinconazole, triticonazole, fluazinam, azoxystrobin, kresoxim-methyl, metaminostrobin, cyprodinil, mepanipyrim, famoxadone, mefenoxam, quinoxyfen, fenhexamid, fenamidone, trifloxystrobin, cyazofamid, acibenzolar-*S*-methyl	42
2001–Present	Picoxystrobin, pyraclostrobin, dimoxystrobin, prothioconazole, ethaboxam, zoxamide, fluopicolide, flumorph, fluoxastrobin, benthiavalicarb, iprovalicarb, mandipropamid, boscalid, silthiofam, meptyldinocap, amisulbrom, orysastrobin, metrafenone, ipconazole, isotianil, proquinazid, ametoctradin, sedaxane, penflufen, isopyrazam, penthiopyrad, bixafen, fluopyram, fluxapyroxad	29 plus other pipeline products

Source: Reproduced and updated from Russell, P.E., 2005. A century of fungicide evolution. Journal of Agricultural Science 143, 11–25.

fungicides for the control of downy mildews and late blight such as metalaxyl and cymoxanil, and the amine fungicide fenpropimorph.

In the following 20-year period from 1980 to 2000, agricultural markets continued to increase at first, but, in time, overproduction of crops such as cereals resulted in a slowing down of the agrochemical market, especially in Western Europe (where a large proportion of the fungicide sales were made). At the same time, new legislation was introduced concerning the requirements to bring new crop-protection products to the market, notably in the USA (Environmental Protection Agency (EPA)), and Europe (introduction of European Directive 91/414). At this time, experts forecasted a dramatic decrease in the numbers of innovative new products that would be brought to the market as a consequence of the new legislations and the concomitant increase in the costs of bringing new products to the markets. Indeed, for a number of years the rate of introduction of new products slowed dramatically because of delays by regulatory authorities in implementing the new rules and the sheer increases in workloads caused. During this period, there were fewer new active substances registered, but innovation continued with an increasing number of different fungicide mixtures, innovative formulation types, and novel packaging solutions to enable manufacturer to continue to differentiate and bring new ideas to the markets. Over time, in fact the investments made by agrochemical companies continued to increase. As a consequence, more than 40 new fungicides were discovered and introduced successfully to the market during that period. These innovations included the next generation of significant new triazoles, including epoxiconazole, and cyproconazole, difenoconazole, as well as completely novel chemistry with new modes of action such as fludioxonil, pyrimethanil, cyprodinil, acibenzolar-S-methyl (ASM), and the groundbreaking new strobilurin fungicides, namely, azoxystrobin and kresoxim-methyl. The triazole and strobilurin fungicides formed the basis for today's continued successes in these chemistries, which consist of a great proportion of fungicide sales around the world.

From the year 2000 up to the present day, industry has continued to invest and has been successful in the discovery of new fungicides. Since the year 2000, many major new introductions have been made to the market, including 'new generation' triazoles and strobilurins, and further chemistries with new modes of action such as metrafenone, mandipropamid, proquinazid, and boscalid. This continued rate of new product introductions by R&D-oriented agrochemical companies is a demonstration of the continued commitment to agriculture by the chemical industry, which has resulted in increasing investment by companies into the future, despite rising costs and the threats of declining markets and generic competition. This contrasts strongly with the pharmaceutical industry where, despite increasing R&D expenditure, the rate of innovation has fallen dramatically.

Overview of the Main Classes and Uses of Modern Fungicides

As discussed in the Section History of Fungicides, many fungicides have been invented and commercialized over the past 50 years with varying levels of success. It is not possible to fully cover each of these fungicide classes and fungicides in this article, only to give a summary overview of those which are of the greatest commercial importance globally at the present date. Comprehensive publications are available that cover these and many more fungicides in more depth, for example, Lyr (1995) and (Krämer *et al.*, 2012). Market statistics for 2011 (McDougall, 2012) given in **Table 3** show that the most important fungicide classes by sales value today are the triazoles and strobilurins, followed by mancozeb and the succinate dehydrogenase inhibitor (SDHI) fungicides. The multisite fungicides chlorothalonil, copper, and mancozeb, and the highly systemic and active benzimidazole and phenylamide fungicides also have significant sales of US$300–600 million. These numbers show the worldwide success of triazoles and strobilurins, which is due to their broad-spectrum nature of disease control and their high levels of efficacy and yield/quality protection. It is equally clear, however, that the fungicide market is dominated in site-specific modes of action by only three, which has an implication in terms of fungicide resistance (see Section Fungicide Resistance and its Management). In addition, it is apparent that the older multisite fungicides have a particular value, largely as tools for use in resistance management mixtures and programs to protect the newer site-specific fungicides. Of course, these multisite fungicides are also important as standalone fungicides in their own right, but usually have limitations in terms of flexibility of application, timing in the disease epidemic (most effective when used completely protectively at the early stages of pathogen attend and not curatively), and, unlike the more systemic modern fungicides, are not able to protect new crop growth. In the 2011 market, the class of SDHIs is mainly represented by the seed treatment carboxin, and also Boscalid, which has significant sales mainly into fruit and

Table 3 Reported sales of fungicides in the year 2011 by chemical class/mode of action

Chemical class	*Worldwide sales 2011 (US$×1000)*[a]
Demethylation-inhibitors (DMI) (triazoles)	3 273
Quinone outside inhibitors (QoI) (strobilurins and others)	3 261
Mancozeb	620
SDHI	581
Copper fungicides	485
Benzimidazoles	452
Phenylamides	405
Other multisites	311
Chlorothalonil	310
Amines	264
Carboxylic acid amides	250
Anilinopyrimidines	245
Dicarboxamides	175
Other fungicides	2 673
Total	13 305

[a]Calculated values based on data from AMIS., 2012. Crop Protection and Seeds Database. Midlothian, UK: AMIS and Phillips McDougall (2012) (www.Phillipsmcdougall.com).

Abbreviation: SDHI, succinate dehydrogenase inhibitor.

vegetable crops for the control of powdery mildews and *Botrytis* but also to an extent into cereals. With the present-day high level of industry innovation and investment into this class of fungicides, it can be expected that over the next 5–10 years, the SDHIs will be at least as significant as the strobilurins in global sales.

Benzimidazoles

The benzimidazole fungicides were introduced in the late 1960s for plant disease control and were very quickly accepted throughout the world. This was due to their unique properties that included high potency at low use rates, very good crop safety, and their ability to protect new growth of the crop due to their systemic activity. Benomyl was the first of the class to be introduced, soon to be followed by carbendazim, thiophanate-methyl, thiabendazole (mainly used in fruit postharvest treatment) and fuberidazole (primarily used for seed treatment). The benzimidazoles are notable for their broad-spectrum activity against a very wide range of diseases, including most ascomycetes, and some basidiomycetes and deuteromycetes. Key economic pathogens controlled include *Botrytis cinerea*, *Cercospora* spp., *Colletochrichum* spp., *Fusarium* spp., powdery mildews in several crops, including *Erysiphe* spp. and *Oidium* spp., and eyespot in cereals. Benzimidazoles are potent inhibitors of β-tubulin polymerization in many species of fungi. Although direct interactions with β-tubulin seem to be the predominant inhibitory processes for this chemical class, interactions with other forms of tubulin as well as differential interactions with tubulin in the free and polymerized states also have been reported. This single-site mode of action was unfortunately soon discovered to be highly prone to resistance problems and, as described earlier in this article, benzimidazole resistance represented the beginning of serious fungicide resistance problems in the agricultural industry. Because of their very success in terms of excellent disease control, these fungicides were used by growers frequently and, in many cases, exclusively – under these conditions, resistance developed rapidly within two to four seasons. However, where mixtures of benomyl and other unrelated fungicides were used from the beginning, resistance was delayed for several seasons (Delp, 1980). In this way, this class of fungicides became a model for the basis of resistance management principles that are still followed today. Although the market potential of the benzimidazoles has been limited by the resistance problems, they are still used in some markets today. Benzimidazoles are classified by FRAC as high-risk fungicides according to their resistance risk classification scheme.

Sterol Biosynthesis Inhibitors

There are four classes of fungicides that comprise the sterol biosynthesis inhibitors (SBIs). Only three of these classes are used as agricultural fungicides: demethylation-inhibitors (DMI) fungicides, amines (formerly called 'Morpholine' fungicides), and hydroxyanilides. All three classes inhibit targets within fungal sterol biosynthesis but differ in regard to the precise target sites they inhibit. SBI fungicides that inhibit the C_{14} demethylation step within fungal sterol biosynthesis are known as DMIs). Besides the triazoles, numerous imidazoles, pyridines, and pyrimidine all have been shown to act as DMIs. The most important members of the SBI fungicide group are described here.

Triazoles

Triazoles are the largest class of fungicides used in plant-protection, both in terms of number of fungicides developed and launched but also in sales in the current market (Table 3). They are members of the DMI class and are generally characterized by their broad spectrum of activity against a range of economically important pathogens on arable crops, top fruit, vines, plantation crops, etc. Fluotrimazole, first presented in literature in 1973, was the first triazoles fungicide to be marketed. This fungicide was narrow in its spectrum of disease control, being limited to powdery mildew, and was very quickly superseded by the first broad-spectrum triazole fungicides such as triadimefon. Triadimefon was launched soon after fluotrimazole in 1973. This was followed closely by triadimenol (more active than its precursor fungicide, triadimenol) in 1977, bitertenol (1978), and propiconazole (1979). Since the introduction of these highly successful fungicides, numerous other triazoles have been launched for a wide variety of plant diseases across crops as well as for foliar, seed treatment, and postharvest uses, and have been equally successful. Despite the success of the early wave of triazole fungicides, and the high number of this class of fungicides being introduced in the 1980s, innovation in the chemistry continued and more modern more potent triazoles have been commercialized more recently – examples are epoxiconazole (1992) and prothioconazole (2004). One reason for the longevity of this class of fungicides is that, although being highly efficient broad-spectrum products, resistance has only occurred over time as a slow shift resulting in a decreased sensitivity to their mode of action rather than a clear and sharp loss of field performance. Although these sensitivity shifts have resulted in some of the less potent triazoles being ineffective in some disease/crop combinations, the intrinsically more active triazoles push the sensitivity curves back to their original ED_{50} values and remain effective. Sales figures for 2011 show the 'top 10 ranking' for triazoles to be prothioconazole, epoxiconazole, tebuconazole, cyproconazole, propiconazole, difenoconazole, metconazole, myclobutanil, flutriafol, and flusilazole. FRAC classify the DMI fungicides as medium resistance risk.

Other DMI Fungicides

Imidazoles include only a small number of compounds that are active against plant pathogens. Imazalil was the first imidazole fungicide for agricultural uses and is mainly used today as a seed treatment in cereals, but it is also used as a foliar treatment in vegetables and ornamentals and as a postharvest treatment in citrus fruits. Prochloraz is a broad-spectrum fungicide with activity against ascomycetes and *fungi imperfecti*, plus lower activity against basidiomycetes. Prochloraz has been widely used in European cereals, particularly for its activity against eyespot (*Oculimacula* spp.) and also for its activity against key foliar diseases in cereals such as net blotch

and *Septoria* spp. Other members of this class are fenapinil (now discontinued) and trifumizole, used mainly in fruits and vegetables against a wide range of pathogens such as powdery mildew, scab, and *Monilinia* spp. but also as a cereal seed treatment against smuts and bunts.

Piperazines, Pyridines, and Pyrimidines

The only fungicide from the piperazines used in agriculture is triforine, which was used primarily as a foliar treatment against powdery mildew, scab, and other diseases in fruits and other horticultural crops and also extensively as a home and garden product (especially on roses). It has also been used as a seed treatment in barley for powdery mildew control. The pyridines are represented by buthiobate and pyrifenox, both used primarily for powdery mildew control in fruits and vegetables; pyrifenox has a greater spectrum of disease control and is also effective against various leaf spots in fruits, vegetables, and peanuts. Both are today commercially small-market fungicides. Two pyrimidine fungicides were developed and marketed: fenarimol and nuarimol. Fenarimol was developed for use in fruits and vegetables (powdery mildew, scab, rust, and leaf spots), whereas nuarimol was developed mainly for use against cereal diseases as a seed treatment to control seedborne pathogens and airborne powdery mildew, and also as a foliar treatment against powdery mildew and *Rhynchosporium secalis*.

Amines

Similarly to the DMIs, the amines also consist of different chemical classes. The first representatives of this group were chemically morpholines. Although representatives of two other chemical groups (piperidines and spiroketalamines) have entered the market, the group is still (incorrectly) commonly termed the morpholines. Amines inhibit to a variable degree two target sites within the sterol biosynthetic pathway, the Δ^8–Δ^7 isomerase and the C^{14} reductase.

Amines have a narrower spectrum of activity than the DMIs and are best known for their excellent control of powdery mildew and rust in cereals, powdery mildew on vegetables and grapes, and black sigatoka of banana. During the 1980s, fenpropidin and fenpropimorph were key fungicides in the European cereal market, whereas tridemorph was used extensively for the control of black sigatoka. This class of chemistry, although having seen some moderate shifts in sensitivity by some pathogens in the past (e.g., sigatoka in Central and South America, powdery mildew in cereals in Western Europe), remains effective and is still extremely valuable in crop protection today, including those uses where historical shifts occurred. Indeed, owing to resistance problems of cereal powdery mildews toward triazole fungicides during the mid-1980s, the morpholine fenpropimorph and the piperidin fenpropidin gained rapidly in importance as partners for the resistance management of triazole fungicides, because amines are not cross-resistant to DMIs. The latest introduction within the amine group is spiroxamine, which is a representative of a new chemical class within fungicidal amines, the spiroketalamines. Other amine fungicides in agriculture are dodemorph and aldimorph. The current ranking of global sales (2011) is: spiroxamine, fenpropidin, fenpropimorph, and tridemorph. Amines can be used alone but are often used in mixtures with DMIs to control powdery mildews and rusts.

Hydroxyanilides

Currently this class is represented by fenhexamid. Hydroxyanilides inhibit the C3-keto-reductase step in ergosterol biosynthesis. Hydroxyanilides have a narrower spectrum of activity than the DMIs and amines – fenhexamid is a specific botryticide, which does not show cross-resistance to other classes of anti-*Botrytis* fungicides.

Dicarboximides

The activity of dicarboximide fungicides was first reported in the early 1970s (Fujinami *et al.*, 1971) with three key commercial products being introduced within 3 years: iprodione (Lacroix *et al.*, 1974), vinclozolin (Pommer and Mangold, 1975), and procymidone (Hisada *et al.*, 1977). They are typically protectant fungicides and, although some claims to systemic activity have been made (Hisada *et al.*, 1977), they are best regarded as protectant materials.

Compared with many other classes of fungicides, their activity spectrum is relatively narrow but includes species from the following genera: *Botrytis*, *Sclerotinia*, *Sclerotium*, *Monilia*, *Alternaria*, *Phoma*, *Didymella*, *Rhizoctonia*, and *Laetisaria* (*Corticium*). Current fungicides in this class on the market are iprodione, vinclozolin, and procymidone. They are sold alone and as components of many coformulated mixtures. Dicarboximides were originally introduced for control of *B. cinerea*, primarily on vines where they were welcomed due to the occurrence at the time of resistance to the benzimidazole fungicides. As mentioned previously in this article, resistance management strategies were poorly understood at the time and this inevitably led to overuse of the products such that resistance developed very quickly. *Botrytis* remains the main fungus at risk, although resistance in other genera can easily be found. Even after approximately 30 years of research, the mode of action of dicarboximides is still not certain. Recent evidence (for review see Yamaguchi and Fujimura, 2005) suggests that they interfere with the osmotic signal transduction pathway consisting of histidine kinase and MAP kinase cascades.

Quinone Outside Inhibitor Fungicides

The quinone outside inhibitors (QoIs) class of fungicides represent one of the most widely used groups of fungicides used today to control agriculturally important fungal pathogens. In addition to the strobilurins, the group includes famoxadone, fenamidone, and pyribencarb, all chemically distinct from the strobilurins but with the same mode of action and contained within the same cross-resistance group. Indeed, eight chemical classes of QoIs can be identified to date. The strobilurins were first commercialized in 1996 with the launch of azoxystrobin and kresoxim-methyl, and since this date there has been a steady stream of new QoI fungicides launched with several more identified in company pipelines.

There was a rapid uptake in the market of the strobilurins and within only a few years they were registered and sold in over 80 crops in 70 different countries (Bartlett *et al.*, 2002). Sales of strobilurins and other QoI fungicides amounted to approximately US$3.2 billion in 2011, representing 20–25% of the total global sales of fungicides. Sales of azoxystrobin alone in 2011 were approximately US$1.2 billion million making it the world's biggest selling fungicide.

The discovery of the strobilurins was inspired by a group of natural fungicidal derivatives of β-methoxy-acrylic acid, the simplest of which are strobilurin A, oudemansin A, and myxothiazole A. These derivatives are produced by the basidiomycetes *Strobilurus*, *Mycena*, and *Oudemansiella* but were found unsuitable to be produced commercially as fungicides because of their photochemical instability and volatility. However, the knowledge of their structures and physical properties provided the starting point for many researchers to start to optimize the chemistry toward commercially viable alternatives. Chemical synthesis programs in the R&D-based chemical companies, most notably Syngenta and BASF, resulted in the discovery of the first synthetic strobilurins, namely azoxystrobin and kresoxim-methyl, which were subsequently commercialized. A few years later, metominostrobin (Clough and Godfrey, 1998; Hayase *et al.*, 1995), trifloxystrobin (Margot *et al.*, 1998), picoxystrobin (Godwin *et al.*, 2000), and pyraclostrobin (Ammermann *et al.*, 2000) were announced. During the 1990s, famoxadone (Joshi and Sternberg, 1996) and fenamidone (Mercer *et al.*, 1998) were discovered. More recently, pyribencarb (Kataoka *et al.*, 2010) has been announced and described as having the QoI mode of action. Other fungicides expected to be QoIs such as coumoxystrobin, dicloaminostrobin, enoxastrobin, pyrametostrobin, pyraoxystrobin, and triclopyricarb have been recently reported. The various QoI fungicides have very different physicochemical properties, which confer different behaviors in the plant. For example, picoxystrobin is the most rapidly absorbed into plant tissue and the most xylem-systemic (Godwin *et al.*, 2000). Azoxystrobin and metominostrobin are also xylem-systemic. In contrast, kresoxim-methyl (Ammermann *et al.*, 1992), trifloxystrobin, and pyraclostrobin are all nonsystemic.

The QoI fungicides are respiration inhibitors – their fungicidal activity comes from their ability to inhibit mitochondrial respiration by binding at the so-called Qo site (the outer quinol-oxidation site or ubiquinol site) of the cytochrome bc_1 enzyme complex (complex III), located in the inner mitochondrial membrane of fungi and other eukaryotes. This inhibition blocks electron transfer between cytochrome *b* and cytochrome c_1, which, in turn, leads to an energy deficiency in fungal cells that halts reduced nicotinamide adenine dinucleotide (NADH) oxidation and adenosine triphosphate (ATP) synthesis, thereby halting the production of ATP. This leads to the stopping of the energy production and the fungus eventually dies. All the QoI fungicides share this common mode of action. The toxophore is similar in all compounds and always carries a carbonyl oxygen moiety, thought to be responsible for binding.

Following their introduction in 1996, the strobilurins rapidly became widely used in many crops around the world. The reason for this was their revolutionary levels of disease control and financial returns, and also their positive physiological effects in many crops, resulting in greener crops and increased yields. Possibly due to this rapid widespread use, resistance issues arose rather soon in some key diseases. Although in Europe, monitoring of the air spora of *Blumeria graminis* f. sp. *tritici* (wheat powdery mildew) in 1996 and 1997, conducted independently by members of the manufacturing industry, did not reveal the presence of any QoI-resistant strains anywhere across the continent, further monitoring throughout Europe during 1998 revealed the presence, for the first time, of resistant spores in northern Germany. It was reported at the time that the presence of such strains in northern Germany influenced the performance of strobilurins against this wheat powdery mildew in a negative way, and should, therefore, be regarded as field resistance. Since these first occurrences of resistance to the QoI fungicides in cereal powdery mildew, intensive studies across crops and continents have shown many further cases of resistance in key plant diseases to this fungicide group (FRAC, Leadbeater, 2012a). However, despite the rather frequent occurrence of resistance, disease, and resistance management strategies based around mixtures, alternations with other fungicide mode of action groups have been implemented and QoI fungicides remain in widespread use today. This is due in main to their continuing broad-spectrum disease control but also at least, in part, to the additional physiological benefits to crops, which includes increased greening and robust yield benefits (Grossmann and Retzlaff, 1997; Grossmann *et al.*, 1999; Bayles and Hilton, 2000).

SDHI Fungicides

The SDHI fungicides were discovered and introduced more than 40 years ago. These 'first-generation' carboxamides, carboxin, and oxycarboxin, although having limited spectra of disease control (mainly the basiodimycetes – smuts, bunts, and rusts), are systemic and, therefore, generated great interest. They represented a new way to control these economically important plant diseases – the treatment of seeds or plants with these chemicals resulted in higher yields of crops not only because of disease control but also because of growth stimulation. These systemic fungicides may be applied to seed, soil, or plants, but seed application is the most practical for the control of smuts and bunts.

Following the introduction of carboxin and oxycarboxin, structural analogs were introduced such as benodanil and fenfuram, followed by a range of SDHIs (e.g., mepronil, flutolanil, furametpyr, and thifluzamide) in the 1980s and 1990s with a focus on rice diseases. Despite the replacement of the 1,4-oxathiin ring in carboxin by a variety of alternative ring systems (e.g., phenyl-, furan-, pyrazole-, or thiazole-rings), the activity spectrum of these early SDHIs remained limited to basidiomycetes (Glättli *et al.*, 2011). However, further innovation in the chemistry of the SDHIs resulted in the discovery of boscalid, an SDHI with a considerable expansion of its disease control spectrum to various ascomycete fungi. Boscalid was the first member of this fungicidal class to control a broad range of pathogens in fruits, grapes, vegetables, and arable crops such as cereals and canola (Stammler *et al.*, 2007, 2008). This discovery caused renewed interest in this group of fungicides and, as a result, a wave of new compounds have been announced

and are expected to be commercialized over the next few years addressing a wide range of specialty crop and cereal diseases; these include benzovindiflupyr, bixafen, fluopyram, fluxapyroxad, penflufen, penthiopyrad, sedaxane, and isopyrazam.

The target enzyme of SDHIs is succinate dehydrogenase (SDH, so-called complex II in the mitochondrial respiration chain), which is a functional part of the tricarboxylic cycle and linked to the mitochondrial electron transport chain (Keon *et al.*, 1991). SDH consists of four subunits (A, B, C, and D), and the binding site of ubiquinone (and of SDHIs) is formed by the subunits B, C, and D. Inhibition of SDH impacts on the TCA cycle and quickly will reduce energy (ATP) conservation. Inhibition will also generate reactive oxygen species (ROS), which may be one of the primary ways that SDHIs exert their effect. Clearly, inhibition of SDH has a strong impact on growth and development. Although the QoI fungicides and the SDHIs modes of action involve the inhibition of fungal respiration, the two groups act on different parts of the respiration chain and show no cross-resistance. Thus, although there is cross-resistance between all members of the SDHI group of fungicides, there is no cross-resistance between that group and other important groups such as the QoIs. This is very important in terms of resistance management. Resistance has never emerged as a practical problem to the earlier generation of SDHI fungicides, although it can be generated quite easily in the laboratory. However, high levels of resistance to boscalid were selected quite quickly in field populations of 'high-risk' pathogens such as *B. cinerea*, *Corynesporim cassiicola*, and *Alternaria alternata*. These indications of a significant resistance risk to the SDHI fungicides led to an early recognition of the need to implement resistance management strategies to protect the mode of action; it also led to the formation of a FRAC Working Group in 2009, ahead of the introduction to the market of the majority of the new generation of SDHI fungicides. Intensive research and monitoring programs are under way in industry and in various institutes and so far no resistance has been detected in key crop/disease combinations for most crops including cereals. Clearly, however, successful resistance management will be key to ensuring the longevity of this valuable group of broad-spectrum, highly effective fungicides in the market place.

Phenylamides

The first and most significant member of the phenylamides, metalaxyl, was introduced to the market in 1977. Metalaxyl brought a completely new level of control to the oomycete-incited diseases such as late blight, downy mildews, and *Pythium* damping-off, through its systemic properties that offered protection to the plants as seed treatments and soil or foliar applications. Metalaxyl was followed by the other commercial phenylamides (furalaxyl, benalaxyl, oxadixyl, and ofurace). The unique properties of phenylamide fungicides, such as the control of all members of the *Peronosporales* and most Pythiales, the longlasting preventive and curative activity, the high systemic activity, and the excellent safety profile have been reviewed by Gisi and Ziegler (2002) and Müller and Gisi (2012). Phenylamide fungicides especially affect hyphal growth and the formation of haustoria and sporangia in oomycetes (Schwinn and Staub, 1995). In 1996, the commercial introduction of the more active enantiomer of metalaxyl, metalaxyl-M (mefenoxam) was announced. The concept of using chiral phenylamides has also been taken up in the case of benalaxyl-M (kiralaxyl) in 2007.

The phenylamide fungicides inhibit ribosomal RNA synthesis, specifically RNA polymerization (polymerases). In mycelium of *Phytophthora megasperma*, metalaxyl affected the polymerase 1 complex of rRNA synthesis, which was considered as the primary site of action (Davidse, 1988). A secondary site of action was postulated for benalaxyl and the chemically related herbicides propachlor and metolachlor by Gozzo *et al.* (1984) and again for kiralaxyl in 2009. However, this effect on membrane function occurred at much higher fungicide concentrations than those needed for rRNA inhibition, suggesting that it might be an unspecific rather than a primary activity.

Shortly after the commercial introduction of metalaxyl, resistant isolates were detected in *Pseudoperenospora cubensis*, *P. infestans*, *P. tabacina*, and *P. viticola*. In most cases, this was linked to a decline in disease control. As a consequence, strict recommendations for the use of phenylamides were introduced to prevent and further delay resistance evolution. These recommendations support the use of phenylamides for foliar treatment only in mixture with other, low-resistance-risk fungicides such as mancozeb or chlorothalonil, and a restriction in the number of applications. These recommendations have been implemented successfully and products containing mefenoxam and metalaxyl remain important fungicides today, despite the fact that resistant isolates can be found in all regions of the world and on many crops.

Carboxylic Acid Amides

The carboxylic acid amide (CAA) fungicides consists of three subclasses: the cinnamic acid amides (dimethomorph, flumorph, and pyrimorph), the valinamide carbamates (benthiavalicarb, iprovalicarb, and valiphenalate), and the mandelic acid amides (mandipropamid). Dimethomorph was the first to be introduced in 1988, followed by iprovalicarb with flumorph, benthiavalicarb, mandipropamid, valifenalate, and pyrimorph introduced later. The reason these fungicides are classified together is there is a common cross-resistance pattern among all members for the vast majority of tested isolates of *P. viticola*. Other common features are the specific and rather narrow spectrum of activity against oomycetes, including pathogens of the Perenosporales such as *Bremia lactucae* on lettuce, *Perenospora* spp. on tobacco, pea, onions, and other vegetables, *P. viticola* on grapes, *P. infestans* on potatoes and tomatoes and several other *Phytophthora* species on other crops such as peppers and pineapple. However, the entire genus *Pythium* is insensitive as are all other pathogens outside the oomycetes. CAAs inhibit the germination of cystospores and sporangia (but not zoospore release and motility). They affect growth of germ tubes and mycelium, thus preventing infection of the host tissue. The CAAs have differing properties but are largely preventive fungicides, although dimethomorph has curative and antisporulant activities. Some systemic activity is found in some members of the class.

The mode of action of CAA compounds is directly linked to the inhibition of cellulose synthesis in the oomycete plant

pathogens (Blum *et al.*, 2010a). Uptake studies with ^{14}C-labeled mandipropamid showed that this fungicide acts on the cell wall but does not enter the cell. Furthermore, ^{14}C glucose incorporation into cellulose was perturbed in the presence of mandipropamid. Gene sequence analysis of cellulose synthase genes in laboratory mutants insensitive to mandipropamid revealed two point mutations in the cellulose synthase (*PiCesA3*) gene. Both mutations in the *PiCesA3* gene result in a change to the same amino acid (Glycine-1105) in the protein. The transformation and expression of a mutated *CesA3* allele in a sensitive *P. infestans* isolate resulted in a CAA-resistant phenotype. Thus, cellulose synthase can be postulated as the primary target enzyme for CAA activity.

Resistance to the CAA fungicides in *P. infestans* and *B. lactucae* has never been detected in field populations even though dimethomorph has been in use for more than 15 years. Mutants resistant to the CAAs have been produced in the laboratory in *P infestans*, but are found to show reduced growth rates, reduced pathogenicity and reduced fitness. In contrast to this, resistance to CAAs in *P. viticola* have been reported since 1994, shortly after the introduction of CAAs in France. Resistance has increased gradually in European countries over the past few years (www.FRAC.info), and resistance has been reported in *P. cubensis* from sites in USA, Israel, and China. Studies on the inheritance of resistance to the CAA fungicides in *P. viticola* show it to be based on one recessive nuclear gene (Gisi *et al.*, 2007; Blum *et al.*, 2010b). Resistance-management practices have been defined for the CAA fungicides by FRAC with particular concern around the higher-risk pathogens, such as *P. viticola*; these fungicides are recommended to be used only in mixture with multisite fungicides or other effective noncross-resistant partner fungicides and are limited in number during the growing season. In addition, although some CAA fungicides demonstrate some curative activity, they are recommended to be used in a preventative manner. In contrast to this, resistance risk in *P. infestans* to the CAA fungicides seems to be low and, therefore, the most active of these fungicides can be recommended for use without mixture partners. However, as a resistance-management precaution, the number of CAA fungicides is limited to no more than 50% of the treatments against this disease.

Control of Bacterial Plant Pathogens

As has been already mentioned in this article, bacterial diseases of plants present special challenges in terms of their control. In contrast to the wide range of fungicides available for the control of fungal plant diseases, there is a very limited range of options available for the control of bacterial diseases. Probably the most commonly used products for bacterial disease control are based on copper, used either alone or in mixture with an ethylene bisdithiocarbamate fungicide such as mancozeb. The level of disease control given by such products is at the level of suppression at best and therefore they must be supported by the use of tolerant or resistant varieties, clean seed, and other good cultural practices. Bacterial resistance to copper fungicides is quite common, further increasing the challenges for growers to control these diseases.

Another option for the control of bacteria is the use of antibiotics. The classic definition of an antibiotic is a compound produced by a microorganism that inhibits the growth of another microorganism. Antibiotics were introduced into the field of human medicine in the 1950s and were heralded as 'miracle drugs' for the control of human bacterial diseases and infections worldwide, and, indeed, still play a major role in human medicine today. Of the many antibiotics used, only two are commonly used on plants for bacterial disease control: streptomycin and oxytetracycline. For the control of certain bacterial diseases of plants, streptomycin was indeed a silver bullet. Unfortunately, just as the emergence of bacterial strains resistant to antibiotics has limited their performance in clinical settings, streptomycin resistance has destabilized plant bacterial disease control. The antibiotic resistance crisis in medicine has been widely publicized and is recognized as a major threat to controlling human bacterial diseases and infections worldwide (Levy, 1998). Efforts to conserve the efficacy of antibiotics in medicine have drawn scrutiny to all antibiotic use within and outside the medical field, including agriculture. For this reason, the use of antibiotics in horticulture and agriculture is not permitted in many countries of the world. There are exceptions to this, such as the United States.

Streptomycin is an aminoglycoside antibiotic. Oxytetracycline is a member of the tetracycline antibiotics. Both streptomycin and oxytetracycline inhibit protein synthesis by binding reversibly to bacterial ribosomes. In the United States, streptomycin use is registered on 12 plant species, but the primary uses are on apple, pear, and related ornamental trees for the control of fire blight caused by *E. amylovora*. Oxytetracyline is used in the USA primarily on peach, nectarine, and pear. It is also used on an emergency basis on apple in specific regions where streptomycin-resistant strains of *E. amylovora* have been documented. Antibiotics provide a protective barrier on the surface of plants that suppresses the growth of the pathogen before infection. Streptomycin has been the antibiotic of choice for fire blight as it kills the pathogen on the plant surface. Oxytetracycline, which reduces the growth rate of the pathogen but does not kill existing populations, is less effective than streptomycin. Tetracycline derivatives are the only antibiotics that are registered for internal use in plants. They are injected into the trunks of palm and elm trees to treat lethal yellows diseases caused by phytoplasmas. This is, however, a labor-intensive and expensive process. Antibiotic injections are practical only for isolated high-value ornamental trees and not vast plantings of agricultural or forest trees. The efficacy of antibiotics for the control of plant diseases has been diminished in some regions due to the emergence of antibiotic-resistant strains of pathogens. However, until effective and economic alternatives become available, antibiotics will remain important tools for the management of some of the most devastating plant diseases.

Control, or suppression, of bacterial diseases of plants can also be achieved by using the natural defense mechanisms of plants and switching them on, or enhancing them, by the use of host defense inducers. Two major types of induced resistance have been identified: systemic acquired resistance (SAR), which depends on salicylic acid (SA); and induced systemic resistance (ISR), which requires jasmonic acid (JA) and ethylene, but not SA. Typically, in nature, SAR is induced by a

limited primary infection caused by a necrotizing pathogen, whereas ISR is induced by nonpathogenic organisms that colonize the roots. Both SAR and ISR confer an enhanced defense capacity. These mechanisms can be triggered in plants by numerous fungi and bacteria, and can also be effectively triggered by the use of a number of synthetic chemicals. The main commercial chemical compounds available so far are inducers of SAR – these products can be shown to have no direct antifungal or antibacterial effect when used *in vitro*, but in combination with a host plant, clearly induce the host plant's natural defense mechanisms to confer protection against pathogenic fungi and bacteria. The level of control of fungal diseases by induced-resistance products is usually significantly less than that achieved by an effective modern fungicide and is usually more complicated because such products must be applied in advance of infection to allow the plant time to activate its defense mechanisms. But in the case of bacterial disease control, where the effectiveness of the available products is often already rather low, resistance-inducing chemicals can offer a good alternative. An additional advantage of induced-resistance compounds is that, due to their unique and rather nonspecific modes of action, the risk of resistance occurring against them seems to be low, which means their effectiveness should be maintained for the future.

Examples of bacterial disease control by induced resistance compounds used commercially are probenazole, tiadinil, and isotianil used in Asia, mainly to control fungal blast disease and bacterial blight in rice. ASM induces a broad resistance spectrum on an extended diversity of dicotyledonous and monocotyledonous plants. It is used as a foliar spray and as a seed treatment in various dicotyledonous crops for the control of a range of diseases, including plant pathogenic bacteria. ASM is, today, successfully registered and sold worldwide in a wide range of crops, including tomatoes, tobacco, pears, bananas, lettuce and other leafy vegetables, nuts, and cucurbits.

Fungicide Resistance and Its Management

Fungicide resistance is the naturally occurring, inheritable adjustment in the ability of individuals in a population to survive a plant-protection product treatment that would normally give effective control (OEPP/EPPO, 1999). Although resistance can often be demonstrated in the laboratory (and is, indeed, an important part of resistance-risk assessment for new fungicides), this does not necessarily mean that disease control in the field is reduced. 'Practical resistance' is the term used for the loss of field control due to a shift in the pathogen's sensitivity to a fungicide. When it occurs in the field, fungicide resistance affects all those concerned with crop health; the growers, advisors, and the industry that provides these with the advice and products necessary to ensure a healthy, productive crop. Without successful resistance management, the effectiveness and eventually the number of modern fungicides available to the farmer and grower will diminish rapidly, leading to poor yields and reduced crop quality. Such a scenario could quickly lead to overuse of affected fungicides as users strive to get products to work (e.g., higher dose rates being used, or an increase in the frequency of application), leading in turn to increased and undesirable loading on the environment.

Growers and the agrochemical industry have lived with resistance problems for many years. Resistance was not considered to be a real problem in the early 1960s – fungicides had been used over many years, quite intensively in several crops, with no obvious signs of problems. At that time, the fungicide market consisted largely of nonsite-specific, nonsystemic, and moderately effective fungicides. There were some reports of resistance to diphenyl and sodium-*o*-phenylphenate in *Penicillium digitatum* in citrus at that time (Harding, 1962), and a failure of hexachlorbenzene to control *Tilletia foetida* in Australia (Kuiper, 1965); in addition, some isolates of *Pyrenophora avenae* in oats in Scotland were found to be resistant to organomercurial seed treatment (Noble *et al.*, 1966), but these were a small number of cases and were not considered to be very economically significant. Moreover, the fungicides had been in use for many years and so were not considered to have important consequences in terms of relevance to other fungicide and disease combinations.

However, the cases of practical resistance to the benzimidazole fungicide benomyl after only 2 years of commercial use in the USA on cucurbit powdery mildew caused far more concern (Schroeder and Provvidenti, 1969). Other reports of resistance to benomyl and other related fungicides followed quite quickly afterward. Reports of resistance to fungicides became more frequent following these early cases and, in the 1970s, reports were published documenting resistance to important fungicides such as dodine, kasugamycin, and the phenyltins. Since the 1970s, cases of resistance to fungicides have increased in number, significance, and geographical spread, with the phenylamides, dicarboximides, SMIs (e.g., triazoles), QoIs (e.g., strobilurins), and, more recently, the SDHIs all suffering from to shifts in sensitivity or full practical resistance in key crops and diseases.

From the above, it can be easily realized that fungicide resistance is a real threat to the effectiveness of many fungicide groups and must be managed, to ensure good product performance in the field for the grower and also to justify sustainable investment by the agrochemical industry into new fungicides. Fortunately, despite a general widespread occurrence of resistance to several fungicides, effective management strategies have limited the impact of this on crop protection and production. Fungicide resistance has been much researched and with the expert knowledge that such research has provided, effective resistance management strategies have been developed and implemented. Because the risk of the impact of resistance being high is directly related to the degree of exposure of the plant pathogen to a fungicide (or a group of fungicides belonging to the same cross-resistance group as defined by FRAC), most resistance management strategies involve limiting the number of applications of the 'at-risk' fungicide in a disease-control program. The other fungicides used in the disease control program must have different modes of action to the fungicide in consideration. Other fundamentals of resistance management include the use of mixtures of fungicides from different cross-resistance groups to avoid reliance on a single mode of action, starting the fungicide spray program early in disease epidemics (to reduce the probability that a chance mutation conferring resistance has happened in

Table 4 Resistance risk classification of fungicides according to the Fungicide Resistance Action Committee (FRAC) Code List 2012[a]

Resistance risk classification	*Number of fungicide groups (FRAC code list)*	*Number of fungicides*	*Worldwide sales 2011[a] (US$×1000)[b]*
High	4	30	4 041
High to medium	4	24	836
Medium	8	51	3 868
Medium to low	11	36	1 269
Low	11	23	2 348
Not known	19	32	718
Others (bactericides, etc.)			225
Total	57	196	13 305

[a]Excluding biologicals.
[b]Calculated values based on data from AMIS., 2012. Crop Protection and Seeds Database. Midlothian, UK: AMIS and Phillips McDougall (2012) (www.Phillipsmcdougall.com).

the fungal population) and to avoid long persistence of a single 'at-risk' fungicide in a crop such as might be experienced by a soil application targeted to control foliar disease in the crop. It is clear from these basic principles of fungicide resistance management that there is a high requirement for many fungicides with different modes of action to be available for the grower to choose from, which includes the preservation in the market place of the older modes of action such as multisites, which have a low resistance risk (Leadbeater *et al.*, 2008; Leadbeater, 2011). The importance of fungicide resistance management becomes more clear when the fungicide market is considered. In 2011, considering the highest selling fungicides and their classes, 62% of the world fungicide market (by value) consisted of only six single-site modes of action (**Table 3**). These six mode-of-action groups are the QoIs, the azoles, benzimidazoles, SDHIs, phenylamides, and amines. Of these six, five are classified by FRAC as high risk or between medium and high risk of resistance occurring. Only 18% fall into the category of low resistance risk (23% if 'resistance not known' fungicides are included; **Table 4**). These statistics do not give the complete picture with regard to treated areas with each mode of action of course, but show clearly what fungicides growers depend on most to provide disease control.

In recognition of the challenge set by the possibility of fungicide resistance developing., and with the experiences of the benzimidazoles and phenylamides, FRAC was formed following a course in resistance in 1980 and a subsequent seminar in Brussels in 1981; FRAC is still extremely active today (Leadbeater, 2012b, www.FRAC.info). The purpose of FRAC is to provide fungicide resistance management guidelines to prolong the effectiveness of 'at-risk' fungicides and to limit crop losses should resistance occur. FRAC members are recognized industry experts in the field of fungicide resistance and are actively engaged in scientific work and discussions and are frequent contributors at educational events such as scientific symposia and symposia. Important resources have been produced by FRAC and are available on the FRAC website, including educational monographs, sensitivity testing methods, classification tables of fungicide mode of action grouping, summaries of records of fungicide resistance cases, and much more. Importantly, the updated situation with regard to resistance to the most important groups of 'at-risk' fungicides is available on the website for consultation and downloading. FRAC does not work in isolation, of course, and the key is cooperation and consultation between FRAC members and researchers, consultants, advisors, and officials in public and private organizations in order to share scientific information and enable all to come to common, supported conclusions, practical advice, and recommendations.

The Future

As discussed already in this article, the costs of discovery and development of new fungicides are continuing to escalate; at the same time the hurdles with regard to registration are increasing. These two driving forces have some obvious consequences for the future. Because of the increasing costs of development and registration, to justify the development of new fungicides they will need to have a large business potential to enable industry to recoup the costs of R&D. This drives product design toward broad-spectrum disease control products on a wide range of crops. However, to realize the full business potential of the new fungicide, it must be able to be registered! This has, of course, always been the case in new product development but tighter requirements will lead in the future to a different approach where the ability to register a new fungicide takes priority over potency and the absolute level of disease control. Hopefully, however, future innovation will be high enough to deliver highly effective products that can be successfully commercialized. These requirements are likely to continue to drive the current trend in the increase of biologicals and biofungicides in the market. Biofungicides, while themselves having some specific technical challenges such as production capacities and consistency, shelf life, and level of performance, and so on, have some advantages of reduced data required for registration (therefore, lower costs), lower likelihood of residues in produce plus the probability of lower resistance risk than a conventional (single-site) fungicide. In the future, therefore, biofungicides are likely to be more successful not only in providing solutions for organic farming but also as integrated elements of successful disease management programs in combination with conventional chemical fungicides. Biofungicides will be especially useful when used close to crop harvest because they are not likely to leave undesirable residues on and in food.

In terms of innovation in conventional fungicides, this is difficult to predict. Clearly, the focus will be on new modes of action in order to overcome current resistance problems, plus the invention of new chemicals that themselves have low

resistance risk. As discussed in the Section Challenges for Developing Chemical Agents for Plant Disease Control, this is a great challenge because 'designing' new modes of action is difficult and the additional requirement of low resistance risk presents an even higher challenge to even be able to determine this when novel chemistry has been found. The current wave of new fungicides of high potential market significance depends greatly on a single mode of action (the SDHI fungicides), mainly because this class of chemicals clearly has a high potential for innovation in structure and disease-control spectrum. However, with a high number of new, potent fungicides entering the market at approximately the same time into the same crops and targets, resistance management will be a particular challenge. With this challenge in mind, FRAC established a specific Working Group for the SDHI fungicides early, and before the market introduction of most of the 'new generation SDHI' fungicides. Hopefully, this approach will result in success in managing resistance in this group of important fungicides.

Beyond the SDHI fungicides, it is difficult to see the next wave of innovative fungicides. Several new active ingredients are announced to be introduced over the next few years, but with few exceptions such as tiadinil, fenpyrazamine, they are mainly further SDHIs. However, it is difficult to be definitive because agrochemical company pipelines are confidential and only limited information can be obtained, for example, by monitoring patents. It can be assumed that at any point in time there is much more in company pipelines than is in the public domain, and although it is increasingly challenging to find truly new modes of action, history has shown that industry is very successful in responding to this challenge in fungicides.

Conclusion

Despite the enormous efforts of research and development into the control of plant diseases over the past decade, crop losses to destructive plant pathogens such as the fungi, oomycetes, and bacteria remain high and are among the most limiting constraints to crop yields worldwide. Current best practice for the control or limitation of plant diseases of crops includes good crop hygiene and cultivation methods, the selection of disease resistant or tolerant varieties, good agricultural practices such as planting times, fertilizer regimes, and the use of effective chemical fungicides. Since the days of the early synthetic chemical fungicides, great advances have been made by science and the chemical industry in inventing and developing lower use-rate fungicides that are safer to humans and the environment. The improved physical and chemical/biochemical characteristics of these modern fungicides has enabled growers to far more effectively control the diseases in their crops. Properties such as systemic activity, curativity, longer duration of control, and improved rain-fastness have enabled the use of novel application technologies (e.g., seed, soil treatment, application in irrigation systems) and have resulted in more flexibility and labor saving for growers worldwide. It is a fact that yield and quality in many crops would be extremely low without the use of modern fungicides and, in some extreme cases, production would today be impossible without their use (e.g., potato late blight, Asian soy rust in Brazil). It is for these reasons that, despite significant increases in the costs and other hurdles involved in the R&D of new crop protection products to the market, the agrochemical industry continues to invest into the invention and development of new chemical fungicides to meet the demanding needs of economic disease control in the modern world.

Experience has shown, however, that chemical fungicides must be used responsibly and in an integrated way with other crop-protection practices to ensure effective disease management for the long term. It can be quite clearly seen from this article that fungicide resistance is a constant threat, particularly to the modern, single-site inhibitors, which must always be considered and addressed in the development of any new fungicide product. The invention of highly effective, highly specific fungicides carries a special risk of resistance development – these often becoming the victims of their own commercial success. It is important that a full evaluation of the resistance risk is made before the commercial introduction of any new fungicide, with management strategies put into place from the start to prolong the effective life of the fungicide(s) in question. Scientific knowledge has progressed tremendously over recent years to enable such risk assessment. It is equally clear that, despite the significant scientific advances in fungicide technologies in recent years, there remains a very important role for the older fungicides, especially those with nonspecific modes of action such as the 'multisite' fungicides, which have a low risk of resistance occurring and, therefore, are valuable to be used in combination with the newer modes of action. There remains a high requirement for diversity in chemistry and in modes of action to ensure the future success of chemical fungicides. It is hoped that, in the future, the next generations of fungicides invented by the agrochemical industry will include novel modes of action, a low risk of resistance, and continuing trends toward even greater safety to crop, humans, and the environment.

See also: Biotechnology: Plant Protection. Climate Change and Plant Disease. Mineral Nutrition and Suppression of Plant Disease. Organic Agricultural Production: Plants. Pathogen-Tested Planting Material. Plant Disease and Resistance. Plant Health Management: Biological Control of Plant Pathogens. Plant Health Management: Crop Protection with Nematicides. Plant Health Management: Pathogen Suppressive Soils. Plant Health Management: Soil Fumigation

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Plant Health Management: Herbicides

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Glossary

Herbicide Any chemical substance or cultured biological organism used to control or suppress plant growth.
Mechanism of action The primary biochemical or biophysical event that the herbicide directly affects.
Mode of action Refers to the entire sequence of events from the introduction of a herbicide into the environment to the death of the plant.
Postemergence Herbicide-application timing targeting weeds that have emerged from the soil.
Preemergence Herbicide-application timing targeting weeds that have not germinated.
Safener A herbicide safener, also termed antidote, antagonist and protectant, is a compound applied to a crop that confers a selective advantage to the crop, lending protection from herbicidal phytotoxic effects without reducing activity in target weed species.
Selectivity A selective herbicide is one that is significantly more toxic to some plants than others within the limits of a specified dosage range, the method of herbicide application, and environmental conditions that follow application.

Introduction

The use of chemicals to control weeds dates back centuries – the use of salt is a prime example of humans using a chemical to manage vegetation. The rigorous use of salts and acids in the nineteenth and early twentieth centuries presaged the development of the selective herbicide, as pesticides that control weeds are known. The modern selective herbicide was born in the early 1940s with the discovery of 2,4-D (2,4-dichlorophenoxyacetic acid) and other synthetic plant growth regulators. The use of 2,4-D as a selective herbicide began the modern era of modern weed management. Since that time, significant advances in herbicide chemistry have delivered multiple herbicide classes that interact with a discrete set of plant processes. The use of herbicides has also significantly changed the farming practices on a global basis – in general, herbicide use results in a reduction in rotational diversity by facilitating the repetitive production of crops of high value.

Herbicide has been defined as any chemical substance or cultured biological organism used to control or suppress plant growth. Herbicides are the most commonly utilized crop-protection compounds in the world. In 2007, worldwide herbicide use was estimated at 951 000 MT. Usage in the United States was estimated at 241 000 MT, or 47% of the total pesticide used in the country (Grube *et al.*, 2011). The total annual amount of herbicide use has not changed in the United States over the past 20 years (Figure 1). Rather, there has been a substantial increase in the use of a single herbicide, glyphosate.

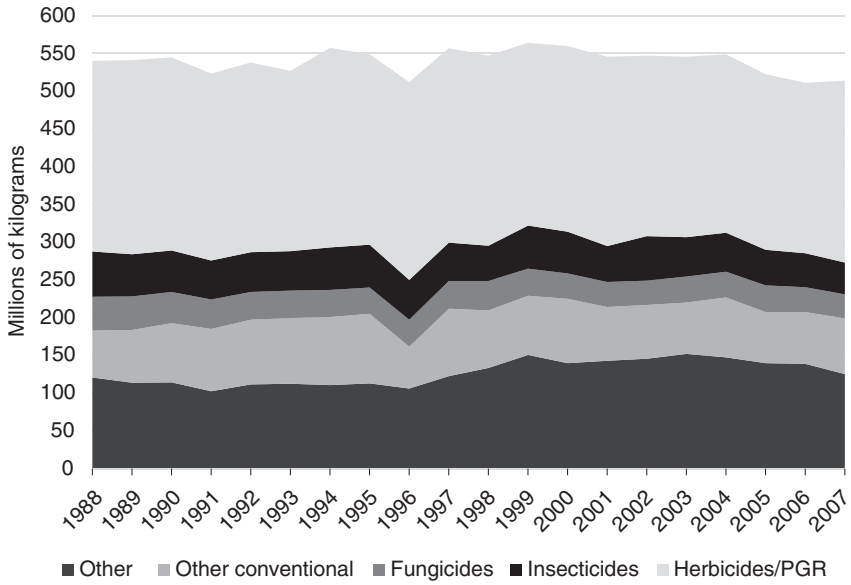


Figure 1 The annual amount of pesticide-active ingredient used in the United States by pesticide type, 1988–2007 estimates in all market sectors. Reproduced from Grube, A., Donaldson, D., Kiely, T., Wu, L., 2011. Pesticides Industry Sales and Usage: 2006 and 2007 Market Estimates. Washington, DC: U.S. Environmental Protection Agency.

Of the top ten pesticides used in the United States, six are herbicides (Grube *et al.*, 2011).

Herbicides are first a labor-reduction tool. Selective herbicides have radically reduced the amount of labor required to manage weeds in crops. Herbicides have also facilitated the adoption of reduced tillage and tillageless (no-till) production systems and weed control in closely seeded crops by controlling weeds within the row. Cultivation, even the most advanced robotic systems, still have difficulty controlling weeds in the crop row. Herbicides also facilitate early planting of crops under adverse soil moisture conditions – tillage often fails to control vegetation when sufficient soil moisture is present to facilitate rerooting. Herbicides offer considerable increases in efficiency compared to human labor inputs. Where labor is scarce or expensive, herbicides offer an efficient, albeit energy-intensive alternative. Where energy inputs have been compared, labor and herbicides are very similar. Ultimately, there is no comparison in terms of cost – herbicides enable far fewer humans to weed much larger areas for about the same energy input and much lower labor costs.

The primary negative attribute of herbicides is a side effect of the beneficial effects. Often, there is a tendency among practitioners to expect a herbicide solution for all weed problems rather than to seek a solution within the framework of the entire production system. There is also a misconception that herbicides offer a complete solution, that there will always be complete control. Such a misconception, coupled with significant selection pressure imposed by the use of herbicides and with marketing and supply chain aspects, has led to widespread herbicide resistance and shifts in weed species composition. A second negative aspect of herbicides is their use necessitates a diminishment of agricultural diversity – they are well suited to the monoculture cropping systems of the twentieth and twenty-first century. Of course there are other primary negative aspects of herbicides and herbicide use. The most common problems associated with herbicides include injury to crops, injury to nontarget vegetation, and herbicide residues persisting in the soil and injuring crops grown in rotation. Less common problems can include effects on nontarget organisms, including fish, although such problems are usually related to applicator error rather than the herbicides themselves. In rare circumstances, high levels of use can couple with less than ideal environmental profiles to result in groundwater contamination and other unanticipated effects.

Since the 1940s, foreign and domestic agrochemical companies have commercialized several hundred herbicide active ingredients. Today there are more than 130 chemical compounds worldwide that are used as selective herbicides and approximately 30 others that are used as nonselective herbicides. In contrast, there are many hundreds of trademarked herbicide products commercially available as there may be more than one manufacturer of a particular herbicide or multiple formulations that contain the same active ingredient. As most herbicides are applied in mixtures containing two or more herbicides, the list of possible herbicide combinations becomes quite extensive as does the knowledge to use such mixtures. As a consequence, there are multiple names associated with herbicides. The active ingredient is the chemical in a herbicide formulation responsible for phytotoxicity and has a chemical name according to the rules of nomenclature of the International Union of Pure and Applied Chemistry. Each herbicidal chemical has one common name that is usually a simplified version of the chemical name. An appropriate authority must approve common names before being accepted by working weed scientists. Authorities include the American National Standards Institute, the Weed Science Society of America, and British Standards Institution. However, growers typically use a trade name by which a commercial product is identified that may contain one or more herbicidal active ingredients.

Selectivity of Herbicides

Selectivity is the most important factor for successful herbicide application – success being defined as the death of the weeds and not the crop. A selective herbicide is one that is significantly more toxic to some plants than others within the limits of a specified dosage range, the method of herbicide application, and environmental conditions that follow application (Harrison and Loux, 1995). Herbicide selectivity is the foundation of successful chemical weed management and is conferred by physical or physiological factors that produce differential herbicide toxicity for crops and weeds (Harrison and Loux, 1995).

Physical factors that confer selectivity by application method significantly reduce or eliminate exposure of the crop plant to the herbicide, and include differential placement or differential absorption. Differential translocation, enzyme target-site resistance, or differential metabolism of the herbicide confers biological selectivity. Selectivity of herbicides among crop plants is usually attributable to a single mechanism – primarily differential metabolism. Often a combination of application method and biological tolerance is required to impart the greatest degree of selectivity over a range of herbicide dosages and environmental conditions (Harrison and Loux, 1995). Virtually all herbicides lose selectivity if applied improperly or under environmental conditions that adversely affect physiological tolerance mechanisms.

Physical placement of the herbicide can achieve significant selectivity. Application of herbicides used for selective control of small-seeded grass and broadleaf weeds in large-seeded annual crops to the soil surface following planting is one example of selectivity by placement. Selectivity is achieved when seeds are positioned in the soil beneath the zone of greatest herbicide concentration where the smaller-seeded weeds are germinating. Directed postemergence sprayers, shielded sprayers, rope-wick applicators, and other specialized herbicide-application equipment that direct herbicide applications on weeds and away from crop plants are examples of herbicide-application selectivity by placement (Harrison and Loux, 1995). Environmental factors such as soil type or moisture availability can modify the selectivity by placement, as can biological factors such woody tissue or root zone development.

Selectivity conferred by differential absorption of herbicides by different plant species is not common, largely due to the effective array of adjuvants designed to aid penetration. When selectivity is conferred by differential absorption, it is based on leaf cuticle thickness and composition. However,

cuticle thickness can vary from plant to plant and even among leaves of the same plant, as cuticle formation depends on environmental conditions. Not surprisingly, plants with thickened cuticles or leaf pubescence are more difficult to control with most foliar-applied herbicides. Adequate soil moisture, sunlight, and high relative humidity are more conducive to penetration by herbicides. Drought or prolonged periods of hot, dry weather can result in an increase in epicuticular wax, cuticle dehydration, and plant stress, and foliar application of herbicides during such periods may result in a loss of effectiveness due to lack of herbicide absorption (Harrison and Loux, 1995).

Once across the cuticle barrier, herbicides are translocated in the apoplast or symplast some distance before reaching their biochemical site of action. Herbicides first undergo short-distance translocation from the epidermis to the vascular tissue. Even during the short transport period, those herbicides moved in the symplast are likely to have substantial effects on the cells they have entered. In foliar tissue, herbicide moves to the xylem or phloem via normal apoplastic or symplastic routes. Herbicides translocated short distances in the root apoplast that are traveling toward the xylem and phloem in the center of the root encounter and must cross the endodermis. Finally, herbicides that cause membrane disruption usually do not translocate appreciably except under special circumstances.

Transport of herbicides (and pesticides in general) is an important criterion and several models have been developed to describe and predict mobility (Hsu and Kleier, 1996; Satchivi *et al.*, 2006 and related citations). Herbicide translocation is dependent on the chemical properties of the herbicide and conditions within the plant. Some herbicides, for example, may undergo reactions on entering into the symplast resulting in anionic or more polar forms of the herbicide that cannot return to the cell membrane. The herbicide is thus 'trapped' in the cytoplasm and is largely confined to translocation in the symplast (Harrison and Loux, 1995). Conversely, nonionic herbicides that move freely across cell membranes and into and out of living cells undergo translocation primarily in the apoplast. Differential rates and extent of translocation sometimes play an important role in determining herbicide selectivity among plants.

The driving force behind apoplastic translocation is transpiration – net movement of apoplastically translocated herbicides in plants is upward from site of entry along the gradient from highest water potential (soil solution or soil water) to lowest water potential (the atmosphere) via the transpiration stream. As a result, apoplastically translocated herbicides are generally soil-applied or require complete coverage of above-ground structures (Harrison and Loux, 1995). In contrast, herbicide movement via the symplast is bidirectional, with direction of movement dependent on the location of areas of greatest assimilation supply and demand within the plant. Photosynthate source and sink relationships determine the rate, direction, and extent of phloem-mobile herbicide translocation and can change spatially and temporally. Perennial weed source–sink relationships are more complex than that of annuals, and response to phloem-mobile, symplastically translocated herbicides is highly dependent on stage of development. Because a key objective in perennial weed management is to destroy overwintering vegetative propagules (e.g., rhizomes, stolons, tubers, etc.) as well as the foliage, phloem-mobile herbicides should be applied based on knowledge of movement to the vegetative reproductive structures.

Herbicide Metabolism

The most common mechanism that confers herbicide selectivity is differential metabolism – rapid metabolism by the crop and little to no metabolism by the weed. Plants are immobile organisms that must adapt to the environmental conditions where they occur. That environment may include exposure to natural and synthetic toxins such as heavy metals, allelochemicals, pollutants, and herbicides (Riechers *et al.*, 2010). A plant that is tolerant to a herbicide through metabolism is capable of altering or degrading the chemical structure of a herbicide through enzymatic and nonenzymatic reactions that render the herbicide nontoxic (Harrison and Loux, 1995). The rate, in addition to the extent of herbicide metabolism, is also an important factor in determining selectivity. Herbicides often undergo biotransformations in plants and can be metabolically deactivated or metabolically activated. Some herbicides are stable in plant systems, although this is not common. The herbicidal detoxifying metabolic processes include the action of several enzymes (Kreuz *et al.*, 1996). The metabolic processes are divided into three distinct phases. Phase I metabolism involves oxidation by cytochrome P450 monoxygenases and hydrolysis by carboxyesterases. As a consequence of oxidation or hydrolysis, herbicide molecules are susceptible to phase II metabolism, including conjugation to glucose (Hatzios and Burgos, 2004) and glutathione (Edwards *et al.*, 2000; Riechers *et al.*, 1997). Conjugation of herbicide not only modifies the physical properties of the molecule, decreasing the ability to interact with the target site, but also enhances transport by multidrug resistance-associated protein to the vacuole, resulting in a sequestering of the molecule in phase III metabolism (Martinoia *et al.*, 1993; Zhang *et al.*, 2007).

Selectivity can also be achieved by the use of herbicide safeners. An herbicide safener, also termed antidote, antagonist and protectant, is a compound applied to a crop that confers a selective advantage to the crop, lending protection from herbicidal phytotoxic effects without reducing activity in target weed species. Many herbicides are developed for their crop selectivity; however, selectivity is often borderline prohibiting their use or diminishing acceptable weed control rates if not for the safener application (Rosinger *et al.*, 2012). Safeners may be used to overcome injury due to damaging residual pesticide levels allowing for more crop rotational flexibility, or in botanically related minor crops not targeted for product development (Davies, 2001). To date, all commercialized safeners have been developed for major crop species, all of which are monocots (maize, sorghum, rice, and cereals such as wheat and barley). Dicot crops have yet to respond to safener treatments. The method of application has evolved from compounds designed for seed treatments to preemergence mixtures and now postemergence safener-herbicide mixtures. Herbicide safeners act by reducing the

ability of a herbicidal compound to reach its active site mainly by stimulating metabolic processes described previously that alter or sequester the active molecule. Other studied safener-herbicide antagonism mechanisms, including reduced absorption and translocation or completion with the active site, have yielded conflicting results (Davies, 2001; Abu-Qare and Duncan, 2002). Herbicide safeners continue to be of value in agro chemistry. Further elucidation of the processes involved in safener-herbicide detoxification in combination with transgene technologies could increase their utility, especially in dicot crop species (Riechers *et al.*, 2010).

Fate of Herbicides

Fate of herbicides constitutes a topic of its own and will only be reviewed briefly here. The major processes that determine the fate of herbicide in soil are adsorption, transport, and degradation. In principle, all three processes occur once a herbicide is introduced to a soil system. However, there is usually a primary process that determines fate, and the primary process is determined by a multitude of abiotic and biotic conditions in addition to the chemical nature of the herbicide itself. There are excellent reviews on the subject addressing tillage (Alletto *et al.*, 2010), leaching (Flury, 1996), runoff (Wauchope, 1978), volatilization (Taylor and Spencer, 1990), and microbial degradation (Aislabie and Lloyd-Jones, 1995). An excellent introduction and overview is provided by Ross and Lembi (2009) (**Figure 2**).

Adsorption of herbicide governs herbicide fate to a greater extent than the other two processes. Adsorption is defined as the adhesion of molecules to the surface of solids (Ross and Lembi, 2009). Herbicide availability in the soil water fraction depends on the amount of water present, the chemical nature of the herbicide, and the colloidal composition of the soil. Herbicides vary significantly in their chemical properties, and are most commonly weak acids or bases. Depending on pH, such herbicides can ionize and bind tightly to soil particles, rendering them unavailable for absorption by plants. Herbicide solubility can also dictate the amount available in the soil–water fraction, as herbicides with relatively low solubility are usually adsorbed to soil particles and division into the soil–water fraction is based on solubility. Clay and organic matter particles are active colloids in soil, and as the fraction of soil composed of either clay or organic matter increases, adsorption usually increases.

Herbicide movement is largely governed by water movement or by volatilization of the herbicide. They can also be moved away from the site of application in plant material or adsorbed to soil particles. Water movement in soil is complex and can be categorized into three main types: runoff, leaching, and diffusion through capillary action. Runoff and soil-particle movement usually occurs during periods of heavy precipitation on unprotected soils. Leaching, or the movement of herbicide downward in soils with water, is of considerable concern and leaching potential is governed by the affinity of the herbicide to bind to soil and degradation pathway. Movement by capillary action is often upward in the soil, and occurs in areas where irrigation or stored soil moisture occur with low relative humidity.

Herbicides degrade in the environment. The degradation rate of herbicides can be quite variable and are dependent on abiotic and biotic conditions for some time after application. Biotic degradation pathways involve microbial degradation by an array of enzyme-mediated reactions, whereas abiotic degradation is largely attributed to photolysis and hydrolysis. Degradation is governed by adsorption, and herbicides do not

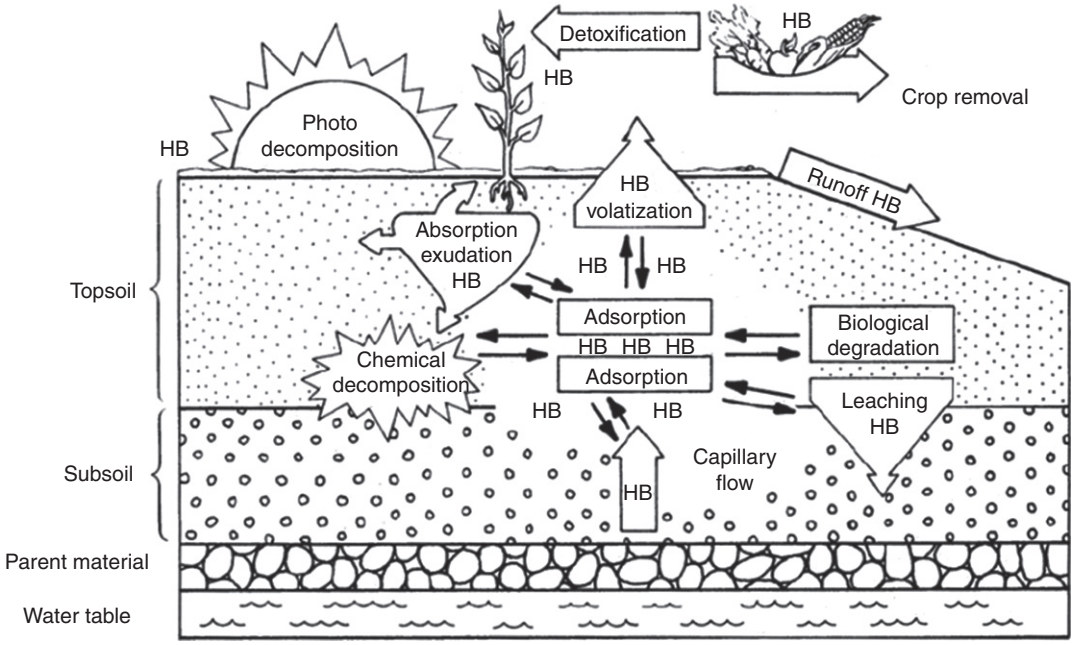


Figure 2 The three primary processes, adsorption, transport, and degredation, that determine the fate of herbicides (HB) in the environment. Reproduced from Ross and Lembi (2009), redrawn from Weber *et al.* (1973).

degrade appreciably when adsorbed to soil particles. Herbicide persistence can be a considerable problem when degradation is slowed by a lack of moisture or temperature to facilitate the reactions, combined with herbicidal activity at very low concentrations.

Herbicide Resistance Action Committee Classification of Herbicides

Herbicides are grouped using a host of attributes. The most common method is by herbicide mode and mechanism of action (the Herbicide Resistance Action Committee (HRAC) and the Weed Science Society of America classification schemes are two examples, (**Table 1**)). Mode of action refers to the entire sequence of events from the introduction of a herbicide into the environment to the death of the plant. The mechanism of action is the primary biochemical or biophysical event that the herbicide directly affects (Monaco *et al.*, 2002). The HRAC proposed a classification system for herbicides according to their enzyme target sites, the similarity of symptoms, or their chemical class (**Table 1**; Menne and Köcher, 2012) and that system will be used here and noted at the beginning of each herbicide mode of action section. Herbicides could be classified by their chemical family, persistence, selectivity, application method, or a host of other attributes. Classifying them by mode of action facilitates communication about risk of herbicide resistance development, as development of resistance can confer cross resistance within a mode of action. Herbicide resistance much more rarely confers resistance across modes of action. Interestingly, a herbicide with a novel or new mode of action has not been introduced since the 4-hydroxyphenylpyruvate dioxygenase (HPPD) inhibitors in the early 1990s. Finally, the modes of action presented here are those for which there are identifiable registered herbicides targeting them – there are a much larger number of target sites for which there is no corresponding registered herbicide.

Acetyl-CoA Carboxylase Inhibitors (Group A)

Acetyl-CoA Carboxylase inhibitors (ACCase; EC 6.4.1.2) are one of the most important modes of action globally, with annual sales estimated to exceed US$1 billion. There are three distinct classes of ACCase inhibitors. The aryloxyphenoxypropionate (AOPP or fop) and cyclohexanedione (CHD or dim) were first identified in the early 1970s, whereas the single member of the 2-aryl-1,3-dione class, pinoxaden, was introduced in 2006. The ACCase inhibitors are widely used in dicotyledonous crops to control grass weeds, and several are used for selective control of grasses in cereals and rice (Hirai, 2002; Hock *et al.*, 1995).

ACCase is a biotin-dependent carboxylase that produces malonyl-CoA from bicarbonate as a source of carboxyl group, and adenosine triphosphate (ATP) as a source of energy. ACCase catalyzes the conversion of acetyl-CoA into malonyl-CoA through the incorporation of a carboxyl group into the acetyl radical of acetyl-CoA. The ACCase herbicides are known to inhibit the carboxylate transferase function of homomeric ACCase found in the plastids of grasses (Hirai, 2002; Menne and Köcher, 2012; Nicolau *et al.*, 2003). These herbicides have specific activity against grass species only – dicots and nongrass monocots are tolerant. Nongrass monocots and dicots have a prokaryotic-type multisubunit plastidial ACCase that is resistant to ACCase inhibitors, as are the eukaryote ACCases from animals and yeast. The transcarboxylation reaction is performed following the two-step process utilized by all biotin-dependent transcarboxylases. Grasses of the Poaceae family contain two eukaryotic-type ACCases – one chloroplastic and one cytosolic. Almost all other plants contain the two well-differentiated forms – a cytosolic eukaryotic-type ACCase and chloroplastic prokaryotic-type ACCase. ACCase inhibitors are complex and often exist as multiple isomers. In the case of the AOPPs, the (*R*)-enantiomer is the most active isomer. CHDs are chiral around a double bond, and the (*E*)-enatiomer is the most biologically active form (Nestler and Bieringer, 1980). As a consequence, products are often reintroduced with formulations containing only the active isomer.

Many studies on the mechanism of action of the ACCase herbicides have been conducted. Nearly all ACCase inhibitors are rapidly absorbed through the cuticle and into leaf cells of both grass and dicot species, where some, particularly the AOPPs, are metabolically activated from esters to acids. The acid is then translocated to meristematic areas of the shoots and roots. The amount translocated is low in relation to the amount applied; however, translocation occurs in both the xylem and the phloem. No significant differences in absorption, translocation, or metabolism of these herbicide, have been reported between dicot and grass species.

Some of these herbicides have soil activity (Gerwick *et al.*, 1988); however, the main activity occurs after postemergence application to emerged grasses. Activity occurs on both annual and perennial grass species, but activity can vary depending on the particular herbicide. Translocation of ACCase herbicides can occur in both the xylem and the phloem, and all generally require the addition of an adjuvant to improve leaf coverage and absorption (usually a crop oil concentrate). These herbicides are more effective when applied to unstressed, rapidly growing grasses. Death of the grass is slow, requiring a week or more for complete kill. Symptoms include rapid cessation of shoot and root growth, pigment changes (purpling or reddening) at the leaves occurring within 2–4 days, followed by a progressive necrosis beginning at meristematic regions and spreading over the entire plant.

Acetohydroxy Acid Synthase/Acetolactate Synthase Inhibitors (Group B)

The discovery that small synthetic compounds could inhibit acetohydroxy acid synthase (AHAS; EC 2.2.1.6) revolutionized weed management. The first AHAS-inhibiting compounds discovered, the sulfonylureas, were safe and had significantly lower use rates compared to other widely used herbicides (Beyer *et al.*, 1988; Levitt, 1991). Some sulfonylureas control vegetation at rates below 10 g ai ha^{-1}. A nearly simultaneous discovery of a second group of structurally distinct AHAS-inhibiting compounds, the imidazolinones, increased interest in the target site. Currently, there are five structurally distinct chemical classes that inhibit AHAS: the sulfonylureas,

Table 1 Herbicide Resistance Action Committee (HRAC) classification system in comparison to Weed Science Society of America (WSSA) and Australian code systems (presented in Menne and Köcher, 2012)

Site of action	*Chemical family*	*HRAC group*	*WSSA group*	*Australian group*
Inhibition of acetyl-CoA carboxylase (ACCase)	Aryloxphenoxy-propionate, cyclohexanedione, and phenylpyrazoline	A	1	A
Inhibition of acetolactate synthase and acetohydroxy acid synthase	Sulfonylurea, imidazolinone, triazolopyrimidine, pyrimidinyl(thio)benzoate, and sulfonylaminocarbonyl-triazolinone	B	2	B
Inhibition of photosynthesis at PSII	Triazine, triazinone, triazolinone, uracil, pyridazinone, and phenyl-carbamate	C1	5	C
Inhibition of photosynthesis at PSII	Urea and amide	C2	7	C
Inhibition of photosynthesis at PSII	Nitrile, benzothiadiazinone, and phenyl-pyridazine	C3	6	C
Photosystem I-electron diversion	Bipyridylium	D	22	L
Inhibition of protoporphyrinogen oxidase	Diphenylether, phenylpyrazole, *N*-phenylphthalimide, thiadiazole, oxadiazole, triazolinone, oxazolidinedione, pyrimidindione, and other[b]	E	14	G
Inhibition of the phytoene desaturase	Pyridazinone, pyridinecarboxamide, and others[b]	F1	12	F
Inhibition of 4-hydroxyphenyl-pyruvate-dioxygenase	Triketone, isoxazole, pyrazole, and others[b]	F2	27	H
Inhibition of carotenoid biosynthesis (unknown target)	Triazole, diphenylether, and urea (also C2)	F3	11	Q
Inhibition of 1-deoxy-d-xylose 5-phosphate synthase	Isoxazolidinone	F4	13	Q
Inhibition of 5-enolpyruvylshikimate-3-phosphate synthase	Glycine	G	9	M
Inhibition of glutamine synthetase	Phosphinic acid	H	10	N
Inhibition of dihydropteroate synthase	Carbamate	I	18	R
Inhibition of microtubule assembly	Dinitroaniline, phosphoroamidate, pyridine, benzamide, and benzoic acid	K1	13	D
Inhibition of mitosis/microtubule organization	Carbamate	K2	23	E
	Arylaminopropionic acid	K2	25	Z
Inhibition of very long chain fatty acids (inhibition of cell division)	Chloroacetamide, acetamide, oxyacetamide, tetrazolinone, isoxazoline[a], other[b]	K3	15	K
Inhibition of cell wall (cellulose) synthesis	Nitrile	L	20	O
	Benzamide	L	21	O
	Triazolocarboxamide	L	28	
	Alkylazine	L	29c	
Uncoupling (membrane disruption)	Dinitrophenol	M	24	
Inhibition of lipid synthesis – not ACCase inhibition	Thiocarbamate and phosphorodithioate	N	8	J
	Benzofuran	N	16	J
	Chloro-carbonic-acid	N		J
Action like indole acetic acid (synthetic auxins)	Phenoxy-carboxylic-acid, benzoic acid, pyridine carboxylic acid, quinoline-carboxylic acid, and other[b]	O	4	I
Inhibition of auxin transport	Phthalamate and semicarbazone	P	19	P
Unknown *Note*: Although the mode of action of herbicides in Group Z is unknown, it is likely that they differ in mode of action between themselves and from other groups.	Pyrazolium	Z	26	
	Organoarsenical	Z	17	Z
	Other[b]	Z	26	

Source: Reproduced from Menne, H., Köcher, H., 2012. HRAC classification of herbicides and resistance development. In: Krämer, W., Schirmer, U., Jeschke, P., Witschel, M. (Eds.), Modern Crop Protection Compound, second ed. Weinheim: Wiley-VCH Verlag GmbH & Co, pp. 5–28.

imidazolinones, triazolopyrimidines, pyrimindinyl (thio) benzoates, and sulfonylaminocarbonyl-triazolinones with more than 50 unique active ingredients. Total global market value is estimated at US$3.0 billion, despite the widespread occurrence of resistance.

AHAS catalyzes the first committed step in the biosynthetic pathway of the branched-chain amino acids and is localized in the chloroplasts. Also referred to as acetolactate synthase (ALS), the multisubunit enzyme begins a series of condensation reactions that result in the formation of leucine,

isoleucine, and valine. The inhibition of AHAS by herbicides is a complex time-dependent process that is not well understood. It also appears that each herbicide interacts in a subtle and unique way with AHAS. Binding is a slow-tight reaction, and has been described as uncompetitive or noncompetitive, depending on the individual active ingredient. Several reviews of both AHAS (Umbarger, 1978; Chipman *et al.*, 1998; Duggleby and Pang, 2000; Duggleby *et al.*, 2004; McCourt and Duggleby, 2006; Duggleby *et al.*, 2008 and of AHAS inhibition (Gutteridge and Thompson, 2012) are available.

The sulfonylurea herbicide chlorsulfuron was the first AHAS inhibitor introduced. It was highly selective for broadleaf weeds in wheat. As more analogs were discovered, however, it became apparent sulfonylurea herbicides were not only highly selective but would also control both grass and broadleaf weeds. Similar levels of selectivity were observed in the other AHAS inhibitor chemical classes. Selectivity is often achieved by slight changes in the herbicide molecule base structure. For instance, imazapyr, imazapic, and imazethapyr vary considerably in selectivity (least to greatest, respectively). The addition of a methyl group to imazapyr (largely nonselective) yields imazapic (selective in peanut) whereas the addition of an ethyl group yields imazethapyr (selective in a broad range of legume crops). Behavior in plants and soil by AHAS-inhibiting herbicides is as variable as the compounds themselves. Selectivity is usually achieved by differential metabolism. Soil breakdown is usually through microbial degradation or chemical hydrolysis; however, the combination of chemical properties and activity at very low concentrations can combine to cause very long plant back restrictions that number in years.

Photosystem Inhibitors (Groups C and D)

Shortly after World War II, the ureas became the first major chemical family of the photosystem II inhibitors to be discovered and developed. However, it was not until 1952 that a series of patents were granted to E. I. du Pont de Nemours & Company. As a result of the success of the patent series, DuPont developed and released diuron, fenuron, monuron, and neburon for commercial use. The triazines were discovered in 1952 in Switzerland and initial patent applications were made two years later. Atrazine, simazine, prometryn, and ametryn were the first major compounds to display unique selectivity. The herbicidal activity of diquat and paraquat, the two herbicides that inhibit photosystem I, was first documented and described by Brian *et al.* (1958). The photosystem II and photosystem I inhibitors are among the most important herbicides, and atrazine was the most widely used pesticide globally until it was recently displaced by glyphosate. The Group C herbicides are used in a wide variety of applications, whereas the Group D herbicides are exclusively postemergence nonselective herbicides.

Inhibitors of photosynthesis act by blocking or diverting energy dissipation or transfer within the photosynthetic apparatus, causing accumulations of membrane-disrupting radicals. The processes are well understood, as several members of this herbicide group were used to elucidate the process of photosynthesis. Photosystem II inhibiting herbicides comprise ten chemical families including the amides, benzothiadiazinones, nitriles, phenylcarbamates, phenyl-pyridazines, pyridazinone, triazines, triazinones, uracils, and ureas. Triazines and ureas are the two largest families of the photosystem II inhibitors and are the most widely used. Photosystem I inhibitors consist of one chemical family (the bipyridilliums) and two herbicides (paraquat and diquat). The light-dependent reactions occur in two photosystems known as the PSII and PSI light-harvesting complexes. The two photosystems are pigment–protein complexes spanning the thylakoid membrane within chloroplasts and are associated with the ATP synthase complex (Cobb and Reade, 2010). Light is required directly or indirectly for the activity of herbicides that inhibit photosynthesis.

Photosystem II inhibitors bind to the D1 protein in photosystem II. There are five hydrophobic amino acid helices in the D1 protein that span the thylakoid membrane. What is known as the Q_B binding niche in the D1 protein consists of five hydrophobic amino acid helices spanning the thylakoid membrane (Tietjen *et al.*, 1991; Xiong *et al.*, 1996). The Q_B binding niche is located near the surface of the membrane on the stroma side between the fourth and fifth span of the D1 peptide. When a herbicide occupies the binding pocket, electron flow is blocked, and the resulting singlet chlorophyll energy cannot be transferred to the photosystem II reaction centers. Triplet chlorophyll is formed as the short-lived singlet chlorophyll molecules accumulate, ultimately resulting in an overloading of the carotenoid system and an initiation of lipid peroxidation. Ultimately, membrane destruction is the end result and results in the primary outward symptom of photosystem II inhibitors, necrosis (Hess, 2000).

Group D herbicides, paraquat and diquat (bipyridiniums), divert electrons away from ferredoxin in PSI by competing with ferredoxin to capture electrons (Percival and Baker, 1991). Both are considered contact-type herbicides and are applied to leaves. Phytotoxicity is not only the result of nicotinamide adenine dinucleotide phosphate and ATP depletion, but also through the generation of free hydroxyl radicals from superoxide and hydrogen peroxide accumulation. After capturing electrons, both chemicals form unstable bipyridyl radical cations (Percival and Baker, 1991). The herbicide radical can react with oxygen to form superoxide radicals (O_2^-). The radical is then dissipated through the activity of superoxide dismutase to form hydrogen peroxide (H_2O_2) and α-tocopherol (Halliwell, 1991; Hess, 2000). Hydrogen peroxide is catalyzed or routed through the ascorbate-glutathione cycle to form oxygen and water. However, excessive production of superoxide and hydrogen peroxide form when the herbicides are present both processes are not able to dissipate the resulting accumulation of superoxide and hydrogen peroxide. Subsequently, these two radicals react with each other to create hydroxyl radicals ($OH^{\bullet}$) catalyzed by iron or copper. Hydroxyl radicals initiate lipid peroxidation causing cell membrane destruction as described previously (Hess, 2000). Interestingly, the herbicide, once it has transferred energy from ferredoxin, is available to repeat the process.

Interestingly, the symptoms of chlorosis and necrosis associated with these herbicides do not result primarily by the inhibition of target sites in Photosystem II and Photosystem I. Rather, membrane destruction is caused by lipid peroxidation

of polyunsaturated fatty acids as a consequence of radical formation resulting from photosystem perturbation (Hess, 2000). Thus, photosystem inhibitors differ in their site and mode of action: Photosystem II, Photosystem I, PROTOX, and carotenoid-synthesis inhibitors cause necrosis of plant tissues due to destruction of membrane integrity via lipid peroxidation (Hess, 2000). The process is facilitated by the production of free oxygen radicals and their effects on polyunsaturated fatty acids such as linoleic (18:2) and linolenic acid (18:3). As Hess (2000) described in a thorough review, there are three steps: initiation, propagation, and termination. Initiation begins when radicals such as singlet oxygen (as generated by Photosystem I inhibitors), a hydroxyl radical (as generated by Photosystem II inhibitors), or triplet chlorophyll react with polyunsaturated fatty acids, a component of plant membranes. In the initiation step oxygen interacts with the lipid radical that generates a peroxidized lipid radical, which then reacts with other fatty acid molecules. The process propagates unstable lipid peroxides within the membrane in the second step. In the termination step, lipid peroxide is degraded to short-chain hydrocarbon gases that ultimately lead to damage of plant membranes (Hess, 2000; Halliwell, 1991).

Protoporphyrinogen Oxidase Inhibitors (Group E)

Herbicides possessing protoporphyrinogen oxidase (PPO) (EC 1.3.3.4) inhibiting properties are diverse with over nine structural classifications. All PPO herbicides are classified together as group E by HRAC or group 14 by the Weed Science Society of America (WSSA). Discovery of PPO herbicides began in 1963 with the patent of the diphenylether nitrofen (Wilson and McRae, 1963). From that release, the agrochemical industry launched extensive research efforts to exploit the mode of action as PPO activity exhibited numerous possibilities for compound development. The potential was diminished as many of the highly biologically active compounds lacked clear crop selectivity (Theodoridis *et al.*, 2012). For this reason, PPOs can be used as a nonselective burndown application. Crop-selective compounds have been developed such as fomesafen, the postemergence soybean-selective compound (Cartwright and Collins, 1981) and preemergence soybean compound sulfentrazone (Theodoridis *et al.*, 2012). The latest registry of a PPO herbicide was made in 2009 with saflufenacil and is labeled for uses as a contact burndown herbicide and for preemergence broadleaf weed control in several row crops (Grossmann *et al.*, 2010). Saflufenacil was introduced in part to manage glyphosate-resistant weeds. PPO inhibitors are used primarily as preemergence and some postemergence applications, and their use has increased recently.

Protoporphyrin IX (PPIX), a tetrapyrrole, is the main structural component of both heme, the red-colored cofactor of hemoglobin, and chlorophyll, the green pigment of plants. Heme proteins have a Fe cofactor positioned near the center of the tetrapyrrole ring that serves as a receptor for gaseous XO molecules (X═C, N, O) (Spiro *et al.*, 2013). The PPIX component of chlorophyll found in plants has an Mg cofactor at the center of the tetrapyrrole ring. The chlorophyll structure acts as a light receptor, absorbing energy that is then transferred by resonance to a specific set of chlorophyll molecules (P680 and P700) at the reaction centers of photosystem II and I. Light energy and transfer causes charge separation, redox reaction and donation of an electron that can move through the electron-transport chain leading to the reduction of NADP and a proton gradient in the thylakoid lumen to generate ATP (Raven *et al.*, 2005). The last step in PPIX synthesis is the oxidation of protoporphyrinogen IX by the enzyme protoporphyrinogen IX oxidase (PPO, EC 1.3.3.4), which utilizes molecular oxygen (Matringe and Scalla, 1988; Matringe *et al.*, 1989a,b). The enzymatic step is conserved for both heme and chlorophyll biosynthesis. Inhibition of PPO by herbicides causes the accumulation of the reaction product (PPIX) but not the substrate protoporphyrinogen IX. Excess PPIX undergoes nonenzymatic oxidation in the presence of light and oxygen, which in turn produces large amounts of single oxygen and hydrogen peroxide (H_2O_2) within the cell (Witkowski and Halling, 1988). Reactive oxygen species cause breakdown of membranes through lipid peroxidation of unsaturated fatty acid bonds. Loss of membrane integrity allows for cellular leakage leading to necrosis and death of leaves (Becerril and Duke, 1989). Symptoms of PPO herbicides include a wetting appearance on the leaves followed by yellowing and necrosis. Because of their fast activity, PPO herbicides are designated as contact herbicides and have little to no translocation. Herbicides are applied both foliarly and to the soil as preemergent applications to control sprouting weeds.

Carotenoid Biosynthesis Inhibition (Group F1, F3, and F4)

Carotenoids are essential secondary metabolites initially derived from 5-carbon isoprene units. There are two known pathways in isoprene biosynthesis, the cytosolic mevalonate (MVA) pathway and the plastidial nonmevalonate. A 20-carbon (4 isoprene) geranylgeranyl diphosphate (GGPP) molecule is the building block of carotenoids and many other isoprene-derived metabolites (diterpenes). Joining of two GGPPs forms the precursor molecule to the first committed step in carotenoid production, phytoene, a tetraterpene (Hirschberg, 2001). Subsequent desaturation of phytoene to z-carotene by the enzyme phytoene desaturase (PDS, EC 1.3.99.30) is the target for herbicides grouped by the HRAC in F_1 or WSSA in group 12 (**Table 1**). PDS-targeting herbicides are characterized as pigment synthesis inhibiting or bleaching herbicides. Symptoms are similar to HPPD-targeting herbicides; indeed, PDS and HPPD inhibitors both disrupt carotenoid biosynthesis albeit at different enzymatic steps, PDS being several steps downstream of HPPD. Carotenoid pigments play an important role in photosynthesis as light-harvesting accessory pigments within the light-harvesting complex (Ritz *et al.*, 2000) with a dual function as electron acceptors in photosynthetic electron transfer (Pillai *et al.*, 2013). Carotenoids, particularly carotenes, protect chloroplasts from photo-damaging effects of high-energy oxidative triplet chlorophyll and singlet oxygen by removing excess light or scavenging high-energy species before they can oxidize lipids, proteins, or deoxyribonucleic acid (DNA) (Di Mascio *et al.*, 1990). For further description of carotenoid synthesis and inhibition, refer the Section 4-Hydroxyphenylpyruvate

Dioxygenase Inhibitors (Group F2). Inhibitors of carotenoid biosynthesis are increasingly important herbicides and are widely used in major row crops in premergence and postemergence applications.

Commercial herbicides in group F_1 include seven major active compounds: diflufenican, fluorochloridone, fluridone, flurtamone, norflurazon, picolinafen, beflubutamid. All commercial products, with the exception of picolinafen and fluridone, are applied as pre or early postemergence for broadleaf weed control. Picolinafen can be applied in postemergence applications in cereals, usually in combination with other cereal herbicides. Fluridone is mainly used as an aquatic herbicide to control submerged and emerged aquatic plants but also has selectivity to cotton. Diflufenican and beflubutamid are exclusively applied in cereals whereas fluorochloridone, flurtamone and norflurazon have uses in other crops such as peanuts, cotton, and sunflower.

Although PDS and HPPD herbicides are the main target sites that inhibit carotenoid synthesis, there are other noteworthy herbicides that share bleaching symptoms but have different and in some cases unknown targets. A plant metabolized product of the herbicide clomazone, 5-ketoclomazone, inhibits an early step of the nonmevalonate plastidial isoprene biosynthesis pathway (Ferhatoglu and Barrett, 2006). The compound 5-ketoclomazone inhibits the enzymatic step that joins pyruvate and glyceraldehyde 3-phosphate to make 1-deoxy-D-xylulose 5-phosphate (DOXP, EC 2.2.1.7) hence the designation as a DOXP synthase inhibitor. Clomazone stands alone as group F_4 or 13 by HRAC and WSSA designations, respectively. Clomazone is a broad-spectrum herbicide labeled for use mainly as a preemergent or early post soil-applied herbicide in several vegetable crops and some row crops (Ferhatoglu and Barrett, 2006).

The cyclization of lycopene, a precursor to carotene that gives tomatoes their red color, is another site of action of carotenoid inhibitors. The substituted diethylamine herbicides *N*,*N*-diethyl-*N*-[2-(4-chloro-phenylthio)ethyl]amine) and *N*,*N*-diethyl-*N*-[2-(4-methylphenoxy)ethyl]amine are noncompetitive inhibitors of lycopene cyclase (Schnurr *et al.*, 1998) although their utility as commercial herbicides has yet to be determined. The commercially applied herbicide amitrole, an amino-substituted triazole, causes the accumulation of lycopene that does not appear to directly inhibit lycopene cyclase but rather, an earlier as yet undetermined step in carotenoid biosynthesis (Agnolucci *et al.*, 1996; Fedtke and Duke, 2005; Schnurr *et al.*, 1998). Amitrole is classified with fluometuron and the diphenylether, aclonifen, as unknown target sites in the HRAC F_3 group.

4-Hydroxyphenylpyruvate Dioxygenase Inhibitors (Group F2)

The discovery of herbicides that inhibit the enzyme HPPD (EC 1.13.11.27) began in 1977 with an observation made by a research biologist Reed Gray while working at the Western Regional Utilization Center in California. He noticed that few weeds grew beneath the bottle brush [*Callistemon citrinus* (Curtis) Skeels] plants in his backyard (Gray *et al.*, 1980). After extraction and fractionation of soil samples collected from under the plants, the natural product leptospermone was isolated as the active compound. Leptospermone had been previously discovered in the volatile oils of Australian myrtaceous plants, but biological activity was not characterized with the original discovery (Hellyer, 1968). Pure leptospermone has unique herbicidal bleaching activity but only at high rates ($\sim 9\ kg\ ha^{-1}$) (Gray *et al.*, 1980).

HPPD inhibitors compete with the substrate hydroxyphenylpyruvate, the first step of tyrosine degradation by inhibiting the dioxygenation step (Moran, 2005). When HPPD is inhibited, homogentisate (HG) cannot be formed. HG is a key biosynthetic precursor of plastoquinones (PQ) and plant tocopherols (vitamin E) (Eckardt, 2003; Schultz *et al.*, 1985). Plastoquinones are essential electron acceptors necessary for carotenoid biosynthesis with dual function as electron carriers of photosynthesis. The associated unsaturated prenyl chains of carotenoid molecules also act as electron quenchers to modulate the degradative effects of triplet chlorophyll, a high-energy form of chlorophyll produced naturally during photosynthesis (Pallett *et al.*, 1998). Triplet chlorophyll can further pass this imbalance of energy to oxygen to create unstable singlet oxygen species. Without the quenching effects of carotenoids, plastoquinones and tochopherols chlorophyll itself is decomposed by singlet oxygen (Di Mascio *et al.*, 1990). Excess singlet oxygen can further cause degradation of membrane lipids, protein, and DNA. Lack of PQ and tocopherol coupled with downstream carotenoid absence causes the aforementioned bleaching symptom of treated plants. Although plants may grow for some time after herbicide exposure, deficiency of photosynthates coupled with accumulation of reactive oxygen species eventually overcomes further growth capabilities.

The structure of HPPD inhibitors stem from the original triketone design and are generally formed around a dicarbonyl ketone linkage of cyclic substructures, including isoxazoles and pyrazoles with multiple variations. The herbicide structures appear to bind the iron cofactor at the HPPD active site by mimicking the alpha-keto acid moiety of the natural substrate, hydroxyphenylpyruvate (He and Moran, 2009; Moran, 2005) as confirmed by homology modeling (Kakidani and Hirai, 2003) and herbicide-bound protein crystal structure determination (Brownlee *et al.*, 2004; Yang *et al.*, 2004).

HPPD herbicides have been selected for release based on crop tolerance, particularly to monocot species. Corn is the main selective crop with tolerance to mesotrione (Mitchell *et al.*, 2001), sulcotrione (Beaudegnies *et al.*, 2009), tembotrione (Santel, 2009), topramezone (Grossmann and Ehrhardt, 2007), and isoxaflutole (Pallett *et al.*, 2001). Pyrazolynate (Kubo *et al.*, 2012) and pyrazoxyfen (Copping and Hewitt, 1998) are labeled for use in rice whereas pyrasulfotole is used in small grains like wheat (Reddy, 2012) and sorghum (Fromme *et al.*, 2012). Use of bicyclopyrone is limited to sugarcane (Michel *et al.*, 2010).

5-Enolpyruvylshikimate-3-Phosphate Synthase Inhibitors (Group G)

Glyphosate, the only inhibitor of 5-enolpyruvylshikimate-3-phosphate synthase (EPSPS; EC 2.5.1.19), was first patented by

Stauffer Chemical Company as an industrial cleaner (American Chemical Society, 1997). Monsanto Chemical Company ultimately patented glyphosate as a nonselective herbicide in 1974. Initially, use of glyphosate was low primarily because it was nonselective and expensive. However, with the advent of transgenic glyphosate-resistant crops and the expiration of patents, glyphosate has become the most widely used herbicide in the world. In the United States, glyphosate has been the most commonly used pesticide since 2001, with >81.6 million kg used in 2007 (Grube *et al.*, 2011).

EPSPS is the penultimate enzyme in the aromatic amino acid pathway that ultimately produces tyrosine, tryptophan, and phenylalanine, and is fortuitously absent from mammals (Haslam, 1993). Inhibition of EPSPS depletes these important amino acids from treated plants; in turn, functional proteins cannot be synthesized. Under normal application conditions plant death usually results from depletion of important secondary plant metabolites, particularly those involved with disease resistance. The enzyme EPSPS is localized in the chloroplasts and converts shikimate-3-phosphate into enolpyruvylshikimate-3-phosphate (Amrhein *et al.*, 1980). The introduction of glyphosate to a plant system results in accumulation of shikimate as shikimate-3-phosphate, which is unstable. EPSPS is a monomeric enzyme composed of two domains joined by protein strands. When shikimate-3-phosphate binds to EPSPS, the two domains tighten together to trap the substrate in the active site (Schönbrunn *et al.*, 2001). Glyphosate then permanently occupies the binding site of the second substrate of EPSPS, phosphoenol pyruvate.

Glyphosate, as a zwitterion, is usually formulated as a salt. Three salts have been utilized: isopropylamine, trimesium, and potassium salts. Various uses exist for glyphosate and are usually built around achieving selectivity by placement, timing, or genetic modification. That topic is covered in another part of this Encyclopedia.

Glutamine Synthetase Inhibitors (Group H)

Glufosinate-ammonium is a nonselective, postemergence herbicide introduced in 1981 for total vegetation control. Glutamine synthetase (GS; EC 6.3.1.2) is the target enzyme for glufosinate-ammonium. GS is an important enzyme in nitrogen metabolism responsible for assimilation of ammonia. Ammonia is present in both the cytoplasm and the chloroplast and is produced by nitrate reductase or by photorespiration and deamination reactions,. The enzyme is responsible for the synthesis of the amino acid L-glutamine from L-glutamate, utilizing ATP and ammonia. Glufosinate-ammonium is a nonselective herbicide used in transgenic glufosinate-ammonium resistant crops and in vegetation management applications.

Glufosinate-ammonium is a structural analog of glutamic acid and inhibits GS at its active site; it is competitive with the substrate glutamate for the GS enzyme. Glufosinate appears to form an enzyme-glufosinate-phosphate complex that result in an irreversible inhibition of the enzyme. Symptomology appears rapidly, usually within 5 days. Although the accumulation of ammonia as a result of inhibition of GS by glufosinate is well documented, phytotoxicity can be remediated by the addition of glutamine despite increased accumulation of ammonia (Seelye *et al.*, 1995). Instead of ammonia accumulation causing the observed herbicidal activity, there is evidence that the loss of glutamate, an amino donor for the glycolate pathway, leads to the breakdown of the transamination reaction of glyoxylate to glycine in the photorespiration cycle. The resulting accumulation of glyoxylate inhibits ribulose-1,5 bisphosphate carboxylase/oxygenase, which in turn leads to an inhibition of the light reaction in photosynthesis (Hess, 2000).

Microtubule Assembly Inhibitors (Group K)

Herbicidal microtubule assembly inhibitors (MAI) are most effective when applied to the soil before weed seed germination to control annual grasses and small-seeded broadleaf weeds. Initially, these herbicides, specifically the dinitroanilines, were used as dyes due to their yellow color imparted by the two nitro groups on the phenyl ring. Classified by chemical structure they can be grouped into five families: the dinitroanilines, phosphoroamidates, pyridines, benzamides, and benzoic acids. The microtubule assembly inhibitors are typically used preemergence in an incredible diversity of crops and are among the most widely used family of herbicides.

Microtubles are hollow polymers made up of stacked proteins consisting of alpha and beta tubulin dimers. These dynamic structures form an intracellular network as part of the cytoskeleton that gives both stability and communication pathways within the cell. Microtubules are an integral component of cellular division ensuring proper dissemination of chromosomes to new cells and assisting in plant cytokinesis. MAIs act by inhibiting the ability of microtubules to perform their normal function, mainly during cellular division. MAI compounds are not readily translocated but are absorbed by meristmatic regions at the tips of roots or, to a lesser extent, apical meristems during seed germination. The major symptom of affected plants is root clubbing as a result of isodiametric cell expansion from a lack of cortical microtublues (Lickfeldt *et al.*, 2012). Inability to form root structures deprives the seedling from acquiring water and nutrients, effectively starving and killing the plant before it can establish.

The molecular sites of action of the MAI structural classes are different but all have the same cell-cycle inhibitory effect. The dinitroaniline herbicides bind specifically to the alpha subunit of the tubulin dimer in higher plants, preventing proper polymerization as demonstrated by *in vitro* experiments (Morejohn *et al.*, 1987) and by analysis of weed-resistance mechanisms (Anthony *et al.*, 1999; Hashim *et al.*, 2012). The phosphoroamidates have the same alpha-tubulin inhibitory effects based *in vitro* studies (Morejohn *et al.*, 1987), three-dimensional electrostatic similarities to dinitroanilines (Ellis *et al.*, 1994) and competitive binding to alpha-tubulin between oryzalin and amiprophos-methyl (Murthy *et al.*, 1994). The pyridine and benzamide herbicides do not bind to microtubules assemblies but rather are proposed to inhibit an unknown microtubule-associated protein (Lickfeldt *et al.*, 2012). Disruption of the microtubule-associated proteins affects spindle fibers during prometaphase, causing a shortening of kinetochore microtubules and an inability to properly

segregate chromosomes (Vaughan and Vaughn, 1987). The site of action for the benzoic acid microtubule disruptor chlorthal-dimethyl is yet to be discovered.

Cellulose Biosynthesis Inhibitors (Group L)

Cellulose biosynthesis inhibitors are a group of chemically unrelated compounds that inhibit the incorporation of glucose into crystalline cellulose as demonstrated by radiolabelled ^{14}C-glucose experiments (Dietrich and Laber, 2012). Compounds known to inhibit cellulose biosynthesis include benzonitriles, benzamides, isoxaben, trizolocarboxamides, alkylazines, thiatriazines, and *N*-aryl lactams. Of the several compounds known to inhibit cellulose biosynthesis, only a few have been commercialized, namely, dichlobenil, isoxaben, and indaziflam. All three have similar use profiles – they are applied preemergence and control weeds in the seedling stage, just after germination. All three are primarily used in the tree-fruit, turf, and ornamental markets, as there is no observable effect on established plants. The similarities end there, though, as the discovery of the individual active ingredients occurred over the span of 40 years, and each sparked site of action research ended inconclusively. Cellulose biosynthesis inhibitors are typically applied preemergence and are mostly used in noncropland and perennial crops such as orchards.

Cellulose biosynthesis is too complex to review here. There has been significant progress in our understanding of cellulose biosynthesis in recent years, much of it gleaned from identification of mutants with cellulose deficiencies in *Arabidopsis thaliana* (Guerriero *et al.*, 2010; Taylor, 2008). However, the application of that knowledge to the identification of the mechanism of action of cellulose biosynthesis inhibitors has not resulted in a definitive identification of a molecular target site. There are several candidates targets including proteins associated with the cellulose synthase complex.

Inhibition of Fatty Acid (N) and Very Long Chain Fatty Acid Biosynthesis (K_3)

According to the current HRAC classification, there are two main groups of herbicides that inhibit lipid metabolism on targets other than ACCase, group N and group K_3. Herbicides in group N have four main structural classes, including the benzofurans, chlorocarboxylic acids, phosphorodithioate and thiocarbamates. In group K_3, delineated as inhibitors of very long chain fatty acid (VLCFA), there are five main structural classes: the acetamides, chloroacetamides, oxyacetamides, tetrazolinones and other nonclassified structures. The K_3 herbicides are described as growth/cell-division inhibitors whereas group N are specified as inhibiting cellular metabolism. Common to compounds in both groups is their ability to inhibit long chain fatty acid metabolism effectively hindering growth in the root or shoot of susceptible species. Chemistries from this mode of action have been in commercial use for more than 60 years (Hamm, 1974) and continue to be robust with limited resistance reported (Heap, 2013).

VLCFAs have a long aliphatic carbon chain of >18 carbon atoms that are derived from stearic acid (C18:0). The extension of saturated carbon atoms to the C18 chain is achieved by a microsomal elongation system located in the endoplasmic reticulum and involves fatty acid elongase or 3-ketoacyl-CoA synthase (KCS) enzymes (Blacklock and Jaworski, 2006; Ghanevati and Jaworski, 2002; Joubès *et al.*, 2008; Todd *et al.*, 1999; Trenkamp *et al.*, 2004). VLCFAs serve several biological functions within the plant cell, including integral components or precursors to suberin, cutin and waxes, all important in leaf cuticle formation (Post-Beittenmiller, 1996); in seed storage triacylglycerols; in periderm and endodermis components; in glycosylphosphatidyl-inositol anchors in plasma membrane proteins; in sphingolipid components of various membranes; and in developmental patterning of plant organs (Bach and Faure, 2010; Nobusawa *et al.*, 2013). VLFCAs are synthesized by a multienzyme acyl-CoA elongase systems bound to the cell membrane that catalyzes a string of reactions similar to fatty acid synthase (Fehling and Mukherjee, 1991). Although these compounds have been grouped into mode of action categories based on symptomology and biochemical and physiological evidences, the identity of specific molecular sites of action has remained elusive but with some progress made in recent years. Molecular-genetic studies utilizing loss-of-function mutants, expression profiling and heterologous expression of candidate genes in yeast have identified the enzyme of the first step in VLFCA biosynthesis, KCS, to be a major target of K_3 herbicides (Trenkamp *et al.*, 2004). Interestingly, the N class herbicides did not have the same inhibitory effect in yeast even though VLCFA inhibition had previously been shown (Abulnaja and Harwood, 1991; Abulnaja *et al.*, 1992) and they phenocopy the VLCFA elongase (VLCFAE) mutant *fiddlehead* (Pruitt *et al.*, 2000; Yephremov *et al.*, 1999). Lack of activity in yeast is potentially due to the inability of yeast systems to make the bioactive form of the compounds, or the low bioavailability of the compounds in yeast cells (Trenkamp *et al.*, 2004).

In general, K_3 and N herbicides are applied preemergence or preplant-incorporated to soil. Major weed targets are annual grass species and some small-seeded broadleafs such as lambsquarters and pigweed. Herbicide is absorbed into the meristematic regions of germinating weed seed with little to no translocation following absorption. Arrest of cellular division in the meristems leads to plant death. The chloroacetamides including metolachlor, acetochlor, flufenacet, dimethenamid and others are among the most widely used herbicides due to their exceptional weed control, long residual activity in soil, and crop selectivity. Chloroacetamide herbicides are used in corn, sorghum, soybean, dry beans, peanuts, peas, cotton, and vegetable crops. The latest compound registered in the K_3 group was pyroxasulfone (2013), intended to be as a selective herbicide in corn, soybean, and wheat. The Group N herbicides, the thiocarbamates, including S-ethyl dipropylcarbamothioate, pebulate, butylate, vernolate, and others are used in much the same way as chloroacetamides; however, soil incorporation is important as many are volatile.

Auxin Mimics (Group O)

Otherwise known as growth regulators, auxin-mimic herbicides act as synthetic analogs similar to the plant-synthesized hormone indole-3-acetic acid (IAA). Auxin-mimic herbicides

have a chemical structure characterized by a planar aryl group with attached carboxyl functionality. Molecules can be divided into four main structural classes: the phenoxy-carboxylic acids, benzoic acids, pyridine/pyrimidine carboxylic acids, and quinoline-carboxylic acids. These herbicides are recognized for their low use rates and relative selectivity to monocot species as opposed to broadleaf susceptibility. Application is usually foliar with subsequent systemic translocation, mainly to meristematic regions. The first auxin-mimic, 2,4-D was registered in the United States in 1948 as a result of post WWII research (Cobb and Reade, 2010). Since the registration of 2,4-D, each decade has seen the release of a growth regulator herbicide. Although widely used, weed resistance has been less severe than that observed in 'newer' herbicide modes of action with 30 documented resistant species (Heap, 2013) most of which have limited distribution (Wright *et al.*, 2011). Owing to the robust nature of this herbicide class and the increase in herbicide-resistant weed species, 2,4-D-resistant transgenic crops have been developed that utilize a bacterial aryloxyalkanoate dioxygenase transgene to metabolically breakdown 2,4-D (Wright *et al.*, 2010).

Although auxin mimics are one of the oldest and most widely used herbicide types, the specific molecular site or sites of action have eluded researchers until recently. The past decade has shed light on molecular targets to auxin herbicide perception and response. The auxin-signaling pathway begins with IAA or an auxin-mimic binding to one of the receptors. The first characterized auxin-sensing protein described in *Arabidopsis* is the TRANSPORT INHIBITOR RESPONSE 1 (TIR1) protein; however, five other auxin-sensing proteins called AUXIN SIGNALING F-BOX (AFB) proteins have also been discovered in *Arabidopsis* and are being characterized (Dharmasiri *et al.*, 2005; Walsh *et al.*, 2006). The auxin receptors are F-box proteins and, in conjunction with SKP-1 and CUL-1 proteins, form a plant E3-Ubiquitin ligase complex. On perception by TIR1 or an AFB, auxin-response-transcriptional repressors AUX/IAA are targeted for ubiquitination and degradation allowing an auxin-response-factor protein, a transcriptional activator, to elicit downstream auxin-responsive gene transcription. Endogenous IAA acts as a plant hormone controlling physiological and morphological plant characteristics such as tropic responses, apical dominance, phyllotaxy, and embryogenesis (Muday, 2001; Jenik and Barton, 2005; Leyser, 2005; Reinhardt, 2005). IAA synthesis occurs in the apical meristem and then translocated throughout the plant where it is subject to intensive regulation at synthesis, transport, localization, derivatization, and degradation (Zhao, 2010). Auxin-mimic herbicides are long-lived xenobiotics that

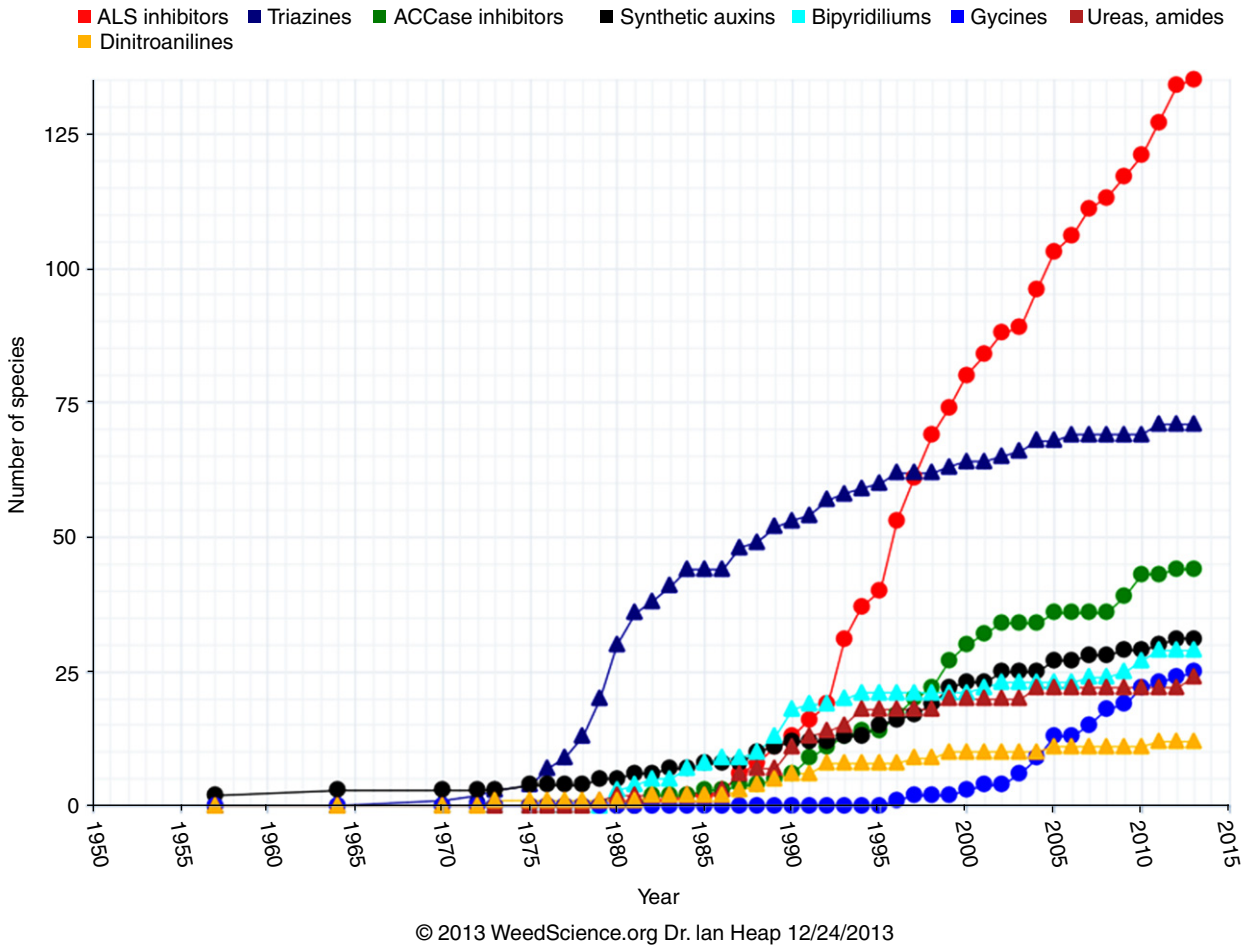


Figure 3 The chronological increase in resitant weeds globally, presented by herbicide mode of action. Reproduced from Heap, I., 2013. International Survey of Herbicide Resistant Weeds. Available at: www.weedscience.org (accessed 15.01.14).

are not subject to endogenous regulation and therefore elicit a prolonged cellular response. At the physiological level, extended auxin signaling by auxin-mimic herbicides causes upregulation in ACC synthase, leading to elevated ethylene levels that, in turn, activates ion channels and $+$H-ATPases, causing abnormal cell elongation and epinasty. Within hours of perception, abscisic acid biosynthesis genes are overexpressed, causing stomatal closure, inhibition of meristematic growth, and senescence. The further production of reactive oxygen species and cyanide leads to membrane degradation, chloroplast damage, and vasculature failure. The summation of metabolic and physiological response causes plant death (Grossmann, 2010).

A main characteristic of auxin mimics is their selectivity, particularly to dicot species. Grass crops do display herbicide injury if applications are made at certain growth stages high rates or applied to environmentally stressed plants. Phylogenetic analysis of the TIR1/AFB receptors from reported plant genomes indicates evolutionary conservation existing before monocot/dicot separation. Indeed, protein comparison between grasses and broadleaf plants reveals little distinction, suggesting that auxin perception is the same (McSteen, 2010). Tolerance in most grass species may be due to differential downstream metabolic and physiological responses (Walsh *et al.*, 2012). It has also been suggested that differences in vasculature anatomy and metabolism may play a role in grass tolerance (Gauvrit and Gaillardon, 1991; McSteen, 2010; Monaco *et al.*, 2002).

Herbicide Resistance in Weeds

Herbicide resistance in weeds, like herbicide fate, constitutes a broad branch of research involving herbicides and is beyond the scope of this article – but it is also the basis for its organization. The development of herbicide resistance in weeds is a major concern because it almost always results in increased costs, particularly in industrialized nations that have embraced the use of herbicides and crops genetically modified to resist them. Herbicide resistance was first documented in the 1970s, although instances of resistance occurred much earlier. There are currently 218 plant species resistant to herbicides globally (**Figure 3**; Heap, 2013), and that number is likely higher as reporting of resistance can be uneven and dependent on active weed science research programs focusing on resistance. Herbicide resistance is first an evolutionary process, and selection for herbicide resistance is dependent on a host of factors involving the genetic basis of the resistance, the biology of the weed species, the attributes of the herbicide, and how it is used (well summarized and reviewed by Powles and Yu, 2010) (**Table 2**). Herbicide resistance, particularly widespread glyphosate resistance in North America, has stimulated a resurgence in herbicide discovery and may well be the impetus for new herbicide modes of action in the future.

Table 2 Factors influencing evolution of herbicide resistance in weed populations

Genetic
Frequency of resistance genes
Number of resistance genes
Dominance of resistance genes
Fitness cost of resistance genes
Biology of weed species
Cross-pollination versus self-pollination
Seed production capacity
Seed longevity in soil seedbank
Seed/Pollen movement capacity
Herbicide
Chemical properties and structure
Site of action
Residual activity
Operational
Herbicide dose
Skills of the operator (treatment machinery, timing, environmental conditions, etc.)
Agro-ecosystem factors (nonherbiicde weed control practices, crop rotation, agronomy, etc.)

Source: Reproduced from Powles, S.B., Yu, Q., 2010. Evolution in action: Plants resistant to herbicides. Annual Review of Plant Biology 61, 317–347.

Summary

There are many herbicides, and there is significant amount of information available on their use, fate, and mode of action. Herbicides are currently the most readily identifiable tool for management of unwanted vegetation, and an integral part of industrialized weed management systems. In general, knowledge of their mode and mechanism of action is not necessary for their everyday use. However, modern weed managers and scientists are required to be familiar with their nature and properties as such information is needed when the use of herbicides results in unexpected results or when seeking new or novel uses.

Herbicides, like all other tools, can be used and misused. Of all the lessons of the herbicide era, the most important appears to be that herbicides have a limited effective life span, and overuse usually results in a shortened life span. Using herbicides in integrated weed management systems, instead of thinking of them as the primary tool for weed management, is the first step in sustaining the herbicide resource for the future.

See also: Advances in Pesticide Risk Reduction. Biotechnology: Herbicide-Resistant Crops. Genomics: Plant Genetic Improvement. Plant Biotic Stress: Weeds

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Relevant Websites

www.hracglobal.com
Herbicide Resistance Action Committee.
www.wssa.net
Weed Science Society of America.

Plant Health Management: Pathogen Suppressive Soils

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Glossary

Antibiosis An antagonistic interaction between two organisms where the outcome favoring one organism over the other is determined by a bioactive chemical to which the unsuccessful organism is sensitive.

Antibiotic A bioactive microbial metabolite that at low concentrations inhibits the growth or metabolic activities of other organisms.

Operational taxonomic units An operational taxonomic unit or taxonomic level of sampling, such as an individual, population, species, genus, or bacterial strain, based on a metagenomic similarity threshold.

Siderophore An iron-chelating compound produced by microorganisms to starve their neighbors of iron and hence have access to other nutrients.

Introduction

Plant diseases caused by soilborne pathogens represent one of the earliest scientific frontiers in plant health management that have seen only minor advances in understanding at the molecular biology and genetics levels in host–pathogen relationships compared with the spectacular advances of the past 25 year for the above-ground pathogens. This is particularly true for the root diseases caused by wide host-range pathogens, such as *Pythium*, *Rhizoctonia*, and *Fusarium* species. Of these three, *Pythium* is the most ubiquitous. Essentially 100% of the plants in a field may have root disease caused by one or more *Pythium* species and more likely one or more *Rhizoctonia* and *Fusarium* species as well. These root diseases can occur so uniformly and completely within a wheat field that they let one to accept the diseased crop as a healthy crop (Cook *et al.*, 1987) or to focus only on whatever disease(s) of the foliage or inflorescence may occur without even considering what may be going on below the ground. Likewise, data on crop losses caused by plant diseases tend to focus on above-ground diseases that are easy to measure using selective fungicides or resistant varieties without considering what the yield of that crop would be if free of root diseases. Nor do data on crop losses account for the environmental effects of root diseases, including nitrogen left unused in the soil, the need for more herbicide because the crop is less competitive with weeds, and less organic matter returned to the soil because of less plant biomass produced (Cook, 1992) – which are all outcomes of unmanaged root diseases. Besides being more difficult to study compared with above-ground diseases, the old adage 'out of sight out of mind' applies to root diseases as well.

Soil fumigation with any one of several gaseous fumigants (methyl bromide, chloropicrin, and metham sodium) is still the best tool to estimate the yield potential of a crop free or nearly free of root diseases. Early work with soil fumigation led to the term 'increased growth response' (IGR), because of the almost universal and often spectacular response of crops to one of these fumigants or to soil solarization (Gamliel and Katan, 2012). However, early and even some contemporary interpretations of the IGR, because it can be so spectacular (commonly 15–20% but also up to 100% greater yield), more often than not discounted root disease control in favor of a response to nitrogen or other nutrients released by the microbial biomass killed by the fumigant. At least four independent studies that went beyond measuring yield increases and also examined the roots came to conclusion that the IGR is due to control of minor root pathogens, especially the ubiquitous *Pythium* spp. (McLaughlin and Melhus, 1943; Bruehl, 1951; Wilhelm, 1965; Cook and Haglund, 1982; Cook *et al.*, 1987). Cook (1992) further showed with wheat at two eastern Washington locations and two fumigants, namely, 1,3-dichloropropane (Telone) and 1,3- dicholorpropane plus 17% chlorpicrin by volume (Telone C17), each at 240 l ha^{-1} injected and roller sealed in the soil, that both caused a flush of ammonium nitrogen in the top 15 cm of soil and that both significantly delayed the conversion of ammonium to nitrate, but only Telone C17 gave the IGR and only Telone C17 eliminated *Pythium* spp. from the soil based on dilution-plate counts on a *Pythium*-selective medium. These results not only confirmed that the flush of nitrogen is real but also experimentally separated the flush of nitrogen from the IGR. A separate study showed that, at harvest, nitrogen was left unused in progressively greater amounts in the wheat rooting zone at incremental depths down to 150 cm in nonfumigated soils but was fully used at all depths down 150 cm in fumigated soils. These results point clearly to the importance of root health to crop growth and use of available nitrogen.

The notion that crop rotation is practiced to maintain the fertility of the soil is erroneous. Other than nitrogen fixed by a legume, crops are net users of nitrogen, phosphorus, and other mineral nutrients. A 3-year wheat/oat/canola rotation or wheat/soybean/sugar beet rotation will deplete the soil of nutrients (that must then be replaced) as completely if not more completely than continuous monoculture wheat, because of less root disease. Yields go down with crop monoculture because the crop is depleted of roots and not because a monoculture crop depletes the soil of nutrients disproportionately more or faster than crops in a rotation. Plants with root disease tend to show symptoms not unlike plants lacking nitrogen, phosphorus, or other nutrient, which, of course, they are lacking, but due to lack of healthy roots and not due to lack of soil fertility.

Options for Management of Soilborne Plant Pathogens

The options available for practical management of soilborne plant pathogens include the following:

- soil treatments, such as fumigation, soil flooding, crop rotation, and soil solarization, to temporarily reduce or eliminate inoculum of soilborne pathogens;
- management of the environment of soilborne pathogens through row spacing, plant density, and planting-date effects;
- reduction of carryover inoculum through burial of infested crop residue and timely elimination of volunteer (self-sown) host plants, also known as green bridge management (Roget *et al.*, 1987; Smiley *et al.*, 1993);
- host plant resistance;
- selective inhibition of pathogens through use of fungicides; and
- biological control, including thorough exploitation of pathogen-suppressive soils.

Of the treatments used to reduce the inoculum load of pathogens in soil, fumigation (Wilhelm and Paulus, 1980), and solarization (Gamliel and Katan, 2012) are not only the most effective but also the most expensive treatments used and therefore are economical only on high-value horticultural crops and nursery plants. Soil solarization is further limited to areas with a hot climate. Soil flooding was once practiced by the United Fruit Company in Central America to control Fusarium wilt of banana (Stover, 1962), which undoubtedly helps to account for the few economically important soilborne pathogens of paddy rice but otherwise is no longer practiced to any extent worldwide. Crop rotations, especially 3-year and longer rotations, allow time for the pathogen(s) of one crop to drop below some economic threshold before planting that same crop in that same field again. However, economic advantages of specializing in one of the two crops have led increasingly to 2-year rotations, double cropping, and continuous crop monocultures worldwide.

Managing the environment of the pathogen is based on the classic host–pathogen–environment triangle, where the host is fully susceptible, the pathogen is both present and virulent, but the environment owing to microclimate effects, for example, dying or warming of the top few centimeters of soil, is less favorable to pathogens, such as *Pythium* and *Rhizoctonia* species. These effects are accomplished with practices such a planting on ridges and spacing the rows wider apart or in pairs rather than uniformly (Cook *et al.*, 2000) but requires the right equipment, timing, and skills. Burial of crop residue by deep plowing can be effective, especially when combined with a 2- or 3-year crop rotation but is also contrary to the need for greater adoption of no-till or direct-seed practices to save soil, water, time, and fuel while improving soil quality and often also providing more habitats for wildlife.

Except for host-specific pathogens, such as those responsible for Fusarium wilts of different crop species, virtually no progress has been made in the development of useful host plant resistance to soilborne plant pathogens. Even for root diseases caused by pathogens with a fairly narrow host range – such as *Gaeumannomyces graminis* var. *tritici*, cause of take-all of wheat and related grasses, and *Fusarium solani* f. sp. *pisi*, cause of root rot of peas – attempts initiated during the past century to find useful variation in resistance/susceptibility within the host species and its wild relatives have been unsuccessful and largely abandoned. Moreover, any evidence of resistance or tolerance in experimental field tests can be so subtle and variable that it requires a fully susceptible check strategically placed at multiple locations throughout the experimental test site so as to always have a check close by for comparative purposes. In addition, distinguishing differences in resistance or susceptibility of plant varieties and lines to a root disease require confirmation, meaning that the plant's roots must be dug from the soil, washed free of soil, and examined, which is inherently tedious work.

There has also been relatively little progress in the development of fungicides for control of soilborne plant pathogens. One exception is the oomycetes, including *Pythium* and *Phytophthora* species. As a research tool, granular metalaxyl applied in-furrow confirmed that *Pythium* root rot of wheat in eastern Washington was so uniform that, without the treated rows for comparison, one would believe that the untreated rows were perfectly healthy wheat (**Figure 1**). In practice, metalaxyl is used only as a seed treatment to protect the germinating seeds and then in combination with a fungicide to inhibit seed and seedling infection by *Rhizoctonia*, thereby avoiding a classic problem of control only of *Pythium* that can lead to more damage from *Rhizoctonia* and vice versa. Unfortunately, today's fungicides applied to seeds protect seeds during germination but do little on nothing to protect roots from infections.

Pathogen-Suppressive Soils Defined

Pathogen-suppressive soils have been defined as "The inhospitality of certain soils to some plant pathogens is such that either the pathogens cannot establish, they establish but fail to produce disease, or they establish and cause disease at first but



Figure 1 Winter wheat direct seeded (no-till) into standing wheat stubble with nitrogen, phosphorus, and sulfur applied below the seed in each seed row at planting, and metalaxyl also applied as a granular in the four indicted seed rows with the seed at planting, for control of Pythium root rot. Note that similar to the response of wheat and other crops to soil fumigation, except for the four treated rows, the check rows would be considered healthy.

diminish with continued monoculture of the crop" (Baker and Cook, 1974). The opposite of soils suppressive to plant pathogens are soils conducive to plant pathogens.

The suppressiveness of soils to pathogens has been further subdivided into 'general suppression' and 'specific suppression' (Weller *et al.*, 2002). General suppression relates usually to the total microbiological activity of the soil in contrast to specific suppression, which relates to the antagonistic activity of a specific group of microorganisms or possibly a single microbial species suppressive to a specific soilborne pathogen, operating in addition to and against a background of general suppression. Another key distinguishing feature is that general suppression is a natural and preexisting characteristic of soil and is not transferrable from field to field, whereas specific suppression develops in response to the presence of the pathogen or disease and is transferable from one soil to another. Although categorizing suppressive soils into these two types is useful for discussion, they should more appropriately be viewed not just as a combination but also as a continuum from general to specific suppression and as the likelihood of general suppression giving rise to specific suppression in response to specific cropping systems or management practices.

The existence of pathogen-suppressive soils has been recognized by growers and plant scientists since early in the twentieth century. Unfortunately, very few studies were carried out in those years to fully document the existence of these soils experimentally, because the priority typically would be to work on diseases that were problematic and not on those that were not problematic or that disappeared more or less spontaneously. Nevertheless, enough of the early day plant pathologists showed enough curiosity to at least document the occurrence of certain pathogen-suppressive soils long before the emergence of the molecular methods used today to characterize and shed light on the novel microbiological properties responsible for biological control of pathogens in these soils.

Today, research aimed at understanding the mechanisms responsible for the suppression of pathogen populations or their ability to cause disease is among the more scientifically interesting and exploitable areas of research on molecular plant–microbe interactions. Moreover, because the basis of soil suppressiveness to pathogens has thus far been shown to be microbiological, and not chemical or physical, pathogen-suppressive soils have never been considered anything other than examples of biological control caused by resident (indigenous) microorganisms. The suppression may be either direct through starvation, parasitic exploitation, or production of an antibiotic inhibitory to the pathogen (Cook and Baker, 1983) or indirect through induced resistance in the host plant to the pathogen (van Loon *et al.*, 1998).

General Suppression

Soilborne plant pathogens spend the great majority of their existence as dormant structures (chlamydospores, oospores, sclerotia, and dead host tissue colonized by the pathogen through parasitism while the host was still alive) waiting for a host root to come to them. Other than the rare exception, such as the production of root-like rhizomorphs by *Armillaria* species, soilborne plant pathogens do not grow through soil seeking a host root. This dormancy, known as 'soil fungistasis,' is universal to all soils (Lockwood, 1964). It is also universally overcome by nutrients, usually the simple sugars and amino acids (also volatiles) that diffuse as exudates from roots as they grow through soil. This is obviously an important survival mechanism for soilborne pathogens, as it assures that they remain dormant and therefore in relative safety until a host is nearby. It can be assumed that the signal(s) that trigger(s) germination or other response of the pathogen also 'tell' the pathogen which way to grow. Not surprisingly, the larger the survival structure or food base, the greater the distance the pathogen can grow to reach a host root, but the distance is still more likely in millimeters and not in centimeters (Wilkinson *et al.*, 1985). Conversely, the more suppressive the soil to that pathogen, the nearer to the root the pathogen must be to infect the root (Wilkinson *et al.*, 1985). Pathogens that survive as relatively small structures (20–50 um in diameter), such as oospores (*Pythium* spp.) and chlamydospores (*Fusarium* spp.), make up for their small size with numbers. Eastern Washington wheat field soils, for example, have an average of approximately 200 propagules of *Pythium* species (oospores and thick-walled sporangia) per gram in the top 15 cm of soil (Cook *et al.*, 1987). At a bulk density of 1.2 g cc^{-1} of soil, this translates to an average of approximately 240 propagules per cm^3 or 1 propagule in per 4 mm^3 of soil. No root as it emerges from a geminating seed and passes through the zone of greatest infestation can avoid coming into direct contact with several of these propagules.

General suppression need to be no more than an outcome of the rate at which root exudates or other nutrient sources are consumed by microorganisms in the rhizosphere. Think of the microbiological activity of soil as a fire burning the available carbon and energy sources as they are released from roots, where the greater the intensity of microbiological activity, the faster the rate of burn, the greater the general suppression, and the nearer the pathogen propagule must be to the root to have any chance of receiving sufficient nutrient to trigger germination and reach the root. Soils rich in organic matter because of regular inputs of decomposable biomass are generally more suppressive than soils naturally low in organic matter, such as arid lands or soils depleted of their organic matter because of years of tillage and removal of crop residue. Organic amendments in the form of barnyard manure and composts were among the first treatments shown already during the first half of the twentieth century to control a wide range of soilborne pathogens without understanding the mechanism(s) involved (Reviewed in Baker and Cook, 1974).

Broadbent and Baker (1974a,b; Reviewed in Baker and Cook, 1974) documented an example thought to be 'pathogen establishes but fails to produce disease' in their work with Phytophthora root rot of organically managed avocado trees in a rain forest environment of south Queensland, Australia. An avocado grove established in the early 1940s was still healthy with large high-yielding trees after 40+ years, in spite of growing in soil infested with *Phytophthora cinnamomi* and with 152 cm average rainfall known to favor this pathogen. In contrast, root rot caused by this pathogen was severe in groves of the neighbors of this grower. Suppressiveness was associated with soil organic matter maintained at approximately

12%, close to the natural surrounding rain forest soils before the orchard area was cleared and planted to avocado. This was accomplished by adding copious quantities of biomass as chicken manure, plowed-down corn stalks, and any other source of plant material that might have been available, along with calcium, with pH maintained between 6.0 and 7.0. In contrast, soils had become more acidic and the soil organic matter was mostly depleted by oxidation in neighboring orchards with extensive root rot and where no effort had been made to maintain a soil organic matter content similar to the surrounding undisturbed rain forest soil.

Essentially the healthy orchard was managed organically and the soil was described as a really 'live soil' based on the diversity and size of the microbial biomass. It would seem likely, therefore, that this is an example of general suppression. Although no particular organism or group of organisms could be shown to account for the suppressive effect, nor was the suppressiveness transferable, it was eliminated by waterlogging the soil and overcome by adding excessive quantities of *P. cinnamomi* inoculum. Increasing the inoculum density of the pathogen would effectively increase the number of propagules in direct contact with the root. No further research has been done to explain more fully the basis for the suppressive effect, but presumably the neighbors will have long ago adopted the organic method of managing their avocado orchards.

Soil solarization has also been shown to result in soil suppressive to pathogens, exemplified mainly by failure (or delay) of pathogens to recolonize the treated soil (Kassaby *et al.*, 1985; Greenberger *et al.*, 1987; Freeman *et al.*, 1990). The relatively mild heat, especially at lower depths, similar to pasteurization, is thought to kill inoculum of pathogens more efficiently than inoculum of saprophytes then left to recolonize the treated soil. Soil saprophytes are typically more thermotolerant than the inoculum of fungal and oomycete pathogens (Cook and Baker, 1983). The rapid colonists and likely antagonists of soilborne pathogens identified after soil solarization include *Trichoderma* spp., strains of the *Pseudomonas fluorescens* group, *Bacillus* spp., *Gliocladium*, and *Talaromyces*.

There is an assumed metabolic cost to propagules during their imposed dormancy in natural soil based on the observation that survival is longer if not indefinite in sterile soil but clearly finite in natural soil. A large metabolic cost and hence a shortened life expectancy for the pathogen owing to an intensely active soil microbiota would be an example of general suppression accounting for a failure of the pathogen to survive until the arrival of its host. The half-life of *Fusarium culmorum*, cause of *Fusarium* root and crown rot of wheat, was estimated at 215 days in a Ritzville silt loam with 250 cm annual rainfall and 350 days in a Palouse silt loam with 500 cm annual rainfall (Inglis and Cook, 1986). Both locations are in eastern Washington. Obviously a 1-year break from wheat or barley would not be long enough to control this pathogen by crop rotation at either location without the means to intensify microbial activity of these soils and thereby increase the metabolic cost to propagules during their dormancy. Unlike the tropical soils of south Queensland, the challenge for eastern Washington with its Mediterranean-like climate (most precipitation occurring during the fall and into spring, with dry summers) is that soils are cold and sometimes frozen when moist enough for microbiological activity and dry when warm enough for microbiological activity.

There is a risk when attempting to increase the suppressiveness of soils to pathogens by addition of organic matter if the biomass added is alive, for example, green manure. Soilborne plant pathogens are typically facultative parasites, meaning they can obtain their nourishment from either dead tissue (as a saprophyte) or live tissue (as a parasite). Thus, as long as the green manure remains alive in the soil, which could be 1 or 2 days or longer in moist soil at a favorable temperature, the only serious competition for colonization of the green tissues by a facultative parasite, such as a *Pythium* species, will be other facultative parasites. Trujillo and Hine (1965) showed that a high rate of mortality of papaya seedlings transplanted into soil where live residue of the previous papaya crop had been incorporated was due to buildup of *Pythium aphanidermatum* and *Phytophthora parasitica* on the live residue, thereby using the residue as a food base to attack the young papaya seedling. Before their work, the problem had been ascribed to toxicity of the papaya residue to the young papaya seedlings transplanted into the soil containing the residue.

However, pathogens that depend for survival between host plants on dead tissues of their host colonized through parasitism while the plant was still alive are then vulnerable to displacement within this food base by strict saprophytes, depending on their ability to maintain possession of this food base until a new host arrives (Bruehl, 1975). This vulnerability can explain why *G. graminis* var. *tritici*, cause of the root disease of wheat known as take-all, is controlled by only a 1-year break from wheat in the southeast United States, where soil microorganisms are active essentially year round, but requires a 2-year break or longer from wheat in the Inland Pacific Northwest, where soils typically are too dry for microbiological activity when warm and too cold when wet. Tang Wen-hua (unpublished) established a mutant strain of the take-all pathogen resistant to the fungicide benzimidozole in autoclaved oat grains that was then reduced to smaller particles in a coffee grinder, infiltrated the particles with a solution of benzimidozole, and added them as an inoculum source in soil in pots planted to wheat. The same oat grain particles colonized by the pathogen but infiltrated only with water were used as the control. The severity of take-all where benzimidozole-infiltrated inoculum was used was double of that where inoculum infiltrated only with water was used. The experimental design was based on the hypothesis that limiting colonization of the take-all pathogen's foodbase by competing fungi with a fungicide, such as benzimidozole, would increase the inoculum potential of this pathogen, which obviously is what happened.

Bruehl *et al.* (1969) showed that *Cephalosporium gramineum*, cause of a vascular disease of wheat known as Cephalosporium stripe, maintains possession of its food base (wheat straws colonized through parasitism) by production of a broad-spectrum antibiotic inhibitory to microorganisms that otherwise would colonize the straw and potentially displace *C. gramineum*. Antibiotic-negative mutants failed to survive, whereas wild-type strains survived in straw buried in soil up to two years. In essence, the antibiotic functions like benzimidozole in the experiment described above for protection of the

take-all pathogen from displacement in its food base by soil saprophytes. In this example, the antibiotic produced by *C. gramineum* serves to counter what otherwise would be an example of the pathogen failing to survive.

Rhizoctonia solani AG-8, cause of root rot of wheat, barley canola, peas, and safflower, among other hosts, lives between host crops as a colonist of roots, typically small roots. Hence, this pathogen is vulnerable to displacement relatively quickly, i.e., within a month or less, owing to colonization and decomposition of its food base by competing microorganisms in soil. Root tissues have a much lower carbon to nitrogen (C:N) ratio than stem tissues consisting of cellulose and lignin and therefore are more rapidly decomposed than stem tissues when dead. However, because of its wide host range, breaks between hosts need to be a plant-free fallow for at least a month when soil conditions are favorable for microbiological activity and longer if the fallow period includes winter months with subfreezing temperatures or an extended dry period (Roget *et al.*, 1987; Smiley *et al.*, 1993).

Suppression of pathogens through competition for their food base, potentially even displacing them in their food base, is one of the more common mechanisms of general suppression exemplified by a failure of the pathogen to survive. This form of suppression is among the most exploitable suppressions using crop rotation where enough time is allowed between host crops for displacement of the pathogen in its food base.

Role of Antibiosis in the Survival and Suppression of Soilborne Plant Pathogens

Antibiosis in the broadest sense of the term is an antagonistic interaction between two organisms where the outcome favoring one organism over the other is determined by a bioactive chemical to which the unsuccessful organism is sensitive. Antibiosis is an example of allelopathy usually applied to describe an antagonistic interaction between plants through production of a phytotoxic chemical. Two well-studied mechanisms of antibiosis postulated to be involved in pathogen-suppressive soils are inhibition by production of an antibiotic (Thomashow and Weller, 1995) and iron starvation by production of an iron-binding siderophore (Schroth and Hancock, 1982). Either mechanism of inhibition provides a means by which one organism can more effectively compete for carbon or other nutrient(s) in short supply, especially with its nearest relatives likely to depend on the same nutrients. Production of antibiotics and siderophores, whether in the rhizosphere, within the food base of a pathogen, or in the bulk soil, are site-specific processes. In other words, soil is not awash in these substances, even soils maintained at 12% organic matter content, such as the avocado orchard in south Queensland. For antibiosis to play a role in suppressive soil, the bioactive substance would need to be produced in the niche(s) occupied by the pathogen and the pathogen would need to be sensitive to the antibiotic or siderophore. More recent work shows further that antibiotics produced by bacteria modulate other processes essential to survival and function of the producing bacteria (Raaijmakers and Mazzola, 2012). Overall, the evidence is clear that antibiosis plays a role in the suppressiveness of soils to pathogens, both general and specific suppression.

Strains and species within the *P. fluorescens* group (within the γ subclass of Proteobacteria) have received the greatest attention because of their ability to produce a wide array of antibiotics and siderophores. Two factors led early to a focus on this large taxon of gram-negative bacteria and their roles in disease suppression: they were readily culturable, which opened the way for microbiologists and chemists to purify and work out the biochemistry of antibiotic biosynthesis; and the development of a semiselective medium (Rovira and Sands, 1970) that made it possible before the days of polymerase chain reaction (PCR) and other molecular methods to quantify their populations in soil and the rhizosphere. At least four antibiotics produced by the *Pseudomonas fluorscens* group, namely, pyoluteorin, pyrolnitrin, 2,4-diacetylphloroglucinol (DAPG), and phenazine-1-carboxylic acid, were early targets of research on their roles in disease suppression (Weller *et al.*, 2002). Moreover, the ability of different strains each to produce one or more of these antibiotics was shown to be highly conserved worldwide in subpopulations within the rhizospheres of different crops. Genome sequencings now reveal that the *P. fluorescens* group is even more diverse and heterogeneous than previously realized. A comparative analysis of the genomes of 10 strains of plant-associated *Pseudomonas* strains or species shown through previous studies to provide biological control of plant pathogens revealed that the core genomes (genes present in all 10 strains) made up only approximately half of the genes in any individual strain (Loper *et al.*, 2012). Roughly the other half of the genes in the ten strains consisted of each strain having hundreds of genes unique to that strain and responsible for the biosynthesis of the antibiotic 2-hexyl-5-propyl-alkylresorcinol, siderophores, and other biologically active metabolites not previously known to be produced by those strains.

In what is the first area-wide study of the natural production and accumulation of an antibiotic in a plant rhizosphere, D. Mavrodi *et al.* (2012) determined the populations of indigenous strains of *Pseudomonas* spp. with ability to produce the broad-spectrum antibiotic phenazine-1-carboxylic acid (Phz+ *Pseudomonas* spp.) in the rhizosphere of wheat collected from 61 commercial fields of winter wheat in an area of approximately 22 000 km^2. The area sampled stretches from north central Washington into northeastern Oregon and northern Idaho and is the largest contiguous cropping area in the Western United States. Cells of *Pseudomonas* spp. recovered from the wheat rhizosphere by dilution planting on the semiselective medium were screened by PCR for the *phzF* gene, one of a seven-gene locus shown earlier (Mavrodi *et al.* (1998)) to account for biosynthesis of phenazine-1-carboxylic acid. Liquid chromatography of processed samples representing wheat roots and tightly adhering soil was used to detect and quantify the antibiotic. Phz+ pseudomonads were detected in all fields sampled in populations ranging from log 3.2 to 7.1 g^{-1} fresh weight of root. The antibiotic was also detected, in nanogram amounts per gram fresh weight of roots from 26 of 26 fields selected, with a highly significant and direct relationship between the population of Phz+ pseudomonads and the amount of accumulated antibiotic. Of particular interest, there was a highly significant inverse

correlation between annual precipitation and root colonization by Phz+ pseudomonads, with the highest proportion of plants with roots colonized by Phz+ pseudomonads in areas receiving 350 mm of annual precipitation or less. This part of what is known as the Columbia Basin has been under cultivation for approximately 125 years, mostly in a dryland (rainfed) 2-year winter wheat/fallow rotation (one crop produced with two years of precipitation). Samples collected in the higher rainfall areas farther east toward and along the Idaho/Washington border (the Palouse) cropped annually in cereal-intensive or cereal/pulse rotations had the lowest frequency of Phz+ pseudomonads.

O. Mavrodi (2012) quantified the comparative frequencies and population densities of both Phz+ pseudomonads and strains of the *P. fluorescens* group with ability to produce the antibiotic DAPG (Phl+) in the semiarid region (150–300 mm annual precipitation) of the Columbia Basin for both rainfed and irrigated wheat. The method used to quantify Phl+ strains was similar to that used by D. Mavrodi for Phz+ strains, using PCR to screen cells with *PhlD*, one of a six-gene cluster shown to account for biosynthesis of this antibiotic (Bangera and Thomashow, 1999). Only Phz+ pseudomonads were detected in the rhizosphere of rainfed wheat. In contrast, of the 10 wheat fields irrigated by center pivot, all were colonized by Phl+ bacteria. From half to 100% of the roots from irrigated fields were colonized by Phl+ bacteria compared with less than half the roots in these fields colonized by Phz+ bacteria. Phz+ pseudomonads were below the detection level in 3 of the 10 irrigated fields.

These remarkable results point clearly to a role of Phz+ and Phl+ production and accumulation in the rhizosphere of wheat as an example of, potentially, a general suppression of what root pathogens provided by indigenous strains of the *P. fluorescens* group. Shifting from historically rainfed to irrigated wheat also shifted the makeup of the two populations from Phz+ dominant to Phl+ dominant. *Rhizoctonia* root rot and *Fusarium* root and crown rots are the dominant diseases in the lower rainfall areas, whereas take-all caused by *G. graminis* var. *tritici*, present at subclinical levels on rainfed wheat in this semiarid region, develops quickly into epidemic proportions once the wheat is irrigated. The widely documented spontaneous decline of take-all with continuous monoculture of wheat under high-rainfall or irrigated conditions and an example of specific suppression (see below) is due to Phl+ pseudomonads achieving threshold populations of log 6–7 g^{-1} fresh weight of wheat roots on essentially 100% of the roots (Weller *et al.*, 2002). *Rhizoctonia* root rot of wheat and barley in both Australia (Roget *et al.*, 1999) and the semiarid Inland Pacific Northwest has been documented to increase in importance with direct seeding but then decline after several more years of the same management (see below). *Rhizoctonia* is highly sensitive to phenazine-1-carboxylic acid that may provide some level of general suppression of this pathogen in the wheat-fallow rotation with mulch tillage but, similar to take-all decline (TAD), exemplify an example of control by induced suppression after several year of continuous wheat and barley sequences with direct seeding.

The role of siderophores in pathogen-suppressive soils received a great deal of attention by researchers in the 1980s (Kloepper *et al.*, 1980a,b; Schroth and Hancock, 1982). These studies also gave rise to the term Plant Growth-Promoting Rhizobacteria, referring to the IGRs when seeds of sugar beets or seed pieces of potatoes, for example, were treated with cell suspensions of siderophore-producing bacteria. Virtually all were members of the *P. fluorescens* group. In one study, soils suppressive to *G. graminis* var. *tritici*, cause of take-all of wheat, and *Fusarium oxysporum* f. sp. *lini*, cause of Fusarium wilt of flax, became conducive to these diseases with the addition of Fe(III)EDTA-, a form of iron highly available to microorganisms (Kloepper *et al.*, 1980a,b). Conversely, when a siderophore-producing pseudomonad or its siderophore psuedobactin were added to the conducive soil, the soil became suppressive to the two pathogens in separate tests. As there has been no clear evidence that siderophores contribute specifically to the suppression of a given pathogen on a given crop to fit with examples of specific suppression, yet are clearly factors in the antagonistic interactions of microorganism and soilborne plant pathogens, siderophore-producing soil and rhizosphere bacteria should be considered part of background (general) suppression.

Reflecting on the lack of genes for host plant resistance to soilborne plant pathogens, Cook *et al.* (1995) hypothesized that the plants may have evolved a different strategy for defense against root pathogens, namely, interactions with antibiotic-producing rhizosphere microorganisms. Stated another way, the widespread and even ubiquitous occurrence of these beneficial bacteria and especially their tendency as in the case of TAD to increase in numbers and activity in response to the disease on monoculture wheat would surely have eliminated or greatly diminished selection pressure on the host for resistant genotypes over the course of the evolution of this plant species and its relatives. Although crops species evolved as polycultures, crop rotation is an artifact of agriculture. Wheat and barley in particular evolved with their close relatives in almost solid stands in the Fertile Crescent, reseeding themselves in the same places and without benefit of tillage over centuries. With the tools now available to detect and quantify populations of antibiotic-producing bacteria over wide areas, as described above for rainfed wheat in Pacific Northwest Columbia Basin, the tools are now available to verify the extent to which this hypothesis is correct.

Specific Suppression

Fusarium Wilt-Suppressive Soils

One of the earliest-reported examples of a pathogen-suppressive soil, althought to result from failure of the pathogen to establish, was soil in Central America tolerant and intolerant to *F. oxysporum* f. sp. *cubense*, causing Fusarium wilt of banana (Reinking and Manns, 1933; Stover, 1962). Soils were classified as short, intermediate, and long life according to the length time required for an orchard to become unproductive because of wilt. Virtually 100% of the banana plants would die from wilt within 3–4 years in short-life soils but remain healthy and productive for 20–30 years in long-life soils. Some long-life soils were only a few yards from short-life soils. Snyder and Walker (1933), working in Wisconsin with the *F. oxysporum* f. sp. *pisi*, cause of Fusarium wilt of peas,

documented what they termed 'wilt-resistant soils,' whereby the pathogen established and spread rapidly in two different loams but failed to establish in Superior red clay, even when this soil was transported to and tested for potential for development of wilt in plots adjacent to the wilt-conducive loams.

Fusarium wilts are caused by different subspecies of *F. oxysporum* known taxonomically as formae speciales or f. sp., usually named after the species name of the host plant – f. sp. *lini* for the wilt pathogen of flax, f. sp. *cubense* for the wilt pathogen of banana, f. sp. *nivem* for the wilt pathogen of watermelon, f. sp. *lycopersici* for the wilt pathogen of tomato, f. sp. *pisi* for the wilt pathogen of peas, etc. Many formae speciales, in turn, are made up of races pathogenic to specific varieties of that plant species. Examples of soils suppressive to Fusarium wilts have been reported for a wide array of formae speciales on their respective host plants (Weller *et al.*, 2002), and soils suppressive to wilt caused by one formae speciales can also be suppressive to wilt caused by other formae speciales (Scher and Baker, 1980). Consistent with the classification of wilt-suppressive soils as examples of specific suppression, the suppressivness is eliminated by moist heat treatment as low as 54 °C (Scher and Baker, 1980) or γ-radiation (Alabouvette *et al.*, 1977) and is transferable by mixing a small amount of suppressive soil into a conducive soil or a suppressive soil rendered conducive by heat or other treatment (Alabouvette, 1986; Scher and Baker, 1980). Moreover, the suppressivness is specific to Fusarium wilts and does not affect *Fusarium* root rots (Weller *et al.*, 2002). In the case of *F. oxysporum* f. sp. *nivem*, suppressiveness was induced following four successive plantings of a moderately resistant variety of watermelon but not by four successive plantings of a fully susceptible variety of watermelon (Larkin *et al.*, 1993).

Most investigations of wilt suppression have identified a role for:

1. nonpathogenic *Fusarium* spp., including nonpathogenic *F. oxysporum* as competitors for carbon in the rhizosphere (Alabouvette, 1986; Larkin and Fravel, 1999);
2. induced resistance in response to certain strains of nonpathogenic *F. oxysporium* (Larkin and Fravel, 1999);
3. siderophore-producing strains of *Pseudomonas* bacteria that starve the pathogen of iron in the rhizosphere or during the infection process (Scher and Baker, 1980); and
4. phenazine (*phzC*+) antibiotic produced by fluorescent *Pseudomonas* spp. acting synergistically with carbon competition from nonpathogenic *F. oxysporum* (Mazurier *et al.*, 2009).

Mazurier *et al.* (2009) compared the frequency of antibiotic-producing fluorescent *Pseudomonas* species in bulk and rhizosphere soils conducive and suppressive, respectively, to Fusarium wilts. The suppressive soil was from the Chateaurenard region of France and shown through extensive earlier studies by Alabouvette (1986) to be highly suppressive to Fusarium wilts of several crops. Fluorescent *Pseudomonas* spp. positive for production of DAPG (PhlD+) were not detected in bulk soil of either the conducive or suppressive soil. In contrast, strains positive for production of phenazine (PhzC+) were detected in bulk-suppressive soil but not bulk-conducive soil. When the populations of these antibiotic-producing bacteria were determined for rhizosphere soil of both flax and tomato, PhzC+ strains were not detected in the conducive soil but were readily detected in the rhizosphere of these two wilt suscepts in suppressive soil. Strains of PhlD+ bacteria were marginally detected in rhizosphere soil of both plants in both conducive and suppressive soils. In tests for biological control, antibiotic-negative (PhlD–) and wild-type strains (PhlD+) were equally suppressive to wilt of flax alone or in combination with nonpathogenic *F. oxysporum*, indicating that the phloroglucinal antibiotic had no role in wilt suppression. In contrast, a mutant strain negative for production of phenazine was also negative for disease suppression when combined with carbon competition from *F. oxysporum*.

Mazurier *et al.* (2009) proposed a model that takes into account all four mechanisms of wilt suppression acting synergistically or sequentially. A greater microbial biomass in the Chateaurenard soil compared with the conducive soil was proposed to provide a naturally more intensely competitive soil environment as a background to the more specific mechanisms of carbon and iron competition and phenazine antibiosis. Their model also takes into account several physical and chemical factors of soil, such as a higher pH in the suppressive than the conducive soil, making iron less available and hence competition for iron more critical.

The fact that Fusarium wilt-suppressive soils have been identified for many different formae speciales of the pathogen and that soils suppressive to wilt caused by one formae speciales are also suppressive to wilt caused by other formae speciales, would suggest a common mechanism of suppression. Induced resistance in response to nonpathogenic *F. oxysporum* could well be that common mechanism enhanced by a background of general suppression includes the other demonstrated mechanisms of suppression – competition for carbon and iron and production of phenazine antibiotic. In one of the clearest examples of induced resistance, Larkin and Fravel (1999) used a split-root system to show that of the three different isolates of nonpathogenic *Fusarium* spp. found earlier to limit the incidence of Fusarium wilt, each provided a level of induced resistance to each of Fusarium wilt of melon caused by *F. oxysporum* f. sp. *niveum* and of tomato caused by *F. oxysporum* f. sp. *lycopersici*, where half of each root system was exposed to one of the nonpathogens and other half in a separate pot was exposed to the pathogen.

The Fusarium wilt syndrome starting with infection and ending with a wilted plant has been worked out by Beckman (1987, 1990) for Fusarium wilt of banana caused by *F. oxysporum* f. sp. *cubense*. The pathogen, residing in soil as dormant chlamydospores, is stimulated by root exudates to begin growth, similar to any other pathogen existing dormant in soil waiting for a host root to grow near it. The pathogen enters the root behind the root tip, in the region not yet differentiated into vascular tissue. As the xylem forms in the region of maturation, the pathogen is now positioned to begin its journey to the top of the plant. It does this by producing microconidia that are carried upward with the water stream in the xylem. Xylem end walls are perforated, so they function like sieves. When a microconidium reaches an end wall, it germinates, grows through an opening in the end wall, and produces more microconidia that are then carried upward in the water stream to the next end wall. This process is repeated until the

pathogen reaches the petioles and ever-smaller veins in the leaves, which is when the plant begins to wilt and then die. The host, meanwhile, is not passive to this process. It reacts by attempting to wall off the pathogen by formation of gels and tyloses within the xylem. Susceptibility is when the pathogen stays just ahead of the walling-off or occlusion process, meaning that the host essentially plugs up its own water-conducing system. The pathogen now distributed inside the dead plant is positioned to begin its saprophytic survival by colonizing and taking possession of its dead host from the inside out. Resistance is when the occlusion reaction is fast enough to stay ahead of the invading pathogen, thereby walling it off near the beginning of its journey to the top.

Nonpathogenic *Fusarium* spp., including or especially nonpathogenic *F. oxysporum*, are ubiquitous in cultivated soils, living mainly as colonists of root cortical tissues, much like endophytes, where they are poised to more fully colonize the root ahead of any competition once the root dies. Like the endophytes of leaves, these root inhabitants are limited to root cortical tissues, presumably by host defenses. A Fusarium wilt-suppressive soil may include the presence within that soil of strains or subspecies of nonpathogenic *F. oxysporum* that not only respond preemptively to the same carbon, energy, and other signals from host roots that trigger growth of the pathogen but also triggers a rapid resistance response of the host in time to wall off the pathogen as well as the non-pathogen. A moderately resistant cultivar might then perform more like a fully resistant cultivar, as was found after four successive plantings of the variety of watermelon moderately resistant to wilt caused by *F. oxysporum* f. sp. *niven* (Larkin *et al.*, 1993).

Although a single mechanism is not likely to explain the many examples of Fusarium wilt-suppressive soils worldwide, the one common and consistent denominator is a clear association with nonpathogenic strains of *F. oxysporum*. Moreover, a study of the genetic diversity of nonpathogenic *F. oxysporum* revealed similar populations in two fields several kilometers apart in the Chateaurenard region of France known for its soils suppressive to Fusarium wilts, as well as evidence that the same genotypes occur and have remained a stable component within the diversity of genotypes of nonpathogenic *F. oxysporum* within these fields over time (Edel *et al.*, 2001) in the same way that long-life soils in Central America have remained stable over time.

Development of Suppressive Soil with Crop Monoculture

One of the earliest documented example of a soil being conducive and then suppressive to a pathogen with continuous monoculture of the host is Phymatotrichum root rot of cotton and other susceptible hosts. *Phymatotrichum omnivorum* has a wide host range, although economically it has been particularly important on cotton in Texas and alfalfa in Arizona. The disease on cotton occurs as patches that become gradually larger but then disappear, according to observations by Scofield (1919); McNmara *et al.* (1931) confirmed the observations of Scofield but noted further that disappearance of the patches in stands of cotton begins in the centers. Similarly in alfalfa, the disease begins as patches that gradually become rings, much like a fairy ring (King, 1923); King (1923) confirmed that alfalfa plants recover over time starting in the center but showed further that cow peas, in spite of their susceptibility to *P. omnivorum*, remained healthy for the entire season when planted into the center of a Phymatotrichum ring in a stand of alfalfa. Apparently, no further research has been done to explain why the rings (or spots) disappear, reappear, or disappear starting at the center.

Common scab of potatoes caused by *Streptomyces scabies* was observed early in the last century to decline with potato monoculture. In plots subjected to different rotations under irrigation in Nebraska during the period 1912–36, with the incidence and severity of common scab recorded for potatoes each year starting in 1929, scab was recorded initially as severe or pitted but then became nonexistent where potatoes were grown continuously. In contrast, both severe and pitted occurred in each of plots where potatoes were grown in a sugar beet/potato, oats/potato, or corn/potato rotation (Goss and Afanasiev, 1938); Weinhold *et al.* (1964) similarly recorded a decline in common scab of potato grown since 1949 as a monoculture under irrigation near Shafter, CA, compared with potato/cotton, potato/sugar beet, and potato/barley rotations. Scab continued to increase on continuous potatoes early in the study until the eighth year and then steadily decreased whereas scab on potatoes grown in rotation continued to increase on each potato crop until 1961, during which there was less scab on potatoes grown in monoculture than those grown in a 2- or 3-year rotation.

Working with common scab of potatoes in the irrigated central Washington State, Menzies (1959) not only associated soils suppressive to *S. scabies* with long-term production of potatoes, what he referred to as 'old' fields, but also made the first transfer of an antagonistic microbiota of a pathogen-suppressive soil from an old field to soil from a 'new' field. Both fields were arid lands, essentially desert lands, brought into production with irrigation and conducive to scab, with the 'new' fields brought into production most recently. Only 10% suppressive soil plus 1% alfalfa meal was required to transfer the suppressiveness, whereas 1% alfalfa meal alone had no effect. It is highly unlikely that the mixing of 10% of one soil with 90% of another soil would change the physical and chemical properties sufficiently to account for transferability of the suppressiveness. Autoclaving eliminated the suppressiveness, further confirming a microbiological basis for the suppressiveness and pointing to an example of specific suppression.

An experimental plot of monoculture potatoes maintained at Grand Rapids, MN for screening potato germplasm for resistance to common scab of potatoes could no longer be used after approximately 20 years because of the soil having become suppressive to scab (Lorang *et al.*, 1995). Soil transferred from the scab-suppressive plot to a scab-conducive plot near Becker, MN also transferred the suppressive factor (Bowers *et al.*, 1996). This 'factor' was subsequently shown to involve the buildup of nonpathogenic *Streptomyces* species or weakly pathogenic *S. scabes* inhibitory to the more pathogenic *S. scabies* (Liu *et al.*, 1996; Lorang *et al.*, 1995). A nonpathogenic strain of *S. diastatochromogenes* and a weakly pathogenic strain of *S. scabies*, each shown to inhibit the highly pathogenic strains by production of an antibiotic (Liu *et al.*, 1996), were

mixed into an *S. scabies*-infested scab-conducive soil with a vermiculite/oatmeal/broth carrier contained in pots held outdoors and each planted to potatoes for four consecutive years. Even the lowest rate (1% by volume) of suppressive *Streptomyces* strains provided significant control of scab already in the first year and continued to provide scab control on the subsequent three consecutive crops of potatoes. The carrier alone mixed into the soil and planted to potatoes provided no control of scab (Liu *et al.*, 1995).

The evidence is clear that scab decline results from a shift in the makeup of the *Streptomyces* populations from highly pathogenic but low producers or nonproducers of antibiotics to weak or nonpathogenic strains inhibitory to the pathogenic strains by production of antibiotics. The outcome is apparently an example of the advantage conferred on strains with ability to inhibit their nearest relatives likely to occupy the same ecological niches and depend on the same nutrients. However, from the practical standpoint, the great majority of potato production worldwide depends on crop rotation and even soil fumigation to control nematodes and other soilborne plant pathogens. Monoculture potatoes might only be practiced today on a small scale, such as in private garden plots.

One of the best documented examples of a disease decline in response to a specific cropping system, but not necessarily the same crop grown in monoculture, is from a long-term cropping systems study conducted with dryland crops near Ritzville, WA (269 mm annual precipitation) (Schillinger and Paulitz, 2006, 2013). This location is well within the rainfed semiarid region described above as the Pacific Northwest Columbia Basin with a high frequency of phenazine-producing pseudomonads in the rhizosphere of wheat (Mavrodi, 2012). The study was launched in 1996 using spring and winter wheat, spring barley, yellow mustard, and safflower, all direct seeded (no till) in a field that had been managed for years with winter wheat alternated with a year of fallow and conventionally tilled. A disease known as 'bare patch' due to severe root rot caused *R. solani* AG-8 began to appear in all crops in the third year of the study and continued to increase in both size and numbers as documented by GPS measurements until the eighth year of the study. During years 5–7, bare patches occupied as much as 18% of land area cropped to wheat or barley. Interestingly, although wheat and barley are equally susceptible to this pathogen, with barley being possibly more susceptible than wheat, 15% of the area in monoculture spring wheat were bare patches during years 6–8 of the study compared with 7% of the area in bare patches in plots managed as a 2-year rotation of spring barley/spring wheat. Thereafter, the patches began to disappear in both monoculture wheat and the wheat/barley rotation until year 11 when the total area of wheat and barley in patches was less than 1%. No patches were present in years 12–15 when the study was discontinued.

Rhizoctonia root rot caused by *R. solani* AG-8 and the less pathogenic *Rhizopus oryzae* (Ogoshi *et al.*, 1990) became more important, including as bare patches in rainfed wheat and barley, in both the northeastern Oregon, eastern Washington, northern Idaho, and the Southern Australian wheat belt with the adoption by growers of the no-till or direct seeding for dryland cereals. The study by Schillinger and Paulitz (2006, 2013), done in the field over a 15-year period, is among the best documented examples of disease decline and the first to document disease decline in response to a 2-year rotation using a no-till (direct seed) planting system. Enduring a decade or longer of bare patches and potentially 15% lower yields during peak years of the disease, not to mention the added cost of controlling weeds in the bare patches, might seem uneconomical as an approach to manage Rhizoctonia root rot of cereals. However, many growers in the rainfed Inland Pacific Northwest and the Southern Australian wheat belt, where this disease is most important, already converted into a direct-seed system 20 years ago and must already be benefiting from this natural biological control. Roget *et al.* (1999) documented a suppression of Rhizoctonia root rot after severe disease in a wheat-based cropping systems in Southern Australia within approximately 15 years of direct seeding in the field. Timely management of the volunteer (self-sown) cereals, known as the 'green bridge,' has also played an important role in lowering the pressure of this disease (Roget *et al.*, 1987; Smiley *et al.*, 1993). Whether it is better management of the green bridge or disease decline in response to increases in phenazine-producing pseudomonads-intensive direct-seeded cereals, Rhizoctonia root rot and particularly the bare patch version of this disease have become rare occurrences compared with the 1980s and 1990s in both the Pacific Northwest and Australia.

Lucas *et al.* (1993) demonstrated the development of soil suppressive to Rhizoctonia root rot caused by *R. solani* AG-8 in each of two wheat field soils from NE Oregon, each planted five successive times to wheat in greenhouse pots, with additional inoculum of the pathogen added with each planting. Of particular interest in their study was that the soils only became suppressive to root rot caused by *R. solani* AG-8 in response to inoculum of *R. solani* AG-8 but not to *R. oryzae*, pointing to this disease decline as an example of specific suppression.

Hyakumachi and Ui (1982) documented a decline of Rhizoctonia root rot with sugar beet monoculture on Hokkaido, Japan. Following up on observations by a local sugar beet company that severe Rhizoctonia root rot one year would be followed by a healthy sugar beet crop in that same field the next year, they designed a field experiment that included monoculture sugar beets in plots with the pathogen introduced and reintroduced in successive years. Rhizoctonia root rot was consistently severe in the first year and absent in the second and subsequent years of monoculture, including in plots with the pathogen reintroduced each year. A single year of severe disease was enough to convert the soil from conducive to suppressive to Rhizoctonia root rot of sugar beet.

Another case of soil suppressive to Rhizoctonia root rot of sugar beet following severe disease in a previous crop was documented in the Netherlands and shown by Mendes *et al.* (2011) to be an example of specific suppression. The suppressive soil greatly limited Rhizoctonia root rot on sugar beet seedlings in contrast to a similar soil from the margin of the field that allowed heavy seedling mortality under the same conditions and dose of *R. solani* inoculum. Heat treatment of the suppressive soil at 50 °C partially eliminated suppressiveness, and heat treatment at 80 °C and γ-radiation totally eliminated suppressiveness. Mixing 10% suppressive soil with 90% conducive soil partially restored suppressiveness.

Mendes *et al.* (2011) used a metagenomic approach to characterize the rhizosphere microbiome for disease-suppressive bacteria. Metagenomic deoxyribonucleic acid (DNA) was isolated from the rhizosphere microbiota of sugar beet seedlings grown in suppressive soil, conducive soil, conducive soil amended with 10% suppressive soil, suppressive soil heat-treated at 50 °C, and suppressive soil heat-treated at 80 °C. A total of 33 346 bacterial and archaeal operational taxonomic units (species equivalents) were detected in the sugar beet rhizosphere microbiome, with no significant differences in the number of bacterial taxa detected among the respective treatments. However, a comparison of the relative abundance of different taxa revealed six clusters corresponding to the six treatments, suggesting that relative abundance of certain bacterial taxa plays a bigger role in suppressiveness than the presence of specific bacterial taxa. The bacterial phyla Proteobacteria (includes Pseudomonaceae, Xanthomonadales ,and Burkholderiaceae), Firmicutes (includes Lactobacillaceae), and Actinobacteria all were more abundant in suppressive soil than in conducive soil as well as in suppressive soil amended with 10% conducive soil. The 50 °C heat treatment would have eliminated the Proteobacteria and Firmicutes but possibly the 80 °C treatment would have been needed to eliminate the Actinobacteria because these bacteria form spores.

Mendes *et al.* (2011) used a high-density 16S ribosomal DNA oligonucleotide microarray, known as the PhyloChip, to further identify bacterial species and genes involved in disease suppression. Interestingly, results of this culture-independent approach to identification of suppressive taxa compared well with a more traditional culture-dependent approach. Of 111 antagonistic bacteria isolated from suppressive soil, 104 were members of the Pseudomonadaceae. Based on DNA fingerprinting by BOX-PCR, these isolates were grouped into 10 closely related (94–98% identity) haplotypes. Three haplotypes represented by 38, 21, and 37 isolates accounted for 90% of the antagonistic bacterial isolates from the *Rhizoctonia*-suppressive soil. When representative isolates of the three haplotypes were tested in sugar beet seedling assays, one provided biological control of *R. solani*. Two mutants of this strain, produced by transposon mutagenesis, showed to no longer protect sugar beet seedlings against infection by *R. solani*, although they colonized the rhizosphere to the same extent as the wild type. The mutated gene was shown to be a nonribosomal peptide synthase gene with 69% identity with the *syrE* gene of *Pseudomonas syringae*. Subsequent genetic analyses revealed a two-gene cluster predicted to encode a chlorinated lipopeptide.

This research takes the study of pathogen-suppressive soils to a new level using the new tools of metagenomic analysis combined with traditional culture techniques. Although the authors cautioned against ruling out other organisms in the suppression of Rhizoctonia root rot of sugar beet, the fact that this one haplotype along with two others out of 10 with 94–98% identity were members of the Pseudomonadaceae is consistent with the putative causes of other examples of suppressive soil. For example, fluorescent pseudomonads were shown to play a primary role in the suppression of black root rot of tobacco caused by *Thielaviopsis basicola* in a soil cropped 24 years to monoculture tobacco (Stutz *et al.*, 1986). Of several potential mechanisms of inhibition investigated, work with *P. fluorescens* CHA0 (now *Pseudomonas protegens* CHA0) obtained from the suppressive soil and one of the premiere model strains for fundamental research pointed to the importance of the antibiotic DAPG in this natural suppression (Keel *et al.*, 1992). The decline of take-all caused by *G. graminis* var. *tritici* discussed in detail below is similarly related to the buildup of specific genotypes fluorescent pseudomonads in the *P. fluorescens* complex (now *Pseudomonas brassicacearum*) with ability to produce the antibiotic DAPG. TAD has become another model for research on understanding the microbiological and molecular bases for the specific suppression responsible for disease decline with continued monoculture of the host and an important source of clues as to the success of intensive cropping (Cook, 2007).

Take-All Decline

Of all the examples of disease decline with continuous monoculture of the crop, none have revealed more about the microbiological mechanisms although serving as a practical means to root disease management than the decline of take-all (*G. graminis* var. *tritici*) with continuous monoculture of wheat or wheat/barley sequences. Fellows and Ficke (1934) working in Kansas were possibly the first to report the appearance of take-all patches in the second crop of wheat, more patches in the third and possibly the fourth crop of wheat, followed by the disappearance of take-all patches with continuous monoculture of wheat. Glynne (1935) working in the United Kingdom noted the same pattern of increase and then decline in take-all with continuous wheat monoculture. However, the first clear documentation of a microbiological basis for TAD was by Gerlach (1968) working with polder soils in the Netherlands newly reclaimed from the North Sea and planted first to reed grass and then continuous wheat. Take-all increased in the first two or three crops but then declined to an economically tolerable level in subsequent crops. He showed in greenhouse studies that a given amount of inoculum produced only mild take-all when introduced into polder soils that had entered TAD but severe take-all in polder soils not yet into TAD. He showed further that the suppressiveness was eliminated by heat treatment of the soil.

Following the lead of Menzies (1959), and working with both arid virgin (soils not yet brought into cultivation) and long-term wheat monoculture soils from the Columbia Basin of eastern Washington, Shipton *et al.* (1973) showed that the suppressiveness to take-all in long-term wheat monoculture soils was transferable with only 1% (by weight) to a virgin soil, and that the suppressiveness was eliminated by heat treatment of moist soil at 60 °C for 30 min using a steam–air mixture. Cook and Rovira (1973) used the experimental system of Shipton *et al.* (1973) to demonstrate further that suppression of the take-all pathogen occurred in the rhizosphere of wheat and not in the bulk soil and provided the first evidence that root-associated fluorescent pseudomonads played a role in the suppression.

Probably no experiment showed more conclusively the existence of an agent or agents responsible for TAD than the results of a field trial conducted over the years 1971–73 by R.J. Cook and P.J. Shipton and reported by Baker and Cook

(1974). Soil from each of three long-term wheat fields along with corresponding soils from each of three close by non-cropped sites, either in grasses or native vegetation (six soils in total), were transported in 120 l containers from eastern Washington to a Washington State University (WSU) research farm in western Washington. There the soils were each applied to the surface of four separate replicate plots, each 1.3 m by 3.3 m and mixed to a depth of approximately 15 cm with a rotovator. Two additional treatments included the local soil mixed in and rotovation only (no added soil). The entire experimental area had been fumigated with methyl bromide before adding the soils to eliminate any native pathogens or resident antagonists. The plot area as part of a larger area was seeded with a standard grain drill with wheat seed mixed with autoclaved oat grains colonized by the pathogen as a source of inoculum. The wheat that grew from that sowing was harvested and the entire plot area reseeded that same fall with only wheat. This harvest/reseed cycle was repeated a third time.

Take-all was uniformly severe in the first year but was almost completely absent in the second year, specifically in the four replicate plots that received soil from a 12-year-wheat-monoculture field of irrigated wheat from near Quincy, WA (**Figure 2**). By the third sowing, TAD has occurred uniformly over the entire experimental site.

A second wheat monoculture experiment was started in the fall of 1968 on 1 ha plot on the WSU experiment station near Lind, WA. The site had been managed for several decades with dryland winter wheat alternated with a year of fallow but was sprinkler irrigated to supplement the average annual precipitation of 25 cm with another 25 cm needed for annual cropping. Take-all is present but detected only by careful examination of roots of dryland wheat alternated with fallow; however, it develops into the classic disease (**Figure 2**) with continuous wheat under irrigation. In the plot near Lind, take-all appeared in the third and subsequent years of monoculture wheat, was most severe in the seventh year of monoculture wheat when the difference between fumigated and non-fumigated plots was striking, but then declined until, by the 15th year, there was no visible difference between fumigated and nonfumigated plots (**Figure 3**).

Bacteria cultured from the rhizosphere of wheat growing in suppressive soils in the presence of the take-all pathogen, including soil from the Lind plot following TAD, revealed strains of fluorescent pseudomonads with ability to produce phenazine-1-carboxylic acid and 2,4-diacetylploroglucinal, as shown in the recent comparison of antibiotic-producing pseudomonads in the rhizosphere of irrigated and rainfed wheat (O. Mavrodi *et al.*, 2012). Both strains inhibited take-all when introduced on seeds planted into soil infested with the take-all pathogen. Similarly, mutant strains no longer able to produce antibiotic phenazine-1-carboxylate (Phz+) or Phl+ lost ability to protect wheat against take-all, and both mutants were restored in ability to protect against take-all when the respective mutant genes were complemented with a wild-type gene (Weller *et al.*, 2002). A seven-gene locus shown to account for biosynthesis of phenazine-1-carboxylic acid (Mavrodi *et al.*, 1998) and a six-gene cluster shown to account for biosynthesis of Phl (Bangera and Thomashow, 1999) served as sources of marker genes for quantification of the respective populations in the wheat rhizosphere by PCR analysis. The results showed that the subpopulations of Phl+ fluorescent *Pseudomonas* species but not the subpopulation of Phz+ rhizosphere-inhabiting bacteria could account for TAD under continuous wheat monoculture in Washington State (Raaijmakers *et al.*, 1997). These results were confirmed for take-all suppressive soils in the Netherlands (Souza *et al.*, 2003).

The threshold population of Phl+ strains of *Pseudomonas* spp. naturally present in the rhizosphere of wheat growing in soils that had undergone TAD was consistently in the range of log 5–6 colony forming units (CFU) per g fresh weight of root (Raaijmakers and Weller, 1998; Raaijmakers *et al.*, 1997).

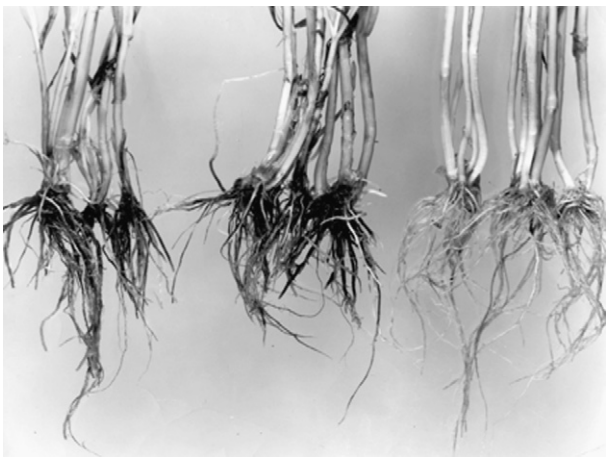


Figure 2 Field transfer of a factor or factors suppressive to take-all of wheat caused by *G. graminis* var. *tritici*. These plants came from plots in the second year of wheat monoculture where, before planting in year one, the plots were amended to a depth of 15 cm by rotovation with soil from an eastern Washington irrigated wheat field in the twelfth year of continuous wheat monoculture (far right), soil from a nearby virgin area under native vegetation predominated by sage brush (center) and no added soil (check, far left). All wheat plants were healthy in the third year of wheat monoculture. The one-time added soil amounted to approximately 0.5% by weight.



Figure 3 Winter wheat in the fifteenth year of continuous wheat monoculture under irrigation near Lind, WA. The man is standing on the border between a plot fumigated with methyl bromide before planting the previous fall (the man's left) and nonfumigated.

Elimination of this subpopulation coordinately eliminated suppression, and its restoration to >log 5 CFU per g root by mixing TAD soil with conducive soil and planting wheat coordinately restored suppression of take-all. The amount of Phl produced in the rhizosphere of wheat by a Phl-producing strain ranging between log 6 and log 7 CFU per g root was calculated at 0.62 ng 10^{-5}CFU (Raaijmakers *et al.*, 1999).

Interestingly, the D genotype (now *P. brassicacearum*) has been identified as the dominant strain in the rhizopsphere of wheat following TAD in both Washington State but a different genotype dominates in the Dutch TAD soils (Weller *et al.*, 2002). One particularly rhizosphere-competent strain, *P. brassicacearum* Q8r1-96, was shown to maintain the necessary threshold population for take-all suppression in natural soil when introduced as a seed treatment.

Logically, it should be possible to 'jump start' or enhance TAD by introduction of *P. brassicacearum* Q8r1-96 as a seed treatment in the same way the earlier introduction of soil from the 12-year continuous-wheat-monoculture field served to jump start TAD at the site in western Washington in the early 1970s. Field trails showed that yields can be increased by seed treatment with single and combinations of strains on wheat after wheat (Cook *et al.*, 2000). However, turning this approach into a commercial technology would require a formulation suitable for commercial use and tests required of the US Environmental Protection Agency for registration of the product as a biopesticide. The alternative strategy in use, knowingly or unknowingly by growers worldwide, is to maintain intensive cereal grain sequences. In the Inland Pacific Northwest, for example, growers use a 2-year rotation of winter wheat alternated with spring wheat or a 3-year rotation of winter wheat/spring wheat/spring barley, both of which maintain an effective level of take-all suppression.

To date, at least 22 Phl+ genotypes of the *P. fluorescens* group have been identified worldwide based on polymorphisms in one of the six biosynthetic genes required for biosynthesis of this antibiotic (De La Fuente *et al.*, 2005); however, the number of genotypes is no doubt greater. Of particular interest is that certain genotypes of Phl+ *Pseudomonas* spp. seem to dominate in certain cropping systems, including in response to certain crop monocultures. For example, on the experimental station of North Dakota State University where each of flax and wheat were grown in monoculture for more than 100 years, roughly 80% of the Phl+ fluorescent pseudomonads were the F and J genotypes in the rhizosphere of flax, whereas 76% of the Phl+-producing fluorescent pseudomonads were the D genotype (*P. brassicacearum*) in the rhizosphere of wheat (Landa *et al.*, 2005) – the same genotype identified in the rhizosphere of monoculture wheat in Washington state. Moreover, population of *P. brassicacearum* on wheat in the Fargo plot exceeded the log 5.0 threshold associated with take-all suppression.

Approximately 50% of US cropland is planted to corn and soybeans each year, as continuous corn in a 2-year corn–soybean rotation. The question arises as to whether any stable cropping system involving the same two crops grown in the same field for decades might enrich for specific genotypes of antibiotic-producing *P. fluorescens* suppressive to soilborne pathogens of one or both of these two crops? McSpadden Gardner *et al.* (2005) working in Ohio found Phl-producing *P. brassicacearum* in the rhizosphere of both corn and soybeans in all 15 counties sampled. Further, it was the most abundant of seven genotypes identified, exceeding log 3.4 on 77%, 84%, and 81% of corn plants sampled in years 2001, 2002, and 2003, respectively, and 78%, 67%, and 52% of soybean plants sampled during those three years, respectively. The average annual yield of soybeans and especially corn have continued to increase over the past 75–80 years, with the credit given as approximately 50% to genetics and 50% to management. Possibly some credit should also go to suppression of known or unknown root diseases by antibiotic-producing strains of *Pseudomonas* in the corn and soybean rhizospheres.

Reverse Fortunes of the Apple Replant Disease

Apple, like other orchard or perennial crops, is a monoculture subject to root diseases like any other crop grown without benefit of crop rotation. However, the real manifestation of root disease on apple becomes evident only when the trees are removed and the same site replanted with young apple trees, a phenomenon known as the apple replant disease. Mazzola (1995) showed for Washington apple orchards that the replant disease is due to a complex of root pathogens, including *Cylindrocarpon destructans, Phytophthora cactorum, R. solani* AG-5, and *Pythium* spp. However, unlike the examples of disease decline with crop monoculture discussed above, soils new to apples are suppressive to the root disease complex but become conducive by the fourth or fifth year of growth, in contrast to old orchard soils that are conducive already in the year of replanting.

The introduction of inoculum of *R. solani* AG-5 into soils collected from sites new to apples and ranging from the first to the fifth year of growth showed that the soil was suppressive in the first and second year but became conducive at the start of the third year. Concomitant with the loss of suppressiveness, populations of *Burkholderia cepacia* and *Pseudomonas putida* decreased, whereas populations of *P. syringae* and *P. fluorescens* biovar C increased. A separate study showed that a *P. putida* population similar to that in first-year apple growth controlled the replant disease on apple seedlings (Mazzola, 1999); Mazzola and Gu (2000a) found in greenhouse experiments that growing wheat resulted in a suppressiveness to the apple replant disease similar to soil not previously planted to apples. This has led to a practice of rotating old apple orchard soil to wheat before replanting apple (Mazzola and Gu, 2000b). The older the trees when infected, the more they can tolerate root infections; moreover, whatever damage does occur is more subtle compared with young trees with roots infected the year they are planted.

Concluding Comments

Although research on the molecular biology and biochemistry of host–plant defenses against above-ground diseases remains focused on host–pathogen interactions, research on the molecular biology and biochemistry of plant–host defense against soilborne pathogens is focused almost entirely on plant-associated microorganisms responsible through competition,

production of antibiotics, and induced host–plant resistance and known as pathogen-suppressive soils. Indeed, to understand the molecular and biochemical mechanisms involved in the *Gaeumannomyces*/*Pseudomonas* interaction responsible for TAD with continuous wheat monoculture is exceeded as a soil microbiological phenomenon only by the understanding of the molecular and biochemical processes involved in nitrogen fixation by *Rhizobium* spp. Furthermore, although the exploitation of nitrogen fixation in agriculture depends more on naturally occurring resident rhizobia than on their introduction with the seed at each planting, exploitation of TAD depends entirely on resident Phl+ genotypes of the *P. fluorescens* group. TAD is a model for similar studies of the mechanisms of pathogen suppression, especially the more intriguing and potentially exploitable examples of disease decline with crop monocultures, double cropping, and 2-year crop rotations.

Of the two types of pathogen-suppressive soils – general and specific suppression – only specific suppression can be managed with any degree of certainty and then largely or entirely by choice of the cropping system. Amending soil with large quantities of compost or other biomass is about the only management option available to reliably increase the level of general suppression. This may be part of the long-term success of direct seeding where crop residue is left to decompose on the soil surface or is mixed superficially into the top few centimeters of soil with the planting operation. In many developing countries, however, rather than adding or conserving the crop residue *in situ*, the trend has long been to remove it for fuel or animal feed. Current research and plans to produce biofuels from corn stalks and wheat straw will need to consider the value of this resource in maintaining an active and pathogen-suppressive soil microbiota of the general type.

There is a risk in depending over a long term on suppression of a specific disease in response to a specific cropping system. The level of disease suppression, being biologically based, will likely vary from year to year depending on local conditions, thereby allowing some level of disease in some years. Shifting the field to a different cropping system can also cause the soil to again become conducive, thereby requiring one of more disease outbreaks in order to restore suppressiveness when returning to a crop susceptible to that disease. Further, most crops are subject to infection by three of four root pathogens, and suppression of one can expose the root system to greater damage from one or two others. After 15 years of irrigated monoculture wheat and essentially full decline of take-all on the WSU research farm near Lind (described above), Rhizoctonia root rot caused by *R. solani* AG-8 appeared in the sixteenth year and increased to a maximum level of severity in the nineteenth year before stabilizing. No attempt was made to document its decline with continued wheat monoculture as done in the study near Ritzville. Dependence on a specific suppression should be considered as only one of several components of an integrated system needed to manage a mixture and not just one root disease.

Crop rotation is clearly the most dependable means to control soilborne pathogens of agronomic crops that cannot justify the expense of fumigation or solarization. This fact notwithstanding, with the need for specialized and expensive equipment to plant and harvest a grain crop, potatoes, sugar beets, or alfalfa hay, together with the need for an efficient and reliable marketing infrastructure, leaves most modern farm businesses little choice but to specialize in the production of two crops, rarely more. Likewise, more and more land planted to agronomic crops, such as corn, soybeans, cereal grains, and canola, are direct seeded rather than tilled as was done for decades, to reduce fuel costs, improve soil quality, and store more carbon that otherwise or eventually is released as a greenhouse gas. Direct seeding of wheat was shown in the early years of adoption to favor both take-all and Rhizoctonia root rot, requiring some form of soil disturbance even if only in the seed row. The fact that both of these diseases have been documented by careful and long-term studies to decline in direct-seed cropping systems speaks well for what might also be happening or has already happened with other crops managed in short rotations and even without benefit of crop rotation.

See also: Mineral Nutrition and Suppression of Plant Disease. Plant Disease and Resistance. Plant Health Management: Biological Control of Plant Pathogens. Plant Health Management: Fungicides and Antibiotics. Plant Health Management: Soil Fumigation. Plant Health Management: Soil Solarization. Soil Fertility and Plant Nutrition

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Plant Health Management: Soil Fumigation

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Introduction

Soil fumigation is a form of soil disinfestation that involves the application of volatile chemical compounds (fumigants) before planting to rid the soil of plant pathogens and pests. Other forms of soil disinfestation include steam sterilization, solarization (the use of clear plastic to heat soil), flooding, and anaerobic soil disinfestation (a combination of flooding and organic amendments). Soil fumigation is practiced on a wide variety of agronomic, fruit, nursery, ornamental, turf, and vegetable crops to control a broad spectrum of soilborne pests including plant pathogens, nematodes, insects and weeds. To be effective, chemicals used for soil fumigation must be extremely toxic to a wide range of organisms encompassing actinomycetes, bacteria, fungi, oomycetes, insects, nematodes, and plants (both seeds and vegetative material). Many popular chemical fumigants are halogenated organic compounds that disrupt basic cellular structure or functions via methylation of protein sulfhydryl groups, interference of the cytochrome-mediated electron transport chain, and/or direct attack on amino and hydroxyl groups. Soil fumigants are unique chemical pesticides. They are highly volatile, enabling them to disperse rapidly through the soil profile following application as a liquid. To achieve this, chemical fumigants should include a number of characteristics, including low boiling points and high vapor pressures; and they should posses a strong affinity to move through air spaces within the soil profile. Henry's law (K_H) constant is employed to measure the partition potential of a compound between the air and water phases. In general, K_H values $> 10^{-4}$ imply that compounds will diffuse more rapidly in the vapor phase and thus will move quickly through the soil profile when the soil is below 50% saturation.

Soil fumigants can be applied either through the irrigation system (drip or overhead) or directly into soil via metal shanks attached to a farm implement (**Figure 1**). Details on the principals and theory of soil fumigation have been reviewed extensively by Goring (1962) and Lembright (1990). Soil fumigation is a popular form of pest control because one chemical application can effectively replace the need for combined applications of soil fungicides, bactericides, nematicides and herbicides, resulting in a substantial financial savings to growers. Soil fumigation is also popular because one simple application can eliminate the need for more complicated knowledge-based pest management programs that require additional information acquisition and processing, decision making, and long-term land management programs such as crop rotation. Initially, an inexpensive method of soil disinfestation, soil fumigant costs have risen dramatically over the past 15 years and in the US can reach US$2766 per hectare and account for 15% of the total operating costs for vegetable production (University of Florida, 2009). Thus, soil fumigation is now typically restricted to high value, intensively managed crop production systems where large monocultures are repeatedly planting in same location, precluding the use of crop rotations or fallow periods to mitigate the build-up of soilborne pests. Another interesting side note is the contribution of soil fumigation, particularly using the chemical methyl bromide, to agricultural and ecological research. Through comparison of yields to fumigated soil, it has been used to access and optimize the performance of more sustainable crop management practices (Cook *et al.*, 2002). It has also been used in ecological field research to experimentally test ecological theories such as island biogeography (Simberloff and Wilson, 1969).

History

The first documented example of soil fumigation using volatile organic compounds dates from 1869, where Baron Paul Thenard applied carbon disulfide (CS_2) to French vineyards infested with the root parasite *Phylloxera vastatrix* (Rohart, 1876; Rommier, 1876). Eventually, over 50 000 ha of European vineyards where fumigated by the end of the nineteenth century. The origin of many chemical fumigants began as waste byproducts of industrial reactions.

A mixture of dichloropropene and dichloropropane (DD) was produced as a byproduct of the production of allyl chloride by Shell Company and presented a disposal problem until its nematicial activity was discovered by Walter Carter in Hawaii (Carter, 1943; Caswell and Apt, 1989). The fumigant methyl bromide, initially manufactured as a flame retardant in the 1920s, was produced as a precursor to safer fire retardants such as BCF and Halon 1211. The popular soil fumigant chloropicrin (trichloronitromethane, CCl_3NO_2) had a more



Figure 1 Traditional shank application of soil fumigants practiced in the southeastern US.

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insidious origin before its introduction to agriculture. Chloropicrin, produced by the reaction of picric acid and bleach, remained largely a laboratory curiosity until World War I when it gained widespread use in chemical warfare, both a lachrymator and a lethal gas. At the closure of World War I, the US had stockpiled an estimated 36 million pounds of chloropicrin (Roark, 1934) and agricultural scientists begin to assess the surplus chloropicrin for insecticidal properties (Cotton and Young, 1929; Moore, 1918). By the late 1950s, soil fumigation with mixtures of chloropicrin and methyl bromide had become the standard soil disinfestation practice for high-value crops such as tomato and strawberry (Geraldson *et al.*, 1965; Wilhelm *et al.*, 1961), replacing other less effective soil fumigants. For 50 years, methyl bromide was widely used as a soil fumigant due to its low cost, ease of handling, performance under a wide range of soil and environmental conditions, low phytotoxicity, and broad range of activity. Globally, it was viewed as indispensable wherever intensive agriculture was practiced (Vanachter, 1975), and in the US a 1990s economic study estimated that a ban on the use of methyl bromide would cost producers and consumers more than US$1 billion annually (Anonymous, 1993).

Biological, Environmental, and Human Impacts

The same combination of acute toxicity and high volatility that make fumigants an effective soil pesticide can also increase the risk of field worker and bystander exposure, contamination of ground and surface water, and environmentally damaging atmospheric emissions, creating a contentious source of conflict between the agricultural industry and consumer and environmental advocates. The registration of ethylene dibromide, at the time one of the most abundantly used nematicides in the world, was suspended by the US Environmental Protection Agency (USEPA) after it was identified in ground waters of Arizona, California, Connecticut, Florida, Georgia, Massachusetts, and Washington (Federal Resister, 1983). A contaminant of DD was detected in municipal drinking wells located near former pineapple production fields on the Hawaiian islands of Kauai, Oahu, and Maui, prompting a voluntary withdrawal by the manufacturer (Oki and Giambelluca, 1987). Use of the popular soil fumigant 1,2-dibromo-3-chloroprane (DBCP) was suspended by the USEPA after it was discovered that one-third of male workers at a DBCP manufacturing plant in California were sterile (Thrupp, 1991). Later, a massive sterilization of approximately 1500 banana plantation workers in Costa Rica from DBCP was also documented (Thrupp, 1991). DBCP was also detected in the ground waters of Arizona, California, Hawaii, Maryland, and South Carolina. In 1991, metam sodium gained national attention when a train derailed spilling over 43 000 l into the Sacramento River, causing catastrophic damage to wildlife and the river ecosystem (Cantara Trustee Council, 2007; Brett *et al.*, 1995). Methyl bromide was identified as a significant ozone-depleting compound, and agricultural soil fumigation was implicated as a major anthropogenic source (Yagi *et al.*, 1993; WMO, 1994). Under obligations of the US Clean Air Act and the Montreal Protocol on Substances that Deplete the Ozone Layer (an international stratospheric ozone protection treaty) a scheduled phase-out of production and sale was initiated in developed countries (USEPA, 1993; UNEP, 1995). Since 1999, production and importation of methyl bromide in the US has declined from 25 500 to 434 metric tons. In Europe, registrations for 1,3-dichloropropene (1,3-D) and chloropicrin were canceled and production and sale of both fumigants were phased out between 2008 and 2012.

Current and Future Status

In the US, the number of chemical compounds registered for use in soil fumigation has diminished to chloropicrin, dimethyhl disulfide (DMDS), methyl isothiocyanate (MITC) generators (dazomet, metam potassium, and metam sodium), and 1,3-D. Their chemical properties have been extensively reviewed by Ajwa *et al.* (2003) and Ruzo (2006), and a generalized summary of their maximum-use rates and relative effectiveness to methyl bromide is available (Noling *et al.*, 2010). A comprehensive reevaluation of chloropicrin, DMDS, and the MITC generating compounds by the USEPA in 2010 led to additional regulations place on their use to increase protection of agricultural workers and bystanders. Some of the new regulations include increased buffer zones of untreated soil between the application sites and neighboring residences, detailed site-specific fumigant management plans, emergency preparedness and response notification, and formal applicator training programs administered by the fumigant registrants (USEPA, 2013). The additional compliance assistance and assurance measures will dramatically restrict the ability to apply soil fumigants, particularly in urbanized areas.

Recent trends in soil fumigation have focused on developing a set of good agricultural practices (GAPs) for fumigant applicators that, when adhered to, enhance the pest control efficacy of alternative chemical fumigants and minimize their environmental and human health impacts. Key features of GAPs include the use of improved application methods and technology to reduce fumigant application rates, improve the precision of fumigant placement within the soil profile, and restrict their atmospheric emissions. For example, low disturbance fumigant application equipment was developed using small vertical colters mounted forward of a soil bed press to improve the precision of fumigant delivery without disturbing the soil profile (**Figure 2**). The combined use of low-disturbance application equipment and a soil surface seal reduced cumulative atmospheric emission of 1,3-D by 21% and chloropicrin by 18% when compared to traditional shank applications (Chellemi *et al.*, 2012). An under-bed fumigator using winged steel shanks mounted behind large vertical colters was developed to deliver soil fumigants underneath existing plastic mulched beds without disturbing the integrity of the beds (**Figure 3**). Significant control of plant parasitic nematodes and weeds with reduced fumigant application rates was achieved when the under-bed applications were made 7 days after planting beds were covered with plastic film (Chellemi and Mirusso, 2006). New formulations of plastic film have been developed and used as tarps to retain fumigants in the soil following application by using layers of ethylene vinyl alcohol resins, nylon, or other polyaminides. A standardized approach for estimating their permeability to soil fumigants was developed and used to assess

their performance under a range of field and application conditions (Papiernik *et al.*, 2011). Total cumulative atmospheric emissions of chloropicrin and MITC were reduced to less than 5% of the material applied when low-disturbance application technology was combined with improved plastic films (Chellemi *et al.*, 2010). Also included in GAPs are the selective inclusion of specific soil and environmental conditions that mitigate the impact of fumigant emissions. They include soil moisture above field capacity and good soil tilth. Soil tilth is defined as the physical condition of soil as related to its ease of tillage, fitness as a seedbed, and its promotion of seedling emergence and penetration (Karlen, 2005). An illustrated comparison of two fumigated planting beds with contrasting levels of soil tilth is presented in **Figure 3**. Ranked in order of impact on the retention of fumigants in the soil are soil water content, soil tilth, the type of plastic film, and soil texture (Chellemi *et al.*, 2011). When GAPs are following during the fumigant application process, many soil fumigants can achieve a spectrum of pest control similar to methyl bromide while maintaining a high level of marketable yields (Ajwa *et al.*, 2002; Chellemi and Mirusso, 2006; Gilreath *et al.*, 1999; Locascio *et al.*, 1997; MacRae *et al.*, 2010).



Figure 2 Use of vertical colters to improve the precision of fumigant placement within the planting bed and to minimize disturbance of the soil profile.



Figure 3 Precision placement of fumigants under plastic mulched beds using vertical colters and winged steel shanks.



Figure 4 A comparison of raised plastic mulched beds prepared in soils with good tilth (left) and poor soil tilth (right).

By definition, soil disinfestation procedures are not sustainable because reinfestation of treated soil occurs during crop production, necessitating the reapplication of soil disinfestation procedures for future crops. Future trends in soil fumigation research will include ways to mitigate the impact of chemical fumigants on nontarget beneficial soil microbial communities as a means of extending the time intervals between fumigant applications (**Figure 4**).

See also: Advances in Pesticide Risk Reduction. Plant Health Management: Crop Protection with Nematicides

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Plant Health Management: Soil Solarization

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Glossary

Biocontrol Reducing pest populations or limiting their activity by means of a living agent.
Integrated pest management A holistic approach to pest control, which also considers environmental issues.
Mulch Covering the soil with organic residues or plastic tarp.
Polyethylene Plastic material, frequently used as sheets in agriculture.
Soil disinfestations Treating the soil before planting for pest control, usually using drastic means.
Soil solarization Solar heating of soil for pest control, usually by use of a plastic mulch.
Solar heating Exposure to solar radiation to achieve elevated temperatures.

Introduction

Soilborne pests, including pathogens, arthropods, nematodes, weeds, and parasitic plants, cause heavy losses to all major crops by affecting both yield and quality. In severe cases, they may totally destroy the crop, forcing the farmer to use drastic and expensive control measures, abandon the land, or shift to less susceptible, but often less profitable crops. There is, therefore, a need to develop cost-effective control methods that are economically, environmentally, and technologically sound to ensure crop productivity and yield stability (Katan, 1996). An effective method of control also prolongs the use of available lands for crop production.

Soil disinfestation is one of the approaches for the control of root diseases that are especially common with intensive and high-value crops, for example, greenhouse and horticultural crops. It is a sophisticated, expensive, and effective approach of control that carries great advantages. The basic principle is to eliminate a wide spectrum of harmful organisms in the soil before planting, usually using drastic chemical or physical means. Although the main goal of soil disinfestation is to eliminate the major pests when their populations reach economically intolerable levels, additional (albeit initially unintended) benefits may also be obtained. The elimination of accompanying detrimental biotic and abiotic agents that have been accumulating in the soil throughout its long history of cropping is an example of such a benefit. However, because of the drastic nature of soil disinfestation, it may also have a harmful effect on nontarget biotic and abiotic components of the soil.

Soil disinfestation consists of four approaches. The first two – steaming and fumigation – were developed at the end of the nineteenth century. A third approach is soil solarization (also called solar heating). Biofumigation or biodisinfestation based on the incorporation of organic amendments under plastic mulch is a fourth approach that has gained interest in recent years.

The history of soil solarization has been summarized (Katan and DeVay, 1991; Gamliel and Katan, 2009, 2012). Many attempts have been made since ancient times to harness solar energy (as a heating tool) for pest control, in soil or in planting material, although until recently this was done by means other than the use of plastic material to enhance and prolong heating. Soil solarization as a preplant treatment for control was first described in 1976, based on studies carried out in the Jordan Valley in Israel (Katan *et al.*, 1976). From the beginning, solarization has been based on covering (mulching, tarping) the soil with transparent polyethylene sheets. This, in fact, represents a modernized application of old mulching principles, using technologies and materials that were not available back then. Today's technologies (and materials) enable more intensive and controlled soil heating and hence more effective and reproducible pest control. Soil solarization represents a shift from the classical use of plastic mulching of soil, because the latter is usually used during cool seasons to elevate low soil temperatures, thereby promoting plant development. With soil solarization, a bare soil is mulched during the hot season to further elevate its maximal temperature (Gamliel and Katan, 2012). Soil solarization is a hydrothermal process that brings about thermal and other physical, chemical, and biological changes in moist soil during, or even after mulching, which may eventually lead to pathogen control (Katan, 1981; Stapleton and DeVay, 1986).

In 1977, following the first publication of the method, American plant pathologists from Davis, California, reported the successful application of solarization for the control of *Verticillium dahliae* (Pullman and DeVay, 1977), indicating the potentially wide applicability of the soil-solarization method. Deep interest in the new soil-solarization approach and its rapid adoption are reflected by a bibliography listing 173 publications on the topic of soil solarization during its first decade, from 22 countries (Katan *et al.*, 1987). Since then, more than 1000 studies on the topic have been published, and soil solarization has been adopted or investigated in 74 countries, both developed and developing (**Figure 1**). Most of the studies have been carried out in relatively hot regions or countries, but important exceptions in cooler or humid regions, with various levels of success, are also known.

Principles of Soil Solarization

Soil solarization is a climate-dependent method that needs to be adapted to the specific region and season in which it is

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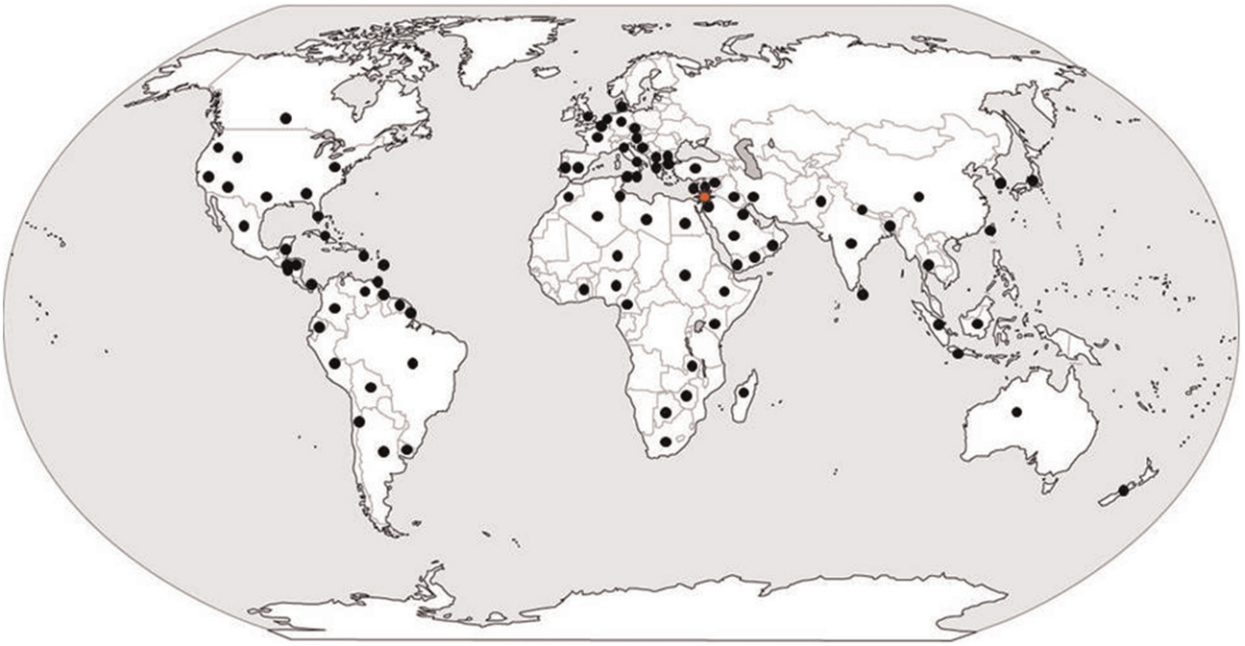


Figure 1 World distribution of sites where soil solarization has been investigated, as of 2012. Reproduced with permission from Gamliel, A., Katan, J. (Eds.), 2012. Soil Solarization: Theory and Practice. St Paul, MN: APS Press.

applied. The basic principles are summarized as follows (Gamliel and Katan, 2012):

1. Moist soil is mulched with transparent polyethylene sheets (Figure 2). Soil mulching should be carried out during periods of long daylight, high temperature, and intense solar irradiation (preferably with little or no precipitation).
2. The best time for soil solarization, i.e., when climatic conditions are the most favorable, can be determined experimentally by mulching the soil and measuring the resulting temperatures. Meteorological data from previous years and predictive models (see below) further facilitate this task. Monitoring changes in the populations of native pathogens or intentionally introduced pathogen inocula as a bioassay is an additional approach to determining the effectiveness of soil solarization.
3. The soil should be kept moist to increase the thermal sensitivity of pathogens' resting structures and to improve heat conduction from the soil surface to its deeper layers.
4. The thinnest polyethylene tarp that can be used for mulching without being easily damaged (35–40 μm thickness) is recommended because it is less expensive, but just as effective as the thicker tarps. Because the upper soil layer is heated more intensely than the underlying ones, the mulching period must be long enough, usually at least 4 weeks, to achieve pest control at all desired depths. The longer the mulching period, the greater the depth of effective control. With growth substrates and soilless culture, where the depth is 10–20 cm, shorter periods of solarization might be sufficient.
5. Solarization heats the soil through a repeated daily cycle. Typical maximal temperatures are within the range of 45–50 °C and 38–45 °C at depths of 10 and 20 cm, respectively, although higher temperatures have been recorded in certain regions. At a depth of 30–40 cm, maximal temperatures are 35–40 °C and are maintained for longer periods of time, although they are reached later in the day (Figure 3). In solarized plots where effective disease and weed control has been obtained, the temperatures are 5–15 °C higher than those in comparable nonsolarized plots.
6. As with any disinfestation method, recontamination of the soil after termination of solarization, for example, by infected propagation material or infested soil or water, should be absolutely avoided.



Figure 2 Soil solarization, showing the soil surface is mulched with a clear polyethylene. Reproduced with permission from Gamliel, A., Katan, J. (Eds.), 2012. Soil Solarization: Theory and Practice. St Paul, MN: APS Press.

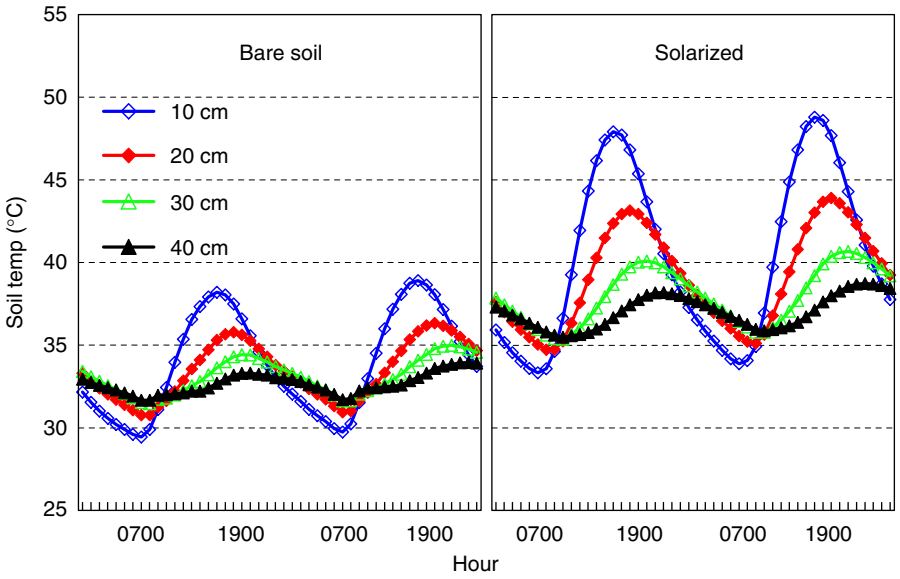


Figure 3 Soil temperatures at various depths during solarization in the summer time in Israel (Rehovot, August 2003), using transparent low-density polyethylene sheets. Reproduced with permission from Gamliel, A., Katan, J. (Eds.), 2012. Soil Solarization: Theory and Practice. St Paul, MN: APS Press.

Soil Solarization for the Mangement of Soilborne Pests

Many studies have been published since 1976 describing the control of a variety of pests by solarization. These include fungi, oomycetes, nematodes, bacteria, weeds, invasive plants, and arthropod pests, as described below, and even some unidentified agents. In most cases, disease control or reduction is accompanied by reduction in inoculum density, yield increase, or both (Figure 4). The most extensively studied pests have been fungi, oomycetes, nematodes, and weeds. Most of the studies were conducted under realistic field conditions (many under farm conditions); therefore, their relevance and applicability to real-life conditions are high. This situation came about because solarization can actually be carried out only under farm conditions; simulation studies for solarization are especially difficult to carry out. The number of soilborne pests effectively controlled by solarization is very large, exceeding that of pests not controlled by solarization. Some pathogens that are highly sensitive to solarization, for example, *V. dahliae* and species of *Phytophthora*, were effectively controlled in most studies, whereas the level of control of moderately heat-tolerant pathogens, such as *Sclerotium rolfsii*, varies from site to site. Certain pathogens and weeds, however, are not effectively controlled by solarization, such as the heat-tolerant fungi of the genera *Macrophomina* and *Monosporascus*. This is not surprising as no single control method can be expected to be effective against all pests.

The following are examples of responses of various pathogens, with various crops, to soil solarization (Katan and DeVay, 1991; Gamliel and Katan, 2012; McGovern and McSorley, 2012; McSoreley and McGovern, 2012). It should be emphasized that these are based on studies carried out under various climatic conditions and with different cropping systems; therefore, any generalization has to be made with caution.



Figure 4 Commercial application of soil solarization to control broomrape in carrots. The small area on the left with stunted plants indicates a nonsolarized plot. Reproduced from Gamliel, A., Katan, J. (Eds.), 2012. Soil Solarization: Theory and Practice. St Paul, MN: APS Press.

The list of fungal pathogens that are frequently effectively controlled by solarization is large and includes, among others: various formae speciales of *Fusarium oxysporum*, for example, *basilici*, *lactucae*, *melonis* and *vasinfectum*, *Phytophthora* spp., *Pythium* spp., *Sclerotinia sclerotiorum*, *Sclerotium cepivorum*, *V. dahliae*, and *Rhizoctonia solani*. Results with *F. oxysporum* f. sp. *radicis-lycopersici* and *F. oxysporum* f. sp. *dianthi* have been variable.

The bacterial pathogens *Clavibacter michiganensis* subsp. *michiganensis*, *Streptomyces scabies*, and *Agrobacterium tumefaciens* are sensitive to solarization, whereas *Ralstonia solanacearum* seems to be more difficult to control.

Various plant parasitic nematodes are effectively controlled by solarization, including species of *Ditylenchus*, *Globodera*, *Heterodera*, *Paratylenchus*, *Pratylenchus*, *Rotylenchulus*, *Xiphinema*, and others. Soil solarization is especially effective at controlling *Ditylenchus dipsaci* and increasing garlic yield.

The effect of soil solarization in controlling *Meloidogyne* spp. root-knot nematodes is variable, apparently due to the fact that this nematode can survive in the deep, less heated soil layers, and later migrate up into the solarized soil layers.

Surprising as it may seem, the incidence of some foliar diseases (e.g., late blight of carrots and leaf spot of peanuts) has been reduced by solarization in certain cases. This might be attributed to a reduction of primary inoculum in the soil, as shown with *Botrytis* (Lopez-Herrera *et al.*, 1994), or to changes in the mineral content of the soil (Chen *et al.*, 1991) that, in turn, might enhance host–plant resistance. An interesting aspect of the effect of solarization on primary inoculum was shown by Philips (1990) with *Sclerotinia sclerotiorum*. Solarization not only reduced the sclerotial populations of this pathogen, but also reduced the ability of the surviving sclerotia to form apothecia. Induced resistance in plants growing in solarized soil has been reported (see Mechanisms of Pathogen and Disease Control and Plant-Growth Improvement). Solarization is also effective in controlling diseases and increasing the yield and biomass of plants grown in artificial growth substrates. For example, yield decline and growth retardation were evident in *Gypsophila* grown in either soil or artificial growth substrate under continuous cropping. In this study, *Pythium* spp. colonized the plant roots, and soil solarization nullified those phenomena and yield was increased by 17–97% (Gamliel *et al.*, 1993).

A long-term effect of solarization on disease control, yield increase, or both, for a second or even third season after the solarization treatment, has been observed in various regions and with a variety of crops (Hartz *et al.*, 1993; Satour *et al.*, 1989). The effect seems to be due to the drastic reduction in inoculum density and the induction of soil suppressiveness (see Mechanisms of Pathogen and Disease Control and Plant-Growth Improvement), which delays reinfestation of the soil by the pathogens. Combining solarization with other methods, especially biological control agents, should enable better and longer-lasting disease control, and may require less frequent application. The long-term effect has economic implications, in terms of reduced costs of control per crop.

Weed control is one of the observable results of soil solarization and can be used as an indicator of its effectiveness (Rubin, 2012). In general, annual weeds are more sensitive to solarization than perennial weeds. Purple nutsedge and *Melilotus* are usually not controlled by solarization. Soil solarization is also effective in reducing the seed banks of the invasive plant *Acacia saligna* despite the seeds' tolerance to heat (Cohen *et al.*, 2008). This seems to be connected with solarization's ability to break seed dormancy and then thermally kill the heat-sensitive seedlings. The parasitic weed *Orobanche* (broomrape) is also effectively controlled by solarization.

A comprehensive study of the effect of solarization on weeds was carried out in a Mediterranean climate at ICARDA in Syria (Linke, 1994). Of the 57 weed species from 25 families, 46 were reduced by solarizaton, 6 were unaffected, and 5 increased in numbers. Most annual weeds were controlled up to 100%. Low- to zero-control, or even stimulation, occurred with weed species having bulbs, heat-tolerant seeds, a deep-lying root system, or other perennial organs.

The possible mechanisms of weed control by solarization are direct thermal killing of seeds and biological control through weakening or other mechanisms, including breaking seed dormancy.

Soil solarization for weed control has advantages over herbicides in that it is a nonchemical method, there is no harmful residual effect, and its weed-killing effect may extend to deeper soil layers and may also reduce the weeds' seed banks.

Mechanisms of Pathogen and Disease Control and Plant-Growth Improvement

Understanding the mode of action of a management measure, as well as the accompanying biotic and abiotic processes, provides an important tool for optimizing pest control, predicting its efficacy, and minimizing undesirable side effects. Once the mode of action is known, the control measures can be better adjusted to the situation, thereby increasing the reliability and reproducibility of pest management. This is especially valid for soil disinfestation, which affects many biotic and abiotic soil components, and even more so for soil solarization, which is a climate-dependent method. The contribution of biological mechanisms toward pest control, beyond thermal killing of the pathogens, was already realized in early studies of soil solarization. Accumulating evidence shows that reduction of pathogen populations was recorded even under sublethal conditions from a climatic point of view, for example, in the lower soil layers. Many studies have shown that biological control processes are frequently induced or stimulated in solarized soil, thus contributing to pathogen and disease control. Below are some typical examples. The long-term effect of soil solarization was an indication that a beneficial shift in soil microbial activity might have occurred in the solarized soil, which indeed was shown in later studies.

The lower disease incidence among plants grown in solarized soils, as with any soil treatment, results from the effects exerted on each of the three living components involved in the disease – the pathogen, the surrounding soil microorganisms, and the host plant – as well as on the physical and chemical components of the environment which, in turn, affect the activities and interrelationships of these biotic components (Cook and Baker, 1983). Although these processes occur primarily during solarization, they may continue to various extents and in different ways after removal of the polyethylene sheets and planting. Soil solarization may affect inoculum density, inoculum potential, or both (Gamliel and Katan, 2009).

The mechanisms of biological control that may be created, stimulated, or suppressed by solarization can be connected with:

1. the inoculum existing in the infested soil – its reduction by direct microbial killing or by suppression of its saprophytic or pathogenic capacity;

2. suppression of reinfestation of the soil after termination of the solarization process, leading to induced soil suppressiveness;
3. induced host–plant resistance, namely, an effect via the plant system.

The above mechanisms have been demonstrated in various pathogen–plant systems. However, not all of the suggested mechanisms have to be realized in each system or even for the same pathogen.

A weakening effect results from exposing pathogen propagules to sublethal heating, which is not initially sufficient to cause immediate thermal killing. The affected propagules are impaired and inferior compared to untreated ones. Consequently, they become weakened and more vulnerable to antagonistic soil mocroorganisms, which are less effective against intact, nonweakened propagules. This may ultimately lead to a reduction in inoculum density and disease incidence. Thus, weakening leads to biological control of the pathogen and is reflected in a decline of the pathogen population (Freeman and Katan, 1988). A solarization-triggered weakening effect has been demonstrated in a variety of pathogens, including *F. oxysporum* f. sp. *niveum* (Freeman and Katan, 1988), *F. oxysporum* f. sp *melonis* and *F. oxysporum* f. sp *radicis-lycopersici* (Eshel *et al.*, 2000), *Sclerotium rolfsii* (Eshel *et al.*, 2000; Lifshitz *et al.*, 1983), *Sclerotinia sclerotiorum* (Philips, 1990), and others.

Flow-cytometric, physiological, and microscopic studies on the viability of sublethally heated *Fusarium* conidia showed that, although they were seemingly unaffected when examined shortly after heating, their population was reduced later on, even under axenic conditions, suggesting delayed mortality (Assaraf *et al.*, 2002). This study again suggests that assessing the levels of pathogen populations shortly after exposure to a control agent does not necessarily reflect the full potential of the weakening phenomenon induced by sublethal treatment in pathogen and disease control. The phenomenon of delayed mortality caused by sublethal heating, its possible connection to programmed cell death, and the implications regarding self-deterioration of the weakened propagules and pathogen control need to be further studied.

In certain cases, weakening is reflected in microscopic changes in the propagule. For example, exposing *Sclerotium rolfsii* sclerotia to sublethal heating under controlled conditions increased the frequency of surface cracks on the sclerotia. This was accompanied by an increase in the concentrations of bacteria in or around those cracks and in the amount of ^{14}C-labeled water-soluble organic compounds that leaked from the sclerotia (Lifshitz *et al.*, 1983).

Studies have frequently shown that solarized soils become suppressive, namely, less receptive to pathogens. This can be regarded as an example of induced soil suppressiveness (Kassaby *et al.*, 1985; Greenberger *et al.*, 1987; Freeman *et al.*, 1990). In solarized and subsequently inoculated soil, the incidences of disease caused by *Fusarium* and *Sclerotium rolfsii* were lower than in untreated infested soil, the population of lytic microorganisms was higher, and suppression of chlamydospore formation was frequently observed (Greenberger *et al.*, 1987). An additional mechanism might be partial or complete nullification of fungistasis in the absence of the host, thus exposing the vulnerable germinating propagules to the antagonistic action of the soil biota.

Various studies have shown stimulation of beneficial microorganisms (e.g., biocontrol agents and plant-growth promoters) in solarized soils. These include microorganisms such as *Trichoderma* spp., fluorescent pseudomonads, *Bacillus* spp., *Gliocladium*, *Talaromyces*, and others (Stapleton and DeVay, 1984; Gamliel and Katan, 1991; Tjamos *et al.*, 1991; Stevens *et al.*, 2003). For example, populations of *Talaromyces flavus*, a thermotolerant antagonist of *V. dahliae*, increased in solarized soils (Tjamos *et al.*, 1991). Soil solarization increased the rate of infection of juveniles of the nematode *Meloidogyne javanica* by the bacterial antagonist *Pasteuria penetrans* for at least 10 months (Walker and Wachtel, 1988). The beneficial microbial shift induced by solarization might appear because thermotolerant saprophytic organisms survive, at least partially, under the mild heating of solarization, because of rapid colonization of the root zone by the surviving microorganisms, or for other unknown reasons. Cook and Baker (1983) indicated that saprophytic microorganisms, compared to parasites, tend to have a wider temperature range over which growth is possible. Frequently, but not always, soil solarization seems to create a soil environment that favors saprobes. It should be noted that in a typical agricultural soil, plant pathogens are only a very small proportion of the total flora; chances are good that certain antagonistic species will survive the mild heating involved in the solarization process.

The stimulation of fluorescent pseudomonads in the rhizosphere of tomato plants, but not in the bulk soil, was connected with changes in the composition of root exudates from plants growing in solarized soil, i.e., increased levels of amino acids and amino compounds (Gamliel and Katan, 1992). It was concluded that the rapid establishment of fluorescent pseudomonads in the rhizosphere of plants in solarized soils is caused by the improved capacity of the bacteria to compete for exudates. These exudates also enhance chemotaxis of the beneficial bacteria toward the roots and affect the balance between various groups of microorganisms in the soil. The signals in solarized soils that trigger these changes in the root exudates are unknown. Pioneer colonists, which rapidly respond and colonize, have a better chance of occupying the soil niches created by the mild heating than do pathogens.

Many studies have examined the effect of soil solarization on microbial activity by quantifying populations of various groups of soil organisms using appropriate culture media. In general, these studies found that microbial activities are reduced to various extents during solarization but resume later, either gradually or rapidly, depending on various factors. In many but not all cases, these results corresponded with microbial population counts.

In recent years, molecular tools such as polymerase chain reaction combined with denaturing gradient gel electrophoresis (DGGE), terminal restriction fragment length polymorphism (T-RFLP), and others have been used to study shifts in soil community structure resulting from solarization, as well as microbial diversity and changes in the genetic structure of soil microbial communities. A marked temporally induced change in the genetic structure of indigenous soil bacterial communities was observed in solarized soil, as evidenced by the DGGE patterns of bacteria, β-protobacteria, actinobacteria

and, to a lesser extent, α-protobacteria (Gelsemino and Cacco, 2006). T-RFLP analyses of extracted soil deoxyribonucleic acid (DNA) revealed significant shifts in fungal community composition following soil solarization, which was sustained in both rice-cropping sites studied (Culman *et al.*, 2006). In another study using DGGE analysis, it was concluded that, in general, soil solarization tends to reduce the richness of bacteria and fungi (Bonanomi *et al.*, 2008). However, the population of fluorescent pseudomonads emerged as the most important factor in crop productivity.

Soil solarization might indirectly affect disease via an effect on host–plant resistance to pathogens. This is not surprising as there are studies that demonstrate physiological – including hormonal – changes in plants growing in solarized soils (Gruenzweig *et al.*, 1993, 2000). In those soils, plant growth is frequently increased. Mineral nutrient levels are also increased, as detailed below, and have the potential to affect host–plant resistance to pathogens. Soil solarization has been shown to reduce some foliar diseases despite the fact that only the roots are in contact with the solarized soil. Stevens *et al.* (1992) and Levy *et al.* (2004) found that reduction of foliar diseases in solarized soil is connected with induced resistance. Because only the roots are exposed to the solarized soil, signals may move upward in the plant, causing physiological changes (Gruenzweig *et al.*, 1993). Solarization frequently stimulates the activity of rhizobacteria, such as fluorescent pseudomonads and *Bacillus* (Stapleton and DeVay, 1984; Gamliel and Katan, 1991; Stevens *et al.*, 2003), which are potential inducers of host–plant resistance to pathogens.

Increased Growth Response of Plants in Solarized Soils

Improved plant growth and a consequent increase in yield are expected to occur when soilborne pests are controlled by any method of soil disinfestation, as has been shown in many studies. However, less expected is the phenomenon of plant-growth improvement by disinfestation of soils in the absence of major visible disease symptoms, but not ruling out minor root pathogens such as *Pythium*. The phenomenon of increased growth response (IGR) was documented in the early days of soil disinfestation and has been validated with all soil-disinfestation methods, including solarization (Wilhelm, 1965; Cook and Baker, 1983; Cook *et al.*, 1987; Chen *et al.*, 1991; Gamliel and Katan, 1991; Gruenzweig *et al.*, 1993, 1999). The increases in plant growth by soil disinfestation ranges from a few to several hundred percent. A thorough historical review of the IGR since the early days of soil disinfestation in Europe at the end of the nineteenth century was described by Wilhelm (1965). Different mechanisms have been suggested to explain this IGR in disinfested soils. These might be connected with either enhancement of potential beneficial agents, for example, beneficial microorganisms, improved mineral nutrition, or the elimination of a biotic harmful agents, including minor pathogens. The ubiquitous root pathogen *Pythium* is such a potential harmful agent that the elimination of which, by soil disinfestation, has been associated with an IGR. This was frequently reported among various crops including strawberry and cauliflower (Wilhelm, 1965), wheat (Cook *et al.*, 1987), and *Gypsophila* (Gamliel *et al.*, 1993), among others. Wilhelm (1965) considered the control of injurious soilborne organisms, for example, *Pythium ultimum*, as a more important factor in plant growth promotion than improving mineral nutrition. The significant role of *Pythium* in plant-growth suppression, and the improvement of plant growth by fumigation or solarizaiton was demonstrated for wheat (Cook *et al.*, 1987). It can be assumed that in various cropping systems different mechanisms might be responsible for the IGR phenomenon. IGR is also connected with a basic question, the definition of plant health, which is beyond disease control.

Soil disinfestation can be also used as a tool for determining the role of certain microorganisms in plant growth suppression (Cook *et al.*, 1987). In another study, the level of soluble organic substances, i.e., humic substances, was higher in the solarized soil. These soluble substances increased the growth of corn plants as well as populations of fluorescent pseudomonads, indicating an additional potential mechanism for improved plant growth (Chen *et al.*, 2000). In another study (Gruenzweig *et al.*, 1993), plant improvement was recorded in shoots of tomato seedlings and significantly higher levels of chlorophyll and protein contents were detected in plants from solarized soil, as compared to those from control soil.

The IGR has very important economic implications, which should be taken into account when considering the use of solarization.

Integrated Management Aspects

The management of soilborne pathogens cannot be based on a single measure, even a highly effective one. Moreover, it has to consider all sources of inoculum, not the soilborne sources only, and should manage them before, at and after planting. Thus, it has to be holistic. With regard to dependency on a single control measure, the methyl bromide (MB) crisis has taught one a painful lesson that must not be repeated.

The concepts of disease control have evolved over the years. In the early days, the goal was to eradicate the pathogens mainly using drastic chemicals. Only later it was realized that, in addition to the pathogen, there are other components in disease development, namely, the host and the biotic and abiotic components of the environment, which can be manipulated to suppress disease. The integrated pest management (IPM) approach became a major pillar in disease management. Consequently, the term 'disease management' replaced the term 'disease control.' The holistic IPM concept gathers all of these elements under one 'roof.' An appropriate IPM program can achieve better control with minimal use of pesticides and environmental hazards, a broader spectrum of control, and even a long-term effect. The diversity of approaches reduces the risks involved when a cropping system depends on a single control method. Combining and alternating methods of control are at the heart of IPM. The following issues should be considered when developing IPM programs for soil disinfestation and specifically for soil solarization (Gamliel and Katan, 2009).

- All pests of the crop, with an emphasis on the major ones, need to be taken into account.

- The IPM program should be in harmony with the cropping system.
- In combining methods of control, priority should be given to nonchemical methods.
- Emphasis should be placed on reducing pesticide usage, not necessarily with the aim of eliminating it entirely.
- Environmental, economic, legal, and social considerations need to be taken into account.
- When possible, decision-making tools should be used.

Combining solarization with other methods of control should be considered from two different angles: as a way of improving solarization; and as a way of improving the other method(s). For example, from the latter point of view, a suitable combination of solarization (or any nonchemical method) with a reduced dosage of pesticide makes the pesticide less harmful (and more acceptable), without reducing control effectiveness, and may even increase its effectiveness. McGovern and McSorley (1997) emphasized the potential necessity of combining solarization with other pest-management practices to ensure acceptable reduction of difficult-to-control pests, especially in suboptimal climates. When two control measures are applied together, the resultant effect on the target pest may be antagonistic, additive, or synergistic. For example, a synergistic effect has been obtained from combinations of soil solarization and biocontrol agents (Ristaino *et al.*, 1991; Sivan and Chet, 1993). The sequence of application of the combined methods is also important (Eshel *et al.*, 2000).

Combining Soil Solarization with Other Control Methods

The concept of combining solarization with other control methods emerged from the need to make use of the advantages of each method while overcoming their specific limitations. Since the beginning of the MB phase-out in 1992, the adoption of solarization and its combination with chemicals have been recognized as feasible and effective strategies. Combining solarization with fumigants and pesticides improves pest control and broadens the spectrum of affected pests. The increased control effect also reduces the required dose of the pesticide. In addition, the combination of solarization with a low rate of an appropriate pesticide may provide the benefit of wider safety margins for ensuring an effective treatment, which is a requirement for commercial users. Soil solarization may also enhance or delay the rate of pesticide dissipation from soil, thus giving the farmer an additional tool to better manage the sequence of soil treatments and crop-management practices.

The combination of organic amendments (organic material, animal manure, compost, and plant residues) with soil solarization can further improve pest control (Gamliel and Stapleton, 1993; Klein *et al.*, 2011). The term 'biofumigation' is often used to describe the incorporation of organic amendments, reflecting the mode of action of active volatile compounds generated by the decomposing biomass in the soil. This is not actually the case, however, as many different chemical and biological mechanisms are involved with organic amendments beyond active volatile compounds. These processes occur during the decomposition of organic material and act directly and indirectly on pathogen survival. Moreover, organic amendments may result in the evolution of 'soil suppressiveness,' i.e., low disease incidence and severity in the presence of a virulent pathogen and a susceptible host. It is regarded as a general soil suppressiveness (Weller, 2012), not being pathogen-specific and demonstrated with various crop residues (Klein *et al.*, 2012). The adoption of organic amendments combined with solarization as a disease-managing approach has been extended to a broad-spectrum of cropping systems. Improvements are continuously being made in providing consistent and reproducible results, and in formulating organic materials as commercial products (as with chemical pesticides) for maximal efficacy and consistency.

Another attractive approach to improving solarization is to combine it with beneficial organisms that can improve plant production both directly and indirectly. The survival and even increase in populations of natural thermotolerant antagonists are common in solarized soils. The application of selected antagonists that can survive solarization is of special interest, for both pre- and postsolarization application of biocontrol agents. Modifying soil conditions through solarization can improve reproducibility and the biocontrol performance of the appropriate organism.

The goal of combining solarization with other agents is to provide additional tools for disease management and enhancement of crop production. To place these tools in the growers' hands, the whole approach (solarization application, commercial formulation of the combined agent (organic material and beneficial organism), as well as its application technology) has to be feasible and economical for commercial implementation.

Technological Aspects

Huge advances in soil solarization as well as the innovations in intensive agriculture are attributed, among other things, to the development and adoption of plastic materials in various forms for different applications. The most common plastic film used for solarization is transparent low-density polyethylene. However, even the simple film must have some important properties to ensure that the plastic holds for several weeks, which might be too long under certain open-field conditions of intensive photodeterioration and wind forces. This is also the major application challenge of continuous solarization relative to soil fumigation: in the latter, the plastic only needs to hold for a few days. For example, the deterioration of transparent plastic is rapid during the hot season, under intense solar irradiation. Therefore, additional characteristics are needed to provide a better film for soil solarization. Indeed, certain additives are incorporated into the film for soil solarization to modify or enhance some specific property, such as irradiation transmittance, protection from ultraviolet (UV) degradation, and increased film strength. Protection of plastic sheets for solarization is done by amending them with various UV-light stabilizers. Water droplets condense rapidly on the under-surface of plastic mulch. The condensed water interferes with the transmittance of irradiation and may reduce the extent of soil heating. Addition of wetting agents causes water droplets to coalesce

and the runoff is returned to the soil. This keeps the film more transparent for maximum sunlight penetration. Antifog (or antidrip) agents act like surfactants, such that the moisture forms a continuous, transparent layer on the undersurface of the film rather than forming droplets that create haze and reduce light transmission.

The thickness of the film has no major effect on soil heating, hence the cost of the film and its strength with respect to the application technology dictate the thickness of the film to be used. In practice, solarization can be applied using a thin sheet of 25-μm thickness.

Applying soil solarization is a relatively simple procedure. It requires soil preparation, which includes removing plant residue from the soil surface and leveling the surface of soil clods by hand or machine. The soil has to be smoothened and irrigated down to a depth of 50 cm before the plastic film is laid, because, as a rule, organisms are more sensitive to heating under moist versus dry conditions (Shlevin *et al.*, 2003). Plastic is normally laid in the field for 4–6 weeks during the appropriate climate, i.e., with maximal ambient temperatures and solar irradiation.

Soil mulching for solarization can be performed manually with relatively small plots, or with special mulching machinery, which is preferred for large fields. In the former, the films are laid manually and anchored by narrow sand windrows. The soil in the windrows can be placed inside clear plastic bags, enabling its solarization as well, and leaving no soil unsolarized.

In mechanized solarization, the plastic film is unrolled and a trench is opened to bury the edge. Soil anchoring is then performed by covering with soil using a roller or disc. Broadcast application aims to cover the entire plot to be solarized. The tarp-laying machine unrolls a plastic strip (2–4 m width) with one edge of the sheet anchored to the soil in a trench on one side of the plot (as described for strip application) and the other edge of the film overlapping and connected by glue or welded to the adjacent plastic sheet laid at the previous pass. An alternative system that involves welding the polyethylene and fusing the sheets together was developed in Israel (Grinstein and Hetzroni, 1991). This technology is now the major method used for broadcast solarization as well as other fumigation applications in Israel.

A different approach to soil solarization is the application of sprayable polymers, which can offer a feasible and cost-effective alternative to the commonly used polyethylene sheet. This approach is based on spraying a water-based formulation of plastic polymer that forms a membrane film on the soil surface. The uniformity and porosity of the membrane depends on the type and formulation of the polymer. In fact, the use of liquid formulations for spray mulch was suggested even before solarization was developed (Bochow, 1989), but these were oil-based. Later, the development of latex-based mulches offered more feasible options for application (Audette and Pole, 1987). In Israel, a sprayable polymer product, Ecotex, was developed along with the technology to apply it economically on soil for a variety of purposes (Gamliel and Becker, 1996). Soil coating with the black polymer formulation using this technology resulted in a membrane film that could raise soil temperatures close to solarization levels (Gamliel and Katan, 2009). The soil-heating process is faster with sprayable mulch than with plastic film, but the soil also cools down to lower temperatures at night. In another study, a water-based varnish made of a biodegradable polysaccharide mixture containing biodegradable plasticizers was suggested. However, its practical use was not demonstrated. Obviously, this approach is promising, especially for open-field conditions, but its adoption requires further improvements.

Solarization in the open field has the advantage of direct exposure to solar irradiation with no interference. However, technical difficulties, such as improper and poorly timed mulch application, maintaining film integrity under harsh conditions for several weeks, and film removal, cause difficulties for commercial implementation of solarization under open-field conditions. Development of innovations in the application of solarization should focus on better mulching technologies, including improved films and polymers, and specifically photodegradable films. Additional development should also aim at plastic removal and disposal. Meeting these challenges, together with the adoption of strategies for IPM, will certainly promote the extended use of solarization for large-scale application in the open field.

Solar Heating of Soil and Pathogen Response to Heating: Principles and Modeling

Reduction of pathogen populations during the solarization process is a key (but not the only) factor for disease reduction. Thermal-killing of the pathogen (in addition to other mechanisms) is responsible for this reduction and is connected with both soil temperature and the pathogen's sensitivity to that temperature. These two topics will be discussed below.

Soil Heating during Solarization

The patterns of solar heating of soil, with or without plastic, are characteristic. Knowing the factors involved in heating enables optimizing the solarization process.

A variety of models for predicting temperatures of solarized soils under various climatic conditions have been developed and validated. The first models were developed for arid conditions (Mahrer, 1979; Mahrer and Shilo, 2012). Simplified models (Cenis, 1989), and those suitable for more humid areas (Wu *et al.*, 1996), were also developed. A 1-cm^2 area outside the earth's atmosphere and parallel to its surface receives 2 cal cm^{-2} min^{-1} (solar constant) of energy in the form of solar radiation; but only about half of that reaches the ground. The energy is lost from the soil in the form of long-wave radiation (depending on water vapor and clouds) through conduction, convection, and water evaporation; the latter being a very important factor in wet soils. The heat that penetrates the soil surface is stored in the soil and, at night, when the thermal gradient is reversed, it is lost again due to a cyclic reversal in the direction of heat flow. In principle, because the rate of heat flow through the soil depends on the soil's thermal properties and the temperature gradient to which it is subjected, the temperature regime at a given depth can be predicted using equations for calculating an energy

budget that take into account all factors involved in soil heating, including plastic properties.

Mahrer (1979) developed a one-dimensional numerical model for such predictions. Indeed, the predicted temperatures in mulched soils were very much similar to the observed ones, the magnitude of error being within the range of 0.6–1.2 °C. Models describing spatial soil temperature regimes in solarized soils and closed greenhouses have also been developed.

Response of Pathogens to Elevated Temperature

The thermal death rate of a population of an organism depends on both the temperature and exposure time, which are inversely related. Various methods have been developed to evaluate thermal effects on organisms and to quantify the time–temperature relationships and the organisms' inherent heat sensitivity. Certain thermal death curves have an exponential nature, which indicates that a constant fraction of the population is killed per unit of time. In some cases, a linear relationship was revealed by plotting logarithms of time required to kill 90% of populations of various pathogenic fungi against temperature (Pullman *et al.*, 1981).

Modeling pathogen control by solarization is usually based on studies of thermal inactivation of pathogens, using data collected under constant elevated temperatures. Based on chemical reaction kinetics at constant temperatures, an exponential inactivation relationship is typically expected. Traditionally, thermal inactivation of microorganisms is considered a first-order reaction, characterized by a logarithmic change in the organism's population with time. Studies on thermal inactivation under fluctuating temperatures, such as those naturally prevailing in the field, are much more complicated because the partial effects of varying temperatures on pathogens are difficult to weigh, and they require numerical integration to account for their complexity (Shlevin *et al.*, 2003). There are other approaches to simulating and modeling pathogen control by solarization, for example, by plotting the level of mortality versus accumulated hours above a certain temperature, i.e., degree–hours (DH). Shlevin *et al.* (2003) developed a model describing the process of pathogen control with time under structural (dry) solarization. In another study on modeling regular (wet) soil solarization, the common DH approach for predicting the rate of heat inactivation was further improved by giving different weights to the different temperatures, thus refining the correlation between temperature data and pathogen survival from $R^2 = 0.324$ to $R^2 = 0.86$.

Soil Solarization in Various Cropping Systems

Since 1976, research into soil solarization has expanded in many countries. Although it is a climate-dependent method, it has been introduced in countries with different climates, soils, and cropping systems. Furthermore, soil solarization has been embraced and adapted for various production systems characterized by different economic structures, agricultural traditions, and farmer attitudes. Therefore, it is not surprising that solarization has developed in different ways, with modifications producing different solutions for specific problems and needs. Nevertheless, research, development, and implementation of soil solarization share common features in the various cropping systems with those in which it was developed (Katan and DeVay, 1991). The success of soil solarization as a practical approach led to the evaluation of solarization in other marginal and cool climates, inside structures or as an outdoor application, as well as in humid areas where cloudy conditions and rain are common during the solarization period (Walters and Pinkerton, 2012). Below are examples from some of those countries.

In Europe, especially in the northern regions, as well as in Japan, the approach of solarizing the soil inside closed greenhouses was developed (Garibaldi and Gullino, 1991; Horiuchi, 1984). This results in further elevation of soil temperatures (and more effective disease and weed control) compared with solarized soils in the open field due to the double plastic layers from both closing the greenhouse and mulching the soil. Greece was one of the first countries to realize the potential of soil solarization, especially in plastic houses and glasshouses, and to a lesser extent with field crops, for a variety of vegetables and flower crops, and perennial crops such as artichoke and olive (Tjamos *et al.*, 2012). They found that many fungal pathogens, as well as the pathogenic bacterium *C. michiganensis* subsp. *michiganensis*, were well controlled. In India, soil-solarization studies have been carried out in many regions, including arid ones, with an emphasis on combining solarization with local organic amendments (Lodha and Mawar, 2012). Soil solarization, especially when combined with low dosages of fumigants, is applied on a large scale in Turkey. In Israel, soil solarization is successfully used with a variety of crops, in both open field and greenhouses, with an emphasis on combining it with other measures (Gamliel and Ausher, 2012). Soil solarization is well-adapted to organic farming and home gardens in many countries.

Technology Transfer and Adoption of Soil Solarization

Technology development in agriculture relies on three components: technology generation, diffusion, and adoption. Successful technology transfer depends primarily, but by no means solely, on a long-term collaboration between research, agricultural extension, and farmers. Advancing and monitoring adoption at the growers' level is an extension task. The development of soil solarization in Israel was first evaluated by farmers and extension specialists in the Jordan valley in Israel where, for the first time, they came across the possible disinfestation effect of transparent plastic mulch during one hot summer (Grinstein and Ausher, 1991). This initial observation was further developed by a multidisciplinary team of researchers and agricultural extension specialists. Therefore, when soil solarization evolved into an applicable technology at the growers' level, it was already well received by both extension workers and growers. Still, for the first 20 years after its release, soil solarization remained a niche treatment, and its wide-scale adoption was slow. This was mainly due to bottlenecks in four major areas: application problems, low efficacy with specific soilborne pests, the cost factor, and the human factor. A lack of awareness of the particular benefits of solarization, as well as a lack of technical information, were also identified as factors impeding large-scale utilization of the method.

From a technology-diffusion perspective, solarization can be regarded as a component of IPM and biological control systems. These systems and techniques are complex and often more expensive than the equivalent chemical control methods. Moreover, solarization was only backed by public research and development organizations, with little or no involvement of the private sector in the promotion or marketing of the whole technological package. Therefore, the dissemination of soil solarization relied mainly on intensive, but limited to, one-to-one advisory contact between researchers and farmers. Although individual extension specialists were involved in the development of solarization right from the start, the method was not yet fully adopted by the Ministry of Agriculture as a system-wide policy at that time, except for the control of pink root rot in onion and broomrape.

Today the use of soil solarization is on the rise. For the most part, this is due to specific crop systems and specific regions pioneering the adoption of solarization in practice, mainly in combination with other methods. Moreover, the phase-out of MB and the fact that many chemical alternatives to MB have deleterious environmental effects have recently boosted the use of solarization. Successful results of solarization used in combination with fumigants such as 1,3-D, 1,3-D/Pic, metham sodium, and dazomet have been reported from different countries and for different crops and cropping systems for many years. The greatest advantage of these combinations is up to 50% reduction in fumigant dosage rates, which minimizes the impact of fumigants on the environment and often lowers costs. From an extension-advisory perspective, the applicability of these formulas has been demonstrated in the field for the major crop/pathogen combinations to ensure its rapid dissemination and adoption.

Other Uses of Solarization

Soil solarization was originally developed as a preplant soil disinfestation tool for annual crops. However, its application and uses have expanded since its early days, and continue to expand to various areas and fields of interest. These unusual uses are based on solar heating. Following are some examples:

1. Soil solarization in existing orchards to control soilborne pathogens (which is impossible to achieve with fumigants) is a deviation from the classical preplant application. It was pioneered by Ashworth and Gaona (1982) for the control of Verticillium wilt in pistachio orchards. The success of this approach depends on a variety of factors, such as the extent of damage inflicted on the trees during solarization and the effectiveness of solarization in shaded areas. Postplant solarization also reduced the incidence of Verticillium wilt in olives (Tjamos *et al.*, 1991) and *Rosellinia necatrix* in apple (Freeman *et al.*, 1990). The recovery of infected trees following the application of solarization is a highly desirable goal.
2. Solarization can be used as a sanitation tool, for example, for disinfestation of tomato supports that transmit *Didymella lycopersici* (Besri, 1983), structural solarization of closed greenhouses (Shlevin *et al.*, 2003), disinfestation in container nursery production (Stapleton and Faddoul, 2012), disinfestation of reused polysterene trays and soil piles (Nico *et al.*, 2003), among other uses.
3. Soil solarization is not practical for rice production. Nevertheless, solarization of rice nursery soils for the production of healthy seedlings is a simple, low-cost, nonchemical soil treatment for the suppression of pathogens in flooded soils. Thus, when rice seedlings were produced in solarized nursery soil, the health of the mature rice plants was significantly improved (Culman *et al.*, 2006; Gamliel and Katan, 2012).
4. Contribution to human health: soil solarization is effective at reducing the incidence of corn ear rots and consequently, produces mycotoxin-free crops and increases the productivity and quality of the corn grains (Yasmin and Ghaffar, 2007). Similarly, it reduced the colonization of peanut pods by *Aspergillus niger*, which is also a source of mycotoxin production (Grinstein *et al.*, 1979).

   Human infection with foodborne pathogens has occasionally been linked to field-soil contamination with fecal pathogenic bacteria, which can be brought to agricultural fields by animal manure. Soil solarization eliminated a population of *Escherichia coli* within 4 weeks of treatment, with no influence on the total direct and viable counts of other bacteria in the soil (Wu *et al.*, 2009). In another study, solarization of soil amended with raw chicken manure resulted in reduced counts of *Staphylococcus aureus*, *Clostridium perfringens*, and fecal coliform bacteria (Barbour *et al.*, 2002). These findings indicate that soil solarization can be useful for biosafety and the control of soil contamination by human pathogens via immature compost or animal manure.
5. Soil solarization for home gardens and landscapes.
6. Solarization of plant-growth media and potting mixes, some of which are difficult to fumigate (Stapleton and Faddoul, 2012).

The use of 'old' (i.e., previously used) polyethylene provides for extremely inexpensive solarization. Avissar *et al.* (1986) found that such used polyethylene can be effective for soil heating.

Concluding Remarks

The initial goal of soil solarization was quite modest: to explore the possibility of effectively using solar heating of the soil for the control of Verticillium wilt in two crops in a specific hot region in Israel. However, its rapid development led to its success in controlling a wide-spectrum of pests, well beyond its initially intended scope. Pest control by solarization has developed from the primary goal of simply killing the pathogen and reducing disease incidence, to the concept of integrating additional objectives, such as economic aspects as well as minimal disturbance of the biotic and abiotic components of the environment. Thorough studies on the mechanisms involved, with emphasis on the biotic ones, were essential for achieving the above goals. The philosophy of IPM is responsible for the evolution of other aspects of soil solarization. Other global changes, such as the phase-out of soil fumigants – mainly MB – further boosted the adoption of solarization in soil-disinfestation programs.

The adoption and implementation of solarization by farmers can be achieved by developing a feasible, cost-effective application technology. The application of solarization, namely, tarping a plastic sheet over moist soil and allowing the sun to do the rest, seems to be an easy way. Nevertheless, many aspects of its application, including soil preparation, tarping, and plastics technology are involved in achieving successful solarization. The need for application methodologies suited to each specific solarization niche, for example, open field, closed greenhouse, and strip solarization, has led to specialized research and development.

The success of soil solarization has led to its implementation in other marginal areas. Solarization has now been shown to be effective in northern regions as well, such as in the Pacific Northwest of the USA. Similarly, solarization has been introduced into humid areas where cloudy weather and rain are common during the summer. The significant role of soil solarization as an element in integrated control should be further expanded. Further developments of predictive meteorological tools and models, as well as other related topics, are essential in providing a more solid background for further development and implementation of solarization. The development of soil solarization clearly demonstrates that even a climate-dependent management method can be harnessed, for certain situations, if it is properly introduced and its expansion is carefully and gradually carried out.

In a dynamic and continuously changing agricultural, social, political, and economic global climate, it is extremely difficult to predict future measures for crop protection. Nevertheless, it is our duty to closely follow and respond to those changes, to improve our research techniques, and to continuously prepare alternative management methods, well ahead of time, rather than only when a solution for a crisis is urgently needed. The IPM concept, which reflects reality and a practical approach, should become more of a central pillar in soil disinfestation than it is today, as it is in solarization. The IPM concept has the flexibility required to better adapt to our agricultural systems, with expected and unexpected changes.

See also: Food Law. Mineral Nutrition and Suppression of Plant Disease. Plant Biotic Stress: Weeds. Plant Disease and Resistance. Plant Health Management: Biological Control of Plant Pathogens. Plant Health Management: Crop Protection with Nematicides. Plant Health Management: Fungicides and Antibiotics. Plant Health Management: Herbicides. Plant Health Management: Pathogen Suppressive Soils

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Plant Virus Control by Post-Transcriptional Gene Silencing

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Abbreviations

amiRNA	Artificial micro RNA
Ath	*Arabidopsis thaliana*
CP	Coat protein
CPMR	Coat protein-mediated resistance
DCL	Dicer like protein
dpi	Days post-inoculation
dsRNA	Double-stranded RNA
miRNA	Micro RNA
ORF	Open reading frame
PTGS	Post-transcriptional gene silencing
RISC	RNA-induced silencing complex
RNAi	RNA interference
siRNA	Small interfering RNA
TGS	Transcriptional gene silencing
UTR	Untranslated region

Glossary

amiRNA An ~21 nucleotide small RNAs generated from the natural miRNA precursors by replacing the natural miRNA sequence in the precursor.
Gene silencing The mechanism by which the functions of one or many genes are inhibited or reduced either before (transcriptional gene silencing, TGS) and or after transcription (post-transcriptional silencing, PTGS).
Guide strand siRNA One of the two strands of duplex siRNA which is complementary to the target messenger RNA.
Micro RNA (miRNAs) Small RNAs of ~21 nucleotide length generated by the processing of self complementary precursor transcript.
Post-transcriptional gene silencing (PTGS) PTGS involves the processes which leads to the sequence specific cleavage of target mRNA or inhibition of its translation.
Resistance It is a state in which a plant shows no or mild or delayed symptoms of virus and undetectable level of virus genome by one of the molecular detection method.
RNA-induced silencing complex (RISC) A multi-enzyme complex effecting the cleavage of the target mRNA. It contains a slicer and guide siRNA strand.
Small interfering RNA (siRNA) A ~21 nucleotide duplex RNA generated from the long dsRNA substrates by the action of dicer-like proteins.
Suppressor of gene silencing A group of proteins usually encoded by the plant viruses which inhibit one or many steps of the gene silencing pathways.
Transgenic plant A plant regenerated by transforming it with a vector containing one or more foreign DNA sequences including promoter sequences.

Introduction

Both single-cell and multicellular organisms control their physiological processes through their genetic material either directly or indirectly by their products, such as various types of ribonucleic acids (RNAs) and proteins in response to internal and external cues. In a multicellular eukaryotic organism, all the genes are not expressed all the time, but genetic and epigenetic factors and processes regulate them spatially and temporally. Eukaryotic organisms, including plants, have evolutionarily conserved mechanisms to evade the invasion by foreign genetic materials, such as transposons, viruses, and bacteria. One such mechanism is post-transcriptional gene silencing (PTGS), also called as RNA interference (RNAi) in animals and quelling in fungi. In PTGS, expression of a gene (endogenous, transgene, or foreign genetic material) is regulated after it is transcribed into a messenger RNA (mRNA). PTGS plays a pivotal role in the development of an organism and in the protection from invading foreign genetic material, including viruses. It acts in a sequence-specific manner by cleaving and by translational suppression of mRNA. PTGS is triggered by the formation of a hairpin-like structure of a mRNA or a double-stranded RNA (dsRNA). RNA hairpin-like structures are thought to be formed by bidirectional transcription of overlapping gene regions, aberrant transcription from inverted repeat regions, and dsRNA genomes of viruses or replication intermediates of viruses.

It is believed that the first report of RNA silencing might have been by Wingard in 1928, in which initially infected leaves with tobacco ringspot virus appeared necrotic and diseased. However, the upper leaves were immune to the virus, asymptomatic and resistant to secondary infection (Baulcombe, 2004; Wingard, 1928). At that time the mechanism of recovery and specificity of resistance to secondary infection was unknown. With the report of a new concept of pathogen-derived resistance (PDR) (Sanford and Johnston, 1985), it was shown that virus-derived sequences, for example, coat protein (CP) gene, conferred resistance to the same or related viruses (Powell-Abel *et al.*, 1986). Many of the initial studies employed pathogen-derived (CP-mediated) resistance strategy (Beachy, 1997) to develop virus resistance and used sense or antisense gene constructs to impart virus resistance in transgenic plants (Yadav

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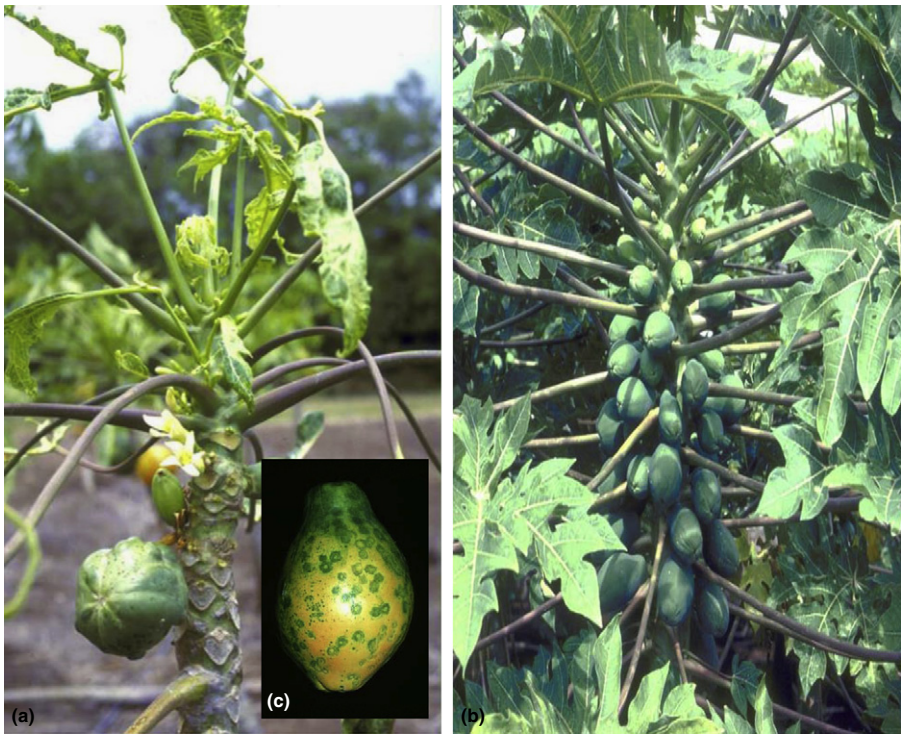


Figure 1 Transgenic papaya resistant to PRSV. (a) Non-transgenic sunrise, (b) transgenic virus-resistant Rainbow papaya (*Carica papaya* L.) in the field, and (c) ringspot symptoms on papaya fruits infected with PRSV. Courtesy of S. Ferreira.

et al., 2007). Several groups reported virus resistance using the coat protein-mediated resistance (CPMR) strategy, although it was unclear for many types of viruses whether the expression of the CP was required for inducing virus resistance, and probably many of them were using the PTGS mechanism, unknown at that time. For the sake of simplicity this article mostly review the cases where PTGS was clearly involved in the resistance; otherwise, the readers are advised to refer to the review of Yadav *et al.* (2007). For example, transgenic papaya transformed with the CP of Papaya ringspot virus (PRSV) was developed and successfully deployed in the field (**Figure 1**, Ferreira *et al.*, 2002). However, the exact mechanism of PDR was not known at that time because both protein-coding and nonprotein-coding virus sequences conferred virus resistance (Tacke *et al.*, 1996).

In the early 1990s Jorgensen's lab reported co-suppression of both the transgene and the endogenous gene when the transgene was over-expressed in petunia (Napoli *et al.*, 1990). Following this report many research groups reported that silencing of endogenous, transgene, or both genes could be achieved by over-expressing the sense or antisense copy of the gene. However, it was not until the report by Andrew Fire and Craig Mello in 1998 that RNA silencing started to receive more attention when they showed that dsRNA is much more efficient in silencing the homologous mRNA than either sense or antisense strand of a gene (Fire *et al.*, 1998; Tabara *et al.*, 1998). Subsequently, it was observed that corresponding small RNAs (of size ~ 21nt) accumulate in the silenced plants (Hamilton and Baulcombe, 1999).

Regarding plant virus resistance, as early as 1993, Lindbo *et al.* (1993) had first demonstrated RNA-mediated resistance against viruses in plants. Central to the RNA silencing mechanism are the small RNAs (Hamilton and Baulcombe, 1999). Small interfering RNAs (siRNAs) are 21–23nt long with 2-nt 3′ overhang that mediates the cleavage of the target RNA (Elbashir *et al.*, 2001a,b). The 3′ structure of the siRNAs suggested that they are the products of enzymatic cleavage and the 2nt overhang suggested features of RNase III endonuclease. There are several classes of small RNAs with diverse structures and functions (**Figure 2**).

The role of innate PTGS for the plant virus control was also suggested by the accumulation of virus-derived siRNAs in virus-infected plants and the increased susceptibility of the plants to viral infections when genes involved in PTGS were mutated (Hamilton and Baulcombe, 1999). Presence of virus-encoded suppressors of gene silencing and their functions in various steps of PTGS further supported their role in the plant virus control (Li and Ding, 2006). Very recently, an antiviral role of RNAi has been shown against mammalian viruses (Li *et al.*, 2013; Maillard *et al.*, 2013). To exploit this innate antiviral mechanism, plants were genetically modified to express virus-specific dsRNAs to trigger the PTGS system (Smith *et al.*, 2000). The gene silencing mechanism used to control viruses based on either short or long hairpin constructs involves the cleavage of dsRNA molecules into short duplex 21–26nt siRNAs (Baulcombe, 2004; Hamilton and Baulcombe, 1999) by the action of RNase III endonucleases, such as four Dicer-like proteins in *Arabidopsis thaliana* (DCL1 to 4) (Golden *et al.*, 2002; Park *et al.*, 2002). One of the strands of duplex siRNAs (guide strand) is incorporated into the multi-subunit endonuclease complex called RNA-induced silencing complex (RISC). RISC consists of a complex of

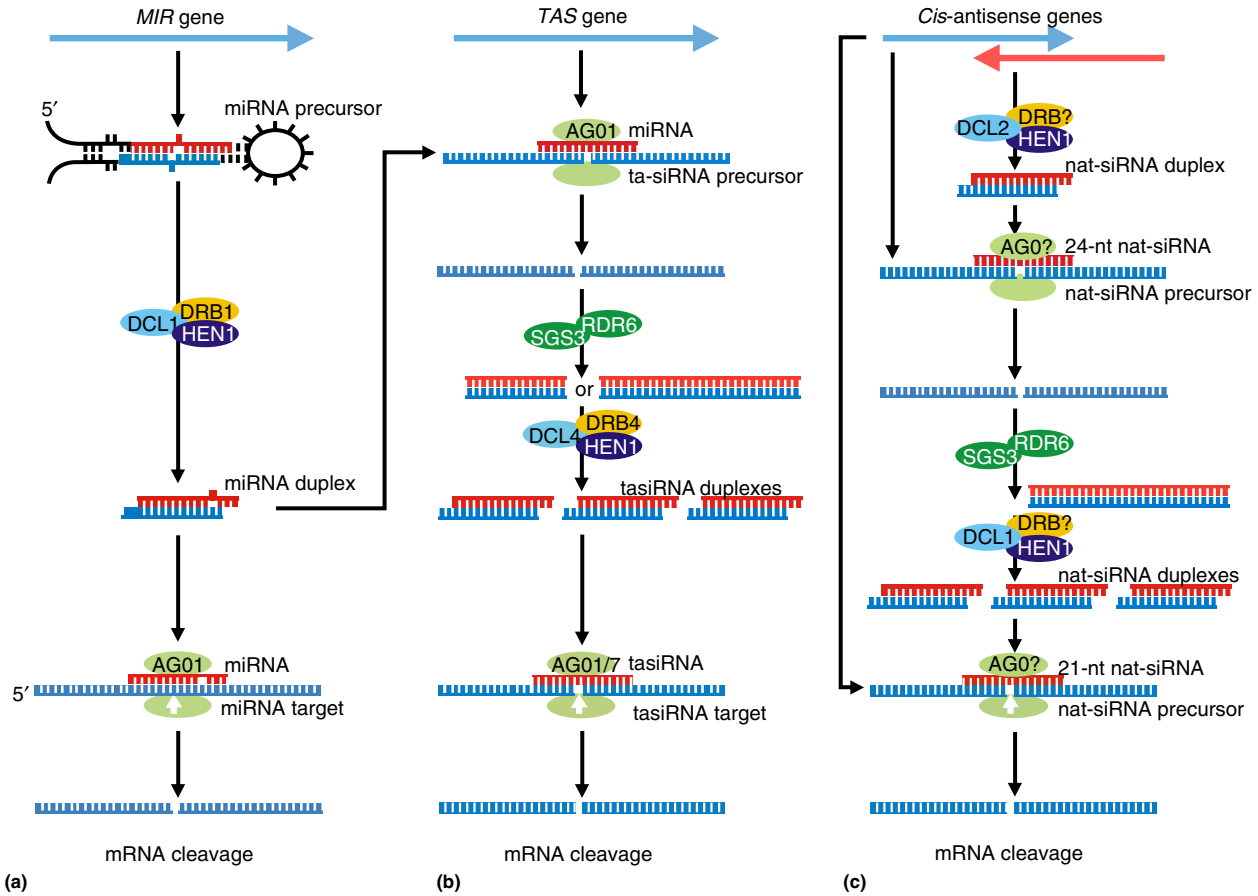


Figure 2 Diversity of small RNA pathways in plants. (a) miRNA pathway, (b) and (c) siRNA pathways. DCL1, Dicer-like protein 1; DRB1, Double-stranded RNA-binding protein 1; HEN1, Hua enhancer protein 1; AGO1, Argonaute protein 1; SGS3, Suppressor of gene silencing 3; RDR6, RNA-dependant RNA polymerase protein 6; ta-siRNA, trans-acting siRNA; nat-siRNA, Natural antisense siRNA. Adapted from Eamens, A., Wang, M.B., Smith, N.A., Waterhouse, P.M., 2008. RNA silencing in plants: Yesterday, today, and tomorrow. Plant Physiology 147, 456–468.

proteins, including one of several Argonaute proteins. There are, for example, at least 10 Argonaute proteins in *A. thaliana*. RISC mediates the sequence-specific cleavage of the target mRNA between the positions 10 and 11 of the ~21nt guide strand, by the slicer function of the Argonaute protein. Primary siRNAs (those generated by the processing of initial dsRNA triggered by the action of DCL proteins) can also bind to the target RNA, and a secondary dsRNA can be synthesized by the action of RNA-dependent RNA polymerases (RdRPs). The siRNAs generated by this mechanism are called secondary siRNAs and the phenomenon is called transitivity because secondary siRNAs can also be produced from the nucleic acid regions beyond the primary target, thus increasing the efficiency of the RNAi (Sijen *et al.*, 2001; Vaistij *et al.*, 2002). In *A. thaliana* there are at least six RdRPs. The presence of multiple paralogs of key proteins involved in PTGS in *A. thaliana*, and most probably other plants, results in diverse siRNA pathways in plants (**Figure 2**) (Eamens *et al.*, 2008; Xie *et al.*, 2004) that can be utilized for engineering virus resistance.

To enhance the production of dsRNAs in the cell to trigger a robust PTGS, plant transformation gene constructs encoding an intron-spliced RNA with a hairpin structure have been shown to be highly efficient when directed against viruses or endogenous genes rather than over-expressing either sense or antisense copy of the gene (Smith *et al.*, 2000). Since this report, hairpin RNA-mediated PTGS has been used as a method of choice to engineer virus resistance in transgenic plants (Baulcombe, 2004; Vanitharani *et al.*, 2005).

Here the authors have discussed chronologically the recent progress reports of proof of concepts and successful applications of engineered plant virus resistance by gene silencing/PTGS for DNA and RNA plant viruses, with future opportunities/prospects and challenges. Owing to space limitations, only selected studies have been reported in order to highlight the breadth of the application of gene silencing technology to control diverse plant viruses in different host plants (**Table 1**). Most of these studies used inverted or hairpin RNA to trigger PTGS, and the virus-resistant plants were characterized by the accumulation of siRNAs specific to transgenes.

Control of Plant DNA Viruses by siRNA-Mediated Gene Silencing

Members of two DNA virus families, Geminiviridae and Nanoviridae, have small, single-stranded DNA genomes in

Table 1 List of transgenic plants where post-transcriptional gene silencing has been used to develop virus-resistant plants

Plant	*Virus*	*Virus gene*	*References*
DNA Viruses			
Nicotiana tabacum	CLCuV	5′-, 3′-AC1, AC2-AC3 overlap	Asad *et al.* (2003)
Manihot esculenta	ACMV	AC1	Chellappan *et al.* (2004)
N. tabacum	TYLCV	Noncoding conserved regions	Abhary *et al.* (2006)
Lycopersicon esculentum	TYLCV	Noncoding conserved regions	Abhary *et al.* (2006)
L. esculentum	TYLCV	C1	Fuentes *et al.* (2006)
Phaseolus vulgaris	BGMV	AC1	Bonfim *et al.* (2007)
L. esculentum	TYLCV	Intergenic region, AC1/AC4	Yang *et al.* (2004); Zrachya *et al.* (2007)
M. esculenta	ACMV	Promoter; AC1	Vanderschuren *et al.* (2007); Vanderschuren *et al.* (2009)
L. esculentum	ToCMoV	AV1-AC1-AC4 overlap	Ribeiro *et al.* (2007)
Nicotiana benthamiana	ToLCTWV	Partial C2 gene	Lin *et al.* (2011)
L. esculentum	ToLCTWV	Partial C2 gene	Lin *et al.* (2011)
N. benthamiana	CpCDPKV	Rep + IR + MP	Nahid *et al.* (2011)
Musa paradisiaca	BBTV	Rep	Shekhawat *et al.* (2012); Elayabalan *et al.* (2013)
RNA Viruses			
Carica papaya	PRSV-P	CP	Fitch *et al.* (1992); Manshardt (1998); Suzuki *et al.* (2009)
Prunus domestica	PPV	CP	Scorza *et al.* (1994); Scorza *et al.* (2001); Pandolfini *et al.* (2003)
Cucurbita pepo	ZYMV, WMV2, and PRSV	CP	Tricoll *et al.* (1995)
Cucumis melo/Cucumis sativa	ZYMV, WMV, and PRSV	HC-Pro	Leibman *et al.* (2011)
Hordeum vulgare	BYDV-PAV	Polymerase	Wang *et al.* (2000)
Beta vulgaris	BNYVV	CP, Replicase	Andika *et al.* (2005); Pavli *et al.* (2010)
N. tabacum	CTV	3′-CTV	Batuman *et al.* (2006)
Citrus macrophylla	CTV	3′-CTV	Batuman *et al.* (2006)
N. benthamiana	CTV	p23 + UTR	Febres *et al.* (2008)
Citrus aurantifolia	CTV	p20, p23, p25 and 3′ UTR	Soler *et al.* (2012)
N. tabacum	TMV	CP; partial MP	Yan *et al.* (2007); Hu *et al.* (2011)
Euphorbia pulcherimma	PnMV	HC-Pro	Clarke *et al.* (2008)
N. benthamiana	CPsV	CP, 54K	Reyes *et al.* (2009)
Citrus x sinensis	CPsV	CP, 24K, 54K	Reyes *et al.* (2011)
N. tabacum	TMV and CMV	Partial MP and Rep	Hu *et al.* (2011)
N. benthamiana	TSWV	N gene	Lin *et al.* (2011)
L. esculentum	TSWV	N gene	Lin *et al.* (2011)
Citrullus lanatus	WSoMV, CMV, and WMV, CGMMV	N gene of WSoMV and CP gene for others	Lin *et al.* (2012)
N. tabacum	CMV	Rep	Ntui *et al.* (2013)
Solanum tuberosum	PVX, PVY, PLRV	ORF2-HC_Pro-CP	Arif *et al.* (2012)
Glycine max	AMV, BPMV, SMV	Rep	Zhang *et al.* (2011b)
N. benthamiana	CBSV	CP	Patil *et al.* (2011)
M. esculenta	CBSV	CP	Yadav *et al.* (2011); Ogwok *et al.* (2012); Odipio *et al.* (2013)
Oryza sativa	RTBV	ORF-IV	Tyagi *et al.* (2008)
O. sativa	RDV	Pns4, Pns12	Shimizu *et al.* (2009)
O. sativa	RSV	SP, CP; pC3, pC4; and CP	Ma *et al.* (2011); Shimizu *et al.* (2011); Zhou *et al.* (2012)
O. sativa	RGDV	Pns9	Shimizu *et al.* (2012)
O. sativa	RGSV	pC5 and pC6	Shimizu *et al.* (2013)
Prunus avium	PNRSV	CP	Song *et al.* (2013)

Abbreviations: ACMV, African cassava mosaic virus; AMV, Alfalfa mosaic virus; BBTV, Banana bunchy top virus; BGMV, Bean golden mosaic virus; BNYVV, Beet necrotic yellow vein virus; BPMV, Bean pod mottle virus; BYDV, Barley yellow dwarf virus; CBSV, Cassava brown streak virus; CGMMV, Cucumber green mottle mosaic virus; CLCuV, Cotton leaf curl virus; CMV, Cucumber mosaic virus; CpCDPKV, Chickpea chlorotic dwarf Pakistan virus; CP, Capsid protein/Coat protein; CPsV, Citrus psorosis virus; CTV, Citrus tristeza virus; HC-Pro, Helper component protease; PLRV, Potato leaf roll virus; PnMV, Poinsettia mosaic virus; PNRSV, Prunus necrotic ringspot virus; PPV, Plum pox virus; PRSV, Papaya ringspot virus; PVX, Potato virus X; PVY, Potato virus Y; RDV, Rice dwarf virus; Rep, Replicase; RGDV, Rice gall dwarf virus; RGSV, Rice grassy stunt virus; RSV, Rice stripe virus; RTBV, Rice tungro bacilliform virus; SMV, Soybean mosaic virus; ToLCTWV, Tomato leaf curl Taiwan virus; TMV, Tobacco mosaic virus; ToCMoV, Tomato chlorotic mottle virus; TSWV, Tomato spotted wilt virus; TYLCV; Tomato yellow leaf curl virus; WMV, Watermelon mosaic virus; WMV2, Watermelon mosaic virus 2; ZYMV, Zucchini yellow mosaic virus.

one or more components, for example, DNA-A and DNA-B in Geminiviridae. DNA-A encodes an essential protein for DNA replication known as Rep or AC1 or C1. DNA-B encodes proteins involved in inter- and intracellular movements (King *et al.*, 2012).

Cotton Leaf Curl Virus (*Begomovirus*, Geminiviridae)

Asad *et al.* (2003) provided the first report of expressing virus-derived sense and antisense RNAs of 5′ and 3′ halves of AC1 and AC2, AC3 overlapping regions of Cotton leaf curl virus (CLCuV) in *Nicotiana tabacum* cv. Samsun without an intron separating them. Transgenic lines showed no symptoms even after 120 days of continuous exposure to viruliferous whiteflies. The presence of dsRNA and siRNAs in selected uninfected sense lines suggested that the likely mechanism of resistance was via PTGS (Asad *et al.*, 2003).

African Cassava Mosaic Virus (*Begomovirus*, Geminiviridae)

Wild type and modified versions of full-length AC1 sense RNA of African cassava mosaic virus (ACMV) were expressed in cassava (*Manihot esculenta* Crantz). High levels of resistance were obtained to both homologous and two heterologous begomoviruses viz., East African cassava mosaic Cameroon virus (EACMCV) and Sri Lankan cassava mosaic virus (SLCMV). The presence of transgene-specific siRNAs suggested that the resistance was through PTGS (Chellappan *et al.*, 2004). Some of the transgenic cassava lines were immune to ACMV and several other geminiviruses infecting cassava (Chellappan *et al.*, 2004). ACMV resistance was also obtained by targeting both the noncoding common region of DNA-A that contains bidirectional promoters (Vanderschuren *et al.*, 2007) and the coding region of partial AC1 gene (Vanderschuren *et al.*, 2009). The authors observed a recovery phenotype in the transgenic cassava lines and, in leaf disc assays, a decrease of more than 90% in virus accumulation of single- or double-stranded DNA forms.

Tomato Yellow Leaf Curl Virus (*Begomovirus*, Geminiviridae)

In a transient virus protection assay, the hairpin construct that contains conserved noncoding sequences of four strains of Tomato yellow leaf curl virus (TYLCV) conferred resistance to the challenge by these viruses. Stable resistance with immunity to TYLCV in tomato was reported using an intronic hairpin construct targeting the 3′end of the C1 gene (Fuentes *et al.*, 2006). This is the first report of use of an 'intronic' hairpin RNA construct for resistance to a plant DNA virus. Similarly, in a transient assay using *Nicotiana benthamiana* and tomato expressing conserved noncoding sequences from several strains of TYLCV, an effective resistance was obtained upon virus challenge either by agroinfiltration or by whitefly transmission (Abhary *et al.*, 2006). Similarly, the V1 gene, which encodes the CP, was used to develop resistance to TYLCV in both transient assays (*N. benthamiana*) and in transgenic tomato plants expressing an intronic hairpin construct targeting V1 RNA (Zrachya *et al.*, 2007). The role of PTGS was also hypothesized in a previous study involving transgenic tomato plants that contain TYLCV intergenic region (IR), Rep, and C4 genes. When challenged by viruliferous whiteflies under field conditions, transgenic tomato plants for partial IR (81nt) and Rep genes (426nt of 5′end) showed best resistance (Yang *et al.*, 2004).

Bean Golden Mosaic Virus (*Begomovirus*, Geminiviridae)

In the case of Bean golden mosaic virus (BGMV) infecting the common bean, targeting the AC1 by intron-spliced hairpin RNA resulted in immunity in one of the transgenic lines (5.1) (Bonfim *et al.*, 2007). These transgenic lines are being evaluated in the field for release to the farmers in Brazil (Aragao and Faria, 2009). In 2011, it was approved for commercialization by the National Technical Commission on Biosafety (CTNBio) of Brazil, but it was also requested to do more multilocation field trials in the country.

Tomato Chlorotic Mottle Virus (*Begomovirus*, Geminiviridae)

An interesting feature of PTGS-mediated virus resistance in the case of DNA viruses is that the presence of virus-specific siRNAs does not seem to guarantee the resistance/protection against the virus as shown by the studies in Tomato chlorotic mottle virus (ToCMoV); similar levels of siRNAs were observed in resistant and susceptible lines of the same *N. benthamiana* line transgenic for a gene hairpin construct derived from the overlapping regions of three genes viz., AV1-AC1-AC4 (Ribeiro *et al.*, 2007).

Chickpea Chlorotic Dwarf Pakistan Virus (*Mastrevirus*, Geminiviridae)

PTGS-based resistant *N. benthamiana* plants have also been developed for the Chickpea chlorotic dwarf Pakistan virus (CpCDPKV), a member of the genus *Mastrevirus*, expressing a chimeric construct that consists of three genes of CpCDPKV (Nahid *et al.*, 2011). Transgenic plants were symptomless and flowered normally, whereas the controls showed symptoms and died at 25 days post-inoculation. The virus accumulation in transgenic versus non-transgenic plants was estimated by PCR to be between 2600 and 28 000 times less.

Banana Bunchy Top Virus (*Babuvirus*, Nanoviridae)

Transgenic bananas (*Musa sp.*) resistant to Banana bunchy top virus (BBTV) were developed by targeting the Rep gene (Elayabalan *et al.*, 2013; Shekhawat *et al.*, 2012). Transgenic banana plants expressing RNAi-BBTV rep were obtained and shown to resist infection by BBTV. The transformed plants were symptomless, and the replication of challenging BBTV almost completely suppressed.

Control of Plant RNA Viruses by siRNA-Mediated Gene Silencing

RNA viruses form a large class of plant viruses. They have either single- or double-stranded RNA genomes in one or



Figure 3 Plum pox virus-resistant transgenic plum (*Prunus* × *domestica* L.) HoneySweet plums, sweet and flavorful, are highly resistant to plum pox virus. Courtesy of USDA ARS.

several segments. In the case of single-stranded RNA viruses the genome can be of positive sense, negative sense, and in some cases ambisense (King *et al.*, 2012).

Papaya Ringspot Virus (*Potyvirus*, Potyviridae)

There are two main strains of PRSV based on host range. PRSV-P (papaya strain) infects both papaya and cucurbits, whereas Papaya ringspot virus (Watermelon strain) (PRSV-W) infects only cucurbits. Based on the concept of PDR, and by expressing the CP gene from a mild strain of PRSV, a virus-resistant transgenic papaya line (55-1) was developed (Fitch *et al.*, 1992). Transgenic line 55-1 was later used to develop two popular cultivars viz., SunUp (red flesh, homozygous for CP transgene) and Rainbow (yellow flesh, heterozygous for CP) (Manshardt, 1998). Although this was one of the early successful cases of CPMR, it was later shown to be a case of PTGS based on two observations: First, resistance was higher to PRSV isolates, which showed higher homology to the transgene; second, homozygous transgenic line showed broader resistance to different PRSV isolates with lower steady state levels of *CP* transgene mRNA compared with hemizygous transgenic papaya (Suzuki *et al.*, 2009).

Plum Pox Virus (*Potyvirus*, Potyviridae)

Plum (*Prunus* × *domestica*) trees transgenic for multicopy CP gene, with a complex integration pattern, were highly resistant to Plum pox virus (PPV) (Scorza *et al.*, 1994). The mechanism of resistance was by transgene methylation (**Figure 3**; Scorza *et al.*, 2001). In another study, a 197bp self-complementary hairpin RNA of PPV expressed under *rolC* promoter conferred systemic resistance to PPV in *N. benthamiana* but no local resistance (Pandolfini *et al.*, 2003).

Zucchini Yellow Mosaic Virus, Watermelon Mosaic Virus 2, Papaya Ringspot Virus (all *Potyvirus*, Potyviridae), and Cucumber Mosaic Virus (*Cucumovirus*, Bromoviridae)

Transgenic summer squash lines with different combinations of Cucumber mosaic virus (CMV), Zucchini yellow mosaic virus (ZYMV), and Watermelon mosaic virus 2 (WMV2) CPs (one to several copies) showed variable field resistance to these viruses. Two of the inbred transgenic lines, ZW-20 and CZW-3, which contain CP genes from ZYMV, WMV2 and CMV, of which ZYMV and WMV2 showed higher resistance, were utilized to develop commercial squash hybrids (Tricoll *et al.*, 1995). The mechanism of virus resistance is believed to be mediated by PTGS. In another study the RNAi construct that contains the self-complementary RNA of ZYMV HC-Pro gene was used to develop transgenic cucumber and melon. The level of siRNAs derived from HC-Pro transgene varied from 6% to 44% of total siRNAs and conferred resistance to ZYMV systemic infection. Resistance to WMV and PRSV was also observed in a cucumber line accumulating 44% of transgene siRNAs and higher levels of RDR1 and AGO1. This study also reported that transgene siRNAs are not uniformly distributed over the transgene but accumulated in hot spots, which may not be responsible for the resistance phenotype (Leibman *et al.*, 2011).

Barley Yellow Dwarf Virus (*Luteovirus*, Luteoviridae)

Barley plants transformed with a Barley yellow dwarf virus (BYDV)-PAV polymerase hairpin construct exhibited extreme resistance (immunity) to BYDV virus challenge. When co-challenged with Cereal yellow dwarf virus-RPV (CYDV-RPV), transgenic plants were susceptible to CYDV-RPV but were resistant to BYDV-PAV, indicating robust homologous specific resistance (Wang *et al.*, 2000).

Beet Necrotic Yellow Vein Virus (*Benyvirus*, Unassigned family)

Nicotiana benthamiana plants expressing a CP read through open reading frame resulted in plants resistant to Beet necrotic yellow vein virus (BNYVV), which was less effective in roots than in foliar tissues (Andika *et al.*, 2005). Recently, Pavli *et al.* (2010) targeted the replicase gene of BNYVV by expressing a replicase-specific dsRNA in the beet roots mediated by *Agrobacterium rhizogenes* hairy root transformation. The transgenic roots showed none to very low virus titer with delayed symptom development (Pavli *et al.*, 2010). In a related study, transgenic *N. benthamiana* lines expressing dsRNA produced from a hairpin BNYVV replicase gene and HrpZ protein (a bacterial protein, found to elicit hypersensitive response in host plant) conferred higher resistance to BNYVV than the individual genes (Pavli *et al.*, 2010).

Tobacco Mosaic Virus (*Tobamovirus*, Virgaviridae)

Tobacco mosaic virus (TMV) is the first virus against which the use of the CPMR was demonstrated (Powell-Abel *et al.*, 1986). At that time PTGS was not discovered and consequently there was no evidence that PTGS was involved, and several subsequent studies demonstrated that the CP was necessary and involved in the resistance mechanism (for more details see Beachy 1997, Yadav *et al.*, 2007). An RNAi construct of TMV coat protein and single copy of partial movement protein gene expressed in tobacco as an inverted hairpin also conferred resistance to TMV (Hu *et al.*, 2011; Yan *et al.*, 2007).

Citrus Tristeza Virus (*Closterovirus*, Closteroviridae)

p23 and 3′UTR sequences of Citrus tristeza virus (CTV) were used in the hairpin constructs and expressed in *N. benthamiana* and Alemow (*Citrus macrophylla*). Transgenic *N. benthamiana* and Alemow plants showed resistance and delayed symptoms, respectively. However, none of the transgenic Alemow plants showed durable resistance (Batuman *et al.*, 2006). In another study in *Citrus paradisi*, most of the transgenic lines transformed with various constructs derived from CTV were susceptible or partially resistant and only one line transformed with 3′end of CTV was virus resistant (Febres *et al.*, 2008). Complete resistance to graft inoculations of homologous CTV strain T36 was obtained in three transgenic lines of Mexican lime transformed with intronic hairpins that consist of untranslatable genes of three suppressors of CTV (p23, P20, and p25) and 3′UTR. Resistance to the divergent CTV strain (T318A) was partial (Soler *et al.*, 2012).

Poinsettia Mosaic Virus (*Tymovirus*, Tymoviridae)

Hairpin RNAi technology was also used in a flowering plant to develop Poinsettia mosaic virus (PsMV)-resistant poinsettia (*Poinsettia pulcherimma*) by expressing PsMV self-complementary CP or RdRP genes (Clarke *et al.*, 2008).

Citrus Psorosis Virus (*Ophiovirus*, Ophioviridae)

In *N. benthamiana*, hairpin RNA constructs derived from both CP and 54K genes of Citrus psorosis virus (CPsV) conferred resistance to the virus infection. In the actual host plant, sweet orange, only the CP-derived hairpin construct gave a high level of resistance (Reyes *et al.*, 2009), whereas hairpin constructs derived from either 54K or 24K genes conferred partial or no resistance. This study highlights the difference between working in model plants and actual crop plants (Reyes *et al.*, 2011).

Tomato Leaf Curl Taiwan Virus (*Begomovirus*, *Geminiviridae*) and Tomato Spotted Wilt Virus (*Tospovirus*, Bunyaviridae)

Several lines of *N. benthamiana* and tomato, transformed with a chimeric RNAi construct that consists of partial C2 gene of Tomato leaf curl Taiwan Virus (ToLCTWV) and the middle region of the Tomato spotted wilt virus (TSWV) N gene, exhibited high levels of resistance to TSWV and no symptoms of ToLCTWV after being challenged with agroinoculation (Lin *et al.*, 2011). This is an example for using a chimeric gene construct to control both RNA and DNA viruses.

Watermelon Silver Mottle Virus (*Tospovirus*, Bunyaviridae); Cucumber Mosaic Virus (*Cucumovirus*, Bromoviridae); Cucumber Green Mottle Mosaic Virus (*Tobamovirus*, Virgaviridae); and Watermelon Mosaic Virus (*Potyvirus*, Potyviridae)

Lin *et al.* (2012) developed a chimeric hairpin RNAi construct with partial sequences of N gene of Watermelon silver mottle virus (WSMoV) and partial CP sequences of CMV, Cucumber green mottle mosaic virus (CGMMV), and WMV to transform watermelon. Two transgenic lines in R_o (first generation) showed resistance to these viruses when infected either individually or in mixture. However, in R_1 the loss of resistance to CGMMV was correlated with the loss of a CGMMV-specific fragment in the chimeric transgene (Lin *et al.*, 2012). In a different approach direct repeats of the CGMMV movement protein was used to transform melon plants. Transgenic melon plants showed high resistance to CGMMV and it was correlated with the transgene methylation (Emran *et al.*, 2012). CMV resistance in transgenic tobacco expressing hpRNA construct derived from a defective replicase gene of CMV-O strain conferred immunity to both CMV-O and CMV-Y strains (Ntui *et al.*, 2013).

Potato Virus X (*Potexvirus*, Alphaflexiviridae), Potato Virus Y (*Potyvirus*, Potyviridae), and Potato Leaf Roll Virus (*Polerovirus*, Luteoviridae)

Using a chimeric RNAi construct for these three potato viruses, with partial sequences from ORF2 of Potato virus X (PVX), HC-Pro of Potato virus Y (PVY), and CP of Potato leaf roll virus (PLRV), assembled into a single transgene, conferred immunity to all three viruses in approximately 20% of transgenic plant lines (Arif *et al.*, 2012).

Alfalfa Mosaic Virus (*Alfamovirus*, Bromoviridae), Bean Pod Mottle Virus (*Comovirus*, Secoviridae), and Soybean Mosaic Virus (*Potyvirus*, Potyviridae)

Zhang *et al.* (2011b) employed several small (150bp) inverted repeats separated by single-stranded sequences to target multiple viruses instead of using one long sequence. They used sequences from the replicase gene of each of the following three legume viruses: Alfalfa mosaic virus (AMV), Bean pod mottle virus (BPMV), and Soybean mosaic virus (SMV) and combined them into a single transgene. Transgenic lines were simultaneously resistant to infection by all three viruses. The design of the construct is such that targets for additional viruses or viruses of other crops could easily be incorporated (Zhang *et al.*, 2011b).

Cassava Brown Streak Virus (*Ipomovirus*, Potyviridae)

Cassava brown streak disease is caused by Cassava brown streak virus (CBSV) or Ugandan cassava brown streak virus (UCBSV). Using hairpin RNA derived from partial CP of UCBSV, transgenic *N. benthamiana* resistant to UCBSV and CBSV were produced (Patil *et al.*, 2011). In cassava the same RNAi construct conferred resistance to UCBSV in graft experiments (Yadav *et al.*, 2011) and to UCBSV and CBSV in the field experiments (**Figure 4**; Ogwok *et al.*, 2012; Odipio *et al.*, 2013). Similarly, a hairpin RNAi construct derived from a conserved region of UCBSV and CBSV CP was used to transform both model (cv. 60444) and farmer-preferred (TME-7) cassava cultivars. Several of the 60444 transgenic lines were highly resistant to both UCBSV and CBSV. All the transgenic lines derived from TME-7, which is naturally resistant to cassava mosaic disease (CMD), showed immunity to both CBSV and UCBSV, and the immunity was maintained when



Figure 4 Tuberous roots of virus-resistant cassava (*Manihot esculenta* Crantz). Symptoms of CBSD on cassava at harvest time: (a) close-up of sections of roots of one plant of the transgenic event 718-001; (b) close-up of sections of roots of one plant of the non-transgenic cv. 60444 control; (c) close-up of the stems of one plant of the transgenic event 718-001; and (d) close-up of the stems of one plant of the non-transgenic cv. 60444 control.

co-inoculated with the East African cassava mosaic virus, one of the causal agents of CMD (Vanderschuren *et al.*, 2012). This study successfully shows the possibility to combine natural resistance with transgenic resistance to increase the range of protection.

Rice Tungro Bacilliform Virus (*Tungrovirus*, Caulimoviridae)

A mild resistance to Rice tungro bacilliform virus (RTBV) was obtained by expressing dsRNA in rice derived from ORF IV (Tyagi *et al.*, 2008).

Rice Dwarf Virus (*Phytoreovirus*, Reoviridae)

Targeting two Rice dwarf virus (RDV) nonstructural proteins (Pns4 and Pns12) by RNAi, Shimizu *et al.* (2009) obtained resistant transgenic rice lines. But lines targeting only the Pns12 gene (critical to virus replication) were also resistant to the RDV virus.

Rice Stripe Virus (*Tenuivirus*, Unclassified)

In the case of Rice stripe virus (RSV), transgenic rice expressing RNAi constructs targeting the special disease protein (SP) and the CP genes of RSV conferred stronger resistance than the lines containing either SP or CP genes alone (Ma *et al.*, 2011). In another study, both the SP and CP genes proved to be efficient in conferring the resistance to RSV in the trans genic rice plants in T_5 and T_7 generations (Zhou *et al.*, 2012). Shimizu *et al.* (2011) targeted each of the genes of RSV and found that two target genes viz., pC3 (encodes nucleocapsid protein) and pC4 (encodes viral movement protein), provided stronger resistance to RSV in transgenic rice plants.

Rice Gall Dwarf Virus (*Phytoreovirus*, Reoviridae)

Transgenic rice plants expressing self-complementary RNA from the Pns9 gene of Rice gall dwarf virus (RGDV) conferred a strong resistance to the RGDV but not to Rice dwarf virus (Shimizu *et al.*, 2012).

Rice Grassy Stunt Virus (*Tenuivirus*, Unclassified)

Similarly, in the case of Rice grassy stunt virus (RGSV), targeting nucleocapsid and movement protein by hairpin RNAi constructs resulted in a strong resistance in the transgenic rice plants (Shimizu *et al.*, 2013).

Prunus Necrotic Ringspot Virus (*Ilarvirus*, Bromoviridae)

Using transgenic cherry rootstocks expressing a hairpin RNA construct derived from the Prunus necrotic ringspot virus (PNRSV) CP gene conferred resistance to PNRSV and related Prunus dwarf virus (*Ilarvirus*, Bromoviridae) in the non-transgenic scions (Song *et al.*, 2013).

From the above examples it is obvious that PTGS-mediated virus resistance is effective against a wide range of RNA viruses in single or mixed infections, and there is great hope that these small-scale studies could be successfully replicated in the field in the near future. The examples of the transgenic papaya and the transgenic summer squash produced in the mid-1990s are still showing high levels of resistance in the fields. Some of the new resistant transgenic lines are now being evaluated in the field, for example, BGMV-resistant common bean (*Phaseolus vulgaris* L.) in Brazil and CBSD-resistant cassava (*Manihot esculenta* Crantz) in East Africa.

Control of Plant Viruses by amiRNA-Mediated Gene Silencing

There are different types of small RNAs involved in PTGS, among them siRNAs and miRNAs are the most studied (Figure 2). miRNAs are chemically and functionally indistinguishable from siRNAs but their origin and mode of action differ. Most miRNA originate from intergenic regions and a few are from gene-coding sequences and introns. Endogenous miRNAs are produced from double-stranded hairpin-like precursors formed by the fold back of primary miRNA transcript synthesized by RNA polymerase II. The stem region of the hairpin is processed into a 21nt mature miRNA duplex in a two-step process. In plants, both the steps take place in the nucleus of the cell by the action of DCL1-like proteins (Golden *et al.*, 2002; Park *et al.*, 2002). The miRNA strand complementary to its target gene is then recognized by the RISC that guides the miRNA to degrade the target mRNA (Bartel, 2004). The plant miRNA-processing machinery was used to target PPV chimera that contain the target sequence of plant endogenous miRNAs, miR171, miR167, and miR159, which resulted in reduced virus infectivity. This reduced virus infectivity was overcome in transgenic plants expressing the silencing suppressor P1/HC-Pro, suggesting that reduced infectivity was caused by the plant PTGS pathway (Simon-Mateo and Garcia, 2006). Two arms of an endogenous miRNA (21nt) on its precursor can be replaced by ~21nt target virus sequences (Fahim and Larkin, 2013). These ~21nt sequences are known as 'artificial miRNAs' (amiRNAs). If the host plant genome sequence is known, then precise antiviral amiRNAs lacking complementary host target sequences can be designed to prevent unintended off-target effects (Simon-Mateo and Garcia, 2006). Moreover, the environmental biosafety concerns of viral sequences that might complement or recombine with nontarget viruses do not apply to amiRNAs (Simon-Mateo and Garcia, 2006). Recently, amiRNAs have also been used to control plant diseases caused by both DNA and RNA viruses (**Table 2**). The general strategy has been to use modified plant miRNA precursor backbones to express 21nt sequences of viral mRNAs coding for vital proteins, including suppressors of gene silencing under strong constitutive promoters, such as the CaMV 35S.

In the first report of the use of amiRNAs to control plant viruses, *A. thaliana* miR159 precursor was modified to express amiRNAs targeting Turnip yellow mosaic virus (TYMV, *Tymovirus*, Tymoviridae) P69 gene and Turnip mosaic virus (TuMV, *Potyvirus*, Potyviridae) HC-Pro and CP genes. The expression of amiRNAs was inhibited in dcl-1 mutants, indicating that the DCL-1 protein is required for the accumulation of amiRNAs. Transgenic *A. thaliana* lines expressing amiR-HC-Pro^{159} and amiR-P69^{159} conferred resistance against TuMV and TYMV, respectively. Similarly, lines expressing amiRNAs against CP of TuMV were also virus resistant (Niu *et al.*, 2006). Transgenic lines expressing amiRNAs against both viruses in a dimeric construct were resistant to both the viruses, suggesting that resistance conferred by amiRNAs can be stacked for multiple viruses.

Similarly, CMV was successfully controlled in *A. thaliana* by expressing amiRNA (amiR-CMV-2b^{171}) in Ath miR171a precursor targeting the CMV 2b protein, a PTGS suppressor. It was done both transiently and in transgenic tobacco plants (Qu *et al.*, 2007). CMV 2b has been shown to block the movement of systemic silencing signals, to inhibit DNA methylation-induced silencing (Hamilton and Baulcombe, 1999) and also to

Table 2 List of transgenic plants where artificial micro RNAs (amiRNAs) have been used to develop virus-resistant plants

Plant	*Virus*	*Virus gene*	*Precursor backbone*	*References*
Arabidopsis thaliana	TuMV and TYMV	HC-Pro and p69	Ath pre-miRNA159a	Niu *et al.* (2006)
Nicotiana tabacum	CMV	2b	Ath pre-miRNA171a	Qu *et al.* (2007)
A. thaliana	CMV	3′-UTR	Ath pre-miRNA159a	Duan *et al.* (2008)
Lycopersicon esculentum	CMV	2a-2b overlap	Ath pre-miRNA159a	Zhang *et al.* (2011a)
N. tabacum	PVX, PVY	p25 and HC-Pro	Ath pre-miRNA159a, 167b and 171a	Ai *et al.* (2011)
Triticum aestivum	WSMV	p1, p3 and HC-Pro	Os pre-miRNA395	Fahim *et al.* (2012)
N. benthamiana	WSMoV	Replicase (L) gene	Ath pre-miRNA159a	Kung *et al.* (2012)
Vitis vinifera	GFLV	CP	Ath pre-miRNA319a	Jelly *et al.* (2012)
N. benthamiana	ToLCNDV	AV1, AV2 of ToCLV	Ath-mir-319a, Sly-mir-159a and Sly-mir-168a	Vu *et al.* (2013)
N. benthamiana	CLCuBV	V2	Ath pre-miRNA159a	Ali *et al.* (2013)

Abbreviations: ACMV, African cassava mosaic virus; Ath, *Arabidopsis thaliana*; BGMV, Bean golden mosaic virus; CLCuBV, Cotton leaf curl Burewala virus; CMV, Cucumber mosaic virus; CP, Coat protein/Capsid protein; GFLV, Grapevine fan leaf virus; HC-Pro, Helper component proteinase; Os, *Oryza sativa;* PVX, Potato virus X; PVY, Potato virus Y; Sly, *Solanum lycopersicum*; ToLCNDV, Tomato leaf curl New Delhi virus; TuMV, Turnip mosaic virus; TYMV, Turnip yellow mosaic virus; UTR, Untranslated region; WSMoV, Watermelon silver mottle virus; WSMV, Wheat streak mosaic virus.

inhibit the AGO1 (slicer) activity (Zhang *et al.*, 2006). The resistance conferred by a 35S promoter-driven amiRNAs was superior to the U6 promoter driving a short hairpin (sh)-derived small RNA targeting the same region (Qu *et al.*, 2007), suggesting that the efficacy of amiRNA-mediated virus resistance depends not only on the amiRNA sequence, but also on the level of expression. Duan *et al.* (2008) used an experimental approach to analyze the effect of target site accessibility and engineer effective anti-CMV silencing in plants by amiRNAs. Transgenic plants expressing amiRNAs that targeted the putative DCL-mediated cleavage sites, such as those in the tRNA-like structure region, showed no protection against CMV infection. Both transgenic *Arabidopsis* and tobacco expressing amiRNAs that targeted the putative RISC accessible sites conferred a higher level of resistance to CMV challenge than those targeting the DCL-mediated cleavage sites. These findings clearly indicated that both processing of the miRNA precursor and experimentally determining accessible target sites are important criteria in designing an efficient virus control strategy (Duan *et al.*, 2008).

Transgenic tobacco plants resistant to PVX (*Potexvirus*, Alphaflexiviridae) and PVY (*Potyvirus*, Potyviridae) were obtained by expressing amiRNAs in *A. thaliana* miR159, miR167, and miR171 precursors against their PTGS suppressors TGB1/p25 and HC-Pro, respectively. Through the expression of dimeric amiRNA precursors, the resistance was obtained to both viruses in mixed infections and the resistance was maintained under laboratory conditions of high virus pressure (Ai *et al.*, 2011).

In the case of Watermelon silver mottle virus (WSMoV, *Tospovirus*, Bunyaviridae), a negative-strand ssRNA virus, six highly conserved motifs of WSMoV were targeted by amiRNAs expressed transgenically using the miR159 precursor of *A. thaliana* in *N. benthamiana* (Kung *et al.*, 2012). Two single amiRNA constructs targeting LB2 and LD motifs delayed the WSMoV symptoms or conferred moderate resistance. Transgenic lines expressing amiR-LB2 also delayed symptoms in a related tospovirus (Peanut bud necrosis virus) that has a single mutation in the target site, as it is known that amiRNAs can tolerate a single mismatch. Complete resistance was obtained when three motifs viz., LB2, LD and LC, were targeted (Kung *et al.*, 2012). Transgenic *N. benthamiana* expressing amiRNA targeting the V2 gene of Cotton leaf curl Burewala virus, a ssDNA virus, (CLCuBV, *Begomovirus*, Geminiviridae) conferred resistance to the homologous virus but not to heterologous viruses infecting cotton (Ali *et al.*, 2013).

Apart from model plants, amiRNA-mediated virus resistance has also been obtained in crop plants such as tomato, wheat, and grapevine. Zhang *et al.* (2011) showed that amiRNA-based resistance to CMV could also be obtained in tomato by targeting both coding and noncoding (3′UTR) regions (Zhang *et al.*, 2011a). The resistance was stable under high virus titer and infection with other viruses, such as TMV and TYLCV, which encode the 126-kDa replicase and AC2, respectively, both PTGS suppressors (Vogler *et al.*, 2007; Zrachya *et al.*, 2007). In another study, high to moderate tolerance was obtained against Tomato leaf curl New Delhi virus (ToLCNDV; *Begomovirus*, Geminiviridae) by two amiRNAs targeting CP (AV1) pre-CP (AV2) overlapping and CP (AV1) regions, respectively (Vu *et al.*, 2013). The study of Zhang *et al.* (2011) also indicated the cell autonomous nature of amiRNAs because there was no evidence showing amiRNAs as a systemic antiviral silencing signal, either in shoot-to-root or in root-to-shoot direction. In contrast, the virus-derived siRNAs served as diffusible antiviral signals to immunize tissues ahead of infection through phloem-mediated long-distance movement (Ding and Voinnet, 2007), and it signified the complexity of silencing by siRNAs and miRNAs (Zhang *et al.*, 2011a).

Using a modified rice polycistronic miRNA precursor (miR395), Fahim *et al.* (2012) expressed in wheat five amiRNAs targeted to the conserved regions of Wheat streak mosaic virus (WSMV, *Potyvirus*, Potyviridae) to obtain virus-resistant transgenic plants (**Figure 5**). This strategy is significant because it used a naturally existing rice polycistronic miRNA precursor. Analysis of T_1 and T_2 transgenic wheat plants revealed three types of responses, including complete immunity to the WSMV (Fahim *et al.*, 2012).

Recently, two amiRNAs constructs targeting the CP of Grapevine fan leaf virus (GFLV, *Nepovirus*, Secoviridae) were transiently expressed in grapevine. Functionality of these amiRNAs were confirmed indirectly using GUS sensor assays, but they have not yet been stably transformed in grapevine (Jelly *et al.*, 2012).

Owing to the small size of approximately 21nt, the use of amiRNAs provides many advantages over long hairpin RNA constructs, including minimal off-target effects, lower possibility of recombination between transgene and nonvirus target viruses, lower possibility of transmission by other viruses through encapsidation or by seed or pollen, or no synergy with unrelated viruses (Niu *et al.*, 2006). However, amiRNA-based resistance is susceptible to breakdown by rapid mutations in the amiRNA target sequence, especially in the seed region, change in the virus population and, by other virus isolates in case of mixed infections (Martinez *et al.*, 2012; 2013). However, these resistance breakdowns have been obtained in the laboratory by successive selection of virus progenies that mutated to overcome the resistance, and it remains to be seen if this would be the case in nature. Moreover, these concerns have also been addressed by choosing the amiRNA from the highly conserved regions (Niu *et al.*, 2006) and by stacking multiple amiRNAs for each virus in a single construct (Fahim *et al.*, 2012).

Overall, great progress has been made in the application of innate antiviral mechanism of using the amiRNA strategy to control a number of RNA and DNA viruses in laboratory/model plants, and it has opened a gateway for translating these results to crop plants.

Applications of the Post-Transcriptional Gene Silencing in the Field

Application in the field of PTGS-based technologies to induce virus resistance has been very limited so far, at least for cases where it has been shown that PTGS was the mechanism of resistance used. Papaya and Summer squash: Transgenic papaya (SunUp, Rainbow) and squash (ZW-20, CZW-3) have been employed successfully in the field with durable resistance and stability for almost two decades (Fuchs and Gonsalves, 2007). Plum: Transgenic plum is the third engineered virus-resistant product, based on PTGS, which has been successfully brought to the field (Pandolfini *et al.*, 2003; Scorza *et al.*,

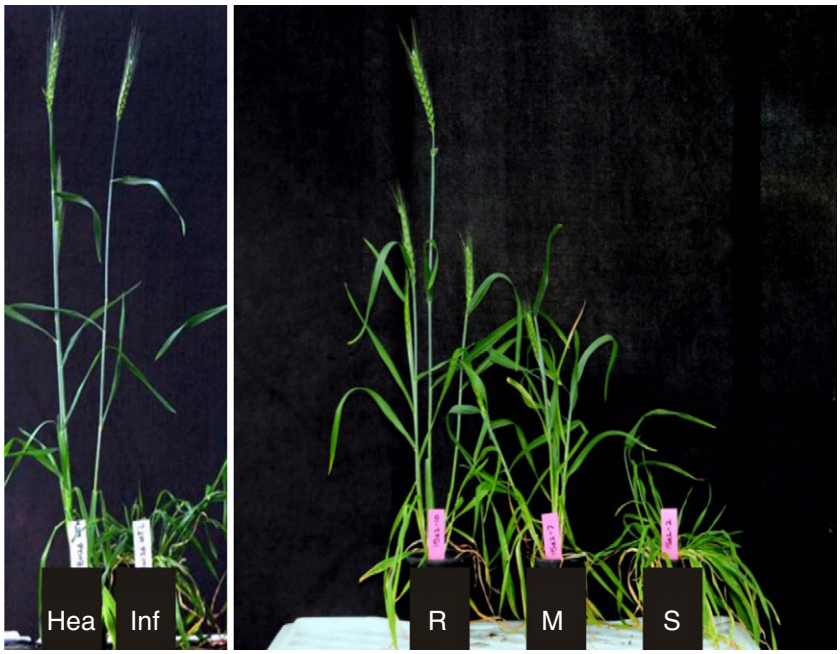


Figure 5 T_1 families of transgenic wheat (*Triticum aestivum* L.) families expressing amiRNAs. (a) Healthy and infected controls. (b) Levels of resistance in the transgenic plants. R, transgenic immune; M, moderate resistant; S, susceptible. Adapted from Fahim, M., Millar, A.A., Wood, C.C., Larkin, P.J., 2012. Resistance to Wheat streak mosaic virus generated by expression of an artificial polycistronic microRNA in wheat. Plant Biotechnology Journal 10, 150–163.

2001). Bean: Two transgenic common bean (*P. vulgaris*) lines transformed with the BGMV AC1 gene are likely to be the first commercial virus-resistant crops to be released in South America (Aragao and Faria, 2009). Cassava: Cassava plants resistant to brown streak disease have been developed as part of the VIRCA (Virus Resistance for Cassava in Africa) project using a hairpin RNA construct against the CP gene of CBSV and UCBSV (Ogwok *et al.*, 2012; Odipio *et al.*, 2013). So far there are no reports of evaluation of transgenic virus-resistant plants developed by amiRNA-mediated strategy in the fields.

Broad-Range Resistance by Silencing Host Proteins

The resistance obtained by PTGS seems to be specific to the virus strain from which it is derived or to very closely related strains. However, if there is a host gene that is essential for the virus replication/biology but dispensable for the host plant that could be used as a target for PTGS, and broad host-range resistance could be achieved. The eIF4E family of eukaryotic translation initiation factors of melon (*Cucumis melo* L.) were found to be essential for the replication of many viruses, mediated through the interaction with the potyviral VPg protein (Kang *et al.*, 2005; Wang and Krishnaswamy, 2012). Transgenic melon plants silenced for the eIF4E gene were resistant to four of the eight different viruses challenged, such as Cucumber vein yellowing virus (CVYV, *Ipomovirus*, Potyviridae), Melon necrotic spot virus (MNSV, *Carmovirus*, Tombusviridae), Moroccan watermelon mosaic virus (MWMV, *Potyvirus*, Potyviridae), and Zucchini yellow mosaic virus (ZYMV, *Potyvirus*, Potyviridae) (Rodriguez-Hernandez *et al.*, 2012). Similarly, transgenic tomato plants silenced for both eIF4E1 and eIF4E2 genes conferred broad-spectrum resistance to potyviruses, whereas the silencing of eIF(iso)4E resulted in susceptibility to potyviruses (Mazier *et al.*, 2011).

Suppressors of Post-Transcriptional Gene Silencing and Plant Virus Control

Suppressors of PTGS are the proteins encoded by plant and animal viruses that are used by both DNA and RNA viruses as a general strategy against the host PTGS (Voinnet *et al.*, 1999). Most of these proteins were previously shown to be pathogenicity determinants and do not share significant sequence homology among them. The success of innate and engineered PTGS against invading viruses partially depends on inhibiting these suppressors. Viral suppressors of PTGS are shown to act at one or more steps of the PTGS pathways (Alvarado and Scholthof, 2009). The mode of action of these suppressors is summarized in **Table 3**. Briefly, viral suppressors act starting from the processing of dsRNA triggers and continuing to mRNA cleavage by the AGO proteins (Alvarado and Scholthof, 2009). It has been shown that the Turnip crinkle virus (TCV) P38, the CMV 2b, and the Cauliflower mosaic virus (CaMV) P6 proteins interfere with the dicer activities, either directly or indirectly, thus preventing the processing of dsRNA into small RNAs (Haas *et al.*, 2008; Thomas *et al.*, 2003; Zhang *et al.*, 2006). The V2 protein of TYLCV was shown to inhibit the

Table 3 Suppressors of post-transcriptional gene silencing and their mode of action

Suppressor	*Source*	*Family*	*Genus*	*Mode of action*	*References*
AC4	ACMV	Geminiviridae	*Begomovirus*	Prevents holo-RISC assembly by capturing siRNAs	Chellappan *et al.* (2004); Chellappan *et al.* (2005)
AC2	MYMV	Geminiviridae	*Begomovirus*	Transactivation of ~30 genes	Trinks *et al.* (2005)
AC2/C2	TGMV/BCTV	Geminiviridae	*Begomovirus/ Curtovirus*	Adenosine kinase inhibition	Wang *et al.* (2005)
γb	BSMV	Virgaviridae	*Hordeivirus*	Unspecified	Bragg and Jackson (2004)
P21	BYV	Closteroviridae	*Closterovirus*	Binding to 3′overhang of siRNAs and HEN1	Yu *et al.* (2006); Lozsa *et al.* (2008)
βC1	CLCuMV-β	Geminiviridae	Betasatellite	Likely interferes accumulation of siRNAs	Cui *et al.* (2005); Eini *et al.* (2012)
2b	CMV	Bromoviridae	*Bromovirus*	Physically interacts with ssRNA bound Ago	Brigneti *et al.* (1998); Zhang *et al.* (2006)
P0	PLRV	Luteoviridae	*Polerovirus*	Likely promotes ubiquitin-dependant Ago1 proteolysis	Pazhouhandeh *et al.* (2006)
CRP	PVM	Betaflexiviridae	*Carlavirus*	Inhibits RNA silencing at the viral replication stage	Senshu *et al.* (2009)
P25	PVX	Alphaflexiviridae	*Potexvirus*	Unspecified	Voinnet *et al.* (2000); Senshu *et al.* (2009)
NS3	RHBV	Unclassified	*Tenuivirus*	Affects accumulation of siRNAs by binding siRNA duplex	Bucher *et al.* (2003)
P19	TBSV	Tombusviridae	*Tombusvirus*	Sequestration of siRNA duplex	Lakatos *et al.* (2004)
P38	TCV	Tombusviridae	*Carmovirus*	Processing of dsRNA precursor	Thomas *et al.* (2003)
Replicase	TMV	Virgaviridae	*Tobamovirus*	Interferes with stability of siRNA	Ding *et al.* (2004); Takeda *et al.* (2005); Vogler *et al.* (2007)
16K	TRV	Virgaviridae	*Tobravirus*	Acts downstream of dsRNA formation	Liu *et al.* (2002); Ghazala *et al.* (2008); Martinez-Priego *et al.* (2008)
NSs	TSWV	Bunyaviridae	*Tospovirus*	Sequestering siRNA and miRNA duplex	Bucher *et al.* (2003); Schnettler *et al.* (2010)
HC-Pro	TuMV	Potyviridae	*Potyvirus*	Interacts with rgs-cam	Anandalakshmi *et al.* (2000)
P69	TYMV	Tymoviridae	*Tymovirus*	Likely inhibits viral amplification	Chen *et al.* (2004)

Abbreviations: ACMV, African cassava mosaic virus; BCTV, Beet curly top virus; BSMV, Barley stripe mosaic virus; BYV, Beet yellows virus; CLCuMV-β, Cotton leaf curl Multan virus betasatellite; CMV, Cucumber mosaic virus; CRP, Cysteine-rich protein; dsRNA, double-stranded RNA; MYMV, Mungbean yellow mosaic virus; PLRV, Potato leaf roll virus; PVM, Potato virus M; PVX, Potato virus X; RHBV, Rice hoja blanca virus; siRNA, small interfering RNA; ssRNA, single-stranded RNA; TBSV, Tomato bushy stunt virus; TCV, Turnip crinkle virus; TMV, Tobacco mosaic virus; TRV, Tobacco rattle virus; TSWV, Tomato spotted wilt virus; TuMV, Turnip mosaic virus; TYMV, Turnip yellow mosaic virus.

amplification of primary small RNAs by binding SGS3 (Glick *et al.*, 2008). PTGS suppressors from Rice hoja blanca virus (NS3), from potyviruses (HC-Pro) along with the well-characterized P19 suppressor of the Tomato bushy stunt virus (TBSV), and the AC4 protein of cassava geminiviruses sequestered the small RNAs by various strategies (Anandalakshmi *et al.*, 2000; Bucher *et al.*, 2003; Chellappan *et al.*, 2005; Lakatos *et al.*, 2004). The TBSV P19 and the P1/HC-Pro of Turnip mosaic virus (TuMV) also affected the stability of small RNAs by interfering with the function of HEN1, a methyl transferase (Lozsa *et al.*, 2008; Yu *et al.*, 2006). Similarly, the 126-kDa protein of TMV and the P21 protein of BYV interfered with the HEN1 activity (Vogler *et al.*, 2007; Yu *et al.*, 2006). Finally, the polerovirus (Beet western yellows virus) P0 protein and the CMV 2b protein) interfered with the slicer activity of AGO1 protein (Pazhouhandeh *et al.*, 2006; Zhang *et al.*, 2006).

Range, Level, and Stability of Gene Silencing-Based Virus Resistance

The virus resistance conferred by gene silencing is highly sequence specific to the cognate virus strain from which the dsRNA trigger is derived and to related strains depending on the sequence identity. Most of the studies reported have not tested their PTGS constructs against related strains or viruses. A few previous studies indicate that sequence identity of 89% or higher is sufficient to confer resistance to related strains (Jones

et al., 1998; Lindbo and Dougherty, 1992). However, in a recent report a hairpin RNAi construct derived from HC-Pro gene of ZYMV conferred resistance in cucumber to WMV and PRSV-W with 67% and 63% sequence identity to HC-Pro, respectively (Leibman *et al.*, 2011). Similarly, a hairpin RNAi construct derived from a partial CP gene of UCBSV conferred resistance to both homologous and heterologous strains of UCBSV and even to isolates of a different species CBSV, in *N. benthamiana* and cassava (Ogwok *et al.*, 2012; Patil *et al.*, 2011). The cross-protection could be explained by the observations that functional siRNAs and miRNAs can tolerate a few mismatches in non-seed region (~7–9 bp). It has also been shown that the resistance to cognate virus is sometimes affected by another virus in mixed infection. In barley, the resistance to BYDV-PAV was not broken down by an unrelated virus species in the mixed infection with CYDV-RPV (Wang *et al.*, 2000), whereas in the case of Potato virus A (PVA, *Potyvirus*, Potyviridae) the resistance to a cognate virus (PVA) was broken down after infection by Potato virus Y (PVY; *Potyvirus*, Potyviridae) (Savenkov and Valkonen, 2001). The range of protection could also be increased by combining transgenic PTGS-mediated resistance with naturally available resistance in some crops, such as cassava (Vanderschuren *et al.*, 2012).

Regarding the level of virus resistance conferred by gene silencing, it is ranging from partial resistance/delayed symptoms to immunity. For both DNA and RNA viruses, immunity to inoculated virus has been obtained by hairpin RNA-mediated resistance in several cases. For example, a single copy of BYDV-PAV polymerase (Wang *et al.*, 2000), line 126 of tomato that contains TYLCV-C1 (Fuentes *et al.*, 2006), line 5.1 of common bean that contains BGMV-AC1 (Bonfim *et al.*, 2007), and line 718.001 of cassava that contains UCBSV-CP1 (Ogwok *et al.*, 2012) all are immune against their cognate viruses. The key is probably to select effective regions of the virus for the hairpin RNAi construct because all regions of the virus genome are probably not equally effective for virus resistance. In addition, by employing different (non-PTGS) resistant mechanisms the level of resistance can be increased (Pavli *et al.*, 2010).

In most of the studies reported using PTGS for virus resistance, the level of transgene expression assessed by the level of target siRNAs produced were not analyzed. It has been demonstrated in the case of the CBSV and UCBSV, in both tobacco and cassava, that there is a correlation between level of expression and the level of resistance (Patil *et al.*, 2011). It could also be possible that the level of expression affects the broad-range protection, by increasing the number of target siRNAs that could potentially prime a nontarget virus (e.g., UCBSV vs. CBSV).

Stability of transgenic virus resistance is a very important requirement for the successful deployment of field resistance, especially in the case of perennial crops. A number of studies have shown the stability of PTGS-mediated virus resistance over several generations and years. Noticeably, papaya, the first commercial product for virus resistance, is still highly resistant in the fields (Ferreira *et al.*, 2002; Fuchs and Gonsalves, 2007). In the case of BGMV, resistance in common bean (*P. vulgaris* L.) line (5.1) for more than 2 years of field trials has confirmed the greenhouse observations of resistance to this virus. Sequencing the target region of line 5.1 in several Brazilian isolates has shown 100% identity or less than one point mutation within the transgene (Aragao and Faria, 2009). The C5 line of plum transgenic for the CP gene was uninfected for more than 4 years in the field with natural aphid vectors, whereas susceptible and non-transformed trees developed severe symptoms within the first year of the study (Hily *et al.*, 2004). It remains to be seen, however, what happens to the resistance when the C5 line of plum is coinfected with multiple PPV strains and with other viruses. In the early field trials of CBSD-resistant cassava, line (718.001) has shown stable resistance for more than two seasons (Odipio *et al.*, 2013). Similarly, several previous studies involving CPMR, many of which were shown later using PTGS, have demonstrated a long-term stability of virus resistance. For example, ZW-20 and CZW-3 lines of summer squash (*Cucurbita pepo* spp. *ovifera* var. *ovifera*) have shown stable and durable resistance for more than two decades (Fuchs and Gonsalves, 2007). Transgenic papaya that contains PRSV CP (Rainbow) has shown to perform well in Hawaii for more than 20 years (Fuchs and Gonsalves, 2007). Therefore, it appears that PTGS-mediated virus resistance would be stable in the fields for very long periods of time.

Future Challenges

The major challenge of the PTGS strategy is the high level of sequence specificity required for degradation of target RNA. This problem is more critical in amiRNA and shRNA constructs than for longer dsRNA constructs. Viruses exist as populations in the field, and mutations in the seed region of the effective small RNAs might result in the breakdown of the resistance. For example, in a study with closely related isolates of CTV, PTGS was highly strain specific and not effective against closely related strains (Febres *et al.*, 2008), whereas for cassava, geminivirus protection was obtained against related virus species (Chellappan *et al.*, 2004). The cross-protection is thought to be conferred by the so-called 7bp 'seed region' of the small RNAs (Lewis *et al.*, 2003). One of the solutions for this problem is to select highly conserved regions of the genes such that mutations in those regions will be lethal to the virus, or by stacking multiple regions of a virus under a separate promoter – or under a single promoter as in the case of polycistronic amiRNA construct used against Wheat streak mosaic virus (Fahim *et al.*, 2012).

Another major challenge is the suppressors of gene silencing that interfere with the host PTGS at one or more steps. In the case of mixed infections, these suppressors are shown to act synergistically and increase the severity of the disease (Vanitharani *et al.*, 2005). For example, transgenic tobacco resistant to PVA became susceptible to PVA after Potato virus Y (PVY) infection (Savenkov and Valkonen, 2001). To be successful under field conditions, PTGS technology has to take into account the prevalence of virus species and their interaction in the host plant besides targeting the sequences of suppressors of gene silencing in the RNAi constructs (Yadav *et al.*, 2007). The breaking of PTGS resistance for a virus by an unrelated virus, as reported by the studies conducted in the laboratories, is less likely to happen in the real field conditions. This can be further avoided by stacking genes of

viruses prevalent in a given geographical area in the design of the hairpin RNAi construct.

Although PTGS technology for plant virus control has been successfully demonstrated in the laboratory against a large number of diverse RNA and DNA viruses, so far only a few studies have been successfully applied under field conditions. Moreover, many studies have been conducted on model plants, such as *N. benthamiana*, *A. thaliana*, or on cultivars responding to tissue culture. Only in the recent past have a few studies been carried forward to the field evaluation, for example, PPV resistant plum in the United States, BGMV-resistant common bean in South America, and Cassava brown streak disease (CBSD) resistant cassava in East Africa. Individual viruses are often less damaging than their synergistic effects in the mixed infections. The field conditions vary widely both in biotic and environmental factors, such as presence of other viruses or strains of the same species as well as light, temperature, humidity, etc. Consequently, these factors, such as biodiversity of the viruses, need to be incorporated into the project right from the beginning. On a laboratory scale, resistance has been obtained against multiple viruses and there are still many opportunities to stack the genes for multiple virus or pathogen resistance. Ultimately, there is an urgent need to translate these findings into field conditions. Many times this requires collaboration among scientists of different disciplines, such as biotechnologists, plant breeders, and plant pathologists, from the public and the private sectors.

Because most of the studies performed and reported provide partial information relative to the PTGS mechanism involved, the length and 'value' of the target sequence, the level of expression, the level and range of resistance obtained, and the stability of this resistance in time and space, it is difficult to have a realistic opinion about the strength, validity, and usefulness of such technology for so many different types of viruses in so many hosts, in various places in the world. There are, however, a few common features that are worth noticing; PTGS has been shown to induce virus resistance for many viruses of RNA and DNA nature, in different types of hosts, which seems to indicate that this technology has a universal capacity, provided it is well developed to produce significant and long-term virus resistance for many hosts. The fact that very few products have been or are being deployed is due to a variety of reasons that are not scientific but rather economical or social. The virus targets are either not commercially supported (cassava and rice) or are not big enough (vegetables and fruits) to warrant development by the private sector, leaving the public sector to make all the necessary development, including biosafety regulations that are not in place in many countries in the world. Finally, the opposition of certain groups of growers or the public to adopt this technology is also impacting the development of this technology, such as for fruit trees and vegetables, where the organic market is now driving the decisions.

See also: Agbiotechnology: Costs and Benefits of Genetically Modified Papaya. Biodiversity: Conserving Biodiversity in Agroecosystems. Biotechnology Crop Adoption: Potential and Challenges of Genetically Improved Crops. Biotechnology: Plant Protection. Biotechnology: Regulatory Issues. Breeding: Plants, Modern. Cloning: Plants – Micropropagation/Tissue Culture. Emerging Plant Diseases. Emerging Zoonoses in Domesticated Livestock of Southeast Asia. Genebanks: Past, Present, and Optimistic Future. Genomics: Plant Genetic Improvement. Intellectual Property in Agriculture. Mineral Nutrition and Suppression of Plant Disease. Pathogen-Tested Planting Material. Plant Abiotic Stress: Temperature Extremes. Plant Biotic Stress: Weeds. Plant Disease and Resistance. Quarantine and Biosecurity. Regulatory Challenges to Commercializing the Products of Ag Biotech. Transgenic Methodologies – Plants

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Policy Frameworks for International Agricultural and Rural Development

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Glossary

Cold chain Set of facilities for keeping a product cool or cold from farm to market.
Comparative advantage Inherent ability to produce and sell in international markets at prices equal to or below those of competitors from other countries, abstracting from policy interventions such as taxes and subsidies.
Competitive advantage The same as comparative advantage but evaluated at prevailing prices including the effects of policy interventions.
Covariance risk The risk that variables may move together, for example, yields for several crops in an area may decline when a drought strikes.
Guarantee fund A fund set up to guarantee part of a loan, so that in the event of default the lender recovers at least part of the funds lent.
Multiplier effect The total effect on consumption in the economy of the successive rounds of spending induced by an initial increase in income in a sector or district.
Social capital The ability of individuals (producers in this case) to work together to achieve common aims that could not be achieved without cooperation.
Usufruct right A recognized right to utilize a natural resource, such as land or forests.
Value chain The entire chain of a product from producer to market, from genetic material (in the case of agriculture) through production and harvest, postharvest management, storage, transportation, processing, packaging, and marketing.

Introduction

The Role of Agriculture in Economic Development

In the early strategies for economic development, the role of agriculture's contribution to national growth was conceived as passive. Its primary role was to release resources for use in other sectors: labor and savings (e.g., Chenery and Syrquin, 1975). A supporting role was to generate foreign exchange earnings for use in purchasing imported inputs for industrial growth. Now it is recognized that agriculture's role is more active, and that through its role in reducing poverty and its multiplier effects on domestic demand, it can be one of the motors of economic development. As Mellor (2000) put it:

> Typically high growth rates are achieved when agriculture grows rapidly. That is because the resources used for agricultural growth are only marginally competitive with other sectors and so fast agricultural growth tends to be additive to growth in other sectors… Block and Timmer's model of the Kenyan economy shows the multipliers from agricultural growth to be three times as large as those for nonagricultural growth.

It has been found that agricultural growth is not only the most effective way to reduce rural poverty, but that it is also more effective than industrial growth in reducing urban poverty. To cite one of the several international studies on the topic, Peter Timmer's analysis of a sample of 35 countries found that

> A one percent growth in agricultural GDP per capita leads to a 1.61 percent increase in per capita incomes of the bottom quintile of the population in 35 developing countries. A similar one percent increase in industrial GDP increases the incomes of the poor by 1.16 percent (Timmer, 1997; a fuller discussion of these points is presented in Norton (2004, Chapter 1)).

Agriculture has been a driver of growth in industrialized countries as well: "The growth of total factor productivity in the OECD countries in agriculture has been greater than in manufacturing during the past quarter century or more. The difference has not been small" (Johnson and Agriculture and the Wealth of Nations, 1997, pp. 9–10).

The role of agriculture in earning foreign exchange continues to be relevant for many developing countries, and given that it is a major user of natural resources (land and water and also forests), agricultural development must be sustainable in its resource management. In brief, the most vital roles of agriculture in supporting the development of the entire economy are

- providing increased food security for rural populations, through both higher per capita rural incomes and production of food for home consumption;
- reducing poverty;
- contributing to stimulating the nation's economic growth;
- generating export earnings; and
- assuring the sustainable management of the natural resource base.

The overarching objectives of agriculture policy are the strengthening of each of these roles, for the benefit of the entire economy and nation. The Comprehensive African Agricultural Development Program, an African-led effort under the aegis of the New Partnership for Africa's Development (NEPAD), places agriculture at the center of strategies for reducing poverty and achieving the other Millennium Development Goals of the United Nations (NEPAD Planning and Coordinating Agency, 2010).

Identifying Agricultural Potentials and Constraints

For the sake of efficiency, sound economic policy should strive to make effective protection rates as uniform as possible across products, on the assumption that producers will expand

output of the most competitive ones. However, in a world of many products and many small farmers who may have experience with only a few products, government programs often try to introduce the most promising products to farmer groups and facilitate the adoption of those products. How are the products identified? One step is to look to export markets. Developing-country exports are usually labor intensive and therefore their growth helps create employment and reduce poverty. Nevertheless, promoting exports successfully requires exploiting comparative advantage.

The challenge for policy and for the private sector is to find comparative advantage and turn it into competitive advantage. Following Porter (1990), competitive advantage can be gained either through cost competitiveness or through product differentiation. In agriculture, differentiation by product quality as well as by type of product is an important consideration in determining competitive advantage. Identifying potentials empirically is complicated by the fact that comparative and competitive advantages are dynamic. They can change rapidly because of both external and internal factors. Mexican cotton disappeared because of increasing costs of pest control in cotton-growing zones. Costa Rican pineapple gained markets because of technology (varieties) and marketing support. Colombian coffee has been losing market share because of lower costs of production in Vietnam and Brazil. Peru went from virtually zero production of asparagus to its world's largest exporter in a few years, in part, because of the opportunity to harvest the crop year round.

Classical methods of calculating comparative advantage, such as the domestic resource cost coefficient, do not capture dynamic factors. Approaches such as the revealed comparative advantage capture past trends but ignore cost-price comparisons. Therefore, empirical methods are often used in agriculture to identify products with competitive advantage or the potential for it, such as

- products in which the country has a recognized quality advantage or can meet international quality standards while remaining competitive on costs (e.g., papaya in Belize, gooseberries in Colombia, and macadamia in Rwanda and Malawi);
- products for which the country was a major exporter in the past (it has to be asked why the exports declined and if the factors involved can be reversed);
- consensus opinions in the private sector: producers, processors, and marketing agents; and
- products with proven potential (on the basis of experience of some producers) for significant improvements in yields and quality.

Above all, in agriculture the value chain has to be analyzed and satisfactory responses are needed for questions all along the chain, from seeds to markets: Are the varieties that farmers plant are the same that the market demands? Is there sufficient volume of disease-free, high-quality planting material? Do farmers cultivate and harvest according to best practices (including harvest timing and selection of the products ready for harvesting)? Do postharvest practices maintain quality (drying, threshing, storage, classification and selection, and initial processing in some cases)? Are transport links and facilities available, including cold chain facilities, that will prevent damage to the products when moved to markets or marketing agents? Are plant or animal hygiene standards met all along the chain? Do processing facilities meet international standards? And so forth. When one or more of these questions is answered negatively but the potential appears to be present, it has to be asked if policies and programs can overcome the bottlenecks at a reasonable cost.

The importance of developing competitiveness along the full value chain has been emphasized in many studies for all regions of the world, as in the following:

> The entire value chain is critical: The need to maintain grades and standards within the value chain, not only in export markets but also in evolving domestic and urban markets, drives innovation in agribusiness… Quality assurance, driven by the search for competitive advantage with domestic markets of access to export markets, in turn requires coordination along the value chain… (Kim *et al.*, 2009, p. 10).

Maintaining competitive advantage over time is another challenge and requires

- continuous adaptation of technology, seeking improvements in yields, reduction in costs, and improvements in quality;
- continuous contact with markets to perceive rapid changes in market preferences and requirements;
- integration of the chain of production, postharvest handling, transport, marketing, and in some cases processing; and
- continuous improvements in public infrastructure, institutions, and policies that support production.

In spite of today's ease of international transport, comparative or competitive advantage sometimes exists not only by product but also with respect to market locations. For example, countries in Eastern Africa and the Indian Subcontinent would have a leg up on the competition in serving markets in the Gulf States and the Middle East.

Agriculture and Rural Development

Agriculture is one instrument of rural development. By raising rural incomes, it provides a basis for broader rural development. However, agriculture alone usually cannot satisfy the requirements for more rural employment and higher living standards. Sources of nonagricultural rural employment are needed along with, over long periods of time, rural–urban migration in quantities that the urban job market can absorb.

Development of high-value products, addition of family livestock, and integration of farmers more fully into value chains can accelerate the generation of nonfarm jobs in rural areas. In all regions of the world, agriculture is becoming a more knowledge-intensive industry and its expansion creates demand for specialized services, including input supply, market information and product development support, business management and consulting, transportation and logistics, quality assurance (including certifications), skills, extension and training, veterinary services, and credit and other financial services. To this list can be added irrigation development and management, paraveterinary services, machinery rental and

repair, product selection and packing jobs, administration of cooperatives and farmer associations, soil analysis, local agricultural processing and associated management of facilities such as cooling centers, and others. Although financial services may originate from urban financial entities, they are provided through rural branches and increasingly through local savings and loan associations and microfinance entities. The role of high-value crops in promoting rural employment generation has been noted by Weinberger and Lumpkin: "If… horticultural production increases, this can lead to increased employment opportunities and rising wage levels. Both can be induced either because of increasing labor demand at the farm level, at the level of input providing industries, or at the level of processing and postharvest industries" (Weinberger and Lumpkin, 2007, pp. 1468–1469).

The demand side of the rural economy also plays a role in fostering the growth of rural nonfarm economy: "technological change in the Rural Non-Farm Economy occurs most frequently in rapidly growing rural regions; growing local demand in the rural economy seems to increase opportunities for market growth and attracts new entrepreneurial activity and investment.…" (Haggblade *et al.*, 2009, p. 17).

Training is required for these many specialized activities and occupations. In addition, the small size of many farms mandates cooperation as a prerequisite for participating in higher value markets, and hence the development of social capital is another requirement. As well as endowments of suitable farmland, successful rural development requires progress along the four axes of 'private' and 'social' forms of human and physical capital:

- Individual knowledge and skills, usually termed human capital.
- Ability to work effectively and productively in groups, or social capital (considerable work has been done in conceptualizing and measuring social capital, e.g., Grootaert and van Bastelaer, 2002).
- Private physical capital or farm improvements, such as cultivated terraces, wells, fencing, stables, storage bins, etc., plus stocks of livestock and plantings of tree crops.
- 'Social' physical capital, which includes jointly owned assets (e.g., cooperative processing facilities) and infrastructure supplied by the state, such as roads, publicly supported irrigation systems, electricity, and health facilities.

Agricultural development can promote, and be the result of, increases in these kinds of capital. Higher levels of human and social capital can be utilized in nonagricultural occupations. These four axes are not alternatives for rural development; serious deficiencies in one of them can hinder the overall progress. Hence, development policy needs to promote advances on all four axes.

As an example of the effects of progress along these axes, for many years international development agencies had refrained from supporting road development, but studies have repeatedly shown that the rate of return to rural roads is very high (although there can be concerns about the environmental consequences of road penetration into unsettled areas). In a recent study, Webb (2013) showed the strongly stimulating effect on rural incomes of simple, all-weather farm-to-market roads in the Peruvian highlands, areas that have been difficult for development.

The Nature of Agricultural Policy Instruments

Agricultural policy is implemented through five kinds of instruments: (1) new legislation, (2) executive decrees, (3) investment projects, and (4) programs, which usually require significant numbers of field staff working with farmers, input supplies, processors and the like, and (5) voluntary collaboration by the private sector. Instruments may be combined; a program may have an investment component, or may require an executive decree before it can be carried out. Legislation and decrees define the rules of the game and establish programs, such as guarantee funds, subsidies targeted on the poor, and the formation of water user associations, among many other examples.

Broad Issues in Agricultural and Rural Policy

Macroeconomic Policy and Agricultural Development

Macroeconomic policy affects agricultural growth prospects, mainly through three instruments: the exchange rate, trade policy, and fiscal policy. Real prices in the agricultural sector are unusually sensitive to the exchange rate because agriculture is a highly tradable sector. It is a major exporter in many countries, and its imports often compete with domestic production, either directly or indirectly through substitution effects in consumer diets. Hence, it has been long accepted that an appreciating exchange rate in real terms brings about a decline in domestic real agricultural prices (two of the earliest studies to document this relationship empirically were Krueger *et al.* (1988) and Schiff and Valdés (1992)). This is not only a question of incentives for growth, but, for many smallholders, a decline in real prices signifies worsening malnutrition.

In most countries, the exchange rate is the main determinant of relative, or real, prices in agriculture. This issue is sufficiently important that the UN Food and Agriculture Organization has stated:

> The maintenance of overvalued exchange rates is of particular significance as they impose a tax on exports and subsidize imports. This tool has been used at a high cost to stabilize and hold down domestic food prices for urban consumers at the expense of the domestic producers of import-competing and exportable agricultural products… (FAO, 1996, p. 294).

Trade policy, principally in the form of tariffs and nontariff barriers, affects real prices also, but usually in the direction of raising them (an exception to this statement has been the practice of eliminating tariffs on food aid imports when for all other products there is at least a standard tariff even if a low one; this kind of policy constitutes price discrimination against producers of the commodities concerned), and sometimes with the result of creating uncompetitive, unsustainable subsectors in agriculture. However, protectionist policies tend to be found more in the agriculture of developed nations than in developing nations, so the concern among the latter is to reduce world levels of trade protection.

Developing agriculture generally pays less in taxes because incomes are lower than in urban areas, so fiscal policy concerns outlays from the government budget. In this area, a large number of issues arise about the priorities for such outlays and their effectiveness in stimulating sustainable growth paths in the sector. Some of these questions are treated in the remaining sections of this article.

The Role of Government and the Private Sector

In agriculture, in a developing market economy, the role of the government is complex, sometimes so much so that it places a heavy management burden on the capacity of a Ministry of Agriculture. Among other things the government is responsible for

- setting fair and transparent rules of the game and enforcing them;
- providing special assistance to bring the poor and marginalized into the ambit of economic development;
- providing economic leadership and programs to catalyze the sector;
- facilitating private sector growth, through public–private partnerships, financial guarantees, assistance in organizing producer groups, and the like;
- providing public goods (a worthwhile discussion of the differences between public and private goods in agriculture is found in Umali-Deininger (1997)), such as infrastructure, some kinds of agricultural research, etc., in which the private sector would underinvest or not provide (e.g., land registries);
- ensuring that other vital productive services are available, from the private sector or if necessary from the public sector (e.g., irrigation water and seed multiplication services in the early stage of developing a private seed network);
- providing assistance for emergencies; and
- mediating conflicts over natural resources and other issues.

Developing and enforcing fair and transparent rules of the game can lead the government into an uncomfortable situation of managing conflicts among interested parties. In this area, central roles of the public sector are to provide

- secure property use rights and clear rules for access to property (land, water, and forests);
- informative guidelines for contracts (land rental, exchange of water use rights, sale of products, and borrowing capital) and swift and impartial enforcement of contracts; and
- clear system of weights, measures, and standards in product markets.

In the area of help for the poor and marginalized, governments may provide

- targeted subsidies for access to land, water, inputs, and extension advice;
- targeted programs of microcredit or seed capital for them;
- participatory agricultural research and extension, involving farmers and using their plots;
- grants for acquiring livestock and tree crops or for covering part of their cost;
- assistance in farmer organization;
- training in marketing and facilitation of links to private buyers and exporters; and
- payments for natural resource management under payments for environmental services schemes.

In regard to economic leadership and facilitation, some examples of public sector roles are the following:

- Fundación Chile created state companies for new technologies and products, launched them, and then sold them to the private sector.
- In Peru, competitive grants have been awarded to groups of small farmers to cover the costs of entering new markets.
- In Rwanda, international specialty coffee buyers were brought into the country to develop links between them and coffee-producing cooperatives.
- Governments sometimes provide seals of quality assurance, or support programs for them, for products sold in foreign markets.
- Competitive grants are given for agricultural research by academic institutions, farmer organizations, nongovernmental organizations (NGOs) and the private sector as well as national agricultural research centers.
- Competitive grants also may be awarded to cofinance small irrigation systems built by farmer groups and NGOs (e.g., Chile).
- Simplifying bureaucratic regulations helps the private sector.
- Helping train and organize farmers, of funding such efforts, facilitates private initiatives.

Many developing countries have experienced takeoffs in their agricultural sectors in recent years, especially in Africa and parts of Latin America. However, continuing agricultural development often requires a progressive shift in the roles of the public and private sectors. The latter needs to take greater responsibility for value chain development: for investments, management of facilities, quality control, farmer advisory services, input marketing, irrigation management (often through water user associations), and many other tasks. This need has been formally recognized in Africa with the recent establishment, under the leadership of the World Economic Forum, of a program called New Vision for Agriculture/GROW Africa, with the express purpose of linking entrepreneurs with producers and identifying promising opportunities. The public sector needs to make it clear that it is withdrawing from these areas and honor that commitment, and at the same time play an effective monitoring and regulatory role including for food hygiene and safety. It can act as a facilitator for partnerships and key actions. Fertilizer is a case in point in which sometimes voucher schemes or other forms of subsidy are used to encourage input uptake on the part of smallholders, and in those cases the allocation and use of input vouchers or other forms of subsidy needs to be consistent with development of a private distribution network and it requires careful supervision.

Often the private sector is better placed to assess markets and to commit resources on the basis of those assessments. It is hard to overstate the importance of promoting a leading role for the private sector in agriculture and, by the same token, inculcating a business attitude in farmers. Passing the baton to

the private sector for many actions has implications for the allocation of public resources in the sector. For example, to facilitate and encourage greater private sector involvement, transitional public sector support and outlays may be needed for programs like the following, among others:

- Training programs in entrepreneurship and cooperative management.
- A venture capital fund for new enterprises and market development in agriculture. An example of a venture capital fund for small agricultural entrepreneurs is Impulso Panamá, put into operation in that country in 2008 with the support of the Inter-American Development Bank. Earlier, the IDEA project in Uganda (a project to link farmers to markets supported by the United States Agency for International Development) also provided grants for business development at crucial points in agricultural value chains. For a discussion of designing and implementing these innovation funds, see The World Bank, Agriculture and Rural Development Department (2010).
- Risk-reducing guarantees for contract farming relationships.
- Sharing the cost of agricultural advisory services; although in many cases they can be contracted by farmer organizations, they can be partially or wholly supported financially by the government in the medium term.
- Public–private partnerships for postharvest activities.

Given these demands on public sector resources, the development of partnerships with the private sector takes on increasing urgency. Equally, it is important that public resources be channeled to the sector in ways that are designed to promote efficiency in the sector. This means targeting support on actions that have sector-wide reach, such as infrastructure development (including irrigation, roads, and land terracing), strengthening human capital, and carrying out interventions that catalyze private sector commitment of resources.

Governments may also present to the private sector opportunities for building irrigation schemes and for leasing nonirrigated land, with benefits to farmers who are already on the land. This kind of participation from the private sector accelerates the construction of needed infrastructure in the sector, introduces new production technologies, and increases production while ensuring that farm household incomes reflect the benefits of the projects.

When there are indications of private interest in fostering growth of particular horticultural products or other export crops, at early stages in the development of these subsectors public sector resources may be effective in providing short-term guarantees to both farmer groups and exporters in order to encourage them to enter into contracts for growing horticultural crops, with technical assistance provided by the exporters. Equally, public support can be effective for private sector market exploration missions and for gathering information on quality standards (grants for market exploration and other activities by smallholders and small-scale rural entrepreneurs were also provided by the Impulso Panamá fund).

Growth among smallholders raises questions of scaling up volumes, because for marketing and other purposes smallholders need to combine their efforts and output. The traditional approach to scaling up has been to stimulate the formation of cooperatives of farmers who agree to plant their contiguous plots in the same crop. That has worked well in many cases, particularly in irrigation schemes and on hillside terraces, but the cooperative approach needs to be complemented with technical assistance in production and marketing, as well as management training for cooperatives and marketing assistance. Hence, it is demanding of resources. For this reason, alternative models for scaling up have been explored, including a model in which entrepreneurs lease land from groups of producers, contract (outgrower) farming, and the nucleus farm model. They may require supervision and guarantees that farmer land rights and incomes are protected.

A guiding principle for public expenditures is for the government to orient its support toward development of basic growth factors (physical infrastructure and human capital); toward transitional programs to stimulate innovation in products and product handling, processing and marketing; toward encouragement of entrepreneurial initiatives in the sector; toward increasing human and physical capital endowments of smallholders and landless families; and toward sharing investment costs with the private sector when necessary, always under an exit strategy for the public sector.

Pricing Policies

Many countries have experimented with controls on the prices of basic commodities but they have almost invariably ended up abandoning them sooner or later. They have a role in temporary emergency situations, but in the longer run they usually prove untenable. In the first place, it is impossible to calculate continuously what a market equilibrium price would be, so administered prices have the effect of generating either shortages or surpluses of each commodity controlled. Second, they do not send appropriate price signals to producers in terms of the relative worth of different commodities, so they tend to lead to misallocations of resources. Generally, price controls are biased in favor of consumers, so the net result is a shortfall of domestic production, and in the long run that tends to defeat the aim of reducing inflation through the controls. A study of the transition from planned to market economies in Eastern Europe reached the conclusion that setting prices free actually leads to lower inflation than a policy of price controls (de Melo *et al.*, 1996).

Agricultural marketing boards have tended to work more effectively in East Asia and some countries of South Asia, than in Africa and Latin America. In this case, effectiveness is measured by the extent to which they actually deliver the announced purchase price to farmers, and their efficiency in handling and selling the products.

Industrial crops such as cotton and sugar, in which there are economies of scale in processing, present a special case in which prices can be distorted by monopolies or oligopolies. In African cotton, there has been a movement away from national processing monopolies toward local monopolies, and this has engendered a degree of competition in the sector. The concern is not only for the level of prices to growers, who only in some cases have a realistic option of shifting to other products, but also for the long-term viability of the processors.

In the end, adequate pricing for these products will depend on governance structures within the sectors.

> Price setting needs to occur in a framework of negotiation, but rules must continue to be reformed to provide reasonable assurance to companies that, if they operate efficiently according to international standards, they will be able to earn a reasonable return on their investment over time. Some level of price flexibility over the course of the marketing season may need to be a part of the revised pricing approaches (Tschirley *et al.*, 2009, p. 176).

Sugarcane presents a more challenging case because it is more difficult for an individual producer in a large cane-producing area to switch to another crop. Here price negotiations with large groups of farmers are routine, and it has been important to move toward pricing systems based on the sugar content of the cane rather than the raw tonnage of cane. It also helps the negotiation process to use as benchmarks international data regarding the ratio of the cane price (to producers) to the processed sugar price.

Gender in Rural Development

In rural areas throughout the developing world, women have more burdens on their time than men do. They are responsible for household management and tasks, for households gardens and small ruminants, and they till fields and work on land improvement projects as much as men do. In South Asia, for example, 60.5% of women work in agriculture as opposed to 42.9% of men. In the flower sectors in Colombia and Mexico, 60–80% of the workers are women, and in the Ugandan flower sector they are 85% of the workers. In Sinaloa, Mexico, women represent 40% of the field workers and 90% of the packers; in the Chilean fruit sector they are 50% of the temporary workers. In the vineyards in Northeast Brazil, women represent 65% of field workers (The World Bank, FAO and IFAD, 2009, pp. 320–321). These examples can be replicated over and over.

In spite of their high rate of participation in agricultural activities, women almost uniformly have fewer legal rights to land, less say in irrigation allocations, and weaker decision power over input purchases and field cropping choices, as well as generally lower rates of participation in farmer groups. Women's rights to land may be severely circumscribed even in customary forms of land tenure, more so if they are unmarried, widowed or divorced, and when modern land titling is introduced in a traditional society often land is titled in the name of the household head, who usually is assumed to be a man. Women often lose the land rights they may have had when modern land registries are introduced (The World Bank, FAO and IFAD, 2009, p. 136).

Recent decades have seen a movement toward greater gender equity at least in legislation affecting rural women:

> Many nations have… modified land and property laws and regulations so as to guarantee women's equal property and inheritance rights… most Latin American nations passed legal reforms in the 1980s and 1990s to remove discriminatory clauses applying to family… and inheritance. They also modified land allocation laws and regulations (e.g., for agrarian reform and land titling programs) to recognize and give women equal land rights explicitly. Similar movements in reform legislation occurred in Africa and Asia (The World Bank, FAO and IFAD, 2009, p. 126).

However, "enforcement of these laws is sporadic, and attempts by women to have the law enforced can be painfully difficult" (The World Bank, FAO and IFAD, 2009, p. 127).

Notwithstanding all these barriers, women are generally more productive than men in agriculture and use limited resources more effectively for reducing poverty. A compilation of case studies by the World Bank brought out the following conclusions:

- Burkina Faso: Shifting labor and fertilizer between men's and women's plots could increase output by 10–20%.
- Kenya: Giving women the same inputs and education as men could increase yields by more than 20%.
- Tanzania: Reducing time burdens for women could increase cash incomes for smallholder coffee and banana growers by 10%.
- Zambia: If women enjoyed the same overall degree of capital investment in agricultural inputs, including land, as their men counterparts, output in Zambia could increase by up to 15% (The World Bank, FAO and IFAD, 2009, p. 3).

Women have also proven to be more reliable clients of microfinance organizations. A study of microfinance in Bangladesh found that:

> Microfinance reduces poverty by increasing per capita consumption among program participants and their families. Annual household consumption expenditure increases Tk 18 for every Tk 100 of additional borrowing by women and Tk 11 for every Tk 100 of additional borrowing by men… Women have proved to be excellent credit risks with loan default rates of only 3 percent – significantly lower than the 10 percent default rate for men (Khandker, 1998, pp. 146–147).

In short, reducing gender bias in agricultural programs is not only a question of fairness but also a significant source of new agricultural growth and improvements in rural household welfare. Programs for this purpose have been introduced throughout the world, and they often start with gender assessments of existing institutions and programs, and move on to issues of how to target women more in agricultural extension services (e.g., dealing with women in groups and employing more female extension agents), bring them into cooperative leadership roles, and the like. The cited Gender in Agriculture Sourcebook is a valuable reference for initiatives in this area.

Policies for Basic Agricultural Resources: Land, Water, Financial Capital, and Technology

Land Tenure Policies in Rural Areas

The importance of land tenure and its policy objectives

Land tenure arrangements everywhere are one of the foundations of agricultural production and natural resource management. The many issues concerning land tenure regimes for agriculture can be grouped around two overarching themes: security of land tenure and access to land. Institutional

frameworks can provide powerful incentives for productive activity, as much as prices can, and land tenure regimes are a preeminent example of such frameworks.

Equally, adequate tenure provisions for forested land, and land to be reforested, can provide incentives for sustainable forest management. Experiences in many countries (Congo, Cameroon, Panama, Ecuador, and Indonesia, among others) have shown that the greatest forest depredations tend to occur when usufruct rights to forests are not clearly defined and administered.

Access to land is one of the most valuable instruments for reducing rural poverty, although it is not a panacea in this respect. Both traditional land tenure systems and governments have emphasized providing access to land for poor rural families.

For land tenure, more than other fields of agricultural development policy, viable approaches depend on the historical and social context of each country. Land tenure is often one of the most heated subjects in agricultural development policy. Whether land is effectively and sustainably used has a strong bearing on agricultural growth and rural poverty. Land ownership often is highly contested and ownership or usufruct rights can be uncertain. In these settings the following policy objectives, sometimes conflicting, tend to govern land decisions:

- Achieving economically efficient allocations of land and conditions of tenure, to provide incentives for production.
- Ensuring equity (fairness) in allocations of land.
- Helping reduce rural poverty by providing poor families with a productive asset.
- Promoting sustainable environmental management of the land resource.

In developing countries the broad issues of land tenure frequently include some of the following:

- How can access to farmland be provided for landless rural families and those with tiny plots?
- How can equity in land distribution be made consistent with productive commercial farming?
- How can farmers be provided long-term security of rights to use farmland, to give them incentives to invest in the land?
- How can grazing rights be made secure and, in cases of transhumance, made compatible with cultivation rights?
- What is the role for land markets, or land rights markets, in allocating land?
- What is an appropriate role for customary village land rights and allocation systems?
- How can land access and land rights for women be promoted?
- What is an appropriate way to make the transition from collective lands to individually farmed lands?
- At what level of decentralization should land tenure be regulated and administered?
- How can a land tenure regime influence the maintenance of forest cover and protection of soils?

An example of how land rights can affect the environment is found in Panama, which has a regime of titled private property. Forested lands belong to the state and thus by definition cannot become private property. Therefore, in light of the weak enforcement of forest protection provisions, some rural families go into the forest and cut the trees down, and subsequently apply for and gain title because the land is no longer forested and hence no longer the exclusive domain of the state.

The nature of land rights

There are seven basic forms of property rights:

- open access lands (usually rangelands and forests),
- communal lands in customary tenure,
- collective farmlands (state-owned),
- lands owned jointly through cooperatives or other forms of farmer organizations,
- individual rights within associative tenure systems.
- private individual land rights, including ownership, leasing, and rental, and
- state-owned lands apart from collective farms, and lands owned by local governments.

These forms of land tenure can overlap, for example, state lands can be given out in long-term tradable leases. Communal lands can include open access lands and lands ceded to individuals with usufruct rights.

Land rights, including private ownership, are rarely absolute. Restrictions and conditions are usually placed on land rights, and different governmental jurisdictions may control them. Examples of facets of land rights include the following:

- A right to use land and prevent others from using it.
- A right to transmit land to heirs.
- A right to control how land is used (e.g., community zoning restrictions).
- A right to transfer all or part of land use rights to others, at a freely negotiated price.
- A right to derive income from a piece of land.
- Immunity from expropriation.
- Residuary rights that take effect when other rights lapse (e.g., recovering land rented out).
- Contingent rights to land (e.g., claims of a creditor).
- Traditional rights to graze on lands farmed by others, or to drive herds of animals across such lands.
- Rights in perpetuity or rights delimited in time.

Statistical studies have shown that secure land title or secure usufruct rights help promote

- access to credit (India, Thailand, and South Korea),
- investment in the land (Costa Rica and Thailand),
- higher intensity of land use (Jamaica), and
- higher land values (Nicaragua).

Experiences with land reform and land markets

Much of Africa is still involved in the process of formalizing land rights and sometimes transforming them. Colonial land tenure regimes tended to favor small groups of expatriates, and customary village tenure regimes often cannot respond well to all the demands of modern agriculture. They evolved to assure at least a subsistence standard of living to all village members, not necessarily to support a growing and technologically changing agriculture. The question usually is not supplanting

one system with another but rather harmonizing traditional forms of tenure with the clarity, certainty, and long-term security that agricultural development requires. Some of the aims and problems associated with this transition have been noted in the following words in Spore (2004):

> In the past ten years, in an effort to confer a degree of legitimacy and legal status on farmers working the land, many countries in West and Eastern Africa have embarked on land reform or introduced new laws. To varying degrees, all these initiatives have tried to take greater account of existing land tenure systems and to bring modern rights into greater harmony with traditional ones, rather than setting one against the other. But since communities are often not consulted, many of them have proved reluctant to accept such solutions. That has been the case in Ethiopia, Rwanda and Tanzania. Elsewhere, ambitious programs to codify land rights, as in the rural land rights plans in Benin, Burkina Faso and Guinea, have clarified a variety of situations.

Experience has shown that when land rights are formalized, it is important to take measures to ensure that traditional, unwritten rights of small producers are respected. Otherwise, they may lose their access to land to informed outsiders who are better able to navigate modern registry systems. It is also important to ensure that traditional, unwritten secondary rights are respected, such as recognized rights of elderly or handicapped persons to collect harvests from fruit trees, or long-standing verbal land rental arrangements, or grazing rights on fallow cropland.

Some countries now have laws that formally recognize customary, unwritten land rights. These cases include Mozambique, Uganda, Tanzania, and also the 1994 Eritrean land law.

In cases of traditional communal lands, formal group titles to the land may be issued (Honduras). For other traditional lands, a village's right to adjudicate land rights may be formally recognized (Tanzania and Mozambique).

Land registry systems are an important component of security of land tenure. However, they are expensive and slow to develop. Therefore, it can be useful to give recognition to traditional (village) land rights for a possibly very long transition period to 'modern' land registry systems.

For state-owned lands, it is worthwhile to seek tenure systems that give producers stability of usufruct rights, so they will have more incentive to invest in land improvements and manage the land in ways that protect the soils. Trinidad and Guyana, for example, have adopted the model of long-term leases on state lands. These leases are tradable at freely negotiated prices, and therefore they can serve as collateral for bank loans, as well as giving farmers incentives to invest their own funds and labor.

Where there was a legacy of state farms and collective farms, a common approach has been to convert them legally into corporations. In effect, the workers on the farm become its shareholders, and part of their remuneration depends on the financial success of the operation. They can also hire and dismiss managers. Some former collective farms have broken up the land partly into individual titled plots and partly into joint property owned by the new corporation. There are three basic options for transforming a state farm or collective farm: (1) entirely into individual plots, (2) entirely as a corporation, or (3) as an intermediate model with individual plots plus jointly owned assets.

When land has a cost to the user, it tends to be put to more productive uses. This cost can take the form of payments on long-term leases, a purchase price, or payment of short-term rental. However, there is a consensus among land tenure experts that poor farmers in developing countries generally cannot afford to pay a market price for land. For example:

> The cost of acquiring agricultural land in the market often is too high for the poor because investors value the land for reasons other than farming – as insurance, as an investment, as a hedge against inflation, as a tax shelter, or as a means by which to gain access to subsidized credit or public infrastructure such as irrigation works (Binswanger-Mkhize *et al.*, 2009, p. 13).

Expropriative land reform has a checkered history. In some countries, such as Brazil and Guatemala, there have been attempts to establish land funds to offer land mortgages to small farmers at subsidized prices, as a mechanism of land redistribution through markets. The most viable conceptual scheme for such funds is that they operate as second-story institutions, lending through intermediaries, and that purchase prices of land are freely negotiated between private economic agents (or NGOs) and landowners. In this scheme, the fund manages the process to ensure that the purchasing entity is committed to breaking up the acquired land in smaller plots and selling it to poor rural families. This is an example of what Binswanger-Mkhize *et al.* (2009) call the 'willing buyer-willing seller' approach. However, in some cases in which that approach has been applied, the state itself was the buyer, which opens the process to possible corruption in the form of the agreed price of the land. In other cases, mechanisms were not always in place to ensure that the acquired land was sold onward to poor families (at subsidized prices).

Land rental is another valuable mechanism for putting land in the hands of the poor. It enables them to farm while they work toward a purchase or long-term lease. The renting-out option also saves farm families from losing their land during periods of illness.

As noted, women often suffer discrimination in access to land or the ability to become owners or lessees of land. It is important that land laws and inheritance laws and family laws be improved so that women have equal rights to land.

Water Management Policies for Agriculture

Irrigation policy issues and objectives

Water availability and its management are becoming major issues of our times. Many countries in the world are suffering increasing water scarcity. Per capita availability of water is declining by more than 25% per decade in many cases. More than 40 countries now have less than 1000 m^3 of water per capita per year, which signifies serious problems in some parts of a country and in drought years.

Some continents, countries, and parts of countries are much better endowed with water. However, water has low value in relation to weight and hence is expensive to transport. Hence, water scarcity necessarily remains a localized problem. Irrigation is a large part of the water problem. Irrigation

accounts for more than 80% of water use in Africa and approximately 70% worldwide.

When irrigation functions well it is the most powerful way to raise agricultural production and incomes. Some of the most notable examples are the irrigation system of the Office du Niger in Mali, the *fadama* irrigation schemes in Nigeria, the irrigation systems of Andhra Pradesh in India, and many irrigation schemes in the Philippines. However, because of water scarcity, in many countries the emphasis in irrigation is shifting away from finding new sources of water and toward managing demand for water. The strategy varies even by watershed, but in many countries agriculture is being asked to give up freshwater, in favor of other sectors.

Other issues that frequently arise with respect to irrigation include (1) irrigation efficiencies of 50% or less in spite of scarcity of water; (2) the fact that the distribution of water may be unequal among all the users in a system; (3) deficient water control structures which make it difficult to always deliver water in the required volumes and in stable flows; and (4) deterioration of many systems, especially the drainage components. It is also widely observed that farmers tend to apply more water than needed. Together with leaky canals, this implies waste of water; and together with inadequate drains, it leads to soil salinization.

The broad objectives of irrigation policy usually encompass sustainability of the systems and irrigation practices, equity among users, and efficiency in use of water. For irrigation, sustainability tends to mean maintaining water and soil quality, guaranteeing water availability for future generations, financial sustainability for system maintenance, social sustainability (including avoiding public health issues such as breeding diseases in water), and institutional sustainability (who manages the systems).

Frequently groundwater resources are not managed sustainably, and information on their exact quantities is usually lacking. In Jordan, for example, annual groundwater extractions are now 180% of renewable resources, and in Yemen they are 140% of renewable resources, which means rapidly dropping water tables.

The equity objective also has special meanings for irrigation. It can be interpreted to imply emphasis on small irrigation schemes for poor rural families, on participatory methods of designing and operating irrigation systems, and on ensuring that all users have equal access to water allotments. In some circumstances it can also refer to compensation of families displaced by system construction.

In the case of irrigation the efficiency objective usually has the following meanings:

- reducing water losses (technical efficiency),
- increasing net economic returns to users, per unit of water,
- recognizing the economic value of water and allowing transfers to higher value uses in the watershed as necessary, and
- avoiding negative environmental externalities in the watershed (for pastoralists, wildlife, soils, marine life downstream, etc.).

There can be cases of conflicts among the distinct benefits of water, for example, for livestock or crops, for wildlife or crops, for urban or agricultural uses.

International experience suggests the following broad prerequisites for successful irrigation projects: (1) adequate crop prices, (2) secure land usufruct rights, (3) effective technology transfer, (4) credit availability, (5) secure water supplies, and (6) appropriate institutional arrangements and sufficient funding for system maintenance and operation (see the summary of irrigation policies and experiences in Norton (2004), Chapter 5). One of the keys to improving irrigation efficiency is the development of effective water users associations (WUAs).

Irrigation water allocation and pricing

In light of the growing scarcity of water in relation to the demands for it, demand management for irrigation water is becoming as important as developing new water supplies. Broadly speaking, there are five alternative systems of water demand management: administrative allocations of water, user-based allocations (by WUAs), joint decisions on allocations by users and government (as in France and Senegal), market allocation of tradable water rights, and individual allocations (both off-farm and on-farm). Market-based and user-based allocation systems are gaining favor throughout the world. Government allocations are most effective at the intersectoral level and in delivering bulk water to irrigation systems, but not in managing distribution within the systems.

In irrigation the price does not play the normal economic role of balancing supply and demand, except for cases of water markets. The main motives for setting irrigation prices are demand management and cost recovery. With regard to demand management, the main objectives of water pricing are to stimulate water conservation, to encourage allocation of water to higher value uses both within and outside of agriculture, and to minimize environmental problems arising from excessive application of irrigation water on fields.

In the area of cost recovery, the principal aim of water pricing policy usually is to generate enough revenues to cover operation and maintenance (O&M) costs in order to avoid system deterioration and therefore expensive rehabilitation. In some cases the aim also is to recover investment costs, but this requires an even higher price and such a price is rarely applied. Irrigation charges are very low worldwide, often at 20–30% of the O&M costs. There is much evidence that farmers are willing to pay more for water provided the supplies of it are reliable (as in the case of wells operated by farmers).

Note that none of these motives for water pricing requires setting the price equal to the marginal cost of supply, or the price equal to the opportunity cost of water. That happens only under water rights markets and private water systems (e.g., private wells). Typically, a price that recovers O&M costs is well below the opportunity cost of water. However, a price corresponding to O&M cost recovery usually is a practical upper limit to water charges.

Administered prices and prices in water rights markets affect farmers in fundamentally opposed ways. A rise in the former effectively represents a tax on farmers and therefore it lowers their income. A rise in the latter (the market price of water) represents a benefit for farmers because they can sell or lease their rights at a higher price and therefore receive higher income.

Of the many irrigation pricing mechanisms, the most commonly practiced ones are area-based pricing (pricing by the area irrigated), volumetric pricing (pricing by amount of irrigation water), crop-based allocations, tiered pricing by volume, two-part pricing (fixed fee plus volumetric fee), and prices determined by water rights markets (The World Bank, Agriculture and Rural Development Department, 2010, p. 46). Area-based pricing is the most common and the simplest to administer. However, area-based pricing schemes do not include incentives for conservation of water or for allocation of it to higher value uses. Equally, allocations based on crop needs for water do not encourage adoption of less water-intensive crops.

International trends in irrigation water pricing are toward higher water prices, prices levied in volumetric form, application of volumetric prices through bulk sales of water by government to WUAs (to a main canal), WUA decisions on internal pricing (and allocation) within the command area, and increasing reliance on water rights markets.

Policies for managing irrigation systems

In the most common mode of management, government is responsible for maintaining and operating headworks (dams and diversion structures) and larger canals whereas farmers are responsible for water distribution and maintenance along lower-level canals. However, there are a range of options in practice: full government control (Malaysia), government O&M with inputs from users; shared management between government and users; user responsibility for O&M; user ownership of the system but with government regulation; and full control by users (Meinzen-Dick *et al.*, 1997).

Experiences with user-managed systems have been varied but generally positive. It must be recognized that a principal beneficiary of management transfer to users is the government, because it saves the fiscal cost of O&M. However, other common benefits of user management of irrigation include a reduction of O&M costs, greater transparency in cost accounting, timely and more adequate water delivery, better system maintenance, reduction of water losses, more equitable water distribution, and greater flexibility in cropping patterns.

The concept of user responsibility for system management can be extended to user ownership of the system, or user possession of a very long lease, with individuals holding shares in the ownership or in the leasehold. A system in Nepal was developed by issuing 50 shares to 27 households, in proportion to their contributions. Share prices have risen and there have been share transactions among farmers. The higher price has led to water conservation, and thus expansion of irrigated area, and greater system efficiency (Rosegrant *et al.*, 1995).

The international consensus on best practices for organizing WUAs includes the following points:

1. Organize users at the outset and involve them in system design. Bring together community organizers and project engineers. Include all stakeholders, including tenant farmers and women, in the WUA, which should build on preexisting cooperation (social capital).
2. Government should allow users to organize themselves as they wish, with a push to include women. WUAs should be established for drainage and flood control as well as irrigation (this often is a weak point). Devolve as many responsibilities as possible to WUAs (partial devolution is less successful).
3. WUA members should be made fully aware of their rights and responsibilities when the WUA is formed. Clear agreement is needed on the criteria for allocating water in periods of shortage. In larger systems it may be useful to form federations of WUAs (Argentina). Establish mechanisms for conflict resolution.
4. WUA water rights and obligations of the government to deliver water to them should be legally established. Mechanisms for supervision of performance of WUAs should be established. Responsibility for rehabilitation or upgrading before system transfer to users should be established (normally it is on the government's side).
5. Responsibility for system rehabilitation after transfer should be made clear (normally it is on the government's side). In larger systems, WUAs below tertiary gates should not be given control of those gates (in those cases the gates often disappear). Agencies supporting WUAs need a service orientation and accountability.

Water rights markets, informal and formal, exist in a growing number of countries. Such markets have a number of benefits but implementing them is demanding and requires careful planning. The principal benefits of water rights markets are: The potential to sell a water right makes it more valuable and thus provides incentives for water conservation and allocation to higher value uses. Moreover, there is greater flexibility because the rights can be leased out for a season or other short period.

An additional benefit of water rights markets is that (when conveyance structures exist) intersectoral water transfers can occur if needed and yet farmers will receive compensation (payment) for them. This advantage has permitted some cities to avoid the cost of building a new dam by purchasing water rights from farmers (Chile).

In water-scarce Yemen informal water rights and rights markets exist. Owners of tanker trucks purchase water from farmers with wells (or take it from reservoirs without authorization) and sell it to urban households. In various ways the government attempts to compensate villages for drilling wells in their territory for supplying water to cities. Similar experiences have been observed in other countries.

Some of the prerequisites for successful functioning of water rights markets include equitable initial allocations of water rights, effective WUAs, defining water allocation rules for times of scarcity, defining the role of water authorities in enforcing rights and resolving conflicts, and defining procedures for treating return flows and third-party rights.

Women are often left out of decision making regarding the design and operation of irrigation systems, and efforts are needed to overcome this bias. Steps that can be recommended are the following:

1. Before designing a system, carry out gender analysis of the communities, with emphasis on identifying agricultural and water-related tasks that women carry out. Consult women's groups without the presence of men during the design process. Include women in WUAs.

2. Include women in demonstration visits to functioning irrigation systems. Explain fully to men and women what their workloads will be under the system. Consider women's financial situation in establishing water tariffs. Train personnel of water agencies to include women in discussion of irrigation issues.

Watershed and soil management

Watersheds are complex, multifaceted ecosystems, and therefore sound watershed management begins with a thorough assessment of its main characteristics and trends, both natural trends and those caused by human activity. Such assessments are being done or have been done in watersheds throughout Africa.

Examples of the topics covered by a watershed assessment include projected water supply–demand balances, costs of developing new water supplies, projection of water pollution and waste assimilation demands on water supplies, interrelations between groundwater and surface water, upstream–downstream linkages, watershed and ecosystem protection needs, and, in some cases, wastewater treatment options. The most basic tool, water balances by month or season, usually does not exist.

Other topics frequently covered in a watershed assessment include the efficiency of existing irrigation systems, the possibilities of water conservation in each use, trends in water quality, likely directions and magnitudes of future intersectoral water transfers, and social issues accompanying water projects (e.g., public health issues related to water, resettlement of populations for dams, and changes in water supplies for pastoralists).

The importance of a careful diagnosis of the issues in a watershed arises from the fact that, according to the World Agroforestry Center, on 10% of the land one can do or control 90% of the damage to streams and rivers. For designing interventions on that 10% of the land, the participation of local communities has been found to be a crucial element:

> User participation is increasingly being recognized as critical for success in watershed development and management projects… Empirical evidence suggests that giving users a role in managing their own watershed resources can lead to projects that are more efficient and effective than their top down predecessors (Johnson *et al.*, 2001, p. 20).

The central role of local participation in watershed management has led to a movement away from strictly physical definitions of watershed boundaries:

> Field experience has led the Project to address watersheds more as geopolitical territories (defined on the basis of their governance and social dimensions) than as hydrological units (as in conventional watershed management initiatives). This shift from a 'hydraulic' to a 'territorial' approach required that the scope of watershed management has to be redefined… (FAO, 2003).

The importance of participation has been emphasized in the African context as well as generally:

> There is more to sound water management than simply saving it. Equal and careful – read sustainable – distribution and use of water requires the initiative and ongoing involvement of stakeholders. It is a permanent process since every solution, every innovation leads to a new challenge. If a community creates a small dam for watering cattle, the resulting unprecedented body of water makes the whole community brim with ideas… This will require new rounds of consensus within the community and with others, upstream and downstream. It requires, too, an explicit say in it by women (Spore, 2001).

Improved watershed management can reduce loss of soils through erosion, but another major threat to soils is loss of nutrients. This trend poses a threat to the long-run capacity to produce food. It occurs because of inappropriate fertilization and because crop residues are not left on the fields. The nutrient issue has been summarized in the following words:

> All African countries, except Mauritius, Reunion and Libya, show negative nutrient balances every year… In the semiarid, arid and Sudano-Sahelian areas that are more densely populated, soils lose 60–100 kg of nitrogen, phosphorus, and potassium (NPK) per hectare each year. The soils of these areas are shallow, highly weathered, and subject to intensive cultivation but with low levels of fertilizer application. Limited water availability and intensified land use due to increasing population size have restricted crop diversification and the adoption of proper management practices. Short growing seasons contribute to additional pressure on the land (Henao and Baanante, 1999).

A precondition for the adoption of soil conservation practices is secure long-term tenure rights to the land. A study of this issue in Benin came to the following conclusion:

> The willingness to invest in the long run is significantly higher on owner-operated fields than on leased, borrowed or pledged fields with only medium or short-term use rights. This is particularly evident in the incidence of tree planting. In this survey, landowners planted more than 200 trees per hectare on average, while the number of trees per hectare on non owner-operated fields with medium and short-term use rights were only 26 and 6.3 respectively… (Neef, 2000, p. 126).

Similar results have been found in a study for small-scale hillside farmers in Honduras. That study concluded, "We found... that ownership of the land is positively associated with the use of soil conservation practices" (Jansen *et al.*, 2003).

Whether the land use rights take the form of long-term usufruct or ownership, the conclusions about the effect of tenure security on soil conservation appear to be quite general. For Eritrea, it has been observed that

> A [tenure] rotation period of 5–7 years is too short for people to have the incentive to make long-term investments in improving the land, such as tree planting, digging water wells, making water canals and soil conservation structures, etc. (Negassi *et al.*, 2000, p. 1).

For these reasons, a sound watershed management plan is vital for agricultural productivity and sustainability, and policy needs to find ways to promote it, in the social, economic, and ecological context of each watershed.

Rural Financial Policies

Most developing countries have struggled with agricultural finance without finding an entirely satisfactory solution. In particular the lack of medium-term finance for activities such as irrigation, livestock investments, and planting tree crops remains a major hurdle in developing countries, and sometimes even export finance is difficult or impossible to obtain.

The reluctance of large commercial banks to lend to agriculture is widespread, especially if they have secure alternatives to invest in such as urban real estate development and government bonds. Many countries have created state agricultural development banks but on the whole their record has been mixed, as governmental agencies often do not possess capabilities as financial managers.

Microfinance has proven to be a viable and rapidly expanding approach in many countries, but often its lending is short term and is more oriented toward urban populations and rural marketing activities. It can be as valuable to work to build capacity in local financial intermediaries such as savings and loan cooperatives. The potential for mobilizing rural savings through the farmers' organizations is enormous. The success of rural banking sector in Kenya and Namibia, for example, speak volumes for this possibility. Rural banking in Kenya and Koshi y'O Muti (Savings Under the Tree) in Namibia, and Badan Kredit Kecamatan in Indonesia, are some of the success stories besides the Grameen Bank and a development NGO, formerly the Bangladesh Rural Advancement Committee in Bangladesh. The discipline generated from these systems has resulted in repayment rates of up to 98%. Rural savings and credit cooperatives have worked elsewhere in stimulating agricultural and other socioeconomic growth, although they may be exposed to a high level of risk because of geographical concentration and sometimes a concentration in a few agricultural products (forms of covariance risk). Adding consumer lending to their portfolio can help reduce the risk, as can an apex organization that manages liquidity to these institutions in multiple geographical areas.

Another option that has proven useful in some countries is the creation of a loan guarantee fund (including for agroexports) or a second-story rediscount line that provides funds to financial intermediaries for on-lending to agriculture or other strategic sectors (Wenner, 2001). Usually, the interest rate charged to the intermediaries is made sufficiently attractive to encourage them to participate in the program, but sometimes these rediscount lines are not fully utilized. A common reason is that banks may already be at their lending limit, as a ratio to capital, in more secure kinds of investments. Neither of these approaches is sustainable over the long run because they require a continuing source of subsidy (i.e., the national treasury).

A consensus has emerged that interest rate ceilings, though still prevalent, are inimical to development of financial institutions, especially for agriculture where financial risks may be higher. For most farmers, the main concern is access to credit, more than its cost, because without access to financial institutions they may pay extremely high interest rates on the informal lending market. Equally, it has been found that holding interest rates on government agricultural loans at artificially low levels is counterproductive. It discourages financial institutions from lending to the sector, and it also tends to encourage allocations of investment funds to less productive uses. When lending rates become negative in real terms, financial institutions see their capital and deposit base eroded over time, with the result of decreasing amounts of loanable funds available in real terms. In addition, low lending rates mean low deposit rates that discourage mobilization of financial savings. One of the lessons of rural finance experience is that farming families need a range of financial services, and not only loans. They need opportunities to make deposits, as their income comes at irregular intervals, and they require facilities such as mechanisms for transfer of funds (these and other conclusions from international experiences are reported in many studies; one of the classic references is Yaron *et al.* (1997)).

Crop insurance schemes have been implemented in an increasing number of developing countries. An issue has been the cost of administering them but a useful approach has been developed in the form of basing indemnity payment decisions on detailed meteorological data by zone and following up with field checks only for outliers with greater damage (two useful references are Herbold (2010) and Roberts (2005)). Other forms of crop insurance include coverage against substandard yields and revenues, and against specific types of damage. The latter is used for livestock.

The nature of collateral has received attention in reviews of financial systems. The consensus is that moves to make land tenure more secure, whether by ownership or leasehold, can improve farmers' access to finance. In addition, legislation is being introduced to widen the kinds of moveable collateral, including invoices and crops in storage (Yaron *et al.* 1997; Fleisig, 1995). Village banks and microfinance entities make effective use of social collateral, in the form of group guarantees. Developing value chain finance can require legislation for these and other forms of collateral, and policy tools to make them available include legislation for and implementation of a program of warehouse receipts (certificates of grain deposit) that gives access to finance based on grain stored in approved facilities, and regulations that facilitate the use of invoices for agroinputs and agricultural sales as collateral (factoring). Input suppliers and agricultural marketing agents are significant sources of agricultural finance, and regulations of this nature contribute to increasing the flow of finance and lowering its cost to borrowers. A common form of value chain finance is the buyer-driven model or triangular finance, in which the buyer repays the production loan on receipt of the harvested commodities (Miller, 2013). In this case, the risk is shared between the bank and the product buyer, because of the possibility that the producer may not deliver the commodities, or may do so in insufficient quantities.

The need for venture capital for agricultural enterprise startups is beginning to be recognized (with the support of the International Finance Corporation, a member of the World Bank group, Mozambique has set up a risk capital fund for small and medium enterprises, and Uganda has venture capital programs for agriculture. Panama's Impulso Panamá program has been an example of this kind of fund). Governments can provide this kind of risk capital, preferably with independent panels to select qualifying enterprises. This will generate shareholdings in the enterprises for the government,

and regulations should establish a deadline (perhaps 5–7 years) at which the government would be obliged to sell the shares, giving first rights of purchase to the enterprise concerned (at the initial valuation). Absent a purchase from the enterprise, the shares would be sold at auction. The entrepreneurs would be required to contribute a specified percentage of the capital. Experience has shown that lack of this form of financing is a significant gap in capital markets, and banks typically are not interested in financing enterprises that involve new products or new technologies, for lack of ability to appraise such projects. Although this kind of finance may not be directly aimed at the rural poor, it can improve their incomes significantly by supporting the development of outlets for their higher value products and enterprises that will provide them employment and technical assistance on issues like quality control. Increasingly, these innovation funds require collaboration among the actors in the value chain (Rajalahti and Larson, 2011).

Another financial policy topic that has been explored more recently is the question of the nature of bank supervision and regulation. Worldwide, it was designed for the purposes of providing adequate supervision to commercial banks, but for that reason it has been found to be inapplicable to microfinance and, increasingly, to agricultural finance. (Fiebig (2001) was one of the first to emphasize the different nature of regulatory requirements for agricultural loan portfolios). Collateral often is informal in microfinance, and in agriculture loan classification, reporting requirements and risk provisioning have to be different, among other issues. Weekly or monthly loan reporting is not feasible for crop loans under which repayment will be lump sum and will take place at harvest time, months after the loan is placed. A number of countries have created a special regulatory window in the Superintendency of Banks for microfinance institutions that wish to take in deposits. However, the need for a special regulatory regime for agricultural lending is only beginning to be recognized.

These findings have led to considerable ferment in developing countries in regard to agricultural and rural financial systems. The development of microfinance is the foremost thrust, but collateral legislation, crop and livestock insurance schemes, venture capital windows, systems of village banks, supervisory requirements, and interest rate regulations are also undergoing development or change. Equally, the role of the state in the financial sector is being reviewed. It is now clear that executive branches of governments are not as well suited as the private sector to provide and manage loans directly, but nonetheless they have a vital role in providing incentives and resources to the financial system, as well as establishing an appropriate regulatory and legislative framework.

In summary, priorities for rural financial policies in developing countries include the following:

- Improve access to credit and other financial services by strengthening the rural financial system with emphasis on enhancing its sustainability.
- Widen the range of types of collateral and financial instruments, including crop insurance, available to the rural population.
- Develop mechanisms such as venture capital funds, guarantee funds, and rediscount lines in order to increase the amount of investment finance available with emphasis on the kinds of productive investments not well covered by existing financial markets.
- Strengthen the demand side for rural financial services through activities to improve financial literacy in rural areas and the capacity of local financial intermediaries.

Policies for Agricultural Technology

Issues concerning agricultural technology systems

Agricultural technology classically embraces research and extension, and for the most part research in developing countries has meant development of new crop varieties and improved methods of crop management in the field. The vision of research and extension systems has been broadened to encompass agricultural knowledge and information systems (AKIS). Research and extension systems have had a number of notable successes, going back to the Green Revolution, but nevertheless several important issues have arisen (Norton, 2004, Chapter 8; Suvedi and McNamara, 2012; and the other publications of the project for Modernizing Extension and Advisory Systems (MEAS), headed by Paul McNamara at the University of Illinois). Some of them are as follows:

- Although many studies have confirmed the very high economic rates of return to agricultural research, funding for it is almost invariably insufficient, and one of the consequences is weak sustainability of many lines of research.
- The sources of agricultural research are often limited to one governmental agency and hence the benefits of tapping into diverse approaches are not realized.
- The priorities in a national agricultural research agenda are often set by research scientists and they may not reflect the needs and priorities of farmers.
- In relation to this issue, research rarely concentrates on high-value crops, instead staying with staple crops, and it almost never extends to technologies for postharvest handling, processing, and packaging.
- Farmers can inform the research process about problems that need to be addressed and also can contribute knowledge to the process from their own experiences. Hence, there is a need to find avenues for greater involvement of farmers in research (one of the early, successful efforts along these lines was the creation by the International Center for Tropical Agriculture (CIAT) in Colombia of the approach of Local Agricultural Research Committees, which has spread to other countries (Ashby *et al.*, 2000)).
- There is a need to orient more research toward the needs of women farmers.
- The institutional incentives for government extension workers are to satisfy the requirements of their institution and not necessarily to address the problems faced by farmers.
- Traditionally extension systems have operated in a top-down manner, delivering messages from researchers to farmers, rather than operating as facilitators in farmers' search for relevant knowledge. The top–down approach is poorly suited to the heterogeneous farming conditions of smallholders in most developing countries.

- Traditionally extension systems have not responded well to the needs of women farmers.
- A one-size-fits-all approach does not fulfill the extension needs in developing countries; rather, the trend is toward pluralistic systems with multiple providers.

Owing to these weaknesses in research and extension systems, the private sector and NGOs have increasingly become involved in those efforts. Moreover, because of the importance of these issues, governmental policies for technology systems are undergoing evolution in many parts of the world.

Policy frameworks for agricultural technology systems

In response to these increasingly urgent issues, policies for agricultural technology systems have been experiencing important changes. Some of the most relevant new policy orientations are the following:

- Some countries have set up competitive mechanisms for awarding research contracts. Funds are awarded on the basis of the quality and relevance of proposals, and typically the national agricultural research agency is eligible to submit proposals as well. In some cases (as in the program of the Panamanian National Secretariat for Science, Technology and Innovation (SENACYT)), proposals can include the fields of postharvest management and agroprocessing.
- Following the examples of CIAT and efforts in Africa, programs are now put in place to carry out selected research activities on farmers' plots, with the participation of farmers.
- Some programs are put in place to attract private investment into adaptive research for high-value products (Rwanda).
- In some cases, reviews of the priorities of women farmers are used as an input into the research agenda.
- To correct the institutional incentives issue for agricultural extension, in some cases the contracting of farm advisors is delegated to farm cooperatives and associations, even though governments may continue to fund all or part of the advisory services via reimbursements of those agencies. This ensures that the advisors address the priorities of those farmer groups.
- Approaches like the Farm Field Schools have been implemented, in which farmers participate in the search for improved cultivation methods and become trainers to work in participatory ways with neighboring farmers.
- More women extension agents and farm advisors are being recruited, and extension services direct some of their activities exclusively to women farmers.

See also: Agricultural Cooperatives. Agricultural Finance. Agricultural Labor: Gender Issues. Agricultural Policy: A Global View. Critical Tracking Events Approach to Food Traceability. Crop Insurance. Food Chain: Farm to Market. Food Security: Development Strategies. Global Food Supply Chains. Markets and Prices

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Poultry and Avian Diseases

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Glossary

Broiler birds Birds bred and raised for meat production.
Gamonts A developmental stage within the life cycle of Eimerian species parasites. Specifically, gamonts are the parasitic forms that occur during the sexual phase of the life cycle, which lead to the formation of oocysts that are spread throughout the feces.
Hazard analysis and critical control point (HACCP) A management system in which food safety is addressed through the analysis and control of biological, chemical, and physical hazards from raw material production, procurement, and handling to manufacturing, distribution, and consumption of the finished product.
Impaction Accumulation of eggs and egg material within the oviduct and is usually a consequence of dystocia, metritis, or salpingitis.
Layer birds Birds bred and raised to lay eggs.
Necrosis Refers to the process when a living cell dies due to irreversible injuries.
Notifiable diseases Diseases that must be immediately reported to health and agriculture authorities.
Oophoritis An inflammation of the ovaries that is mainly caused by bacterial agents, such as *Escherichia coli* (*E. coli*).
Pathognomonic A term used to denominate the characteristic clinical signs or lesions of a particular disease or condition.
Poultry Birds used for the purpose of production, which include mainly chickens and turkeys; however, according to the region, ducks, geese, partridges, quails, and ostriches are also used.

Poultry Production: Economical Perspective and Public Health Impact of Diseases

The demand of poultry products has increased parallel to the continual rise in the human population. This can possibly be explained as poultry meat and eggs represent an efficient source of protein and have low cost of production in comparison with other sources of protein, such as pork and beef (Service, 2013). Nowadays almost every world region (Africa, North and Central America, South America, Asia, Europe, and Oceania) has to improve their production systems to accomplish the global demand of richer and more nutritional diets. Besides, global trading of poultry products has also increased, especially between the major producers (i.e., the United States, Brazil, and China) and the rest of the world (Stenhouse, 2008).

All infectious agents, toxics, and nutritional imbalances have an impact on the performance of the farm and consequently on the local poultry industry. Additionally, some diseases of birds, such as influenza virus, imply a potential zoonotic risk to the population and the notification of some strains related to high virulence involves commercial restrictions (ban on poultry imports/exports) and therefore reduce profitability (Yin *et al.*, 2013). Therefore, the goals of any production system (conventional or sustainable) will always be to prevent the risk and consequences of diseases.

Sustainable Production Systems in Poultry

Sustainable or organic production systems consist of a series of strategies developed to decrease the environmental footprint to a minimum in the process of production. In poultry farms, the environmental pollution is generated during the process of growing animals, producing feed, generating manure, and obtaining housing accessories (litter materials and heating devices). Therefore, these systems have to implement measurements at the level of housing, lighting, fencing, and adequate feeder and waterer designs as well as management of litter, composting, and land (Xin *et al.*, 2011).

These organic farming systems consist of several types of production methods that invariably allow access to pastures and involve less density of birds per square meter (Castellini *et al.*, 2006), implying improvements that maximize animal welfare (Beaumont *et al.*, 2010). Examples of these types of sustainable production systems include the following: free range, pastured poultry, semi-intensive, and others (Fanatico, 2007). An important point for the promoters of these systems is the search of alternatives to medication, and especially to antibiotics, which could reduce the emergence of antibiotic-resistant strains of bacteria in the birds themselves or/and the presence of residues in meat and eggs that induce resistance to infected humans (Fanatico, 2008).

Although sustainable and conventional production systems require completely different management strategies, their success depends on the establishment of adequate preventive and control measures to reduce the detrimental effects of diseases in the flock.

Basic Understanding of Disease, Prevention, and Control

Disease may be defined as an impairment of normal physiological function that reflects some structural or functional alteration in the cells or organisms (Slauson and Cooper, 2002). These may be caused by a single factor or more commonly by a combination of different factors. Multifactorial diseases are

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more difficult to diagnose and sometimes require an epidemiological approach. This approach allows assessing all possible etiological agents and associated risk factors, selecting the most adequate laboratory tests to determine the cause of the disease. It is also important to take the intrinsic factors (such as species, breed or strain, immune status, and age of bird) into consideration that can determine the presence of a disease (Sjaak de Wit, 2008).

Prevention and control of disease require a careful evaluation of the entire farm and establishment of a series of biosecurity measures that allow assessing the possible challenges and their impact on the production system. Once established, all factors determining disease can be better recognized and corrected. In general, the recommended approach is to perform a risk assessment and establish the Hazard analysis and critical control point (HACCP) principles on the poultry farm, determining the points where potential hazards could occur and biosecurity measures have to be implemented (Collett, 2013). Biosecurity involves measures at the level of environmental control and management, including elaboration of vaccination and medication programs and also application of effective cleansers, sanitizer, and disinfectants. These biosecurity measures are essential to control the diseases and reduce their economic and public health significance (Lister, 2008).

In summary, prevention and control of diseases depend in part on the ability to recognize the clinical signs, lesions, and all possible etiological agents related to them. For this reason, in the following section on poultry and avian diseases, emphasis was given to the identification of the agent, mechanism of disease, and lesions observed in the affected birds.

Viral Diseases

Influenza Virus

Influenza viruses are segmented negative-stranded ribonucleic acid (RNA) viruses belonging to the family Orthomyxoviridae. Avian influenza viruses are divided according to their virulence in highly pathogenic avian influenza virus (HPAIV) and low-pathogenic avian influenza virus (LPAIV). Influenza viruses are also classified on the basis of the nucleocapsid and matrix proteins into three types (A, B, and C), but especially type A genera cause disease in birds. In addition, influenza A viruses (IAVs) may further be classified into subtypes according to 16 hemagglutinin (H) and 9 neuraminidase (N) antigens. Only the IAVs belonging to the H5 and H7 subtypes are notifiable to health authorities, because they are frequently involved in HPAIV outbreaks and almost all zoonotic viruses have been from these subtypes (OIE, 2013a).

The most susceptible species to infection are gallinaceous species, such as chicken and turkeys (Perkins and Swayne, 2003). Wild birds are the main reservoir of IAVs and disseminated the virus directly to the poultry farms. Birds are infected mainly through the fecal–oral route, although the virus can also be transported mechanically (Prosser *et al.*, 2013).

Clinical forms depend on the virulence of each IAV. LPAIVs are associated with suppurative pneumonia, sinusitis, kidney lesions, and occasionally pancreatitis. However, the HPAIVs cause hemorrhagic and necrotic lesions in different visceral organs, such as the heart, pancreas, and adrenal gland (**Figure 1**; Swayne *et al.*, 2013).

Newcastle and Other Paramyxoviruses

Newcastle disease virus (NDV) is a nonsegmented, negative sense, single-stranded RNA virus of the family Paramixoviridae and genus *Avulavirus*. Specifically, Newcastle disease is caused by serotype 1 viruses (APMV-1) (King *et al.*, 2012c).

NDV induces different clinical conditions with variable severities or pathotypes. These pathotypes include the following: viscerotropic velogenic NDVs (induce hemorrhagic lesions in the intestinal tract), neurotropic velogenic NDVs (produce high mortality and respiratory and nervous signs), mesogenic NDVs (induce respiratory signs with low mortality), lentogenic respiratory NDVs (cause slight respiratory signs), and asymptomatic enteric NDVs (induce an unapparent enteric infection). In the field, these are usually overlapped between pathotypes and exacerbation by secondary pathogens (Alexander, 2008).

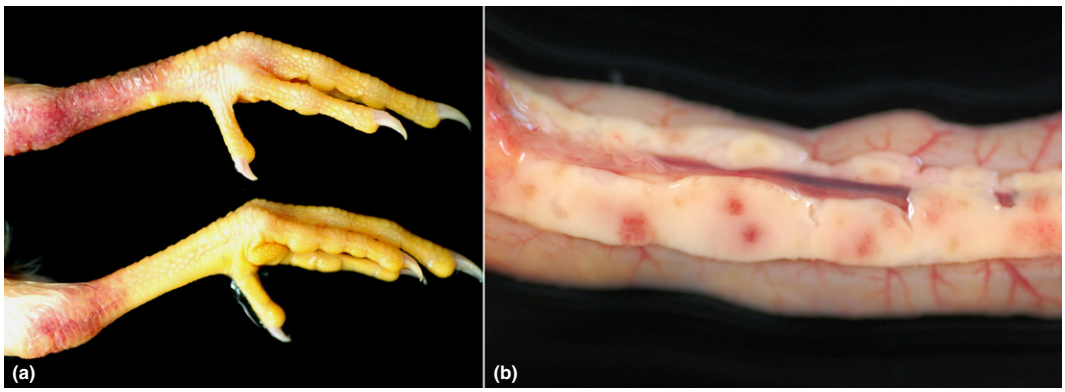


Figure 1 Gross lesions caused by HPAIV H7N1 in specific pathogen free (SPF) chickens. (a) Severe subcutaneous hemorrhages around the hock joint and shank of birds. (b) Multifocal petechial hemorrhages and necrosis in the pancreas of chickens intranasally inoculated with HPAIV A/chicken/5093/99 (H7N1), 5 days postinfection. Photos provided by Natàlia Majó i Masferrer, SDPV (Servicio de Diagnóstico de Patología Veterinaria)-CReSA (Centre de Reserca en Sanitat Animal, Barcelona).

Approximately 250 species of birds can be infected by NDV, through fecal-oral or respiratory route of infection, according to the clinical presentation. Wild birds are the main reservoir of NDVs. As mentioned previously, the lesions are variable; viruses causing respiratory disease produce hemorrhages in the trachea, whereas the enteric viruses cause hemorrhages in the intestinal tract, particularly in the proventriculus (Miller and Koch, 2013).

NDV is zoonotic and has been reported in people with eye infections who are involved in activities related to NDV diagnosis and in poultry production (Conan *et al.*, 2012).

Poxvirus

Fowlpox virus (FWPV) is caused by an *Avipoxvirus* that contains a double-stranded DNA genome and replicates in the cytoplasm of the cells. Poxvirus infections have been recognized in 230 species of birds (Gyuranecz *et al.*, 2013). *Avipoxvirus* is a large virus that contrary to most of the virus is not filterable and consequently the viral particles could be visualized by light microscopy (inclusion bodies containing elementary particles). *Avipoxvirus* is highly host specific; therefore, infection with one type of poxvirus does not protect against others. In fact, poxviruses are named according to the susceptible host species (i.e., Fowlpox virus, Canarypox virus, Pigeonpox virus, Psittacinepox virus, Turkeypox virus, etc.) (Tripathy and Reed, 2013).

Avipoxvirus is transmitted by means of desquamation of skin lesions or by the biting of insects that sting the unfeathered skin areas, producing the characteristic papular, vesicular, and crusty lesions visible in the nares, eyelids, and legs. Birds can also ingest or inhale viral particles, producing diphtheritic lesions in the oral cavity, pharynx, larynx, and trachea (Tripathy and Reed, 2013).

Avian Encephalomyelitis Virus

Avian encephalomyelitis is produced by a nonenveloped, icosahedral, single-stranded RNA virus of the family Picornaviridae (Todd *et al.*, 1999). The disease affects mainly chickens and occasionally turkeys, pheasants, Japanese quail, and pigeons. Clinical signs include reduction in hatchability and nervous signs in young birds, whereas adult birds show enteric signs. Gross lesions are frequently unapparent. Microscopic changes are considered pathognomonic and include diffuse gliosis and central neuronal chromatolysis in the brainstem and midbrain, as well as presence of gliosis in the molecular layer of the cerebellum. Additionally, lymphoid perivascular aggregates are seen through the central nervous system as well as in the dorsal root ganglia, proventriculus, gizzard, pancreas, and other viscera.

Other Picornaviridae family viruses causing serious diseases in birds include the following: Duck hepatitis virus (causes hemorrhagic lesions and necrosis in the liver of duck) and Turkey viral hepatitis (induce similar lesions in turkeys) (Suarez, 2013).

Infectious Bursal Disease

Infectious bursal disease (IBD) virus is a pathology to chickens and is caused by a nonenveloped, double-stranded RNA virus, that is member of the Birnaviridae family (Muller *et al.*, 1979). The viruses causing IBD are divided into two serotypes (serotypes 1 and 2), but only viruses of the serotype 1 infect B cells. The high mutational rate of IBD viruses induces high genetic diversity and continual emergence of more virulent forms, which are able to overcome the previous acquired immunity and persists in the population, such as the European very virulent viruses (vvIBDV) (Maas *et al.*, 2001).

The main target organ of IBDV is the bursa of Fabricius, where the virus causes lymphocytolisis and persists within the macrophages. Chickens with a well-developed bursa of Fabricius (between 3 and 6 weeks of age) are most susceptible. Gross lesions consist of petechial hemorrhages in the leg and thigh muscles, swelling of the bursa of Fabricius and petechiae, and sometimes petechiae in the mucosa of the proventriculus. Besides, there may be splenomegaly, swelling of the liver, and nephrosis (Eterradossi and Saif, 2013).

Reovirus

Reovirus corresponds to a nonenveloped virus that contains ten segment of double-stranded RNA. Reovirus causes arthritis and tenosynovitis in domestic fowl (De Gussem *et al.*, 2010), but it also has been associated with a multisystemic disease in African gray parrots (Sánchez-Cordón *et al.*, 2002). In addition, Reoviruses have been detected in budgerigars, black-tailed gulls, pheasants, bobwhite quail, pigeons, and mallard duck; however, only in a few cases they have been related with disease (Jones, 2013). Lesions commonly found (especially in broiler chickens) consist of tenosynotivis and arthritis, affecting the hock joints and rupture of the gastrocnemius tendon in chronic cases. Reovirus has been also related with ulcerative enteritis, acute and chronic respiratory disease, pericarditis, hydropericardium, anemia, acute hepatitis, inclusion body hepatitis, malabsorption syndrome in broilers, and poult enteritis and mortality syndrome (PEMS) in turkeys (Jones, 2013).

Rotavirus

Rotavirus also belongs to the family Reoviridae, and its genome contains 11 segments of double-stranded RNA. Rotaviruses have been detected in chickens, turkeys, pheasant, partridges, ducks, guinea fowl, ratites, pigeons, and parrots. In these species, Rotavirus may cause subclinical infections (predominantly in chickens and turkeys) and malabsorption and secretory diarrhea of different severity. The target cells of Rotavirus are the mature villous epithelial cells of the small intestine, causing villous atrophy (Day, 2013).

Circovirus

The family Circoviridae contains nonenveloped, icosahedral viruses with single-stranded circular DNA genomes. This family includes the genus *Gyrovirus*, which is represented by Chicken anemia virus (CAV), and the genus *Circovirus*, which contains Psittacine beak and feather disease virus (BFDV), Pigeon circovirus (PiCV), Canary circovirus (CaCV), and Duck circovirus (King *et al.*, 2012b).

CAV infects only domestic fowl and does not have zoonotic potential. Clinical signs are observed in the progeny of breeder flocks that are infected for the first time (vertical transmission) and that are susceptible (i.e., chickens without maternal antibodies). In these birds, CAV causes anemia, aplasia of the bone marrow, and atrophy of the thymus, spleen, and bursa of Fabricius (Santen *et al.*, 2004).

Adenovirus

Adenoviruses are nonenveloped double-stranded DNA viruses that replicate in the nucleus of the cell, producing inclusion bodies. The family Adenoviridae includes four genera, but only three of them (*Avidenovirus*, *Siadenovirus*, and *Atadenovirus*) are related to diseases in birds (King *et al.*, 2012a).

The *Aviadenovirus* of domestic fowl has been associated with several conditions that include the following: inclusion body hepatitis (IBH), hydropericardium syndrome, respiratory disease, tenosynovitis, diarrhea, drop in egg production, and poor performance (Hess, 2013).

The *Siadenoviruses* are represented by the Turkey Adenovirus A, which causes sudden death consequence of severe hemorrhagic enteritis (Pierson and Fitzgerald, 2013).

Egg drop syndrome is induced by an *Atadenovirus* that replicates primarily in lymphoid tissues and massively in the pouch shell gland region of the oviduct, producing eggshell changes (loss of shell pigmentation, thin and soft shells, and shell-less eggs) (Smyth, 2013).

Parvovirus

Parvovirus is a single-stranded DNA virus. In birds there are two important diseases caused by viruses of this genus: Derzsy's disease cause by Goose parvovirus (GPV) and Muscovy duck parvovirus. GPV affects young gosling and Muscovy ducks and is also known as gosling plague, goose hepatitis, enteritis, or infectious myocarditis. GPV causes a multisystemic disease, which is characterized by the induction of Cowdry type A intranuclear inclusions in myocardial cells, enterocytes, and smooth muscle cells (Glávits *et al.*, 2005).

Infectious Bronchitis Virus

The avian infectious bronchitis virus is a positive-sense, linear, single-stranded RNA virus of the family Coronaviridae and genera *Coronavirus* (Jackwood, 2012). Avian coronavirus causes respiratory signs and renal damage in broilers as well as drop in egg production in laying hens. Gross lesions consist of catarrhal exudate in the nasal cavity, sinuses, and trachea, sometimes affecting the low respiratory tract. Some IBV strains cause interstitial nephritis and visceral gout. Recently, there have been reports of IBV strains that affect the development of the reproductive tract, inducing the 'blind or false layers,' consequence of agenesia or hypoplasia of the oviduct (Cook *et al.*, 2012).

Infectious Laryngotracheitis Virus

Infectious laryngotracheitis is a respiratory disease of domestic fowl that is caused by Gallid herpesvirus 1 (Iltovirus: ILT-like virus) (King *et al.*, 2012a). The disease is observed mainly in young male birds of heavy breeds between 3 and 9 months of age. The virus can remain in the trigeminal ganglia of birds latently infected, which begin to intermittently reexcrete the virus on stress conditions (Williams *et al.*, 1992).

The clinical presentation is restricted to the upper respiratory tract and can be peracute, acute, mild, or asymptomatic. In the peracute form, birds are found dead without prodromal signs due the induction of necrosis and hemorrhagic tracheitis. Acutely affected birds show caseous diphtheric exudates and hemorrhages in the trachea, which obstruct the respiratory pathways. In mild forms, there are mucous and caseous exudates in the trachea, and histologically it is possible to see pathognomonic Cowdry type A intranuclear inclusion bodies and multinucleate cells (syncytia) in respiratory and conjunctival epithelial cells.

Other important member within the Herpesviridae family is the Anatid herpesvirus 1 that causes Duck enteritis virus or Duck Plague (García *et al.*, 2013).

Arhtropod-Borne Viruses

Within this group are included the arboviruses (arthropod borne), which are viruses transmitted by hematophagus arthropods to vertebrate hosts. This group includes 535 viruses. Among these, six families of viruses have been isolated in birds and ornithophilic arthropods: Togaviridae, Arenaviridae, Flaviviridae, Bunyaviridae, Reoviridae, and Rhabdoviridae (Capua, 2008).

Highlands J virus

Highlands J virus (HJV) causes disease in Chukar Partridges and turkeys. HJV corresponds to an *Alphavirus* of the Togaviridae family. HJV causes ovarian atrophy and mortality in young poults (Ficken *et al.*, 1993) and encephalitis and myocarditis in Chukar Partridges (Eleazer and Hill, 1994).

Easter equine encephalitis virus

Easter equine encephalitis virus (EEEV) infects birds and humans and has been reported in North and South America. EEEV is transmitted by a highly ornithophilic mosquito (*Culiseta melanura*), which feeds mainly from passerine birds (Hassan *et al.*, 2003) EEEV causes encephalitis and occasionally myocarditis in pheasants, turkeys, ducks, Chukar Partridges, and chickens (Guy, 2013).

Western equine encephalitis virus

Western equine encephalitis virus (WEEV) also infects humans and other mammalian host, besides birds. WEEV is found in the Americas and is transmitted by ornithophilic mosquitoes of the *Culex* genus. WEEV has been isolated from pheasants, turkeys, and Chukar Partridges. In Chukar Partridges, WEEV has been related to high mortality (Guy, 2013).

Venezuela equine encephalitis virus

Venezuela equine encephalitis virus infects more than 100 species of birds and is transmitted among them by mosquitoes belonging to the genus *Culex* (Capua, 2008).

West Nile virus

West Nile virus (WNV) belongs to the Flaviviridae family and its presence has been described in Africa, Asia, Europe, and North America. The virus can be transmitted by at least 43 mosquito species from 11 genera. WNV infects birds, reptiles, amphibians, mammals, mosquitoes, and ticks; however, birds are the main reservoir. Infection has been detected in geese, ducks, Chukar Partridges, pheasants, and a wide variety of feral and captive birds (Himsworth *et al.*, 2009). Some WNV strains present in North America and the Middle East have evolved to become more virulent (Isr98), causing meningoencephalitis, myocarditis, and splenomegaly in humans (Guy, 2013).

Crimean–Congo hemorrhagic fever virus

Crimean–Congo hemorrhagic fever virus (CCHFV) is an *Arbovirus* transmitted by ticks that infects birds and causes disease in humans. CCHFV is found in Asia, Africa, the Middle East, and Eastern Europe and in the European Union. CCHFV have been reported in ostriches, chickens, and guinea fowl, but it does not cause clinical signs (Bente *et al.*, 2013).

Marek's Disease

Marek's disease (MD) is a lymphoproliferative and neuropathic disease of chickens, and occasionally turkeys, quails, and geese. This disease is caused by a cell-associated lymphotropic herpesvirus of the genus *Mardivirus*. The genus *Mardivirus* contains three serotypes, but MD is induced only by viruses of serotype 1. Viruses within this serotype show variable pathogenicity, which are subdivided into different groups: mild (mMDV), virulent (vMDV), very virulent (vvMDV), and very virulent+ (vv+MDV) (Witter, 1998).

Transmission occurs through direct and indirect routes (airborne route). The virus replicates in keratinizing epithelia cells of the feather follicle, so the desquamated cells and feathers serve as a source of infection (Jarosinski, 2012).

There are different clinical forms of the diseases that include the following: the classical form, acute form, acute cytolytic form, and transient paralysis syndrome. The classical form involves neural lesions that cause partial or complete paralysis of the legs and wings, torticollis, and paralysis. The acute form is characterized by the induction of lymphomas in visceral organs. The acute cytolitic form is caused by vvMDV strains, which produce severe atrophy of the lymphoid organs and high mortality in birds between 10 and 14 weeks of age. Transient paralysis occurs in birds between 5 and 18 weeks of age and consists of vasculitis and edema that induce flaccid paralysis (Schat and Nair, 2013).

Avian Leukosis, Reticuloendotheliosis, and Other Lymphoproliferative Diseases

The retroviruses are RNA viruses that cause neoplastic cells transformation and tumor development. Retroviruses affecting birds include the following: Avian leukosis/sarcoma group viruses (ALSV), reticuloendotheliosis viruses (REV), and lymphoproliferative disease virus of turkeys (LPDV) (King *et al.*, 2012d).

ALSV belongs to the genus *Alpharetrovirus*, which is able to induce erythroid, lymphoid, and myeloid leukoses and other kind of tumors in chickens and other species of birds. Lymphoid neoplasms (B cell origin) are usually induced by ALVs subgroups A and B. The erythroid leukosis originates from bone marrow cells and is induced by subgroup J ALVs. Myeloid leukosis derives from myeloid (granulocytic) cells of the bone marrow and produce myeloblastosis and myeolocytomatosis (Venugopal *et al.*, 2000). Additionally, ALSVs and specially ALV-J are associated with the induction of other tumors, such as fibrosarcomas, chondroma, hystiocytic sarcoma, endothelioma, hemangioma, nephroblastoma, and hepatocarcinoma. Furthermore, these viruses are able to induce osteopetrosis (Nair and Fadly, 2013).

REV includes several viruses isolated from game birds (order *Galliformes*) and waterfowl (order Anseriformes). REVs induce an acute multisystemic and neoplastic disease in chickens and turkeys, or in chronic cases, formation of B-cell or T-cell lymphomas (Nair *et al.*, 2013).

Bacterial Diseases

Avian Cholera

Fowl cholera is caused by *Pasteurella multocida*, which is a Gram-negative, nonmotile, non-spore-forming, rod-shaped bacterium. The species *P. multocida* includes the subspecies multocida, septica, and gallicida. Additionally, *P. multocida* is divided into 16 somatic serovars (1–16) and five capsular serovars (A, B, C, D, and E). All capsular and somatic serovars (with exception of 8 and 13) have been isolated from birds. However, subspecies multocida serovar A is the most frequently isolated one in cases of fowl cholera. All types of birds are susceptible to the infection, but turkeys, partridges, and pheasants are highly susceptible.

Pasteurella multocida first colonizes the upper respiratory tract and lung and later disseminates, causing two clinical presentations. The peracute/acute form is related to septicemia, inducing petechial to ecchymotic hemorrhages in the heart, the mucous membranes of the gizzard, and in the abdominal fat. In chronic cases, lesions involve the respiratory tract (fibrinonecrotic pneumonia and fibrinopurulent pleuritis), the conjunctiva, infraorbital sinuses, and the reproductive tract. *Pasteurella multocida* is also related to fibrinonecrotic dermatitis affecting the dorsum, abdomen, and breast (Glisson *et al.*, 2013).

Pasteurella multocida infections are notifiable due to their zoonotic potential (Wilson and Ho, 2013).

Mycoplasmosis

Mycoplasmas are assigned to the class mollicutes, which comprises the smallest known prokaryotes able to replicate in cell-free medium. There are 23 recognized avian mycoplasma species, but only four species are important in poultry.

Mycoplasma gallisepticum

Mycoplasma gallisepticum infects chickens, turkeys, pheasants, partridges, duck, geese, guinea fowl, quail, peafowl, racing

pigeons, and other species of free-living birds. *Mycoplasma gallisepticum* causes catarrhal rhinitis, tracheitis, pneumonia, edema of the air sac walls, and sinusitis (Gharaibeh, 2011).

Mycoplasma synoviae

Mycoplasma synoviae strains vary in their virulence and tropism. *Mycoplasma synoviae* affects primarily chickens and turkeys, and less frequently guinea fowl, ducks, geese, pigeons, quails, pheasants, Red-legged Partridges, and house sparrows. *Mycoplasma synoviae* may cause respiratory lesions or suppurative and caseous arthritis of the foot and hock joints (Osorio *et al.*, 2007).

Mycoplasma meleagridis

Mycoplasma meleagridis is a specific pathogen of turkeys that causes airsacculitis, osteodystrophy, and low hatchability in mature birds (Chin, 2013).

Mycoplasma iowae

Mycoplasma iowae contains six serovars, which vary in their virulence. *Mycoplasma iowae* causes embryo mortality in turkey, poor-quality poults, and chondrodystrophy (Bradbury and Raviv, 2013).

Chlamydiosis – Chlamydophilosis

Avian chlamydophilosis is produced by bacteria belonging to the family Chlamydiacea, which is divided in two genera: *Chlamydia* and *Chlamydophyla*. The species that affect birds belong to the genus *Chlamydophyla* and include the following: *Chlamydophyla pecorum* and *Chlamydophyla psittaci*. These are Gram-negative, coccoid bacteria that depend on the intracellular environment for their multiplication. (Vanrompay, 2013).

Chlamydophyla psittaci infects parrots and other psittacine birds as well as domestic poultry and free-living birds. Infected birds can transmit the infection to mammals (Beeckman and Vanrompay, 2009).

Severity of the disease varies according to the strain of *C. psittacine*. High-virulent strains are related to acute epidemics and high mortality, whereas low-virulent strains spread slowly and cause slightest lesions. Birds affected acutely show fibrinous peritonitis, pericarditis, myocarditis, pneumonia, and enlargement of the liver and spleen, which also show multifocal necrosis. Chronically infected birds show hepatomegaly and splenomegaly, which may lead to rupture of these organs (Vanrompay, 2013).

Ornothobacterium and *Riemerella*

Ornothobacterium and *Riemerella* genera belong to the family Flavobacteriaceae.

Ornithobacterium rhinotracheale

Ornithobacterium rhinotracheale is a slow-growing, Gram-negative, pleomorphic or rod-shaped bacterium that has been isolated from chicken, Chukar Partridge, duck, goose, guinea fowl, gull, pheasant, ostrich, partridge, pigeon, quail, rook, and turkey. Infection in broiler chickens induces purulent airsacculitis, pleuritis, and pneumonia (Chin *et al.*, 2013). Young birds can also have purulent inflammation of the brain and osteomyelitis of the skull bones (Moreno *et al.*, 2009).

Riemerella anatipestifer

Riemerella anatipestifer is a Gram-negative, nonsporulated bacterium that causes disease not only in young ducks but also in galliform birds, such as turkeys, pheasants, and partridges. Lesions produced by *R. anatipestifer* include fibrinous airsacculitis, polyserositis, sinusitis, pneumonia, meningitis, mucopurulent, or caseous salpingitis (Ruiz and Sandhu, 2013).

Enterobacteriaceae

The family Enterobacteriaceae consists of rod-shaped, Gram-negative aerobic or facultative anaerobic bacterium. This family includes bacteria within the genera *Salmonella*, *Escherichia*, *Shigella*, *Citrobacter*, *Klebsiella*, *Proteus*, and *Yersenia* (Lister *et al.*, 2008).

Salmonella

This genus consists of two species: *Salmonella enterica* and *Salmonella bongori*. The former contains 6 subspecies that are also classified in serovars according to the antigenic specificity. In the veterinary field, the most important serovars are: *Salmonella* pullorum (pullorum disease), *Salmonella* gallinarum (fowl typhoid), *S. enterica* subsp. *arizonae* (Arizonosis), and other salmonella infection-causing serovars (Salmonellosis, paratyphoid infection) (Lister *et al.*, 2008).

- Pullorum disease: Almost all species of birds can get infected with *S.* pullorum, but only chickens, turkeys, guinea fowl, quail, and pheasant show clinical disease. Clinical signs are usually observed in birds less than 3 weeks of age, which are found dead in shell or die quickly after hatching, due to peritonitis and septicemia (Shivaprasad, 2013b).
- Fowl typhoid (*Salmonella* gallinarum infection): *S.* gallinarum causes disease mainly in adult or growing chickens and turkeys but also affects ducks, pheasants, guinea fowl, peafowl, grouse, and quail. Acute cases of infection are related to septicemia. In subacute outbreaks, there are dead-in-shell embryos, or dead chicks on the hatching trays. Chronically affected birds show anemia and focal necrosis in the liver (**Figure 2**), heart, intestines, and pancreas (Lister *et al.*, 2008).
- Salmonellosis, paratyphoid infection: Within this group are included *Salmonella* serovars associated with foodborne human disease. This group includes *Salmonella* enteritidis and *Salmonella* typhimurium. Members of this group are found in a wide range of species (birds, mammals, reptiles, fish, and insects). Paratyphoid *S. enterica* produces typhlitis in young birds with dissemination toward the spleen, lungs, liver, spleen, and kidneys (Gast, 2013).
- Arizonosis (*S. enterica* subsp. *arizonae*): Arizonae infection affects avian, mammal, and reptilian species. Avian arizonosis is recognized mainly in turkeys but also is found in chickens and ducks. Clinical signs are similar to the observed in cases of salmonellosis, but additionally the



Figure 2 Liver from a bird naturally infected with *Pasteurella*, showing hepatomegaly and multifocal-coalescing pale foci of necrosis and hemorrhages. Photos provided by Alejandro Alfaro, Universidad Nacional de Costa Rica.

arizonosis is characterized by the induction retinitis and encephalitis (Shivaprasad, 2013a).

Collibacillosis

Escherichia coli (*E. coli*)species are Gram-negative bacteria, flagellated rods that are normal inhabitants of the digestive tract in birds and mammals. Collibacillosis entitle all disease conditions that are caused by the pathogenic serovars of *E. coli*, including Colisepticaemia, egg peritonitis, and yolk sac infection or omphalitis, coligranuloma, swollen head syndrome, and others syndromes (Lister *et al.*, 2008).

- Colisepticemia is observed in chickens, turkeys, ducks, and pheasants. Birds affected show pericarditis, perihepatitis, airsacculitis, and peritonitis.
- Egg peritonitis is observed in chickens, turkeys, ducks, and geese. Gross findings include peritonitis, salpingitis, and impaction of the oviduct.
- Yolk sac infection occurs by contamination of the unhealed navel or by contact of the hatching egg with the contaminated shell. Chickens affected show septicemia and yolk sack inflammation.
- Coligranuloma consists of several hard, yellow, nodular granulomas that are found in the mesenteries and wall of the intestines, especially in the cecum.
- Swollen head syndrome (SHS) is observed in chickens, turkeys, and guinea fowl and consists of an acute to subacute cellulitis affecting the periorbital tissues (Nolan *et al.*, 2013).

Clostridia

Clostridia are large Gram-positive, rod-shaped, toxin-producing bacteria that generate endospores to survive. Clostridia are ubiquitous worldwide and are found in the soil, dust, animals, and insect larvae. They are considered normal inhabitants of the intestinal tract (Kaldhusdal *et al.*, 2008).

Clostridium perfringes *(necrotic enteritis-NE and hepatic disease)*

Clostridium perfringes causes two types of diseases: necrotic enteritis (NE) and colangiohepatitis. NE is caused by *C. perfringes* toxin types A and C and is observed mainly in chickens and turkeys but also found in ostriches, wild geese, wild crows, domestic geese, and ducks. NE occurs when predisposing factors (such as infection with *Eimeria*) induce overgrowth of *C. perfringes*, which through its toxins destroys the cell membranes, causing pseudomembranous enteritis (**Figure 2**) and endotoxemia. Cholangiohepatitis is related to *C. perfringes* toxin type A producers that arrive to the liver via the portal blood or bile, causing cholangitis, and occasionally focal necrosis, granulomas, and rarely massive liver necrosis (Opengart and Glenn Songer, 2013).

Clostridium colinum *(ulcerative enteritis)*

Clostridium colinum affects mainly quails but also infects chickens, turkeys, pheasants, partridges, grouse, pigeons, robins, and lories. *Clostridium colinum* induces ulcerative, pseudomembranous enteritis that affects the small intestine, ceca, and upper large intestine. The ulcers may become perforated, generating peritonitis (Songer and Uzal, 2013).

Clostridium botulinum *(botulism and limberneck)*

Botulism is a paralytic disease caused by toxins produced by *C. botulinum*. There are seven toxins (A–G); Toxin type C is the most important and common one. Presence of type C botulism has been described in chickens, turkeys, ducks, gulls, pheasants, and ostriches (Skarin *et al.*, 2013).

Gangrenous dermatitis (malignant edema and cellulitis)

Gangrenous dermatitis is observed in chickens and turkeys. The disease is caused by *Clostridium septicum* and *C. perfringes* type A, and occasionally *Staphylococci aureus* (Opengart, 2013).

Campylobacter

The genus *Campylobacter* consists of curved-rod, Gram-negative, flagellate bacteria, which grow at high temperatures (42–43 °C). These organisms are found normally in the intestinal tract of a wide variety of animals, including birds (Whiley *et al.*, 2013). Their significance lies in the ability to cause disease in humans, producing catarrhal diarrhea and self-limiting fever or in severe cases nervous system manifestations. In birds there are three main species: *Campylobacter jejuni*, *Campylobacter coli*, and *Campylobacter lari*. *Campylobacter jejuni* is usually found in poultry but can also be isolated from game birds, pigeons, and several wild bird species. Besides, poultry farm workers act as carriers and can spread the infection between broiler houses and farms. Therefore, all biosecurity

measures have to be directed to reduce the horizontal transmission of the bacteria (Hermans, 2012).

Tuberculosis

Avian tuberculosis occurs in companion, captive exotic, and wild and domestic birds throughout the world. *Mycobacterium avium* consists of a complex group of mycobacterial organism, which is divided into four subtypes: *M. avium* subsp. *avium*, *M. avium* subsp. *hominissuis*, *M. avium* subsp. *silvaticum*, which are pathogens of birds, and *M. avium* subsp. *paratuberculosis*, which is a pathogen of mammals (Dhama, 2011).

Mycobacterium avium infects all species of birds, among which the most susceptible ones are the domestic species (such as chickens, ducks, and geese), game birds (pheasants), and birds kept in zoos (Moreno *et al.*, 2011). In poultry, *M. avium* subsp. *avium* serotypes (1, 2, and 3) are the most virulent ones and are most frequently found. *Mycobacterium avium* subsp. *avium* produce tubercular granulomas that may be found in the intestines, liver, spleen, bone marrow, and other tissues (Fulton and Sanchez, 2013).

Other Bacterial Diseases

Yersinia pseudotuberculosis *(Yersiniosis)*

Yersinia pseudotuberculosis (Yersiniosis) is a Gram-negative coccobacillus that causes severe enteritis, splenomegaly, hepatomegaly, and lung lesions in young turkeys. In chronic cases it is possible to observe caseous tubercle-like lesions in the liver, spleen, and lungs (Lister *et al.*, 2008).

Avibacterium paragallinarum

Avibacterium paragallinarum is a Gram-negative, non-spore-forming, capsulated rod-shaped bacterium that causes coryza in chickens. The lesions consist of catarrhal and fibrinopurulent inflammation of the nasal passages, infraorbital sinuses, and conjunctivae in old birds (Blackall, 1999).

Gallibacterium anatis

Gallibacterium anatis is a Gram-negative, rod-shaped, or pleomorphic bacterium that is a normal inhabitant of the upper respiratory tract and the lower genital tract. *Gallibacterium anatis* produces purulent salpingitis and oophoritis in chickens, turkeys, geese, ducks, pheasants, partridges, cage bird, and wild birds. In chronic cases purulent peritonitis may be found (Paudel *et al.*, 2013).

Bordetella avium

Bordetella avium is a Gram-negative, rod-shaped bacterium. *Bordetella avium* causes turkey coryza, which is an acute respiratory tract disease in young turkeys. Lesions consist of mucopurulent pneumonia and respiratory stress syndrome. *Bordetella avium* also infects young Muscovy ducks, quail chicks, and cockatiels (*Nymphicus hollandicus*) (Jackwood and Saif, 2013).

Erysipelothrix rhusiopathiae

Erysipelothrix rhusiopathiae is a Gram-positive, rod-shaped bacterium. There are 26 serovars of *E. rhusopathiae*, but only the serovars 1, 2, and 5 produce outbreaks. *Erysipelothrix rhusiopathiae* is found in pigs, rodents, fish, and birds, and rarely in sheep. In birds, *E. rhusopathiae* infects turkeys, chickens, ducks, geese, emus, pigeons, and game birds. Birds acutely affected show lesions indicative of septicemia, such as petechial hemorrhages in the myocardium, epicardium, gizzard serosa, mesentery, liver, and pleura. In chronic cases, there is vegetative endocarditis and fibrinopurulent arthritis (Bricker and Saif, 2013). *Erysipelothrix rhusiopathiae* in humans may cause erysipeloid (localized infection of the fingers and hands), generalized cutaneous infections and septicemias (Wang *et al.*, 2010).

Staphylococci, Streptococci, and enterococci

- Staphylococci consist of Gram-positive cocci belonging to the family Micrococcaceae and genus *Staphylococcus*. The genus includes 40 species, of which *Staphylococcus aureus* is the most important and common one in poultry. *Staphylococcus aureus* may cause septicemia, fibrinous arthritis and tenosinovitis, chondronecrosis, and osteomyelitis (also called femoral head necrosis) in chickens, turkeys, ducks, and geese (Andreasen, 2013).
- Streptococci and Enterococci of importance in poultry include *Streptococcus gallinaceus*, *S. gallolyticus*, *S. equi* subsp. *zooepidemicus*, *Enterococcus hirae*, *E. durans*, and *E. faecalis*. Lesions associated with infections by Streptococci and Enterococci consist of septicemia (common in chickens, ducks, and pigeons), caseous cellulitis (caused by *S. dysgalactia* in chickens and turkeys), encephalomalacia (associated with *E. durans* and *E. hirae*), vegetative endocarditis (caused by *E. hirae* in young birds and *E. faecalis* in older birds), and amyloid arthropathy (observed in chickens infected with *E. faecalis*) (Thayer and Waltman, 2013).

Fungal Diseases

Fungi are eukaryotes that nourish through absorption and can exist as single-celled or multicelled organisms. They are opportunistic pathogens of all species of birds and cause disease by tissue invasion or by means of the production of toxins (Dykstra *et al.*, 2013)

Aspergillosis (Brooder Pneumonia)

Species of *Aspergillus* associated with disease include the following: *Aspergillus fumigatus*, *A. flavus*, *A. niger*, *A. glaucus*, and *A. terreus*. *Aspergillus* species are soil saprophytes. Birds are infected by inhalation of conidia, which may germinate and produce granulomatous lesions in the respiratory tract and air sacs epithelium (**Figure 3**). Besides, conidia may invade the blood vessels and spread to other tissues, such as the brain, pericardium, bone marrow, kidneys, and other soft tissues. Keratoconjunctivitis or panophthalmitis can also be observed (Dykstra *et al.*, 2013).

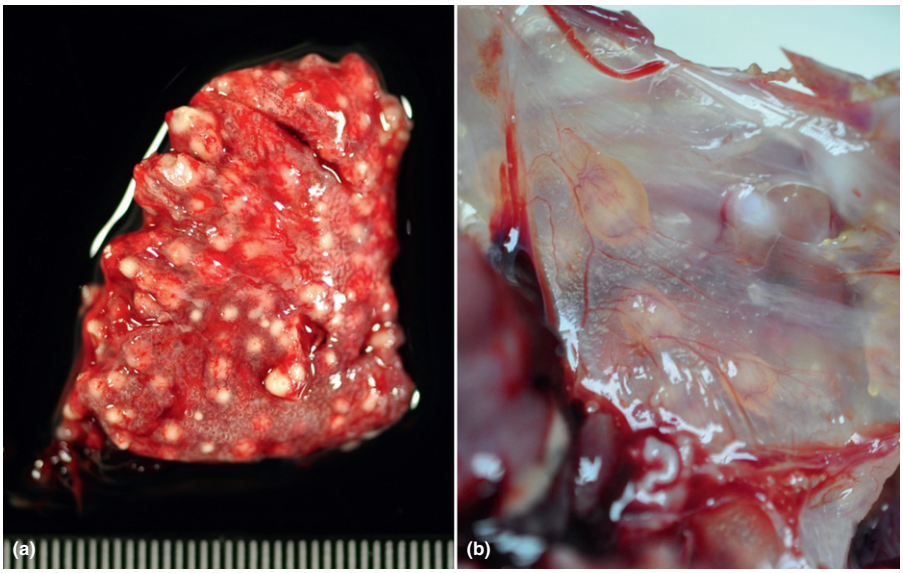


Figure 3 (a) Lung and air sacs. (b) Lung from naturally infected chickens showing numerous caseous nodules characteristic of respiratory asperigllosis. Photo (a) was provided by Natàlia Majó i Masferrer, SDPV (Servicio de Diagnóstico de Patología Veterinaria)-CReSA (Centre de Reserca en Sanitat Animal, Barcelona) and Photo (b) was provided by Alejandro Alfaro, Universidad Nacional de Costa Rica.

Other Fungal Diseases

Ochroconosis

Ochroconiosis (formely Dactylariosis) is a rare neurological disease of chickens and turkeys poults that is caused by *Ochroconis gallopava*.

Candidiasis (crop mycosis, thrush)

Candida albicans yeast produces pseudomembranes and diphtheric membranes in the oral cavity, esophagus, and crop of immunosuppressed birds. In rare cases, it is associated with neurological, renal and intestinal disease.

Favus (white comb, ringworn)

Favus is a skin disease caused by *Microsporum gallinae* (formely *Trichophyton gallinae*) that affects mainly the unfeathered skin (comb, wattle, and shanks) and occasionally the feathered skin (Dykstra *et al.*, 2013).

Mycotoxicosis

Mycotoxins are chemical by-products produced by fungi that are toxic to animals (mycotoxins) and/or to bacteria (antibiotics) or both. They are produced when the fungi invade the grain or feed, and there are adequate temperate, moisture, and grain substrate to growth. The most frequent mycotoxicosis in birds include the following: aflatoxicosis, ochratoxicosis, and tricothecene mycotoxicosis (Hoerr, 2013).

Aflatoxicosis

Aflatoxins are toxins produce by *Aspergillus flavus*, *A. parasiticus*, and *Penicillium puberulum*, which are found in corn, millet, sorghum, and other feed grains. Fungi growth is favored by warm and high humidity conditions. Aflatoxins consist of several mycotoxins (B1, B2, G1, and G2), of which the most toxic and usual one is Aflatoxin B1. This aflatoxin is biotransformed in a highly reactive metabolite that binds to the DNA and RNA, impairing the protein synthesis and immunity. Aflatoxins cause liver enlargement due to lipidosis and hyperplasia of the biliary ducts. Blood clotting factor synthesis and capillary stability are altered; as a result birds may show petechial hemorrhages or bruises.

Ochratoxicosis

Ochratoxin is a dihydroisocoumarin derivative produced mainly by *Aspergillus ochracues* and *Penicillium veridicatum*. Ochratoxin A is the most common and toxic one. Ochratoxin A inhibits proteins synthesis, producing anemia, immunosuppression, and decrease in egg production and hatchability. It also causes acute necrosis in the kidneys and visceral gout.

Trichothecene mycotoxicosis

Trichothecene mycotoxins are found in wheat, corn, and other grains contaminated with species of *Fusarium*, *Stachybotrys*, and other genera of fungi that prefer cold and moist conditions for growth. Trichothecene mycotoxins cause lesions through two mechanisms: direct epithelial necrosis or radiomimetic effects. For example, T-2 toxin and DAS cause necrosis of the epithelial cells of the commissures of the mouth, hard palate, the dorsal surface of the tongue, and rostral part of the oropharynx. Mycotoxins inducing radiomimetic effects inhibit the synthesis of proteins and reduce cellular life span and therefore affect the hematopoiesis, lymphopoiesis, immune response, and the replication of feather follicle epithelium and enterocytes (Hoerr, 2013).

Other Micotoxicosis

Fusarium *fungi – Moliniformin*

Moliniformin is produced by *Fusarium verticillioides* (formerly *F. moliniforme*) and other *Fusarium* spp. This toxin causes reduced performance and diarrhea. Experimentally, it induces acute myocardial necrosis, nephrosis, and death.

Fumonisins

Fumonisins are also produced by *Fusarium verticillioides* and cause catarrhal enteritis, liver necrosis, villous atrophy in the intestines, lymphoid depletion, and rickets.

Fusarochromanone (TDP-1)

TDP-1 is produced by *Fusarium* spp. and is related to leg deformities and tibial dyschondroplasia in chickens.

Oosporein

Oosporein is produced by *Chaetomium* spp and induces acute proximal tubular nephrosis and gout.

Ergotism

Ergotism is an acute disease caused by alkaloid toxins produced by *Claviseps* species, particularly *Claviseps purpurea*. Ergotism causes vascular, neurological, and endocrine disorders. Birds affected may show reduced growth and egg production, diarrhea, and necrosis as well as ulcers affecting the unfeathered skin of the comb, wattles, beak, and feet (Hoerr, 2013).

Parasitic Diseases

Coccidiosis

Coccidiosis is one of the most important diseases of poultry caused by parasites worldwide. Coccidia are intracellular protozoa parasites that belong to the phylum Apicomplexa. In poultry, most coccidia are classified within the genus *Eimeria*, which are highly host specific.

Chicken coccidiosis may be attributed to seven species of *Eimeria*, which are: *E. brunetti*, *E. necatrix*, *E. tenella*, *E. acervulina*, *E. maxima*, *E. mitis*, and *E. precox*. *Eimeria tenella* and *E. necatrix* are the most pathogenic species and are associated with necrohemorrhagic typhlitis. *Eimeria. acervulina* and *E. maxima* are the most prevalent ones and cause lesions in the small intestine. Turkeys are infected by coccidian of the following species: *E. adenoeides*, *E. meleagridis*, *E. gallopavonis*, and *E. meleagrimitis*. Intestinal coccidiosis can also be seen in geese, ducks, game birds, and pigeons. Infected birds may show diarrhea as a consequence of catarrhal to necrohemorrhagic enteritis. In general, infection with one species of *Eimeria* does not ensure protection against other species, neither does maternal antibodies; however, repetitive exposure to low numbers of oocyst does give protection (McDougald and Fitz-Coy, 2013).

Cryptosporidiosis

Cryptosporidia are apicomplexan protozoa parasites that affect mammals and birds. *Cryptosporidium baileyi* causes respiratory disease and *C. meleagridis* produces enteric infections. Cryptosporidia parasitize the margin of the epithelial cells, where it is enclosed by the cell membrane. Infection and disease have been reported in chickens, turkeys, ducks, pheasant, quail, peafowl, and other birds. In the respiratory form, cryptosporidia causes sinusitis, conjunctivitis, pneumonia, and airsacculitis. The enteric infection is associated with poor performance (McDougald, 2013a).

Histomoniasis (Blackhead)

Histomoniasis is an enterohepatitis caused by the protozoan *Histomonas meleagridis*. It is observed mainly in turkey poults but game birds, chickens, and guinea fowl may also be affected. Birds get infected after ingestion of eggs of the cecal nematode *Heterakis gallinarum* female parasites (intermediate host), which are transported by earthworms or remain alive in the soil (Armstrong and McDougald, 2011). *Histomonas meleagridis* causes ulcerative or hemorrhagic typhlitis and multifocal zones of necrosis in the liver. Liver lesions, which appear 10–12 days postinfection, are pathognomonic (Hess and McDougald, 2013).

Other Protozoa Parasites

Spironucleosis-Hexamitiasis

Spironucleus meleagridis causes slight catarrhal enteritis in turkey poults and young game birds.

Trichomonas gallinae

This pathogen produces necrotic and caseous lesions in the mouth, crop, and esophagus of pigeons and squabs and rarely in turkeys and chickens. Occasionally, there are systemic lesions involving the liver.

Leucocytozoonosis

Leucocytozoon spp. infects blood and tissue cells and is described in ducks and geese (*L. simondi*), turkeys (*L. smithi*), and chickens (*L. caulleryi, L sabrasezi*, and *L. choutedeni*). Within its life cycle, schizogony is found in the liver, lungs, heart, brain, and spleen, whereas gamonts are contained within blood cells. Infected birds show weakness, anemia, and mortality (Hess and McDougald, 2013).

Nematode Parasites

In birds there are a great number of nematode parasites; however, their prevalence in poultry birds is low, because half of them require an intermediate host. Therefore, they are more frequent in free-range, backyard, and wild birds. Most nematodes affect the gastrointestinal tract, such as *Capillaria*, which causes enteritis (*C. obsignata, C. annulata, etc.*), *Heterakis* (important in the life cycle of *Histomonas*), and Ascaridia (*Ascaridia galli* that affects performance in heavy infestations). In addition, there are nematodes that have affinity for the respiratory tract, such as *Syngamus trachea* and *Cyathostoma bronchialis*. The first one affects wild and domestic birds and causes blockage of the trachea, whereas *C. bronchialis* is a parasite of geese (McDougald, 2013b).

Cestodes and Trematodes

Cestodes and trematodes require intermediate hosts in their life cycles. Cestodes employ arthropods, whereas trematodes need molluscan. Therefore, their importance as pathogens of modern poultry production systems is insignificant. However, they are still relevant in free-range rearing, game, and wild birds, causing digestive and reproductive tract lesions (McDougald, 2013b).

Ectoparasites

Ectopasites of birds include species of lice, such as *Menacanthus stramineus*, *Cuclotogaster heterographa*, and *Menopon gallinae*, which feed on feathers and skin scales causing irritation.

Moreover, birds may be seriously infested by mites that cause anemia due to their blood-sucking habits. The most important mites in poultry are *Dermanyssus gallinae* (red mite) and *Ornothonyssus sylvarum*. *Dermanyssus gallinae* infects chickens and other species of birds.

Fleas may also cause irritation and blood loss. Fleas infest the host and persist in the environment; some of them, such as *Echidnophaga gallinacea*, can be attached to the host for months. Finally, ticks may cause poor food conversion, depressed egg output, and anemia (Hinkle and Corrigan, 2013).

Nutritional Disorders

Nutritional imbalances may arise from deficiency in the diet, destruction or inactivation during feed processing and manufacture, antagonism between nutrients, or impaired absorption and metabolism. Each of the 36 essential nutrients of poultry has specific functions that account for the distinctive diseases associated with its deficiency (summarized below). However, in the field, only rarely these changes are related to deficiency of one specific element (mineral, vitamins, etc.), making the clinical diagnosis a difficult task (Klasing, 2013).

Vitamin A (Retinol, Retinoic Acid, and Retinyl Ester)

Vitamin A is necessary to maintain the epithelial function and structure and also for a normal egg production. Consequently, its deficiency is related to epithelial and mucous metaplasia of the respiratory, intestinal, and urinary tracts. Pathognomonic hyperkeratotic lesions are observed in the cornea and the skin of the mouth and esophagus. The excess of this vitamin induces deficiency of vitamin E and D_3 (Klasing, 2013).

Vitamin D (Cholecalciferol-Vitamin D_3)

Vitamin D acts as a hormone to regulate calcium and phosphorus metabolism. Deficiency of vitamin D causes growth retardation, rachitic deformities, osteomalacia, osteoporosis, tibial dyschondroplasia, and egg abnormalities in layers. Excess of vitamin D is toxic, as a consequence of the deposition of calcium in several soft tissues (Klasing, 2013).

Vitamin E (α-Tocopherol)

Vitamin E is an antioxidant that has a major role in the protection of cellular membranes. Clinical conditions associated with its deficiency include the following: embryonic mortality in breeders, encephalomalacia, exudative diathesis, and nutritional muscular dystrophy in young birds (**Figure 4**). The security index of vitamin E is very high and therefore toxicity is improbable (Klasing, 2013).

Vitamin K (Vitamin K_3-Menadione)

Vitamin K participates in the formation of prothrombin and so in blood coagulation. It also contributes in calcium metabolism. Deficiency causes delayed blood clotting (Klasing, 2013).

Vitamin B_1 (Thiamin)

Vitamin B_1 participates in the metabolism of carbohydrates. Deficiency of this vitamin is rarely seen in the field, unless feed that contains thiaminase (such as fishmeal) or treatments with the anticoccidial amprolium have been used. Deficiency affects the overall performance (Klasing, 2013).

Vitamin B_2 (Riboflavin)

Riboflavin acts as coenzymes in several enzyme systems; many of them are related with oxidation–reduction reactions in the process of cellular respiration. Deficiency causes reduced egg production. Hatched chickens may be dwarfed, show depigmentation, and 'curled toe paralysis' due to the presence of degenerative changes in nerve trunks (Cai *et al.*, 2009).

Vitamin B_6 (Pyridoxine)

Vitamin B_6 participates in the metabolism of amino acids. As a consequence, there is no specific list of signs related to its



Figure 4 Pectoral muscles of a chicken affected with vitamin E and selenium deficiency, showing severe locally extensive areas of degeneration and necrosis, which is noted by the presence of light colored streaks of affected muscle. Photos provided by Natàlia Majó i Masferrer, SDPV (Servicio de Diagnóstico de Patología Veterinaria)-CReSA (Centre de Reserca en Sanitat Animal, Barcelona).

deficiency. Birds showing deficiency may have anemia, demyelinization, weakness, paresis, and chondrodysplasia (Klasing, 2013).

Niacin (Nicotinic Acid and Nicotinamide – Vitamin B_3)

Niacin is part of the coenzymes involved in metabolism of proteins, carbohydrates, and fats. Deficiency in birds causes poor growth, feather disorders, inflammation of the mucous membranes of the alimentary tract, nervous degeneration, and chondrodystrophy in young birds (Klasing, 2013).

Pantothenic Acid (Vitamin B_5)

Pantothenic acid is required to synthesize coenzyme A (CoA), which has a role in energy and fatty acid metabolism, citric acid cycle, neural function, antibody formation, and endocrine function (steroid hormones). Deficiency causes dermatitis, drop in egg production, embryo death, and stunted and weak chickens (Klasing, 2013).

Biotin (Vitamin H)

Biotin is necessary for the production of fatty acids, carbohydrates, and proteins; therefore, it is essential for growth, epidermal and tissue maintenance, bone development, and reproduction. Deficiency induces reduced growth and hatchability, deformed embryos, dermatitis (footpad, toes, and periocular), and beak deformities. Occasionally, there is chondrodystrophy and fatty liver and kidney syndrome (FLKS) in young broilers and layer pullets (Klasing, 2013).

Folic Acid (Folacin)

This vitamin acts as a coenzyme in the synthesis of specific amino acids (e.g., purines, choline, threonine, and histidine). Consequently, it is indispensable for nucleic acid synthesis and cell mitosis. Folic acid deficiency causes macrocytic megaloblastic anemia, defective feather development and pigmentation, chondrodystrophy, and cervical paralysis in young birds. Breeding birds show reduced hatchability and presence of embryo deformities (Klasing, 2013).

Vitamin B_{12}

Vitamin B_{12} is involved in metabolism of proteins, carbohydrates, and fats. Deficiency produces embryonic death and lowered hatchability. Chick embryos affected show malposition, myopathy, and chondrodystrophy (Klasing, 2013).

Choline

Choline is part of various phospholipids (e.g., lecitin) and is necessary to maintain the cell structure (especially of cartilage) and fat metabolism. Choline also participates in nerve transmission (forms the acetylcholine) and protein synthesis as methyl group donor. Deficiency causes reduced growth rate and hatchability, chondrodystrophy, and fatty liver (Klasing, 2013).

Calcium and Phosphorus

Calcium and phosphorus are part of body fluid electrolytes. Calcium participates in nerve cell excitation, neuromuscular transmission, muscular contraction, and blood clotting. Phosphate is necessary to maintain the acid–base balance and protein and carbohydrate metabolism. Calcium and phosphorus imbalance may cause rickets in growing birds and osteomalacia or osteoporosis in mature animals. Affected laying hens produce eggs with thin or soft shell and may show paralysis, fractures, and have skeletal deformities. However, excess of calcium causes nephropathy with renal fibrosis, atrophy, and visceral gout. An excess of phosphorus decreases the quality of the eggshell and increases bone fragility in layer birds (Klasing, 2013).

Sodium Chloride

Sodium chloride is a component of the intra- and extracellular fluids; as a result, it is important to maintain the acid–base and water balance as well as for transfer of metabolites across membranes and nerve impulse transmission. Birds fed with low levels of sodium show severe drop in egg production, pecking behavior, and cannibalism. An excess of sodium produces diarrhea, excessive thirst, progressive muscular weakness, convulsions, and death. Young birds show severe kidney damage with presence of visceral gout (Klasing, 2013).

Manganese

Manganese is necessary, along with magnesium, in the activation of several enzymatic systems and formation of DNA complex. Deficiency in young birds produces growth retardation and bone deformities (e.g., chondrodystrophy). Laying or breeding birds may show decreased egg production and hatchability, in addition to embryo mortality, ataxia, and tetanic spasms in newly hatched chicks (Klasing, 2013).

Zinc

Zinc participates in almost every metabolic function in the organism; therefore, its deficiency has a great impact on the development of the skeleton and in the reproductive system. Growing birds exhibit poor feathering and scaly skin, in addition to chondrodystrophy. Laying birds show decreased egg production and hatchability. Embryo mortality with presence of deformities is observed around mid-incubation (Klasing, 2013).

Selenium

Selenium forms part of the cell enzyme glutathione peroxidase and acts in accordance with vitamin E as antioxidants. Deficiency causes muscular dystrophy (**Figure 4**), exudative diathesis, and encephalomalacia (Klasing, 2013).

Toxicants

Toxicity is almost always determined by the dose, because it is possible to find cases of toxicoses related to the use of apparently innocuous substances, such as feed constituents or therapeutic agents. Many of these toxicoses cause unspecific clinical signs that could be confused with infectious and metabolic diseases. Diagnosis depends on the compilation of a

Table 1 List of diagnostic methods and sample selection for the most important – notifiable viral diseases of poultry

Methods of diagnosis for viral-origin poultry and avian diseases

Infectious agent	*Samples of choice*	*Serological techniques – Immune status*	*Etiological diagnosis – Antigen detection*
Avian influenza virus	● Live birds: oropharyngeal and cloacal swabs and serum ● Dead birds: feces, trachea, lung, air sacs, intestines, spleen, kidney, brain, liver, and heart	● AGID ● HA test and HI test ● ELISA	● Virus isolation in SPF embryonated chicken eggs ● AC-ELISA ● Immunofluorescence and immunohistochemistry ● RT-PCR and rRT-PCR techniques
Newcastle virus	● Live birds: oropharyngeal and cloacal swabs and serum ● Dead birds: oronasal swabs, lung, kidneys, intestines, cecal tonsils, spleen, brain, liver, and heart	● HA test and HI test ● ELISA	● Virus isolation in SPF embryonated fowl eggs ● RT-PCR and rRT-PCR techniques
Infectious bronchitis virus	● Live birds: oropharyngeal swabs and serum ● Dead birds: oropharyngeal swabs, trachea, lung, kidneys, and oviduct	● HA test and HI test ● AGID ● VN ● ELISA	● Virus isolation SPF embryonated chicken eggs ● TOC ● Immunofluorescence and immunohistochemistry ● RT-PCR ● RT-PCR-RFLP
Infectious Laryngotracheitis virus	● Live birds: tracheal, oropharyngeal or conjunctival swabs, and serum ● Dead birds: tracheal samples and mucosal scrapings	● AGID ● ELISA	● Virus isolation in SPF embryonated chicken eggs or cell cultures. ● Immunofluorescence ● Histopathology (Cowdry type A inclusions) ● PCR and PCR-RFLP
Poxvirus	● Cutaneous tissue samples or smears of the diphtheritic lesions and serum	● Passive HA test ● AGID ● VN ● ELISA	● Smears stained with Giménez method. ● Virus isolation in SPF embryonated chicken eggs or cell cultures. ● Histopathology (intracytoplasmatic inclusions – Bollinger bodies), Immunofluorescence and immunoperoxidase ● PCR-RFLP ● Immunoblotting or Western Blotting
Infectious bursal disease	● Live birds: serum ● Dead birds: bursa of Fabricius tissue samples	● AGID ● VN ● ELISA	● Virus isolation in specific antibody-negative chicken embryos or cell cultures Immunofluorescence ● AC-ELISA ● RT-PCR and RT-PCR-RFLP
Marek's disease	● Blood samples (Buffy coat cells), lymphoma and spleen tissue samples, and feather	● AGID ● ELISA	● Virus isolation in cell cultures. ● PCR ● Real time quantitative-PCR

Abbreviations: AGID, agar gel immunodiffusion; HA, hemagglutination; HI, hemagglutination inhibition; ELISA, enzyme-linked immunosorbent assay; SPF, specific pathogen free; AC, antigen capture; RT-PCR, reverse transcription polymerase chain reaction; rRT-PCR, real time RT-PCR technique; VN, virus neutralization; TOC, tracheal organ culture; and RT-PCR-RFLP, RT-PCR-restriction fragment length polymorphism.

Source: OIE, 2013a. Manual of diagnostic tests and vaccines for terrestrial animals: Avian influenza. In: Terrestrial Manual. International Standard Setting, seventh ed. World Organization for Animal Health, pp. 436–454 (Chapter 2.3.4) and OIE, 2013b. Chapter 2.3.4. Avian influenza. In: I. S. S. T. Manual (Ed.), World Organisation for Animal Health. Paris, France: World Organisation for Animal Health, Section 2.3 (Chapters: 2.3.1., 2.3.2., 2.3.3., 2.3.4., 2.3.5., 2.3.6., 2.3.9., 2.3.10., 2.3.11., 2.3.12., 2.3.13., 2.3.14).

good history, field visits, detection and recognition of the clinical sings, necropsy findings, and examination of the samples collected in specialized laboratories (Fulton, 2013).

Toxics Found in Feed and Water

Mycotoxins

Mycotoxins were reviewed in the section of fungal diseases.

Biogenic amines and plant toxins

Biogenic amines, such as gizzerosine, are derived from overheated fish meal. Gizzerosine causes gizzard erosion syndrome. An example of a plant toxin is found from the unselected strains of rapeseed that contains erucic acid, which causes anemia and cardiomyopathy.

Nutrient additives

Some examples of poisoning caused by an excess of vitamins and elements (such as iron, zinc, calcium, sodium, etc.) were briefly described in the section of nutritional disorders.

Coccidiostats and other therapeutic drugs

Toxic coccidiostats in poultry include polyether ionophores, such as monensin, lasalosid, salinomycin, narasin, and maduramicin. These ionophores are characterized by the induction of myonecrosis in the skeletal muscles and occasionally the myocardium.

Sulfonamides are used to treat several infectious diseases; however, their therapeutic indices are very narrow, making likely an overdose. Sulfonamides induce vitamin K deficiency and consequently produce anemia, multifocal hemorrhages, jaundice, and bone marrow depression (Fulton, 2013).

Table 2 List of diagnostic methods and sample selection for the most important notifiable bacterial diseases of poultry

Methods of diagnosis for bacterial-origin poultry and avian diseases

Infectious agent	*Samples of choice*	*Serological techniques – Immune status*	*Etiological diagnosis – Identification of the agent*
Fowl typhoid and pullorum disease: *Salmonella*	● Aseptically taken samples of tissues (spleen and liver), intestinal (cecal tonsil) or cloacal content, eggs, embryos, oviduct, fecal droppings and cloacal swabs, and hatcher debris	● Rapid whole blood plate or serum agglutination test	● Culture (MacConkey agar, xylose lysine, brilliant green agar, Rappaport–Vassiliadis soya, etc.) and biochemical test (API system for Enterobacteriaceae) ● PCR-RFLP
Fowl cholera: *Pasteurella*	● Bone marrow, lung, liver, spleen, gonads and heart blood, and caseous exudates	● Rarely used for diagnosis of Fowl cholera	● Culture (Blood agar, trypticase-soy agar, and dextrose starch agar) and biochemical test ● Somatic typing procedure using gel diffusion precipitin test ● REA
Chlamydiosis	● Live birds: pharyngeal and nasal swabs, intestinal excrements, and conjunctival scraping ● Dead birds: Inflammatory or fibrinous exudates (peritoneal or in organs); ocular and nasal exudates; impression smear of the liver; whole blood; and tissue samples of the kidney, lung, pericardium, spleen, liver, and colon contents or excrements	● ELISA, AGID ● CF test, modified direct CF test, latex agglutination, and elementary body agglutination	● Isolation in embryonated chicken eggs or cell culture ● Cytochemical staining of smears or immunohistochesmistry ● Conventional and real-time PCR, restriction length polymorphism, DNA microarray, and sequencing
Mycoplasma	● Live birds: choanal cleft, oropharynx, eyes cloaca, and phallus swabs ● Dead birds: nasal cavity, infraorbital sinus, trachea, air sacs, esophagus, joint cavities, and material of egg yolk or embryos	● RSA test ● ELISA ● HI test	● Culture in specific media ● Basic biochemical test (i.e., fermentation of glucose and failure to hydrolyze arginine) ● Immunofluorescent antibodies and immunoperoxidase test
Tuberculosis	● Liver or spleen tissue samples and bone marrow	● Tuberculin test ● Blood stained-antigen agglutination test	● Detection of acid-fast bacilli in smears or tissue sections from affected organs ● Culture (Lowenstein–Jensen, Herrol'd medium and other media) ● Typing methods: ELISA and HPLC ● PCR, multiplex-PCR, and PCR-RFLP

Abbreviations: AGID, agar gel immunodiffusion; API, analytical profile index; CF, complement fixation; ELISA, enzyme-linked immunosorbent assay; HI, hemagglutination inhibition; HPLC, high-performance liquid chromatography; PCR, polymerase chain reaction; PCR-RFLP, PCR-restriction fragment length polymorphism; REA, restriction endonuclease analysis; and RSA, rapid serum agglutination.

Source: OIE, 2013a. Manual of diagnostic tests and vaccines for terrestrial animals: Avian influenza. In: Terrestrial Manual. International Standard Setting, seventh ed. World Organization for Animal Health, pp. 436–454 (Chapter 2.3.4) and OIE, 2013b. Chapter 2.3.4. Avian influenza. In: I. S. S. T. Manual (Ed.), World Organisation for Animal Health. Paris, France: World Organisation for Animal Health, Section 2.3 (Chapters: 2.3.1., 2.3.2., 2.3.3., 2.3.4., 2.3.5., 2.3.6., 2.3.9., 2.3.10., 2.3.11., 2.3.12., 2.3.13., 2.3.14).

Pesticide Toxicoses

Insecticides

Chlorinated hydrocarbon insecticides, such as DDT, chlrodane, heptachlor epoxide, etc., are not found in farms nowadays as they are banned due to their prolong persistence, high toxicity, and carcinogenicity in animals and humans. Organophosphorus (OPs) insecticides have a cholinesterase-inhibiting action and some of them are specifically toxic to birds. OPs compounds, such as diazinon, fenthion, and parathion, cause locomotor and respiratory muscular weakness, dyspnea, and paralysis. Carbamate anticholinesterase insecticides (bofuran, methomyl, and bendiocarb) produce similar clinical signs to the OPs, but it is more acute with marked tremors and convulsions. Finally, another insecticide widely used is the pyrethroid (permethrin, cypermethrin, and deltamethrin); however, they are very secure and only rarely cause toxicity. Clinical signs of hyperactivity, tremor, and salivation are observed in the affected birds.

Rodenticides

Rodenticides used in poultry buildings comprise first-generation anticoagulants and the most widely used second-generation anticoagulants as well as other less commonly used rodenticides (sodium strychnine, cholecalciferol, zinc phosphide, and sodium fluoroacetate). First-generation anticoagulants include warfarin, coumatetralyl, chlorphacinone, and diphacinone that can induce a subacute hemorrhagic syndrome in birds, whereas second-generation anticoagulants (brodifacoum, bromadiolone, difenacoum, difethialone, and flocoumafen) are highly toxic and are related to mortality in raptors and owls.

Toxicoses from the air or litter

Ammonia toxicity is common in poultry exposed to wet litter. Ammonia causes poor food conversion and eye and lung lesions. However, an example of air pollutant that causes toxicoses in birds is carbon monoxide, which induces ataxia and dyspnea and bright red blood (Fulton, 2013).

Diagnosis

Each laboratory test has been developed to accomplish an objective, which may be to confirm or exclude a presumptive clinical diagnosis, to perform an epidemiological study, to certificate a health status, or to monitor responses to vaccination. All pathogens have their mechanism of induction of lesions and disease; therefore, this knowledge is valuable to adequately select which samples have to be chosen and which diagnostic methods can give you better information to your purposes. In this section were summarized the diagnostic methods used to diagnose all notifiable diseases of poultry (Tables 1 and 2).

See also: Animal Health: Global Antibiotic Issues. Animal Health: Mycotoxins. Climate Change: Animal Systems. Marek's Disease and Differential Diagnosis with Other Tumor Viral Diseases of Poultry. Organic Livestock Production. Vaccines and Vaccination Practices: Key to Sustainable Animal Production

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Precision Agriculture: Irrigation

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Glossary

Conservation Reserve Program Land conservation program administered by the Farm Service Agency, whereby participating farmers receive a yearly payment to remove environmentally sensitive land from agricultural production and plant species that will improve the health and quality of the soil.
Deficit irrigation Applying (meeting) less than full crop evapotranspiration requirements.
Irrigation scheduling A scientific method of determining when to irrigate and how much water to apply.
Low elevation spray application An irrigation technique in which the spray plate is 30–60 cm above the soil surface.
Low energy precision application An irrigation method in which the spray plate hangs near the ground, or a canvas sock is attached to the end of a drop hose. Water flows through openings in the sock as it drags along the ground.
Prescription maps Instructions or coding to direct variable rate irrigation sprinkler systems as to where and how much to irrigate.
Remote sensing In agriculture, the noncontact sensing of plant canopy or soil to acquire information.
Thermography Thermal images produced by cameras that detect radiation in the infrared region of the electromagnetic spectrum. In agricultural applications, digital thermal images have been used to map crop water stress and phenotyping.
Variable rate irrigation Applying different rates of irrigation in different locations throughout a particular field.
Wheat streak mosaic virus A virus that is vectored by curl mite. Extensive infections have been experienced within wheat fields across the Central Great Plains region.

Introduction

The High Plains region of the North American Great Plains includes portions of Texas, New Mexico, Colorado, Oklahoma, Kansas, Nebraska, and Wyoming. In most of the region, the primary cropping system is a corn/wheat rotation, and because of irrigation from the Ogallala Aquifer and high solar radiation, this is one of the most agriculturally productive regions in the United States. Total corn acreage in the High Plains area that overlays the Ogallala Aquifer is approximately 14.3 million acres (5.67 ha), and 2.4 million acres (1 millon ha) of irrigated winter wheat are planted in this region each year (USDA and NASS, 2008). Much of this wheat is dual purpose, i.e., planted as winter forage for livestock as well as for grain production if winter and spring precipitation are adequate. Although the economics of this corn/cattle/wheat agricultural production system are dominated by the cattle component, the sustainability of the system is dependent on the cropping component, which with corn in the mix is dependent on irrigation in the semiarid High Plains environment. However, the economic sustainability of irrigated crop production in the High Plains is increasingly at risk. Widespread adoption of irrigation, high pumping rates, and limited recharge have resulted in a precipitous decline in the Ogallala Aquifer's water table. Furthermore, increased temperatures and drought, associated with climate change, only exacerbate these problems; hence, the sustainability of crop production in the High Plains, as currently practiced, is clearly at risk. This decline in crop production affects not only those who farm the land but also those living in rural communities that are economically dependent on agriculture-related economic activity (Almas *et al.*, 2004). The overarching challenge for High Plain's agriculture is to maintain economically viable crop productivity, in the presence of increasing abiotic and biotic stresses, with a continually decreasing amount of water.

In the High Plains, the major stabilizing force against drought has been, since the Dust Bowl of the 1930s, the advent of irrigation. Almost all irrigation in the High Plains is from the Ogallala Aquifer, and development of irrigation in this region significantly increased beginning in the 1950s and continued until the early 1970s when fuel prices caused a decline in irrigation. In an attempt to reduce the inherent risks associated with agriculture, farmers have developed and implemented practices to improve efficiency and productivity, and one of the most successful of these has been irrigation. Irrigation allows farming in environments that would not otherwise support crop production. Typically, irrigation results in significantly greater yields than nonirrigated crops and substantially reduces the overall risk of production agriculture. Over most of its area, however, the Ogallala is essentially a closed system with minimal recharge. The dramatic increase in water extraction for crop irrigation resulted in a significant decline in the water table; in some areas it was up to 50% reduction in saturated thickness (Colaizzi *et al.*, 2008).

In addition, with irrigated agriculture comes a new set of issues and potential challenges, including preservation of the water resource, abundance, and quality; high initial costs of advanced irrigation systems; application method, amount, and scheduling; nutrient management; and erosion control and disease management. Over the years, depletion of the aquifer has spurred development of better irrigation application technologies and a variety of methods to improve crop water use efficiency (WUE = economic yield per unit of water used by the crop) (Stewart *et al.*, 2010), including precision irrigation equipment and management methods. The focus of this article

is on precision irrigation strategies that have been implemented and others that are currently in development.

Need and Benefits of Precision Irrigation Management

Although precision agriculture as a collection of technologies aims to control a number of inputs for optimal farm productivity, precision irrigation management is a subset of this technology that focuses on site-specific delivery of required amounts of irrigation water to specified management zones within a field. Site-specific delivery infers spatial control of irrigation water, whereas required amounts refer to volumetric control of irrigation water. The main objective of precision irrigation management focuses on maximizing the benefit-to-cost ratio of irrigation. This includes goals of improving crop yield, crop quality, and water use efficiency by applying the appropriate amount of water when and where needed. By achieving these goals, precision irrigation management can help to reduce excessive irrigation, resulting in adverse environmental impacts from runoff or deep percolation, and address water resource sustainability at the farm and regional levels.

Not only is excessive irrigation wasteful and expensive, but it can also reduce soil aeration and provide a favorable habitat for soilborne pathogens, which may increase crop vulnerability to disease (Allmaras *et al.*, 1988; Carter and Johnston, 1989). Soils with high matric potential (wetter soils) are usually more conducive to the growth, reproduction, and spread of soilborne pathogens (Cook and Duniway, 1981; Cook and Papendick, 1970; Duniway, 1979). Some soilborne pathogens, and the diseases they cause, are favored by lower soil matric potential (drier soils) and associated plant water stress, for example, *Macrophomina phaseolina* and *Fusarium* spp., which cause root and stem rots in a number of crop species. For these reasons, root diseases are often the major biological constraint to profitable crop production in irrigated agricultural systems, even those in extremely arid environments. Thus, if a grower's standard irrigation practices are responsible for increased losses from diseases, then the potential exists to reduce losses by modifying those irrigation practices so as to neither under- nor overirrigate.

Excessive irrigation can also reduce yields by leaching nitrogen past the root zone, thereby increasing crop vulnerability to weed pressure. However, water deficits can retard plant development, reduce crop quality and yield, or even cause complete crop failure. Applying only the amount of water that a crop actually needs helps to alleviate problems associated with over- or underirrigation. Water requirements for healthy crops are dependent on climatological factors, crop species, soil texture, and developmental stage. To further complicate irrigation management, diseased plants or those infested with pests may show limited water or nutrient uptake, due to root or foliar damage. Therefore, in order to maximize its potential, precision irrigation must include decision support for determining the incidence and severity of diseased or pest-infested areas within a field, the estimated value of decreased yield potential (based on quantity and quality), and whether to continue or withhold irrigation.

Precision irrigation practices are still evolving, but these irrigation systems rely on the integration of scientific principles and methods, plant and soil water sensors, and mechatronics to address within-field variability. The term mechatronics was coined by an engineer from the Yaskawa company to describe the integration of power, electronics, and mechanical systems – using hardware, software, and network systems – for control or automation (Acar, 2010). The framework for precision irrigation management is a systems approach that uses mechatronics for precision irrigation delivery with the objective to optimize crop productivity or yield per unit of irrigation water applied (**Figure 1**). A primary challenge is to adapt decision support to variable crop needs in the field, over space and time.

Spatial and Temporal Variability

In addition to inherent physical variations in soil type, slope, aspect, and elevation, abiotic and biotic stresses may be responsible for heterogeneity of crop status across agricultural fields. Examples of abiotic stresses include nutrient deficiencies, water stress, extreme temperatures, high winds, hail, and chemical damage. Biotic stresses are negative influences caused by other living organisms, and in production agriculture they typically refer to damage caused by insects, plant parasitic nematodes, disease, or weeds. In addition to being spatially variable, trends (progression of spread) and severity, or infestation levels in the case of biotic stresses, these stressors can vary over time and impact irrigation management decisions, for example, whether to irrigate, when to irrigate, or how much to irrigate. The ability to identify and analyze these stresses in crops is prerequisite to effective precision irrigation. Sensors and sensor network systems are used to detect spatial and temporal variability of plant and soil properties related to stress, and decision support algorithms are developed to determine the type of stress (disease or insect damage, too much or too little soil water, presence or absence of nutrient deficiency, which nutrient, and so on and so forth).

Spatial statistics can be used to augment information from sensors and predict patterns that manifest themselves in spatial variability. Methods for predicting a pattern at nonmeasured points using known values at neighboring points can generally be described as kriging (Matheron, 1963) or other interpolation methods. Kriging methods use semivariance statistics derived from a spatially related dataset of measured values in a field to interpolate a value for an unmeasured point based on the statistics and measured values of points surrounding the unmeasured point. Confidence intervals for the value at the unmeasured point(s) can also be derived with this method. Kriging has been used to map an integrated crop water stress index (CWSI) in a variably irrigated field (O'Shaughnessy *et al.*, 2011), which can lead to mapping potential yield based on crop stress indices.

Other models or datasets that have been developed to address variability within a field that could be applicable to decision support for precision irrigation include the model developed by Starr (2005) to scale the variance of soil water content measurements over space at any given time for

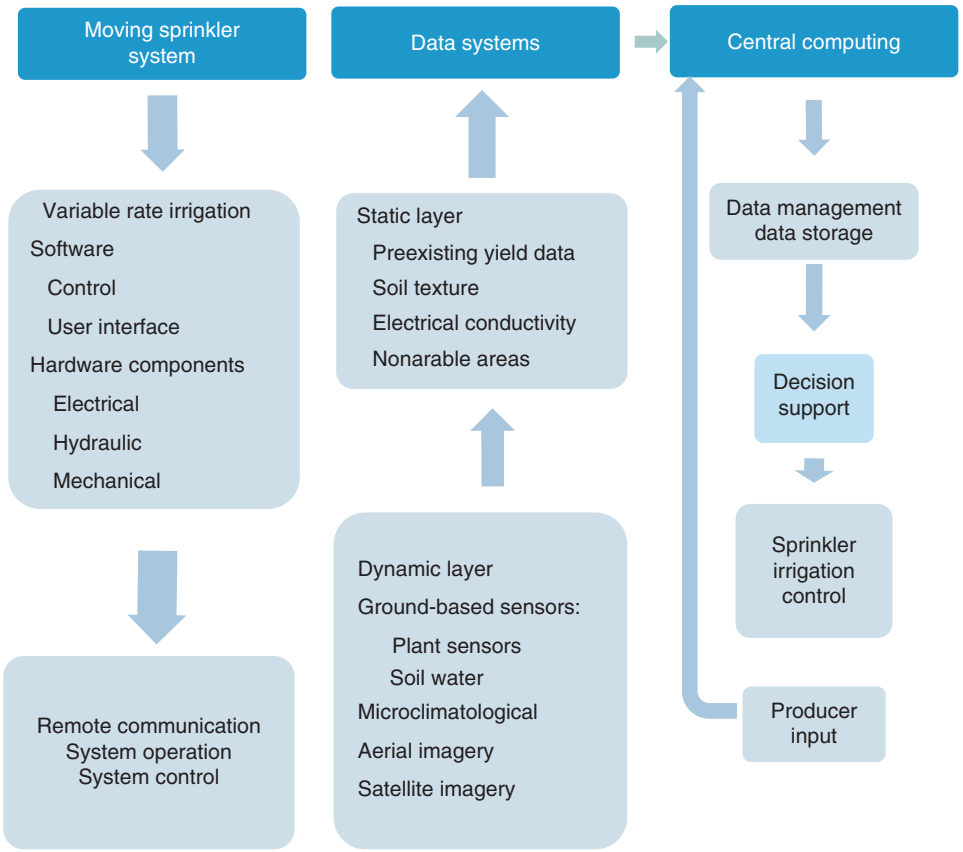


Figure 1 Overview of technology integration for precision irrigation management.

different points within a field and direct site-specific irrigation of potatoes. Also, mapping historical crop yields can offer insight into variability that is not obvious. Blackmore *et al.* (2003) developed trend maps to evaluate crop yields at the 'same point' over a number of years. This type of evaluation requires adjusting for year-to-year differences in climatic conditions. Machado *et al.* (2002) used biomass measurements (plant height and weight) to formulate irrigation scheduling for corn and predict yields. Workneh *et al.* (2009) formulated a structural time series model as a state space model to predict yield values as a function of disease intensity.

Identifying and monitoring spatial and temporal changes within a field is critical to executing precision irrigation. Initially, spatial variation within a field is used to configure boundaries for management zones and establish the configuration of irrigation zones. Over time, the detection or prediction of abiotic and biotic stresses within these management zones can allow decision making related to precision irrigation management throughout the growing season. The prediction of variability in time and space can be useful when monitoring crops by sensor network systems, but these can be limited by the number of available sensors (spatial limitation), such as soil water sensors. Similarly, there may be temporal limitations, as in the example of a moving sensor network system of infrared thermometers or passive spectral radiometers, whose useful measurements are made only during the daylight hours.

Physical Within-Field Variability

The optimal field for agricultural production has minimal slope, variation in soil type, and drainage requirements. Irrigation systems should be properly designed for the inherent topography of the field, soil and crop characteristics, and quantity and quality of the water supply. However, a number of physical variations usually exist within agricultural fields. These variations range from differences in soil texture, salinity, pH level, and topography to natural nonarable land attributes, such as roads, pump houses, waterways, and rock outcroppings (**Figure 2**). Differences in soil texture, restrictive layers, and depth can affect rooting and plant soil water extraction. Soil properties and water-holding capacities have been strongly associated with yield differences for crops (sorghum (Tolk and Howell, 2008); corn (Tolk *et al.*, 1999); wheat (Lawes *et al.*, 2009); soybean (Cox *et al.*, 2003); cotton (Ping *et al.*, 2008); and sugarcane (Johnson and Richard, 2005)). Precision irrigation systems can utilize georeferenced data and be programed to apply customized amounts of irrigation based on differences in soil texture or topography (e.g., Sadler *et al.*, 2005).

However, precision irrigation systems can be used to avoid irrigation of nonarable land areas in order to preserve structures, maintain access, or comply with environmental regulations. An example is irrigation application for animal production systems (e.g., dairies or hog farms) where the sprinkler system is used to apply liquid animal waste.

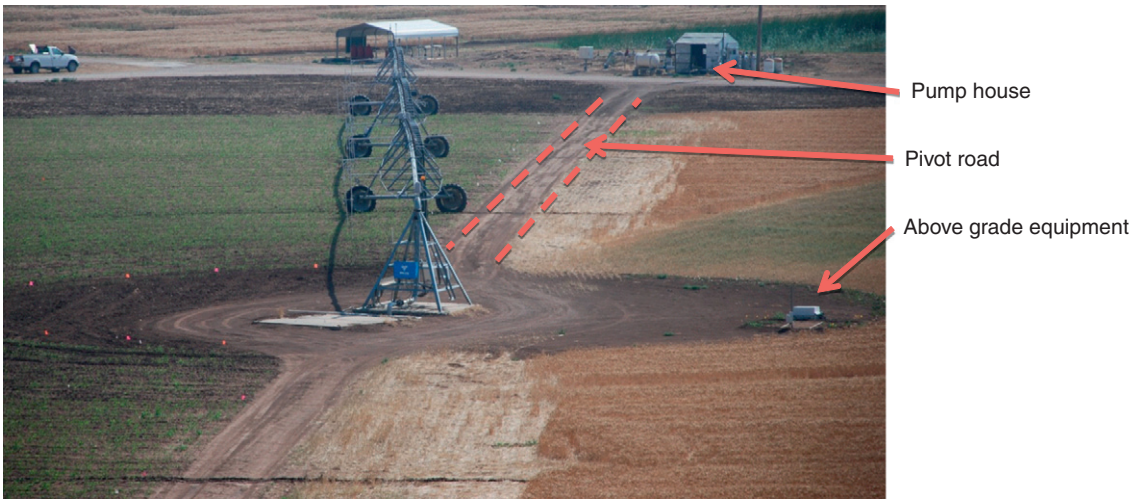


Figure 2 Center pivot field/examples of areas to avoid irrigating include pivot road, pump house, and above-grade equipment.

Precision irrigation systems can be used to insure compliance with setbacks from wells, surface water impoundments, or to avoid areas that are prone to nitrate leaching (Kranz *et al.*, 2012).

Other types of within-field variability may occur because of long-term agricultural practices, short-term farming mishaps (equipment failure causing overfertilization, overapplication of herbicide, chemigation spills, or over- or underseeding), or poor irrigation system design or maintenance (e.g., nozzle sizing and nozzle plugging). These latter types of imposed variations must be addressed first by changing farming practices, using proper engineering design, and performing ordinary maintenance. Precision irrigation management technologies cannot overcome extreme physical irregularities. Yet, this advanced technology could help to mitigate irregularities by maximizing water infiltration, reducing overwatering and deep percolation (leaching nutrients below the root zone), and minimizing runoff and run-on (Sadler *et al.*, 2000, 2002).

Prescription maps to address physical variations within a field are typically derived from soil surveys, electrical conductivity surveys (Lesch *et al.*, 2005), remote sensing images, historical yield maps, and as-built plot plans. These instructions are uploaded into the computer control panel of the irrigation system at the start of the irrigation season. These maps typically remain static throughout the cropping season. Although software is available to allow a producer to manually change the irrigation rates, the task can be time consuming and overwhelming for a novice user.

Implementation of Deficit Irrigation Schemes and Risk Management

As quality water resources for irrigation become scarcer, efficient use of water for maximum economic return and agricultural sustainability become more critical. Irrigation management strategies that are used to cope with declining and nonrenewable groundwater resources include deficit irrigation (DI) schemes. Precision irrigation management is a tool to implement these practices. DI, i.e., applying less than full crop evapotranspiration (ET) requirements, can be implemented by applying a percent of crop ET demands throughout the irrigation season. This scheme requires the estimation of crop ET, which is crop, soil (Tolk *et al.*, 1999; Tolk and Howell, 2012), and climate specific and is discussed in more detail later in this article. The second method of DI management is managed DI (MDI), which involves varying water application amounts according to critical growth stages (Doorenbos *et al.*, 1979). The goal in both DI and MDI is to maximize crop water use efficiency. DI practices have demonstrated sustained yields at levels that are economically feasible while reducing water use in many crops (Payero *et al.*, 2009). However, it is typical for farmers to use the 'conserved' water on other acreage.

The execution of DI implies knowledge of actual crop ET (ET_c), crop responses to the timing and severity of water deficits, and the economic impacts of yield reduction strategies (Pereira *et al.*, 2002). The key to DI management is to provide the appropriate amount of water to the crop to minimize damaging effects from crop water stress. Signs of crop stress include leaf wilt, scorched leaves, leaf senescence, abscission, pollination failure, and shoot and growth inhibition. Visual observations of water stress may come too late for the crop to help detect crop water stress or biophysical changes that signal advancement in crop growth stage. However, sensors can be instrumental in early detection of plant stress and in directing precision irrigation management.

If precision irrigation management is used to schedule DI yet avoid uneconomic reduction in yield quantity or quality, the system requires that crop stress and growth stage be assessed continuously throughout the growing season to avoid temporary severe crop stress that leads to uneconomic yields. Visual signs of crop water stress are specific to the crop species but in general can include leaf wilting, curling or burn, decrease in hue or brightness of crop canopy, retarded development, limited pollination, and reduced grain fill. In case of MDI, sufficient irrigation is applied at or just before critical growth stages (e.g., emergence to establish plant stand, at the onset of the reproductive stage through anthesis, and at grain fill). Sensors to help detect crop water stress or biophysical

changes that signal advancement in crop growth stage can be instrumental in directing precision irrigation management.

Methodology of Precision Irrigation

Fundamentals of Irrigation Scheduling

Precision irrigation management requires scientific irrigation scheduling to determine when, where, and how much to irrigate. Three main methods for scientific irrigation scheduling are: (1) weather-based crop ET (ET_c) calculations; (2) monitoring soil water status; and (3) monitoring plant canopy status. Algorithms that have been used to determine when to irrigate are numerous but are primarily based on the assessment of an established threshold; once the threshold is exceeded irrigation is triggered. Thresholds have been established for soil water depletion levels in the root zone or as thermal-based stress indices, such as the theoretical (Jackson *et al.*, 1981) and empirical (Idso *et al.*, 1981) CWSI, the Water Deficit Index (Moran *et al.*, 1994), and the Biologically Identified Optimal Temperature Interactive Console (BIOTIC, Patent No. 5 539 637 (Upchurch *et al.*, 1996) otherwise known as the time–temperature threshold method.

For healthy crops, the basic goal behind calculating the appropriate amount of irrigation to deliver, using precision irrigation management, is to meet deficiencies in crop water availability caused by shortages in precipitation and exacerbated by inadequate soil moisture storage capacities (Cuenca, 1989) for each management zone. Precipitation can be measured accurately with an electronic rain gage placed in close proximity to a specific field and measurements autologged and stored for retrieval by the irrigation controller. However, determining soil water content or energy potential properties that are representative of an entire field is challenging. Nonetheless, *in situ* soil water sensing and measurement (e.g., with neutron probe, tensiometers, capacitance, gravimetric core samples, moisture blocks, and time domain reflectometry (TDR)) have been used pervasively to decide when to irrigate (Evett, 2007). Some of these methods require manual measurements (neutron probe, gravimetric sampling, some capacitance, and TDR systems), which can be cumbersome, whereas other soil sensor systems, particularly those based on capacitance, can be sensitive to changes in temperature and bulk electrical conductivity (Evett *et al.*, 2012; Evett *et al.*, 2006; Schwartz and Evett, 2011), which are highly variable in time and space for many soils (Evett, 2007).

The most prevalent scientific method used to determine how much water a crop needs is based on estimations of crop water use or ET. If weather data are available (wind speed, air temperature, solar radiation, and humidity), reference ET (ET_0) can be calculated on a daily basis using the standardized American Society of Civil Engineering-Environmental and Water Resources Institute Penman–Monteith equation (Allen *et al.*, 2005). Crop water use is estimated as the product of ET_0 and the appropriate crop coefficient (K_c) (Allen *et al.*, 1998). Crop coefficients are species, region, and growth stage dependent. For a precision irrigation management system, the base station computer can collect microclimatological data from a nearby weather station and calculate ET_0 and ET_c using a predefined table of K_c values (as a function of growing degree days (Wang, 1960) or by relating K_c to normalized difference vegetative index (NDVI) values). ET estimates can also be derived from satellite- or aircraft-based imaging systems (with a thermal band) using surface energy balance algorithms, such as the two-source model (Norman *et al.*, 1995), surface energy balance models (Kustas *et al.*, 1994; Bastiaanssen, 1995), METRIC (Allen *et al.*, 2007), and RESET (Elhaddad and Garcia, 2011).

Soil water balance simulation models can be used to predict soil water content and therefore the amount of irrigation to apply. They range from simple models, such as a soil water budgeting process of irrigation scheduling (Fox *et al.*, 1993; KANSCHED, Rogers, 2009), to more complicated energy and water balance models, such as ENWATBAL (Van Bavel and Lascano, 1993; Evett and Lascano, 1993).

Soil water sensors or soil water balance models can be used in conjunction with the management allowable depletion method to schedule irrigation. This method uses the fundamental parameters of field capacity (fc) and permanent wilting point (pwp) properties, which are dependent on soil texture and bulk density, to develop a threshold for determining not only when to irrigate but also how much water to apply. An acceptable depletion level in the crop's root zone is established and then the percent depletion (%Depletion) is calculated on a daily basis:

$$\%\text{Depletion} = \frac{\theta_{fc} - \theta v}{\theta_{fc} - \theta_{pwp}} \times 100\%$$

where θ_{fc} is the soil water content at field capacity, θ_v is the current volumetric soil water content, and θ_{pwp} is the soil water content at the permanent wilting point (all in $m^3\ m^{-3}$). When the established threshold of percent depletion is reached, irrigation is signaled and the amount of irrigation is calculated as replenishment of soil water depletion to field capacity or to a percentage of field capacity (i.e., more or less than field capacity as indicated by factors, such as drainage rate and rate of soil water extraction by the crop). The base station computer of the precision irrigation system can manage daily calculations and provide decision support. Work by Thompson *et al.* (2007) illustrated a parallel method for irrigation scheduling and demonstrated how rates of soil water content changes measured by soil water sensors could be used to monitor an established lower limit of soil water change for irrigation management.

Precision irrigation management should establish fundamental methods for irrigation scheduling and then use sensor systems to refine irrigation scheduling and decision support. In addition to irrigation needs, decision support should inform the producer or irrigation manager about the health status of the crop, the growth stage, and if diseased, the severity level of the disease. Sensor systems and decision support are addressed in more detail in subsequent sections.

Irrigation Delivery

Field boundaries

To put site-specific irrigation management into practice, a field must be divided into geospatially defined areas or

management zones. Perhaps Vrindts *et al.* (2005) defined it best, "a management zone in a field expresses a subregion within a field that has a relatively homogeneous combination of yield-limiting factors, for which a single rate of a specific crop input is appropriate." Management zones delineated in a field are defined by geospatial coordinates, in addition to the attribute of interest. The basis for the boundaries of management zones within a field, as discussed previously, can be nonarable physical attributes, soil and topographical properties, historical crop yield data, etc. or a combination of datasets. For example, Schepers *et al.* (2004) used spatial data layers of bare soil brightness, elevation, soil bulk electrical conductivity, and crop yield data to characterize spatial variation in soil chemical properties and grain yield patterns.

Irrigation zones

The size of an irrigation zone may be limited by the design and flexibility of the irrigation system. The flexibility and resolution of a precision irrigation system are defined by the number of zones capable of being controlled and the width of those zones (O'Shaughnessy *et al.*, 2013). For moving irrigation systems, the minimum width of a management zone is determined by the number of drops or nozzles within an individually controlled set (e.g., under the control of a single solenoid valve), whereas the length could be determined by the pattern of variability in the direction of the traveling sprinkler or the length of the zone in the case of subsurface drip irrigation. For sprinkler irrigation systems, precise applications depend on wind speed and on the overlap from the wetted sprinkler patterns between management zones irrigating at different rates along the sprinkler lateral and in the direction of sprinkler movement when irrigation rates change. Low energy precision application (LEPA) drag socks (Lyle and Bordovsky, 1983; **Figure 3(a)**) offer perhaps the best method for precise irrigation application, followed by low elevation spray application (LESA) (**Figure 3(b)**).

In case of moving irrigation systems, variable rates of water can be applied by either speed or nozzle set control. By increasing the speed of a moving sprinkler irrigation system over a specific area, less water is applied; by decreasing the speed over the same area, more water is applied. Speed control is limited in that it only allows application rates to be varied in the direction of sprinkler travel but not along the sprinkler lateral. Nozzle set control, however, affords variable water application rates in both the direction of sprinkler travel and along the lateral pipeline. The benefit of speed control alone is that a limited amount of additional hardware is required for implementation. However, the limitation is the inflexibility to address variability along the length of the sprinkler lateral.

Irrigation machinery

The first commercially available mechanized irrigation systems were introduced in the United States in 1954 by Frank Zybach and A.E. Trowbridge (Morgan, 1993). After purchasing the marketing rights, Valley Industries revised the design and put the center pivot sprinkler irrigation system on the market. Since then, other manufacturers, such as Zimmatic, Reinke, and T-L Irrigation, have developed self-propelled sprinkler irrigation systems, either center pivots (a lateral with one end anchored) or linear move systems (unanchored lateral moves). Traditionally, these systems were designed to apply water uniformly across a field while delivering a specific application depth.

In the 1990s, several research groups (Washington State University, University of Georgia-Tifton Campus, University of Idaho, and USDA-ARS locations in Ft. Collins, CO, Sidney, MT, and Florence, SC) developed variable rate irrigation (VRI) equipment to manage irrigation spatially (Sadler *et al.*, 2005). Related efforts occurred at the USDA-ARS location in Bushland, TX (drip irrigation zone control, Evett *et al.*, 1996), which was controlled using plant status feedback based on IR thermometry, and at the Texas A&M AgriLife research location at Halfway, TX (center pivot speed and sprinkler set control, Bordovsky *et al.*, 1992). The first commercially marketed VRI package was jointly developed by the University of Georgia, and FarmScan (Hobbs and Holder, LLC) (LaRue, 2011). Key components for these new systems included: (1) hardware and software integration for mechanized control, (2) the incorporation of a global positioning system (GPS) receiver for navigation or spatial control, and (3) a programmable logic



(a) (b)

Figure 3 (a) Double open-ended low energy precision application (LEPA) drag socks located in alternating furrows in cotton planted in concentric rows and (b) Low elevation spray application (LESA) applied with a lateral move.

controller to operate and synchronize the pulsing of the sprinkler banks. Research work by Evans *et al.* (1995), McCann *et al.* (1997), Dukes and Perry (2006), Sadler *et al.* (1996, 2000), and King *et al.* (1995) sought to work through the complexities of integrating hardware into the existing moving irrigation systems. The objective was to deliver variable rates of irrigation along the sprinkler lateral and in the direction of sprinkler movement.

The following description covers only VRI systems for moving sprinkler systems. Computer hardware and software systems enable the overall control of the irrigation delivery hardware. VRI systems must have a control panel, consisting of a computer module that is capable of receiving and sending data regarding the operation of the irrigation system, and a controller. Software for VRI systems is the set of instructions for the controller, which manages the variable rate delivery of water per management zone as the sprinkler moves across the field. System management also involves the use of GPS data to map the system position relative to management zones so that system speed and nozzle sets (Figure 4(a)) can be controlled. In case of control via values that pulse nozzle flows, the synchronization of zone 'On' and 'Off' time is important to prevent water hammer or the system pump from shutting down due to low water pressure. The third purpose of the VRI software is to provide a graphical user interface (Figure 4(b)), to allow easy uploading of instructions by a producer, and verification of spatial instructions.

The combination of hardware and software allows site-specific irrigation scheduling customized for a particular field (Figure 4(c)); however, the prescription map is considered static if it is uploaded a single time and used throughout the growing season for irrigation scheduling. Initial prescription maps are generally based on inherent physical variability within a field, such as soil texture, salinity, pH, nonarable areas, and topography, as mentioned previously. For producers to address temporal variability, such as abiotic or biotic stress, prescription maps must be dynamic or modified throughout the growing season to address temporal changes.

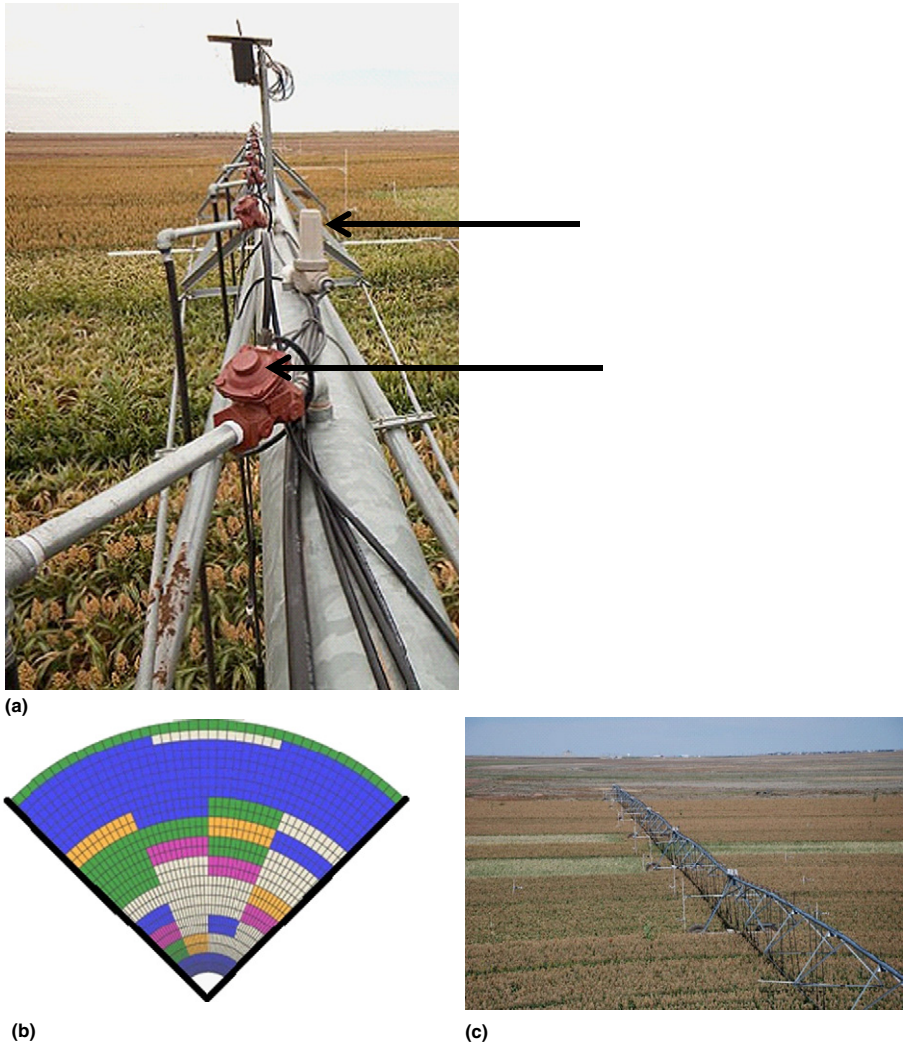


Figure 4 (a) Commercial variable rate irrigation (VRI) system mounted onto a center pivot irrigation system, (b) prescription map built with commercial software, where the different colored sections represent different levels of irrigation, and (c) irrigation field study with irrigation treatment plots established with a VRI system.

Dynamic instruction sets require the use of sensors and sensor network systems to detect the location of within-season variability over time and algorithms to decide where, when, and how much to irrigate or whether to withhold irrigation.

Sensors for precision irrigation management

Although major irrigation companies are now providing easy-to-use soil water and microclimatological sensors that provide information to the producer about the field environment, there are only a few precision irrigation systems that exist with sensors and algorithms fully integrated with the irrigation machinery to control irrigation scheduling. These advanced systems are used in research. Examples include an *in situ* sensor network system of soil water and thermocouple sensors to control the irrigation scheduling of a linear move irrigation system (Kim *et al.*, 2009) and center pivot irrigation systems using wired (Peters and Evett, 2004, 2008) and wireless (O'Shaughnessy *et al.*, 2012) sensor network systems of infrared thermometers to control irrigation scheduling using plant feedback methods.

Infrared thermometers assess a small portion of a field at any one time. However, Wanjura *et al.* (2004) demonstrated that when canopy size is sufficient to overcome the contributions of soil background, canopy temperatures measured from a small area by infrared thermocouples were comparable to those from a larger area viewed by a thermal scanner. If the infrared thermometers are mounted onto a moving irrigation system and are continuously collecting data, thermal information can be provided over space and time (Sadler *et al.*, 2002) and used to control irrigation (Peters and Evett, 2008). Continuous crop monitoring allows the assessment of temporal variation of crop water stress within a field. For example, O'Shaughnessy *et al.* (2011) documented the temporal trend of an empirical CWSI in a cotton field for the duration of an irrigation season and demonstrated its relationship to seasonal crop yield.

Both abiotic and biotic factors can induce stress in a plant, thus affecting transpiration rate, crop water use, leaf color, morphology, and crop density, each of which, in turn, affects the optical properties of the canopy (West *et al.*, 2003). To differentiate between abiotic (such as water stress) and biotic stresses (such as disease or insect infestation), it can be useful to outfit a precision irrigation system sensor network with more than one type of sensor. The incorporation of multiband optical sensors could provide timely detection of a crop disease or pest infestation within a field. Plants suffering from severe levels of disease are easier to detect than those beginning to suffer from early effects. The challenge is to discriminate healthy plants from those suffering from early, or less severe, levels of stress.

Digital imagery

Digital imagery has the advantage of providing data in a format that can be viewed and more easily validated. Digital images (visible, infrared, and hyper spectral) are processed using various methods that separate the image into pixels and then transform the spectral intensity in the various bands within a pixel to produce information related to plant status. For example, the red, green, and blue (RGB) components of each pixel of interest can be transformed into a more meaningful representation (**Figure 5**).

Since the 1990s, it has been known that thermography could detect plant disease earlier than visual observation could (Balachandran *et al.*, 1997). Aerial thermal imagery has been used to assess the heterogeneity of plant stress in orchards, vineyards, and over cotton fields. Falkenberg *et al.* (2007) demonstrated that images from a thermal infrared camera were able to detect biotic (root rot) and abiotic stress (drought) in cotton, using a camera with GPS and GIS capabilities. Unfortunately, thermographic images do not contain enough data to differentiate between such stressors. Data from thermal images enable the formulation of large area maps that indicate the location of water-stressed crops. Gonzalez-Dugo *et al.* (2013) extracted single tree crown temperatures from imagery using automated object-based methods to exclude mixed pixels of soil and vegetation. Ben-Gal *et al.* (2009) measured average tree canopy temperature with a thermal camera to calculate a theoretical and empirical CWSI over trees irrigated at different levels of potential ET. Aerial thermography has also been used to spatially map the water status of cotton (Alchanatis *et al.*, 2010) and vineyard plants within a field and then develop maps with leaf water potential levels for irrigation scheduling (Cohen *et al.*, 2005).

Visible imaging sensors are less costly than their thermal infrared counterparts and have the advantage of assessing color or color intensity using the RGB components of pixels. Commonly available visible imaging sensors are also sensitive to the near-infrared and ultraviolet light if left unfiltered. Visible imagery has been used to identify visual symptoms of plant disease remotely (Camargo and Smith, 2009), identify weeds (Tellaeche *et al.*, 2008; Burgos-Artizzu *et al.*, 2010), and distinguish vegetation from soil (Zheng *et al.*, 2009; Xue *et al.*, 2012). Digital images could be useful for decision making in precision irrigation management, if image processing is automated.

Spectral reflectance measurements

Optical sensors include nonimaging spectroradiometers, either multispectral radiometers (e.g., Crop Circle, CropScan, and Exotech) that provide reflectance measurements from a few bands or hyperspectral radiometers that have a broad spectral range (typically 400–1050 nm) with fine resolution (e.g., 1.4 nm). Radiometers are often augmented with a GPS unit to provide georeferenced data and are then useful for assessing spatial variability. Changes in canopy reflectance in healthy green plants are greatest in the near-infrared region (NIR), due to an increase of biomass and light scattering, whereas the visible region shows less seasonal variation (Hatfield *et al.*, 2008). Spectral reflectance in diseased or pest-infested plants (Yang *et al.*, 2009) is generally reduced in comparison with healthy plants, especially in the NIR region. One of the most useful vegetative indices (ratio of reflectance bands) is the NDVI (Rouse *et al.*, 1973):

$$(\mathrm{NIR} - \mathrm{Red})/(\mathrm{NIR} + \mathrm{Red})$$

where NIR is reflected radiation in the near infrared region (band width 790–1000 nm) and Red is reflected radiation between approximately 650 and 780 nm. This vegetative index

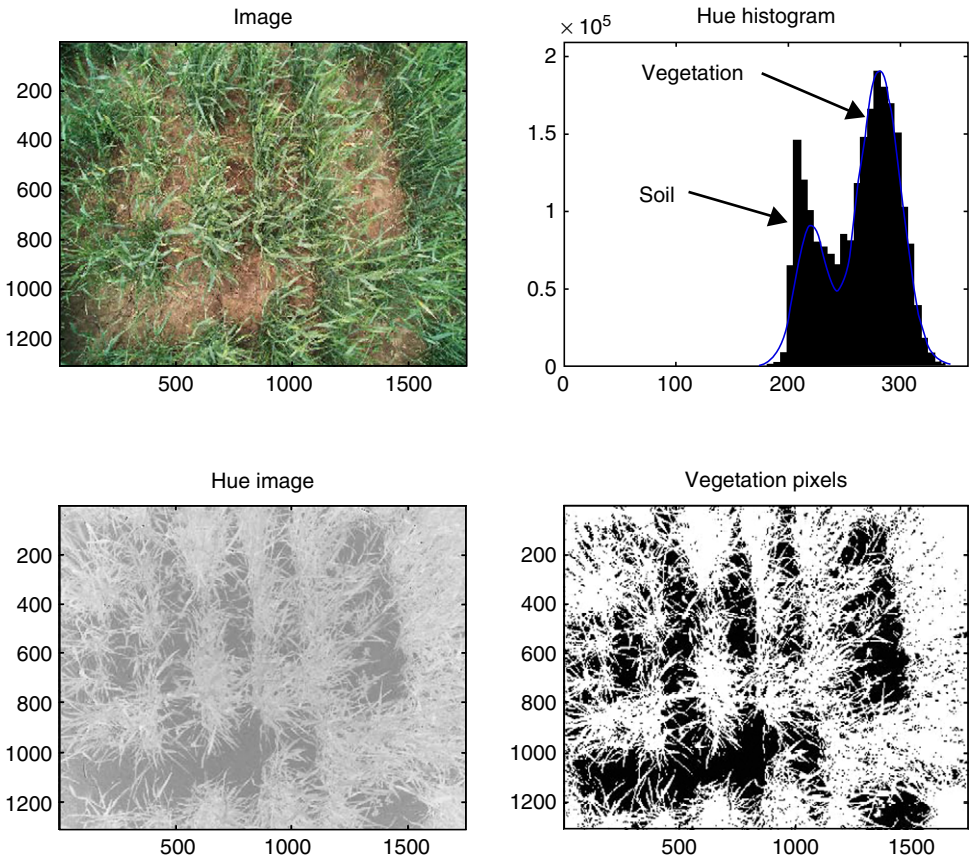


Figure 5 Digital visible image segmented by hue values calculated from red–green–blue components of the pixels of a digital image. Hue values were then separated into soil and vegetation using the expectation maximization algorithm (Moon, 1996).

has been used extensively to estimate plant canopy cover and crop coefficients for Et_c estimation (Hunsaker *et al.*, 2003, 2005). NDVI can also serve to indicate the presence of nitrogen and water stress. Plant *et al.* (2001) found the spatiotemporal pattern of NDVI-reflected stress factors and was approximately coincident with the onset of measurable water stress. Other vegetative indices have been used to estimate crop yield and to detect patches of weeds, disease, and insect infestation. Rumpf *et al.* (2010) demonstrated that vegetative indices from a hyperspectral reflectance instrument were able to discriminate between healthy sugar beet leaves and diseased leaves with an accuracy of 97%. They also confirmed presymptomatic detection of plant diseases with accuracy between 65% and 90%, using a support vector machine classification method and eight spectral indices as parameters (support vector machines are supervised learning models used in machine learning with associated learning algorithms to analyze and classify data). More recently, airborne hyperspectral imaging was used by Garcia-Ruiz *et al.* (2013) for early detection of citrus greening (Huanglongbing), which affects citrus production worldwide. Although data regarding crop canopy cover and crop status are available from satellite- or aircraft-based sensors, there is still the need to overcome the drawbacks of inadequate spatial and temporal resolution of the data, particularly in the case of satellite data (Ha *et al.*, 2013). Downscaling algorithms (e.g., Anderson *et al.*, 2003), more frequent satellite passes, and cloud computing may facilitate the integration of satellite-based information with precision irrigation management.

A requirement for complete precision irrigation management is to use sensors in a manner that provides information over the whole field. Therefore, any *in situ* or ground-based sensors should be wireless to reduce cost and maintenance (required for wired systems) and to prevent interference with farming equipment and tasks. If sensors are mounted onto moving irrigation systems, two sensors should be installed on opposite sides of each management zone, the sensors should face each other to reduce sun angle effects, and be oriented toward the canopy at an oblique, not nadir, downlooking angle to reduce effects of soil background. In case of drip irrigation/sprinkler for orchards, the wireless sensors should be located over representative areas within each specific management zone. Although images from aerial and satellite platforms are able to provide data over large areas, the images will need to provide adequate resolution to detect spatial variability within a single field. For all sensors and sensor network systems, access to useable data must be timely to meet irrigation scheduling requirements.

Algorithms

Algorithms for precision irrigation management should control an irrigation system so that it responds to within-field variability caused by abiotic and biotic stresses over the length of an irrigation season in an optimal manner (maximizing the

benefit-to-cost ratio of irrigation). Algorithms can be procedures or mathematical models to interpret data and provide decision support for sprinkler control and irrigation scheduling. Automatic control involves system input and feedback. Feedback for precision irrigation scheduling must provide a mechanism, process, or signal that is looped back into the irrigation system to control the timing and amount of water applied. In a closed-loop system for irrigation scheduling, a controller uses information from any number of inputs (microclimatological, soil matric potential, soil water content, canopy temperature or reflectance, or simulation models) and assesses the results of previous actions of the system to calculate the next action. If feedback is based on a prediction, for example, a rainfall event, the control is termed 'feed-forward.'

Kim *et al.* (2009) used a closed-loop feedback system to control the movement and irrigation scheduling of a commercial variable rate linear move system. Feedback control was established using a distributed network of soil water sensors. Sensors were strategically placed in a field mapped with a soil bulk electrical conductivity-sensing system. Irrigation was initiated when soil water deficits reached a preestablished threshold. Another closed-loop plant feedback method, the CWSI and Time Threshold (CWSI-TT) algorithm, was used to control irrigation scheduling of a center pivot outfitted with a VRI system (O'Shaughnessy *et al.*, 2012). In addition to irrigation control, the algorithm was used to control crop water use efficiency of grain sorghum hybrids. The algorithm for the CWSI-TT (based on the theoretical CWSI (Jackson *et al.*, 1981)) required scaling a remote one-time-of-day canopy temperature with a reference temperature measured throughout the day to estimate the diel temperature of the area represented by that remote location (Evett *et al.*, 1996 as implemented by Peters and Evett, 2004). The scaling algorithm allowed not only estimation of a diel temperature for a remote location but also comparison of canopy temperature for a large-scale area at the same time of day. This information can provide spatial and temporal CWSI maps over an irrigation season (O'Shaughnessy *et al.*, 2011), and it can be used to estimate seasonal grain yield. The algorithm for plant feedback irrigation scheduling included the use of varying threshold levels of the CWSI to initiate irrigation (**Figure 6**). Once a signal was generated, the irrigation amounts were always the same, i.e., twice (a function of irrigation frequency) the daily peak crop water use. The theory was that greater threshold values would result in less frequent irrigation, resulting in a controlled soil water-deficit condition (O'Shaughnessy *et al.*, 2012). The secondary calculation of crop water use (ET_c) was to enable irrigation for prolonged periods of cloudy skies for which infrared temperatures would not indicate crop water stress.

Model prediction or feed-forward control methods have been used extensively in simulations for precision irrigation control. Examples include the integration of crop development models with predictive control algorithms, including the VariWise framework (McCarthy *et al.*, 2010) and algorithms that model water dynamics in the soil–plant–atmosphere continuum, as used by Romero (2011) for controlling irrigation in almond orchards. These algorithms use historical measured data input streams, such as microclimatological data, soil water content, plant growth stages, and fruiting parameters in order to predict an outcome. The optimized outcome becomes the decision-making factor. Predictive methods are important because combined frameworks are needed to accomplish robust precision irrigation management. Such systems are data intensive and complex. Nonetheless, this type of arrangement has all the components of a supervisory control and data acquisition system and is on the cusp of commercialization.

For precision irrigation management in production agriculture, Romero *et al.* (2012) suggested the combination of feed-forward, feedback, and mathematical models to provide advanced irrigation control. Casadesús *et al.* (2012) developed a feed-forward irrigation-scheduling algorithm for tree crops based on the combination of microclimatological, plant, and soil water sensors. The integration of sensors to detect biotic stresses will expand the above algorithms and enable decision support to either continue or withhold irrigation. Finally, it should be noted that whatever the algorithm or combination of algorithms is, decision support procedures can allow producer interaction or they can be completely automated.

Information Technology for Remote Monitoring, Data Access, and Decision Making

Maintenance and oversight of the operation of precision irrigation machinery and sensor network systems require remote monitoring by wireless technologies. These technologies include fixed location systems, such as point-to-point microwave and stationary satellite systems, which generally operate at high baud rates. There are also near-fixed systems, local area network (IEEE802.11, 2012), and personal area network systems (Bluetooth, IEEE802.15.1, 2005; and Zigbee; IEEE802.15.4, 2011) that provide limited mobility over shorter transmission paths. Finally, wide area mobile systems, such as paging and cellular, provide extended mobility (Moring, 2004).

At present, the majority of commercially available remote monitoring systems focus on equipment operation and malfunctions. However, agricultural researchers and a limited number of commercial companies specializing in agricultural applications (e.g., CropMetrics and SmartCrop) are beginning to integrate plant sensors, for example, infrared thermometers (O'Shaughnessy and Evett, 2010), RFID tags (Sjolander *et al.*, 2010), soil water sensing (Kim *et al.*, 2009), and microclimatological networks with irrigation systems for precision irrigation control. With the addition of wireless field-based sensor systems, it becomes necessary to access data remotely to evaluate connectivity, troubleshoot network system issues, and perform quality analysis and quality control on the data. In the future, it is more likely that central data storage and sharing will be the basis for combining satellite and aerial imagery to provide for optimal irrigation scheduling and control. The advent of cloud-based computing, a term used to express services that are commoditized and delivered (Buyya *et al.*, 2009), could facilitate faster computing time and larger data storage.

Precision Irrigation for Disease Management

In many regions of the United States, particularly those areas where irrigation water is scarce, irrigation with center pivot

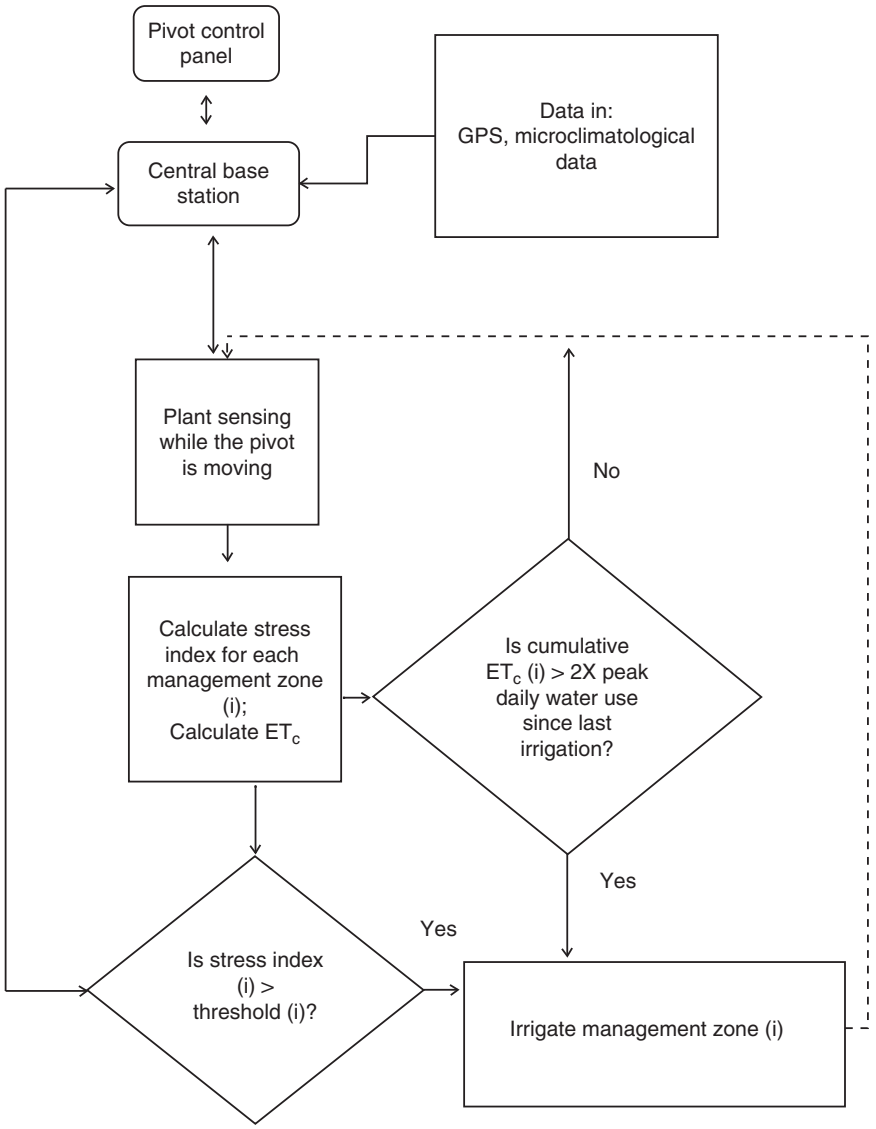


Figure 6 Process for precision irrigation scheduling using a plant feedback system; input from network of infrared thermometers and microclimatological data. ET_c, Estimation of crop evapotranspiration.

irrigation systems has largely replaced furrow irrigation. Many producers in areas of high evaporative demand still over-irrigate because they fear 'getting behind' and not being able to supply the crop with adequate water. In these situations, farmers often turn on the pivot and let it run continuously. As a result, soils in these fields may remain constantly wet, creating conditions conducive to disease. Fahnert (1999) conducted a study to evaluate the effects of different irrigation amounts and frequency on incidence and severity of disease in sugar beet. A center pivot system was equipped to deliver varying percentages of the normal amount of water applied at the usual (farmer determined) frequency or with on/off valves that allowed the grower to irrigate at different frequencies. At harvest, the final number of harvestable beets, disease incidence and severity, and root yield and quality were determined. With regard to disease incidence and severity, irrigation frequency had a greater impact than total irrigation. Reducing irrigation frequency to half the norm resulted in significantly less disease, higher percent sucrose, and higher root yields than beets irrigated at the usual frequency. After this and a number of other studies, there was no question that irrigation could affect disease incidence and severity, but it was also clear that disease incidence and severity could be reduced by improved irrigation management, i.e., applying the correct amount of water at the right time and frequency.

Framing a New Question

In all irrigated agricultural cropping systems, it is imperative for farmers to understand how irrigation management can impact disease, crop water use, yield, and quality of their crops. In many areas of the United States, however, high quality water for irrigation is becoming increasingly scarce and expensive to apply (McGuire, 2007). In some instances,

disease incidence and severity may not be directly impacted by irrigation amount or frequency, but if disease is present in the field, the farmer must decide whether the cost of applying additional irrigation (both in terms of actual expense and also depletion of a limited resource) is economically and environmentally sustainable. This decision is greatly complicated when the disease is progressive and increases in both incidence and severity over time. Wheat streak mosaic virus (WSMV) is a prime example of such a disease.

Development of an Economic Threshold for Site-Specific Variable Rate Irrigation of Fields with Wheat Streak Mosaic

In the Southwestern Great Plains, which includes parts of Texas, Oklahoma, Colorado, and Kansas, disease caused by mite-vectored viruses is the predominant biotic constraint to economically sustainable wheat production (Appel *et al.*, 2007; Burrows *et al.*, 2009). A recent wheat virus survey revealed that WSMV and Triticum mosaic virus were both common throughout the Great Plains, especially in the Texas Panhandle (Burrows *et al.*, 2009). These viruses are vectored by the wheat curl mite (*Aceria tosichella* Keifer) and cause significant reductions in root growth, WUE, and grain yield and quality (Price *et al.*, 2010; Workneh *et al.*, 2010).

Factors that impact mite populations and subsequent disease development are poorly understood, but disease epidemics are typically associated with hot, dry weather conditions. In most cases, mites are introduced into recently planted wheat fields from patches of volunteer wheat, native pastures, or land taken out of production by the US federally funded Conservation Reserve Program and planted to grasses that serve as oversummering reservoirs for the mites. Disease first appears at the edges of fields and as mite populations increase, they are blown across the field over time. In this manner, WSM develops disease severity gradients across fields, typically with the most severe disease occurring near the edge of the field where mite populations and plant infections were first established, and gradually decreasing in severity with increasing distance from the edge. To quantify this disease severity gradient and its effect on plant–water relations, Workneh *et al.* (2010) used a handheld hyperspectral radiometer to measure reflectance at 555 nm, which correlates well with visual disease severity ratings. These severity ratings were taken at regularly spaced points along the disease gradient when plants were at Feekes Scale 8, and gravimetric soil water content and plant yield parameters were also taken at each point. Plants from more than 90% of the sampled points tested positive for WSM, but disease severity ratings were strongly correlated with distance from the initial infection locus at the edge of the field. Additionally, as distance from the edge increased, disease severity decreased (indicative of later infections), soil water content decreased, and WUE and grain yields increased. Although most of the plants in this field eventually became infected, those infected later in the season were still capable of producing good grain and forage yields, and therein lies the management problem for farmers. The progressive nature of WSM makes it difficult for producers to know whether additional crop inputs, such as fertilization, pesticides, and multiple spring irrigation, are economically feasible.

Currently, most farmers manage their irrigated wheat fields as a single unit, applying inputs uniformly across the field, despite recognized variations in yield potential. The recent advances in irrigation technology discussed above may soon allow farmers to modify their current center pivot irrigation systems for site-specific variable rate applications. Such systems would be ideal for differentially irrigating wheat crops affected by WSM. However, in order to maximize the potential benefits of site-specific VRI of diseased wheat, an economic threshold for WSM is required.

Most studies relating disease severity of WSM to final yield have relied on disease ratings made relatively late in the season, well after the majority of inputs have been made. What is needed is a risk assessment model that could take disease severity ratings in early spring, before the majority of inputs have been applied, and predict yield potential for the entire field. Unfortunately, such a model does not exist, and due to the lack of knowledge concerning ecology and epidemiology of WSM, it would take years to develop such a model. However, continuous monitoring for disease severity using wireless pivot-mounted or stationary remote sensing devices potentially could provide timely detection and quantification of disease severity and provide a sensitive 'trigger' for site-specific irrigation.

As an alternative to ground-based imaging, satellite imaging has shown promise for quantifying the incidence and severity of WSM and the potential to apply this information for irrigation decision support. A study was conducted to evaluate Landsat 5 TM imagery for detection, quantification, and mapping of WSM in irrigated wheat fields. Imagery was acquired biweekly, beginning in early March, and diseased wheat was separated from healthy wheat using a subpixel classifier with $>91\%$ accuracy (Mirik *et al.*, 2013). In this study, early stages of WSM in which symptoms were just beginning to develop were not included in the classification, but based on previous studies (Workneh *et al.*, 2009, 2010), infections first appearing in mid-April or later had minimal impact on final yield. Although the 30 m pixel size of Landsat 5 imagery would restrict its usefulness for detection of some diseases, it was adequate for detection of WSM in commercial irrigated fields; moreover, 30 m would represent a reasonable irrigation management zone. The ease in acquiring low-cost, large-scale, biweekly images that can be used to accurately detect, quantify, and map WSM in commercial wheat fields qualifies this technology for potential use in site-specific irrigation of diseased wheat.

The incidence of WSM in large-sized pivot fields across the Texas Panhandle is one example for the application of precision irrigation management in production agriculture. It illustrates the need for site-specific irrigation to meet variable crop water needs of healthy and diseased wheat. The progression and changing levels of severity in WSM requires continuous crop status monitoring to provide spatial detection of disease and temporal information on severity level throughout the growing season. Algorithms factoring in disease severity level can provide decision support to farmers for irrigation scheduling of wheat that has the potential to produce economical yields or withholding irrigation in the case of severely diseased wheat. In this manner, irrigation management focuses on maximizing the benefit-to-cost ratio of irrigation.

See also: Climate Change, Society, and Agriculture: An Economic and Policy Perspective. Plant Abiotic Stress: Temperature Extremes. Plant Abiotic Stress: Water. Plant Disease and Resistance

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Production Economics

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Glossary

Conditional factor demand Input use, x_i, chosen for least-cost production of output, y, when input prices are $w_1,\ldots, w_n$: $X_i(y, w_1,\ldots, w_n)$.

Cost function Least amount of money needed to purchase inputs to produce a specified output level, y. When the prices of inputs are $w_1,\ldots, w_n$, the cost function is written $C(y, w_1,\ldots, w_n)$.

Production function Agricultural yield expressed as a function of the use of inputs, such as water, nitrogen, labor, land, and equipment. If the physical quantities of inputs are $x_1,\ldots, x_n$ and the physical quantity of output is y, then the production function is mathematically represented as $y=F(x_1,\ldots, x_n)$.

Profit function Maximum farm earnings net of production costs as a function of output price, p, and input prices, $w_1,\ldots, w_n$. Profits are total revenues from farming less total costs of farming; the profit function, π, is written as $\pi(p, w_1,\ldots, w_n)$.

Supply curve Profit-maximizing output level as a function of output price, p, and the prices of inputs, $w_1,\ldots, w_n$: $Y(p, w_1,\ldots, w_n)$.

Unconditional factor demand Input use, x_i, chosen for profit-maximizing production when input prices are $w_1,\ldots, w_n$ and output price *is* p: $X_i(p, w_1,\ldots, w_n)$.

The Basic Theory of Production

Production Functions

Production economics begins with the production function – a mathematical relationship between the inputs used for farming and the resulting output. The production function F is purely a technical relationship. It summarizes knowledge about the production process but implies nothing about the behavior of farmers or of markets.

Economists assume that the production function has several properties. First, output is nondecreasing in each input. That is, if use of one input increases, all other inputs held constant, then output should increase or, at least, not decrease. Mathematically, the partial derivative of F with respect to each input is nonnegative. In agriculture, it is possible that output will decrease if the input (such as fertilizer or manure) is applied excessively (first derivative becomes negative), but it is usually assumed that such applications are outside of the range of what farmers would use.

Second, each additional unit of input usually adds less to output than the unit before, a phenomenon referred to as diminishing marginal product. Mathematically, the second partial derivative of output, with respect to that input, is nonpositive.

Third, production functions have constant or decreasing returns to scale. A production function has constant returns to scale if doubling all inputs doubles output. (Returns to scale are decreasing if doubling all inputs leads to less than a doubling of outputs. They are increasing if doubling all inputs leads to more than doubling of outputs.) When output is analyzed as a function of physical inputs, such as land and fertilizer, agricultural production functions can reasonably be assumed to have constant returns to scale. In other words, if a farm is doubled in size, output should double. Because, as farm size increases, farmers are often able to specialize and make better use of certain inputs (such as labor and machinery), the production function may have increasing returns over much of the relevant size range. In wheat farming, for instance, the ability to use large implements on large tractors makes it possible for a large farm to use less labor per unit of output than a small farm.

A production function with constant returns to scale can be written on a per-acre basis. That is, if x_1 is the number of acres, then $y/x_1=g(x_2/x_1,\ldots, x_n/x_1)$. A frequent way to analyze agricultural output is to write separate equations for per-acre production and for acreage in the crop. Acreage is assumed to adjust to changes in profits from one crop relative to profits from an alternate crop.

Pesticides and other damage-control agents do not behave like ordinary inputs in that they do not increase yields directly. Instead, they limit the reduction in yield from pests or other damaging agents. To reflect the difference between damage-control agents and other inputs, a production function can be specified as

$$y=f_1(x_2,\ldots,x_n)+f_2(x_2,\ldots,x_n)G(x_1)$$

where x_1 is the damage-control agent and $x_2,\ldots, x_n$ are other inputs. The function $G(x_1)$ is the proportion of the pest damage that is controlled by use of the input x_1; it has a range between 0 and 1. Any cumulative probability distribution function is a potential choice for a functional form for G. When damage is uncontrolled, the output is f_1. When it is perfectly controlled, it is f_1+f_2.

Cost Minimization

In most production processes, different techniques can be used to produce a given level of output. Irrigated crops, for example, can produce the same output with flood irrigation (more water and less equipment) or sprinkler irrigation (less water and more equipment). Economists assume that, for any specified level of output, firms choose the combination of techniques to produce that output at least cost. In the example above, if water were expensive relative to irrigation equipment,

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sprinklers would be adopted. If water were inexpensive relative to equipment, flood irrigation would be used.

More technically, firms choose inputs, $x_1,\ldots, x_n$, to minimize the cost of those inputs, $w_1\times_1+\cdots+w_nx_n$, subject to the constraint that a given level of output, y, is achieved: $y=F(x_1, \ldots, x_n)$. Levels of input use chosen as a function of input prices and output are conditional factor demands, $X_i(y, w_1,\ldots, w_n)$. The cost function is $C(y, w_1,\ldots, w_n)=w_1\times_1(y, w_1,\ldots, w_n)+\cdots+w_nX_n(y, w_1,\ldots, w_n)$.

A conditional factor demand decreases as its own price increases. Effects of other input prices on this curve depend on whether inputs are substitutes or complements. For most inputs, increased output shifts factor demands out; these are termed normal inputs. Inputs whose use decreases when output increases are called inferior inputs.

Other facts about conditional factor demands are derived from economic theory as well. First, $\partial x_i/\partial w_j=\partial x_j/\partial x_i$. That is, the effect of the price of input j on factor i is the same as the effect of the price of input i on factor j. Second, they are characterized by homogeneity of degree 0, which means that doubling all prices with output held fixed does not change the input mix. This assumption implies that only relative prices (the ratio of each input price to one designated 'numeraire' input price) matter.

Profit Maximization

Each firm engaged in agricultural production supplies only a tiny fraction of the market for that product. No single farm can significantly affect market volume or market price. Such firms are called price takers. A reasonable approximation of their behavior is derived by assuming that they maximize profits. There are two steps to maximizing profits: deciding how much to produce and choosing inputs to produce that amount at minimum cost. Because the input decision problem is summarized in the cost-function analysis, the remaining problem for the firm is to choose the output level to maximize profits, which are revenues less costs, $py-C(y, w_1,\ldots, w_n)$. The y chosen to maximize profits yields the decision rule $Y(p, w_1,\ldots, w_n)$, called the supply function. The supply function gives the profit-maximizing level of output for any set of input and output prices. The profit function summarizes the output and input decisions in the same way that the cost function summarizes input decisions and is written as $\pi(p, w_1,\ldots, w_n)$.

Economic theory predicts that the supply function is nondecreasing in output price and nonincreasing in input prices. In practice, one expects that an increase in the output price will increase the quantity supplied, whereas an increase in an input price will decrease the quantity supplied. Finally, the supply function is homogenous of degree 0 in output and input prices. If all output and input prices double, production should remain unchanged. Thus, only relative prices matter.

The supply function from profit maximization can be substituted for y in the conditional factor demands. The resulting functions (which give input use as functions of input prices and output price) are termed unconditional factor demands, because they are no longer conditioned on output. Properties of the unconditional factor demands are the same as those of conditional factor demands.

Risk

Agricultural firms bear considerable yield and price risks. Weather, world demand conditions, government programs, and pest problems are a few sources of risk in agriculture. A better approximation of farm behavior than simple profit maximization includes a consideration of farmer attitude toward those risks and of the actions farmers can take to avoid those risks.

Risk-averse farmers are willing to take lower expected profits to lower the variability of their profits. Consider two possible outcomes for farm income: high income, H, which happens with probability λ, and low income, L, which happens with probability $(1-\lambda)$. A risk-averse individual prefers a certain income equal to the average, $\lambda H+(1-\lambda)L$, to the uncertain income stream. In fact, such an individual may be willing to take a payoff lower than $\lambda H+(1-\lambda)L$ to avoid the uncertainty.

Risk aversion can lead farmers to alter their practices in a number of ways. For instance, they may choose to spend more on inputs if they can reduce the uncertainty in crop yield. Instead of growing just the most profitable crop, farmers may choose to grow many crops in the hope that some crops will do well even if others do not.

Duality

Although it is most natural to think of the physical relationships of production being summarized in the production function, the same information is contained in the cost and profit functions because of their derivations from the production function. This property of cost, profit, and production functions is called duality. Its practical consequence is that all technical information about production can be recovered from the cost function (which depends on prices and output) or from the profit function (which depends only on prices).

Shepard's lemma

The problem of minimizing cost for given output makes direct use of the production function and leads to conditional factor demands. Those same factor demands can be found in a second way. The calculus can be used to prove that the derivative of a cost function with respect to input price is the conditional factor demand. Because the same input decisions are found either by working out the minimization problem, using a production function, or by taking the derivative of a cost function; these two functions contain the same information.

Hotelling's lemma

Just as conditional factor demands can be found directly from the cost function, unconditional factor demands can be found from the profit function. The derivative of the profit function, with respect to output price, is the supply function. The negative value of the derivative with respect to an input price is an unconditional factor demand.

Multiproduct Model

Most farm operations have more than one output. Hog farms often produce corn and soybeans, cotton farms tend to grow alfalfa, and farms in the developing world frequently include

several types of livestock as well as vegetables and grains. The formal analysis for such operations is an extension of the single-product analysis presented above. Instead of only one output, y, let $y_1,\ldots, y_m$ represent the m possible outputs. The multiproduct production function, H, is commonly written in an implicit form, such as $H(y_1,\ldots, y_m, x_1,\ldots, x_n)=0$. The cost function is $C(y_1,\ldots, y_m, w_1,\ldots, w_n)$; the profit function is $\pi(p_1, \ldots, p_m, w_1,\ldots, w_n)$; and so forth. With a suitable choice of functional form, these relationships can be used directly. Although there are examples of work at this level of generality, such as a study of expansion effects and substitution possibilities for Canada, there is a tendency, particularly among those interested in farm management, to place more structure on the problem.

The most common method of analyzing a multiproduct system is first to examine the production relationships of each activity (crop or livestock production) individually and then to examine the profit-maximizing choice of activities.

Farmers have many reasons for producing more than one crop. First, different soils may be suited to different crops. Second, if labor, capital, or other input requirements for two different crops are complementary, then both can be grown with the same inputs and greater production can be achieved with little increase in cost. Third, producing a variety of crops reduces risk, because factors that may cause one crop to fail may not be factors that will destroy another crop. Even if one crop is destroyed, the farmer can still earn profits from those remaining. Fourth, rotations may be desirable to control pests or maintain soil characteristics. Various programming methods, described below, can be used to solve this allocation of scarce resources among crops.

Estimating Production Relationships

The previous discussion has presented the economic theory of production. The next step in analyzing production relationships is data collection and analysis. Data collection and analysis are used to determine empirical production, cost, and profit functions and associated factor demands. These functions are used for policy analyses and farm-management recommendations.

Data Sources

Data derived from a range of sources can be used to develop estimates of production, cost, and profit functions. Some of these data sources are experimental, farm survey, county data, and cost and return estimates.

Experimental

Agronomic field trials provide data that include different input combinations and their resulting output. Examples include experiments to find responses of various crops to nitrogen, potassium, and water.

Farm survey

The U.S. Department of Commerce, Bureau of the Census, conducts a census of agriculture every 5 years. Every farmer in the US is asked information on their farm operations, including input applications, irrigation methods and amounts, acreage in different uses, size of farming operations, market value of assets and debts, and other areas. Every year as well, the National Agricultural Statistics Service of the U.S. Department of Agriculture surveys a subset of farmers and collects similar information for specific crops. The USDA Risk Management Agency collects extensive data needed to administer crop insurance programs; this data and similar data from private crop insurers is just beginning to see use. Other surveys are often conducted by researchers interested in specific issues or regions.

County data

The local government in most states in the US collects acreage, output, and value of output by crop for the major crops in each county. This information can be used to construct countywide agricultural land-use models.

Cost and return estimates

Land-grant universities in most states in the US estimate how much it will cost to produce a crop and what revenues to expect on a representative farm. These estimates are based on a standard set of inputs, management techniques, and level of output, determined by consultation with farmers and local crop experts, and with specified prices for inputs and output. They are used for a wide range of purposes, including determining whether an investment in a particular crop is worthwhile, examining the effects of alternative management practices on profits, estimating the value of land in production of a crop, and analyzing whether the costs on a particular farm are relatively high or low.

In addition, the U.S. Department of Agriculture conducts a Farm Costs and Returns Survey for a range of crops (including all crops involved in federal crop support programs) every 5 years. This survey reports how much, on average, farmers spend for production of each crop and how much they earn.

Statistical Techniques and Functional Form

Statistical estimation of crop production functions requires not only data on inputs applied and output attained, but also a class of assumed mathematical forms to relate the inputs and output. A class of functions is determined up to r numerical values, $\alpha_1,\ldots, \alpha_r$, called the parameters of the function. A choice of the form of the function $F(x_1,\ldots, x_n; \alpha_1,\ldots, \alpha_r)$ is necessary to conduct most analyses. Statistical techniques are used to determine the parameters that make the equation fit the data as accurately as possible.

Data never conform perfectly to a functional form chosen to approximate the true production function. Measurement error, omitted variables, and error in the choice of functional form all contribute to the imperfect fit. These discrepancies between actual yield and the yield predicted by a production function are called error terms, ε. The relationship between inputs and output is assumed usually to be of the form

$$y = F(x_1, \ldots, x_n; \alpha_1, \ldots, \alpha_r) + \varepsilon$$

This form means that, for each observation (year and farm, field, county, or state), the output for that observation is

related to the inputs for that observation plus an error term. Assumptions about ε, such as normality, lead to particular types of estimation.

A common choice for an agricultural production function is a quadratic function. With two inputs, the function is written as

$$y = \alpha_1 x_1 + \alpha_2 x_2 + \alpha_3 x_1 x_2 + \alpha_4 x^2{}_1 + \alpha_5 x^2{}_2 + \alpha_6$$

In this function, six parameters need to be determined by statistical techniques. Generalizations of the quadratic include higher-order polynomials, polynomials in square roots, and polynomials in logarithms (called translog).

As noted above, diminishing marginal product is commonly assumed in economics and commonly observed in reality. This assumption is incorporated by limiting the choice of forms (or parameters) to those that permit positive first derivatives and negative second derivatives. In addition to polynomials, the following functional forms (given for the two-input case) are frequently used and have these characteristics.

Mitscherlich	$y = (1-e^{\alpha_1 x_1})(1-e^{\alpha_2 x_2})$
Von Liebig	$y = \min(\alpha_1 x_1, \alpha_2 x_2)$
Cobb–Douglas	$y = \alpha_0 x_1^{\alpha_1} x_2^{\alpha_2}$
Translog	$\ln y = \alpha_0 + \alpha_1 \ln x_1 + \alpha_2 \ln x_2 + \alpha_3 (\ln x_1)(\ln x_2)$

Pope/Just Production Function

The Pope/Just production function generalizes the other functions described by including the possibility that different inputs have different effects on the variability of output. Let the function $g(x_1,\ldots, x_k)$ include only those k inputs that affect yield variability, either positively or negatively. The Pope/Just function is then written as

$$y = f(x_1, \ldots, x_n) + g(x_1, \ldots, x_k)e$$

where e is the error term. This generalization of the error term can be used to analyze situations where farmers use inputs that are relatively expensive but that reduce risk and reduce use of inputs that increase risk.

Estimation of Multicrop Production Functions

The estimation of individual production functions for each crop in a multicrop system is hampered by lack of data. Farmers often keep records of the inputs purchased for the whole farm, but they rarely keep records of which inputs were used for which crops. For instance, a farm might have records on the total purchase of nitrogen fertilizer and output of soybeans and corn but no records about the amount of fertilizer allocated between soybeans and corn. Without the allocation of the input between the two crops, it is not possible to determine directly the effect of changing fertilizer use on the production of either crop.

One solution is to use an aggregate function, with the underlying assumption that fertilizer is allocated optimally between the two crops. The added information from this behavioral assumption gives the problem enough structure to be solvable.

Statistical Techniques and Problems

The most common technique to determine the parameters, α_1, …, α_r, is to find the set of parameters that minimizes the sum over all observations of the error terms squared, ε^2. (The error term is squared to prevent positive and negative errors from canceling each other out without finding a good fit.) This method, called least-squares estimation, is used with an additive error term. Using the least-squares estimation, inputs are assumed not to be related to the error term and parameters that best explain the relationship between the inputs and output are found.

Another class of models are those in which the error term is assumed to be inside the function, such as $y=F(x+\varepsilon)$. For instance, the von Liebig function with two inputs, when the error term is incorporated, can be written as

$$y = \min(\alpha_1 x_1 + \varepsilon_1, \alpha_2 x_2 + \varepsilon_2)$$

A switching regression can be used to estimate the parameters of this function.

A requirement for consistent estimation of a production function by least squares is that inputs are independent of the error term. For instance, inputs may be related to planting, whereas the error term might consist largely of weather which occurs after planting has taken place. In this case, the assumption of independence is reasonable. In more managed agricultural systems, however, the input data available often violate this assumption. For instance, the number of pests, which is difficult to count, is an omitted variable and thus part of the error term. If pesticide inputs are applied after the pests are observed, then their use is correlated with pest presence and violates the independence assumption. Similarly, the amount of water applied often correlates with weather (a frequently omitted variable). This violation of assumptions leads to estimators with very poor statistical properties: the estimated parameters do not approach the true parameters even with a large amount of data. Statistical methods for estimating production functions in these circumstances call generally for some measure of the omitted variables – pests or weather in the above examples. An alternative is to estimate the cost function or factor demands, because these forms do not have the same problem.

Prediction and Extrapolation

In agricultural work, the major reasons to estimate a production function are to predict yields in new circumstances or to assess the efficacy of changing the input mix. Standard statistical methods would seem to suffice for assessing the effect of a small change in inputs. Typically, investigators try many functional forms and different sets of variables before deciding which combination is 'right.' As a result, the statistics calculated for a single regression tend to give confidence intervals smaller than the true intervals, because they do not reflect all prior analyses that were rejected. Partly for this reason, predictions from estimated equations tend to be worse than the regression statistics suggest.

Estimation of Cost Functions

In managed agricultural systems, where least squares yield inconsistent estimates of a production function, the estimation of conditional factor demands or cost functions provides an alternative. This alternative is also used with data aggregated over many crops or many regions. Because input prices can be assumed not to be correlated with an error term reflecting weather or pest conditions, estimating factor demands avoids the problem of the interrelatedness of inputs and the error term.

A system of factor-demand equations is often estimated together. A typical equation for conditional demands is of the form

$$x_i = X_i(w_1, \ldots, w_n, y)$$

In unconditional factor demands, output price p substitutes for output y. Properties of factor demands, described earlier, are imposed as restrictions on the equations.

The Supply Function

To examine the effects of government policies on farm output, economists need to know the relationship among those policies, prices, and farmer behavior – a relationship contained in the supply function. If prices can be considered to be unaffected by the behavior of the farmers whose output is being studied, the supply function can be estimated by least squares. This situation holds if price is not determined with output simultaneously.

Under several circumstances, this assumption is plausible. First, if the supply function is estimated for a small segment of the overall market, such as a small region, farmers can be considered to be price takers. Second, if output price is determined by government policy rather than by market forces, then price truly is determined before output. Third, if it can be assumed that farmers base their planting decisions on the price expected for the crop at the end of the season and if actual price at harvest is related to actual harvest (which is determined by exogenous factors, such as weather and pests), then output is determined before actual price. In this case, price, rather than output, is the dependent variable.

However, if a supply function is estimated for the entire market of an output and if output price and quantity are not set separately, then price is determined by interaction of the supply function with the demand function which reflects consumer desires for the commodity at a range of prices. In this case, information about consumer demand behavior is also necessary to find the supply relationship. Estimation techniques, such as two-stage least squares and instrumental variables, are used to solve this problem.

Response to Weather

Global climate change should have first-order effects on agriculture (Schenkler and Roberts, 2009). Finding the response of agricultural yields to weather is the first step in finding the effects of predicted climate change on agriculture. Because it is only the effect of weather that is of interest, a response function is estimated as a function of many weather variables and the effects of prices and soil (or other place dependent variables) are all absorbed by fixed effects. Hotter weather is neither always bad nor always good, so response to temperature needs to be modeled flexibly. Using the PRISM data for the US, temperature for each place (e.g., 4 km×4 km square) is summarized as the number of hours in the growing season by temperature bin. Examples of temperature bins are the number of hours at 10 °C and up, the number of hours at 12 °C and up, etc. Let X_{itb} be the number of hours that the temperature is in bin b place i at time t. The vector of the X_{itb} is $X_{it}=(X_{it1},\ldots,X_{itn})$ where there are n bins of temperature. A conformable coefficient n-vector is β. Similarly let y_{it} be the yield in place i at time t, δ_i be a dummy variable that is one only in place i, and ω_t be a dummy variable only when the time is t. With an error terms ε_{it}, the equation to be estimated is

$$y_{it} = X_{it}\beta + \delta_i + \omega_t + \varepsilon_{it}$$

This regression captures the response to temperature, accounting for place-related things like soil and time-related things like prices through the dummy variables. The framework can be enlarged by including precipitation, by breaking the variables down by month (e.g., temperature above 10 °C in June), by including richer functional forms (e.g., translog, quadratic, etc.), and by including spatial autocorellation in the error terms.

Use of the Basic Theory of Production

The theory of production and the techniques used to develop quantitative estimates of the theoretical relationships are outlined in the previous description. The ultimate reasons for conducting studies of farm production are to improve farm production (the field of management economics) or to examine the effects of government policies (the field of agricultural policy). The use of the theory and quantitative relationships for examining input levels, farm-level resource allocation, regional modeling of agriculture, and agricultural policy analysis is described in the following section.

Input Intensity

Although it is often safe to assume that farmers use levels of inputs that maximize their profits, at times it is useful to examine effects of alternative levels of input use and production technologies, such as irrigation techniques. The choice of functional form for the production function makes a great difference to recommendations for input use. When a polynomial or Cobb–Douglas form is used, recommended input levels will often be less than when a von Liebig form is used. According to empirical evidence, the von Liebig form is closer to being correct for experimental plots, though nonuniformity in fields leads to arguments for the use of other functional forms.

The choice of irrigation technology involves a trade-off between cost and uniformity. Less expensive techniques can lead to parts of the field receiving more water than necessary and other parts of the field receiving far less water. Because excess water often does not adversely affect crop growth, farmers may 'overirrigate' parts of the field to get sufficient water to the drier parts of the field. Alternatively, farmers can

invest in more expensive technologies that distribute water with great uniformity and reduce water use. A more surprising result is that irrigation equipment can be used to substitute for land! The more expensive technology could be more profitably used by increasing water per acre, which increases yield per acre, and by decreasing the number of acres.

Whole-Farm Models and Planning

Input decisions involve choosing methods to maximize profits for a given crop. In contrast, whole-farm planning involves choosing how many acres to devote to each crop. Depending on the nature of the research question, researchers use several forms of programming techniques to allocate acreage among crops and practices.

Linear programming

The simplest of these techniques is linear programming which is used to analyze static systems with no uncertainty. The linear-programming analysis begins by determining the fixed inputs available to the farm. Fixed inputs are those that cannot be adjusted quickly or easily, such as the total acreage available, soil types, and major capital equipment. The next step is calculating revenues, purchased inputs, and needs for fixed inputs for each crop on a per-acre basis. Finally, total profits (revenues minus costs of variable inputs per acre) are maximized, subject to the constraints on fixed inputs. If fixed inputs are used similarly for each crop, then only the crop with maximum profits per acre will be grown according to the linear-programming algorithm. More generally, the number of crops that will be grown depends on the number of fixed inputs. For instance, if different land types grow a different crop more profitably or if both water and land are in fixed supply, then the programming solution will put acreage into more than one crop.

A simple example is the choice of growing corn and growing sorghum, with profits per acre of π_1 and π_2, respectively. With a total of A acres, A_1 is allocated to corn, and A_2 is allocated to sorghum. The linear-programming problem for crop choice and profit maximization is

$$\max_{A_1,A_2} A_1\pi_1 + A_2\pi_2$$

subject to

$$A_1 + A_2 = A$$

With more complicated production relationships (for instance, with a restricted profit function rather than the simple profit per-acre formulation), nonlinear programming is necessary to solve the problem. In these cases, multiple outputs are more likely than with strictly linear problems.

Quadratic programming

The generalization of the whole-farm planning problem either to a regional model or to a model that accounts for risk involves quadratic programming. Risk is usually incorporated in these models by assuming that a farm operator maximizes profits less a term reflecting the risk aversion of the farmer. In terms of the simple example,

$$\max_{A_1,A_2} A_1\pi_1 + A_2\pi_2 - \lambda Var(A_1\pi_1 + A_2\pi_2)$$

subject to

$$A_1 + A_2 = A$$

where λ is a coefficient reflecting risk aversion and Var refers to variance with

$$\mathrm{Var}(A_1\pi_1 + A_2\pi_2) = A_1^2\mathrm{Var}(\pi_1) + A_2^2\mathrm{Var}(\pi_2) + A_1A_2\mathrm{Cov}(\pi_1,\pi_2)$$

This is a quadratic function in the choice variables A_1 and A_2.

Dynamic programming

Many agricultural problems include dynamic aspects. For instance, because soil loss happens over many years, a model to examine its effects must look a number of years into the future. Similarly, pesticide resistance and fertilizer carryover are multiyear problems. Using dynamic-programming methods, time aspects of these issues are incorporated.

In the dynamic-programming framework, farmers are assumed to care about future as well as current profits. At the same time, it is assumed that current profits are more valuable than future profits because of the existence of alternative investment possibilities and uncertainty about the future. In other words, future profits are discounted relative to present profits. The discounted value of future profits, found by dividing future profits by a discount factor related to the interest rate, is termed the present value of future profits. The dynamic-programming problem involves maximizing the sum of present-value profits over time.

Constraints on the maximization problem, such as the effects of practices on soil erosion and, therefore, on soil quality, involve multiple years. These equations are termed 'equations of motion' because they describe how variables, such as soil quality or pest resistance, change over time.

Controlling pests over 2 years provides an example of dynamic modeling. Let $s(t)$ be pest population at time t, and let j (s) be the year to year increase in pests. With pest control, v, applied at a cost of w per unit, profits with a given pest level are $\pi_1,(p, s)$- vw in year t. With the discount rate, r, the dynamic problem for a 2-year model is

$$\max_v \pi_1(p_1, s_1) - v_1w + \pi_2(p_2, s_2)/(1 + r) - v_2w/(1 + r)$$

subject to

$$s(2) = s(1) + j[s(1) - v_1]$$

Because the function, j, is generally not linear, the problem is not linear in the choice variable, v, and requires nonlinear programming.

When the equation of motion is influenced by a random element, ε, the resulting problem is a stochastic dynamic-programming problem. Because profits are no longer deterministic, expected profits are maximized. In terms of the example,

$$\max_v \mathrm{E}\{\pi_1(p, s) - vw + \pi_2(p, s)/(1 + r)\}$$

subject to

$$s(2) = s(1) + j[s(1) - v_1] + \varepsilon$$

where **E** is the expectations operator. There are computer codes to solve these problems, but computational difficulties increase greatly as the number of equations increases. Thus, the decision to add stochastic and nonlinear elements to a model comes usually only with less thorough modeling of other elements, such as seasonality in labor or number of crops modeled.

Regional Models

Supply functions and demand functions (amount of product purchased by consumers as a function of price) can be combined to give equilibrium (quantity supplied equals quantity demanded) models of agriculture on a regional (or even national) basis. These models are used to analyze the effects of such issues as how government policies affect cropping patterns, the optimality of water use rules, and the costs of soil preservation. In California, water is allocated to districts based on political and historical factors. Regional production models are used to determine how much more money could be made in the farm sector if water were allocated to maximize profits. In Iowa, a soil preservation law requires great care in farming very erodible land. A regional model was used to determine the cost of existing regulation and compare it to more and less restrictive regulations. Linear and quadratic-programming methods are used generally to analyze these types of models.

Implications for Agricultural Policy

Policy issues are often centered on farmer response to government-imposed price policies. The aggregate supply curve for a crop can be used to analyze the effects of price changes on production. For instance, if the government lowers the support price for a crop, the supply curve would indicate by how much production would decrease. To determine who gains and who loses from agricultural policy, both aggregate supply and aggregate demand curves are necessary to determine the effects on consumers. In the above case, a drop in price would hurt producers, but consumers would benefit from lower prices.

A more complicated example is the probable effects of a mandate for the use of ethanol or other biofuel. Such a mandate would increase corn output (requiring an estimate of the supply curve for corn). It would also produce byproducts that compete with soybeans, lowering soybean demand. The supply curve for soybeans is also needed to determine the effects on the soybean market. Complicated analyses of this nature are underlain always by the estimated supply relationships of the crops.

Issues in Economics

It is assumed that agriculture is a relatively static industry in the proceeding analysis. In other words, farmers operate in basically the same way year after year and change their behavior only in response to input and output prices. Of course, this assumption is wrong. Farming has changed substantially over time, in response to changes in technology, regulations, and altered market circumstances. These changes are reflected in contemporary work in production economics.

Technological Change

Supply curves change over time because of technical change. Technical change involves increases in output above that which can be accounted for solely by changes in input use. Examples include improvements in varieties, invention of the tomato harvester, and better pest management. The challenge is to measure the increases in output (or savings in inputs) caused by new technologies. Three approaches are used: experimental plots, time trends, and proxy variables.

For a discrete event, such as hybrid corn, experimental plots are planted with the old and new varieties. If the new variety has desirable characteristics, such as greater output, pest or drought resistance, etc., then it is a possible improvement. To be a technical change (and a real improvement), it must also increase profits (or decrease risk).

The time-trend approach involves estimating a production function with a trend term, for instance

$$y = e^{rt} f(x_1, x_2)$$

where t is time and r is the rate of technical change. In this case, the cause of the change is not specified.

The last approach is to use proxies, such as agricultural experiment station expenditures, for new techniques. An example of such a functional form would be

$$y = I^{a} f(x_1, x_2)$$

where I is the expenditure on research and development. Estimates of productivity that account for research and development show that the returns to research activities are quite high.

Technical progress causes major problems for agricultural price-support activities because it increases output. Price-support authorities find it necessary to purchase ever larger quantities of product, or to restrict output, to continue to support prices.

Farm Size

Returns to scale have real consequences for farm demographics. Middle-sized farms in the US are decreasing in number, whereas larger and smaller farms both seem to be increasing. One of the driving economic forces in this revolution (at least for wheat) is returns to scale. If a farm is operating with increasing returns to scale, it can increase its output more quickly than its costs increase; the farm will expand. If a farm is operating with decreasing returns, it will benefit by reducing its size. The range of output where the farm faces constant returns to scale yields the minimum cost per unit of production and is termed the minimum efficient scale. Many crops, such as wheat, are grown in vast expanses to take advantage of large equipment. The large equipment is less costly per acre if the farm has enough acres to average out the capital costs.

Overproduction Trap

Supply curves may not be the same for a price increase and a price decrease because factors of production can easily move into agriculture but not out. Capital (such as tractors), for which farmers paid large sums, cannot be resold at the same price.

For example, the Russian Wheat Deal led to greatly increased wheat prices and the expectation that high prices would continue. In response, farmers purchased considerable quantities of equipment to expand output. When wheat prices subsided, the additional investments could not be converted into other uses and remained in the hands of farmers. The farmers continued to produce high output because they already owned the equipment and had already prepared the land.

This phenomenon is called the overproduction trap. Production economics is used to estimate how fast production will respond to increased prices and to make a separate estimate of how fast production will respond to lowered prices.

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Public–Private Partnerships in Agroforestry

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Glossary

Agricultural extension The application of scientific research and new knowledge to agricultural practices through farmer education.

Biofuels Fuels produced from renewable biological resources, such as plant biomass and treated municipal, and industrial waste.

Collective action Voluntary action taken by a group with common interests. In agriculture this can include the formation of producer groups, farmers' associations, or cooperatives in order to increase economies of scale, for cost effectiveness or to better access services or markets.

Commercialization The process by which a new product or service is introduced into the general market. In smallholder agriculture, this often refers to moving from subsistence production to market-oriented production.

Consultative Group of International Agricultural Research (CGIAR) A global partnership that unites organizations engaged in research for a food secure future. Research is carried out by the 15 centers who are members of the CGIAR Consortium in close collaboration with partner organizations.

Eco-certification Where an independent agency, such as a government, nongovernmental organization, or an industry consortium tests or verifies that a certain more sustainable practice has been followed in the production of goods or services.

Latex The colorless or milky sap of certain plants, such as rubber trees, that coagulates on exposure to air.

Medicinal species Plants whose components, such as bark, roots, or leaves, are used as natural medicines.

Payments for ecosystem services (PES) An umbrella term for a variety of schemes, in which the beneficiaries or users of ecosystem services provide payment to the stewards or providers of ecosystem services.

Silviculture The branch of forestry dealing with the development and care of forests.

Background

In agricultural research for development, partnerships are commonly formed to achieve specific outcomes through combining the strengths of different organizations. As in many areas of crop research and development, the breadth of the field of agroforestry is beyond the capacity of a single institution to manage. Partners bring different skills and experience, such as research to generate knowledge and innovation, local knowledge and expertise, upscaling to translate knowledge into action, capacity development and education, policy and institutional reform, and finance.

Partnerships are established between organizations that include research institutions, agricultural organizations, donors, private sector organizations, and government and nongovernment agencies. In agroforestry, which often sits somewhere between the mandates of agriculture and forestry institutions, partnerships cross the boundaries of agriculture, forestry, environment, conservation, and climate change.

Partnerships between public and private sector organizations in agricultural research and development are viewed as having the potential to reduce the cost of research, facilitate innovation, and enhance the impact of research on smallholder farmers and other marginalized groups in developing countries (Spielman *et al.*, 2007). Such partnerships may also be able to increase the level of private sector investment in poorly performing agricultural value chains (Poulton and Macartney, 2012).

Public–private partnerships (PPPs) can broadly be defined as collaborations between public sector and private entities who share costs, risks, and benefits in order to jointly plan and implement activities toward shared objectives (Spielman *et al.*, 2010). The aim of these collaborative initiatives is to overcome constraints, such as market failure, institutional constraints, and systemic weaknesses, in order to produce agricultural knowledge and technology (Spielman *et al.*, 2007).

Spielman *et al.* (2007) have emphasized the importance in partnerships of clearly defining a problem, its solution, and the resources required, and of having effective monitoring, decision-making and communication mechanisms in place. These factors are crucial to achieving trust between public and private partners (Poulton and Macartney, 2012) and in coordinating knowledge amongst multiple actors (Spielman *et al.*, 2007).

On the basis of PPPs among Centers of the Consultative Group of International Agricultural Research (CGIAR), Spielman *et al.* (2007) classified five types of PPPs according to the role of partners in contributing finance, carrying out research and development, deploying products, monitoring, evaluating, and planning.

1. Resourcing: private partner contributes funding or expertise.
2. Contracting: private partner contracts CGIAR facilities or expertise.
3. Commercialization: private partner commercializes, markets, and distributes CGIAR research findings.
4. Frontier research: private partner conducts research jointly with the CGIAR.
5. Sectoral/supply-chain development: private partner contributes within a partner network to supply chain development.

Almost half of the PPPs in the CGIAR aim to convert research results into products for the poor. Approximately 30%

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of the PPPs reviewed in the study are geared toward sector or supply chain development (Spielman *et al.*, 2007). Within this type of PPP are activities aimed at strengthening collective action, developing technologies, building market linkage, and infrastructure (Spielman *et al.*, 2007).

The case studies analyzed in this article – three out five of which involved a CGIAR Center – tended to be a combination of Spielman's categories with most involving resources from the private sector, joint research, and some aspect of supply chain development among private and public partners. All were strongly geared toward poverty alleviation among smallholder farmers and several incorporated strong elements of improved environmental management.

Public–Private Partnerships in Agroforestry

The involvement of PPPs in agroforestry is a relatively new phenomenon in which private companies wishing to increase their market supply of a product, develop 'new' commodities to meet market demand, and improve the functioning of supply chains formally collaborate with public partners, such as international and national research organizations. Typically, the objectives of these collaborative arrangements are to protect the natural resource base of a commercially important tree species and to develop improved tree crop varieties with increased quality or productivity. In addition, such partnerships embrace government ministries engaged in the important role of formulating and enabling policies as well as nongovernmental organizations (NGOs) working with farmers and product processors.

PPPs in agroforestry involve partners in a number of different roles and approaches. What determines the effectiveness of successful partnerships, the achievement of partnership goals, and the challenges and future opportunities for PPPs in agroforestry commodities are examined here. The focus is on agroforestry products that currently command a private value – via income generation, subsistence value, or reduction of production shocks (Gruère *et al.*, 2006) – or those that have potential to generate income from market transactions in the future. The hope is that the lessons learned from current PPPs in agroforestry can be integrated into future partnerships that focus on intermediary and underdeveloped agroforestry commodities that have the potential for livelihood and environmental gains.

This article examines well-established agroforestry products and their market potential as well as the factors specific to agroforestry supply chains, and their development for products considered intermediary and underdeveloped. Consideration is also given to the complementary role of agroforestry in natural resource management. Six case studies of agroforestry PPPs from a range of countries are included to provide examples of how different public and private sector stakeholders are contributing resources, expertise, skills, and financial investment to enhance market supply of agroforestry products and improve environmental sustainability.

The role of PPPs in payments for ecosystem service (PES) schemes is also discussed as a form of PPP that involves public and private sector actors as providers and buyers of services that include carbon sequestration, watershed protection, and biodiversity protection, many of which can be provided by agroforestry systems.

PPPs are also emerging in tertiary agricultural education with the aim of overcoming a variety of constraints. An overview of these partnerships and their benefits to businesses and universities is given in relation to their ability to stimulate joint research, innovation, greater funding, and improved dissemination of knowledge in agroforestry and other fields of agriculture.

Smallholder Farmers and Agroforestry

An estimated 2.5 billion people around the world are involved in full- or part-time smallholder agriculture (FAO, 2008). Asia and Africa have the highest proportion of small farms, with farm size ranging from 1 to 1.3 ha (IFAD, 2013). Although smallholders contribute significantly to poverty reduction and food security through cultivating field and tree crops as well as livestock, fish, and other aquatic organisms, they also comprise the majority of the world's undernourished population and most of those living in absolute poverty (IFAD, 2011). Of the 1.4 billion people living in extreme poverty (on less than US$1.25 a day) 75% live in rural areas of developing countries, especially subsaharan Africa and southern Asia where agriculture is their main source of livelihood (IFAD, 2011). There are an estimated 870 million people considered food insecure and even more suffering from 'hidden hunger' caused by micronutrient or protein deficiencies (FAO, 2013).

There are strong links between improvements to smallholder agriculture and poverty reduction. Irz *et al.* (2001) estimated that for every 10% increase in farm yields, there was a 7% reduction in poverty in Africa and more than a 5% reduction in Asia. The introduction of new crops and the promotion of underexploited traditional food crops among smallholder farmers have the potential to improve nutrition through providing a variety of foods and in sufficient quantities (Negin *et al.*, 2009).

Smallholder farmers grow 70% of the world's food, in cocoa as much as 90% (Fairtrade Foundation, 2013), yet they receive only a small percentage of the final retail price, just 7–10% of the supermarket retail price for coffee growers and less than 3% of the retail price for smallholder tea producers.

Commercialization of smallholder production (i.e., moving from subsistence-based production to market-oriented production) has been shown to result in welfare gains and poverty alleviation through gains from specialization and comparative advantage, larger-scale production and regular interaction, and exchange of ideas and technological change (Barrett, 2008).

One of the main issues with the commercialization of agroforestry products is the time lag between planting and harvesting (Ajayi *et al.*, 2007), which can be 10 years or more in some cases, although this can be reduced on occasions when alternative propagation methods are adopted, such as vegetative methods, for the propagation and early production of fruit trees (Leakey, 2004). Keeping farmers and others along the supply chain (as well as investors where private or public funding is involved) motivated during this period is a significant

challenge. A lack of business skills and ability to link agroforestry products with markets can be another constraint.

The increased complexity of agricultural markets means that the actors along market chains must collaborate in order to successfully harness business opportunities (Humphrey and Memedovic, 2006). Interventions aimed at developing supply chains look beyond individual actors, such as input suppliers, producers, processors, or traders in order to increase the benefits to smallholders from participating in markets (Donovan *et al.*, 2013).

PPPs are one key element to facilitate smallholders benefiting from market opportunities (World Bank, 2007). Interest in PPPs has increased in recent years because of the potential of such partnerships to improve the functioning of supply chains (Poulton and Macartney, 2012).

Agroforestry, Supply Chains, and Markets

Agroforestry, Its Products, and Services

Agroforestry – the integration of trees in agricultural landscapes– is a traditional land use practiced by farmers throughout most of the world. Zomer *et al.* (2009) found that 48% of the world's farmland has greater than 10% tree cover which represents more than 1 billion hectares of land and 558 million people. Six million square kilometers – or 27% of agricultural land globally – has more than 20% tree cover. Agroforestry systems range from home gardens to subsistence livestock and pastoral systems, staple crops, on-farm timber production, tree crops of all types integrated with other crops, and biomass plantations.

Agroforestry commodities can be clustered according to their use (**Table 1** for the main product groups), including:

- Trees that produce edible fruit, nuts, or oil for human food, such as *Allanblackia* sp, *Theobroma cacao*, and *Dacryodes edulis*.
- Timber and fuelwood trees for shelter and energy, such as *Acacia* and eucalyptus.
- Fodder trees that improve smallholder livestock production, such as *Calliandra calothyrsus*.
- Medicinal trees, such as neem (*Azadirachta indica*), clove, cinnamon, and *Warburgia ugandensis*.
- Trees that produce gums, resins, or latex products, such as rubber (*Hevea brasiliensis*).
- Biofuels, such as *Jatropha curcus*.

Many trees and agroforestry systems are multipurpose and in addition to providing commodities have been shown to deliver ecosystem services and environmental benefits,

Table 1 Suggested classification of agroforestry products and markets

Product	*Intensity of production*[a]	*Scale of an individual enterprise*	*Current demand*[b]	*Market actors*	*Market geography*[c]	*Potential future market value*[d]	*Potential sustainability threats*[e]
Liquid biofuels		Large scale	+	Formal	L-R-I	?	
Solid biofuels	−	Small scale	+	Informal	L-R	−/+	
Charcoal	−	Small scale	++	Informal	L-R	+	Deforestation
Timber	+/−	Large and small scale	++	Informal-formal	L-R-I	+	Deforestation
Fodder	−/+	Small and large scale	+	Informal	L	+/−	
Indigenous fruit	−	Small scale	+	Informal	L-R	−/+	Unsustainable harvesting
Exotic fruit	−/+	Small and large scale	++	Informal-formal	L-R-I	+	Intensity of external input use
Medicinal species	−	Small scale (Africa) and large scale (China)	+	Informal	L	−/+	Unsustainable harvesting
Industrial products (oils and resins)	−/+	Small to large scale	+	Formal	I	?	Unsustainable harvesting
Seeds, seedlings, and other planting material		Generally small scale	+	Informal	L	?	Poor quality material resulting in poor quality trees and products

[a]Low level of on-farm production, i.e., mostly extractive resource use from the existing on-farm, communal area, or forest resource base, + on-farm production.
[b]++ High.
[c]L, Local; R, Regional; I, International.
[d]Growth potential + high −/+ medium.
[e]The drivers behind sustainability threads may be complex, for example, population growth and land and tree tenure systems may drive unsustainable harvesting practices and deforestation.

including biodiversity conservation, soil enrichment, erosion control, and air and water quality (Jose, 2009). Select agroforestry species can also provide nitrogen fixation (Sileshi *et al.*, 2008) and shelter for livestock and crops; increasing production. Tree-based production systems may also support biological, economic, and social resilience under anthropogenic climate change (Thorlakson and Neufeldt, 2012).

Agroforestry supports food and nutritional security through the direct provision of food, raising farmers' incomes to buy food, providing fuel for cooking to make food suitable for consumption and through various ecosystem services that support food production, such as pollination (Jamnadass *et al.*, 2013). Agroforestry also provides dietary diversity and variety in food flavors. In addition, agroforestry products have value in cosmetic and pharmaceutical industries.

Although it is estimated that forests and trees outside forests contribute in some way to the livelihoods of more than 1.6 billion people globally (World Bank, 2008), the varying levels of dependence of different communities on tree products and services and how this changes over time is often not well described or adequately acknowledged in rural development practice (Byron and Arnold, 1997). This reflects the ubiquity of tree products and services and the complex interconnecting pathways by which trees impact livelihoods.

Agroforestry Supply Chains and Their Development

The global export market value of agroforestry commodities is estimated to be in the tens of billions of US$ per annum (Place *et al.*, 2011; Dawson *et al.*, 2013). Yet agroforestry is still often viewed more as a natural resource management activity than a commercial enterprise (Russell and Franzel, 2004).

Tree products are observed to play a vital role in rural livelihoods in the tropics – used in almost every community for construction, fencing, furniture, foods, medicines, fibers, fuels, and fodder – yet quantifying their value and that of the environmental services provided by trees is complex. The many and varied sources of tree products and services (both inside and outside forests) are characterized in different ways by national governments' departments of forestry and agriculture (de Foresta *et al.*, 2013).

Some tree products enter local, national, and international markets, whereas others (although not widely sold) meet basic human needs and are of particular cultural significance (Place *et al.*, 2011). Tree products, such as timber have an investment role for smallholder producers, whereas edible fruit in addition to serving as cash crop has a nutritional security function (Jamnadass *et al.*, 2011).

Informal trade in unmonitored local markets, direct household provisioning, and the exclusion of wild-harvested resources from most large-scale household surveys (Shackleton *et al.*, 2007, 2011; Angelsen *et al.*, 2011), are all reasons why the FAO (2010) figures of US$19 billion for nonwood forest products from forests is unable to adequately represent actual value.

The supply chains for tree products and services generated under agroforestry systems vary considerably in their level of development. A significant focus for PPPs in agroforestry is the further development of these supply chains, from tree domestication for higher quality, greater uniformity and increasing production to better techniques for harvesting and storage, improving processing, and ensuring available markets.

The general components of the agroforestry supply chain are similar to those found in the supply chains of other agricultural products (**Figure 1**). This generic structure has been developed further to illustrate specific agroforestry supply chains (Facheux *et al.*, 2006; Holding Anyonge *et al.*, 2011).

Many agroforestry tree species are wild or semidomesticated (defined by Gruere *et al.* (2008) as underutilized) although they are of high value to local communities, such as the fruit of the baobab tree (*Adansonia* sp.). Some species have been the subject of two decades of intensive domestication (Leakey *et al.*, 2012) and are widely marketed. Underutilized species are generally in abundance locally rather than globally and have high levels of local rather than scientific knowledge and limited current relative to potential value (Gruere *et al.*, 2008). There is emerging interest in species, such as baobab, *Allanblackia*, and tamarind, all of which have European Commission approval for human consumption, and there is high potential for domestication of a range of tree species for on-farm production through the development of cultivars based on market needs.

There has been considerable research generated by both public and private sectors on well-established agroforestry products, such as coffee, palm oil, citrus, and conventional fruits such as apples and olives, which are in production across the world (Jamnadass *et al.*, 2011). However, there is evidence of substantial neglect in some cases, relative to the importance and potential of some products, i.e., horticultural crops (Weinberger and Lumpkin, 2007).

Those products considered intermediary, such as some natural gums and certain indigenous fruits, may be highly commercialized commodities with national as well as regional trade, for example, kola nuts in West and Central Africa (Facheux *et al.*, 2006). Others, such as safou and marula, are highly valued and traded at the local level and have traditional and cultural importance. There are five main aspects which set agroforestry products apart from those of other agricultural crops, some of which are already the focus of PPPs.

1. For agroforestry products, markets for seed and seedling supply may be weak or missing (Lillesø *et al.*, 2011).
2. Information on plant production and plant management may be constrained.
3. Owing to their perennial nature, tree crops experience a longer time lag between planting and harvesting as compared with annual crops. However, their production may be more resilient to seasonal weather variations that can reduce the production of annual staples, and they are more likely to be produced in mixed farming systems that support some resilience in production.
4. In many countries, agroforestry as a subsector is located somewhere between the responsibilities of the Ministry of Agriculture (MoA) and the Ministry of Forestry and may therefore 'fall through the cracks' in the provision of suitable support (Temu *et al.*, 2010).
5. Trees have dual functions in providing important wider environmental services at the same time as the production of fruit, timber, medicines, and other products (Leakey,

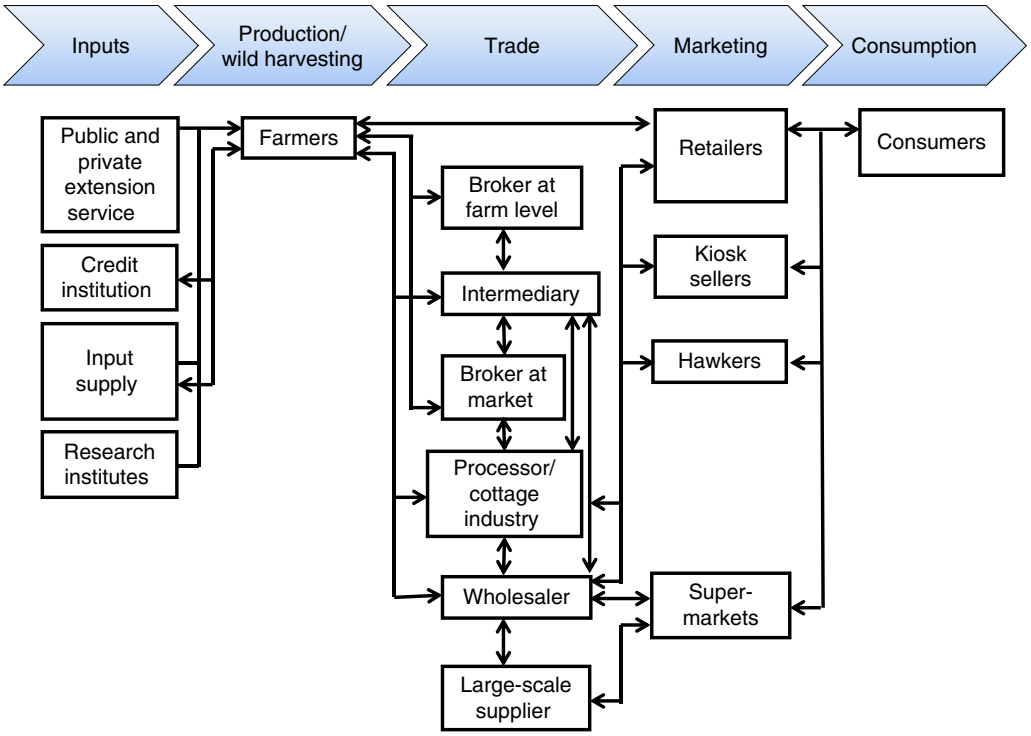


Figure 1 Generic agroforestry supply chain (arrows show product, information, service, and financial flows).

2001). The opportunity to support environmental service provision and production gives added value that can be exploited through PPPs.

The first two aspects are constraints potentially shared with other underdeveloped/underutilized crops and limit supply and its ability to respond to expanding demand. Aspects (3) and (4) are particular to the core characteristics of tree products.

With regard to policy constraints, Place *et al.* (2012) outline three key policy areas that can contribute to agroforestry benefits being more widely distributed: land and tree tenure, equitable supply systems for seeds and seedlings, and increased investment in agroforestry.

Gruère *et al.* (2006) identified the necessary conditions for achieving successful commercialization of underutilized plant species over time, namely: expansion of demand, improved efficiency of production, marketing channels, and supply control mechanisms (Gruère *et al.*, 2006, p. 25). Aspects (1)–(3) can be summarized under Gruere *et al.*'s 'improved efficiency of production and marketing channels.' The process of meeting conditions for successful commercialization of underutilized crops and the position of selected agroforestry products within this process are highlighted in Figure 2.

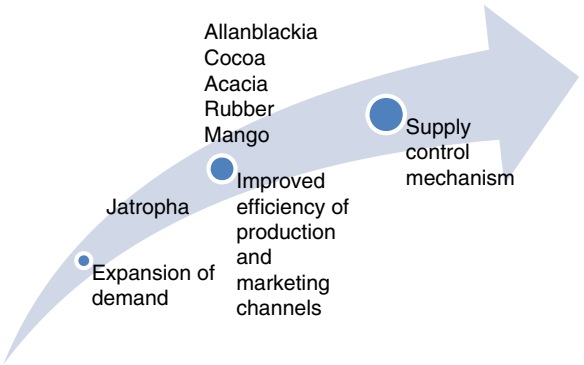


Figure 2 Process of commercializing underutilized crops. Adapted from Gruère, G., Giuliani, A., Smale, M., 2006. Marketing underutilized plant species for the benefit of the poor: A conceptual framework. Environment and Production Technology Division (EPT) Discussion Paper 154. Washington, DC: International Food Policy Research Institute (IFPRI).

Case Studies

The following six case studies illustrate how different PPPs have emerged in agroforestry to meet specific challenges, primarily: research to improve product quality and supply, the further development of supply chains, enhancing farmer participation in markets, and improved environmental management. The products on which they are focused vary from well-known crop (*Acacia*, cocoa, mango, and rubber) to underdeveloped (*Allanblackia* and *Jatropha*) ones.

The common goal among the partnerships profiled is the alleviation of poverty through increasing the commercial viability of agroforestry products. For this reason, the case studies are presented according to their perceived level of impact in terms of improving farmer livelihoods and increasing the value of agroforestry products.

The scale at which the partnerships are operating vary from local (mango, rubber, and *Jatropha*) to regional (cocoa), national (*Acacia*), and multinational (*Allanblackia*).

The level of current and potential future success varies among the PPPs in the case studies as does their long-term sustainability. Although *Acacia* growing in Vietnam is currently highly successful, there are potential risks from pests and diseases. The partnership for cocoa in Côte d'Ivoire is working well at the regional level but there is substantial investment required to scale up efforts. For rubber in Indonesia and mango in Kenya, local-level impact has been achieved but the partnerships have not been extended further. For the allanblackia partnership to achieve the desired impact, considerable work is required in the area of domestication of the species.

Public partners involved in the six case studies include government agencies, international and national research organizations, development organizations, national and international NGOs, donors, certification bodies, universities, and other tertiary education institutions. Private sector partners include multinational companies, public–private enterprises, processing companies, producer associations, and in some instances farmers themselves.

The way in which each of the partnerships is managed varies from informal agreements (*Acacia* and *Jatropha*) to cofinancing arrangements (mango) and contractual agreements overseen by steering and technical committees (cocoa, *Allanblackia*, and to some extent rubber).

Acacia mangium and *Acacia auriculiformis*

There are more than 1300 species of *Acacia* throughout the world with more than 900 of these found in Australia. Many *Acacia* species are valuable for their timber, which is used for fuelwood, sawn timber, and pulpwood for the paper industry, whereas some species also yield tannins and gums. *Acacia* trees are leguminous and many are able to fix nitrogen in the soil. They tend to tolerate soils with low fertility.

Background

In 1943, Vietnam had 14.3 million hectares of forest (Braidotti, 2012). By 1995 approximately 42% of this had been destroyed, largely due to overharvesting and conversion to agriculture during decades of war and severe poverty (Braidotti, 2012). The use of the herbicide Agent Orange in southern Vietnam during the war years of the 1960s and 1970s compounded the situation.

As part of their landholdings, many smallholder farmers in Vietnam have some land that is not arable, such as hilly slopes with shallow, rocky, and degraded soils. These marginal conditions severely limit the income they can gain from agricultural crops.

In the 1980s, due to a shortage of timber supply and as part of a major reforestation program, the Forest Science Institute of Vietnam (FSIV) began to investigate fast-growing tree species that could be grown in short rotations on degraded soils.

The partnership

Partnerships were formed – involving the following – to progress the development of an industry in short rotation *Acacia* plantations:

- FSIV – breeding programs, training, and extension.
- Australian Center for International Agricultural Research (ACIAR) and Australia's Commonwealth Scientific and Industrial Research Organization – expertise on commercial tree growing in developing countries.
- Swedish international development agencies – financial and technical support.
- Provincial and local forest development companies (usually a combination of public and private interests).
- Smallholder farmers.

The type of partnerships established between forest development companies and smallholder farmers range from formal contracts under which companies provide seedlings, fertilizer, technical advice, and other inputs, and farmers provide land and labor with an agreed sharing of returns, to less formal agreements.

In trials of possible species, two Australian *Acacias* proved especially suitable: *A. mangium* and *A. auriculiformis*. Clonal plantations of the interspecific hybrid *A. mangium* × *auriculiformis*, developed through FSIV's own research program are now the most widely planted *Acacia* variety (Dinh Kha *et al.*, 2012) after *A. mangium* and grown from the north to south of the country, including in the Mekong Delta.

Acacia trees are generally grown in Vietnam in small woodlot plantations on short rotation, although intercropping in early years of the rotation does occur with crops such as cassava, and some farmers grow *Acacias* at wider spacing over crops, such as tea, or in rotation with other crops. *Acacia* trees are easy to cultivate and grow quickly.

Plantations can be harvested to yield small logs after 5–7 years (Braidotti, 2012), depending on site quality, providing farmers and companies with early returns. Logs of larger diameter can continue to be grown on longer rotations, earning higher returns after a few more years.

Acacia timber provides excellent fiber for pulp and is good for furniture manufacture; a major industry in Vietnam. The productive *Acacia* plantations support many processing factories across the country. Farmers sell their trees either to company buyers, independent wood contractors (who function as 'middle men'), directly to pulpmills, woodchip mills, sawmills, or veneer mills.

To improve plantation productivity, the FSIV established breeding programs to produce genetically improved *Acacia* planting stock for growers. They also developed technical systems and associated training for nurseries. Clonal nurseries producing elite acacia hybrid clones certified by Vietnam's MoA and Rural Development are either by government- or privately run and some farmers also grow *A. mangium* seedlings for sale in small roadside nurseries.

Extension packages recommending simple establishment and plantation management procedures have also been developed and promoted through the national forest extension service and widely adopted.

Other research has focused on silvicultural methods that protect site resources and support sustainable production over successive rotations. The importance of retaining harvesting residues on site and minimizing soil disturbance by avoiding burning and repeated cultivation has been demonstrated but not yet widely adopted. Thinning and pruning techniques to

increase the production of larger diameter sawlogs have been researched but likewise are not yet widely adopted.

ACIAR-supported projects have helped to build technical capacity in Vietnam and developed advanced *Acacia* breeding programs. Breeding populations and seed orchards have been established to produce improved varieties of the parent species and for hybrid breeding.

Successes

Acacia trees now cover approximately 3% of Vietnam's land surface: 600 000 ha of *A. mangium*, 90 000 ha of *A. auriculiformis* and 400 000 ha of clonal plantations of *Acacia* hybrid (*A. mangium* × *auriculiformis*) (Harwood and Midgley, 2012). About half of these are cultivated by smallholder farmers on less than 10–20 ha. The remainder are owned and managed by forest companies and state enterprises.

The timber processing industry has shifted from state-owned enterprises to private companies through Vietnam's economic liberalization policies. By 2008, the timber-processing sector had expanded into a US$3 billion industry (Putzel *et al.*, 2012), one of Vietnam's top five export sectors and a major source of demand for logs and sawnwood.

In 2011, *Acacia* trees provided approximately 90% of Vietnam's woodchip exports of more than 5 million bone dry metric tonnes (Harwood and Midgley, 2012). In addition, the *Acacia* timber that supplies local pulp mills, sawmills, and downstream wood processors make a significant contribution to rural employment.

The development of a country-wide industry in short rotation *Acacia* plantations has been successful in Vietnam largely because of many reliable commercial markets for the wood that pay a good price for small logs, within easy transport distance of the plantations. Widespread smallholder adoption has also been attributed to the availability of suitable land for planting, land reforms conferring unambiguous ownership of trees, the wide availability of appropriate germplasm for planting, and simple farm establishment requirements (Fisher and Gordon, 2007; Griffin *et al.*, 2011).

Acacia trees help to prevent soil erosion through the development of a heavy litter layer and strongly fix atmospheric nitrogen, thereby improving soil fertility for the next crop. Food crops or other cash crops, such as rubber, can be grown after a rotation of acacias.

Challenges

Although famers and companies have made good profits with *Acacia* growing in Vietnam, the local price of woodchips has only marginally increased in recent years, whereas the Vietnamese Dong has depreciated against other currencies. Relying primarily on exporting woodchips is a risky strategy because of varying commodity prices.

As both furniture manufacturers and pulpwood markets demand the same species, competition exists between these manufacturing sectors, which is good for growers but can create an incentive for premature timber harvesting (Putzel *et al.*, 2012). If smallholders are able to produce higher quality or certified timber, they can often receive greater benefits. There is currently a lack of domestic supply of certified timber which results in Vietnam's furniture companies importing raw materials.

On better soils in Southern and Central Vietnam, rubber plantations can provide more attractive return on investment and timber plantations will increasingly need to be established on less productive land.

Although pests and disease have had little negative impact on wood production of *Acacia* plantations in Vietnam during a 20-year period of widespread planting, they remain a real threat. *Acacia* plantations in Sumatra, Indonesia have been seriously impacted by diseases, in particular Ganoderma and Ceratocystis (Tarigan *et al.*, 2011). Illustrated manuals in both English and Vietnamese language for pest and disease identification have been developed (Thu *et al.*, 2010) and disease surveillance networks are being built. Pathologists with the Vietnamese Academy of Forest Science (VAFS) are screening acacia breeding populations to identify disease-resistant genotypes, and Vietnam has the capacity to rapidly mass-produce resistant varieties. VAFS is also researching and developing other tree genera for plantation forestry, including *Eucalyptus*, *Manglietia*, *Melaleuca*, and *Pinus*.

Concerns have been raised about the environmental impacts of the rapid expansion of large-scale plantations in Vietnam. However, if slow-growing species had initially been chosen for the deforested hillsides of Vietnam, the poverty alleviation benefits would not have been as great as those that have been achieved with fast-growing *Acacias*. If the country now decides to move toward slower-growing species for its plantations, more land under plantations would be needed to produce the same amount of wood that acacias deliver.

Vietnam requires large volumes of timber to supply its US $4 billion processing industries, and 75% of this is imported. The growing of *Acacias* in plantations – half of which are owned and managed by smallholders, with the majority of the remainder under local management – is servicing this industry, providing an alternative to the use of timber from natural forests in Vietnam or timber imported from overseas.

Research focus is increasingly being placed on sustaining productivity within *Acacia* plantations. Highly productive plantations are able to make very efficient use of a small proportion of Vietnam's land base to meet the country's industrial wood requirements, opening up greater opportunities for landscape diversification.

Although distributing improved *Acacia* germplasm to smallholder growers has been highly effective, it is much more difficult to spread improved plantation management practices to tens of thousands of growers. This is an area requiring further research.

Cocoa

The cacao tree, *T. cacao*, is native to southeast Mexico and the Amazon basin. Cacao pods borne on the stems of this small tree typically contain 20–60 beans which are dried, fermented and then used to make cocoa powder, the main ingredient of chocolate. Today, cocoa is mostly produced in West Africa, with more than 30% of the world's supply coming from Côte d'Ivoire. Although cocoa used to be a plantation crop, up to 90% is now grown by smallholders (Fairtrade Foundation,

2011). In Cote d'Ivoire the cocoa industry supports more than 6 million people (Sustainable Cocoa Initiative, 2012) and globally cocoa is grown by 30 million smallholder farmers (Fairtrade Foundation, 2013).

Background

Globally over the past decade, cocoa production has been declining and its quality has varied due to depleted soils, lack of improved planting material, aging trees, pests and diseases, changing weather patterns, and weak rural infrastructure. At the same time, demand for cocoa is increasing and it is estimated that at least 1 million additional tons of cocoa will be needed by 2020 to meet the demand (Fairtrade Foundation, 2011).

Mars Inc., one of the world's largest chocolate producers, launched its sustainability initiative in 2010 with the aim of using only certified cocoa in all of its products by 2020. Research and on-ground projects initiated by Mars toward this goal and increasing the productivity and quality of cocoa are underway in Indonesia, Vietnam, Papua New Guinea, and Côte d'Ivoire.

In Côte d'Ivoire, Mars is focusing its efforts on the country's primary cocoa-producing area of Soubré in the southwest of the country. Land shortages in Côte d'Ivoire limit agricultural expansion, so increasing production requires intensification. Revitalizing the cocoa sector in Côte d'Ivoire necessitates bringing together the private sector, government, and civil society organizations.

The partnership

The Vision for Change program was created in 2010 by Mars in partnership with the Ivorian government, national agricultural institutions and the World Agroforestry Center. The program is strongly geared toward raising farmers out of poverty by helping them to improve their incomes through more productive farms. The goal is to sustainably increase yields for 150 000 farmers in the Soubré region from an average of approximately 400–1500 kg ha^{-1} or more by 2020 through the establishment of 75–100 Cocoa Development Centers, each of which will support up to 20 Village Cocoa Centers.

The major partners in the Vision for Change program and their roles are as follows:

- Mars Inc. – investing in and steering the program.
- World Agroforestry Center – program management, facilitation to coordinate program activities, expertise and resources in cocoa agroforestry, soil management, and tissue culture.
- Center National de Recherches Agronomiques – collaboration on propagating selected high-yielding clones and creating gardens for tree culture.
- Agence Nationale d'Appui au Development Rural – conducting on-farm trials to demonstrate good agricultural practices and rehabilitation of old plots through grafting, and community development activities to benefit farming communities.
- Université de Cocody Department of Statistics – baseline socio economic and cocoa production system survey.
- Université de Bouaké Department of Anthropology and Sociology – baseline socio-cultural survey and cultural analysis.
- National School of Agriculture – strengthening capacity, conducting soil research and training.
- Conseil du Café et Cacao – monitoring, governance, and coinvestment for cocoa community empowerment.

The program also involves other stakeholders and sector investors including the Cocoa Board of Côte d'Ivoire, the World Bank, World Cocoa Foundation, bilateral donors, commercial suppliers, certifiers, and NGOs. The partnership is overseen by a high-level steering committee and a technical secretariat.

The Vision for Change program comprises three concepts: farm-level rehabilitation, community-level empowerment, and sector-level reform. At the farm level this involves the following:

- Providing farmers with quality planting material which relies on research into improved varieties through plant genetics and breeding.
- Rehabilitation of cocoa farms to produce high-yields through using modern, environmentally sustainable agricultural practices.
- Assisting farmers with the skills and tools needed to implement good agricultural practices that can reverse soil nutrient loss and reduce the need to expand cocoa farming into protected forest areas. This includes the effective application of fertilizers, sustainable soil management, pest and disease management, and improved postharvest practices.

Cocoa Development Centers, staffed by agronomists, showcase the best methods for improved and sustainable cocoa production, especially in rehabilitating old cocoa plots with superior planting material. They also provide training to staff of government agencies, local organizations, and private companies who can train farmers in good agricultural practices. Village Cocoa Centers operate as businesses in their own right run by local entrepreneurs. At these centers, local farmers can see best practice in operation, buy superior plant varieties as well as other farm inputs, and receive technical and agronomic advisory services. At the community level, the Vision for Change approach involves community empowerment activities aimed at improving the quality of life in cocoa communities and facilitating better access to public and private development funds.

At the sector level, Mars together with the Cocoa Board of Côte d'Ivoire and MoA work on policy issues and securing ongoing support and investment from public and private sectors. Although the program is currently only operating in Soubré, the partners hope that through effective demonstration of the Vision for Change approach, similar initiatives will operate in other cocoa producing areas of Côte d'Ivoire.

Successes

The success of the Vision for Change partnership depends on an alignment of the problem (i.e., the gap between supply and demand) and agreement on a common goal and vision among all partners. The interventions and activities of the program

support the Ivorian Government's 2QC Program (Program de Qualité, Quantité, Croissance (Quality, Quantity, and Growth Program)) to ensure the sustainability of coffee and cocoa production in the country. Mars is committed to a better supply of cocoa and farmer education because their business depends on the outcome. The effective engagement of national partners has required the private sector to understand the different mandates of government agencies and to invest considerable time and effort in capacity building and advocacy, making use of personnel with the right skills.

Achievements to date under the Vision for Change program include the following:

- The program has already reached 10 000 farmers through the establishment of 16 Cocoa Development Centers and 40 Village Cocoa Centers by 2013.
- Successful propagation of superior germplasm through grafting, embryo culture, and seed gardens; of 11 clones tested from 2010 to 2012, 40% were early maturing and produced 40–60 pods per year 15–18 months after grafting.
- Through rapid appraisal and rapid market appraisals, several indigenous plant species have been identified for diversification on cocoa farms based on farmer's preferences and market potential, including *Milicia excelsa* (Iroko), *Ricinodendron heudelotii* (Akpi), *Spathodea campanulata*, *Beilschmeidia manii*, and *Cola nitida*.
- Funding secured for community empowerment projects, such as the establishment of schools and village water supply systems.

Challenges

Not long after the Vision for Change program was launched in 2010, disputed elections in Côte d'Ivoire triggered a period of intense armed conflict and civil unrest, a great exodus of refugees, and the temporary paralysis of the cocoa industry. Donors and the private sector were initially hesitant to invest amid instability within the country and its government.

There have been ongoing challenges with the partnership, including ensuring timely delivery and technical and financial reporting. Clarifying the need to decentralize the production of planting material to ensure access by farmers and the use of different plant propagation methods to respond to demand were also preliminary challenges.

When the project was first proposed, many farmers believed that Mars and its partners wanted to increase production in order to reduce prices. There was considerable effort invested in communication from Mars, supported by national partners, to convince them that this was not the case. There has also been a need to overcome a mindset of extensive farming and resistance to grafting techniques through the establishment of demonstration sites.

Risk management activities have had to be implemented to address the threat of Cocoa Swollen Shoot Virus Disease. This has involved reviewing the state of knowledge of the disease, organizing training visits to neighboring Ghana and proposing a risk management protocol, and other measures to deliver planting material without spreading disease.

The challenge ahead of the Vision for Change program is to reach 150 000 farmers in Soubré through 1500–2000 Village Cocoa Centers by 2020. To achieve this goal, the program will focus on improved farm inputs that produce measurable income increases, integration of research outcomes into expanded extension services, diversification to ensure sustainable environmental rehabilitation and development of a business model for nursery operators, and the use of additional farm income for improved social services. It is expected to see a transformation of cocoa farming in Côte d'Ivoire from subsistence to entrepreneurial models leading to diversification within value chains and beyond.

Allanblackia

There are nine tree species in the *Allanblackia* genus, all of which are found in the moist forests of West, East, and Central Africa regions extending from Tanzania to Sierra Leone. The *Allanblackia* tree has been used for centuries as a source of edible oil, medicine, and timber. The seeds of the *Allanblackia* tree contain a solid white fat which has traditionally been used for cooking and soap making. It has now been identified as a potentially valuable ingredient for food products and cosmetics. With mature trees able to produce more than 10 kg of oil per year, 3 kg of seed can yield 1 kg of oil (Attipoe *et al.*, 2006).

Background

Around 2000, the multinational consumer goods company, Unilever, analyzed allanblackia oil and found that the oil's composition and structural properties were perfect for products like margarine and confectionary, and decided to explore using allanblackia oil in their supply chain. They began working with subsistence farmers in a number of African countries with the intention of creating a new edible oil crop for Africa grown in agroforestry systems. The strategy now being developed is to use participatory tree domestication to ensure that the farmers are beneficiaries of this initiative.

The partnership

An initial partnership was set up to develop wild harvesting supply chains for *Allanblackia* in Ghana and Tanzania. When it was realized that wild harvesting would not generate sufficient quantities of oil to make it commercially sustainable – only producing a maximum of 200 ton $year^{-1}$ – the initiative sought to create a planting program involving local farmers, focusing on domestication, and growing and planting as many trees as possible, while maintaining existing supply chains.

The Novella Africa partnership was formed in 2002 to work on establishing a sustainable supply of allanblackia oil through domestication techniques, tree management practices, and conservation strategies. The partnership involved more than 30 organizations at the international, national, and local level. Contributions were voluntary at the time, which allowed the project to become established with relatively limited investments. In 2006, a research and development program was established, led by the World Agroforestry Center, to generate the knowledge required to domesticate the species in village nurseries.

Difficulties in managing the project with respect to focus, mass, speed, and accountability led to a restructuring of the

partnership in 2009. A core team was formed, consisting of the following organizations, each of which bring specific expertise to the project and its key goal of proving that *Allanblackia* can be successfully scaled-up at large volumes with attractive prices:

- Unilever – business components, market outlet for *Allanblackia*, investment in product development and establishment of a supply chain.
- Local allanblackia companies: Novel Development Ghana Ltd., Novel Development Tanzania Ltd, and Project Novella Nigeria/Rivers State Sustainable Development Agency – implement local wild harvesting supply chain, link to farmers, and implement components of the domestication activities (planting).
- World Agroforestry Center – development of propagation methods, gene conservation, and integration of *Allanblackia* into agroforestry farming systems.
- World Conservation Union (IUCN) – research into the ecology and abundance of *Allanblackia*, sustainable harvesting, and biodiversity conservation.
- Union for Ethical Biotrade – certification to organic and fair trade standards.
- Form International – designing and implementing planting models.

The collaboration has been formalized via contracts between Unilever and the World Agroforestry Center, the local allanblackia companies and Form International. An independent chairperson heads the team. There is also a technical team that meets and reports regularly, and a web-based tool has been established to share project information.

Each of the partners is contributing to the project in-kind and financially. In addition to this, donors are and have been contributing to the project, including the International Fund for Agricultural Development (IFAD), The Dutch Ministry of External Affairs, Austrian Development Agency, Danish International Development Agency, UK Department for International Development, European Commission, German Federal Ministry for Economic Cooperation and Development (BMZ), Deutsche Gesellschaft für Internationale Zusammenarbeit (GIZ), the Swiss State Secretariat for Economic Affairs (SECO), Swiss Agency for Development and Cooperation (SDC) and Mars Inc.

The team composition and way in which the supply chain for *Allanblackia* operates varies in the three countries. In Tanzania, there is a shift from farmers' groups to a cooperative structure with greater private sector involvement. In Nigeria, the supply chain is government led.

Once collected, the *Allanblackia* seeds are dried and brought to collection centers where they undergo quality certification. The seeds are sent to central oil extraction facilities for extraction under the supervision of the local allanblackia companies. Most of the oil produced is being purchased by Unilever, although the food company Nutriswiss and a cosmetic company have also purchased allanblackia oil.

The World Agroforestry Center is leading the domestication process together with the NGO (Form International) and the local allanblackia companies. Initially, very little was known about the species and the seeds of the tree have proved difficult to germinate, taking more than 7 months. In the wild, a tree needs up to 10–12 years until it starts producing fruit. Although there is still significant work to be done, the first successes of the domestication program have been reported: seed germination has been reduced from 7 months to 90 days and the first generation of *Allanblackia* started fruiting after 6 years from seed.

Domestication efforts will continue to further develop 'superior trees,' through vegetative propagation, that will bear fruit in less than 4–5 years, grow vigorously, and fruit regularly with large fruit. Scientists are working with farmers to capture the most desirable traits from wild trees and reproduce superior types as clonal cultivars.

Experiments are performed on farms, in rural resource centers and specific pilot plots. Rural Resource Centers have been set up to disseminate allanblackia knowledge to farmers managed by national agriculture institutes, community groups, and local NGOs. These serve as diffusion hubs for new technologies, germplasm and knowledge. They have their own tree nurseries, motherblocks (plots with female trees with desirable traits) and demonstration plots, and train farmers in allanblackia propagation and cultivation techniques. The seven Centers also support private satellite nurseries in villages nearby remote farmers (Asaah *et al.*, 2011).

Currently, efforts are focusing on the mass production of seedlings of selected, superior trees, and the development of sound agroforestry systems for large-scale integration of *Allanblackia* with other crop production systems on farms.

Successes

The Novella Africa partnership is very much an African venture, with African research institutes, universities, and NGOs playing a key role. They actively work alongside harvesters, farmers, buyers, oil-seed crushers, and others in the private sector. The involvement of international institutions and significant donor support has been vital to establishing the project.

The commitment of current partners is demonstrated by the time and resources they are investing in the project. The success of the partnership relies on various factors, primarily:

- Transparency.
- Agreement on a common goal leading to common key performance indicators and the development of an agreed work plan.
- Sharing of information, best practices, and areas of key learning.
- Contractual arrangements, which specify the needs to be delivered.
- Monitoring (through a neutral arbitrator) to ensure medium- and long-term goals are met.
- Acknowledgment of successes.

More than 10 000 farmers have planted 200 000 *Allanblackia* seedlings in Tanzania, Ghana, and Nigeria. Functioning local supply chains are in operation in all three countries and there are approximately 250 local buyers that provide a link between harvesters and buyers. Fifteen rural resource centers are providing training and seedlings to farmers.

In terms of domestication, seedlings from 121 mother trees have been established in three genebanks and protocols for vegetative propagation (cuttings, grafting, and marcotting)

developed. Success rates in propagation continue to improve with close to 80% rooting achieved with cuttings and 70% with marcotting. The long seed dormancy period that has frustrated farmers in efforts to produce planting stocks is being reduced with 66% germination being achieved in 90 days.

A monitoring and evaluation program is being implemented which will provide the data needed to assess the future viability of the allanblackia business.

As far as environmental conservation is concerned, IUCN has produced guidelines on best practice for wild harvesting of *Allanblackia* and efforts are being made to ensure that the domestication program enhances biodiversity. For example, the integration of *Allanblackia* into small-scale cocoa farms is being promoted in West Africa to support more biodiverse and resilient agricultural landscapes (Jamnadass *et al.*, 2010).

Challenges

Currently, the potential market demand for allanblackia oil (estimated at more than 30 000 ton year^{-1}) cannot be met by harvesting fruits of wild *Allanblackia*, which yields about 200 ton year^{-1} although this fluctuates (Ofori *et al.*, 2013).

It may be 10–15 years before the first yields of significant size will become available, so keeping farmers interested and enthused is a challenge. Maintaining the wild harvesting supply chain is instrumental as it sets the example of how *Allanblackia* could contribute to increased and diversified income for farmers.

At the start of the project, the main challenge was to realize alignment between partners and for each to understand each other's interests. Individual organizations involved in the partnership are also under pressure from competing priorities and projects they are responsible for in addition to their work on *Allanblackia*.

The Novel Company that was originally established to implement the supply chain in Nigeria dissolved, although its role has now been taken over by the government-run, Rivers State Sustainable Development Agency. Novella Ghana is experiencing problems with supply chains.

As the project progresses through different stages, the partnerships are being reviewed on a regular basis to ensure the right organizations are involved for the right activities. When a partner no longer fits the criteria of the partnership it will be replaced.

In parallel with market-oriented and organizational challenges, the domestication of *Allanblackia* faces a number of constraints, especially in refining appropriate propagation protocols and in devising more efficient methods for delivering superior planting material to growers that is productive and meets farmers' needs. In addition, considerable work is required in understanding how to manage *Allanblackia* trees once they have been introduced into farmland in order that they are productive (Jamnadass *et al.*, 2010).

The project partners believe that several million farmers in Africa could benefit from the trade in *Allanblackia*, which could potentially grow in value to several million US dollars a year and become another significant cash crop in Africa. However, meeting the gap between current demand and supply will require on-going commitment from partners, additional investment in research, and buy-in from national governments and national organizations that can manage the supply chain and make it self-sustainable. In 2016 the project is expected to deliver sufficient data to conclude on the feasibility of upscaling *Allanblackia*.

Mango

The mango tree (genus *Mangifera*) is native to South Asia from where it has been distributed worldwide to become one of the most cultivated fruits in the tropics. It had been introduced to East Africa by the fourteenth century. There are currently more than 350 mango varieties propagated in commercial nurseries and orchards, with many more 'wild' varieties occurring on farms throughout the tropics.

Background

Poor mango production practices in Kenya have led to low-quality produce. Insect pests such as fruit fly and mango weevil, and diseases such as Anthracnose and powdery mildew are major challenges to increased production of quality mangoes. Lack of quality planting material, premature harvesting of fruits, the high cost of harvest losses associated with poor infrastructure, financial constraints, and limited access to markets prohibit smallholder farmers from receiving greater benefits from the mangos they produce. Little is known about the introduced varieties of mango in Kenya and most trees are of unknown seed origin.

The partnership

From 2006 to 2008, a PPP operated that involved cofinancing among the following partners:

- KEVIAN fruit processing company liaised with farmer groups and the out growers for quality control, organized collection of produce, processed fruits, forged links with potential consumers, and promoted local consumption of fruit juices.
- Kenya Gatsby Trust.
- International Center of Insect Physiology and Ecology.
- United Nations Development Program.
- German Technical Cooperation – provided funding for training, equipment, packaging materials, collection centers, and for personnel.
- MoA – trained farmers on the technical aspects of mango production, harvesting, postharvesting, handling, and marketing.
- Kenyan Federation of Agricultural Producers – contributed to organizing farmer groups and associations, trained farmer groups on agribusiness and assisted them in drawing business plans, and networking with stakeholders.

The project was geared toward poverty alleviation of smallholder mango farmers in specific districts in the Eastern, Central, Coastal, and Rift Valley provinces of Kenya through employment creation and local economic development. The aim was to achieve this through promoting mango marketing and value addition/sector development.

The partnership investigated more sustainable use of smallholder mangoes as raw material for cottage industries and for local processing of frozen concentrated mango juice for the domestic, regional, and overseas markets.

Combined, the investment by both public and private partners amounted to approximately €159 000 (US$233 411). These funds were used for activities ranging from training, equipment, packaging materials, collection centers, and personnel.

Successes

The partnership resulted in an improvement in the marketing position of 450 smallholder mango growers which led to an average increase of 42% in their income. Losses at the farm level were decreased by 40% and reduced wastage from farms and at the processing plant decreased by up to 40%. Links were also established between producer groups/associations and the processor.

Challenges

The group approach proved to be a challenge for the partnership, especially with regard to high transaction costs in managing the groups. It was also difficult to ensure quality standards as many smallholder farmers grow different varieties of mangoes leading to limited quality uniformity which negatively affects their income as well as that of the company. It proved to be more beneficial for large-scale farmers to have individual contractual agreements with the processing company but the disadvantage of this approach may be that poverty reduction is more limited. If focus is shifted to large-scale farmers, such as PPP would reach fewer people who in most cases are more resource endowed.

Rubber

The rubber tree (*H. brasiliensis*) is native to the Amazon rainforests of Latin America, but is now grown in many countries around the moist tropics. Latex is extracted from rubber trees using a spout that is inserted into the bark across the latex vessels, just deep enough to tap the vessels without harming the tree's growth. The latex contains approximately 25–40% dry rubber content. There has been a growing trend in recent years away from large-scale plantations to increased smallholder production from plantations, largely due to plantation owners switching to less labor intensive crops.

Indonesia is the second largest rubber producer in the world, supplying approximately 2.3 million tons per year. An estimated 87% of rubber cultivation in Indonesia occurs on smallholder farms averaging 2 ha in size.

Background

The production of rubber in smallholder agroforestry systems (jungle rubber) has been practiced by the communities of Muara Bungo district in Jambi province, Sumatra, Indonesia since 1904 and is the main source of income for smallholder farmers in the district. Rubber-tree gardens are grown in a multistrata system, which forms a secondary forest. Rubber trees are planted alongside other trees that provide local fruits, medicines, and timber for self-use or sale.

Ecologically these jungle rubber agroforests are important; they act as buffer zones for national parks, help maintain local biodiversity, provide watershed protection, and carbon sequestration (Ekadinata *et al.*, 2010). Approximately 60–80% of plant species found in neighboring forests can also be found in the rubber agroforests (Gouyon *et al.*, 1993).

Jungle rubber systems are under threat of extinction because of their low economic viability (Budidarsono *et al.*, 2010) compared with rubber monocultures or oil palm, an industry that is rapidly expanding in the province with plantations dominated by large companies.

Jungle rubber systems produce only about a third of the latex that is produced in intensive monoculture plantations. This is mainly because the trees are generally old and suboptimal planting material is used (Akiefnawati *et al.*, 2010). The quality of the rubber is also lower due to poor harvest and postharvest techniques.

Farmers generally sell their rubber at a low price to local traders, known as 'toke,' who tend to determine the price of rubber subjectively. Farmers can sell their rubber at a higher price to a biweekly rubber auctioneer but this can involve queuing for 2–3 days for the auction and payment. Farmers with higher quality rubber can sell directly to rubber-processing factories for up to 60% more than the cost they would receive from the toke, however, many farmers cannot afford to transport their rubber to a factory.

The partnership

Bridgestone Corporation learnt that the World Agroforestry Center had been working with farmers in Jambi and was keen to support the Center's efforts through its operations in nearby Medan, and to investigate the potential for increased 'dark-green' rubber supply. A Memorandum of understanding was signed by both organizations initially to investigate the potential for ecosystem-friendly (green) natural rubber and later to work together on improving the productivity and quality of jungle rubber.

A partnership was formed with the aim of improving the profitability of jungle rubber (and thus farmers' livelihoods) in the hope that farmers would be more willing to conserve their agroforestry rubber-tree gardens and be less likely to convert them into monoculture rubber or oil palm. The organizations involved and their roles were as follows:

- Bridgestone – funding for economic research and research into productivity.
- World Agroforestry Center – acting as an intermediary providing scientific inputs, sensitizing and connecting farmers with Bridgestone, and documenting outcomes of the work.
- Lembaga Ekolabel Indonesia (Indonesian Ecolabeling Institute) – feasibility study into eco-certification cofinanced by the Rewarding Upland Poor for Environmental Services (RUPES) project funded by the IFAD.
- Konsorsium Komunitas Indonesia – Warung Informasi Konservasi, a NGO – capacity development support in improved rubber harvest and postharvest techniques and environmental aspects of rubber agroforests.
- Waseda University Environmental Research Institute – economic research concerning jungle rubber.

Activities under the partnership were undertaken in the village of Lubuk Beringin, including:

- Investigating the potential for eco-certification of jungle rubber (i.e., whether farmers might be able to receive a

premium price for their rubber in return for maintaining the environmental services of jungle rubber ecosystems).
- Improved techniques for tapping rubber and use of different harvesting tools.
- Introducing a special acid as latex coagulant during postharvest and other techniques to: maintain the full dry content of rubber, produce slabs with regular form, and reduce wastage.
- Rejuvenation of some gardens with superior rubber clone seedlings (type PB 260) that can produce approximately three times more latex (Wibawa *et al.*, 2008).
- Organization of collective transportation to rubber processing factories through the establishment of the Agro Pores farmer's group.

Successes

Improving rubber quality can increase farmers' income from agroforestry, demonstrating that quality improvement could have an impact on conserving rubber agroforestry.

Wulan *et al.* (2006) and Roshetko *et al.* (2007b) have shown that the successful promotion of higher yielding rubber clones (rather than the collection of self-regenerated seedlings) and the better management of plants to reduce input costs and retain some biodiversity in rubber agroforests have led to greater profits for many Indonesian smallholders.

For eco-certification to succeed requires supportive policy. The information gained from the partnership will assist local government to address livelihood, conservation and land use planning issues, and determine what benefits can be gained from well-managed rubber.

Two farmer groups in Lubuk Beringin (Agropores: 15 farmers and Senamat Ulu 10 farmers) have been able to improve their harvest and postharvest techniques, resulting in higher quality rubber and higher quantities. This has given them the option of selling directly to rubber production factories and gaining higher prices.

Some farmers have changed the establishment and maintenance of their rubber gardens, for example, applying chemical herbicide and fertilizers, and fencing their gardens. Some have also used chemicals to catalyze and increase latex production.

The establishment of the farmer-led Agro Pores group has reduced transportation costs enabling farmers to sell direct to rubber-processing factories.

Farmers from Lubuk Beringin are now interacting directly with Bridgestone.

In the neighboring village of Senamat Ulu (not part of the partnership's work), some farmers have begun to implement the new techniques, demonstrating that the information is being transferred to some extent.

Challenges

The risk of farmers converting their agroforestry systems into monoculture into enhance their profitability remains. The achievements under the partnership have so far been limited to the village of Lubuk Beringin and there are no formal agreements that the innovations they have benefited from are a reward for their practices to maintain environmental services.

Different attitudes toward eco-certification exist within different companies, and though some are seriously considering investing in eco-friendly rubber, others are carefully considering that purchasing the product at a premium price may have a distorting effect on the global market.

There is a strong need for raising awareness about the ecological importance of rubber agroforestry and support needed for district and provincial level governments to champion eco-certification or implement any reward scheme that would protect jungle rubber from conversion into other land uses.

Jatropha

Jatropha (*Jatropha curcas*) is indigenous to Central America and produces a seed that can be processed into biodiesel suitable for diesel cars or further processed into jet fuel. The tree is grown extensively in India as well as in the Philippines, Pakistan, and Brazil for its oil.

For many years, farmers across subsaharan Africa have grown *Jatropha* as a fence, hedge, or windbreak. In many parts of Kenya it has been grown as a support for vanilla vines. In recent years, it has been widely promoted as a biofuel crop.

Background

The company, Energy Africa Ltd., was established as a social business in Kenya in 2006 with the aim of working with farmers to redefine local agriculture to produce new environmentally friendly food and oil crops that would be competitive and attractive to an international clientele. The company planned to reinvest profits from the production of *Jatropha* back into its operations.

At the time, the growing of *Jatropha* for biofuel feedstock was being aggressively promoted in Kenya by the private sector and NGOs for its potential to grow well almost anywhere, be resistant to pests and unattractive to browsing animals.

Energy Africa collaborated with 100 farmers in the Shimba Hills area, on the south coast of Kenya, to grow *Jatropha* trees for oil production. The farmers were provided with seedlings, information on how to manage the trees, and assistance with pest control. The trees were intercropped on farmers land, mostly as a support for passion fruit vines and grown alongside maize, beans, and other vegetables and fruits.

The seeds produced by the farmers are bought by Energy Africa for a guaranteed minimum price. They are pressed and filtered at a small facility the company has in the Shimba Hills and sold to select tourist establishments in Diani beach as an ecofriendly lighting source in place of imported paraffin or diesel.

The partnership

When Energy Africa was establishing its operations in Kenya, they felt a need to partner with local organizations also interested in *Jatropha* production for biofuel. Informal partnerships were formed among the following:

- Energy Africa – *Jatropha* growing as a social business.
- Norwegian University of Life Sciences – joint learning on the viability of *Jatropha* production.

- World Agroforestry Center – joint learning on the viability of *Jatropha* production.
- Global Environment Fund project – technical collaboration.
- Deutscher Entwicklungsdienst (the German Development Service) – development of various *Jatropha* products, in particular oil lamps.

Energy Africa together with the World Agroforestry Center established a test plot of *Jatropha* for provenance trials to determine the best planting material for the local area. This proved to be an expensive and time-consuming undertaking for Energy Africa.

Successes

Energy Africa continues to support 60 smallholder farmers who are growing *Jatropha*. The company purchases the seed produced by the farmers at a fair price and processes it into oil for one large hotel and other buyers.

The partnership has had success in linking farmers with markets but not in the development of *Jatropha* as a viable commodity in Kenya. Energy Africa is operating at a loss with regard to *Jatropha*; however, their work in securing investors and establishing networks of farmers and local partners has enabled the company to establish a successful business in fruits and vegetables. They work with approximately 10 outgrowers in Shimba Hills and sell fresh produce to a growing local market.

Challenges

Energy Africa ventured into *Jatropha* growing when it was being promoted as easy to grow, with high returns anticipated for biofuel feedstock. The farmers they collaborated with had high expectations for the trees they planted.

The reality proved quite different. Little information was made available on the difficulties associated with growing *Jatropha*, production costs proved much higher than expected and yields were low. The 60 000 trees that are still grown produce just 2 ton year^{-1} of seed from two growing seasons.

A survey of yields by Iiyama *et al.* (2013) found 79% of farmers in Kenya growing *Jatropha* obtained just 0.1 kg of seed per tree and 41% of these obtained no seed at all. The low yields were due partly to the use of inferior germplasm as well as poor farm management and to the planting of *Jatropha* in inappropriate environmental conditions. The study urges against the growing of *Jatropha* by smallholders in Kenya until further research can determine how best to increase yields. It suggests that significant returns for Kenyan farmers – and a useful contribution to climate change mitigation – would only be possible with the coordinated introduction of more productive planting material that is environmentally matched to local conditions and the adoption of suitable farm management methods.

There was considerable outside interest in the activities of Energy Africa and the informal partnerships which were established prolonged the company's investments in *Jatropha*.

Initially the company produced soap and locally made *Jatropha* lamps that it hoped would be popular in the local market. These proved too costly for farmers so now only some lamps are manufactured on demand.

The company has since shifted to growing vegetables and fruit with outgrowers and relies more on the resources within the company and local knowledge than on time-consuming partnerships with major institutions.

Other Examples of PPPs Relevant to Agroforestry

Partnerships through PES schemes and in tertiary agricultural education are broadly discussed here as types of PPPs that have relevance to agroforestry.

Payments for Ecosystem Services

PES schemes may be viewed as a form of PPP whereby a buyer provides monetary or in-kind incentives to a provider to implement activities that maintain ecosystem services.

Trees in forests, woodlands, agroforests, and elsewhere provide important ecosystem services including soil, spring, stream and watershed protection, animal and plant biodiversity conservation, and carbon sequestration and storage; all of which can ultimately benefit local communities' livelihoods (Garrity, 2004). Individual farmers can be encouraged to preserve and reinforce these functions in agroforests through PES schemes which provide them with monetary or in-kind rewards for their efforts.

The United Nations' Millennium Ecosystem Assessment (2005) established that the natural resource base is declining partly due to the lack of mechanisms to value aspects of nature (Redford and Adams, 2009), assigned as public goods and excluded from market transactions. A conceptual framework of ecosystem services categorized as provisioning, regulating, supporting, and cultural was developed to guide the understanding of the value of nature in order to better manage it. PES acts as a mechanism to enable these nonmarket values of ecosystem services to be included in economic transactions as incentives for local actors to provide such services (Engel *et al.*, 2008).

PES is perceived to be efficient and fair because of its use of positive incentives to cause improved environmental service production. Because the beneficiary directly pays the environmental service providers, PES has potential to reduce donor dependence (Kumar and Muradian, 2009). PES exists in many different forms with different levels of conditionality, efficiency, and fairness (Wunder, 2005; van Noordwijk and Leimona, 2010; Swallow *et al.*, 2009).

Examples of effective schemes

In Costa Rica, upstream land owners are paid to retain forest cover and implement other catchment conservation practices using a compulsory fee charged on top of tariffs from downstream water users (Pagiola, 2006). It is implemented countrywide ensuring that all watersheds are sustainably managed.

A Wildlife Works project in Kenya pays landowners a lease with some restricted-grazing easement for restoration of a wildlife migratory corridor between two national parks. Revenue from avoided CO_2 emissions, through farmers no longer practicing forest-burning methods and instead managing pasture, is shared with landowners. Local communities also

benefit through employment in a garment factory run by the company involved in partnership with big brand companies.

The CARE-WWF project, Equitable Payments for Environmental Services in Naivasha, Kenya operated from 2006 to 2011. It promoted PES between upstream landowners and downstream flower irrigation farmers. By supporting start-up costs, through capacity building and provision of inputs, desirable conservation practices, such as grass strips and the growing of fruit trees, were established which also improve household incomes. The local benefits rather than the regular payment from the downstream buyers are driving farmer performance. Many more farmers are seeking to join the scheme, however, the buyers cannot afford to pay them all.

A similar project promoted PES in the subcatchment of the Mfizigo River in Uluguru Mountains of Tanzania. The scheme was aimed at provision of watershed services by more than 450 farmers upstream to buyers downstream (the Dar-es-Salaam Water and Sewerage Corporation and Coca Cola Kwanza Ltd.). Payments were allocated according to hectares of land converted and the type of conservation practice adopted. The scheme was briefly successful but is now experiencing challenges dues to leadership changes within the companies.

The partnerships

Almost all PES projects have been initiated by NGOs, and many evolve from existing conservation projects and build on existing networks to introduce PES as a new approach. Community members are generally engaged through meetings and policy makers through policy briefs, publications, and workshops. Various methods are used to determine communities' willingness to engage, such as reverse auctions and household surveys.

Private sector engagement is facilitated through iterative dialog to raise awareness and present potential business cases for engagement. Research organizations, such as the World Agroforestry Center, often partner with local implementers to provide evidence (household surveys, models, biophysical, and action research) of the potential for various conservation interventions and PES approaches to deliver the desired outcomes for different stakeholders in natural resource management. The provision of biophysical and socioeconomic tools also enables parties to dialog and develop agreements for PES.

PES successes and challenges

Most PES projects involve initial investment of donor funding in capacity building and dialog with stakeholders through NGOs.

The strongest driving force for a successful PES scheme is the existence of demand for the ecosystem service by beneficiaries who also have the capacity to pay. This demand can be voluntary, mandatory, or a combination of the two. Voluntary schemes coming from a perceived business case of using PES play a small role in the markets and are sometimes transient. For example, in the Mfizigo River catchment, once the personalities that believed in PES left the companies PES was abandoned (Tom Blomley pers. Comm). Public support, mainly through legislation, is essential to drive the demand for PES; for example, through legal assertion of a minimum standard with sanctions for noncompliance. Alternatively, it can enforce payments by embedding them into regular obligatory public fees or tariffs, which are then distributed to landowners on conditional delivery of the ecosystem service (e.g., Costa Rica – Pagiola, 2006).

A satisfactory payment that is guaranteed drives performance; for example, Singkarak, Indonesia and Ecotrust (Carter, 2009) but this can depend on the level of satisfaction perceived by the parties. A project in the Sasumua watershed in Kenya through the World Agroforestry Center's Pro-poor Rewards for Environmental Services in Africa program estimated a potential net annual saving of approximately US$20 000 in sediment treatment costs from PES with grass strips. This was perceived to be too small to persuade the downstream potential buyer, Nairobi Water and Sewerage Company, to engage in PES (Mwangi *et al.*, 2011).

PES engagement needs to be perceived by both buyers and sellers as mutually beneficial. When downstream beneficiaries invest in start-up costs for interventions that have potential for local business spinoffs, local engagement can be sustained without dependence on regular subsequent payments, for example, Wami Mbiki (Richards, 2009).

With regard to agroforestry, Roshetko *et al.* (2007a) observed that the most important factor in determining smallholders' tree planting and retention behavior is the direct products and services they receive from trees. Smallholder agroforestry systems have the advantage of not only providing wider ecosystem services but also directly producing other marketable products (Leakey, 2001, 2010).

PPPs in Tertiary Agricultural Education

PPPs are emerging in Tertiary Agricultural Education Institutions (TAEI) to overcome constraints that include: decreased funding leading to insufficient and degraded teaching facilities and materials (Buchert, 2002; Atteh, 1996; Rivera, 2006); depleted human resources due to brain drain and exodus of experienced staff to other professions (Maguire, 2000); HIV (Gakusi, 2010); and in some cases conflict situations. PPPs serve to address the limitations of human resources and facilities to accommodate increasing student numbers (Atteh, 1996).

In relation to agroforestry, as in other fields of agricultural science, partnerships between the private sector and publically funded tertiary institutions offer opportunities for joint research, innovation, greater funding, and improved dissemination of knowledge.

Through PPPs, universities benefit from enhanced student learning, research production, enhanced interdisciplinary research, the creation of innovation Kezar and Lester (2009), and faster technology transfer (Krattiger, 2007). They are also in a better position to access investments in laboratories and equipment, student scholarships and funding for graduate research (Ssebuwufu *et al.*, 2012), and more likely to receive external funding (Kvale and Brinkman, 2009).

The private sector can benefit from collaboration with universities through shared facilities, university offered services, access to the expertise of universities and spread of new knowledge. Ssebuwufu *et al.* (2012) observed that African universities can play a central role in producing and spreading technical solutions for local challenges. In situations where a large number of students are attached to an industry or research institution, this provides an inexpensive labor force and

can also generate innovation. Organizations partnering with universities may also have the opportunity to influence TAEI curricula so that it can better fit current needs.

The UniBRAIN program

UniBRAIN is one such PPP that is currently being implemented through consortia in five African countries, linking education, research institutions, and businesses with the aim of improving education systems within agriculture, fostering innovation, increasing production, and improving supply chains. Each consortium manages an incubator project and among them are projects aimed at supply chain development for commodities that include coffee, tea, honey, mango, banana, and other local fruits. The incubatees vary from start-up enterprises to small and medium enterprises as well as enterprises that are expanding, diversifying, or experiencing challenges. **Figure 3** provides a simplified diagram of relationships and benefits among UniBRAIN consortia members and incubatees.

Success in incubator projects relies on effective collaboration between all partners, and that each UniBRAIN member gains certain benefits from participation, such as:

- Universities: career-enhancing research and research opportunities for postgraduates; funding for on-campus research related to innovations; access to private enterprise and research communities; opportunities for student placements; support for curricula change; and fostering of linkages and interactions with nonAfrican universities and capacity building institutions.
- Private sector: specialized technical support; premises with facilities and services; and the receipt of student placements. The existence of incubators can address supply chain challenges in a very direct way, for example, a business start-up can be formed specifically to address one step in supply addition for an agroforestry commodity.
- Research institutions: partnerships with business for commercializing products and technologies; collaborators and temporary staff support through attachments and internships; and collaboration in research to combine human and physical assets (ANAFE, 2013; FARA, 2013).
- Incubatees: assistance with business and financial planning; specialized technical support; mentoring; and premises with facilities and services and the receipt of student placements.

In general, all partners benefit through UniBRAIN from greater efficiency, effectiveness, and improvement of governance and management. Tang *et al.* (2010) argues that

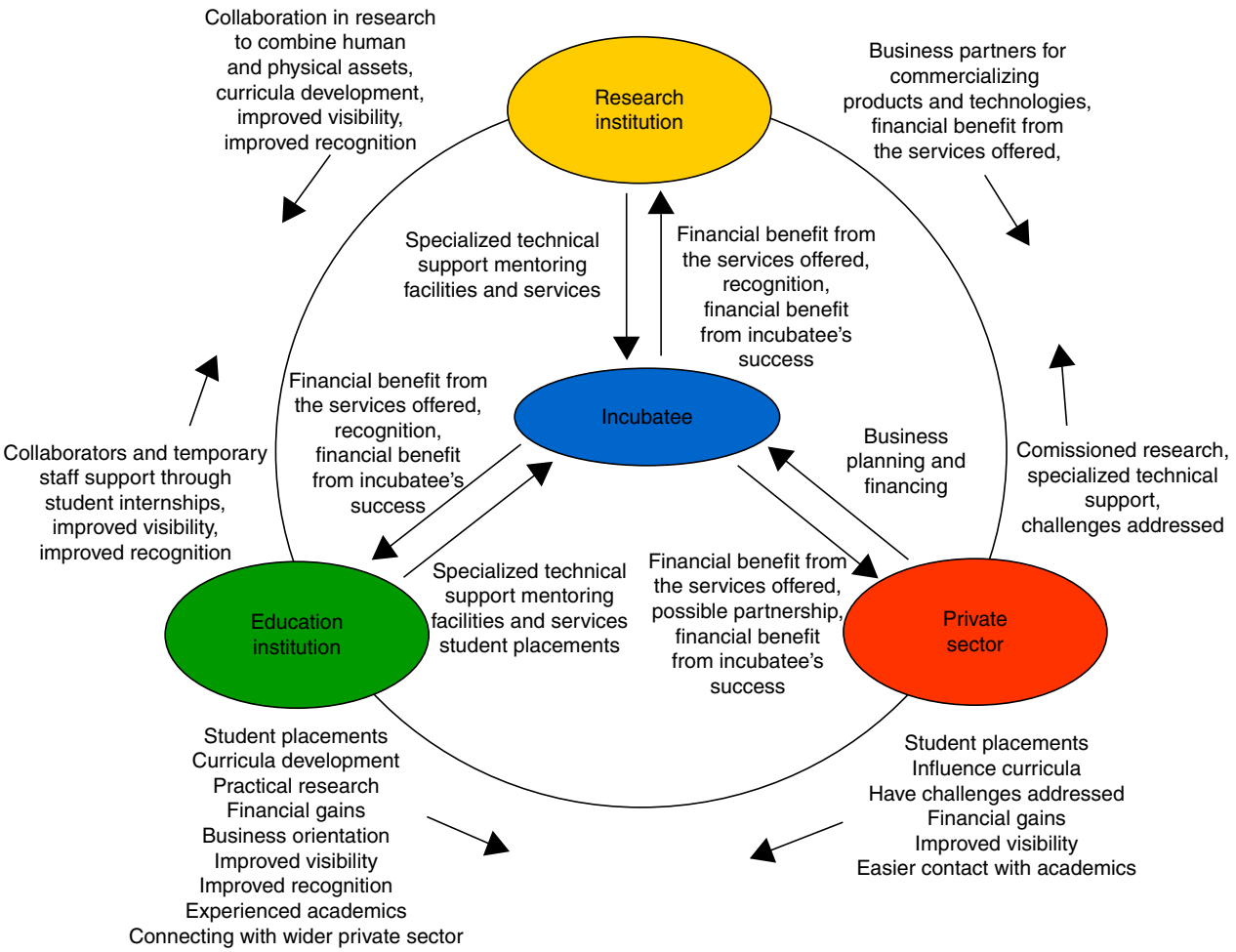


Figure 3 Simplified benefit flow among UniBRAIN members and incubatees.

UniBRAIN enables better risk management, clearer government policies, revealed critical success factors, improved maturation of contract, and more appropriate financial analysis.

Discussion

In agricultural research and development, PPPs are increasingly viewed as an effective way to conduct advanced research, develop new technologies, deploy new products for the benefit of smallholder farmers, and other marginalized groups in developing countries (Spielman *et al.*, 2007).

The PPPs in agroforestry profiled in this article can broadly be shown to be:

- Helping to lift smallholder farmers out of poverty through research and new technologies that improve the productivity and quality of agroforestry products and further develop new products.
- Helping farmers to benefit from market participation through establishing and improving the functioning of supply chains.
- Generating innovation through joint research.
- Integrating production with environmental management.

In the six case studies on PPPs in agroforestry analyzed for this article, poverty reduction was a central aim. The extent to which this is currently occurring or likely to occur in the future depends on the scale at which the partnership is operating, the particular product and the type of intervention. PES schemes that involve beneficiaries directly paying providers of ecosystem services are also geared toward poverty alleviation.

A number of the PPPs discussed in this article are helping to improve the functioning of supply chains and commercialize intermediary or underdeveloped agroforestry species; including: improving the marketing position of growers (rubber and mango), improving productivity (cocoa and *Allanblackia*) and expansion to meet demand (*Acacia*).

The PPPs concerning *Allanblackia* and cocoa provide examples of where private and public organizations are jointly conducting innovative research to develop and improve emerging and established agroforestry products. This is contrary to the findings of Spielman *et al.* (2007) whose analysis of PPPs in the CGIAR system did not find evidence of joint research on cutting-edge science with the private sector to generate innovation. Kezar and Lester (2009) found that universities can benefit from the creation of innovation through PPPs.

The partnerships in place to develop *Allanblackia*, cocoa, and rubber all incorporated strong elements of environmental management. These, together with PES schemes involving agroforestry, highlight the multipurpose nature of agroforestry in its ability to provide both commercial commodities as well as valuable environmental services.

Another potential impact of PPPs according to Spielman *et al.* (2007) is that they provide research organizations with insight into industry perspectives and change the way some centers do business, such as the shortest route to launching a product, the need to terminate projects when they fail to perform, and the importance of demand-side or market analysis. Although research organizations involved in the case studies presented here may be learning such approaches and in some cases adopting them, differences in the modes of operation between private and public organizations were often cited as challenges to the maintenance of effective partnerships.

Building Effective Partnerships in Agroforestry

The PPPs described in this article point to several factors that ensure partnership effectiveness, namely: agreement to a common goal, effective governance, monitoring, and the sharing of information. This supports the elements of a successful partnership outlined by Spielman *et al.* (2007): clear definition of the problem, its solution, and the resources needed to achieve the solution; establishment of benchmarks to gauge progress and decide on next steps; and effective communication channels to all key stakeholders through which to exchange knowledge, resolve conflicts, and change course as needed.

In nearly all cases, both public and private sectors were shown to be working toward a common goal in their partnerships.

Contracts, memorandums of understanding, steering, and technical committees were the common platforms for partnership management in the PPPs analyzed for this article. For a partnership to operate successfully, it was considered important to have a forum or system in place for addressing tensions or instances where one partner does not deliver on its obligations.

The monitoring of partnership progress in meeting medium- and longer term goals was deemed important under the majority of agroforestry PPPs and tended to occur at the strategic level.

Attipoe *et al.* (2006) suggest that open and constant communication between partners from different backgrounds is the only way to deal with misconceptions. This allows consensus to be reached and encourages innovation in reaching new solutions. At the technical level, information exchange in the agroforestry PPPs analyzed occurred primarily through meetings and reports. The potential for the withholding of information to threaten efforts and trust within partnerships makes information exchange a vital component to the success of any PPP.

Overcoming Obstacles in Agroforestry Partnerships

The main challenges associated with agroforestry PPPs covered in this article related to issues of difference in culture between private and public sector partners, investment of time and effort, overcoming risks, obstacles associated with public policy, and failures in reporting and delivery. Spielman *et al.* (2007) acknowledges that PPPs require contributions of knowledge from multiple actors across both time and space; contributions that are often difficult to manage and evaluate.

Although trust between private and public agencies is cited as an obstacle to PPPs – with Poulton and Macartney (2012) stating that it maytake time for private agents to gain trust in public sector partners – this did not appear to hamper the efforts in the agroforestry PPPs analyzed (**Table 2**). Private

Table 2 Goals, success factors, and challenges associated with public-private partnerships (PPPs) in agroforestry

		Allanblackia	*Cocoa*	*Rubber*	*Jatropha*	*Acacia*	*Mango*
Goals	Poverty reduction	x	x	x	x	x	x
	Market participation	x	–	x	–	x	x
	Innovation	x	x	–	–	–	–
	Environmental protection /management	x	x	x	–	–	–
Success factors	Common goal	x	x	x	x	x	x
	Governance	x	x	–	–	–	–
	Monitoring	x	x	x	–	x	–
	Information sharing	x	x	x	x	x	x
Challenges	Trust or attitudes	x	x	–	–	–	–
	Investment of time and effort	x	x	x	x	–	x
	Risks	x	x	–	x	–	–
	Policy	x	x	x	–	–	–
	Reporting	x	x	–	–	–	–

sector culture varies from that of research institutions and the public sector in general. The private sector is often interested in quick returns on investments, whereas researchers are keen to ensure the validity of their results. Researchers have an interest in publishing results which can provide a challenge when the private sector is hesitant about research entering the public domain before they have benefited from their investment.

Experience gained by the World Agroforestry Center more than the past 15 years in finding the most effective balance between different activities for the promotion of a new tree crop has shown that a coordinated strategy is needed that incorporates market, cultivation, and conservation elements (Leakey *et al.*, 2005, 2007; Leakey and Akinnifesi, 2008; Tchoundjeu *et al.*, 2006). Crucially, this involves addressing the different perceptions of various specialists involved in particular areas of work. For example, those supplying goods to markets can find it difficult to understand why it takes so long to conduct the research needed to bring a species into cultivation for the first time. At the same time, cultivation specialists operating in the public sector have only limited insights into the commercial pressures of markets, and they prefer to continue their research until optimal rather than sufficient solutions – which would be adequate for the private sector – have been developed for planting and farm management. There is frequently skepticism among conservation specialists about whether private industry is committed to long-term sustainable production.

The time and effort required to maintain an effective partnership is considerable, and for the majority of those involved in the partnerships presenting in this article, seen as vital to effective future cooperation.

According to Spielman *et al.* (2007) PPPs, carry some very unique risks, including those associated with coordinating diverse partners and interests; protecting the mandates, missions, and reputations of partners; and exchanging proprietary knowledge assets between public and private sectors. In the PPPs analyzed, communication between partners and more broadly to other organizations and stakeholders, together with investment in activities that ensure the continued commitment of partners, are important strategies to mitigate these risks.

Enabling policies and political commitment can be a constraint to private investment in supply chains (Poulton and Macartney, 2012). Although acacia production in Vietnam has succeeded because of government investment and motivation, future high-level investment in the cocoa sector in Côte d'Ivoire will require further efforts in policy development.

Ineffective or reporting failures and failure to deliver on commitments were described as partnership challenges in some of the agroforestry PPPs analyzed. This underlies the importance of putting sound governance structures in place to address tensions and conflicts.

Future Potential for PPPs in Agroforestry

Spielman *et al.* (2007) note that the number of cases where PPPs are leveraging private investment in poorly functioning agricultural supply chains is still limited. This is contrary to the number of collaborative efforts to develop new technologies between public and private sectors in the health sector, catalyzed by health investment funds that in recent years have led to companies seeking new models of drug development that combine social responsibility and commercial viability (Poulton and Macartney, 2012).

Challenge funds in agriculture that disburse grants on the basis of periodic competitive bidding processes do exist, and according to Poulton and Macartney (2012) encourage or hasten investment with high social returns.

The reliance on donor funding in addition to private sector investment of several of the agroforestry PPPs analyzed supports the need for further funds within the field of agricultural research to catalyze PPPs. Similarly for PES schemes, donor funding has been required in the early stages to build capacity and dialog. Poulton *et al.* (2006) identified that investments by both private and public actors are required to support service delivery to staple food producers in Africa.

Increasing pressure on government budgets across the world, especially in developing countries, necessitates partnerships between the public sector and the private sector to allow risks and benefits to be appropriately shared. Private expenditure on agricultural research and development is

Box 1 Enabling PPPs in kenya

Kenya's increasing population has compounded the challenge of ensuring food security in the country. A history of land grabbing and successive subdivision of family holdings prompted an overhaul of Kenyan land regimes, including the introduction of a new Constitution in 2010 with significant focus on land issues, in particular ensuring the equity, efficiency, productivity, and sustainability of land in Kenya (National Council for Law Reporting, 2012). The Constitution sets out the principles of sustainable and productive management of land resources, sound conservation practices and protection of ecologically sensitive areas. New legislation in the form of PPPs Act 2013 has also been enacted to regulate the relationship between the Government's resources and private market's growth potential. Under the Act, PPPs are defined as arrangements between a governmental party and a private party under which a private party:

- undertakes to perform a public function or provide a service on behalf of the contracting authority,
- receives a benefit for performing a public function by way of: compensation from a public fund, charges or fees collected by the private party from users or consumers of a service provided to them, or a combination of such compensation and such charges or fees, and
- is generally liable for risks arising from the performance of the function in accordance with the terms of the project agreement.

PPPs under the Act may be proposed in one of the two ways. A governmental party may procure a PPP through the determination of a project and the initiation of a tender process in which private sector participants (either individually or through a consortium) may bid. Alternatively, a private party may initiate a 'privately initiated investment proposal' provided that the private party can determine that there is significant urgency, the private party has expensive or unique intellectual property rights attached to the project, or they meet any other criteria which the minister may prescribe. Though no criteria have been prescribed as yet, it is likely that these will include projects involving agroforestry.

The types of PPPs specified in the Act vary considerably and include arrangements whereby a private party could lease land, operate and manage a facility or concession, or perform services on behalf of a public authority. Depending on the nature of the PPP project, a number of the options provided for in the Act may be appropriate for use in agroforestry partnerships.

The recent legislative and constitutional changes in Kenya taken together are profound and create an enabling environment for agroforestry PPPs. In addition, in order for the Government of Kenya to undertake its constitutional obligations under Article 69, it would be desirable for the Government to mobilize private sector resources through PPP structures.

increasing in some developing countries with greater domestic and global market opportunities, progress in the development of advanced agricultural technology, and stronger regulatory regimes that favor private investment (Pray and Fuglie, 2001; Pray, 2002). The introduction of the PPP Act in Kenya is one example of an initiative that may well open up new opportunities for private investment in agriculture (see **Box 1**).

In agroforestry, there are intermediary and underdeveloped products that have considerable potential with greater investment and private sector involvement. Ofori *et al.* (2013) believe the PPP for the domestication of *Allanblackia* provides a good model for the domestication of a traditionally important forest tree species of high economic potential which could be expanded to species, such as baobab, tamarind, and the medicinal species *W. ugandensis* and *Prunus africana*.

Ultimately, PPPs in developing-country agriculture are about reducing poverty by providing smallholders and other vulnerable social groups with new technological options. The case studies in this article reveal the potential for a variety of partnership approaches to be adopted in the development of new agroforestry commodities or to improve the market supply and functioning of supply chains for established agroforestry products to alleviate poverty.

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GUIDE TO USING THE ENCYCLOPEDIA

Structure of the Encyclopedia

The material in the encyclopedia is arranged as a series of articles in alphabetical order.

There are four features to help you easily find the topic you're interested in: an alphabetical contents list, cross-references to other relevant articles within each article, and a full subject index.

1 Alphabetical Contents List

The alphabetical contents list, which appears at the front of each volume, lists the entries in the order that they appear in the encyclopedia. It includes both the volume number and the page number of each entry.

2 Cross-References

Most of the entries in the encyclopedia have been cross-referenced. The cross-references, which appear at the end of an entry as a See also list, serve four different functions:

i. To draw the reader's attention to related material in other entries.
ii. To indicate material that broadens and extends the scope of the article.
iii. To indicate material that covers a topic in more depth.
iv. To direct readers to other articles by the same author(s).

Example

The following list of cross-references appears at the end of the entry Critical Tracking Events Approach to Food Traceability.

> *See also*: Agribusiness Organization and Management. Food Chain: Farm to Market. Food Labeling. Food Law. Food Packaging. Food Security: Development Strategies. Food Security: Food Defense and Biosecurity. Food Security, Market Processes, and the Role of Government Policy. Food Security: Postharvest Losses. Global Food Supply Chains. Government Agricultural Policy, United States. Regulatory Conventions and Institutions that Govern Global Agricultural Trade

3 Index

The index includes page numbers for quick reference to the information you're looking for. The index entries differentiate between references to a whole entry, a part of an entry, and a table or figure.

4 Contributors

At the start of each volume there is list of the authors who contributed to that volume.

SUBJECT CLASSIFICATION

Agriculture and People

Agribusiness Organization and Management
Agricultural Cooperatives
Agricultural Ethics and Social Justice
Agricultural Finance
Agricultural Labor: Demand for Labor
Agricultural Labor: Gender Issues
Agricultural Labor: Labor Market Operation
Agricultural Labor: Supply of Labor
Agricultural Law
Agricultural Policy: A Global View
Analyses of Total Phenolics, Total Flavonoids, and Total Antioxidant Activities in Foods and Dietary Supplements
Changing Structure and Organization of US Agriculture
Climate Change, Society, and Agriculture: An Economic and Policy Perspective
Computer Modeling: Policy Analysis and Simulation
Consumer-Oriented New Product Development
Crop Insurance
Determining Functional Properties and Sources of Recently Identified Bioactive Food Components: Oligosaccharides, Glycolipids, Glycoproteins, and Peptides
Farm Management
Food Chain: Farm to Market
Food Labeling
Food Law
Food Marketing
Food Security, Market Processes, and the Role of Government Policy
Food Security: Development Strategies
Food Security: Food Defense and Biosecurity
From Foraging to Agriculture
Global Food Supply Chains
Government Agricultural Policy, United States
Human Nutrition: Malnutrition and Diet
Industrialized Farming and Its Relationship to Community Well-Being
Intellectual Property in Agriculture
International and Regional Institutions and Instruments for Agricultural Policy, Research, and Development
International Trade
Investments in and the Economic Returns to Agricultural and Food R&D Worldwide
Markets and Prices
Mathematical Models to Elaborate Plans for Adaptation of Rural Communities to Climate Change
Policy Frameworks for International Agricultural and Rural Development
Production Economics
Quantitative Methods in Agricultural Economics
Regulatory Conventions and Institutions that Govern Global Agricultural Trade
Rural Sociology
Safety of Street Food: Indonesia's Experience
Social Justice: Preservation of Cultures in Traditional Agriculture
Vitamins and Food-Derived Biofactors

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Air: Confined Animal Facilities and Air Quality Issues
Air: Greenhouse Gases from Agriculture
Biodiversity and Ecosystem Services in Agroecosystems
Biodiversity: Conserving Biodiversity in Agroecosystems
Climate Change: Agricultural Mitigation
Computer Modeling: Applications to Environment and Food Security
Crop Pollination
Dust Pollution from Agriculture
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Economics of Natural Resources and Environment in Agriculture
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Natural Capital, Ecological Infrastructure, and Ecosystem Services in Agroecosystems

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Soil: Conservation Practices
Soil Greenhouse Gas Emissions and Their Mitigation
Soil: Nutrient Cycling
Virtual Water and Water Footprint of Food Production and Processing
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Precision Agriculture: Irrigation
Public–Private Partnerships in Agroforestry
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PREFACE

Food is absolutely necessary for human existence, yet for most in wealthy nations it is largely taken for granted because of its abundance. Sufficient food is a concern, however, for about 1 billion of the earth's inhabitants today who often go to bed hungry. Food security in a broad sense is becoming a worry of the future for those who understand the limitations of our earth's ecosystems. Malthusian prophecies have so far been wrong, but there is growing concern that we are rapidly reaching the point where feeding the world's growing and richer population will be at the cost to our environment that is unacceptable. In the next few decades we face the challenge of growing more food, with less water, with less fertilizer on less land – because of the growth of urban areas on prime agriculture land. We also face the largely unknown consequences that global warming will have on agricultural production. During the last century agricultural scientists were able to bring cutting-edge science into traditional agricultural practices and increase food production sufficiently to prevent global food shortages. The hope that new scientific discoveries will provide the means to keep ahead of world food demand is complicated by a growing public discomfort with biotechnology being applied to food production.

The concept of services being provided by the ecosystems of the earth is a fairly recent attempt to understand and place value on functions of natural lands that have historically been assumed to have few limits. In the past, if more food was needed, new lands were converted from forests or steppe lands into farm land and new water systems developed to provide the water needed for agriculture. When human populations were low our activities were largely buffered by the abundance of forest and steppe, but too late, we are beginning to understand that these provisioning services of our ecosystems are being overused and are no longer buffered by the abundance of wild lands and waters. We are rapidly losing our planet's biodiversity, irreplaceable ground water is being unsustainably consumed, and major river systems are being overused and polluted. Our oceans, the last place on the planet that still support our hunter and gathering traditions may not be able to sustain these activities into the future. And, food production and processing activities contribute to the greenhouse gas emissions that are rapidly warming our planet. Agriculture is the single greatest user of the earth's land and water resources. In the concept of ecosystem services, provisioning or providing food for all organisms is one of the services provided by ecosystems. Human population growth has and will continue to overtax the ecosystems we inhabit. The ultimate outcome of this major diversion of nature's resources into provisioning the human species is unknown, but it is critically important for us to understand what we must do to sustain our planet.

The breakthrough discovery about 10 000 years ago that plants and animals could be bred to provide a more abundant and secure food source was the foundation upon which all other human activities were able to flourish. Activities other than finding food now became possible and our diverse cultures were able to develop because of agriculture. Until fairly recently, however, the majority of the population of most nations was still directly involved in producing food. Mechanization of agriculture and continued improvements in genetics, fertilizers, and pesticides made food production very efficient in developed nations. In the United States, the leading nation in value of agricultural exports, less than 2% of the workforce is currently employed in producing food. The United States, however, is alone among the most populous nations of the world in having such a small population employed as farmers. In countries such as China, India, Indonesia, and Nigeria the majority of people are rural and involved in agriculture either directly or indirectly. But, as food production becomes more efficient in these countries, and as wages increase in other sectors, a major shift is occurring from rural to urban occupations. This revolution is potentially as important in affecting our cultures and community structures as was the development of agriculture. Many nations are currently experiencing a very rapid transition from rural to urban living with all of the social and logistic problems associated with such rapid structural changes. While this transition in our social and cultural structures is a broad subject, it does have significant impacts on agriculture and our food systems. To mention just a few, agriculture labor, food transport, food safety, and access to healthy food.

There is genuine concern among agricultural scientists that human populations and changing diets are outpacing our ability to meet the increasing food needs of the planet. In the first iteration by Academic Press in 1994 of the *Encyclopedia of Agricultural Science*, Noble Prize Winner Normal Borlaug wrote in its forward:

> Had the world's 1990 food production been distributed evenly, it would have provided an adequate diet (2350 calories, principally from grains) for 6.2 billion people – nearly one billion more than the actual population. However, had the people in Third World countries attempted to obtain 30% of their calories from animal products – as in the United States, Canada, or European Economic Community countries – a world population of only 2.5 billion people could have been sustained – less than half of the present world population.

The issue raised by Dr. Borlaug is probably the most important challenge we face. Human behavior and the food choices of consumers will determine the outcome of the race between food supply and population. Population control has been advocated for decades, and in some cases has become part of national policy, but the world's population continues to grow. Science breakthroughs cannot solve our food security and environmental quality challenges if consumers reject food that is not traditionally produced. Likewise, if meat products and other inefficiently produced food continue to be in high demand by consumers, there will be increased pressure on our food production systems. As supplies become short, prices rise. While this may be good for farmers, high food prices and food shortages will probably undermine our efforts to preserve the

world's remaining arable land as natural lands. We must change human behavior to solve the problems we face.

Food choices, nutrition, diets, food cultures, water and air quality, GMOs, global warming, food security, and similar topics are daily in the news throughout the world. We are all concerned about these issues, yet with all of the information easily available in the popular media about food there seems to be too little informed discussion on these various topics. In planning the *Encyclopedia of Agriculture and Food Systems* the editorial committee chose to organize the topics primarily by issues, rather than to focus on a traditional topic approach. We organized the issues that would be discussed in the chapters around the broad topics of Agriculture and People, Agriculture and the Environment, Agricultural Products, Plant Health Management, Animal Health Management, and Agriculture and Science. The issues raised in this preface are the ones that we felt needed to be addressed in this encyclopedia.

The associate editors joined me in the development of topics for the encyclopedia and were responsible for working with the authors – they deserve particular recognition. I was fortunate to be joined by a very distinguished group of colleagues who, I hope, are still friends. They spent much more time and effort in bringing this project to completion than any of us anticipated. I want to thank our authors who while overly committed and overworked, fulfilled their commitments to contribute to this work. I have been impressed with the quality of their contributions. The editorial staff of Elsevier have had the professionalism and patience to work with scientists who do not work under the same time and budget constraints that the staff work. I want to particularly thank Kristi Gomez, Donna de Weerd-Wilson, and Simon Holt who, each in succession, oversaw this effort, and I especially thank the project managers, who worked directly with me, and the associate editors, Kate Miklaszewka-Gorczyca, Will Bowden-Green, and Sam Mahfoudh.

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Quantitative Methods in Agricultural Economics

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Glossary

Computable general equilibrium These models are a class of theoretically based economic models that simulate the reaction of an economy to various changes in terms of prices, production, factor use, household income, and other items.

Econometrics Is the term given to a set of statistical and mathematical techniques used to analyze empirical data. Generally, econometric analysis aims at quantifying economic theories, testing hypotheses, forecasting future values of economic variables, and quantifying the effects of alternative government, firm, or individual decisions on economic outcomes.

Hypothesis tests They are statistical techniques used to determine whether or not a specific conjecture is supported by a particular data set. Hypothesis tests are formally stated as a null hypothesis that the specific conjecture is true and an alternative hypothesis that the conjecture is not true. A test statistic is constructed from observed data assuming that the null statement is true and the hypothesis is rejected if the calculated test statistic exceeds a critical level for its known distribution.

Linear programming Is a special case of mathematical programming where the objective function is linear as are the restrictions on the decision variables.

Mathematical programming It refers to a class of problem-solving techniques where one is trying to find the appropriate values of a set of decision variables so that an objective is optimized while obeying a set of restrictions on the allowable decision variable values.

Operations research It refers to the application of mathematics and the scientific method to decision making with the intent to improve the design and operation of the system studied.

Regression analysis Is a statistical tool for quantifying the relationship of one or more independent/explanatory variables to a dependent variable. Properly implemented, regression analysis can be used to determine a probabilistic statement of the extent to which changes in explanatory variables are related to changes in the dependent variables. The most commonly used regression technique is ordinary least squares.

Simulation It refers to a problem analysis method where one develops a computerized model of a system then uses that model to depict the reaction of the system to different operating decisions and/or levels of external stimuli.

Simultaneous equations They refer to econometrically estimated multiequation systems involving multiple interdependent variables. In simultaneous equation models, several dependent, or endogenous, variables are jointly determined by a set of explanatory, or exogenous, variables and error terms. Each equation may have one or more endogenous variables and one or more exogenous equations.

Introduction

Generally, agricultural economists use quantitative methods for three purposes. First, quantitative methods can be used in conjunction with observed data to discover how individuals behave when confronted with various economic stimuli and, in cases, to test the accuracy of economic theory. Second, quantitative techniques can be used to forecast economic trends and project the consequences of alternative decisions. Third, quantitative techniques can be used to resolve choices among decision alternatives. The methods employed for satisfying the above purposes can be broadly classified into econometric techniques that focus primarily on model estimation and hypothesis testing, and operations research (OR) techniques that are most commonly applied in agricultural economics research to optimization and simulation and often utilize model parameters obtained using econometric methods.

Econometric Estimation

Econometrics is concerned with describing and evaluating the relationship between a target variable, called the dependent variable, and one or more explanatory variables, often called independent variables or regressors. Under certain conditions a causal relationship is presumed from the explanatory variable

to the dependent variable and an equation is estimated in which the dependent variable is expressed as a function of the independent variables. However, many analyses are concerned with systems of simultaneous equations where independent variables influence a set of dependent variables, which also influence each other. In either case, economic theory and empirical observation guide the model specification and method of estimation. For general treatments of econometric modelling, see for example, Judge *et al.* (1985), Maddala and Lahiri (2009), Wooldridge (2010) and Greene (2011).

The basic ingredients in an econometric model are an assumed functional relationship between the dependent variable and the independent variables and an error term that allows deviations between predicted values of the dependent variable and its observed values. A widely used econometric model incorporates a linear functional relationship between the dependent variable and independent variables, along with an additive error term. This model is given as:

$$y_i = \beta_0 + \beta_1 x_{1i} + \beta_2 x_{2i} + \beta_3 x_{3i} + \ldots + \beta_k x_{ki} + e_i,$$

where, for the ith observation, y_i is the dependent variable, x_{1i}–x_{ki} are the independent variables, e_i is the stochastic error term or disturbance, and β_0–β_k are unknown parameters. The regression problem generally involves finding the β's so that some function of the error terms across the observations is minimized. Alternative functional forms can be used to express the relationship between the dependent variable and the independent variables and, generally, the error term need not be additive.

A model specification is not complete without specifying the characteristics of the error term. There are two main sources of randomness incorporated in the error term: unpredictable randomness in human behavior and the effects of a large number of unimportant omitted variables. It is commonly assumed that the error term has a mean value of zero and an equal finite variance for all observations.

Given data for the dependent and independent variables, the objective of econometrics is to obtain estimates for unknown parameters β_0–β_k. To achieve this goal, certain prerequisite conditions (assumptions) must be met. These assumptions vary depending on the estimator selected, but the following are commonly used.

1. The expected value (mean) of e_i is zero (i.e., $E(e_i)=0$, for all i, where i indexes the number of observations in the data set).
2. The variance of e_i is equal for each observation (i.e., $V(e_i)=\sigma^2$, for all i).
3. The explanatory variables x_1–x_k are nonstochastic (i.e., the explanatory variables are presumed to be determined from forces outside the equation and not related to the error term e_i).
4. Each explanatory variable contributes a unique influence on the dependent variable y (i.e., the explanatory variables are not perfectly multicollinear).
5. The model is correctly specified.

The first assumption is not restrictive. The second assumption is sometimes referred to as homoskedastic errors. Homoskedasticity can be violated in two distinct ways. First, the variances in error terms can be correlated across observations such that the probability of a positive error in one observation influences the error in adjacent observations. When the data are for sequential time periods (called time series data), this is referred to as serial (or auto) correlation, or more generally, intertemporal dependence. Second, the variances can differ by observation depending on the values of some subset of the explanatory variables. This condition is termed heteroskedasticity and is most common in cross-sectional data, which invoke observations across individuals or firms. The third assumption is sometimes referred to as fixed regressors. It implies that the explanatory variables come from an experimental process where the investigator sets the level of the independent variables and then observes the outcomes of the dependant variables; a rare occurrence in economic modeling. In fact, the explanatory variables can be stochastic so long as the distribution of the error term does not depend on any explanatory variable. The fourth assumption implies that the data representing the explanatory variables are not perfectly multicollinear; i.e., there is not an exact linear relationship among any subset of the regressors. The fifth assumption implies that the correct functional form is truly linear, that the model contains all relevant variables, but does not include any irrelevant variables, and that the model has an additive error.

Although it is not necessary, another commonly used assumption is that the error term is normally distributed. In small samples, statistical inference (hypothesis testing) is based on assumed normality of the error term. If sample size is large, approximate normality for inference can be established through the central limit theorem.

Each of these assumptions can be relaxed to obtain estimates of the unknown parameters β_0–β_k, and variance of the error term, σ^2. In addition, the validity of each assumption can be determined using appropriate hypothesis tests.

Empirical Estimation

Econometric estimation uses available data plus any additional information about the probability distribution of the error term to provide estimates of unknown model parameters, which form the predictive equation. The true, but unknown, parameter values are called population parameters. Parameter values obtained from data are called estimates. The criterion for obtaining parameter estimates from data is called the estimation method or simply an estimator.

Because estimation methods employ functions involving data that include the dependent variable, which by assumption contains error, the resultant parameter estimates are random variables. Only by coincidence will an estimated parameter estimate equal its 'true' population value, but as random variables, parameter estimates have sampling properties. Evaluating estimators' distributional properties amounts to characterizing their sampling distributions.

Desirable estimator properties

Unbiasedness means that if a parameter is estimated repeatedly from different data samples, the average value of the estimated parameter will equal the underlying population parameter. An estimator is efficient if it is unbiased and has no

greater variance than any other alternative unbiased estimator. Unbiasedness and efficiency are small sample properties that can hold for all sample sizes. But, if any assumption discussed in the Section Econometric Estimation is violated, unbiased, and hence, efficient estimators are not available. In such cases it is customary to apply estimators with desirable large sample properties. Consistency ensures that as sample size expands, the probability of an estimator being close to its true parameter value will increase. Sufficient conditions for consistency are that bias and variance both tend toward zero as sample size expands. Asymptotic efficiency is the large sample analog of finite sampling efficiency. An estimator is asymptotically efficient relative to any other if it is a consistent estimator and the variance of its limiting distribution is smaller than that of any other consistent estimator.

Some commonly used estimators

Estimators can be grouped into one of three categories: minimum distance estimators (including the most common technique, ordinarily least squares regression), maximum likelihood estimators, and method of moment estimators.

The commonly used ordinary least squares (OLS) criterion is a minimum distance criterion that produces parameter estimates that minimize squared prediction errors. Given a data sample of T observations, the least squares estimator obtains values for β_0–β_k that minimize the sum-of-squared residuals.

$$S = \sum_i e_i^2 = \sum_i (Y_i - \hat{Y}_i)^2,$$

where

$$\hat{Y}_i = \beta_0 + \beta_1 x_{1i} + \beta_2 x_{2i} + \ldots + \beta_k X_{ki}$$

OLS offers two major advantages over alternative estimators. First, it does not require specifying the error term's underlying distribution. Second, if assumptions 1–5 are met, OLS parameter estimates are unbiased and efficient.

Maximum likelihood estimation yields estimates of the unknown parameters that have the largest probability of giving rise to the sample that was actually selected. Maximum likelihood estimation requires assumption of a particular probability distribution function for the error term and computes the probability of the sample occurrence. The resultant equation is the probability function of the dependent variable outcome as a function of the values of the unknown parameters. Maximum likelihood estimates are those resulting from maximization of this function with respect to parameters to be estimated. When the error term is normally distributed, the maximum likelihood estimator is the same as the method of moments and OLS estimator just discussed. Under fairly general conditions, maximum likelihood estimators are consistent and asymptotically efficient.

Method of moments estimators simply replace population parameters with their sample counterparts. For example, the sample mean can be substituted for the population mean. A more general family of estimators, called general methods of moments (GMM) estimators, offers a flexible framework of econometric modeling. Compared with the maximum likelihood estimators, GMM estimators do not require distributional assumptions and therefore provide a viable alternative especially when plausible or manageable distributional assumptions are not available.

Statistical inference

Many times the investigator is only interested in estimating parameters for forecasting or simulation. Other times, the purpose of analysis is to test whether a particular independent variable is a significant factor in the equation for the dependent variable. In these cases estimates can be useful in their own right. In addition, more advanced hypothesis tests can be constructed that answer the question of whether the observed difference between a function of the estimated parameters and some hypothesized value is real or is due to chance variation. In application, test statistics are used to check hypothesis tests. Test statistics are based on estimated parameters and their sampling distribution. Two simple test statistics appropriate in small samples and when the error term is normally distributed are the t-test and F-test. The t-test is used to test a hypothesis concerning a single parameter (e.g., is β_0 statistically different from zero?) and is constructed as the ratio of an estimated parameter to its standard error. The F-test is used to test the truth of multiple parameter restrictions such as does a subset of the β's sum to zero and is constructed as the adjusted percent loss in sum-of-squared predicted errors from imposing a hypothesized linear restriction on a group of parameters.

Three more hypothesis testing procedures are available to test the truth of multiple parameter restrictions: Wald, likelihood ratio, and Lagrange multiplier (score) tests. The Wald test and score test can generally be implemented using any estimation procedure, but the likelihood ratio test requires maximum likelihood parameter estimation. The Wald test requires estimating only the unrestricted model and specifying the hypothesized restriction. This can be advantageous when the restricted model is difficult or impossible to compute. The likelihood ratio test requires estimating both the restricted and unrestricted model parameters. The likelihood ratio test statistic is computed as the ratio of the likelihood function evaluated at the restricted parameter estimates and the likelihood function evaluated at the unrestricted parameter estimates and hence is easy to implement when both the restricted and unrestricted models can be estimated. The score test requires estimating only the restricted model. Under the null hypothesis all three test statistics are distributed according to a Chi-square distribution with degrees of freedom equal to the number of parameter restrictions imposed. The null hypothesis is rejected when calculated test statistic values exceed critical values associated with a chosen level of significance.

Lastly, if the asymptotic distribution of a test statistic is overly complicated or one is concerned about the reliability of large sample approximation, there exist inference methods based on resamplings, such as the bootstrap and Jackknife methods. These methods are generally more reliable in finite sample settings, albeit computationally expensive.

Violation of Model Assumptions

In application, the assumptions stated above may be violated. In this section each model assumption will be considered

from three perspectives: (1) How can the validity of each assumption be checked? (2) How are the parameter estimate sampling properties altered if a particular assumption is violated? (3) What alternative estimators can be used to obtain desirable parameter estimates when standard techniques are inappropriate?

Homoskedastic errors

So far it has been assumed that the error terms are homoskedastic; the error terms have common variance at each observation. One possible violation of homoskedasticity is heteroskedasticity. Heteroskedastic errors have different variances and generally occur in cross-sectional data. An often cited example of heteroskedasticity comes from household savings models. In any particular time period, households can use earnings for consumption or savings. Suppose savings are modeled as a function of income. Low-income households must spend nearly all income on consumption items, but high-income households can consume or save. As a result, high-income households exhibit greater variance in savings than do low-income households. The error term in predicting savings is therefore generally found to be correlated with income. Under heteroskedastic errors, the OLS estimator is still unbiased, but it is not efficient. More importantly, estimated parameter variances from OLS are biased, invalidating significance tests and hypothesis testing.

A number of tests are available for detecting heteroskedasticity. Tests involve examining whether residuals from a regression are significantly affected by values of independent variables either through a second regression of the error term on a function of the independent variables or by examining whether groupings of the error terms for different ranges of the dependent variables have statistically different variances.

Estimation methods may be altered to correct for heteroskedasticity. Generalized least squares (GLS) estimators use a three-step estimation process to obtain efficient parameter estimates. First-round OLS estimation is used to compute error terms at each observation, then these errors are squared and regressed on the independent variables. The dependent variable and independent variables are then divided by the square root of estimated variance for each observation and OLS estimation is reapplied to the transformed data. GLS estimators are biased in small samples but they are consistent and asymptotically efficient.

Autocorrelation of residuals is another phenomenon that invalidates the homoskedasticity assumption. Autocorrelation occurs when error terms are correlated; i.e., when error term e_i is correlated with error terms e_{i+1}, e_{i+2},..., and e_{i-1}, e_{i-2},..., and so on. One explanation for autocorrelation is that factors omitted from the model are correlated across time periods. Autocorrelation results in unbiased but inefficient parameter estimates and makes hypothesis testing inappropriate. The most widely used test for autocorrelation is the Durbin–Watson test. It is based on OLS residuals and is appropriate for testing first order autocorrelation – correlation between e_i and e_{i-1} – when the model does not contain lagged dependent variables. Similar tests are available for testing higher-order autocorrelation and for testing autocorrelation in the presence of lagged dependent variables.

Maximum likelihood and GLS estimators are available that correct for autocorrelation. The GLS estimator involves transforming the data to correct for autocorrelation and then obtaining second-round parameter estimates using OLS. The data transformation requires estimating the correlation between error terms from OLS residuals, transforming the data to eliminate correlation between errors, and reestimating the transformed model using OLS.

Stochastic or endogenous regressors

Until now, it has been assumed that each model contains a single endogenous, or dependent variable; all other variables appearing in the model are independent or exogenous. This assumption is sometimes referred to as 'fixed regressors.' The crucial assumption is that each explanatory variable is independent of the error term, i.e., that random changes in the error term are not associated with changes in the explanatory variables. If this condition is not satisfied, the OLS estimator is both biased and inconsistent.

The fixed regressor assumption can be violated in two ways. First, an explanatory variable can be measured with error that is correlated with the disturbance term. Second, the economic system being examined may involve simultaneously determined 'endogenous' variables appearing as independent variables. Such variables are necessarily correlated with disturbance terms appearing in each equation. The classic example in agricultural economics models is a supply-and-demand model where price, quantity supplied, and quantity demanded are simultaneously determined. Consider a simple demand-and-supply model:

$$q_d = a_0 + a_1 p + a_2 I + e_d, \text{ demand function}$$

$$q_s = b_0 + b_1 p + b_2 C + e_s, \text{ supply function}$$

and

$$q_d = q_s, \text{ market identity}$$

where p is market price, q_s is quantity supplied, q_d is quantity demanded, I is income, C is production cost, a_0–a_2 and b_0–b_2 are unknown parameters, and e_s and e_d are stochastic error terms. Here p, q_s, and q_d are endogenous variables whereas I and C are the exogenous variables. Equilibrium price, quantity supplied, and quantity demanded can be obtained as the solution to the system of equations. A change in production cost, C, shifts the supply function causing a change in equilibrium price and quantities. Similarly, realization of an external shock through either error term reveals itself through a change in equilibrium quantities and price. As a result, price and quantities are stochastic variables that are correlated with the error terms in each equation. Both supply and demand are functions of price, a stochastic variable correlated with the error terms; hence, OLS is an inappropriate estimator for the unknown parameters. Before estimation can be considered, the fundamental question of whether the unknown parameters of interest in a simultaneous equations model are estimable must be addressed. The question that arises is: given information about the underlying model structure, is more than one theory, or set of equations, consistent with the same data? If so, the two models are observationally equivalent and

model parameters cannot be estimated. This issue is referred to as the econometric identification problem. For linear models, a necessary, but not sufficient, condition for parameter identification in any equation is that the total number of exogenous variables excluded from the equation must be at least as great as the number of included endogenous variables, less one. This result is known as the order condition of identification. A necessary and sufficient condition for parameter identification is given by the rank condition. In simultaneous equations models, each equation must be checked for econometric identification before any estimation technique is applied.

A general method for obtaining consistent parameter estimates when stochastic regressors are a problem is the instrumental variable (IV) method. An IV is one that is uncorrelated with the error term but is correlated with the explanatory variables in the equation. In the simultaneous equations model above, income would be a good instrument for price in the supply equation and production cost would be a good instrument for price in the demand equation. One special IV estimator is two-stage least squares (2SLS). 2SLS estimation is achieved by applying OLS in two stages. First, OLS is used to obtain predicted values for each endogenous variable using all exogenous variables in the system as explanatory variables. Second, endogenous explanatory values are replaced with their predicted values and OLS is used to obtain parameter estimates. 2SLS is a biased but consistent estimator; it is not efficient. Asymptotically efficient estimation must account for potential correlation among error terms across equations at the same observation. Systems estimators account for cross-equation correlation of error terms and are asymptotically efficient. Three-stage least squares is an IV type systems estimator. Maximum likelihood estimators are also available for simultaneous equations systems.

Hausman's specification test is a very general hypothesis test that can be constructed to detect endogenous variables. An OLS estimator is both consistent and efficient when the explanatory variables are exogenous, but is inconsistent in the presence of endogenous explanatory variables; in contrast, the IV estimator is consistent regardless of the endogeneity problem, but less efficient than the OLS estimator in the absence of endogenous variables. Hausman's test is based on the comparison between the OLS and IV estimators. The presence of endogenous variables cannot be rejected when the two set of estimates are significantly different.

The testing for and handling of endogeneity plays a fundamental role in modern econometrics, which strives to distinguish association from causal inferences. The former refers to functional or statistical relationships among multiple variables, whereas the latter indicates that a change in one factor is responsible for corresponding change in another variable. The main obstacle to establishing a causal relationship in social science such as economics is the endogeneity problem wherein both the explanatory variable and outcomes may be determined simultaneously, sometimes by other (confounding) factors. The IV approach is a popular method to tackle the endogeneity problem. Alternatively, one can use methods in the program evaluation literature, such as matching, propensity score, regression discontinuity, for causal inferences.

Multicollinearity

Multicollinearity is the term used to describe a problem that occurs when the independent variables are linearly dependent, i.e., when one or more independent variables can be exactly explained as a linear function of other explanatory variables. Multicollinearity causes one to be unable to isolate the individual effects of explanatory variables and leads to inflated variances in the estimated parameters. The problem is most extreme when each explanatory variable does not exert an independent effect on the dependent variable resulting in a situation of perfect multicollinearity where model parameters cannot be estimated. Multicollinearity appears most often in time series data where observations on the variables are over a number of time periods. Tests and corrective procedures for multicollinearity, such as ridge regressions, principal component analysis, and regularization methods, are available, but generally result in biased parameter estimates.

Functional form

Obviously, the adequacy of an estimated equation is greatly influenced by the choice of functional form. There are three important considerations in making such a choice. These are: (1) not excluding explanatory variables that should be included; (2) excluding superfluous explanatory variables; and (3) specifying an exact functional relation between the independent variables and the dependent variable. Exclusion of relevant explanatory variables results in biased and inconsistent parameter estimates and renders hypothesis tests inappropriate. Including extraneous explanatory variables results in loss of efficiency but does not induce bias in parameter estimates. Inappropriate functional form results in biased and inconsistent parameter estimates. Various model selection hypothesis tests are available for detecting whether or not an explanatory variable should be included in a model and the appropriateness of the assumed functional form.

Instead of imposing a fixed functional form, a flexible alternative is to let data determine the functional relationship between the dependent variables and independent variables. This approach is called nonparametric estimations. Popular nonparametric estimators include the kernel regression methods, spline regression methods, and neural networks. These methods are generally guided by some data-driven principles with the objective of minimizing certain loss criteria such as the mean square errors. Compared with parametric methods such as the OLS, nonparametric methods are more flexible albeit less efficient.

Special Situations

A number of special situations require alternative estimation methods. Three important situations occur with limited dependent variable models, nonstructural time series models, and panel data models.

Limited dependent variable models

There are many situations where the dependent variable of interest involves a yes or no, 1 or 0, outcome. Such models are called limited dependent variable or qualitative choice models. For instance, in analyzing farmer participation in

government programs one might have data on whether or not any particular farmer participated, along with explanatory variables for expected returns from participating and expected returns from not participating. Parameter estimates for models involving binary dependent variables are obtained using limited dependent variable estimation methods. In such a case, the outcome of the discrete choice is viewed as a reflection of an underlying continuous valued index function

$$y_i^* = \beta_0 + \beta_1 X_{1i} + \ldots + \beta_k X_{ki} + e_i,$$

where y_i^* is an unobservable index representing farmer i's desire to participate in the government program. The estimation technique is based on an assumed distribution and an approach that maximizes the probability of producing the decisions actually observed in the sample. The unknown parameters are typically estimated using either the probit model assuming the errors are normally distributed or the logit model when the errors are assumed logistically distributed. Both models are widely used and in practice there is little difference in the estimation results.

The regression coefficients from either model cannot be directly interpreted as the marginal effect of the associated explanatory variable on the dependent variable as is generally the case in linear models. The marginal effect of any explanatory variable on the probability of a yes decision outcome of the dependent variable is:

$$\partial E\frac{[y]}{\partial x_i} = f(\beta_0 + \beta_1 X_{1i} + \ldots + \beta_k X_{ki}).\beta_i,$$

where $f(.)$ if the probability density function of the error term.

Similar methods are available for other kinds of limited dependent variable models. For instance, multinomial logistic or probit models are commonly used to model multiple choice (e.g., mode of transportation), Poisson or negative binomial models are used for counting data (e.g., number of traffic incidents), and Exponential or Weibull models are used for duration analysis (e.g., length of unemployment).

Time-series models

Economic Time Series Analysis refers to the study of economic data observed in time sequence. Here, order of the observations is an important consideration, as the economy (e.g., agricultural economy) is viewed as evolving through time. The position of the economy in the past has something to say about its current and future position. Early work in this area studied univariate processes (representations for a single series of data, say wheat prices). The single series of data (X_1, X_2, …, X_T) is said to be covariance stationary if it returns to its historical mean and variance/covariance in a finite number of observations. Formal tests of nonstationary data were developed by Dickey and Fuller (1979), others followed in the literature. Here the null hypothesis in the series is nonstationary. If one fails to reject this null, usual practice is to consider the process that generates the first time difference of the series ($w_t = X_t - X_{t-1}$, $t = 2,\ldots,T$). If one rejects the null hypothesis of nonstationary on X_t, analysis is confined to the original series X_t. The number of differences is referred to as the order of integration and represented as $I(0)$ for no differences, $I(1)$ for 1 difference, etc. In economics it is common to find price series are integrated of order 1 (i.e., they are $I(1)$). Following the influential work of Box and Jenkins (1976) the series X_t or the stationary-induced series (w_t) can be parsimoniously modeled as an autoregressive integrated moving average (ARIMA) process:

$$\Phi(B)(1-B)^i X_t = \Theta(B)e_t,$$

where $\Phi(B) = (1-\varphi_1 B^1 - \varphi_2 B^2 - , \ldots , \varphi_p B^p)$ is a polynomial in the lag operator (B) such that $B^i X_t = X_{t-i}$ (post multiplying B^i by X_t takes p back in time i periods); $\Theta(B) = (1-\vartheta_1 B^1 - \vartheta_2 B^2 - , \ldots, \vartheta_q B^q)$; and e_t is a white noise innovation term ($E(e_t = 0)$ and $E(e_t, e_{t-k}) = 0$ for $k \neq 0$ and σ^2 for $k = 0$). The variables p and q in the above representation are finite integers, 0, 1,...,. Empirical work oftentimes finds these to be 0, 1, or 2. Specifying the orders p and q was originally accomplished by studying the autocorrelation and partial autocorrelation functions on data separated by k periods. More recent work studies statistical loss metrics, following Akaike (1971).

Generalization of the ARIMA representation over several variables ($X_{1,t}, X_{2,t}, \ldots, X_{M,T}$) has been studied as a vector ARIMA representation (Reinsel (1997)). Here X is indexed by both t ($t = 1,\ldots,T$) and m ($m = 1,\ldots,M$). Economic theory (or other relevant information) is used to select the set of M variables to study. Although the general Vector Autoregression-Moving Average (VARMA) representation is of some interest, most analysis is confined to the Vector Autoregression (VAR) or Vector Error Correction (VEC) process – arguing that the moving average components of the VARIMA representation can be approximated by a high-order autoregression. Sims (1980) introduced economists and agricultural economists to the VAR form and Engle and Granger (1987) introduced economists to the VEC form. The VAR and VEC forms summarize the correlation properties in contemporaneous and lagged time among the levels of the multiple time series (a levels VAR), their first differences (a VAR in first differences), or mixtures of levels and first differences (VEC). Here the Dickey–Fuller test of nonstationarity (or one of its alternatives) plays an essential role in model specification.

Early versions of multiple time series representations were labeled as atheoretic, as they placed few, if any, *a priori* restrictions on how the data interact in contemporaneous or lagged time. As such, they were heavily used in forecasting. More modern adaptations of the VAR and ECM forms look for structural restrictions on the contemporaneous innovations, garnering the former the label structural VAR (Sims, 1986). Structural VARs are often used in policy settings. Adaptations of structural VARs with statistical dimension reduction techniques and factor VARS are used in settings where the number of series (M above) is large (Bernanke *et al.*, 2005).

The parameters of the univariate ARIMA and the multivatiate VARIMA forms can be estimated by maximum likelihood methods. If we constrain our study of the VARIMA form to the VAR with every variable in every equation (what is known as the unrestricted VAR) OLS, estimated equation by equation can be used for efficient estimation. If one considers VARs where some variables are not included in the lag representations of other variables (a subset VAR) seemingly unrelated regressions provide efficient parameter estimates (Hsiao, 1979). The ECM is generally estimated with maximum

likelihood methods following Johansen (1988). A two-step procedure for a two variable ECM is described by Engle and Granger (1987).

Panel data models

Panel data refers to the type of data in which multiple units are observed for more than one period (Wooldridge, 2010). For example, if a household or farm survey follows the same set of households or farms for multiple periods, it is called a panel or longitudinal study. Panel data offer opportunities and challenges, both arising from the presence of unit-specific effects. Suppose each unit in a panel data has a time invariant individual effect, observing the same unit overtime allows researchers to account for the influence of unobserved individual effects, which is not feasible if each unit is observed only once. However, the pooled OLS is generally not efficient because of the individual effects, which violate the independence assumptions of the error terms. There exist two estimation methods that account for the individual effects: the fixed effects estimator and the random effects estimator. The former estimates the individual effects using dummy variables for the units, or removes the individual effects via demeaning or first differencing. The latter treats the individual effects as random parameters and uses an error component approach to construct a GLS estimator wherein the variance covariance matrix reflects the influence of individual effects. Generally the random effects estimator is more efficient, but is restrictive because it requires that individual effects are not correlated with the explanatory variables.

Operations Research Techniques

The field of OR is a broad one. Virtually all of the techniques in the field have been employed in agricultural economics applications. However, the most common applications involve mathematical programming and simulation.

Mathematical Programming

Mathematical programming is used to solve the problem of finding the best decision strategy from a set of allowable decisions constrained by scarce resources, minimum requirements, and other considerations. The mathematical representation of this problem is:

$$\begin{aligned} &\text{Max} \quad f(x) \\ &g_1(x) \leq b_1 \\ &g_2(x) \geq b_2 \\ &g_3(x) = b_3 \\ &x \geq 0, \end{aligned}$$

where the set of possible decisions is depicted by X, $f(X)$ is an algebraic expression of the objective to be maximized by the choice of X. The X decisions represent a set of nonnegative possibilities, which must also satisfy the constraints defined by the $g_i(X)$ functions. Here, each of the $g_i(X)$ and b_i relations are vectors so that multiple restrictions are potentially defined by each constraint equation plus some can be null so only particular types of constraints may be present. The solution to such a model contains information about the optimum values of the decision variables (X) as well as information on whether constraints are restrictive. Solution information is also provided, which tells how much the objective function would change with changes in the constraint constants (b_i).

A common use for such models involves the choice among production alternatives so as to maximize firm profits subject to resource availability limits. However, many applications involve objectives that are designed to simulate economic behavior (i.e., maximizing agricultural sector consumers'/producers' surplus yields a solution simulating a perfectly competitive agricultural sector).

The linear programming problem

The linear program (LP) is a special case of the above problem where all the functions are linear. In the LP context, the model becomes

$$\begin{aligned} &\text{Max} \quad CX \\ &A_1X \leq b_1 \\ &A_2X \geq b_2 \\ &A_3X = b_3 \\ &X \geq 0 \end{aligned}$$

Here, X is a vector of decision variables, whereas C gives the contribution of one unit of the decision variables to the objective function, and A_1, A_2, and A_3 give the usage of each constraining item by each decision variable.

There are two types of assumptions underlying the use of such a formulation. The first set of assumptions are mathematical and indicate that: (1) returns and constraint effects are strictly proportional to the level of the variables (proportionality); (2) there are no interaction terms between the variables (additivity); (3) the X values are continuous with fractional parts allowed (continuity); and (4) all parameters are known with certainty (certainty).

The second type of assumptions involves the model's ability to portray the actual decision problem. These are that the objective function, variables, and constraints are appropriate.

The linear programming model is the most common mathematical programming technique and can be applied to a wide range of problems. Consider two examples. First, suppose one is trying to decide on a least cost livestock diet while satisfying the animal's nutrient needs. An LP formulation of that decision problem involves minimization of feed cost (the objective function) whereas the variables depict the amount of ingredients, such as corn and soybeans, purchased. Simultaneously, the constraints impose dietary nutrient (e.g., calorie and protein) requirements that must be met (e.g., Saxena and Chandra, 2011; Masset *et al.*, 2009). Second, suppose one is trying to predict how one might coordinate operations across a food supply chain. In that case, LP formulations might be assembled depicting operation of different firms across that chain. The models then could be used to examine the gains from coordination and the effects see the review in Ahumada and Villalobos (2009).

Much of the mathematical programming literature reflects attempts to appropriately formulate LPs for different situations and ways of relaxing the LP assumptions to investigate the effects of the various model assumptions.

Relaxing linear programming assumptions

The following discussion elaborates on the character and relaxation of the LP assumptions.

- Proportionality
  The assumption in linear programming that the objective function value and the resource usage be strictly proportional to X is commonly relaxed both within and outside of linear programming. The LP-based techniques deal with cases where there are diminishing returns to scale. These techniques basically involve specifying multiple variables that represent the effects of the nonproportional phenomena over different ranges of activity. Thus, one might specify a variable that earns a $2.00 return for selling the first two units of firm output with a constraint limiting sales to two, then another variable selling an additional two units at $1.50, etc. This involves incorporating multiple variables and constraints with resulting discrete jumps in returns and/or costs. It is also possible to model a continuous change in returns by using more general nonlinear programming techniques. The most common involves techniques called quadratic programming (QP). This technique only relaxes objective function proportionality. The QP objective function is

$$\text{Max } cx + x'Qx,$$

  where $x'Qx$ reflects interactions between variables and negative entries on the diagonal of Q reflect declining returns to increases in X. One common application of this involves incorporating demand and supply functions into formulations.

  Proportionally can also be relaxed in the constraints by using multiple variables or through the use of general nonlinear programming techniques.
- Additivity
  The additivity assumption prohibits interactions among variables. Thus, the quantity of one commodity cannot affect the marginal returns or resource use of another commodity. This assumption can be relaxed within linear programming by specifying multiple activities, but its formal relaxation requires nonlinear programming techniques. QP formulations are commonly used to allow objective function interactions. Namely, when the off diagonal elements in the above defined Q matrix are nonzero then there are interactions between variables. Relaxation of the additivity assumption within the constraints requires the use of general nonlinear programming where, for example, production could be modeled as a nonlinear function of multiple inputs given that the inputs individually and collectively reflect diminishing returns to scale.
- Certainty
  The certainty assumption requires that the modeler assert that each and every parameter in the model is known without question. This is quite often unrealistic in that parameters in agriculture are often subject to weather variations and other random events. The most common way of relaxing the assumption involves the parameters in the objective function. Concepts from financial portfolio theory have been adapted where decision makers are assumed willing to reduce expected return to achieve a reduction in the variance of return. This is usually modeled within the QP model where the constant terms reflect average returns to X and the Q matrix reflects a measure of risk aversion times the variance covariance matrix of returns.

  There are many additional modeling techniques for handling other forms of uncertainty. Typically, the models depict reactions to uncertainty such that a conservative strategy is followed (e.g., one might maximize variability discounted returns while being limited by variability deflated resource availabilities). Uncertainty models also reflect varying assumptions about how uncertain events arise. The key differentiating factor involves the interrelation of decision timing and uncertainty resolution. Nonsequential models assume decision makers commit themselves at the beginning of the year and then discover the uncertain outcomes at the end of the year. Sequential formulations (commonly called stochastic programming with recourse) model an interrelated stream of decisions and uncertainty resolution. For example, when modeling an agricultural operation in a sequential setting, planting decisions are made under planting and harvesting season uncertainty but harvesting decisions are made with knowledge of what happened during planting season (e.g., see Chen and McCarl, 2000).
- Continuity
  The continuity assumption allows any variable to take on any value including fractional values. However, certain variables may only make sense if they take on discrete values. This is commonly the case when one is modeling capital investment where equipment must be purchased in whole units. If this is the case, then integer programming must be used. Integer programming restricts the values of certain of the decision variables to have integer values thus prohibiting fractional values.
- Appropriate objective function
  The final commonly relaxed assumption involves the choice of a single appropriate objective function. This assumption is relaxed by using multiobjective programming techniques, which define a set of several simultaneous objectives. When using this technique one simultaneously models all the objectives and establishes goal preferences under an assumed utility function structure. The portfolio model discussed in the Section Relaxing linear programming assumptions is the most common example of this approach where expected returns maximization and variance minimization are the two objectives. Such models are also common in developing country applications of model and in technology development settings (see Lee *et al.*, 1995 or Pohekar and Ramachandran, 2004).

Duality

An important aspect of mathematical programming involves duality. The solution of a model actually yields two types of

information: (1) allocation data involving both solution levels of the variables and quantities of resource usage and (2) valuation (or duality) data involving both valuation of constraint resources and estimates of the costs of forcing variables into the solution.

The duality information gives the objective function implications of a right hand-side alteration. Often this is interpretable as a resource value. For example, in a model maximizing profits subject to land and labor constraints, then the duality output would tell how much profits would increase with more land and labor. Duality information would also be present in a cost-minimizing diet model indicating the marginal costs of meeting dietary nutrient constraints. Solution valuation data are called the shadow prices and are found in all MP outputs.

The duality information also gives indications of how much it costs to force unutilized variables into the solution. For example, in a diet model, if a particular feedstuff was not used, the model would contain information indicating the cost of forcing the use of that feedstuff.

Other programming methods

The above review, by its nature, is an overview and does not cover many possible programming techniques. Other techniques include:

1. Analytical programming methods wherein solutions are characterized in an abstract fashion to gain theoretical insight into problem solution properties. In such a setting the theories involving duality, Lagrangian multipliers, Karush–Kuhn–Tucker conditions, and optimal control are relevant.
2. Dynamic programming and optimal control theory methods, which are concerned with optimizing multiperiod problems.

Simulation

Another commonly used OR technique is computer simulation. However, this technique, unlike the Mathematical Programming or Econometric techniques discussed above, does not have a fixed structure. Simulation models may use *ad hoc* functions, theoretically derived functions, and/or econometrically derived functions. The models may incorporate numerically based or mathematical programming-based techniques. Further, one may simulate certain or uncertain systems. Simulation has been used in many settings; worth brief mention here involve econometrically based, firm financial-, process-, biophysical-, and programming-based. The econometrically based simulations include cases where an econometric model with dynamic properties is simulated over time under, for example, alternative policies. The firm financial simulations depict wealth, debt, as set accumulation, etc., under differing firm decisions and/or policy environments. The process-based simulations depict firm performance under changes in firm characteristics (e.g., truck congestion at a grain elevator as affected by new dumping capacity). The biophysical-based simulations depict plant or livestock growth under differing management and environmental regimes. The programming-based simulations use mathematical programming models to depict reactions of the modeled entity to alterations in parameters caused by the firm investment, the environment, or policy alterations. Given this wide variety of uses, a rigorous discussion of simulation techniques is not possible in this short space; rather the reader is referred to the Survey of Agricultural Economics Literature.

Computable General Equilibrium

Computable general equilibrium analysis generally refers to a situation where a whole economy is modeled and one incorporates commodity price formation, total production, household consumption, household income formation, income, price-related consumption demand, factor price formation, factor supply, intermediate goods consumption, and factor/commodity price-dependent production. The overall model is generally set up to simulate an overall equilibrium in the product and factor markets with household consumption driven by household income and intermediate consumption driven by an input–output (social accounting) matrix. A set of simultaneous nonlinear equations characterizes this equilibrium (see Dixon and Jorgenson (2012) or Burfisher (2011) for broad coverage). Such models are typically applied in settings where the items being studied have broad implications across the economy or where agriculture is a dominant sector. Both of these settings involve major implications for household income and in turn consumption. From an agricultural viewpoint, applications often involve highly aggregate representation of agricultural commodities (sometimes all goods, other times groupings into major classes like grains, oilseeds, livestock, and other), regions, and factors (often capital and labor with some representing land, water, and fossil fuels). Hertel (2002) discusses the character and relaxation of such representations. Computable general equilibrium is a complex broad field and readers wishing details are referred to Burfisher (2011), Hertel (2002), Dixon and Jorgenson (2012), and Löfgren *et al.* (2001).

Using Quantitative Techniques

Quantitative methods are applied in agricultural economics as a means of achieving an end. As such, the authors close with a discussion of how the methods reviewed are used in the three problem settings mentioned at the beginning of the article.

First, let us consider the use of quantitative methods to discover information about the influence of certain factors. In such cases, econometric techniques are commonly used to fit functions based on observable data. The accompanying statistical significance tests allow investigation of whether particular items significantly influence our ability to predict behavior and whether the influences conform with economic theory. However, the line between the techniques is blurred as it is quite common at present to develop econometric estimates using mathematical programming techniques. It is also common to use programming, computable general equilibrium, and simulation models in a comparative statics setting to see how certain policy, resource, or other changes influence economic outcomes.

The second problem posed above involved forecasting economic trends and the consequences of decisions. Econometric techniques are most amenable to forecasting future values of various economic items of interest. For example, one may construct a forecast of the near term inflation rate. However, as the time frame gets longer and more variables become involved in the process, one needs to move toward simulation. Econometrical simulation forecasts are most appropriate where the forecasted behavior is felt to be reasonably extrapolated from the past observations used in forming the econometric model. Forecasts from programming computable general equilibrium and noneconometric-based simulations are relevant when the extrapolation of past behavior is not felt to be in order. However, the use of such techniques requires adoption of a considerably larger set of assumptions. Namely, under the econometric technique one must choose independent variables and functional form whereas under the other techniques all the data must be specified as well as the objectives or market clearing conditions pursued, the functional forms, the variables, and the constraints. Nevertheless, if one assumes that an OR model adequately represents the decision situation, then one can use it to predict the consequences of things that alter model data. This includes forecasts of the consequences of technological change, environmental change, alterations in farm policy, and new equipment investments.

The traditional role of mathematical programming, computable general equilibrium, and simulation models is widely felt to be in the third problem setting where one is trying to resolve choices among decision alternatives. However, this is not the most common use of such techniques in agricultural economics. Usually these models are not adequate enough to directly resolve choices but rather are used as decision-making aids and forecasting tools identifying the consequences of select developments or decisions. Finally, such models are commonly supported by data derived through econometric or simulation-derived estimates of parameters.

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Quarantine and Biosecurity

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Glossary

Containment The application of phytosanitary measures in and around an infested area to prevent spread of a pest.
Control (of a pest) The suppression, containment, or eradication of a pest population.
Emergency action A prompt phytosanitary action undertaken in a new or unexpected phytosanitary situation.
Entry (of a pest) The movement of a pest into an area where it is not yet present, or present but not widely distributed and being officially controlled.
Eradication The application of phytosanitary measures to eliminate a pest from an area.
Incursion An isolated population of a pest recently detected in an area, not known to be established, but expected to survive for the immediate future.
Introduction (of a pest) The entry of a pest resulting in its establishment.
Outbreak A recently detected pest population, including an incursion, or a sudden significant increase of an established pest population in an area.
Pest Any species, strain, or biotype of plant, animal, or pathogenic agent injurious to plants or plant products. Note: In the International Plant Protection Convention, plant pest is sometimes used for the term pest.
Pest-free area An area in which a specific pest does not occur as demonstrated by scientific evidence and in which, where appropriate, this condition is being officially maintained.
Pest risk (for quarantine pests) The probability of introduction and spread of a pest and the magnitude of the associated potential economic consequences.
Pest risk management (for quarantine pests) The evaluation and selection of options to reduce the risk of introduction and spread of a pest.
Quarantine The official confinement of regulated articles for observation and research or for further inspection, testing, or treatment.
Surveillance An official process which collects and records data on pest occurrence or absence by survey, monitoring, or other procedures.

Introduction

Biological security or biosecurity is a set of measures that protect the economy, environment, and community from harm from pests and diseases. This can be simplified to safeguarding of resources from biological threats (Sharma *et al.*, 2008). Biological threats can be defined as any organism (including biological material) that has the potential to harm people's health and life, food and agriculture, the environment, and the economy. Biosecurity encompasses all policy, planning, legislation, science, and underpinning operations to minimize the introduction, establishment, spread, and impact of harmful organisms that pose threat to our resources.

An Internet search for the word 'biosecurity' provides over a million hits with several definitions that may vary in scope and priority but their intent is broadly very similar. Biosecurity is a more proactive concept, a multilayered approach, a shift from zero risk to managed risk, from barrier prevention to border management (Beale *et al.*, 2008).

Quarantine versus Biosecurity

Border quarantine is an integral component of biosecurity. The term 'quarantine' has its origin in the Italian word '*quarantina*,' which means 40-day period and is largely associated with isolation, segregation, and disinfestation at the border. It includes a period of time during which the carrier of a suspected harmful organism is detained generally at a port of entry under enforced isolation to prevent the harmful organism from entering a country. It is an enforced isolation or restriction of free movement imposed to prevent the spread of the harmful organism.

The term 'biosecurity' is much broader in scope than quarantine. The origin of the term 'biosecurity' is not known; however, according to New Zealand's publication Biosecurity Issue 35 (May 2002) …New Zealand's Biosecurity Council chair John Hellstorm can take credit for coining use of the word biosecurity from his days at the Ministry of Agriculture and Forestry when a term was being sought for what eventually became the Biosecurity Act 1993. …The word acceptable to all the interested parties and the rest, as they say, is history. …It should be noted, though, the international use of the word biosecurity is still limited.

Bioterminology

The term biosecurity is often used in the same context as biosafety, bioterrorism, and in some instances biodiversity (biological diversity). The four terms are also often interchanged, with some believing that they have the same meaning, when in actual fact both biosafety and bioterrorism are parts of biosecurity, whereas biosecurity aims to protect biodiversity.

Biosafety refers specifically to the safety procedures and containment requirements associated with working with certain biological material. It includes products arising from biotechnology, such as living modified organisms. For example, as a biosafety measure, scientists working on the Ebola virus are required to adhere to strict biosafety regulations to ensure that they are not exposed to the virus and to prevent its escape from the laboratory.

Bioterrorism generally refers to the deliberate introduction or misuse of biological organisms or their products with the aim of causing harm. For example, the deliberate introduction of a biological organism into a food supply chain would be considered bioterrorism. The broader management of the bioterrorism event (containment, eradication, detection, diagnosis, risk assessment, and mitigation) falls within the scope of biosecurity.

The Convention on Biological Diversity (CBD) defines biodiversity as the variability among living organisms from all sources including terrestrial, marine, and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species, and of ecosystems. Effective biosecurity is an important requisite for the conservation of biodiversity. Preventing the introduction and spread of invasive species including pests, diseases, and other organisms through biosecurity measures is important, not only for food security and agricultural health, but also links directly with the prevention of biodiversity loss (Outhwaite, 2010).

Globalization and Biosecurity

There are approximately 70 000 pest species and diseases that damage agricultural crops worldwide (Pimentel, 2009). Many of these pest species and diseases are localized in distribution. The likely consequences of globalization raise significant biosecurity concerns because of the unprecedented increase in the movement of goods and people, which can be potential carriers of pest species and diseases. Approximately 1 billion people travel internationally and over 8 billion tons of goods are transported via sea and air routes every year. The danger of globalization is the potential for international and intercontinental distribution and establishment of harmful organisms in different ecological regions. Incidents of infectious diseases appear to be increasing.

The plant sector, the source of food and feed worldwide, is facing increasing outbreaks of pests and diseases that significantly diminish food production and availability. There are frequent reports of detections of new pests or diseases in different parts of the world. Stem rust of wheat (caused by the fungus *Puccinia graminis* f. sp. *tritici* Ug99 strain), citrus greening (caused by three strains of the bacterium *Candidatus Liberobacter*), Pierce's disease (caused by the bacterium *Xylella fastidiosa*) of grapevine, citrus canker (caused by the bacterium *Xanthomonas axonopodis*), zebra chip disease of potato (putatively caused by the bacterium *Candidatus Liberibacter solanacearum*), and Varroa mite (*Varroa destructor*) pest of honeybee are just a few examples of threatening pests and diseases spreading to new regions during the past 15–20 years.

With the massive increase in movement of people and goods, accompanied by climate change, an increase in the emergence of new pest and disease threats is inevitable. Named plant viruses have risen from less than 380 species in 1991 to more than 1000 species today (Brendan Rodoni, personal communication). There is enhanced potential for the dispersal of potential pest species, creating fresh opportunities for them to move to new geographical regions, find new vectors, new hosts, new environments, and new opportunities for some to hybridize and form new species, strains and biotypes. Exotic invasive pest species and diseases are estimated to cause a US$ 1.4 trillion loss per year worldwide (Pimentel *et al.*, 2001). These pest and disease-induced losses are likely to increase significantly if potential pest species and diseases continue to spread to new regions. As such losses are much higher in developing countries, which lack effective biosecurity systems to safeguard their plant and animal resources from pests and diseases.

Drivers Underpinning Biosecurity

The three key drivers that underpin biosecurity are the economy, the environment, and social factors.

Economic drivers reflect the impact pests and diseases can have from a commercial perspective, including farm production losses (crops, meat, and milk), trade (import and export), and market access. Pest and disease incursions can affect the ongoing supply of agricultural products to the domestic market, and the commerce associated with the entire supply chain is also at risk. For example, an exporting country must show that their product is of acceptable quality to the importing country, which includes being able to demonstrate that the products are free of the pests and diseases appearing in the regulated pest and disease list of the importing country.

Environmental drivers include the impact that pests and diseases can have on both the natural and built environments. This includes natural ecosystems (flora and fauna), amenity (parks and gardens etc.), sustainability of crops and land for cropping, and buildings and infrastructure. Most pests and diseases have at least some commercial impact, but many also cause environmental problems and it is difficult to estimate their economic impact. For example, in 2009, the US Forest Service estimated that throughout the US approximately 169 million acres of forested habitat with maple species is vulnerable to attack from Asian longhorned beetle (ALB), Anoplophora glabripennis (Motschulsky). The estimated maximum potential national urban impact of ALB is a loss of 34.9% of total canopy cover, 30.3% tree mortality (1.2 billion trees) and value loss of US$ 669 billion (Nowak *et al.*, 2001).

Social drivers are those that may affect our social or psychological well-being and include the destruction of growers' crops or farm viability, loss of recreational facilities (e.g., walking/hiking trails), and food availability (food security). Consider the effect that destruction of a crop that is affected by a pest or disease might have on a growers' annual (or longer term) income. Lifestyle and livelihoods are not something that most people would consider when they think of a pest or disease; however, these must be taken into consideration when assessing the impact a pest or disease may have.

The International Biosecurity Framework

Globally, biosecurity is governed by several international agreements. The International Plant Protection Convention (IPPC) covers the protection of plants and plant products, animal biosecurity is governed by the World Organization for Animal Health (Office International des Epizooties; OIE), and international public health (human biosecurity) falls under the World Health Organization (WHO). As biosecurity underpins trade, the World Trade Organization's (WTO's) Sanitary and Phytosanitary (SPS) Agreement applies to all SPS measures that may, directly or indirectly, affect international trade. These measures must be developed and applied in accordance with the provisions of this agreement. In addition, through the framework of the CBD there is an increasing interest from the environment sector in utilizing existing standards, capacity, and expertise, when it is relevant to invasive species in the environment. Governments that are signatories must abide by the obligations outlined in these agreements or conventions.

Animal Biosecurity

The importance of animal diseases and their control led to the creation of the OIE through an international agreement signed in 1924. In 2003 the Office became the World Organization for Animal Health but kept its historical acronym OIE. The OIE is the intergovernmental organization responsible for animal health and biosecurity worldwide. It is recognized by the WTO and in 2012, has a total of 178 member countries and territories. The OIE maintains permanent relations with 36 other international and regional organizations and has offices on every continent. The mission of the OIE is to guarantee the transparency of animal disease status worldwide; to collect, analyze, and disseminate veterinary scientific information; to provide expertise and promote international support for the control of animal diseases; and to guarantee the sanitary safety of world trade by developing rules for international trade in animals and animal products.

Plant Biosecurity

The IPPC is an international plant health agreement, established in 1952, that aims to protect cultivated and wild plants by preventing the introduction and spread of pests and diseases. It is aimed at securing a common and effective action to prevent the spread and introduction of pests and diseases of plants and plant products, and to promote appropriate measures for their control. The IPPC extends beyond the protection of cultivated plants to the protection of natural flora and plant products. It takes into consideration both direct and indirect damage by pests and diseases, so it includes weeds. It also covers vehicles, aircraft and vessels, containers, storage places, soil and other objects or material that are potential carriers of pests and diseases. The IPPC provides a framework and a forum for international cooperation, harmonization and technical exchange between contracting parties. Its implementation involves collaboration by National Plant Protection Organizations, the official body that must be established by governments to conduct the functions specified by the IPPC and Regional Plant Protection Organizations (RPPOs), which can act as coordinating bodies at a regional level to achieve the objectives of the IPPC.

Although the IPPC uses the term pest to define both invertebrates and pathogens for greater clarity this article refers to both pests (invertebrates and nematodes) and diseases (caused by pathogens).

Human Biosecurity

The WHO is the directing and coordinating authority for health within the United Nations system. It is responsible for providing leadership on global health matters, shaping the health research agenda, setting norms and standards, articulating evidence-based policy options, providing technical support to countries, and monitoring and assessing health trends (www.who.int). Through WHO, governments can jointly tackle global health problems and improve people's well-being. Increasingly the OIE and WHO are working together toward a 'One Health' concept, due to the strong link between animal and human diseases. Together the OIE, WHO, and FAO have created the Global Early Warning System, a platform shared by the three organizations to improve early warning on animal diseases and zoonoses (those diseases that are naturally transmitted between vertebrate animals and humans) worldwide.

The Sanitary and Phytosanitary Agreement

The SPS Agreement came into force with the establishment of the WTO on 1 January 1995 and concerns the application of food safety and animal and plant health regulations. The basic aim of the SPS Agreement is to maintain the sovereign right of any government to provide the level of health protection it deems appropriate, but to ensure that these sovereign rights are not misused for protectionist purposes and do not result in unnecessary barriers to international trade. It allows countries to set their own standards on SPS measures (i.e., measures to maintain animal and plant health and biosecurity), but such measures must be based on science. They should be applied only to the extent necessary to protect human, animal, or plant life or health and they should not arbitrarily or unjustifiably discriminate between countries where identical or similar conditions prevail.

All countries maintain measures to ensure that food is safe for consumers, and to prevent the spread of pests and diseases among people, animals and plants. Member countries (signatories to the SPS Agreement) are encouraged to use international standards, guidelines, and recommendations where they exist. However, members may also use measures that result in higher standards if there is scientific justification. These SPS measures can take many forms, such as requiring products to come from a pest and disease-free area, inspection of products, specific treatment or processing of products, setting of allowable maximum levels of pesticide residues, or permitted use of only certain additives in food. Sanitary (human and animal health) and phytosanitary (plant health) measures apply to domestically produced food or local animal

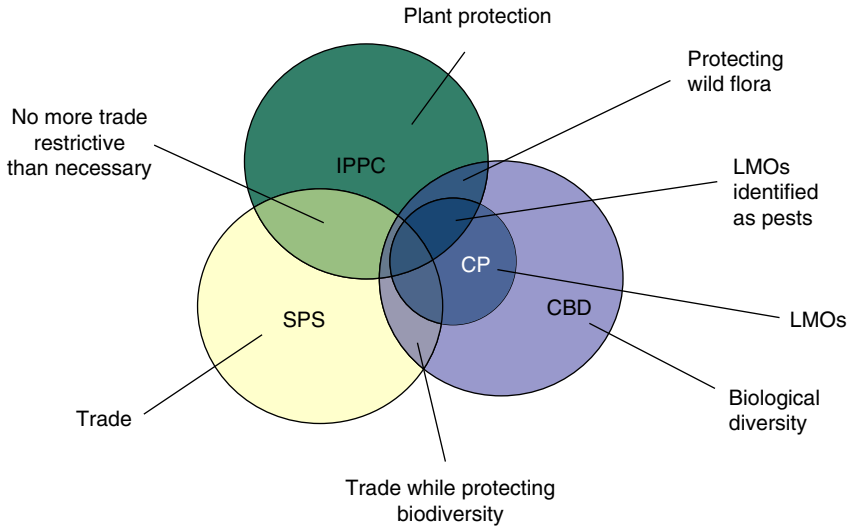


Figure 1 The international regulatory framework for plant biosecurity, comprising the International Plant Protection Convention (IPPC), the Sanitary and Phytosanitary (SPS) Agreement, the Convention on Biological Diversity (CBD), and the Cartagena Protocol (CP). LMO is defined as living modified organism. The main area of governance of each is indicated by a solid line, and the intention of each is indicated by a dotted line (http://www.phytosanitary.info/sites/phytosanitary.info/files/1198163278743_Day_1_A_Welcome_and_IPPC_lecture2_1.ppt).

diseases and plant pests and diseases, as well as to products coming from other countries.

The Convention on Biological Diversity

The CBD is a global, comprehensive agreement addressing all aspects of biological diversity, genetic resources, species, and ecosystems. On 29 January 2000, the Conference of the Parties to the CBD adopted a supplementary agreement to the Convention known as the Cartagena Protocol (CP) on Biosafety. The protocol seeks to protect biological diversity from the potential risks posed by living modified organisms resulting from modern biotechnology. It establishes a procedure for ensuring that countries are provided with the information necessary to make informed decisions before agreeing to the import of such organisms into their territory. In 2005, the Secretariats of the IPPC and the CBD signed a Memorandum of Cooperation to promote cooperation and avoid unnecessary duplication in the field of plant biosecurity. The joint work program between the two Secretariats includes regular consultations to provide input on one another's activities. The relationship between the IPPC, CBD, and CP is indicated in Figure 1.

National and Regional Biosecurity Frameworks

International conventions and agreements are generally signed with national level governments, but how this then impacts on subnational governments is dependent on domestic arrangements. In Australia, for example, the states operate their own biosecurity system within a national framework, while some activities (e.g., national border security) remain a national responsibility. National governments have signatory obligations under international agreements and conventions such as the IPPC.

The role of subnational groups, including semiautonomous government bodies, formal industry groups, informal alliances or individuals, all play a role in biosecurity, directly or indirectly. The role of subnational governments (e.g., state and provincial governments) in biosecurity may vary from nation to nation. It is important to remember that stakeholders below the national level play a role in influencing national policy, which in turn influences international policy.

Regional groups also play a significant role in biosecurity. Under the IPPC, RPPO work on plant biosecurity at a regional level. At present there are 10 RPPO:

- Asia and Pacific Plant Protection Commission (APPPC)
- Comunidad Andina
- Comite de Sanidad Vegetal del Cono Sur
- Caribbean Plant Protection Commission
- European and Mediterranean Plant Protection Organization
- Inter-African Phytosanitary Council
- Near East Plant Protection Organization
- North American Plant Protection Organization
- Organismo Internacional Regional de Sanidad Agropecuaria
- Pacific Plant Protection Organization (PPPO)

Case Study – the Australian Biosecurity Framework

Australia is a party to the WTO and belongs to two RPPO – the APPPC and the PPPO. It cooperates with both RPPOs to develop regional standards for phytosanitary measures. The Australian biosecurity system encompasses the full range of activities undertaken by governments, industry, natural resource managers, custodians or users, and the community across the biosecurity continuum, including prevention, emergency preparedness, detection, response, recovery, and ongoing management of pests and diseases.

The federal (Commonwealth) government has formal responsibility for international government-to-government

relations and Australia's compliance with international obligations under the SPS Agreement, the IPPC, and the CBD. In 2013, the main federal government department that is responsible for biosecurity for plants, animals (including aquatic animals), and marine life is the Department of Agriculture, Fisheries and Forestry (DAFF), which oversees the Quarantine Act 1908. DAFF has primary responsibility for managing Australia's biosecurity system. Environmental biosecurity is covered partly by the Department of Sustainability, Environment, Water, Population, and Communities, which administers the Environment Protection and Biodiversity Conservation Act 1999.

Beneath the Federal government, every state and territory of Australia has its own government, and each of these has additional legislation regarding biosecurity. In Western Australia, for example, the Biosecurity and Agricultural Management Act 2007 is the main legislation. Within a state or territory there may also be regional regulations that apply to certain areas or regions. However, at all levels of government, compliance with international obligations must still occur. Generally, this compliance is contained with the federal and/or state legislation. Therefore, if a company wants to export a product from a particular state of Australia to another country, the company must negotiate with that country through DAFF and demonstrate compliance with all relevant legislation applicable for Australia and the importing country.

The federal, state and territory governments (with exception of Tasmania) signed an Intergovernmental Agreement on Biosecurity in January 2012 to enhance Australia's biosecurity system and strengthen the collaborative approach between the federal and state and territory governments (IGAB, 2012). The intergovernmental agreement recognizes that biosecurity is a shared responsibility and sets out the principles that underpin the operation of a national biosecurity system; describes the key components and features for the national biosecurity system, primarily for animal and plant pests and diseases in both aquatic and terrestrial environments, including pest animals, weeds, and zoonotic diseases; describes steps to strengthen the working partnerships and to enable biosecurity measures to be implemented consistently and efficiently across the biosecurity continuum; establishes nationally agreed approaches to prevent, prepare for, detect and mitigate biosecurity risks, and respond to, manage and recover from biosecurity incidents should they occur; and identifies national priorities to strengthen the national biosecurity system and sets out a process for identifying and reviewing priorities.

The goal of the Australian biosecurity system is to minimize the impact of pests and diseases on Australia's economy, environment, and the community, with resources targeted to manage risk effectively across the biosecurity continuum, while facilitating trade and the movement of animals, plants, people, goods, vectors and vessels to, from, and within Australia. The objectives of the national biosecurity system are to provide arrangements, structures and frameworks that:

- Reduce the likelihood of exotic pests and diseases, which have the potential to cause significant harm to the economy, the environment, and the community (including people, animals, and plants), from entering, becoming established or spreading in Australia;
- Prepare and allow for effective responses to, and management of, exotic and emerging pests and diseases that enter, establish or spread in Australia; and
- Ensure that, where appropriate, significant pests and diseases already in Australia are contained, suppressed or otherwise managed.

The Biosecurity Continuum

The changing global environment means there is a need for a greater emphasis on managing the whole biosecurity continuum, onshore, at the border and offshore, rather than focusing primarily on interventions at the border. Effective biosecurity management requires activities offshore to reduce risks reaching the border, and actions onshore to deal with incursions.

With an increasing biosecurity risk scenario, an effective biosecurity continuum is needed to facilitate safe movement of goods and people and maintain the health status of human, animal and plants and the environment in general. It provides the necessary regulatory framework that governs trade within and between countries. The biosecurity continuum reduces the probabilities of incursions of harmful organisms and increases the probability of successful eradication of pest and disease incursions. Biosecurity policies and regulations across the continuum help to maintain existing markets and create new and improved trade opportunities. Communication, education and awareness of quarantine issues are integral parts of the biosecurity continuum (EPPRD, 2013).

In the past, border quarantine was the mainstay of protection from exotic pests and diseases; however the enhanced risk of invasion by biosecurity threats has necessitated the need for implementation of a continuum of biosecurity approach to manage pest and disease risks where they can be most effectively managed. The biosecurity continuum approach comprises a coordinated system of pest risk analysis, inspection, surveillance and control using risk mitigation measures preborder, border, and postborder to prevent the entry, establishment, and spread of harmful organisms.

Preborder Biosecurity

Preborder biosecurity risk management includes the use of international agreements such as the SPS Agreement or the IPPC for the imposition of import standards, preborder checks and treatments of goods to be imported, as well as information-sharing and international networking between research and development and biosecurity agencies.

Preborder activities seek to prevent biosecurity risks reaching borders of a country or region. Threat identification and risk assessment are significant components of preborder risk management. The preclearance of passengers or goods in their country of origin is consistent with the principle of managing biosecurity risks preborder. Offshore preclearance as part of the preborder biosecurity is gradually expanding; for

example, it may include overseas fumigation certification for full containers and preclearance of some fruits and thus maintaining the quarantine pest risk offshore. The risk mitigation measures are implemented consistent with the obligations under the SPS Agreement and the basic obligations are that biosecurity risk mitigation measures must:

- Be applied only to the extent necessary to protect life or health and not be more trade restrictive than required;
- Be based on scientific principles and not maintained without sufficient scientific evidence; and
- Not constitute arbitrary or unjustifiable treatment or a disguised restriction on trade.

The SPS Agreement encourages WTO member countries to harmonize their measures by developing their biosecurity risk mitigation measures on agreed international standards. Where relevant international standards do not exist, the member country must base its measures on proper scientific assessment of the risks.

Border Biosecurity

Border biosecurity risk management includes checks by the border quarantine authorities of incoming goods and passengers that have potential to be pathways for pest and disease introduction. Declarations of risky items by passengers, mail screening for biological material, and postentry quarantine screening for high-impact pests and diseases are some of the key activities of border biosecurity risk management programs. Border biosecurity primarily aims to minimize the likelihood of entry of biosecurity threats through operation of effective quarantine inspection measures consistent with international obligations. It facilitates the safe international and interstate or regional movement of goods, people and trade in biosecurity risk material through the provision of inspection and certification services. The border biosecurity involves the following activities:

- Screening of all imported material for quarantine pests and diseases;
- Examination of material on arrival;
- Examination of health certification accompanying consignments for compliance with import permit conditions;
- Managing the risk associated with variations of the import permit conditions to ensure equivalence; and
- Liaising with overseas certifying authorities to ensure the certification is consistent with the permit conditions.

Postborder Biosecurity

Postborder biosecurity risk management includes the use of subnational (state and regional) boundaries to monitor and restrict the movement of biosecurity risk materials, surveillance, and monitoring activities for pests and diseases and incursion response planning. Monitoring and surveillance for pest and disease incursions, pest and disease spread and establishment in new regions are some of the key activities of postborder biosecurity program. Pest surveillance information is vital to claim pest and disease freedom status of a region or country. The postborder surveillance is necessary to demonstrate area freedom in order to meet trading partner requirements, as well as to demonstrate successful pest or disease eradication at the end of an eradication response. Pest and disease surveillance programs include targeted active surveillance, generally undertaken by specialists, while passive surveillance often engages growers and general community in reporting any suspect pest or disease to the biosecurity institutions. The efficiency of passive surveillance depends on growers and general public awareness and interest in reporting any unusual sightings of pests and diseases and their symptoms.

Active pest surveillance involves deliberate, coordinated searching, diagnosis, and reporting of pests and diseases. Passive pest surveillance includes observations by growers or investigations of pest or disease occurrences by private consultants or agricultural specialists. Growing volumes of tourism and trade are putting pressure on the biosecurity system and, while interventions at the preborder and border prevent many pests and diseases from entering a country, a well developed surveillance program is necessary to detect the pests and diseases that manage to get in. The postborder surveillance activity aims to minimize the risk of establishment of exotic pests and diseases by implementing early pest or disease detection strategies. Early detection of pest or disease incursion is crucial for successful incursion management. The postborder biosecurity programs keep a 'vigilant eye' on any new biological threat and develop appropriate strategies to eradicate pest and disease incursions.

Postborder biosecurity programs develop best-practice procedures and contingency plans to deal with incursions of exotic pests and diseases for eradication, containment or appropriate control. The approach involves preparation of biosecurity plans for each industry, including farm biosecurity plans where appropriate. The industry biosecurity plans pro-actively identify the key threats to productivity, sustainability and marketability, and outline preventive and response strategies. Each industry biosecurity plan summarizes surveillance and monitoring for the high-risk threats, incident response in the event of a pest or disease incursion, containment, eradication and other management measures, research and development priorities, and biosecurity communication and training needs.

The postborder biosecurity includes farm biosecurity measures for maintaining farm hygiene to prevent introduction of biosecurity threats to plants and animals into the farm from anywhere. Fodder, seed, stock, machinery, vehicles, and people can carry weed seeds, pest eggs, or pathogen spores as well as contaminated soil. Accessing clean material from known pest-free sources minimizes pest and disease risk. Farm biosecurity aims to keep land, crops, and stock free of pests and diseases by managing the movements of stock, produce, and equipment most likely to carry pests and diseases. Farm biosecurity measures minimize the entry and spread of pests and diseases and these measures include:

- Put up a sign to inform farm visitors that all machinery, vehicles, bins and boxes coming onto the farm property must be clean to reduce the potential of any pest or disease introduction;

- Advise visitors that their vehicles, boots and hand tools must be clean of potential pests and diseases;
- Restrict the use of visiting vehicles, using your vehicle to carry visitors around the farm where possible;
- Check the cleanliness and quality of any seed or grain before it comes to the farm. Use pest-and disease-free certified or accredited stock, seed and planting material;
- Ensure that agricultural machinery and equipment are cleaned of plant material and most soil before being moved to a new work site;
- Consider washing footwear and hand equipment before entering and leaving high-risk sites when working in nurseries, animal houses, stockyards and seed crop areas; and
- Identify pest and disease infested/infected areas, if any, on a farm and avoid pest and disease spread to clean areas.

Introduction of an exotic pest or disease may pose a threat to a country's agriculture, economy, environment, and trade. Therefore, the primary goal when a new pest or disease is detected is to eradicate it. Successful eradication relies on preparedness and implementation of appropriate response plan for eradication.

Core Biological Disciplines

The core disciplines that underpin biosecurity are pathology (fungi, oomycetes, bacteria, viruses, nematodes, viroids, and phytoplasmas), parasitology/entomology (insects as well as mites and snails), and weed science. Within each of the key science disciplines biosecurity is reliant on many different specialists. Ebbels (2003) further described that as a branch of applied biology, with an endless variety of problems and circumstances that have to be dealt with, quarantine can involve almost any branch of science. Beale *et al.* (2008) stated that biosecurity requires knowledge to exclude, eradicate, or effectively manage the biological threats to the economy, environment, or community. The combination of science disciplines provides the knowledge to understand the potential impact of these pests and diseases on an organism and its ecosystem. Biosecurity should be considered a melding of many scientific disciplines and not a discipline on its own merit.

Science disciplines contribute to providing knowledge of the pest biology. This includes determining the risk posed for the introduction of a pest or disease and the capacity for it to establish in a new environment. Once established, will the pest or disease spread and what will be the social, economic, and environmental impact? The science disciplines provide advice to decision makers on the application of risk mitigation measures such as containment, eradication, or exclusion. The specific pest or disease information enables decision makers to achieve the desired outcome from a biosecurity response utilizing the most appropriate actions. However, by its nature there are often information gaps and decisions must be made on the best judgment/advice of the discipline experts and may lead to the initiation of research activities to fill the information gaps (Susan Worne, personal communication).

Diagnosis of the Pest

Diagnostics is the core of any countries biosecurity system. Countries that do not have this capability cannot satisfy the requisite international agreements for trade and are unable to protect against the introduction of exotic pests and diseases (Kong *et al.*, 2012). The accurate, repeatable, and often rapid diagnosis of pests and diseases of concern is critical when inspecting a product entering a country, products leaving the country as trade or assessing the presence or absence of a pest or disease. Diagnosis needs to utilize numerous tools from traditional (morphology) taxonomy through to the latest molecular and digital methods. Although there is a growing reliance on molecular methods for diagnosis of pests and diseases, taxonomy based on the morphology of the organism must always to be available and for some disciplines it is in danger of disappearing (Crous, 2005).

Kong *et al.* (2012) confirmed this position by stating that the loss of taxonomic expertise is a global trend and comes at a time when, because of WTO and SPS regulations, there is greater emphasis on high-level pest and disease identification. New molecular and digital tools are assisting in addressing the growing shortage of specific expertise but there are limitations. Deoxyribonucleic acid barcoding is one such tool but its role is still dependent on the support of traditional taxonomists (Kipling *et al.*, 2005). Digital tools provide the opportunity to remove all but the final definitive identifications from taxonomists (Kong *et al.*, 2012). As identified by Guest (2009), there is a continuing decline in investment in key taxonomic positions in plant protection disciplines such as plant pathology and nematology in developed countries and trends indicate this situation is unlikely to improve. A biosecurity system that utilizes various new tools, such as molecular or digital, and is more strategic about its use of key traditional taxonomic expertise will be the most successful in the future.

The use of new tools does present some perils in a biosecurity context. For example, under the IPPC, biosecurity/quarantine decisions are made based on the diagnosis of an organism (ISPM 1). This is in contrast to the animal sector where decisions are made based on the presence/absence of a disease. This presents a challenge for plant pathology as the availability of new tools is resulting in identification of many new organisms for which there is no ascribed disease. For example, the number of named plant viruses has increased from 380 to over 1000 since 1991 (Rodoni, personal communication). If decisions are made by trading countries to decline access of product based simply on the presence of an organism and not symptomatology, then unnecessary significant losses may be incurred. The same scenario exists when eradication operations are undertaken. Valuable plant material may be destroyed because of the presence of an organism even though no symptoms of a discernible disease are present. International policy governed through the IPPC will need to address this issue in the near future and consider the redefining from organism to disease with identifiable symptoms (McKirdy *et al.*, 2012).

Ecology and Epidemiology

Once an exotic pest or disease has been identified in a new area, decision makers need to initiate control or eradication activities. Ecology and epidemiology are critical skills in developing appropriate contingency plans and putting these

plans into action should a detection be made. Surveillance activities are utilized to confirm pest or disease area freedom and to assist in delimiting the area infested by an exotic organism. Ecological and epidemiological skills are necessary when developing a survey plan. Epidemiologists within the disciplines of plant pathology and entomology assist decision makers through their knowledge of the behavior of organisms in the field. Epidemiology has been described in detail by Madden *et al.* (2007) and Berryman (1978).

Defining the genetic relationships between strains/biotypes, describing how a pest or disease is able to survive and spread within an ecosystem, identifying the pathogenicity/vigor/fitness and providing knowledge to enable commencement of appropriate quarantine, eradication and management plans are the role of scientists with expertise in ecology or epidemiology.

Modeling

Skilled modelers play an important role in assisting ecologists/epidemiologists in providing advice. Numerous models have been developed/utilized to assist decision makers in determining the best options when addressing the detection of an exotic pest or disease or in planning for the potential introduction of a pest or disease. Modeling should be considered a tool that can assist rather than provide the definitive system on which decisions are based. Biosecurity provides significant challenges for modeling in that there are often large gaps in available knowledge and there is not the capacity to ground-truth. If dealing with a local pest or disease, modelers working with pest biologists can commission research to address key information gaps or to ground-truth the outputs of a model. By its very definition, biosecurity is dealing with pests or diseases that are not present so there is no capacity to ground-truth outputs. The data available on specific pests or diseases are in most cases gained from areas where the pest or disease is endemic. Researching an endemic pest or disease does not necessarily raise the same questions that arise when decision makers are considering the introduction, establishment and spread of a pest or disease into a new area.

Statistics

Barrett *et al.* (2010) described the role that statistics can play in designing an appropriate surveillance strategy when addressing plant biosecurity threats. Statistical modeling can assist in the detection of pests or diseases while addressing the challenges of multiple data sources, stratifying for differential risk, managing costs, and providing the required power of detection (Barrett *et al.*, 2010). This modeling can also assist in determining the resources to be utilized for detection while meeting the resource constraints.

Economics

Economics is an essential part of any decision-making process in biosecurity. Economists play an important role in determining the potential impact of a pest or disease introduction, prioritizing and managing risks, assessing the merits of eradication versus containment versus management, assessing appropriate compensation for affected stakeholders following a biosecurity incident and estimating the social welfare effects of market access issues or new pest or disease introductions (Liu *et al.*, 2011; Carrasco *et al.*, 2012; Mumford, 2011).

Bioinformatics/informatics

A growing challenge for biosecurity is the storing, maintenance, accessibility, and the usability of data. A country's biosecurity position is dependent on it being able to provide evidence of the status of pests and diseases of concern. This status is critical for both setting restrictions on the importation of product and in gaining market access. The capacity for all stakeholders to gather data on the status of pests and diseases is growing at ever increasing rates as technologies, such as application of the various *–omics*, for their detection continually improve (Alkan *et al.*, 2011). However, the storage of these data are presenting biosecurity systems with the challenge of being able to store the data with the capacity to retrieve and use the data as required. Bioinformatics/informatics applies information technologies to allied fields such as biosecurity. Bellgard and Bellgard (2011) stated that bioinformatics starts at the farm gate and extends through the 'chain of custody' and the challenge is to embrace bioinformatics to ensure biosecurity endeavors can deliver food security.

Social Science

Biosecurity can be a costly and complex issue and, for it to be successful, it requires the shared responsibility of all stakeholders. The stakeholders include government, industry, and the general community (Beale *et al.*, 2008). Social scientists play an important role in achieving the engagement of all sectors of community. Community engagement has been described as a continuum of participation from passive receipt of information, consultation, involvement, partnership through to self-empowered communities that independently initiate actions (Kruger, 2011).

Social science also plays an important role in addressing biosecurity effectively across international borders. Falk and Wallace (2011) stated that the geographic divide between countries introduces both politicoeconomic and sociocultural differences. No one of these aspects, political, economic, social or cultural, is more significant than the other in terms of managing biosecurity effectively (Falk and Wallace, 2011). Social science has a critical role to play in the effective operation of any biosecurity system.

Risk Assessment and Management

Prevention

It prevents the introduction of exotic pest or disease into a region. This strategy focuses on blocking the potential pathways for pest or disease entry. The prevention strategies destroy the pest or disease population before it arrives or establishes in a new area (Gamliel and Fletcher, 2005).

Containment

The containment strategies are implemented after a pest or disease has been introduced in a new area with the objective to prevent and restrict its further spread by reducing the pest or disease population and activities to prevent new infestations and spread (Gamliel and Fletcher, 2005).

Eradication

The eradication strategies are aimed at destroying the pest or disease incursion from the invaded area. It involves elimination of all the existing pest or disease populations from all infested sites, hosts within the area and buffer zone (Gamliel and Fletcher, 2005).

Management

The management strategies are implemented when the pest or disease incursion has established and spread. The aim of management strategies is to minimize the economic and environment impact of pest or disease (Gamliel and Fletcher, 2005).

Communication

Biosecurity communication plans identify relevant stakeholders, internal as well as external, develop key messages, engage with stakeholder groups and monitor the effectiveness of communication. Stakeholder interests and responsibilities may be significantly affected by regulatory risk-management decisions and consultation with external stakeholders throughout the risk-management process is needed. Biosecurity risk communication activities involve a number of mechanisms to inform and update stakeholders via scheduled meetings with stakeholder representatives, and publication of relevant information in stakeholders' journals and periodicals. Successful risk communication requires expertise in conveying understandable and usable information to both internal and external stakeholders.

A key driver for any research in biosecurity is the effective delivery and adoption of research outputs. Scientists can apply their innovation to key challenges and deliver outputs that have the potential to significantly change the mode of operation. However, as biosecurity is very tightly regulated by both national and international regulations, the rate of adoption is often very slow. Regulators need to have a high level of confidence that the implementation of any new research output will still enable all regulatory requirements to be met and, as such, are very conservative. Scientists often find it hard to accept the slow rate of adoption of new research as it is clear to them that a new output will greatly improve the operations of biosecurity. The adoption phase of any research output often involves mundane steps that result in loss of interest for researchers who are continually seeking new innovation. The introduction of social scientists to improve the communication between the innovators (researchers) and the conservative regulators and to develop processes to enable the gradual adoption of research outputs is needed. This will enable the researchers to continue being innovators and focused on the needs of the regulators, without losing interest in a topic as the tasks become more mundane as well as convincing the regulators that new outputs will benefit the operations they undertake in order to meet regulatory requirements.

The disciplines and skills discussed above are not a definitive list of those used in biosecurity. As new challenges are identified in ensuring that a country maintains and adheres to its biosecurity status, there will be a continuing need to seek input from other disciplines of science as well as, for example, engineering, geographic information system, and educators.

Concluding Remarks

Biosecurity is a relatively new concept and its meaning and scope is still evolving. It is emerging as one of the most important issues facing the global community, for a number of reasons (Cock, 2003):

1. Producers' livelihoods can be destroyed by pests and diseases of animals and plants.
2. Processors rely both on high-quality primary produce and on stable consumer demand, based on trust in their products. They are at severe economic risk if either is compromised, either through an external failure of biosecurity measures, or through internal risks, such as contamination in the course of processing.
3. Ecosystem stability, and hence maintenance of ecosystem services to the environment and society, can be threatened by unwanted changes resulting from the introduction of invasive alien species or genotypes.

There is a growing need for countries to establish biosecurity systems to safeguard their resources from new and exotic biological threats. Two main factors have increased the risk of biosecurity threats, namely, the increased global movement of biological materials and the rapid development of technologies associated with genetic modification (Cock, 2003).

Biosecurity safeguards agriculture, the economy, the environment, and human health from the risks of introduced pests, diseases and weeds. As well as preventing new animal and plant pests, diseases and weeds from arriving, biosecurity involves controlling those already present.

The plant sector, the source of food and feed worldwide, is facing an increasing number of pest and disease outbreaks that can significantly affect food production and availability and adversely impact natural biodiversity. A significant proportion of food that can feed well over 1 billion people is being lost to pests and diseases every year.

Pests and diseases are causing significant production and postharvest food losses worldwide, particularly in many food-insecure developing countries. The increase in detection and spread of threatening pests and diseases to new areas has revealed the need for a commitment and shared responsibility for global biosecurity to limit pest and disease impacts.

The outbreak of the Ug99 strain of the stem rust pathogen of wheat in Uganda, to which the world's major wheat varieties have no resistance, is alarming. This strain is apparently spreading in Uganda, Kenya, Ethiopia, Sudan, Yemen, and Iran and has potential to cause significant impact on global wheat yields and thus on food security. The total world area planted to wheat is well over 200 million hectares. Wheat varieties resistant to Ug99 may exist but there is not enough

seed available to plant in millions of hectares even in areas in eastern Africa, the near East and central and south Asia that are at are at high risk of exposure to this strain.

The threat posed by Ug99 to global food security is aptly captured on blog.

> *…So even with a best case scenario, in which there is ample money and cooperation from all parties involved, it would take years to obtain enough Ug99 resistant wheat seed for only a small portion of the wheat fields of the world. In the meantime, the wheat harvest could be devastated. Wheat provides about 20% of the world's total agricultural production, in terms of caloric content of the food. It is one of the top staple crops. (The others are: maize, rice, soy, and barley.) If the wheat crop is devastated, then every other food will be in higher demand. Food prices would rise across the board. The world is so heavily dependent on just a few major staple crops, that any major widespread problem with just one of those crops will cause worldwide problems with agriculture and food.…*

This situation would be disastrous if one more staple food crop in the near future is threatened by Ug99-like virulent strain.

Development and implementation of a global biosecurity strategy has become a necessity to minimize the exposure of global food security system, natural biodiversity, lifestyle and human health and well-being to biosecurity threats.

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Regulatory Challenges to Commercializing the Products of Ag Biotech

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Glossary

Abiotic stress Outside (nonliving) factors that can cause harmful effects to plants, such as soil conditions, drought, flooding, and extreme temperatures.

Bacillus thuringiensis A naturally occurring microorganism that produces a toxin protein that only kills organisms with alkalineing stomachs, namely such as insect larvae. As and when delivered as a part of the whole killed organism, this toxin protein has been used for biological control for decades. The genetic information that encodes the toxin protein was identified and moved into plants to make them insect tolerant.

Biotechnology Development of products by a biological process. Production may be carried out by using intact organisms, such as yeasts and bacteria, or by using natural substances (e.g., enzymes) from organisms.

Biotic stress Living organisms that can harm plants, such as viruses, fungi, bacteria, and harmful insects. See Abiotic stress.

Composition analysis The determination of the concentration of compounds in a plant. Compounds that are commonly quantified are proteins, fats, carbohydrates, minerals, vitamins, amino acids, fatty acids, and antinutrients.

Conventional breeding Breeding of plants carried out by controlled transfer of pollen from one plant to another followed by selection of progeny through multiple generations for a desirable phenotype. This method has also often included irradiation or mutation of plants or seeds to induce extra variation in the donor material.

Genetic engineering A technology used to alter the genetic material of living cells in order to make them capable of producing new substances or performing new functions, or to increase, decrease, or eliminate an existing substance or function.

Genetically modified organisms A genetically modified organism is an organism whose genetic material has been altered using genetic engineering techniques.

Risk A function of the probability of an adverse health effect and the severity of that effect, consequential to a hazard(s).

Risk management The process, distinct from risk assessment, of weighing policy alternatives, in consultation with all interested parties, considering risk assessment and other factors relevant for the health protection of population and for the promotion of fair practices, and if needed, selecting appropriate prevention and control options.

RNAi RNA interference (RNAi) is a phenomenon whereby small double-stranded RNA (referred as small interference RNA or siRNA) can induce efficient sequence-specific silencing of gene expression.

Substantial equivalence In the report of the 1996 FAO/WHO Expert Consultation, substantial equivalence was identified as being "established by a demonstration that the characteristics assessed for the genetically modified organism, or the specific food product derived therefrom, are equivalent to the same characteristics of the conventional comparator. The levels and variation for characteristics in the genetically modified organism must be within the natural range of variation for those characteristics considered in the comparator and be based upon an appropriate analysis of data." In the Codex Guideline for the Conduct of Food Safety Assessment of Foods Derived from Recombinant-DNA Plants (2003), the concept of substantial equivalence is described as "a key step in the safety assessment process. However, it is not a safety assessment in itself; rather it represents the starting point which is used to structure the safety assessment of a new food relative to its conventional counterpart. This concept is used to identify similarities and differences between the new food and its conventional counterpart. It aids in the identification of potential safety and nutritional issues and is considered the most appropriate strategy to date for safety assessment of foods derived from recombinant-DNA plants. The safety assessment carried out in this way does not imply absolute safety of the new product; rather, it focuses on assessing the safety of any identified differences so that the safety of the new product can be considered relative to its conventional counterpart."

Introduction

There is nothing new about introducing novel traits into plants and animals just the methods used to do this have evolved over time. Agriculturalists have been genetically modifying crop plants through crossbreeding, mutation selection, and culling those with undesirable characteristics for hundreds of years. Thus, from a scientific perspective the term 'genetically modified (GM) organism' is not an accurate descriptor of the products produced solely of modern biotechnology, as virtually all domesticated crops and animals have been subjected to varying degrees of genetic modification. On balance, neither the weight of scientific research nor the great majority of the scientific community support the view that organisms modified using the present-day biotechnology pose novel or greater dangers to the environment or human health than organisms developed by other means. Ironically, many of the daily staples would be banned if subjected to the rigorous standards to which biotech crops are subjected. Potatoes and tomatoes contain glycoalkaloids, and if one were to follow labeling to its logical conclusion, one should display a warning label that may contain genes from deadly nightshade. Indeed, biotechnology approaches can be employed to downregulate or even eliminate the genes involved in the metabolic pathways for the production and activation of such plant toxins and also allergens, such as globulins in peanuts.

Over time, and especially during the past century, plant and animal breeders expanded the tools of genetic manipulation beyond conventional crossbreeding to use a variety of other breeding techniques. In the case of plants, these tools include aneuploidy, polyploidy, embryo rescue, protoplast fusion, somaclonal variation, anther culture, colchicine for chromosome doubling, and mutation breeding through either radiation or chemicals. Examples of crops subjected to these breeding techniques include bananas and watermelons (aneuploidy, 3X chromosomes); bread wheat (allopolyploidy, 6X chromosomes from three different species, an old event); broccoflowers (embryo rescue); male sterility in cauliflower (radish cauliflower protoplast fusion); barley (anther culture to speed up development of improved varieties) and asparagus (colchicine chromosome doubling for 'super males'); tomatoes (wide crosses with high toxin glycoalkaloid relatives); and Asian pears, grapefruits, and pasta wheat (irradiation breeding for fungal resistance in the former and modified gluten proteins in the latter). These techniques do not allow any control at the genome level; rather, multiple genes are transferred together or mutated and unwanted traits are eliminated through subsequent selection and backcrossing. Plants created by these conventional phenotypic selection techniques undergo no formal food or environmental safety evaluation before introduction into the environment and marketplace, other than normal agricultural variety testing. Despite the extensive genetic manipulation of crop plants by these diverse methods, cases of novel or completely unexpected adverse consequences for commercialized varieties of these crops are extremely rare. At the deoxyribonucleic acid (DNA) level, the massive accumulation of sequencing data shows extensive genetic similarity among genomes of diverse organisms that are only remotely related. For example, parts of the nucleic acid sequence of a common bacterium present in our guts, *Escherichia coli*, have been found in the DNA of organisms such as oilseed rape, amphibians, birds, grasses, and mammals, including humans. Such findings put in doubt the value of assigning genes to a particular species and the validity of using terms such as 'species-specific' DNA.

Thus, risk assessment should have this fact as a basis and be undertaken within a regulatory framework that ensures adequate protection of the consumer and the environment while not stymieing innovation. Science-based risk assessment identifies potential hazards, quantifies the probabilities of occurrence of those hazards, and accounts for uncertainty with significant safety thresholds – typically set at 1000 times the likely level of a risk to occur. The data that are currently used for the safety assessment of GM crops have focused on the potential perceived risks associated with modern biotechnology. There are now worldwide data from more than 17 years of commercial use of GM crops and almost three decades of research experience and no verified adverse consequences have been reported. These results have allayed the fears of many and have for the most part resulted in the greater acceptance of GM foods. Indeed, many scientists question the painstaking premarket safety assessment of GM crops as practiced in some countries and recommend that the extent and type of data that is part of a current safety assessment be updated to reflect this long-term safe experience with GM crops coupled with new information about plant genome plasticity (Bradford *et al.*, 2005a,b; Kalaitzandonakes *et al.*, 2007; McHughen, 2007; McHughen and Smyth, 2008). They suggest that refinements to the process could include incorporation of factors, such as 'familiarity' (e.g., for commonly used proteins, such as CP4 EPSPS, Cry1Ab, and PAT) and the source of the gene (e.g., when the gene is from the same crop species or is one with a history of safe use), into the overall safety assessment, influencing the extent to which event-specific data are needed. This is considered to be a sensible and pragmatic approach to regulatory oversight.

Despite clear asymmetry and lack of consensus in regulatory systems worldwide and in many instances almost insurmountable challenges, by 2012 GM crops were grown commercially on 175 million hectares, which is 15 million hectares more than that in 2011 with a 9% growth since then. There was a 100-fold increase in hectarage from 1.7 million hectares in 1996 to 175 million hectares in 2012, making biotech crops the fastest adopted crop technology in the history of modern agriculture (James, 2013). Developing countries grew more than 50% of global biotech crops in 2012 and for the first time exceeded industrial countries hectarage. Of the 28 countries planting biotech crops in 2012, it is noteworthy that 19 were less developed countries. Of the 17.3 million farmers, who grew biotech crops, more than 90%, or 16 million, were small resource-poor farmers in developing countries. In addition, biosafety regulations are in place in 57 countries. Although North America still leads in research, more than half of the 63 countries engaged in biotech research, development, and production are developing countries. Adoption is further expanded on in another part of this encyclopedia.

The vast majority of biotech products approved to date are in the area of agronomic traits, especially the area of pest control but with an increasing interest in abiotic stress tolerance, which is gaining prominence as external pressures from climate

change to land-use change. The coming generations of crop plants can be grouped into four broad areas each presenting what, on the surface, may appear as unique challenges to regulatory oversight. The present and future focus is on continuing improvement of agronomic traits, such as yield and abiotic stress, in addition to the biotic stress tolerance of the present generation; crop plants as biomass feedstocks for biofuels and 'biosynthetics'; value-added output traits, such as improved nutrition and food functionality; and plants as production factories. Animals will also enter the regulatory net and although they may parallel plants at some level of application, namely disease resistance, yield, food quality, and as pharming factories, they have clear departures on many significant levels. The issues of ensuring biosafety for the consumer and the environment are of prime concern, irrespective of whether the organism is a microbe, plant, arthropod, or animal. All organisms continuing improvements in molecular and genomic technologies are contributing to the acceleration of product development. One of the subtler modification systems that will provide a challenge for regulatory oversight is, what may be referred to as, next generation directed mutagenesis. Genome editing, specifically genome editing with engineered nucleases, is a form of fine-tuned gene modification using novel nucleases (such as zinc finger nucleases, transcription activator-like effector nucleases, and clustered regularly interspaced short palindromic repeats) that results in minor insertions, replacements, or deletions in a highly targeted manner (Esvelt and Wang, 2013). Genome editing with these nucleases is different from silencing the gene of interest by short interfering ribonucleic acid (RNA) in that the engineered nuclease is able to modify DNA-binding specificity and therefore can, in principle, cut any targeted position in the genome and introduce modification of the endogenous sequences for genes that are impossible to specifically target by conventional RNAi. But even with RNAi, JR Simplot has petitioned for deregulation of their 'Innate' technology based on RNAi suppression of undesirable traits in potatoes on the idea that their potatoes do not contain any transgenes. This is expanded on in another part of this encyclopedia.

The above approaches and evolving tools have tremendous capabilities of introducing very targeted modifications that call into question the notion of 'genetic engineering' and present a problem for regulatory authorities if they, without justification, decide they need to capture them for review as it is, for all intents and purposes, impossible to detect, so enforcing oversight proves to be a challenge. These new products and approaches on the horizon require a reassessment of appropriate criteria to manage risk while ensuring that the development of innovative technologies and processes is encouraged to provide value-added commodities for the consumer.

Other systems, such as synthetic biology (the design and construction of new biological parts, devices, and systems) and genome-scale engineering, are being enabled through advances in high-throughput DNA sequencing, and large-scale biomolecular modeling of metabolic and signaling networks will be contributors to food and agriculture production systems in the future.

Current US Regulations

The United States has been grappling with these regulatory issues considerably longer than most other countries. It also has the largest stake in the technology. Regulations in other jurisdictions, including the European Union (EU), Australia/New Zealand Authority, India, Japan, China, and South American and African countries, are still evolving and are being influenced by the US experience.

At the federal level, the United States has attempted, with mixed results, in developing a coordinated, risk-based system to ensure that new biotechnology products are safe for the environment and human and animal health. However, the trigger for oversight in all instances is still the process of genetic modification. The United States uses health and safety laws that were in the books before the advent of modern biotechnology to review genetically engineered (GE) products. To date, the United States has not issued any new legislation for these products. Established as a formal policy in 1986, the Coordinated Framework for Regulation of Biotechnology (Federal Register, 1986, 51 FR 23302) describes the Federal system for evaluating products developed using modern biotechnology. The Coordinated Framework is based on health and safety laws developed to address specific product classes. The move from the laboratory to the field proved a challenge for the relevant agencies. In the short time that elapsed between the initial development of the capabilities of recombinant DNA technology, the controversy over this research shifted focus from the presumed risks associated with the possible escape of genetically modified organisms (GMOs) from research laboratories to the nature of the long-term environmental impact of GMOs that are intentionally released.

Under the Coordinated Framework, agencies that were responsible for regulatory oversight of certain product categories or for certain product uses are also responsible for evaluating those same kinds of products developed using genetic engineering. Three agencies share primary responsibility for regulating the organisms, products, and processes of recombinant DNA technology, irrespective of whether they are designed for closed systems or for environmental release: the Food and Drug Administration (FDA), the United States Department of Agriculture (USDA), and the Environmental Protection Agency (EPA) (Table 1). Regulations under the Occupational Safety and Health Administration cover those working with rDNA, whereas the Department of Health and Human Services

Table 1 Oversight authority for agricultural biotechnology products

Agency	*Products regulated*
US Department of Agriculture (USDA)	Plant pests, plants, veterinary biologics, animals, fish, and arthropods
Environmental Protection Agency (EPA)	Microbial/plant pesticides, new uses of existing pesticides, and novel microorganisms
Food and Drug Administration (FDA)	Food, feed, food additives, veterinary and human drugs, and medical devices

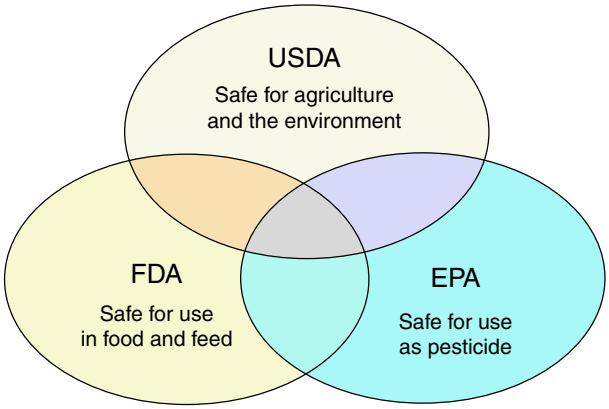


Figure 1 Distribution of federal oversight responsibility.

oversees the health of the general public. Their responsibilities are complementary and, in some cases, overlapping. The USDA–APHIS has jurisdiction over the planting of GE plants. The EPA has jurisdiction over planting and food and feed uses of pesticides engineered into plants. These are referred to as plant-incorporated protectants or PIPs. The FDA has jurisdiction over food and feed uses of all foods from plants. The agencies have developed a coordinated website to keep the public informed (Unified Biotechnology Website; **Figure 1**).

This framework has allowed the United States to build on agency experience with organisms and products developed using conventional techniques. Accordingly, the agencies base their analysis of oversight not principally on any presumed theoretical 'exotic' risks but rather exploit the vast cache of accumulated knowledge that has been amassed over years of research using highly developed scientific procedures for assessing field tests and planned introductions. Using such a scientific approach deduced from first principles is probably the most effective mechanism regulatory bodies can take in crafting effective regulations. The laws currently used to regulate the products of modern biotechnology are the Plant Protection Act (PPA); the Federal Food, Drug, and Cosmetic Act (FFDCA); the Federal Insecticide, Fungicide, and Rodenticide Act (FIFRA); and the Toxic Substances Control Act (TSCA). New regulations have been developed under these statutes as needed to address GE products developed. New regulations, policy statements, and guidelines will continue to be developed as needed.

The details of which items are regulated, such as organisms and processes, and how both may be regulated (time frames, permitting processes, and penalties) are written by each Agency that has the appropriate authority. All formal Federal regulations are published in the Federal Register and also in the Code of Federal Regulations, a large multivolume series. For example, those regulations for Agriculture and the USDA comprise 15 volumes and those governing biotechnology as overseen by APHIS-BRS are found in Volume 7, Section 340. The USA (under USDA–APHIS as described below) uniquely operates deregulation, allowing applications to request that a specific GM product be considered equivalent to crops modified using all other breeding techniques and therefore should no longer be regulated. All GM crops on the USA market currently have achieved a deregulated status.

Many states and local authorities were not satisfied with existing oversight and some 14 states and several municipalities enacted their own biotechnology legislation, many of which have since been modified or revoked. The most recent attempt was the required labeling of products that included 'GMO ingredients' under Proposition 37 in California. It went down to defeat following a concerted campaign that largely focused on the arbitrary nature and potential for capricious lawsuits that the draft language would facilitate.

Agencies must also adhere to the umbrella National Environmental Policy Act (NEPA), which is binding on all federal agencies. Depending on its intended use, a product may or may not be reviewed by all three regulatory agencies.

There have been 96 approvals for deregulation since 1990; these comprise examples from alfalfa, canola, corn, cotton, flax, rose, papaya, plum, potato, rice, soybean, squash, sugar beet, tobacco, and tomato. Those not already on the market, are likely to proceed to full commercial development. There are also 13 applications pending decision which represent the next group of GM crop varieties available on the market; these include alfalfa (1), apple (1) (nonbrowning), corn (1), cotton (1), creeping bentgrass (1), eucalyptus (1) (cold tolerance), potato (1) (reduced acrylamide), and soybean (6) (Information Systems for Biotechnology, 2013a,b). The most recently deregulated products are glyphosate tolerant canola (oil seed rape) (Pioneer/Monsanto), glyphosate tolerant corn, and a novel F1 hybrid seed production system for corn (Monsanto) (USDA, 2014).

The numbers of US GM field trial applications are shown by crop and GM trait in **Figures 2** and **3**, respectively. Each of these applications may cover a range of GM lines of a particular crop grown in one or more locations, and all commercial products will have been tested under this system over a period of several years and at several locations.

In 2013, there were 601 trials, with herbicide tolerant corn representing the largest category.

The United States Department of Agriculture

Scope for coverage is food and fiber products. Although its authority is as equally applicable to GM animals, plants, and microorganisms, it is in one sense outside the circle of ecological safety in that its primary concerns are the safety of crop plant and food animals and the safety and wholesomeness of food products.

The USDA has nine divisions that deal with biotechnology:

- The Agricultural Research Service (ARS)
- The Food Safety and Inspection Service (FSIS)
- The Animal and Plant Health Inspection Service (APHIS)
- The Agricultural Marketing Service (AMS)
- The Cooperative State Research Service (CSRS)
- Extension Service
- The National Agricultural Library
- The Forest Service (FS)
- The Economic Research Service (ERS).

The USDA's policy on the regulation of biotechnology, consistent with the overall federal policy, does not view GMOs as fundamentally different from those produced using traditional methods. The USDA considered that the products of the

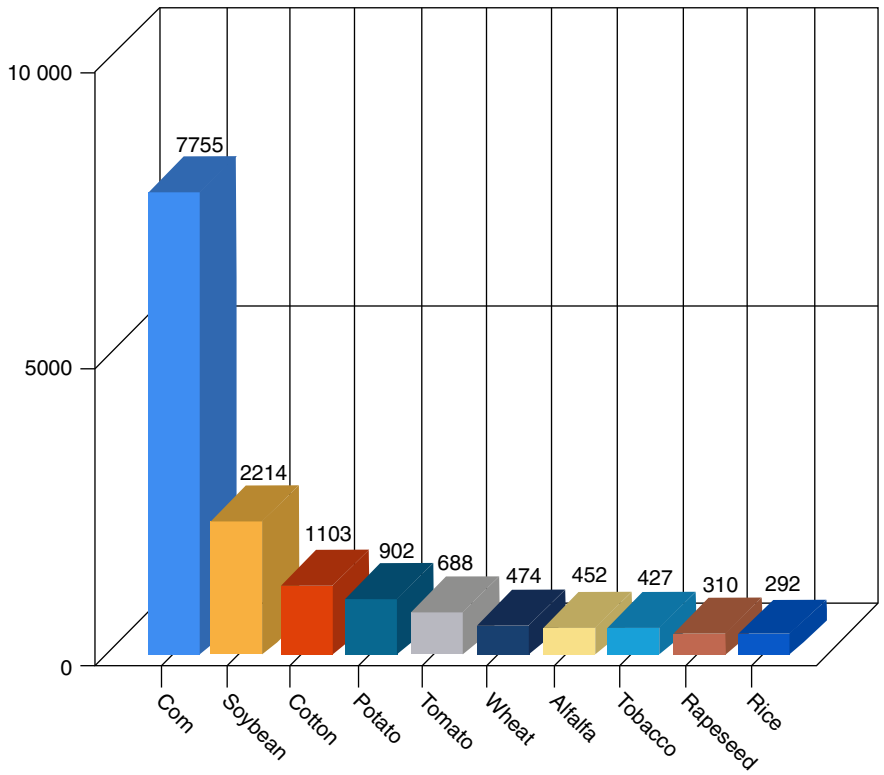


Figure 2 Numbers of field trial permits by crop. Data from Information Systems for Biotechnology, 2013b. Release Summary Data and Charts (1987–Present). Available at: http://www.isb.vt.edu/release-summary-data.aspx (accessed 03.03.14).

new techniques of biotechnology were in principle covered by regulations that had been implemented for existing technologies. They did, however, consider that the assessment of the products of the new technologies in some instances required specific information that necessitated the introduction of some new regulations and the updating of some existing ones.

Within the USDA, the Animal and Plant Health Inspection Service (APHIS) is responsible for protecting agriculture from pests and diseases. The Federal PPA (7 USC. §§7701 *et seq.*) is the primary statute under which the APHIS regulates agricultural biotechnology. Enacted in 2000, this statute replaced the former Federal Plant Pest Act. Originally intended to prevent the introduction and interstate movement of plant pests, the Plant Pest Act had been adapted by the APHIS to regulate GE plants so that they do not become 'plant pests.' The section within the APHIS with prime responsibility is the APHIS Biotechnology Regulatory Services APHIS-BRS. Under the PPA, the USDA–APHIS has regulatory oversight over products of modern biotechnology that could pose such a risk. Accordingly, the USDA–APHIS regulates organisms and products that are known or suspected to be plant pests or to pose a plant pest risk, including those that have been altered or produced through genetic engineering. These are called 'regulated articles.' A regulated article is defined in the APHIS regulations as "any organism which has been altered or produced through genetic engineering" if the donor organism, recipient organism, vector, or vector agent is a 'plant pest' (7 C.F.R. § 340.1). The APHIS defines a plant pest broadly to include 'any living stage' of insects, bacteria, fungi, viruses, or various other organisms that can damage or cause injury to plants or plant parts (7 C.F.R. §340.1). Many plant pathogens commonly used as vectors or promoters in agricultural biotechnology, such as *Agrobacterium* species and cauliflower mosaic viruses, are considered plant pests under the APHIS regulations (7 C.F.R. §340.2(a)). Use of any of these plant pests to make a transgenic plant makes that plant a regulated article. The agency may also designate any product of genetic engineering as a regulated article that the agency determines or has reason to believe is a plant pest (7 C.F.R. §340.1). The USDA–APHIS regulates the import, handling, interstate movement, and release into the environment of regulated organisms that are products of biotechnology, including organisms undergoing confined experimental use or field trials. Regulated articles are reviewed to ensure that, under the proposed conditions of use, they do not present a plant pest risk through ensuring appropriate handling, confinement, and disposal.

In 1993, with modifications in 1995 and 1997, the USDA introduced the final rule notification in lieu of permit process for GMOs that are field tested in accordance with specific safety criteria. The amendment simplifies procedures for the introduction of certain GE organisms, expedites review for certain determinations of nonregulated status, and adjusts procedures for the reporting of field tests conducted under notification to the biology of the test organisms. This enables the APHIS, when appropriate, to extend the existing determination of nonregulated status for new products that do not raise new risk issues. The USDA–APHIS regulations provide a petition process for the determination of

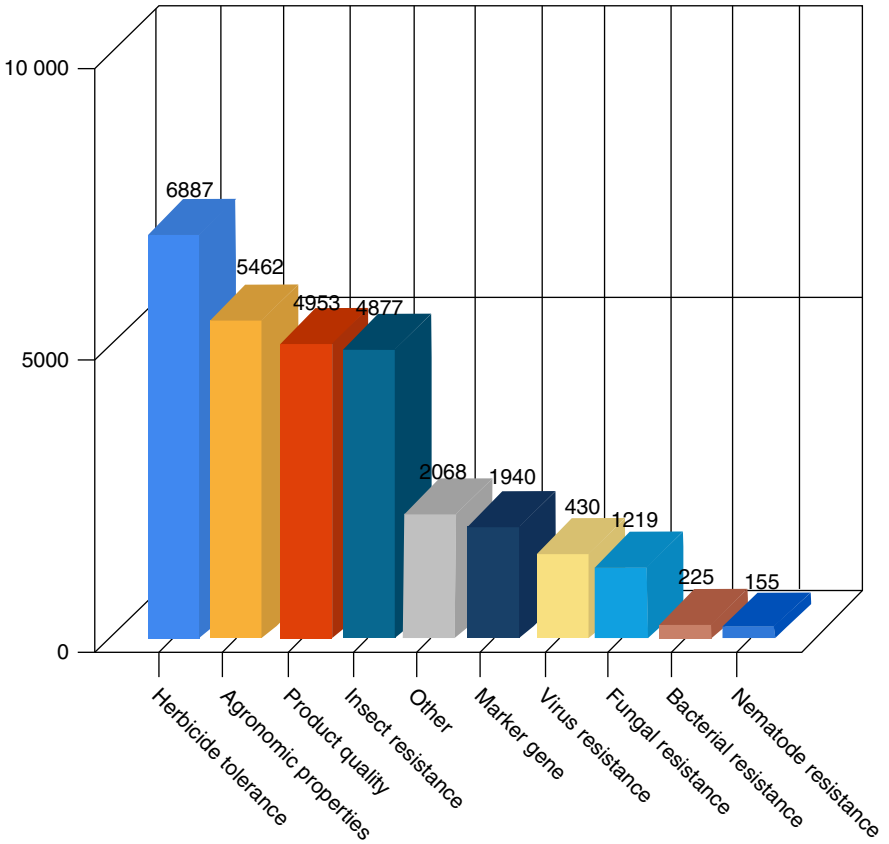


Figure 3 US field trial permits by trait. Data from Information Systems for Biotechnology, 2013b. Release Summary Data and Charts (1987–Present). Available at: http://www.isb.vt.edu/release-summary-data.aspx (accessed 03.03.14).

nonregulated status (USDA Petition). If a petition is granted, that organism will no longer be considered a regulated article and will no longer be subject to oversight by the USDA–APHIS. The petitioner must supply information such as the biology of the recipient plant, experimental data and publications, genotypic and phenotypic descriptions of the GE organism, and field test reports. The agency evaluates a variety of issues, including the potential for plant pest risk; disease and pest susceptibilities; the expression of gene products, new enzymes, or changes to plant metabolism; weediness and impact on sexually compatible plants; agricultural or cultivation practices; effects on nontarget organisms; and the potential for gene transfer to other types of organisms. A notice is filed in the Federal Register and public comments are considered on the environmental assessment and determination written for the decision on granting the petition. Copies of the USDA–APHIS documents are available to the public.

One exception to the notification process described above is for plants that have been modified GM to produce pharmaceutical or industrial products (40 C.F.R. § 340.3(b)(4)(iii)). These plants require a permit before field-testing or interstate shipment. APHIS policy is to inspect all field trials involving such organisms at least annually, and the Agency has stated that such organisms would never be eligible for 'deregulation' (White, 2000). Currently, test plots for crops engineered to produce are regulated by the APHIS permit system.

The USDA regulations require developers to have clearly written procedures in order to handle wastes properly and maintain production and control records. Plant-made pharmaceuticals also come under the US FDA purview. The FDA monitors the manufacturing process as well as the purity and consistency of the products under its 'good manufacturing practices' guidelines. Nevertheless, both the USDA and the FDA recognize that this is a new application of the technology and are in the process of coming up with new guidance, specifically for pharmaceutical plants.

The growing and harvesting of the crop itself must comply with principles of confinement, which essentially means keeping the crop and its products on the land where it was grown until removed for processing with no inadvertent exposure to the public and minimal exposure of products to workers and the environment. Adequate analytical methods for detection of expression (i.e., protein) products must be demonstrated and all confinement systems and procedures must be based on sound scientific principles. Identity preservation within a closed loop system to prevent comingling of pharm crops with food crops will be a prime directive for industry as well as regulatory agencies.

In addition to the above, under the NEPA, the USDA has a responsibility for ensuring ecological safe utilization of crops, livestock, and veterinary products produced both from traditional and recombinant DNA methods. The FSIS assures the safety and wholesomeness of food products.

More than 10 000 field tests, involving more than 200 organisms at thousands of sites throughout the United States, have been analyzed by the USDA. The agency has assessed the biotech plants for their efficacy, performance, and suitability for release in the environment. Globally, approximately tens of thousands of field trials have been conducted on hundreds of organisms in 45 countries (International Field Test Sources, 2007). There has not been a single report of any unexpected or unusual outcome. The APHIS also issues licenses and permits for production, importation, sale, and experimental use of various types of biological products. Specific information that must be submitted for GMOs and products includes detailed information on stability, genetic constructs and vectors, and the effects of any insertions and deletions in the organism.

Some of the more recent deregulations include novel products, such as maize genetically modified to produce a common enzyme called alpha-amylase that breaks down starch into sugar, thereby facilitating a vital step in biomass conversion in ethanol production and apples with RNAi-suppressed oxidizing enzymes to prevent browning. There also has been controversy in some of the processes. In 2007, a court rescinded the approval of glyphosate-tolerant alfalfa, which had been deregulated in 2005 on the grounds that the agency failed to complete an Environmental Impact Statement (EIS) addressing the issue of gene flow and coexistence between GE and conventional varieties. In 2010, the USDA completed the EIS and three alternatives were proposed (1) no deregulation, (2) complete deregulation, and (3) partial deregulation with conditions and restrictions. In a highly unusual move the USDA Secretary Vilsack met with interest groups to try to foster coexistence and avoid lawsuits. In 2011, the second alternative was chosen and GT alfalfa was again deregulated.

In 2008, the USDA revisited the deregulation process and proposed new rules to be phased into use. They proposed a multitiered permit system for field-testing bioengineered plants wherein higher risk products were subject to tighter controls; they also considered conditional decisions and postmarketing monitoring requirements for commercialization of certain bioengineered plants; they recommended more coordination with the FDA and the EPA to include early food safety assessments to address low-level intermittent presence of unapproved traits in the food supply; and proposed new policies for field-testing and commercializing plant-made pharmaceuticals and plant-made industrial products. There was significant push back by the scientific community based on the lack of science underpinning the review process and the trigger points for regulatory overview. Despite providing a comprehensive and thorough prolog that quite clearly delineated the history, issues, and process involved in promulgating the proposed regulations, the suggested amendments that appeared in the Federal Register (2008a,b) in October 2008 had little basis in science or proportionality. The proposed regulations placed little value on precedent, experience, or history basically reducing the regulatory process to assessment on a case-by-case basis. If implemented, this would have greatly increased the burden of proof and placed such an onus on meeting regulatory requirements that it may very well have had a detrimental effect on all agricultural biotech research.

The Environmental Protection Agency

The EPA claims that its biotechnology regulatory program is based on five important principles that guide its decision-making policy. The principles are – using sound science, ensuring transparency of the decision-making process, maintaining consistency and fairness, collaborating with its regulatory partners, and building public trust.

Under the NEPA, the EPA has broad jurisdiction over environmental impact. It mostly considers GMOs under the aegis of the 'TSCA and the FIFRA. In general, the TSCA will not be triggered if the microbes are used to produce foods, additives, drugs, vaccines, cosmetics, or medical devices and are regulated by the FDA or the USDA. Other than those listed exemptions, all other new or new-use chemical end products from microorganisms, which themselves may be considered new, are subject to the TSCA. Consent orders and negotiated agreements are used as the mechanisms to cover environmental introductions.

The FIFRA mandates the registration of pest-control products and 'economic poisons' before production and sale. To test a product, an applicant must submit complete data. Product evaluation includes the equivalent to an Environmental Assessment or EIS. Since 1984, notification of intent to field-test GMOs and nonengineered, nonindigenous pathogenic and nonpathogenic microorganisms was required, regardless of testing site size.

The EPA currently regulates chemical pesticides and biopesticides that are externally applied to plants. In the 1990s, the agency expanded its federal regulatory powers over the characteristics of plants that help plants to resist diseases and pests. The agency coined a new term for these characteristics, calling them 'plant pesticides.' All plants are able to prevent, destroy, repel, or mitigate pests or diseases. That ability occurs naturally, and some crops have been bred for resistance to specific pests. The EPA proposed to single out regulation for those pest-resistant qualities that were transferred to the plant through recombinant DNA technology. Eleven Professional Scientific Societies took grave objection to the suggested regulations and they responded by developing a document entitled 'Appropriate oversight for plants with inherited traits for resistance to pests: A report.' They determined that evaluation of the safety of substances in plants should be based on the toxicological and exposure characteristics of the substance and not on whether the substance confers protection against a plant pest. A compromise was reached, and the EPA now regulates 'PIP.'

The PIPs Rules were issued on 17 January 2001. The rules consider the impact on beneficial insects and nontarget organisms; toxicity of pesticidal compound; safety for human consumption; and ecological hazards and insect resistance. The specific tests for the FIFRA PIPs clearance are wildlife exposure studies for PIPs on nontarget organisms; feeding studies on beneficial insects, including honeybees, ladybird beetles, lacewings, earthworms, birds, fish, and mammals at 10–100 times the concentration; and environmental fate, that is, how long it takes for the PIP protein to degrade in plant material left on or in the soil. Reviews are conducted on a case-by-case basis based on the product and the risk and not the means by which the organism was created. However,

interestingly, despite this assertion, no experimental use permits (EUPs) are required for undirected mutagenesis, most transconjugants, and plasmid-cured strains, yet EUPs are required for all live rDNA GMOs, irrespective of product or risk.

Under the TSCA, the EPA acquires information in order to identify and regulate potential hazards and exposures. The TSCA applies to the manufacturing, processing, importation, distribution, use, and disposal of all chemicals in commerce, or intended for entry into commerce, that are not specifically covered by other regulatory authorities (e.g., substances other than food, drugs, cosmetics, and pesticides). The TSCA's applicability to the regulation of products of biotechnology is based on the interpretation that organisms are chemical substances under the TSCA. The EPA's TSCA Biotechnology Program of the Office of Prevention and Toxic Substances currently regulates microorganisms intended for general industrial uses. The program conducts a premarket review of 'new' microorganisms, i.e., microorganisms formed by deliberate combinations of genetic material from organisms classified in different taxonomic genera. Developers must notify the EPA 90 days before manufacture or 60 days before field-testing of a product regulated by the TSCA. Proposed modifications are issued in the federal registrar for comment. For example, on 5 September 2012, the EPA issued a notification proposing to add two microorganisms (specific strains of the fungus *Trichoderma reesei* and specific subspecies of the bacterium *Bacillus amyloliquefaciens*) to the list of 10 recipient microorganisms (40 CFR 725.420) that are eligible for exemptions from full chemical notification requirements under the TSCA. They took comments on the proposal until 5 November 2012.

The EPA also sets tolerance limits for residues of pesticides on and in food and animal feed, or establishes an exemption from the requirement for a tolerance, under the FFDCA.

Meanwhile, the benefits of biotechnology crops experienced by larger-scale farmers in both industrialized nations and lesser developed countries are already considerable. Research by Brookes and Barfoot (2012a) showed that in 2010 the direct global farm income benefit from biotech crops was US$14 billion. They estimated that this is equivalent to having added 4.3% to the value of global production of the four main crops of soybeans, maize, canola, and cotton. In addition, in their retrospective analysis over the 15 years, from 1996 to 2010, they estimated that farm incomes increased by US$78.4 billion. Biotech crops are, moreover, making important contributions to increasing global production levels of the four main crops. They have, for example, now added 97.5 million tons and 159.4 million tons, respectively, to the global production of soybeans and maize since the introduction of the technology in the mid-1990s. (Brookes and Barfoot, 2012b) In addition, the environmental footprint associated with pesticide use was reduced by 15.4%; there was a reduction in carbon dioxide emissions in 2010, equivalent to taking nearly 10 million cars off the road for a year.

Biotech, primarily herbicide-tolerant crops, facilitates the switch to reduced-till, or conservation, agriculture, which means healthier soil, with reduced erosion and far less carbon dioxide release. In general, cultivation is not a sustainable practice. It is energy intensive and exposes soil to wind and water erosion. It allows rain to compact the soil and increases the oxygen content of the soil, allowing organic matter to oxidize away. In turn, lower organic matter in the soil allows more compaction and more nutrient loss. Pesticide use fell by more than 286 million kg (− 7.8%: equivalent to approximately 40% of the annual volume of pesticide-active ingredient applied to arable crops in the EU). Less spraying means fewer tractor passes, contributing to lower carbon dioxide emissions. Insect-resistant maize also has a collateral effect – less insect damage results in much less infection by fungal molds, which reduces mycotoxins that are known health risks causing problems such as liver cancer to humans and animals. The only 'natural' way to control those fungi is the use of copper sulfate, which has one of the highest toxic hazard ratings of acceptable pesticides and is selected for antibiotic-resistant bacteria in the soil as expanded in another part of this encyclopedia.

Food and Drug Administration

The FDA regulates biotechnology under the authority of the Food, Drug, and Cosmetic Act (FDCA) and the Public Health Services Act. The agency has a mandate to ensure efficacy and safety of food and pharmaceutical products. The agency has a major responsibility in biotechnology in that the majority of the current market share of biotechnology products passes through the agency for review, and it has already reviewed thousands of biotechnology products.

The FDA is responsible for ensuring the safety and proper labeling of all plant-derived foods and feeds, including those developed through bioengineering. All foods and feeds, whether imported or domestic and whether derived from crops modified by conventional breeding techniques or by genetic engineering techniques, must meet the same rigorous safety standards. Under the FDCA, it is the responsibility of food and feed manufacturers to ensure that the products they market are safe and properly labeled. Generally, whole foods, such as fruits, vegetables, and grains, are not subject to premarket approval. The primary legal tool that the FDA has successfully used to ensure the safety of foods is the adulteration provisions of section 402(a)(1). The Act places a legal duty on developers to ensure that the foods they present to consumers are safe and comply with all legal requirements. The FDA has authority to remove a food from the market if it poses a risk to public health. Foods derived from new plant varieties developed through genetic engineering are regulated under this authority. A second section of the Act that the FDA relies on is the food additive provision (section 409). Under this section, substances that are intentionally added to food are food additives, unless the substance is generally recognized as safe (GRAS). Food additives are subject to review and approval by the FDA before they may be used in food. When requested to do so, the FDA also reviews and affirms the GRAS status of food ingredients.

In May 1992, the FDA issued a policy statement on regulating biotechnology food products. The FDA requires premarket review only for foods into which substances are intentionally introduced, significantly changing the structure, function, or amount currently found in the food (Statement

of Policy: Foods Derived From New Plant Varieties (1992)). If a new food product developed through biotechnology does not contain substances that are significantly different from those already in the diet, it does not require premarket approval. To help sponsors of foods and feeds derived from GE crops comply with their obligations, the FDA encourages them to participate in its voluntary consultation process. All foods and feeds from GE crops currently on the market in the United States have gone through this consultation process. With one exception, none of these foods and feeds was considered to contain a food additive and so did not require approval before marketing. The consultation process under the FDA's 1992 Statement of Policy was updated in 1996 and 1997. On a number of occasions, the FDA stated that they would publish a proposed rule mandating that developers of bioengineered foods and animal feeds notify the agency when they intend to market such products and that they would require that specific information be submitted to help determine whether the foods or animal feeds possess any potential safety, labeling, or adulteration issues. However, consultation still remains voluntary (Food and Drug Administration, Center for Food Safety and Applied Nutrition (FDA/CFSAN), 2000).

On the 'labeling' issue, the FDA's policy guidelines state that foods produced through biotechnology will be subject to the same labeling laws as all other foods and food ingredients. Labeling would be required for biotech products in some instances, but not because the products were made using biotech. The FDA requires that labeling of a food or food ingredient or additive be truthful and not misleading and that the product be declared by its common or usual name. In general, the information on the label pertains to the composition and attributes of the food or food ingredients or additive but not to the details of agricultural practices or the manufacturing process. The question of whether foods derived from organisms containing recombinant DNA should be specially labeled has received a great deal of attention. The FDA's (1992) approach to the labeling of foods, including those GE or otherwise novel, is that the label must be accurate and 'material' to it. There are only two situations in which the FDA can require that a transgenic origin or ingredient be disclosed on the food label (1) the FDA may mandate the disclosure of facts on a product label that relate to material consequences, which can follow the consumption of a food (e.g., kidney beans that must be soaked and cooked before eating) and (2) the FDA can require that a label reveal facts necessary to correct or balance other representations made by the manufacturer or seller. Accordingly, labeling is required "if a food derived from a new plant variety differs from its traditional counterpart such that the common or usual name no longer applies, or if a safety or usage issue exists to which consumers must be alerted." The policy statement also emphasizes that no premarket review or approval is required unless characteristics of the biotech food explicitly raise safety issues and that – in as much as the genetic method used in the development of a new plant variety does not meet either of the two criteria for 'materiality' – the FDA cannot require the labeling to include this information. Obviously, many of the novel nutritionally enhanced foods expected on the market in the next few years will be labeled as they will differ from their traditional counterparts, and in most instances the company marketing them will want to proclaim their enhanced nutritional value.

In 2006, to address the possibility that material from a new plant variety intended for food use might inadvertently enter the food supply before its sponsor has fully consulted with the FDA, the FDA announced the availability of a draft guidance document entitled 'Guidance for Industry: Recommendations for the Early Food Safety Evaluation of New Non-Pesticidal Proteins Produced by New Plant Varieties Intended for Food Use.' It discussed the early food safety evaluation of new proteins in new plant varieties, particularly in new bioengineered varieties that are under development for possible use as food for humans or animals. The draft guidance also described procedures for communicating with the FDA about this evaluation. The issuance of draft guidance was proposed in August 2002 in a Federal Register Notice (67 FR 50578) published by the Office of Science and Technology Policy as part of proposed Federal actions to update field test requirements and to establish early voluntary food safety evaluations for new proteins produced by bioengineered plants.

They opined that rapid developments in genomics are resulting in dramatic changes in the way new plant varieties are developed and commercialized. Scientific advances are expected to accelerate, leading to the development and commercialization of a greater number and diversity of bioengineered crops. As the number and diversity of field tests for bioengineered plants increase, the likelihood that cross-pollination due to pollen drift from field tests to commercial fields and commingling of seeds produced during field tests with commercial seeds or grain may also increase. This could result in low-level presence in the food supply of material from new plant varieties that have not been evaluated through FDA's voluntary consultation process for foods derived from new plant varieties (referred to as a 'biotechnology consultation' in the case of bioengineered plants). The FDA believes that any potential risk from the low level presence of such material in the food supply would be limited to the possibility that it would contain or consist of a new protein that might be an allergen or toxin.

Although the FDA has not found and does not believe that new plant varieties under development for food and feed use generally pose any safety or regulatory concerns, this guidance is consistent with the FDA's policy of encouraging communication early in the development process for a new plant variety. Such communication helps to ensure that any potential food safety issues regarding a new protein in such a new plant variety are resolved before any possible inadvertent introduction into the food supply of material from that plant variety.

Depending on its intended use, a product may or may not be reviewed by all three regulatory agencies. A food crop plant developed using genetic engineering to produce a pesticide in its own tissue provides an example that is reviewed by all three regulatory agencies. A common example of this type of product is Bt corn, which has incorporated a gene isolated from the soil bacterium *Bacillus thuringiensis* (Bt). The *Bt* gene encodes a pesticidal protein (Cry). The USDA–APHIS under the PPA regulates the corn as a regulated article based on the procedures used to introduce or express the *Bt* gene. The

USDA–APHIS oversight begins early in the development cycle and continues until the developer applies for and is granted nonregulated status for the plant because it can be shown that the plant is not a plant pest. Until such time as the developer is granted nonregulated status for the plant, the USDA–APHIS oversees the transportation (including importation), field-testing, and disposal of the plant. Developers of Bt crops also consult with the FDA about possible other, unintended changes to the food or feed, for example, possible changes in nutritional composition or levels of native toxicants. Although this consultation is voluntary, all of the food/feed products commercialized to date have gone through the consultation process. The consultation with the FDA serves to ensure that safety or other regulatory issues that fall within the agency's jurisdiction, including appropriate labeling of the food, are resolved before commercial distribution.

When an unregulated event falling under all three jurisdictions is detected in commercial distribution, all three coordinate to mitigate the misadventure. For example, in February 2008, the three agencies coordinated efforts following notification by Dow AgroSciences' subsidiary Mycogen that the company detected extremely low levels of an unregistered GE plant-incorporated protectant (PIP) in three of its commercial GE hybrid corn seed lines. They quickly determined that the unregistered product produces proteins that are identical to a registered product and issued a statement that the USDA, EPA, and the FDA have concluded that there are no public health, food, or feed safety concerns. Additionally, the USDA and the EPA have determined that the unregistered GE corn PIP poses no plant pest or environmental concerns (Event 32, 2008). **Table 2** outlines some examples of shared coordination.

Animal Biotechnology

Biotechnology, as it relates to animals, is largely comprised of three main thrust areas, namely biologics (including vaccines and 'therapeutics') and agricultural and biomedical applications.

As with plants, the two principal agencies that oversee animal biotech applications are the USDA and the FDA. Within the USDA, primary jurisdiction for biologics lies under the Virus, Serum, Toxin Act. The USDA–APHIS Veterinary Services inspect biologics production establishments and license veterinary biological substances, including animal vaccines that are products of biotechnology. Within the FDA the Center for Veterinary Medicine (CVM) is the primary center responsible for approving recombinant products. For example, recombinant bovine somatotropin (rBST), a growth hormone injected into dairy cows, fell under CVM jurisdiction. The CVM considered the additions of rBST (or the genetic modifications involved in producing rBST) to constitute the addition of an animal drug, making the product subject to its premarket approval authority.

Although any transgenic animal is yet to be approved for human consumption, regulations are in place to cover their use. As with plants, the principal federal regulation of transgenic animals and fish is governed by the Food, Drug, and Cosmetics Act.

As far back as 1986, the FDA asserted jurisdiction over transgenic animals and fish on the grounds that the transgene and any expressed proteins affect the 'structure and function' of the receiving animal analogous to the modalities of alternative veterinary drug formulations. This gene-based modifications of animals for production or therapeutic claims fall under CVM regulation as new animal drugs. They work in consultation with the other FDA Centers for food and feed safety evaluation. The FDA jurisdiction has been upheld by the federal courts. Perhaps more so than for plants, the principal focus for transgenic animal production is their use as bioreactors for the production of biotherapeutics in milk, serum, and other bodily fluids. So it makes logical sense that they would be regulated as Institutional New Drugs under CVM. However, faced with regulatory decision making regarding the ever-evolving GM and cloning pipeline, the FDA asked the National Research Council (NRC) to identify and prioritize science-based concerns posed by animal biotechnology. The NRC released its report, Animal biotechnology: Science-based concerns to the public on 21 August 2002, drawing the attention of scientists, the biotech industry, nongovernmental organizations, and the national media.

Their concerns fell into three areas – medical, food, and environmental. On the medical side, the principal concerns

Table 2 Example of coordination of oversight between agencies

New trait/crop	*Agency*	*Review*
Insect resistance in food crop (Bt corn)	USDA	Agricultural and environmental safety
	EPA	Environmental, food/feed safety of pesticide
	FDA	Food/feed safety
Herbicide tolerance in food crop (glyphosate-tolerant soybeans)	USDA	Agricultural and environmental safety
	EPA	New herbicide use
	FDA	Food/feed safety
Herbicide tolerance in ornamental crop (glufosinate-tolerant azaleas)	USDA	Agricultural and environmental safety
	EPA	
	FDA	New herbicide use
Modified oil in food crop (omega three canola)	USDA	Agricultural and environmental safety
	EPA	
	FDA	Food/feed safety
Modified flower color (purple carnations)	EPA	Agricultural and environmental safety

were modification of animals for biomedical purposes, especially xenotransplantation mobilization of new infectious agents. On food issues, they focused on new proteins, and food safety concerns posed by biological activity, allergenicity, or toxicity that they determined should be evaluated on a case-by-case basis. The key issue regarding cloned animals is whether and to what degree the genomic reprogramming results in altered gene expression that raises food safety concerns. They concluded that although it is difficult to quantify concerns without data comparing the composition of food products from cloned and noncloned animals, there is no current evidence that food products derived from adult somatic cell clones or their progeny present a safety concern. Their greatest concern was surprisingly environmental, specifically the potential for GM organisms to escape and become established in the natural environment. They specifically considered that the existing regulatory framework might not prove adequate, particularly with regard to transgenic arthropods. Understandably, not only were there concerns regarding the potential for this technology to cause pain, physical and physiological distress, behavioral abnormality, and health problems but also noted that potential existed to alleviate or reduce those problems. Broadly, they expressed concern about the technical capacity of the agencies to address potential hazards.

As noted under CVM, investigational applications are filed for genetic modifications under the authority of an investigational new animal drug exemption (INAD) or a similar provision. The INAD regulations are published in the Code of Federal Regulations, Title 21, Part 511.1(b). As part of the INAD submission, researchers must document their plans regarding the disposition of all investigational animals after their participation is completed. This is important in the case of food animal species where, with a showing of adequate safety data, the sponsor may request disposition of animals by slaughter for food or for processing into animal feed components. Although no transgenic animals have been approved for use as human food, a very limited number have been approved for rendering into animal feed components. In September 2008, the FDA published for public comment proposed regulations that crystallized the notion that every transgenic animal expressing a novel trait would be subject to the procedures and regulations for drug approval. In January 2009, the FDA issued a final guidance for industry on the regulation of GE animals. The FDCA defines ''articles (other than food) intended to affect the structure or any function of the body of man or other animals'' as drugs. An rDNA construct that is in a GE animal and is intended to affect the animal's structure or function meets the definition of an animal drug, irrespective of whether the animal is intended for food or used to produce another substance. Under this guidance, developers of these animals must demonstrate that the construct and any new products expressed from the inserted construct are safe for the health of the GE animal and, if they are food animals, for consumption. Many consider that this 'new drug' paradigm does not fit transgenic animals well. Miller (2008) proposed that a better model was the approach taken by the Center for Food Safety and Nutrition that placed the burden of ensuring safety of foods and food ingredients on those who produced them.

In December 2003, California found itself in the national spotlight when it became the only state to ban the sale of a GE pet fish, called the GloFish, based on the potential for negative ecological impact.

The first transgenic animal that is more likely to receive commercial approval is a salmon from the AquAdvantage Company, which reaches maturity twice as fast as the wild type. The fish is an Atlantic salmon that contains the Chinook salmon growth hormone gene, a stably integrated α-form of the *opAFP-GHc2* gene construct at the α-locus in the EO-1α line under the control of an antifreeze protein promoter from the ocean pout permitting year-round expression (Staveley, 2010). The AquAdvantage Salmon reaches market size twice as fast as traditional salmon, but they do not grow to be larger than their conventional counterparts. The salmon are grown in land-based contained tanks and with reproductively sterile females, which precludes the threat of interbreeding among themselves or with native populations, eliminating the risk to wild populations or the environment.

Animal Clones

On 15 January 2008 (CVM and Animal Cloning, 2008) after years of detailed study and analysis, the FDA issued an advisory that concluded that meat and milk from clones of cattle, swine, and goats, and the offspring of clones from any species traditionally consumed as food, are as safe to eat as food from conventionally bred animals. Interestingly, they considered that there was insufficient information for the agency to reach a conclusion on the safety of food from clones of other animal species, such as sheep. The release was advisory rather than regulatory as withholding of clones from the food and feed supply was voluntary because no regulations exist banning this practice.

The advisory consisted of three documents on animal cloning outlining the agency's regulatory approach – a risk assessment, a risk management plan, and guidance for industry. The documents were originally released in draft form in December 2006. Since then, the risk assessment has been updated to include new scientific information. That new information reinforces the food safety conclusions of the drafts, namely that milk and meat products from cloned cattle, pigs, and goats are safe for consumers to eat because cloned cattle between 6 and 18 months of age are 'virtually indistinguishable' from their conventional parents and can give birth to healthy offspring. The agency said that any risk was small, given that the group that could pose problems, live neonatal clones, is unlikely to enter the food supply; it poses an extremely limited risk for consumption. The proposed plan outlines measures that the FDA might take to address the risks that cloning poses to animals involved in the cloning process. These risks have been observed in other assisted reproductive technologies currently in use in common agricultural practices.

The draft guidance for industry addresses the use of food and feed products derived from clones and their offspring. The guidance is directed at clone producers, livestock breeders, and farmers and ranchers purchasing clones. It provides the agency's current thinking on use of clones and their offspring in human food or animal feed.

In the draft guidance, the FDA does not recommend any special measures relating to human food use of offspring of clones of any species. Because of their cost and rarity, clones will be used as any other elite breeding stock – to pass on naturally occurring, desirable traits, such as disease resistance and higher quality meat, to production herds. Because clones will be used primarily for breeding, almost all of the food that comes from the cloning process is expected to be from sexually reproduced offspring and descendents of clones and not the clones themselves.

International Perspective on Food Safety

Biotechnology is a worldwide industry. In the case of GM crops alone, more than 100 000 field trials have been done on more than 200 crops in more than 50 countries, including many of the 27 countries of the EU. Despite the fact that almost 80% of these trials take place in the United States, the regulatory issues are of concern to all, and biotechnology issues are front and center in many international fora. For instance, several nations are working on the United Nations' (UN) Biosafety Protocol. The purpose of the protocol is to protect biological diversity from potential adverse effects resulting from the transboundary movement of living modified organisms, including those made through biotechnology. It also addresses the needs of developing countries to develop the capacity to assess and manage potential risks. The Codex Alimentarius Commission has established the Codex Committee on Food Labeling to arrive at a common international position on labeling. A number of countries and regions have established threshold levels for labeling. For approved varieties, commonly tolerance thresholds are established below which a product does not have to be labeled as containing or derived from GMOs. Threshold levels vary for each legislation. Since 2004, the labeling threshold for food products in the EU is 0.9%. Current EU regulations demand control through analysis and traceability. Food and feed products that contain or are derived from GMOs must be labeled. For products that are highly refined, documentation of their conventional, non-biotech source material is now required. The labeling threshold in Japan is 5%, in South Korea 3%, and in Australia and New Zealand 1%.

However, notwithstanding labeling requirements in different jurisdictions, the consensus of scientific opinion and evidence is that the application of GM technology introduces no unique food/feed safety concerns and that there is no evidence of harm from those products that have been through a regulatory approval process. This conclusion has been reached by numerous national and international organizations (e.g., Food and Agriculture Organization/World Health Organization of the UN (FAO/WHO), Organisation for Economic Cooperation and Development (OECD), EU Commission, French Academy of Sciences, NRC of the National Academy of Sciences, Royal Society of London, and Society of Toxicology).

Some summary statements of these leading science organizations include: "No effects on human health have been shown as a result of the consumption of such foods by the general population in the countries where they have been approved."(WHO); "No adverse health effects attributed to genetic engineering have been documented in the human population." (National Academy of Sciences); "The science is quite clear: crop improvement by the modern molecular techniques of biotechnology is safe." (American Association for the Advancement of Science); "There is no scientific justification for special labeling of bioengineered foods. Bioengineered foods have been consumed for close to 20 years, and during that time, no overt consequences on human health have been reported and/or substantiated in the peer-reviewed literature." (American Medical Association); "No scientific evidence associating GMOs with higher risks for the environment or for food and feed safety than conventional plants and organisms." (European Commission); "All criticisms against GMOs can be largely rejected on strictly scientific criteria." (French Academy of Science); "In consuming food derived from GM plans approved in the EU and in the USA, the risk is in no way higher than in the consumption of food from conventionally grown plants. On the contrary, in some cases food from GM plants appears to be superior in respect to health." (Union of German Academics and Scientists); and "Foods can be produced through the use of GM technology that are more nutritious, stable in storage and in principle, health promoting – bringing benefits to consumers in both industrialized and developing nations." (Joint Statement of the Science Academies of Brazil, China, India, Mexico, Third World Academy of Sciences, Royal Society of the UK and the National Academy of Sciences of the US).

There now exists a significant body of evidence that demonstrates that all forms of plant breeding introduce a variety of changes in DNA, ranging from point mutations and single base pair deletions and insertions, loss or acquisition of genes, to changes in numbers of whole chromosomes. When compared with classical plant breeding methods, transgene insertion has been observed to produce less unintended DNA modification. In contrast to traditionally bred crops, a rigorous safety-testing paradigm has been developed and implemented for GM crops that utilizes a systematic, stepwise, and holistic safety assessment approach (Cockburn, 2002). The resultant science-based process focuses on a classical evaluation of the toxic potential of the introduced novel trait and the wholesomeness of the GM crop. In addition, detailed consideration is given to the history and safe use of the parent crop as well as that of the gene donor(s). The overall safety evaluation is conducted using the process known as 'substantial equivalence,' a model that is entrenched in all international crop biotechnology guidelines. This provides the framework for a comparative approach to identify the similarities and differences between the GM product and an appropriate comparator that has a known history of safe use. By building a detailed profile on each step in the transformation process (from parent to new crop) and by thoroughly evaluating the significance, from a safety perspective, of any differences that may be detected between the GM crop and its comparator, a comprehensive matrix of information is constructed. This information is used to reach a conclusion about whether food or feed derived from the GM crop is as safe as food or feed derived from its traditional counterpart or the appropriate comparator. Using this approach in the evaluation of more than 50 g crops that have been approved worldwide, the conclusion has been reached that foods and feeds derived

from GM crops are as safe and nutritious as those derived from traditional crops. The lack of any proven adverse effects resulting from the production and consumption of GM crops grown on more than one billion cumulative ha over the past 17 years supports these safety conclusions.

The US NRC in 'Genetically Modified Pest-Protected Plants: Science and Regulation' (NRC, 2000) determined that no difference exists between crops modified through modern molecular techniques and those modified by conventional breeding practices. The NRC emphasized that the authors were not aware of any evidence suggesting that foods on the market today are unsafe to eat because of genetic modification. In fact, the scientific panel concluded that growing such crops could have environmental advantages over other crops.

In a 2003 position paper, the Society of Toxicology (SOT, 2003) corroborated this finding and noted that there is no reason to suppose that the process of food production through biotechnology leads to risks of a different nature than those already familiar to toxicologists or to risks generated by conventional breeding practices for plant, animal, or microbial improvement. It is, therefore, important to recognize that it is the food product itself, rather than the process through which it is made, that should be the focus of attention in assessing safety.

The OECD and the WHO have embraced the concept of substantial equivalence as the cornerstone of safety assessment for GM foods and crops. The most complex regulatory and political situation is in the EU, especially with regard to labeling for consumers. The OECD's Working Group on Harmonization of Regulatory Oversight in Biotechnology decided at its first session, in June 1995, to focus its work on the development of consensus documents that are mutually recognized as among member countries. These consensus documents contain information for use during the regulatory assessment of a particular product. The consensus documents comprise technical information for use during the regulatory assessment of products of biotechnology and are intended to be mutually recognized among OECD member countries. These documents focus on the biology of organisms (such as plants, trees, or microorganisms) or introduced novel traits.

Variations due to breeding and the application of modern biotechnology have been studied frequently by scientific experts sponsored by organizations such as the UN FAO, the European Commission, the Royal Society, and the US National Academy of Sciences. In each case, the conclusions were that modern biotechnology is no more likely than conventional breeding to produce unintended effects. Indeed, many expert reviews have concluded that the greater precision and more defined nature of the changes introduced into crops via modern biotechnology may actually be safer than changes produced by conventional plant breeding.

Studies have also shown that GM crops are often more closely related to the isogenic parental strain used in their development than to other members of the same genus and species with respect to their transcriptomic, proteomic, and metabolomics profiles (Ricroch *et al.*, 2011; Baker *et al.*, 2006; Catchpole *et al.*, 2005). For example, metabolomic studies in *Solanum tuberosum* have shown that conventional plant breeding produces both intended and unintended effects and that insertion of transgenes can occur with little apparent effect on composition, even when the GM variety produces significant quantities of a new metabolite (e.g., inulin). Indeed, when the introduced gene product (DP2–3 fructans) was removed from the analysis parameters, multivariate statistical analysis showed no significant variation in the metabolic phenotype, including harmful glycoalkaloids, between the GM crop and the progenitor lines, whereas other, conventionally bred cultivars, showed clearly separated metabolic phenotypes (Chassy *et al.*, 2008). Similar results have been observed at the proteome level for other plant species.

It should not be overlooked, however, that in most plant-breeding programs, successive rounds of planting and selection are used to cull out events with obvious and undesirable phenotypes and select plants with unchanged/superior agronomic and phenotypic traits. Regardless of the method of breeding applied to select genetic changes, the candidate plants that are advanced for potential distribution and planting should closely resemble their parental lines – with the sole exception of the intended modification. It also appears that environmental and cultural conditions have more impact on plant composition than breeding and selection programs (Ricroch *et al.*, 2011). Transcriptomic and metabolomic studies in wheat and potatoes, respectively, show greater variation within and between conventionally bred cultivars and even growth locations than between GM and parental variety except for the intended change. To reinforce this observation, differences within lines between sites were generally greater than differences between lines at the same site for both.

However, transcriptomics may be of limited value because assessing potential effects of gene expression on metabolic or phenotypic traits, since so far, in understanding of biological networks is limited and prevents any valid predictions. It is better to directly measure the outcome of genotype–environment interactions instead of trying to predict potential side effects. Metabolomics is a more valid assessment system. These applications follow a two-tiered approach: they can be used for sample discrimination and classification (e.g., for GM comparator analysis) or they can be used for biochemical and mechanistic studies. These tools can be employed to understand which parts of larger biochemical networks respond to genetic modification. Unbiased and comprehensive assessments of potential and immediate risks should, therefore, focus solely on proteins and metabolite analyses, accompanied by necessary developments in validation, statistical assessments, and databases. Where compositional differences are suggested by fingerprinting studies of GM crops, the comparative assessment process, using validated and quantitative compositional analysis methods, can be guided by the fingerprinting results to reach a more informed understanding of the fingerprint results in order to determine whether additional safety assessments are needed.

It is well recognized that absolute safety is not an achievable goal in any human endeavor, and this is relevant with respect to food and feed. The safe use of food or feed has typically been established either through experience based on its common use or by application of generally recognized scientific assessment procedures. Starting in the 1990s, novel (especially GM) food and feed crops have been held to the standard that they should be as safe as an appropriate counterpart with a history of safe use. Based on this with respect to

potential risks to human health, the consensus of scientific opinion and evidence is that biotechnology-derived foods and feeds present no new or unusual dangers to the environment or human health FAO/WHO, OECD, Seven Academies Report, French Medical Association, Royal Society of London, NRC, and Society of Toxicology).

In 2001 and 2011, the European Commission released two reports that cover 25 years of research on GM crops or food on human health or the environment: (EU Commission Report, 2011) 'A decade of EU-funded GMO research (2001–2010)' and 'EC-Sponsored research on the safety of GM organisms (1985–2000) (EU Commission Report, 2001).' Indeed, they concluded that the use of more precise technology and the greater regulatory scrutiny probably make them even safer than conventional plants and foods. The more recent was a compendium of 50 research projects on the safety of GMOs over the past decade. The Commission funded research from 130 research projects involving 500 independent research groups over 25 years, concluding that "There is, as of today, no scientific evidence associating GMOs with higher risks for the environment or for food and feed safety than conventional plants and organisms." A declaration signed by more than 3500 scientists, including 25 Nobel Laureates, reiterates this position.

The medical community has also supported the introduction of biotechnology-derived plants and foods. The American Medical Association states, "it is the policy of the AMA to endorse or implement programs that will convince the public and government officials that genetic manipulation is not inherently hazardous and that the health and economic benefits of recombinant DNA technology greatly exceed any risk posed to society." Although France has been among the most skeptical countries about this technology, the French Academy of Medicine report, Les plantes génétiquement modifiées "Genetically Modified Plants" (ADSF, 2003), called for an end to the European moratorium on GM crops as there was no demonstrated concern from a human health or environmental impact perspective. These crops have been approved for import and sale in the dozens of countries and for growth as crops in more than 30 countries. For example, Bt maize, herbicide-tolerant soybeans, and herbicide-tolerant canola, among others, have been approved for import into the EU and Japan.

The main principles of the international consensus approach are listed below. They serve to illustrate the variety of principles that have been at the center of the discussions and that are continuously being updated:

Substantial equivalence – this is the guiding principle for the safety assessment. In short, substantial equivalence involves the process of comparing of the GM product to a conventional counterpart with a history of safe use. Such a comparison commonly includes agronomic performance, phenotype, expression of transgenes and composition (macro- and micronutrients), and identifies the similarities and differences between the GM product and the conventional counterpart. Based on the differences identified, further investigations may be carried out to assess the safety of these differences. These assessments include any protein(s) that is produced from the inserted DNA. Reports have demonstrated that GM crops are often more closely related to the isogenic parental strain used in their development than to other members of the same genus and species.

Potential gene transfer – where there is a possibility that selective advantage may be given to an undesirable trait from a food safety or environmental impact perspective; this should be assessed, for example, in the highly unlikely event of a gene coding for a plant-made pharmaceutical transferred to commodity to corn. Where there is a possibility that the introduced gene(s) may be transferred to other crops, the potential environmental impact of the introduced gene and any conferred trait must be assessed.

Potential allergenicity – as most food allergens are proteins, the potential allergenicity of newly expressed proteins in food must be considered. A decision tree approach introduced by International Life Science Institute (ILSI)/International Food Biotechnology Council (IFBC) in 1996 has become internationally acknowledged and updated by Codex (FAO/WHO, 2002). Allergy safety assessments use a panel of characteristics to evaluate novel proteins for allergenic potential. The starting point for this approach is the known allergenic properties of the source organism for the genes. Other recurrent items in this approach are structural similarities between the introduced protein and allergenic proteins, digestibility of the newly introduced protein(s), and eventually if needed, sera-binding tests with either the introduced protein or the biotechnology-derived product. If a novel food protein is not similar to allergens and is not derived from allergenic protein families, it is unlikely to provoke allergy. Moreover, if a protein is degraded in simulated gastric fluid, is small in size (e.g., < 10 kDa), and is not glycosylated, the likelihood that it will be an allergen is also unlikely (Lehrer and Bannon, 2005; Sánchez-Monge and Salcedo, 2005). There are many factors that may elicit food protein allergy, including extrinsic factors such as food use and processing; however, this is not well understood and is a continuing topic of research and discussion. It is important to note that many proteins possess one or more of the properties characteristic of an allergen, and yet they do not cause allergy. The likelihood that a novel biotechnology-derived protein will be an allergen is very low for proteins without sequence similarity and physical properties comparable to known allergens. From a safety perspective, the risk of allergy due to introduction of a novel protein into a crop remains low, regardless of whether proteins are introduced through conventional crop breeding or modern biotechnology.

Potential toxicity – some proteins are known to be toxic, such as enterotoxins from pathogenic bacteria and lectins from plants. Commonly employed tests for toxicity include bioinformatic comparisons of amino acid sequences of any newly expressed protein(s) with the amino acid sequences of known toxins with those of introduced proteins, as well as rodent toxicity tests with acute administration of the proteins. Currently, appropriate toxicity studies are typically needed for the introduced protein in GM crops. The assessment often includes studies such as conducting a bioinformatic comparison of the new protein's amino acid sequence with a database of all publicly available protein sequences (e.g., protease inhibitors and lectins) and testing the newly introduced protein's stability to heat or processing and to degradation in suitably representative gastric and intestinal model systems. Appropriate toxicity studies may be needed in cases where the protein

present in the food is dissimilar to proteins that have previously been consumed safely in food. Such studies should also take into account the biological function of the protein in the plant, when known. In addition to purified proteins, whole grain from GM crops has been tested in animals, commonly in subchronic (90 days) rodent studies.

Unintended effects – besides the intended effects of the modification, interactions of the inserted DNA sequence with the plant genome are possible sources of unintended effects. Another source might be the introduced trait unexpectedly altering plant metabolism. Unintended effects can be both predicted and unpredicted. For example, variations in intermediates and endpoints in metabolic pathways that are the subject of modification while undesirable are predictable and while switch on of unknown endogenous genes through random insertion in control regions is both unintended and unpredictable. The process of product development that selects a single commercial product from hundreds to thousands of initial transformation events eliminates the vast majority of situations that might have resulted in unintended changes. The selected commercial product candidate event undergoes additional detailed phenotypic, agronomic, morphological, and compositional analyses to further screen for such effects.

Long-term effects – it is acknowledged that the premarket safety assessment should be rigorous to exclude potentially adverse effects of consumption of foods or feeds derived from GM crops. Nevertheless, some have insisted that such foods should also be monitored for long-term effects by postmarket surveillance. The cost to benefit of such surveillance is severely skewed toward the cost side. This observation is predicated on a number of facts. In the first place, no international consensus exists as to whether such surveillance studies are technically possible without a testable hypothesis in order to provide meaningful information regarding safety. Second, any GM crop with a testable safety concern will not pass regulatory review as the deregulation process is so thorough. In fact, there is probably a greater probability of a non-GM crop slipping through as they are not subject to any premarket surveillance. Finally, the practical feasibility of implementing such a process is also not trivial. One potential method would be the use of measurable biomarkers; however, these would need to be determined for all foods and feeds, irrespective of the source and the question of reasonable economic burden arising. Most probably, the marketplace would not support such a requirement as the value gained would not be considered a counter to the costs.

Besides the international organizations, such as the FAO/WHO, OECD, ILSI, and the IFBC, other organizations have also formulated their views and recommendations on the oversight of GM crops.

It can be expected that bioengineering the increase of a certain metabolite or introducing novel pathways may have side effects on the overall metabolic network by redirecting some of the metabolic fluxes and by unforeseen metabolic reactions due to potential lack of substrate specificity of the introduced enzymes. However, compared with the plethora of allelic interactions that result from conventional crosses and classical breeding procedures, such directed and limited molecular interventions cannot be regarded as a less safe intervention per se and hence any considerations of extended safety assessments would need to be forced onto varieties that are derived by either technology, breeding, or molecular techniques. Still, GM plants with improved stress responses are very likely to adopt such desired performances by drastically altering their metabolite compositions, hence potentially falling outside the compositional ranges set by classical varieties. For example, the introduction or overexpression of suite of transcription factors might trigger many different events, some of which could potentially lead to unwanted side effects, such as increased levels of antinutrients or toxicants. Hence, the extent of such changes needs to be determined by appropriate analytical tools and useful statistical estimates for a range of genotype–environment interactions.

Targeted Analysis

The term 'safety' itself is not a purely scientific and objective measure but is clearly defined by society, risk tolerance, and policy settings. Industrialized nations with slow or negative population growths tend to be very risk adverse and thus emphasize potential, but not actual, dangers of novel technologies or developments, whereas regions with severe food shortages, high population growths, or high variability of environmental stress factors clearly and rightfully may emphasize current needs and may demand rapid improvements of the available plant germplasm. Consequently, it cannot be anticipated that there are global, universally applicable risk thresholds that are set independent from societal and political environments. Instead, safety assessments should distinguish between immediate and potential implications of altered food compositions. Immediate requirements for improved ('novel') foods are based on comparisons with its closest comparator lines with respect to phenotypic characteristics (e.g., taste and texture), macro- and micronutrients, and antinutrients and toxicants, in addition to agronomic traits such as yield. The safety of these compositional values is based on historic experience and should be tightly regulated and critically assessed if a given single food provides the overwhelming nutritional basis for the majority of a population in a specific region. Fortunately, there are many validated and approved target methods available to test for the concentrations of nutrients and known toxicants so that any novel food, or any newly bred variety, can easily be tested for its compositional quality at comparatively low costs. To prevent malnutrition or intoxications, safety assessments on these target compounds should be made mandatory for any newly introduced variety. The OECD has developed international consensus documents on the suite of metabolites that should be analyzed for specific crops (OECD, 2003). By selecting the nutritionally and antinutritionally relevant compounds, this strategy provides considerable protection against unintentional changes that might affect human or livestock health and well-being.

However, in the OECD countries, public concerns about potential side effects in novel foods go beyond such historically established baselines of 'safe' food usage. In principle, it cannot be excluded that allelic interactions or molecular tools may generate allergenic proteins or potentially harmful concentrations of toxic metabolites, and examples of both are published in the literature at least for classically bred plants. The plasticity of plant metabolism is astounding, giving rise to

more than 200 000 different known plant metabolites. Only a very small number of these metabolites have ever been tested for antinutrient or toxic activity. Structural properties of proteins or metabolites alone cannot establish their potential for adverse effects or safe minimal concentrations of these. Hence, additional techniques are sought that may be used to analyze metabolic and protein compositions in a comprehensive manner. Over the past decade, such techniques have been developed and are increasingly used not only in research and development but also in assessing novel foods and GM plants. Although in principle even DNA or mRNA products may be investigated for differential expression in novel foods compared with previously introduced lines, there is no indication that RNA themselves may play any role in nutrition or cause potential toxic effects, more likely due to their direct digestibility and lack of potential harmful structural modifications or catalytic activities. In research, studies aim at linking the potential effects of gene expression on metabolic or phenotypic traits, but so far, understanding of biological networks is limited and prevents any valid predictions. Consequently, it is more straightforward to directly measure the outcome of genotype–environment interactions instead of trying to predict potential side effects. Unbiased and comprehensive assessments of potential and immediate risks should, therefore, focus solely on proteins and metabolite analyses, accompanied by necessary developments in validation, statistical assessments, and databases.

Approaches to identify unintended effects

In a similar manner to 'safety,' the term 'unintended effects' is equally ill defined and subject to change corresponding to societal and political reassessments. In metabolic bioengineering, one may assume the intended effect only to be altered levels of a target metabolite, but in reality, other metabolites closely involved in biosynthetic routes will also be affected. In this sense, such effects may be regarded unintended but surely not unexpected. On a case-by-case basis, a list of potentially affected metabolic by-products may complement the target studies on known nutrients, antinutrients, and toxicants. Such approach combining a larger set of predefined analytical targets is called 'metabolite profiling,' because it serves as a general overview of important compounds and relevant biochemical pathways. However, due to the high plasticity of plant metabolism, further unintended and unexpected effects cannot be excluded a priori, especially if the output trait of the novel plant lines were geared toward improved agronomic traits, such as stress resistance. If political and societal decisions are made that risk assessments of novel foods should extend to potentially new molecules, under the precautionary principle, then studies could comprise tests if there are (1) any totally novel compounds that were synthesized by potentially novel biochemical routes and (2) compounds that are beyond the upper or lower range of a set of comparable, already marketed plant lines under a set of environmental conditions.

It is important not solely to compare, for example, a stress-resistant plant line to comparator lines under normal growth conditions but also under stress conditions because the stress-resistant plant line may already be preadapted and hence metabolically different to the comparator lines before even the stress situation (drought, cold, salinity, etc.) takes place. If safety is defined by historic experience of safe use, then this experience surely includes food that was derived from stress-grown plants, and hence the ranges of metabolic compositions must include these situations. It would be far too demanding if any novel food would need to pass a suite of growth trials under different environmental conditions. Instead, unintended and unexpected effects could be assessed by comparing the compositions of novel foods in relation to publicly available, untargeted (unbiased) databases. Such comprehensive and untargeted compositional analysis that would necessarily screen for unidentified structures is called 'metabolomics.' In a similar manner, proteomic databases could be used to assess the range of naturally occurring proteins and protein abundances. A range of techniques can be used for comprehensive metabolomics, and equally broad are possibilities to use proteomic methods. Efforts are underway in both areas to standardize the reporting structure of such –omics – data and to recommend current best practices. These are important steps to harmonize workflows and to enable queries of the proteomes or metabolomes of novel foods against databases in order to find unintended and unexpected events. So far, no public repositories on baseline metabolomes and proteomes of crops are available, and it would demand significant budgets to establish such databases. However, in principle, technologies are available and their proper use and data storage can be established, standardized, validated, and monitored. Reasonably, databases for staple crops would need to be established first before moving to feeds and foods with lesser use. It is depending on societal and political decisions if funds are made available to establish and curate such databases based on risk–cost–benefit discussions.

Analytical methods for detection of unintended effects

As stated above, the most reasonable approach to look for unintended effects is to quantify the amounts of known and biologically relevant macro- and micronutrients, including vitamins, antinutrients, allergens, and toxic compounds. Analyses must be carried out using validated techniques, at best in certified laboratories, that perform at-cost assessments of the compositional profiles. Even when just two lines are compared, severe statistical constraints must be obeyed, as pointed out in a thorough statistical paper by Hothorn and Oberdoerfer (2006). For evaluating the relevance of compositional differences in novel foods, which may include GM crops, it is important to compare nutrient levels with the range of concentrations that can be observed in other cultivars or varieties and not only in the direct parental lines. The more the compounds are screened and the more the individual samples are analyzed, the more likely it is that a number of levels turn out to be 'significantly different' from the parental lines. This fact is based on simple considerations of statistical probabilities and has nothing to do with nutritional relevance. It is, therefore, sensible to test if the levels of target compounds are out of range of corresponding counterparts that are regarded as 'safe' for human or livestock consumption. In this respect, the ILSI database may be regarded as important cornerstone to emphasize the breadth of natural variability, especially with respect to genotype–environment interactions. Owing to differences in growing conditions and environmental stress

factors, nutritional values cannot be standardized in a global manner. For certain compounds like glycoalkaloids, upper levels have been defined by the OECD as safeguard against unwanted side effects of either breeding or biotechnology efforts. It might be useful to define further concentration limits for further target compounds, both on upper and lower limits, based on physiological and medical evidence. If these ranges would only be given by agricultural practices, it might otherwise appear that a certain (classic) variety under very specific stress conditions would result in a compositional profile that was vastly different from usual compound levels. Hence, comparisons of concentrations against nutritional databases should also consider frequency distributions of normally reported levels, and not take outliers as out-of-range limits.

As stated above, there is no reason to embark on gene expression or microarray analyses for food safety assessments. These techniques are surely useful for basic science, plant research, and crop development but yet lack to prove that useful predictions of antinutritional or toxic effects can be made that would not be picked up in (more cost efficient) targeted or nontargeted metabolic or protein profiles.

Proteomics – Proteomics and protein profiling have been used for more than 30 years as research tool for comprehensive analyses of protein abundance and protein identifications. In a similar manner to metabolic compounds, there are proteins that are known to cause allergenic or other toxic effects and thus should be monitored in principle with highly selective and sensitive techniques, such as western blots or 'mass westerns,' which employ liquid chromatography (LC) and triple quadrupole mass spectrometry (MS) for specific fragments and mass transitions of target proteins. Unfortunately, there is no prediction tool that would allow an unbiased calculation of the likelihood that any given protein, or a specific protein post-translational modification (e.g., glycosylation, phosphorylation, or any of the other 200 known modifications), would raise safety concerns with respect to potential toxic or allergenic effects. If nontarget 'fishing' for novel proteins is sought, which may be used as a preliminary indication of potential concerns, validation and statistical strategies have to be taken that are highly similar to targeted or nontargeted metabolite analyses. First, the proteomic techniques have to prove that they can be used in a robust and reliable manner, giving precise quantification results for a wide range of proteins. In principle, two methods can be applied for the nontargeted comparisons of relative protein abundances: either classical two-dimensional gel electrophoresis (2D gels) using visual staining for detection or chromatography-based separations followed by mass spectrometry detection and quantification (LC/MS). 2D gels can be used today at comparatively low costs and high precision; however, integral membrane lipophilic proteins and proteins of either very high or very low masses are usually not detectable by this technique. In addition, spot detection, gel alignments, and automated quantifications have to be shown to work reliably for standard food and feed crops, before proteomic databases can be set up to define again out-of-range limits of proteins. Recently, Ruebelt and others published a series of papers (Ruebelt *et al.*, 2006a,b,c) demonstrating 2D gel proteomics of *Arabidopsis thaliana* seed samples that the method itself can be worked out to reproducibly detect and quantify spots, but that there was a wide range of protein abundances when 12 different *Arabidopsis* varieties were compared, covering the abundance range of GM *Arabidopsis* lines. A similarly thorough study on potato varieties and GM lines concluded that proteome dissimilarities between different individual cultivar lines were far larger than comparing a GM line to its progenitor (Lehesranta *et al.*, 2005). In principle, 2D gel proteomics may be used if efforts are made to ensure quality controls and a high enough sample throughput to cope with the statistical challenges.

Another approach in proteomics is to utilize LC/MS on fractionated or partly fractionated proteome samples, for example, by using online cation exchange fractionation steps before LC/MS separation of trypsin-digested proteomes. Such approaches can be used with or without labeling with stable isotope intermediates that are often employed in order to enhance the precision of quantification results. No reports have yet been published on plant proteomes with the same diligence on precision and range assessments as with the 2D gel approach. In principle, proteome fractionation with subsequent LC/MS quantifications may work but is still plagued by some fundamental challenges called ion suppression and retention time alignments. For either of the two general approaches on proteome quantifications, laboratories have to prove that they can perform protein quantifications in a high-throughput manner using quality control charts and precision analyses as minimum quality checks to be able to populate range assessments of crop proteome databases.

Metabolomics – Products of metabolism present a very important part for assessing potential unintended effects, due to the lack of substrate specificity of many enzymes and the resulting large metabolic plasticity in plants. A broad-scale analysis of metabolites can, therefore, provide three aspects to evaluating the similarity, and hence unlikelihood of safety concerns, when comparing novel foods to comparator lines. First, novel compounds may be detected that are absent in any of the classically bred ('safe') cultivars. Novel metabolites themselves cannot be regarded a safety concern because mammalian metabolism is ideally adapted to cope with a wide range of compounds. However, it would be important to associate chemical structures or characterize the substance classes in order to unravel potential similarities to known toxicants or antinutrients. Second, known and structurally uncharacterized metabolites may be present out of range compared with the levels found in metabolomic databases or at least compared with the concentrations detected in a given range assessment study using multiple comparator lines. In a similar manner to presence or absence of novel compounds, the sheer finding that certain compounds are at higher or lower concentrations compared with similar plant lines does not substantiate safety concerns. Nevertheless, it would be important to evaluate the magnitude of differences, the number of different compounds, and their chemical structures to found the basis of the assessment of potential risks. Third, any test on the similarity of individual compound levels might obscure the overall dissimilarity of metabolic patterns. Each individual compound could in principle be barely found to be within range, but the total composition might still be quite different, with many compounds highly upregulated and many others with downregulated levels.

Metabolomic techniques have advanced during the past 5 years. Four different areas of metabolite analysis can be

distinguished: (1) metabolite target analysis, as outlined above; (2) metabolite profiling, aiming at a limited number of compounds or a few selected pathways, using a single specific analytical technique; (3) metabolomics, which necessitates use of a number of different techniques to (ideally) identify and quantify all metabolites present in a given biological situation; and (4) metabolite fingerprinting, which globally assesses the complement (pattern) of metabolites without necessarily identifying individual compounds. The latter approach is usually the most cost-effective method and provides a first broad overview and pattern analysis of overall similarity. Particularly for nuclear magnetic resonance studies (NMR), instrumental parameters can be controlled in such a way that many samples can be analyzed with high precision of quantification results. Although resolution and sensitivity of classic NMR analyses prevent the unambiguous identification of low abundant metabolites, a number of compounds can still be associated to proton NMR shifts. An NMR study on GM wheat revealed surprisingly high differences when lines were grown on two different locations within the United Kingdom, providing evidence for the importance of gene–environment interactions in substantial equivalence studies. Another study including 40 potato GM lines derived from two progenitor varieties further confirmed that the largest differences were detected between the varieties but not between GM and non-GM lines in general (Defernez *et al.*, 2004). Differences associated specifically for individual GM lines were generally within the range given by the cultivars except for intended effects (e.g., in polyamine pathways) or for phenotypically severely hampered lines.

If newer correlation spectroscopy methods are used, particularly total correlation spectroscopy and selective total correlation spectroscopy, NMR metabolite fingerprints may reveal dozens of metabolites in highly quantitative manner (Cloarec *et al.*, 2005). So far, however, no study on crop metabolite fingerprinting has been performed utilizing two-dimensional NMR techniques. Alternatively, various techniques in mass spectrometry-based metabolomics can be applied to study metabolic compositions. In a field trial on transgenic potato lines overexpressing two genes for engineering high fructan contents, Catchpole from the Fiehn laboratory and collaborators from the University of Aberystwyth, UK (2005) suggested a metabolomic hierarchy for testing substantial equivalence. First, overall similarity was assessed by metabolite fingerprinting, which was carried out by direct infusion mass spectrometry. Differences between mass spectra of six GM lines to six non-GM comparator potato lines could be associated to fructan-derived signals that were confirmed by metabolic profiling using hydrophilic interaction chromatography–mass spectrometry. However, even after removing the 15 most abundant fructan ions, differences between GM and non-GM lines remained for low molecular masses. Hence, the investigation was extended to gas chromatography–mass spectrometry, a technique specifically powerful for metabolites below 500 Da. It could be shown that residual differences were related to fructans with a degree of polymerization of two and three, without any further compound detected above out-of-range limits that were defined by the six comparator cultivars. Removing the DP2–3 fructans resulted in a total collapse of GM metabolic phenotypes with the Desiree progenitor lines in multivariate statistics plots, whereas the other classically bred cultivars still showed clearly separated metabolic phenotypes. Finally, metabolite fingerprinting and metabolite profiling approaches were complemented by metabolite target analysis for glycoalkaloid contents (Zywicki *et al.*, 2005) for both potato peel and potato flesh concentrations. It was shown using two different LC-MS/MS techniques that concentrations of these harmful compounds also remained within the limits given by the comparator lines, hence proving that no safety concerns could be deduced from this comprehensive metabolomic study.

In addition to univariate and multivariate statistical analyses used in this potato study, the Fiehn lab at UC Davis has developed a metabolite database that combines metabolomic data acquisition readouts with the underlying experimental design metadata (SetupX and BinBase, Fiehn *et al.*, 2005). This database enables capturing even structurally unidentified compounds in order to assess the variability of these metabolites across species and experiments. As part of these efforts, Fiehn *et al.* have developed new distance metrics that robustly recognize coregulation of pairs of metabolites that can then be visualized and compared by network graphs using Bayesian likelihood models. Ultimately, changes in these networks can be related back to interactions with the underlying biochemical pathways, protein–protein interactions, and genetic networks that can be used to understand the relationship between the different cellular components in GM and comparator plants.

Conclusions

It remains mandatory to monitor novel foods and feed by metabolite target analyses for nutritional value and antinutrient and toxicant levels. In addition to range levels that are recommended for these compounds based on health considerations, it is recommended to extend and establish metabolic composition databases that enable assessing natural variability in crops that result from gene–environment interactions. In addition to such direct approaches, nontarget methods have been established for both protein and metabolite compositions that may enable detecting specific differences between novel plant lines and a variety of comparator lines, if natural variability and quality control measures are adequately addressed. Profiling gene expression levels is regarded unnecessary for safety evaluations at the current state because no accurate predictions can be made from such array studies with respect to potentially harmful allergenic proteins or levels of novel metabolites. It is recommended that profiling database for crops are established spanning different environmental conditions in order to enable baseline assessments to which profiles of metabolites and proteins in novel foods may be compared, irrespective of these being generated using molecular biology techniques or otherwise.

The consensus of scientific opinion and evidence from more than 600 studies worldwide is that biotechnology-derived foods and feeds present no new or unusual dangers to the environment or human health (American Medical Association, WHO, OECD, Seven Academies Report, Royal Society of London, NRC, and Society of Toxicology). Worldwide, tens

of millions of livestock, including chickens, pigs, and cows, are fed with GM soybeans mostly imported from Brazil and Argentina. With the current regulatory environment and monitoring by veterinary authorities, any health impacts related to the consumption of GM crops should be have been reported if there were any safety concerns. This has not been the case for almost two decades since biotech products were first approved by the EU. An estimated 2 trillion meals containing GM ingredients have been eaten around the world over the past 13 years without a single substantiated case of ill health.

The most that can be expected of any oversight regimen is that foods developed using all methods should receive the same level of evaluation both with regard to impact on the environment and safety to the consumer. Millions of people have already eaten the products of genetic engineering and no adverse effects have been demonstrated. Both current science and long-term experience support the repeated conclusions of learned bodies that it should be the product, not the process by which it is developed, that should be evaluated for both risk and benefit. Scientists are confident that if one abandons the scientific method in judging the safety of the food supply and the impact on the environment, one will slow or destroy the advances that will reduce the use of unsafe chemicals and less safe agricultural practices in this country and will limit the potential for improved nutrition and quality that promise to increase food security and enhance sustainability worldwide.

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USDA Petition.
http://www.fda.gov/bioconprocguidance
US Food and Drug Administration.

Regulatory Conventions and Institutions that Govern Global Agricultural Trade

C Zepeda, US Department of Agriculture, Fort Collins, CO, USA

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Glossary

Codex Alimentarius (Codex) International food standards, guidelines, and codes of practice that contribute to the safety, quality, and fairness of this international food trade.

International Plant Protection Convention (IPPC) An international agreement on plant health that aims to protect cultivated and wild plants by preventing the introduction and spread of pests.

Phytosanitary Measure (Measure) A legislation, regulation, or official procedure to prevent the introduction and/or spread of quarantine pests, or to limit the economic impact of regulated nonquarantine pests. (Source: ISPM 5).

World Organization for Animal Health (OIE) The intergovernmental organization that is recognized by the WTO and is responsible for improving animal health worldwide.

World Trade Organization (WTO) The only global international organization dealing with the rules of trade between nations. At its heart are the WTO agreements, which are negotiated and signed by the bulk of the world's trading nations and are ratified in their parliaments. The goal is to help producers of goods and services, exporters, and importers conduct their business.

The Agreement on the Application of Sanitary and Phytosanitary Measures

The Uruguay Round of Multilateral Trade Negotiations of the General Agreement on Tariffs and Trade (GATT) concluded in 1994, after 7.5 years of negotiations, with the signature of the Final Act, in Marrakesh, Morocco on 15 April 1994. This became known as 'the GATT of 1994' and led to the creation of the World Trade Organization (WTO) on 1 January 1995 (WTO, 2013). Among the agreements that were included in the treaty that established the WTO, is the Agreement on the Application of Sanitary and Phytosanitary Measures (SPS Agreement), which sets out the basic rules for the protection of public, animal, and plant health during international trade (WTO, 1995).

The SPS Agreement has changed the way in which trade decisions related to agricultural products are made. Its main intent is to facilitate trade and avoid the use of sanitary and phytosanitary measures as unjustified barriers to trade. The Agreement dictates that all measures must be scientifically based and not unnecessarily restrictive, while recognizing the right of countries to protect human, animal, or plant life or health.

The Three Sisters

The SPS Agreement demands that all sanitary and phytosanitary measures should be science-based and nondiscriminatory, and encourages the application of international standards. The WTO relies on three international organizations to develop standards for animal health, plant health, and food safety. These organizations, colloquially known as the 'three sisters' are: the World Organization for Animal Health (OIE, based on its former name 'Office International des Epizooties'), the International Plant Protection Convention (IPPC) and Codex Alimentarius (Codex).

World Organization for Animal Health

Established in 1924 and headquartered in Paris, the OIE is the organization responsible for setting international standards for animal health. The World Assembly of Delegates, comprised by the 178 Delegates of all member countries, is the highest authority of the OIE and meets at least once a year (OIE, 2013). The objectives of the OIE are to:

- Ensure transparency in the global animal disease situation;
- Collect, analyze, and disseminate veterinary scientific information;
- Encourage international solidarity in the control of animal diseases;
- Safeguard world trade by publishing health standards for international trade in animals and animal products;
- Improve the legal framework and resources of national Veterinary Services;
- Provide a better guarantee of food of animal origin and to promote animal welfare through a science-based approach.

The standards are laid out in the Terrestrial Animal Health Code, the Aquatic Animal health Code and their corresponding Manuals for Diagnostic Tests and Vaccines which are updated annually (OIE; 2012a,b,c).

International Plant Protection Convention

Established in 1952, the IPPC is an international plant health agreement that aims to protect cultivated and wild plants by preventing the introduction and spread of pests. The IPPC has 178 signatories. The Commission on Phytosanitary Measures is the governing body of the IPPC, providing guidance to the IPPC Secretariat on strategic direction, cooperation, financial, and operational management. The Secretariat is provided by the Food and Agriculture Organization of the United Nations with headquarters in Rome.

The IPPC coordinates with relevant international, regional, and national organizations to:

- Protect farmers from economically devastating pest and disease outbreaks,
- Protect the environment from loss of species diversity,
- Protect ecosystems from loss of viability and function as a result of pest invasions,
- Protect industries and consumers from the costs of pest control or eradication.

International standards developed by the IPPC primarily cover international trade of plant and plant products, but also include, among other topics, plant pests and their vectors, research materials and germplasm.

Codex Alimentarius

Established jointly by FAO and WHO in 1963, the Codex is the organization responsible for developing international standards for food safety. There are 186 Codex members that collectively cover 99% of the world's population (FAO/WHO, 2013).

Codex standards deal, among other things, with characteristics of food products, maximum residue limits, food additives, and labeling. In addition, Codex Codes of Practice deal with practices related to hygiene, production, processing, manufacturing, transport, and storage. Finally, Codex guidelines outline principles to define policy and provide guidance in the interpretation of the provisions of the Codex general standards (FAO/WHO, 2006). The standards are compiled and published in the Codex Alimentarius.

Key Provisions

The SPS agreement lays out five key provisions: harmonization, equivalence, risk assessment, regionalization, and transparency.

Harmonization

Harmonization is the establishment, recognition, and application of common sanitary and phytosanitary measures. The SPS agreement encourages countries to base their measures on international standards developed by the relevant international organizations. Countries may apply SPS measures that are more stringent than the international standards as long as they are scientifically justified and based on a risk assessment.

Although membership of the reference international organizations is not mandatory, the SPS Agreement has led to an increase in the number of countries belonging to, and actively participating in, these organizations. The development of international standards requires significant scientific input from specialists in a wide array of technical fields.

Equivalence

The concept of equivalence implies the consideration and acceptance of different SPS measures as long as they achieve similar results. Exporting countries have to justify the scientific basis of the procedures used and objectively demonstrate that they achieve the level of protection required by the importing country. Member countries are encouraged to develop bilateral or multilateral equivalence agreements.

The main tenet of equivalence is the emphasis on results rather than methods or approaches. This allows for flexibility in the organization of official animal, plant, and food safety services and allows for countries to direct their efforts on key areas, according to resources and priorities.

The three international standard setting organizations encourage their member countries to adopt the concept of equivalence. For example, the OIE Code contains a chapter related to the SPS agreement (OIE, 2012a) that discusses principles and outlines a step-wise process to be used in determining equivalence. Furthermore, the chapter emphasizes that equivalence may apply to specific measures (e.g., comparison of different diagnostic procedures) or on a system-wide basis (e.g., equivalence of surveillance systems). There is a need to develop and establish methods to recognize equivalency by developing scientific procedures enabling an unbiased comparison of different approaches.

Risk Assessment

The SPS Agreement defines risk assessment as the "evaluation of the likelihood of entry, establishment, or spread of a pest or disease within the territory of an importing member according to the sanitary or phytosanitary measures which might be applied, and of the associated potential biological and economic consequences; or the evaluation of the potential for adverse effects on human or animal health arising from the presence of additives, contaminants, toxins or disease-causing organisms in food, beverages or feedstuffs." (WTO, 1995).

The article on harmonization states that in the event that an international standard does not exist or does not meet the level of protection required, a country has the right to establish SPS measures based on a scientifically sound risk assessment. The OIE Code contains a section on import risk analysis (OIE, 2012a). Similarly, the IPPC has produced a framework for pest risk analysis IPPC (2007) and a section of Codex' procedural manual (FAO/WHO, 2007) outlines the process. It is interesting to note that the SPS Agreement refers to risk assessment, while the OIE and IPPC use the term risk analysis, within which risk assessment is one of the components of the process.

A common perception is that if an importing country applies the risk-mitigation recommendations set by the relevant international organizations, a risk analysis is not necessary. While it is true that an in-depth risk analysis may not be necessary, the establishment of import requirements involves at least a partial application of the risk analysis process. Part of the complexity in developing import requirements is that multiple hazards can be identified for each commodity. However, the recommendations for animal and plant health are based on an individual disease or pest basis. The question then becomes how to merge the recommendations with the hazards that were identified? Risk analysis in its simplest form provides a framework to establish a link between the hazards identified for the specific commodity, the sanitary status of the exporting and importing countries and international

recommendations. There is a need to promote a better understanding among decision-makers of the concept of risk analysis, its application and limitations. Although each risk assessment is likely to be different, there are common methods, tools and techniques that can be used.

Training is essential to develop the capability to perform rigorous risk assessments. A survey conducted among OIE member countries showed that the majority of countries still require training in risk analysis methods despite the fact that the same survey found that most countries had already received some type of training in this area (Zepeda, 2002). In the field of animal health, the OIE Collaborating Center for Animal Disease Surveillance Systems and Risk Analysis developed a series of short training courses on epidemiology and risk analysis and has organized and conducted several training sessions internationally. Similarly, other institutions worldwide are offering short courses on risk analysis. However, there is a lack of formal training opportunities in risk analysis within universities at the graduate or postgraduate levels.

Risk is defined as the probability of occurrence and the magnitude of the consequences (Ahl et al., 1993). A complete risk assessment should include all the relevant steps outlined by the reference organizations; this is a requirement under the dispute settlement process of the WTO. The Canadian salmon dispute was the first animal health case to go through the WTO dispute settlement process. The Appellate Body report reviewing the Canadian salmon dispute established three conditions to assess if a risk analysis can be considered valid. These include (1) identifying the diseases that may be introduced and their associated consequences, (2) evaluation of the likelihood of entry, establishment; and spread of the diseases identified as hazards as well as the biologic and economic consequences; and (3) evaluation of the likelihood of entry, establishment, and spread of the diseases according to the SPS measures that might be applied (WTO, 1998). A more thorough description of the findings of the Panel is given under the dispute settlement section of this article.

Risk management requires comparing the results of the risk assessment with the country's acceptable level of protection (ALOP). The SPS Agreement recognizes that establishing the ALOP is a prerogative of the importing country (WTO, 1995,1998). However, it does not define how to establish the ALOP, although the process by which it is established must be transparent and applied in a nondiscriminatory fashion. The difficulty in defining the ALOP resides not only on developing good quality risk assessments, but also needs to consider economic implications and societal values.

The application of the risk analysis process requires expertise and a multidisciplinary approach. In several developing countries, this expertise does not exist, emphasizing the need for training and establishing mechanisms to enable access to relevant scientific information.

Regionalization

In the past, when a disease agent existed in a country, the entire territory was considered as infected. The SPS Agreement recognizes that it is possible to consider all of a country, part of a country, or all or parts of several countries free from disease/infection based on the epidemiology of the disease and other criteria. This provision is generally known as zoning or regionalization. It is worth noting that both terms are considered synonymous and can be used interchangeably.

Regionalization requires effective surveillance systems and good quality animal and plant health services both at the national and regional level. When determining the status of a country or zone consideration of several factors has been suggested (CFR, 2013):

- Scope of the evaluation being requested,
- Veterinary control and oversight,
- Disease history and vaccination practices,
- Livestock demographics and traceability,
- Epidemiological separation from potential sources of infection,
- Diagnostic laboratory capabilities,
- Surveillance practices,
- Emergency preparedness and response.

Although these eight factors were developed specifically for animal health, the considerations to assess the status of a country or zone for plant health issues are similar. The quality of the official services both at the national and at the regional level plays a crucial role in preventing the reintroduction of disease. Surveillance systems are essential in providing information for the recognition of disease-free zones and to conduct scientifically valid risk assessments.

Different approaches to zoning and regionalization have been adopted:

- Zoning to contain disease outbreaks.
- Zoning of disease-free areas.

Although the same principles are applied, the emphasis is different. From a risk point of view, the application of zoning as a reaction to disease incursion is not the same as the application of zoning as a measure of progress of a disease eradication program. In the first instance, a zone is a way to separate a diseased area in an otherwise disease-free country; in the second, the zone is a way to secure a free area in an otherwise infected country.

A zone that is defined on grounds of infection, after an outbreak, is less stable. Producers within the zone have to abide by a series of measures that are imposed on them and will affect their normal activities. Movement controls, although strict, may not be efficient and there may be incentives for producers to circumvent them. The disease may spread and the zone's boundaries may need to be modified accordingly. A certain amount of time is needed to achieve stability and demonstrate that the disease is effectively contained within the zone.

A zone that achieves disease eradication and claims freedom is much more stable, it reached that status through a structured disease control program, animal movement controls, active surveillance and producer participation. Furthermore, usually the rest of the country is also under a disease control and eradication program, reducing the risk of reintroduction.

Compartmentalization

A new concept for the management of animal health is compartmentalization, which is a procedure to define animal

populations of different animal health status based on management and biosecurity. Compartments are defined on the basis of the functional relationships of the units within them. The concept of compartmentalization is better suited to vertically integrated production systems such as the poultry or swine industries, where all the units within the system are under the same management and biosecurity practices.

Compartmentalization can be applied in situations where different production systems coexist such as commercial and subsistence farming. In general, commercial farms are in a better position to control and eradicate disease and maintain their status. Having reached this status it is possible through appropriate biosecurity measures to effectively avoid the reintroduction of disease from the affected compartment.

As is the case with regionalization, credibility is the basis for recognition of the status of the compartment. Credibility can only be achieved by effective surveillance, movement controls, producer participation, and most importantly, transparency.

Regionalization has allowed resources to be directed more efficiently by allowing access to export markets from disease-free areas without the need to achieve eradication in the entire territory of a country (Zepeda, 1998). From a scientific perspective, disease freedom cannot be conclusively demonstrated. There is a need for the development of methods to substantiate disease freedom claims that include evidence from structured random surveys as well as nonrandom data sources, such as information from passive surveillance systems. Quantification of the joint probability of detection of all the components of a surveillance system allows reaching a high level of confidence of the absence of disease, higher than any of the components individually (Cannon, 2002; Cameron *et al.*, 2003). There is also a need to include economic considerations in defining the intensity of surveillance and deciding on the optimal combination of surveillance components of a system.

Transparency

The SPS Agreement requires countries to notify the WTO about changes in measures that have an impact in international trade. SPS measures must be published and accessible through an official inquiry point. The transparency provision also includes control and inspection procedures as well as risk assessment. Throughout the process, confidentiality of commercial information is maintained (WTO, 1995). In many countries, the transparency provision has led to review the process of regulation drafting, resulting in more open processes that allow input from all interested parties.

The concept of transparency also applies to reporting of the disease situation in a country. OIE and the IPPC have reporting requirements for their members and the information is made publicly available. Transparency on the sanitary and phytosanitary status is the basis for trust in international trade.

Dispute Settlement

WTO member countries have the right to invoke the dispute settlement procedure; however, bilateral settlements are always encouraged. The OIE has set up a procedure for 'in house' dispute settlement (Chapter 1.3.1, OIE Code) (OIE, 2012a; Vallat and Wilson, 2003). Countries using the dispute settlement procedure must be ready to defend their positions with scientifically valid arguments.

The WTO dispute settlement procedure is a lengthy procedure that can be very costly (WTO, 2003) and often requires legal advice and a continuous presence at WTO's headquarters. Therefore, it is a procedure best suited for issues that imply large amounts of trade. It is possible that developing countries may not be willing to elevate a dispute to this level due to financial constraints, leading to an inequitable application of the rights embedded in the SPS Agreement.

Article 12 of the SPS agreement establishes the creation of the SPS Committee to provide a forum for regular consultations. Further, the article encourages the Committee to facilitate negotiations and discussions between parties involved. The SPS Committee acts as the first forum in which SPS-related disagreements can be discussed once bilateral talks have been exhausted. Often, the fact of raising an issue at the SPS Committee level leads to renewed bilateral discussions resulting in very few disputes needing to go through the entire dispute settlement process. In fact, only three cases related to SPS issues had been through the complete formal WTO dispute settlement procedures.

In all formal disputes, risk assessment has been the central part of the technical and scientific evidence submitted to the expert panel. The Appellate Body reviewing the Canadian/Australian salmon case underscored the importance of submitting complete risk assessments and defined a three-pronged test to assess if a study can qualify as a risk assessment under Article 5 and the definition in annex B. According to the panel, an import risk assessment needs to (WTO, 1998):

1. "Identify the diseases whose entry, establishment or spread a Member wants to prevent within its territory, as well as the potential biological and economic consequences associated with the entry, establishment or spread of these diseases;
2. Evaluate the likelihood of entry, establishment or spread of these diseases, as well as the associated potential biological and economic consequences; and
3. Evaluate the likelihood of entry, establishment or spread of these diseases according to the SPS measures which might be applied."

The Appellate Body report emphasized the importance of a solid scientific basis and the coherence between the risk assessment and the resulting SPS measures that are applied. Evidently, good epidemiology is the basis to satisfy this requirement. The report also distinguished between possibility – instead of likelihood or probability – of disease entry, stressing that the second test requires the evaluation of the likelihood (not mere possibility), without there being a need for this evaluation to be done necessarily in a quantitative way.

Challenges and Opportunities

Regionalization, compartmentalization, and risk assessment allow for trade to occur even if a disease has not been

completely eradicated within a country. This has allowed countries to access export markets that were previously inaccessible due to the presence of specific diseases, and, in turn, has led to increased transparency, as countries are more willing to share information on the sanitary and phytosanitary situation within their territories. It must be recognized, however, that although science has become increasingly important in the process of decision-making, other factors such as politics and economics will continue to play a role in the process.

A common misconception is that countries that are not planning to export are not impacted by the SPS Agreement. Both importing and exporting countries need to be able to justify the application of SPS measures to their trading partners and to their own consumers, producers, and industry groups.

Meeting the requirements of the SPS Agreement entails strengthening sanitary and phytosanitary services in several areas of competence. However, economic crises and the resulting budget constraints have resulted in significant challenges to achieve full compliance. To bridge this gap, official sanitary and phytosanitary services in many countries have resorted to the accreditation of private professionals to carry out official actions, to privatization of services under the regulation and supervision of the state and have also implemented schemes of mixed financial participation with specific objectives such as disease eradication campaigns (Zepeda, 1998).

Sound science is the cornerstone for successful implementation of the SPS Agreement.

See also: Agricultural Law. Agricultural Policy: A Global View. Food Security, Market Processes, and the Role of Government Policy. International and Regional Institutions and Instruments for Agricultural Policy, Research, and Development. International Trade. Quarantine and Biosecurity

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Root and Tuber Crops

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Introduction

Root and tuber crops are plants yielding starchy roots, tubers, rhizomes, corms, and stems. They are used mainly for human food (as such or in processed form), animal feed, and for manufacturing starch, alcohol, and fermented beverages including beer. Many of the developing world's poorest producers and the most undernourished households depend on root and tuber crops as an important source of food and nutrition (Scott *et al.*, 2000). Root and tuber crops produce large quantities of energy per day, in comparison with cereals. They have been playing more and more important roles in global food and energy security. The major root and tuber crops – potato, sweet potato, cassava, and yam – occupy approximately 53.93 million hectares worldwide and produce 736.747 million tonnes annually (FAO, 2008). Individually, potato, sweet potato, cassava, and yam rank among the most important food crops worldwide in terms of annual volume of production. Potato, sweet potato, and cassava rank among the top ten food crops produced in developing countries. This article describes origin and distribution, botany and physiology, breeding and cultivation, diseases and insects, and uses and economic importance of the three crops: potato, sweet potato and cassava.

Potato

Origin and Distribution

The center of origin of potato is known to be the Andes of southern Peru and northern Bolivia. The first potatoes were cultivated approximately 8000 years ago in this region, where the potato became intimately connected with Andean culture and religion and was reflected in myths and legends describing the bounties of the Pachamama or Mother Earth. The historical record of the first European to see potatoes was in 1537, when a band of Spaniards led by Jiménez de Quesada penetrated into the highlands of what is now Colombia. Potato in Chile received first mention by Francis Drake in 1578. Apparently there were two introductions into Europe, one into Spain in 1570 and the second into England in 1590. Potatoes in the North American colonies were received first from Bermuda in 1691. British missionaries took potatoes to India and China in the seventeenth century and they were introduced into Japan and parts of Africa at about the same time. They appeared in New Zealand in 1769 and were grown by the Maoris by 1840. Thus, the potato became one of the important crops in more than 300 years (Hawkes, 1994). Now, there are more than 150 countries growing potatoes. The most important cultivated potato belongs to the species, *Solanum tuberosum* L., 2n = 4x = 48. In addition to *S. tuberosum*, there are seven other cultivated species and 228 wild species. They possess the same base number ($x = 12$) of chromosome as the cultivated potatoes and range from diploid ($2n = 2x = 24$) to hexaploid ($2n = 6x = 72$) (Hawkes, 1994).

Botany and Physiology

Cultivated potato is a vegetatively propagated crop. A potato tuber, actually a modified stem, is both a storage organ and a reproductive organ. The face of each tuber has 'eyes,' which are undeveloped leaf buds. Each eye has three buds, one being primary and the others axillary. When the tubers for breaking dormancy eyes begin to grow while exposed to light, they generally form short stem with leaves. As potato stems elongate, leaves form in a spiral pattern; the first leaves forming at the bottom of the plant and the younger leaves developing from the top as the stem continues to grow upward. Each point where a leaf attaches to the stem is called a 'node,' and each attachment point to the stem represents a single compound leaf, which consists of a terminal leaflet and a row of opposite leaflets all attached to a petiole.

Early- or short-season potato cultivars are often limited to vine growth. These plants will generally form 10–13 leaves and then produce a flower. Once the leaves and flowers have matured, further vine growth stops. Long-season potato cultivars are often 'indeterminate,' meaning that vine growth and flower production continue throughout the season. As with short-season cultivars, the first inflorescence will occur at the 10th–13th node. However, growth does not cease at this point, and one of the side or axillary buds just below the flower will begin elongating into a new stem, which will produce another inflorescence. With a sufficiently long season and good nutrition, this process can repeat.

The flowers are actinomorphic and calyx. The five stamens alternate with the petals and are borne on the corolla tube. The anthers enclose the pistil. At maturity, the stamens have short, stout filaments and long anthers. Pollen is shed through pores at the tips of the anthers. There are usually two carpels, the primordia of which are formed simultaneously. These fuse to form a syncarpous, bilocular, superior ovary with a long style and a bilobed stigma. Under proper condition, flower can pollinate and develop into a mature fruit and seed. Each seed inside of a potato fruit is genetically different, and each seed is potentially a new potato variety. Potato breeders use these fruits to produce new varieties.

Once the potato vines are well established, plants will produce stolons underground, which are modified stem that grow horizontally. With appropriate conditions, the tips of stolons will soon hook and begin to swell, resulting in the initiation of new tubers.

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Breeding

Cultivated potato from *S. tuberosum* is a tetraploid, which displays tetrasomic inheritance. The crossbreeding is main breeding method of potato. Compared with other crops, because the parents are not homozygous, potato F_1 is a segregating population. Although regional breeding procedures have certain differences, the basic process is the same (Table 1).

At present, most widely cultivated varieties are created by crossbreeding or natural pollination seeds. The main breeding targets may differ between countries or regions. Generally speaking, the concerns mostly include tuber yield, maturity, resistance to biotic and abiotic stresses, and characteristics of tubers like size, shape, nutrient components, etc. There are several famous potato varieties in the world worth mentioning. Much elder one is 'Bintje,' bred by K. L. de Vrie, Netherlands in 1905 from a cross between 'Munstersen' and 'Fransen.' It produces a moderate to high yield and has moderate drought resistance. Tubers are oval to long oval with smooth, pale yellow skins. It is the variety which cooks slightly moist and firm, with light yellow flesh and good shape. Now the variety is widely used for genetic engineering research as it has the good culture response *in vitro*. 'Russet Burbank,' another well-known potato variety, was identified and selected by Lou Sweet of Colorado in 1914. The tuber is long, slightly flattened with medium russet skin. Russet Burbank has good storage, processing, and culinary qualities. Currently, widely used chip variety is 'Atlantic,' which was released in 1978 by the USDA-ARS-Beltsville. Its tubers are round to oval and buff colored. It is suitable for processing into potato chips directly from the field and from short-term storage. A famous French fry variety is 'Shepody,' which was released in 1980 by Agriculture Canada in New Brunswick. Tubers are long and white skinned with light netting. The utilization is direct-delivery processing into frozen-fried products. Up to now, there are more than thousands of potato varieties in the world, of which more than 300 varieties have been developed in China in the past 50 years.

Recognition of the primary sources of genes for disease and pest resistances lacking in cultivars of *S. tuberosum* has led to numerous collecting expeditions during the early twentieth century. Several potato germplasm collections have been established worldwide: the Vavilov collection in Russia, the Dutch–German genebank in Braunsweig, Germany, the Commonwealth Potato Collection (CPC) in the UK, the US potato genebank in Sturgeon Bay, the wild species collection at Balcare in Argentina, and mainly *S. tuberosum* varieties collection in Chile. Probably the largest collection has been established at the International Potato Center (CIP) in Peru.

In the origin centers of diversity from South America, 228 wild tuber-bearing *Solanum* species have been recognized, according to the latest taxonomic interpretation and partitioned in 21 taxonomic series. There are two barriers in interspecific hybridization between *Solanum* species. One is prezygotic barriers and the other is postzygotic barriers. Prezygotic barriers are expressed between pollination and fertilization as nongermination of pollen on stigma; germination, but no penetration into stigma; or penetration, but inhibition of pollen tube growth to ovary or ovule. Postzygotic barriers are expressed during and after fertilization in ovules, or more specifically, in embryo sacs and also during growth and flowing of F_1 plants or even later in generations. Embryo development may be arrested in its early stages due to the acting of deleterious genes, due to degeneration of the suspensor of the embryo cutting off the nutritive supply, and most frequently due to endosperm degeneration (Hermsen, 1994). Endosperm failure is associated with endosperm balance number (EBN). To explain the crossing behavior of different species, each species is assigned a hypothetical value in the endosperm. The hypothetical value is named EBN. An interspecific hybrid embryo is obtained when both parent species have the same EBN. EBN can be manipulated by 2n gametes or mitotic chromosome doubling and by haploidization (Carputo *et al.*, 1997). The role of 2n gametes in overcoming critical stages in introgression breeding schemes has been well documented, in which the use of bridging species has also been exploited to bring introgression from distantly related species to potato cultivars (Carputo *et al.*, 2000); also, the favorable alleles of 2x parent can be transferred to the 4x cultivars via 2n gamets (Ortiz *et al.*, 1997).

Somatic hybridization may be a rapid and efficient way to get the interspecific hybrid. In this approach, the success of somatic hybridization of some wild species with *S. tuberosum* demonstrates its potential because most of the somatic hybrids introgressed the valuable trait, like resistance, from distant

Table 1 General breeding procedure

Season 1	Sexual hybridization. Greenhouse crosses or field crosses in proper condition. The true seeds are harvested from each cross
Season 2	Potato family populations are developed by planting the seeds to grow minitubers
Season 3	The potato family minitubers are planted 1–4 hill in the field. Selections are made on phenotypic characteristics – appearance field, disease resistance, and maturity
Season 4	Selected tuber clones are planted in the field as 5–10 hill. Evaluation is conducted in the field for integrative plant performance and the selections are harvested
Season 5	Selected clones are planted 10–20 hill in a 2-replecation trial and go through another year of phenotypic evaluations, selections, disease testing, and quality testing
Season 6	The field evaluation for the selected clones are carried out with three replicated agronomic trials. Selections are recognized as advanced breeding lines. These lines are transferred to tissue culture laboratory where virus- and disease-free plantlets are grown on nutritional media in test tubes
Season 7–8	During these seasons, regional test organized by authorities is conducted. Adaptation, tuber quality, and disease and insect resistance are further evaluated
Season 9–10	On-farm trials are carried out. Large-scale agronomic and storage testing are conducted. Variety Release and Plant Variety Protection is considered. Certified potato seed tuber production is initiated. Contracts with seed growers are prepared

species to cultivated variety (Zimnoch-Guzowska *et al.*, 2003) and some somatic hybrids can be sexually backcrossed to potato cultivars (Helgeson and Williams, 1991; Guo, 2011).

Genetic transformation has gained its fast development in potato. It is potentially the shortest procedure for introgressing alien genes into a crop species, and hybridization barriers are not relevant. Transformed cells must have the ability to regenerate into plants. Fortunately, the potato in general has a good regeneration and transformation ability, but the genetic differences are the limited factors for making progress with certain genotypes. Another drawback may be somaclonal variation among the regenerated transgenic plants.

With the development of molecular biology, many important genes have been identified from potato. Elucidation of gene functions has opened brand avenues for understanding the genetic network and manipulating the performance of a trait. Some *R* genes resistant to potato late blight have initiated pyramid breeding by using more and more *R* genes in a variety against this disease. The global transcriptomics have identified at least 428 genes contributed to the quantitative resistance of potato to late blight (Wang *et al.*, 2005; Li *et al.*, 2009), some of them have been cloned and functionally tested to play critical roles in the resistant pathways.

The genes related to tuber quality may be represented by *StvacInv1* and *StInvInh2*, which encode potato vacuolar invertase and the invertase inhibitor. These two genes have recently been well documented to control the reducing sugar content of cold-stored potato tubers through their interaction (Liu *et al.*, 2013). The reducing sugar content is a key factor influencing quality of frying products, because of which most of the potato varieties are not suitable for frying processing.

Other genes which are lacking in potato cultivars could be identified in wild species and relative cultivated specie, such as species showing pest resistance, frost and draught resistance or tolerance, specific nutrient components, etc. Development in high-throughput sequencing in combination with the platforms of proteomics, metabolomics, as well as computational tools will accelerate the innovation to deepen the understanding in how a trait have been controlled and how to control a trait more efficiently.

Cultivation

Potatoes are grown in a wide variety of regions more than other crops, except maize, that is, from tropic to temperate zone and from sea level to 4000 m high hills. Although potatoes can grow under various environmental conditions, an appropriate cultivation is essential for a good harvest.

Like other vegetatively propagated plants, degeneration caused by viruses is one of the main factors impacting on tuber yield. Use of certified seed tubers, which are produced initially by *in vitro* virus elimination and subsequent propagation in protected region and selected fields for minimizing disease and insect infection, can be the first choice to ensure a high yield. A desirable size of seed tubers is approximately 50 g. The seed tuber bears a number of sprouts; a sprouting level represents the physiological age of the tuber. Relatively younger seed tubers would have a stronger capacity of production.

Each seed tuber can develop a various number of stems, a variety-dependent trait but largely associated with mother tuber size. Because each stem has its own root system and forms tubers independently, number of stems per unit area is propitious to term the plant density of a potato crop. Many experiments have proved that number of tubers and tuber size are strongly affected by number of stems. A negative exponential model developed by Xie (1989) is predicable to estimate tubers of each size category. The higher the plant density is, the more the tubers and smaller the tuber size will be. A desirable plant density is determined by the variety used and demand for the products. For example, large tubers are profitable for a ware crop and a relative small size is better for seeds; therefore, a lower plant density can more easily be applied to the former than to the latter.

Field management is important for any crop. Mineral nutrition required by the plants is obtained from the soil and fertilizers applied. Potatoes need optimal level of essential nutrients throughout the growing season to ensure normal plant growth and tuber development. Potato plants with tuber yields that range from 50 to 60 ton ha^{-1} will take up approximately 220–270 kg N, 28–40 kg P, 310–360 kg K, 20–27 kg S, 55 kg Ca, 45 kg Mg, 2 kg Fe, 0.2 kg B, 0.1 kg Zn, 1 kg Mn, and 0.1 kg Cu. Potatoes usually take up approximately 40–50% of their seasonal nitrogen and potassium requirements and approximately 30–40% of their phosphorus and sulfur requirements by the time tuber bulking begins.

High tuber yields are dependent on an adequate supply of soil water, and water supply is a major cause of year-to-year variation in yield. Potato yield can be reduced by both over- and underirrigation. Generally, approximately 10% deviation from optimum water supply for the growing season may begin to decrease yield. Available soil moisture in the root zoon (0–45 cm) should be maintained at 65% to avoid yield and quality losses. Normally, it is better to keep the available soil moisture between 70% and 85% during the active growth period for optimum results (**Figure 1**).

Diseases and Insects

Potatoes are easily attacked by many kinds of pathogens which cause serious yield loss. The most devastating disease of potato is late blight, which leads to losses of billions of dollars annually to modern agriculture and also impacts on subsistence farming in developing countries (Kamoun and Smart, 2005). Late blight is caused by the oomycete pathogen *Phytophthora infestans* (Mont.) de Bary, which induced the Irish famines in the mid-nineteenth century. *P. infestans* is an adapted pathogen that can affect the whole plant of potato. Water-soaked lesions appear on foliage. The disease is favored by temperatures between 10 and 25 °C, accompanied by heavy dew or rain. Tubers infected by spores washed by rain from the leaves and stems into the soil have brownish surface discoloration and finally rotted. Sources of inoculum are mainly neighboring fields of potato or tomato. Soil survival occurs wherever the oospores exist as a result of the presence of the A1 and A2 mating types, which can lead to early infection. There are cultivars with various levels of resistance. However, the disease is mainly controlled by spraying protective and/or systemic fungicides.



(a) (b)

Figure 1 Potato plants in a field (a) and storage tubers harvested (b).

Many fungal diseases are well described. The widely occurred ones include powdery scab of tubers caused by *Spongospora subterranea*; ward – the tumors developed on stems, stolons, and tubers – caused by *Synchytrium endobioticum*; pink rot of tubers caused by *Phytophthora erythroseptica*; powdery mildew of leaves caused by *Erysiphe cichoracearum*; early blight that can infect both leaves and tubers, caused by *Alternaria solani*; and stem rot (*Sclerotium rolfsii*) and black rot (*Rosellinia* sp.); both result in rot of stem base just below the soil line. Host resistance and fungicides are available for control of most fungal diseases.

Some important diseases are caused by bacteria. The well-known one is bacterial wilt, which is the most serious bacterial disease of potato in warm regions of the world. The pathogen *Ralstonia solanacearum* infects phloem of stem and results in wilt of part of leaves, branches, or whole plant. Latent tuber infection occurs when infected seed is planted in cool locations or in tubers infected late in the growing season. Wilt develops rapidly at high temperatures. Neither the high-level resistances in cultivated varieties have been identified, nor are there any efficient chemical available for bacterial wilt control. Crop rotation is most effective with race 3 (also known as potato strain) of the pathogen but difficult with race 1, which also infects many other crops and weeds.

Bacterial diseases widely distributed also include blackleg (*Erwinia* spp.), ring rot (*Clavibacter michiganensis* ssp. *sepedonics*), and common scab (*Streptomyces scabies*). Using healthy seed is recommended. Overirrigation should be avoided for control of blackleg and soil pH levels should be maintained at 5–5.2. Acid-forming fertilizers of sulfur for control of common scab are preferable.

More than 20 viruses and viroids can infect potatoes, resulting in serious yield loss known as 'degeneration.' The most important potato viruses are considered to be eliminated in many seed potato certification systems, including Potato Virus X (PVX), Potato Virus Y (PVY), Potato Leaf Roll Virus (PLRV), Potato Virus A (PVA), Potato Virus S (PVS), Potato Virus M (PVM), as well as Potato Spindle Tuber Viroid (PSTV). Potato plants can be infected by a single virus or by multiviruses, the latter usually cause much more severe plant symptoms than caused by the former. Resistance to individual viruses can be found out in modern varieties, but a pyramid breeding is not applicable to build up the multiresistance to all these important pathogens; degeneration would occur if a variety is susceptible to any of the viruses. Therefore, the most effective way of controlling virus diseases is adaptation of the seed potato certification system, by which healthy seeds can be supplied.

Nematodes are a serious cause of potato diseases in some of the main potato-growing areas. Cyst nematodes (*Globodera pallida* and *G. rostchiensis*) are native to Andes and have now spread to some temperate zones and high-altitude tropics. Root-knot nematodes (*Meloidogyne* spp.) occur normally in warm regions, particularly in sandy soils. These two nematodes also increase incidence of infection by bacterial and *Verticillium* wilt. Other nematodes include false root-knot nematodes (*Nacobbus aberrans*) and lesion nematodes (*Pratylenchus* spp.) that occur in cold Andean areas and in temperate climates. Use of healthy seeds and long rotation can reduce the damage caused by nematodes.

In addition to the green pitch aphid (*Myzus persicae*) – the most important potato aphid that can damage plants directly by feeding and indirectly by transmitting viruses to the plants – the potato tuber moths (*Phthorimaea operculella*, *Symmetrischema plaesiosema*, *Tecia solanivora*, and *Srobipalpula absoluta*) and the Colorado potato beetle (*Leptinotarsa decemlineata*) have attracted great attention because of their increasing impact on yield and difficulties for control.

Potato tuber moths attack potatoes in both fields and stores. They are widely distributed in warm, dry areas. *P. operculella* is the most damaging type and is generally of greatest importance in warmer climates; the larva can bore through the plant terminals and stems, mine the leaves, and bore through the tubers in the field. Severe damage can occur in stores in a short time. *S. absoluta* damages only leaves and sprouts, whereas both *S. plaesiosema*and *T. solanivora* principally attack tubers in stores. The pest incidence can be reduced through cultural practices such as not planting potato in the warmest and driest seasons, proper irrigation to prevent soil cracking that allows moth to reach the tubers, and occasionally using a selective insecticide. Biological insecticide treatments such as *Bacillus thuringiensis* or *Baculovirus* can be used with tubers in stores.

The Colorado potato beetle is an insect dangerous to potato in North America and some other areas of the world. Potato yields are reduced and plants are sometimes killed by adult and larval leaf feeding. More serious yield loss can be caused by leaf feeding when it occurs within 2 weeks of flowering. The high reproductive potential, and the fact that this insect has become resistant to almost all insecticides used against it, make Colorado potato beetle difficult to control. Crop rotation can help to delay or reduce beetle pressure. Control of volunteers and weeds can limit the early food source of overwintering beetle adults. Chemical control is a main way but should be rotated with each application to avoid development of resistance to any one compound.

Uses and Economic Importance

In 2008, the United Nations declared the International Year of Potato with the slogan 'Hidden Treasure.' This global activity has attracted attention on the role of potato providing food security and eradicating poverty in support of achievement of the internationally agreed development goals including the Millenium Development Goals (Lutaladio and Castaldi, 2009). There are more than 1 billion undernourished people in the world and majority of them live in developing countries. The poorest and most undernourished farm households depend on potatoes as a primary or secondary source of food and nutrition. The potato produces more nutritious food more quickly on less land and in harsher climate than any other major crops. It is estimated that the world potato demand is going to double by 2020 of that in 1993. Besides for human consumption, potatoes can also be used for industrial purposes such as starch production. Potato starch can be processed in textile, papermaking, glue, coating, sizing, flocculating agents, and building materials. More uses can be anticipated for the future, such as in biopharmaceuticals for encapsulation and controlled release of functional ingredients.

According to the statistics of FAO (http:faosta.fao.org), in 2011, the potato area harvested in the world was 19.25 million hectares with output of 374.38 metric tonnes. The gross production value of potato was accounted for 2.64% of that of agriculture in total. The world potato sector is undergoing tremendous changes. Until the early 1990s, most potatoes were grown and consumed in Europe, North America, and countries of the former Soviet Union. Since then, there has been a dramatic increase in potato production and demand in Asia, Africa, and Latin America, where output rose from less than 30 million tonnes in the early 1960s to more than 165 million tonnes in 2007. FAO data show that in 2005, for the first time, the developing world's potato production exceeded that of the developed world (http://www.potato2008.org/en/world/index.html). China is now the biggest potato producer, and almost a third of all potatoes is harvested in China and India.

Accelerated and sustainable development of the potato sector is essential both to guarantee the food security of the world's growing population and as a source of added value to drive economic development in countries dependent on agriculture. Potato is already helping in development and food security in Africa, Asia, and Latin America, where potatoes have become an important staple food and cash crop. But further progress requires both increases in the productivity, profitability, and sustainability of potato-based farming systems and a stronger commitment by the international community to agricultural and rural development.

Sweet Potato

Origin and Distribution

Sweet potato, *Ipomoea batatas* (L.) Lam., was originally domesticated at least 5000 years ago in tropical America (Yen, 1982). The exact center of origin and domestication of sweet potato has not been well defined, nor has the wild ancestor of this species been found (Rossel *et al.*, 2001). Based on the numerical analysis of key morphological characters of sweet potato and the wild *Ipomoea* species, Austin (1988) postulated that sweet potato originated in the region between the Yucatán Peninsula of Mexico and the Orinoco River in Venezuela, within which the four major American taxa of the *batatas* group are distributed. Recent reports using molecular markers to assess diversity have found the highest diversity in Central America, supporting the hypothesis that Central America is the primary center of diversity and most likely the center of origin of sweet potato (Huang and Sun, 2000; Zhang *et al.*, 2000).

Sweet potato was one of the first plants introduced from the Americas into Europe by Columbus in 1492. From Europe, this crop was taken by the Portuguese explorers of the sixteenth century to Africa, India, Southeast Asia, and the East Indies. This is the so-called '*batata* line' of dispersal. The *camote* line (from the Nahuatl word *camotli*) represented the direct transfer of Mexican sweet potatoes by Spanish trading galleons between Mexico and the Philippines in the sixteenth century (Rossel *et al.*, 2001). In the Asia and Pacific region, there have been complex interchanges of sweet potato after early introductions. The introduction of sweet potato to the Pacific islands before the era of European exploration was considered to be the third line of prehistoric transmission (Yen, 1982). Fossil carbonized storage roots of sweet potato found in northern New Zealand have been dated back to approximately 1000 years (Yen, 1991), probably by Peruvian or Polynesian voyagers (Yen, 1982). The linguistic links between the Quechua and Polynesian names for sweet potato, and their variations, support the Peruvian origin and human transfer of the Polynesian sweet potato (Rossel *et al.*, 2001). The successful drift voyages of the Kon-Tiki expedition in 1947 (Heyerdahl, 1950) further put this sweet potato issue within the context of the wider problem of the origin of the Polynesian people. Using complementary sets of markers (chloroplast and nuclear microsatellites) and both modern and herbarium samples, Roullier *et al.* (2013) provide the support for prehistoric transfers of sweet potato from South America (Peru–Ecuador region) into Polynesia. Today, the 'Kumara' area includes many sweet potato-producing countries in Oceania, including New Zealand, Tonga, Samoa, and the Cook Islands (Yen, 1974), where sweet potato is a widely used staple food.

Sweet potato is an ancient crop of Peru (Yen, 1974; Austin, 1987). Examples unearthed at numerous archeological sites representing both Inca and preInca cultures suggest that sweet

potato was one of the most important crops in this region (Urgent and Peterson, 1988). However, whether Peru was a major source of sweet potato to Oceania is still unsettled. The studies based on molecular markers showed that Peruvian sweet potatoes were not closely related to those from Papua New Guinea (Zhang *et al.*, 1998) and were also different from those of Mesoamerica (Zhang *et al.*, 2000). Understanding the level of genetic diversity and geographic differentiation is critically important to germplasm conservation. Conservation strategies and methods depend largely on this kind of information from within a given gene pool (Rossel *et al.*, 2001). It was suggested that the sweet potato from Oceania probably came from Central America through nonhuman dispersal (Rossel *et al.*, 2001). The crop was apparently introduced to China in the late sixteenth century by ship from Luzon in the Philippines to Fujian of China (O'Brien, 1972). Other data give information that sweet potato was introduced to China from Vietnam, India, and Burma. Extension of sweet potato inside China was apparently from south to east along the coast and from south to north through the Yangtze River and the Yellow River valleys.

In 2000, CIP published *A Global Geo-Referenced Database of Sweetpotato Distribution*, by Huaccho and Hijmans, based on data from many country-level sources and the Food and Agriculture Organization of the United Nations (FAO). Hijmans, through updating the Database, described a new global geo-referenced database of the distribution of sweet potato and used it to provide a preliminary description of the current distribution of the crop. The results are as follows: sweet potato is grown in areas where it can be grown year round as well as in areas where it can be grown only in the summer (warm) season and approximately half the global sweet potato area occur where it is an obligatory seasonal crop because of low temperatures during part of the year. Most sweet potatoes are grown in the temperate zone between 20°N and 40°N. This peak includes nearly all the areas in China, India, and North America. The sweet potato area at these latitudes is virtually all in lowlands. The second peak in sweet potato distribution by latitude is between 10°S and 15°N. This peak includes most of the sweet potato areas in Africa and some areas in Asia and northeastern Brazil. A large part of the sweet potato areas at these latitudes occur at mid-elevation.

Botany and Physiology

Sweet potato is a member of the family Convolvulaceae, Genus *Ipomoea*, section *Batatas*. The number of chromosomes in the sweet potato plant is 2n = 6x = 90. This indicates that it is a hexaploid plant with a basic chromosome number x = 15. Among the wild species, *I. tabascana* and *I. tiliacea* are tetraploids with 2n = 4x = 60. The other species are diploids with 2n = 2x = 30. Polyploid species are *I. cordatotriloba* with 2x and 4x and *I. trifida* with 2x, 3x, 4x, and 6x (Huaman, 1992). Morphological analysis of the related species indicates that *I. trifida* is the closest wild relative to sweet potato but *I. tabascana* is also morphologically very close (Austin, 1977, 1987). Austin (1987) suggests that natural hybridization between *I. trifida* and *I. triloba* resulted in generation of the wild ancestors of the present *I. batatas* (L.) Lam., Jarret *et al.* (1992) supported a hypothesis that *I. trifida* (H.B.K.) G. Don and wild Mexican tetraploids are putative ancestors of the cultivated sweet potato. Species in section *Batatas* have been shown to contain unreduced gametes (Bohac and Jones, 1994), but the derivation of the hexaploid sweet potato remains unknown. Shiotani (1988) considered it an autopolyploid derivative of *I. trifida*, whereas others favor an allopolyploid origin involving *I. trifida* and an unidentified tetraploid parent. Tetrasomic segregation patterns in microsatellite primers are consistent with an allopolyploid (Buteler *et al.*, 1999). Zhang *et al.* (2001) also found tetrasomic patterns of inheritance in sweet potato. The most compelling evidence of an allopolyploid origin is cytological data reported by Magoon *et al.* (1970). Meiotic patterns showed various pairing configurations among the chromosomes, for example, duplicate, triplicate, and quadrivalents. Their data suggest that *I. batatas* consists of two related and a third more distant genome (Firon *et al.*, 2009).

The cultivated species, *I. batatas* (L.) Lam., includes plants that are very variable in their morphology. Sweet potato is a herbaceous and perennial plant. However, it is grown as an annual plant by vegetative propagation using either storage roots or stem cuttings. Its growth habit is predominantly prostrate with a vine system that expands rapidly horizontally on the ground. The types of growth habit of sweet potato are erect, semierect, spreading, and very spreading.

The sweet potato root system consists of fibrous roots, which absorb nutrients and water and anchor the plant, and storage roots that are lateral roots, which store photosynthetic products. A sweet potato stem is cylindrical and its length depends on the growth habit of the cultivar and on the availability of water in the soil. The stem color varies from green to totally pigmented with anthocyanins (red-purple color). The hairiness in the apical shoots, and also in the stems of some cultivars, varies from glabrous (without hairs) to very pubescent. The leaves are simple and are spirally and alternately arranged on the stem in a pattern known as 2/5 phyllotaxis. The edge of the leave lamina can be entire, toothed, or lobed. The shape of the general outline of sweet potato leaves can be round, reniform (kidneyshaped), cordate (heart shaped), triangular, hastate (trilobular and spear shaped with the two divergent basal lobes), lobed, and almost divided. The leaf color can be green yellowish, green, or can have purple pigmentation in part of or the entire leaf blade. The leaf size and the degree of hairiness vary according to the cultivar and environmental conditions (Huaman, 1992).

Sweet potato cultivars differ in their ability of flowering. Under normal conditions in the field, some cultivars do not flower, some produce very few flowers, and others flower profusely. The inflorescence is generally a cyme in which the peduncle is divided in two axillary peduncles; each one is further divided in two after the flower is produced (biparous cyme). Some cultivars produce white flowers. The flower is bisexual. The androecium consists of five stamens, and the anthers are whitish, yellow, or pink. The gynoecium consists of a pistil with a superior ovary, two carpels, and two locules that contain one or two ovules. The stigma is receptive early in the morning and the pollination is mainly by bees. The fruit is a capsule, more or less spherical with a terminal tip, and can be pubescent or glabrous. The capsule turns brown when mature. Each capsule contains from one to four seeds that are slightly

flattened on one side and convex on the other. Seed shape can be irregular, slightly angular, or rounded; the color ranges from brown to black; and the size is approximately 3 mm. The embryo and endosperm are protected by a thick, very hard, and impermeable testa. Seed germination is difficult and requires scarification by mechanical abrasion or chemical treatment. Sweet potato seeds do not have a dormancy period but maintain their viability for many years (Huaman, 1992).

The storage roots are the commercial part of the sweet potato plant, and sometimes are mistakenly named 'tubers.' Most cultivars develop storage roots at the nodes of the mother stem cuttings that are underground. However, the very spreading cultivars produce storage roots at some of the nodes that come into contact with the soil. The parts of the storage roots are the proximal end that joins to the stem, through a root stalk, and where many adventitious buds are found from which the sprouts are originated; a central part which is more expanded; and the distal end that is opposite to the root stalk. The adventitious buds that are located in the central and distal part usually sprout later than those located in the proximal end.

Breeding

Crossbreeding is the main breeding method for sweet potato. Two major difficulties have been encountered in the development of sweet potato's scientific-breeding methods. First, sweet potato is polyploidy. Second, it is almost always self-incompatible and male sterile. However, since the 1950s, breeding programs have been implemented, mostly in temperate climates, in the US, China, and Japan.

Rossell *et al.* (2007) reported that more than 6000 accessions of landraces, breeding lines, and advanced cultivars of sweet potato were held by CIP in its genebank. The choice of varieties to grow appears to depend largely on how the produce – the root – are utilized, whether as food either directly or in processed forms, as feed component, or as sources of industrial starch. For food varieties, preferences also seem to vary among and even within countries. The dominant varieties in some of the major sweet potato-growing countries are presented below (Carpena, 2009).

In China, 'Xushu 18' (purple skin and white-yellow flesh) was bred by Xuzhou Agricultural Research Institute, Jiangsu in 1972 and is today the leading variety with an annual area of 1.5 Mha. 'Nanshu 88' (pale red skin and pale yellow flesh) was released in 1988 by Nanchong Agricultural Research Institute, Sichuan and is mainly used for food as fresh roots and feed processing (Zhang *et al.*, 2009).

In the US, the leading variety, 'Beauregard' (copper-rose skin and yellow flesh), is a polycross selection released by the Louisiana State University and occupies nowadays approximately 65% of the area planted annually (Smith *et al.*, 2009). Another important variety in the US is 'Covington,' released by North Carolina Agricultural Research Station in 2005, which is estimated to occupy 30% of the sweet potato production area (Carpena, 2009).

In Japan, the leading table variety, 'Beniazuma' (deep red skin and yellow flesh), was released by the National Institute of Crop Science in 1981 and new cultivars with high anthocyanin content and high yields are being developed. 'Ayamurasaki,' for example, is now recommended as a superior source for the production of foods with health benefits (antioxidants) and some foods and beverages already use the anthocyanin pigments (Suda *et al.*, 2003).

In Uganda, 'Tanzania,' a selection from Ugandan landrace germplasm is the most widely grown sweet potato variety and was officially released in 1995, along with three other landrace selections, namely, 'New Kawogo,' 'Bwanjule,' and 'Wagabolige' and a selection from the progenies of a polycross involving 18 popular farmers' cultivars in Uganda, namely, 'Sowola' (Mwanga *et al.*, 2001).

In Papua New Guinea (PNG), sweet potato is the no. 1 food crop, accounting for more than 60% of the total production for 18 staple food crops in 2000, based on the data presented by Bourke (2006). In 2004, the National Agricultural Research Institute released varieties resistant to scab disease (*E. batatas*) with high dry matter: 'K9,' 'B11,' 'Nuguria 5,' and 'SI 278'.

Utilization of the wild relatives of sweet potato in sweet potato improvement has resulted in the release of several varieties such as 'Minamiyutaka' (Japan) and 'Jishu 98' (China). Storage root-bearing somatic hybrids between sweet potato and its wild relatives have been developed (Yang *et al.*, 2009). Genetic engineering offers a great potential for improving disease, pest, or stress resistance as well as nutritional quality of sweet potato. Several agronomically important genes; carbohydrate metabolism-associated SRF1 and IbSnRK1; carotenoids biosynthesis-associated IbLCY-ε and IbLCYe; stress tolerance-associated SWPA2, IbNFU1, and IbP5CR; and disease resistance-associated IbMIPS have been cloned from sweet potato (Liu *et al.*, 2011; Wang *et al.*, 2013; Kim *et al.*, 2013). Transgenic sweet potato plants have been obtained, which exhibit enhanced salt tolerance, disease resistance, or herbicide resistance (Liu *et al.*, 2011; Fan *et al.*, 2012). Molecular markers linked to nematode resistance gene and QTLs for dry-matter , starch, and β-carotene content have been identified (Cervantes-Flores *et al.*, 2011; Liu *et al.*, 2011). These works represent an important step forward in sweet potato improvement through molecular breeding.

Cultivation

Sweet potato is cultivated throughout the tropics and warm temperate regions of the world. Storage root yields respond to native soil fertility. Surface soil is usually scrapped into mound, heaps, or ridges into which several crops are planted. Sweet potato cannot tolerate excessive moisture in soil or drought without irrigation. Some varieties tolerate drought or low soil moisture; however, it is suggested not to plant vines into dry soils. Some varieties tolerate moist soils near waterways and wetlands. Seedbeds (20–30 cm of loose soils) facilitate storage root thickening through less resistance to penetration. Well-drained sandy loamy soils are best, whereas heavy clayey soils produce rough bad-shaped storage roots.

Unlike most vegetables and fruit crops, sweet potatoes are not planted directly as seeds in fields and gardens. They are transplanted as cuttings, which are young shoots that emerge from storage roots. Storage roots produce cuttings in a starter bed. Planting actively growing 25–30 cm apical vines with 4–6



(a) (b)

Figure 2 (a) Sweet potato plants in a field and (b) storage roots harvested.

nodes are best, with a planting density of 45 000–60 000 plants ha^{-1} (Figure 2). The higher the plant density is, the more the storage roots and the smaller the storage root size will be. A desirable plant density is determined by the variety used and demands for the products.

Field management is important for any crop. For weed control in sweet potato, it is a common practice to apply Oxadiazon or Glyphosate before planting. Mineral nutrition required by the plants are obtained from the soil and fertilizers applied. Fields before planting are fertilized with compost and NPK. It is very important for the soil to be rich in organic matter for better soil fertility and higher water retention capacity. Sweet potato requires a generous contribution of potassium to favor the thickening of storage roots. However, excessive nitrogen fertilization causes great development of the stems but smaller storage roots. Removing weeds from around the young sweet potato slips avoids competition for nutrients. Once the plants begin maturing, their sprawling vines and leaves are often sufficient to deter weedy plants. The soil around the plants should be kept moist but not saturated. Overwatering encourages the growth of soilborne fungi that harm sweet potato plants.

According to cultivation techniques, not watering sweet potato during the last month of their growth improves the harvested roots' quality as well as prevent decay. Around October or December, when the plant leaves begin to lose its dark green color and the soil begins to crack, the storage roots are harvested. Harvesting entails cutting off shoots, carefully digging out storage roots with hoe or pickax, and then remove adhering soil (Figure 2). They are classified into three classes: the bigger and larger storage roots for consumption; the smaller and lightweight roots for the next crop; and the tiny and wounded roots for livestock.

Diseases and Insects

Although sweet potato can withstand many adversities, numerous diseases and insects have been reported on this crop from different regions of the world and the species of diseases and pests are different in different regions.

Sweet potato diseases generally fall into three types: bacterial, fungal, and virus. Major bacterial and fungal diseases include sclerotial blight (*Sclerotium rolfsii* Sacc.), black rot (*Ceratocystis fimbriata* Ell. & Halst.), scurf (*Monilochaetes infuscans* Ell. & Halst. ex Harter), foot rot (*Plenodomus destruens* Harter), and stem and leaf scab (*Sphaceloma batatas* Saw). Sclerotial blight is a common soilborne fungus that infects a wide array of crops. It is a common disease of sweet potato in the USA. Black rot has been reported on sweet potato in China, Japan, Kenya, and the USA and is apparently widely distributed (Clark and Moyer, 1988; Farr *et al.*, 2007; Kihurani *et al.*, 2000). Scurf has been reported from Africa, Asia, Australia, Europe, North and South America, and New Zealand. Foot rot has been reported as a problem in Argentina, Brazil, Burundi, New Zealand, Rwanda, South Africa, Tanzania, and the USA. Stem and leaf scab has been reported in Australia, Asia, many Pacific Islands, the Caribbean (Puerto Rico), Mexico, South America (Brazil) but is absent from the USA, except Hawaii (Farr *et al.*, 2007). It is most prominent at elevations in the tropics where conditions are wet and cool to warm.

More than 20 viruses have so far been reported to infect sweet potato, among which sweet potato feathery mottle virus (SPFMV) and sweet potato chlorotic stunt virus (SPCSV, also known as SPSVV) are the most common sweet potato viruses worldwide. Most sweet potato cultivars infected by SPFMV alone show no or only mild circular spots on their leaves or light green patterns along veins. However, when infected together with the whitefly-transmitted SPCSV stunting of the plants, feathery vein clearing and yellowing of the plants are observed (Loebenstein *et al.*, 2009).

One of the major pest groups that cause considerable damage to sweet potato is that of plant parasitic nematodes. There are a number of genera and species that feed on sweet potato. The latest report indicates that 25 genera and 55 species of nematodes are associated with sweet potato (Coyne *et al.*, 2003). The incidence of certain species can be as high as 96% of the field in some area (Iwahori and Sano, 2003) and may cause considerable losses to sweet potato. The root-knot nematodes are generally considered to be the most important nematodes in the production of sweet potato around the world. Other types of nematodes that are known to cause

serious problems of sweet potato are lesion nematode and stem nematode (Overstreet, 2009).

Most recently, 270 insect and mite species are listed as pests of sweet potato around the world. Many insects reduce the quality and yield of sweet potato, either by feeding directly on the storage roots or by defoliating leaves and/or boring into vines. Aphids, whiteflies, and leafhoppers can also transmit many of the viruses known to infect sweet potato. Sweet potato storage roots are injured by a complex of Coleopterous soil insects. Soil insects that damage the root are the most harmful ones because they can cause significant economic losses even in low numbers. In contrast, many foliage-feeding insects do not cause yield reductions because sweet potato plants can often compensate for high levels of defoliation. Insect losses reach 60–100%. The sweet potato weevil, *Cylas formicarius* Fab., is the most destructive insect affecting sweet potato. Other insects such as wireworms, rootworms, and flea beetles also cause damage to sweet potato (Sorensen, 2009).

As to sweet potato disease control, the following measures can be adopted: selecting and using the disease-resistant varieties; attaching importance to the quarantine inspection of the seed and seedlings; cultivating disease-free and strong seedlings or using virus-free seedlings; using medicaments; implementing an integrated program of crop rotation; strengthening water and fertilizer management and so on. The pest shall be controlled as follows: eliminating the pupas by cleaning the crop lands after harvest; treating seedling with medicaments; spraying chemicals on the plants during the larval phase of the pests, etc. With more attention and investment to sweet potato industry and further researches on sweet potato diseases and pests, new control methods and medicaments will be applied to sweet potato production.

Uses and Economic Importance

Sweet potato is regarded as the seventh most important food crop in the world (FAO, 2009). In most developing countries, it is a smallholder crop tolerant of a wide range of edaphic and climatic conditions and grown with limited inputs. Sweet potato provides more edible energy per hectare per day than wheat, rice, or cassava and is an essential food source with very high production per capita across the relatively humid areas of Africa. From 2000 to 2011, global sweet potato cultivation declined slightly in area harvested, yield, and production on the whole, but several years indicate some rebounding based on FAO (2011) production data.

Asia is the largest sweet potato-producing region, with approximately 80% of the world's production and more than 52% of the world's area; Africa is the second largest sweet potato-producing region, with almost 17% of the world's production and more than 42% of the world's area (**Figure 3**; FAO, 2011). The vast majority of production remains in eastern Asia; China alone accounts for approximately 72% of world production, with more than 43% of the global area (FAO, 2011). In addition to China, there are considerable concentrations of sweet potato in Cuba and Haiti in the Caribbean region; in Java (Indonesia), the island of New Guinea (both in Indonesia and in Papua New Guinea), and Vietnam in Asia; and in Africa, particularly in the Lake Victoria area (Burundi, Rwanda, Uganda, and the Democratic Republic of Congo) and in Ghana, Nigeria, and Madagascar.

Use of sweet potato as food

Storage roots are most frequently used after boiling, baking, or frying. They are also processed into starch, flour, or puree to make secondary food products. Baking sweet potatoes in country ovens has been an old mode of processing storage roots in countries viz. China, India, Japan, Bangladesh, Indonesia, Kenya, Papua New Guinea, etc. Storage roots are dehydrated to enhance the shelf life of stored roots. Canning of sweet potato is widely practiced in the US. As high as 86% of the carotene content of the roots are reported to be retained in them even after canning (Elkins, 1979). Sweet potato roots are transformed into more stable edible products like fried chips, crisps, French fries, etc., which are very popular in Japan, the USA, China, the Netherlands, Peru, etc. Sweet potato is processed into noodles in many countries of the Far East. Sweet potato leaves, although a rich source of vitamins, minerals, and proteins, have been much less used as a human food. Sweet potato green tips are used as a vegetable in some parts of the world. The nutritive value of sweet potato leaves has been attributed to the high content of antioxidants, especially phenolic compounds in them (Islam *et al.*, 2002; Yoshimoto *et al.*, 2005).

Industrial utilization of sweet potato

Sweet potato starch is commercially utilized for the production of a number of commodity chemicals like citric acid, monosodium glutamate, microbial enzymes, etc. Storage roots with 20–30% starch are one of the major sources for the commercial extraction of starch. The roots are extensively used for starch extraction in China, Japan, and Korea. Sweet potato starch is similar to any other starch source for use as a raw material for the production of alcohol (Padmaja, 2009).

Roots and vines as livestock feed

Sweet potato roots and vines have been used as animal feed for many years in China and Japan. Besides, the wastes from starch and alcohol factories are also used as animal feed. Many studies are available dealing with the use of sweet potato roots as cattle, pig, poultry, and fish feed (Padmaja, 2009).

Sweet potato as a health-protectant food

Sweet potato is increasingly recognized as a health food due to several of its nutraceutical components viz. dietary fiber, vitamin A, vitamin C, phenolic acids, carotenes, protein, amino acids, mineral nutrient, xanthophylls, anthocyanins, etc. Storage roots are considered as a highly functional, low-calorie food with antidiabetic effects (Kusano and Abe, 2000).

Cassava

Origin and Distribution

Cassava (*Manihot esculenta* Crantz), also called Tapioca in Asia; Manioc in Africa; Manioca, Yucca, and Mandioca in Latin America, originated in South America. It is a perennial woody

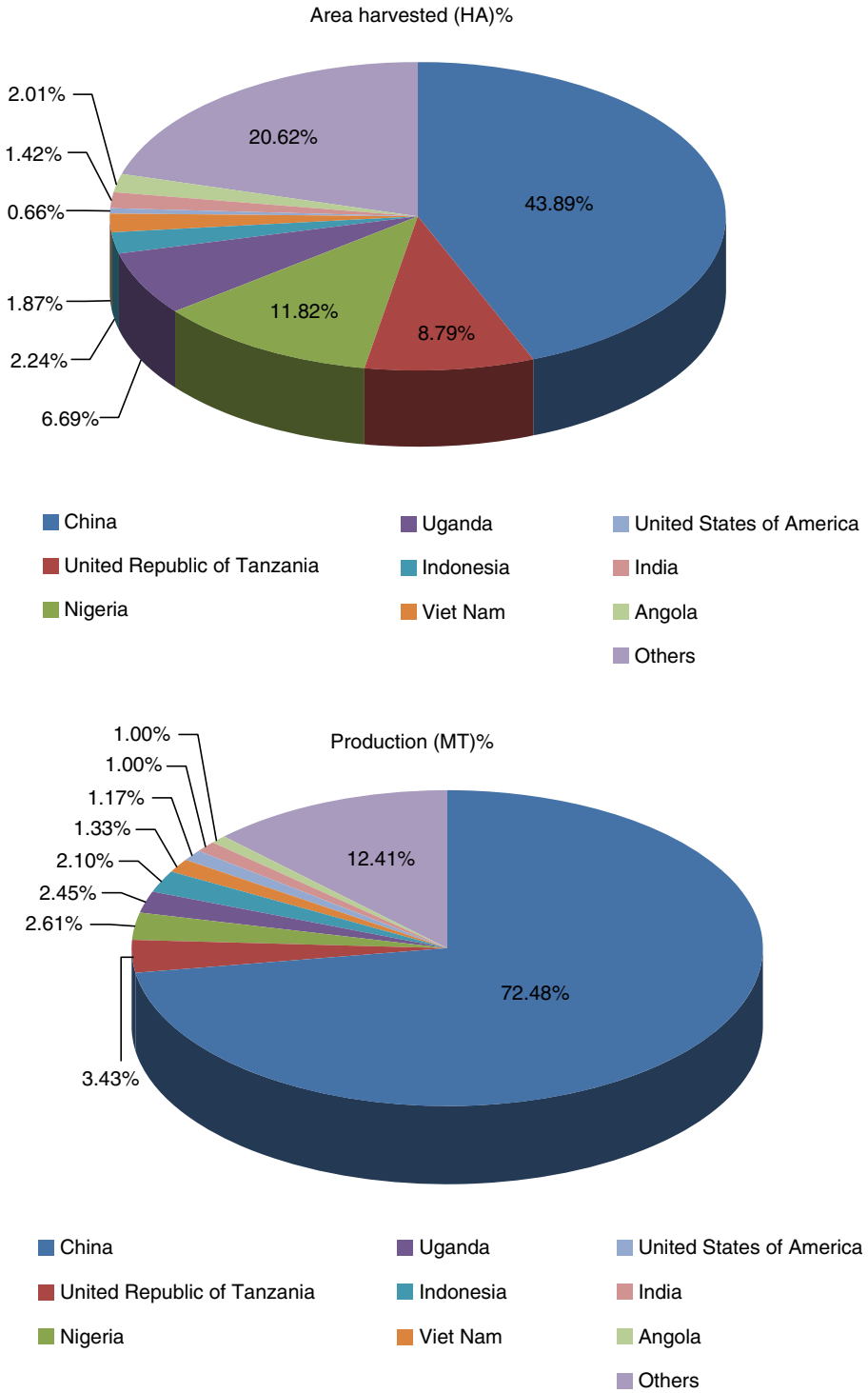


Figure 3 Sweet potato area harvested (7 953 196 ha) and production (104 259 988 metric ton (MT)) of leading countries and geographic groupings in 2011 (FAO).

shrub of the Euphorbiaceae (spurge family) and has been extensively cultivated as an annual crop in tropical and subtropical regions for its edible starchy, tuberous root (Figure 4(b)). The *Manihot* genus has approximately 100 species, and cassava is the only commercially cultivated one. Wild populations of *M. esculenta* subspecies *flabellifolia*, shown to be the progenitor of domesticated cassava (Olsen and Schaal, 1999), are centered in west-central Brazil, where it was more likely first domesticated more than 10 000 years ago. By 6600 BC, cassava pollen appears in the Gulf of Mexico lowlands, at the San Andrés archeological site. The oldest direct evidence of cassava cultivation comes from a 1400-year-old Maya site, Joya



(a) (b)

Figure 4 (a) 10-month old cassava plants in a field and (b) storage roots harvested from 10-month old cassava plants.

de Cerén, in El Salvador, but the species *M. esculenta* more likely originated in Brazil and Paraguay.

Cassava cultivation most probably began from northeast part of Brazil/Paraguay to Mexico/Guatemala more than 4000 years ago. It was introduced to west coast of Africa in the year 1588 by Portuguese traders after discovery of American continent and cultivated in Gulf of Guinea and the Congo Basin first. Around 1750, the cultivation of cassava was spread to Madagascar and east coast of Africa. And in the middle of the nineteenth century, cassava became more and more important as staple food and was widely planted in Africa between 15 degrees latitude north and south. From the very beginning of the eighteenth century, Spanish merchants used to transport cassava seedlings into India for large-scale plantation. At the end of the eighteenth century, cassava was widely spread in Asia and was planted in Indonesia, Sri Lanka, Malaysia, and other countries of tropical and subtropical Asian regions. Nowadays, as an important tropical crop, cassava's horizontal distribution is restricted between 30 degrees latitude north and south; vertical distribution is under altitude of 2000 m. The global cultivation area is approximately 19 million hectares: 55% in Africa, 27% in Asia, and 18% in Latin America (FAO, 2012).

Botany and Physiology

Owing to highly variable genetic diversity, the phenotypes of different germplasms are highly variable (Alves, 2002). However, different cassava possesses the same organs such as roots, leaves, stems, flowers, and seeds. Storage roots are the main storage organ of cassava, which accumulate plenty of starch (Figure 4(b)). The storage roots result from secondary growth of the fibrous roots, which contain three distinct tissues: bark (periderm), peel (or cortex), and parenchyma. The typical composition of the cassava storage roots is moisture (70%), starch (24%), fiber (2%), protein (1%), and other substances including minerals (Tonukari, 2004). Leaves of cassava are palmate, with uneven number of lobes, generally ranging from three to nine. The adaxial surface is covered with a shiny, waxy epidermis, and most stomata are located on the abaxial surface of the leaves. Cassava is a monecious species, which produces both male (pistillate) and female (staminate) flowers on the same plant. The fruit of cassava is a trilocular capsule with six straight, prominent longitudinal ridges or aristae. Each locule contains a single carunculated seed.

Owing to low fertility of seeds, cassava is usually propagated by stem cuttings (Figure 4(a)). From planting to harvest, cassava has five progressive developmental stages, i.e., emergence of sprouting (5–15 DAP, day after planting), beginning of leaf development and formation of root system (15–90 DAP), development of stems and leaves (90–180 DAP), high carbohydrate translocation to roots (180–300 DAP), and dormancy (300–360 DAP). The development of leaf, which starts from emergence of buds (folded, 1 cm long) and ends when it reaches its full size, usually requires 10–12 days. And the leaf life (from emergence to abscission) is commonly 60–120 days, depending on cultivar, shade level, water deficit, and temperature (Cock, 1984). All cassava organs, except seeds, contain cyanogenic gulcoside (CG). Cultivars with CG <100 mg kg^{-1} fresh weight (FW) are called 'sweet,' whereas cultivars with CG 100–500 mg kg^{-1} FW are 'bitter' cassava. The most abundant CG is linamarin (85%), with lesser amounts of lotaustralin. Total CG concentration depends on cultivars, environmental condition, cultural practices, and plant age (Ngudi *et al.*, 2003). Cassava storage roots have the shortest shelf life of any of the major root crops. Roots are highly perishable and usually become inedible within 24–72 h after harvest, due to a rapid physiological deterioration process in which synthesis of simple phenolic compounds that polymerize occurs, forming blue, brown, and black pigments (Bayoumi *et al.*, 2010).

Temperature influences cassava sprouting, leaf formation and size, storage root formation, and consequently general plant growth. The behavior of cassava under the temperature variations indicates that its growth is favorable under annual

mean temperatures ranging from 25 to 29 °C, but it can tolerate from 16 to 38 °C. At low temperature (<16 °C), sprouting of the stem cutting is delayed and rate of leaf production and dry weight (DW) of total storage roots are decreased. Sprouting is hastened when the temperature increases up to 30 °C but is inhibited with temperatures >37 °C. Because the differences in day length in tropical regions are very small, varying from 10 to 12 h throughout the year, photoperiod may not limit cassava root production in this region (Bolhuis, 1966). Long days increase shoot growth and decrease storage root development, whereas short days promote growth of storage roots and reduce the shoots, without affecting total DW. Cassava is also intercropped with perennial vegetation. Thus, in an associated cropping system, cassava is always subjected to different degrees of shading and low-light intensity in the early stage of development (Okoli and Wilson, 1986).

Cassava is a drought-tolerant crop as it is commonly grown in areas receiving <800 mm rainfall year^{-1} with a dry season of 4–6 months. Growth and yield could be also decreased by prolonged dry periods. The reduction degree in storage root yield depends on the duration of the water deficit and the sensitivity of a particular growth stage to water stress. The critical period for water-deficit effect in cassava is from 1 to 5 MAP (month after planting) – the stage of root initiation and tuberization (Vandegeer *et al.*, 2013). A primary response to water stress is stomatal closure, which decreases photosynthetic CO_2 assimilation and, in turn, growth. When water is available, cassava maintains a high stomatal conductance and can keep internal CO_2 concentration high. As a stress hormone, ABA accumulates in both expanding and mature leaves under water deficit condition but completely reverses in respect of control levels after 1 day of rewatering (Alves and Setter, 2004).

Breeding

Cassava can be propagated either by stem cuttings or by sexual seed, but the most common practice is stem cuttings by farmers for multiplication and planting purposes (**Figure 4(a)**). Unlike sweet potato (*I. batatas*), the cassava root is not a reproductive organ. Propagation from true seed occurs occasionally in farmers' fields. The common breeding approach in cassava is through hybridization among appropriate parents. Cassava is monecious, with female flowers opening 10–14 days before the male ones on the same branch. Self-pollination can occur because male and female flowers on different branches or on different plants of the same genotypes can open simultaneously (Jennings and Iglesias, 2002). Cassava is a cross-pollinated species and seldom gets self-pollinated; it has a slow multiplication rate and the production of botanical seed from crosses is expensive. Seedlings with desirable traits are selected and subsequently propagated clonally. Stem cuttings can only be stored for a limited period of time; planting material requires special phytosanitary management (Ceballos *et al.*, 2012). Overall, cassava breeding is time consuming and inefficient in comparison with other major crops, for example, grains.

Therefore, several new approaches have been taken to address this situation in recent years. Modifications of the breeding scheme have been implemented for a more dynamic recurrent selection system and for obtaining valuable information on the breeding value of parental lines (Ceballos *et al.*, 2004). Biotechnology tools have been adapted to cassava and are currently incorporated in different projects for its genetic improvement. Genome sequence of cassava has been released and is publicly available (Prochnik *et al.*, 2012). A high-density molecular map has been developed, and marker-assisted selection is currently used for key traits. Genetic transformation protocols are available and have been used successfully for the incorporation of different genes (Liu *et al.*, 2011).

To date, major agronomic traits of cassava addressed by breeding include high yield and high starch content, good plant type (tall and no or little branching), early harvest and early bulking capacity, improved nutritional quality, virus resistance, reduced cyanide content, and delayed postharvest physiology deterioration in storage roots. Many farmer-preferred landraces and new-bred cassava cultivars had been widely cultivated in regions. For example, in Nigeria, cultivars TMS 30572, TMS 00/0203, TMS 01/0040, NR 01/0004, and CR 41–10, which are high yielding as well as disease and pest resistant, have been released and adopted in varying degrees in different ecological zones of Nigeria. In Thailand, Kasetsart 50 (KU50), Rayong5, Rayong90, Rayong72 are major new released cassava cultivars in the past decades and the KU50 becomes the most popular cultivated cultivar in the ASEAN countries. In China, SC205 and NZ199 are most popular cultivars for decades, covering more than half of total planting area.

Cultivation

Good cultivation practices are important for increasing cassava productivity. The practice includes variety selection, soil preparation, appropriate time for planting and harvesting, planting techniques, weed and disease control, fertilization, and irrigation.

The soil should be plowed in depth to loosen soil structure and ridge according to terrain before planting, which is advantage for root formation and soil moisture retention. It is suitable for cassava growth under moisture climate and the temperature exceeding 15 °C. Therefore, farmers usually plan the planting date based on natural rainfalls. It is very crucial to employ good cassava varieties with high yield, high resistance to diseases, adaptation to different environment stresses, good plant features, and high stem quality (Ayemou *et al.*, 2011). Planting materials should be free from pests and diseases and had better be taken from plants ranging from 8 to 18 months of age. To prevent dehydration during storage, the harvest stems should be as long as possible before planting. Stem should normally be cut in the range of 15–25 cm in length. The plant spacing is approximately 1.0×1.0 m, which can be more or less, depending on soil fertility and plant branching. It is useful to spray or submerge the stems in a solution with an insecticide and a fungicide before planting (Sriroth *et al.*, 2010). There are three kinds of planting patterns including vertical planting, tilting planting, and horizontal planting. Vertical planting has higher resistance to wind and drought. Tilting planting has the higher sprout rate and horizontal planting is easy for harvest but the resistance is lower. This

constant cropping system can rapidly deplete the soil fertility, so sustainable and productive cropping systems are needed (Örjan, 1993). Intercropping or shifting cultivation is a good choice for cassava productivity, and this method has been widely applied (Staver, 1989). There are several intercropping methods including cassava as principal crop intercropping with short-period crops, perennial woody plants as majority intercropping with cassava, and one kind of crop planted instantly following cassava planting.

Weed and pest control are very critical after planting. Weed should be removed either manually or by chemicals. When chemicals are used, it should be considered that the chemicals do not cause any harm to cassava plants. Basal fertilizer and applying fertilizer in the later period are important for increasing root and top biomass (Cadavid *et al.*, 1998), especially potassium fertilizer. Nitrogen fertilizer is not too much, because it can induce the higher cyanic acid content in storage roots. Sprouting rate was strongly influenced by the N, P, and K contents in the stakes. Stakes from plots with moderate level of N, P, and K application resulted in plants that had the highest roots production in both fertilized and unfertilized soils (Molina and E1-Sharkawy, 1995). Cultivation under a very dry condition can be improved by additional water irrigation. Water-dripping system is currently introduced to some cassava planting areas.

The root can be harvested after 10 months of plantation (**Figure 4(b)**). Harvesting can be delayed or advanced, depending on root prices. Fresh roots harvested in the rainy period usually contain less starch contents. Some stems with good stake quality are reserved for new crop propagation and the rest including other biomass are used for fuel and infield fertilizer. Stems can be stored as they have been harvested from the field. There are different storing methods such as heap storage method in the open, trenching storage method, and cache method.

Diseases and Insects

Cassava cultivation is associated with a wide range of diseases and insect pests that reduce cassava yields substantially, posing a threat to food security throughout the developing world. The rapid geographic expansion of the cassava mosaic disease (CMD) pandemic, caused by cassava mosaic geminiviruses, and outbreaks of cassava brown streak disease (CBSD) from Uganda and other parts of East Africa, caused by potyviruses, have devastated cassava crops in most African countries (Legg *et al.*, 2006). Both of these viral diseases are transmitted by whiteflies (*Bemisia tabaci*). Conventional host plant resistance is the most widely practiced control measure for CMD. High levels of resistance to all cassava mosaic geminiviruses (CMGs, Family Geminiviridae, and Genus Begomovirus) have been developed through conventional breeding programs using two different sources of resistance (Dixon *et al.*, 2003; Hahn *et al.*, 1980) and resistant varieties have been widely deployed in CMD management programs. CBSD is caused by two virus species: Cassava brown streak virus (CBSV) and Ugandan cassava brown streak virus (UCBSV) (picornalike (+) ssRNA viruses, genus Ipomovirus, and family Potyviridae). Contrary to CMD, limited natural resistance to CBSD, in a few cassava genotypes, has been identified and demonstrated for one of the viral species (UCBSV) causing CBSD (Winter *et al.*, 2010). The deployment of CMD-resistant cassava with different levels of susceptibility to viruses causing CBSD continues to impact production and alters the distribution and occurrence of UCBSV and CBSV in the field. Transgenic strategies have been developed to engineer the dual resistance to both viruses and transgenic plants undergoing field trials in several countries in Africa (Zhang *et al.*, 2005; Vanderschuren *et al.*, 2012).

Besides being transmitted by the whitefly, for which numerous invasive species have been described, transmission via human-mediated transport of infected stems is today postulated to play an important role in the spread of CMGs and CBSD. Currently, various CMG and CBSV species are widely distributed throughout Africa (Patil and Fauquet, 2009; Ndunguru *et al.*, 2005) and ongoing monitoring of cassava indicates that some CMG and CBSV species are in the process of expanding their geographic ranges.

The most serious pests of cassava are generally those that have coevolved with the crop, especially the cassava green mite (CGM; *Mononychellus tanajoa*), mealybugs (*Phenacoccus herreni* and *Phenacoccus manihoti*), whitefly (*Aleurotrachelus socialis* and *Aleurotrachelus aepim*), hornworm (*Erinnyis ello*), lacebugs (*Vatiga illudens*), and stemborers (*Chilomina clarkei*) (Bellotti *et al.*, 2012).

Disease- and pest-control practices have physical, chemical, mechanical, and biological controls. A successful integrated pest management (IPM) program in cassava will depend on having effective, environmentally sound, and low-cost pest management technologies available to cassava farmers in developing countries. Biotechnology tools currently available offer the potential to develop improved pest resistant varieties (Duan *et al.*, 2013) and enhance the effectiveness of natural control organisms including parasitoids and entomopathogens.

Economic Importance and Uses

Cassava is one of the most important starch crops, and the storage root is mostly used as a source for food and starch products. The total production of cassava all over the world was approximately 184 million tonnes in 2002 and 250 million tonnes in 2012 (FAO, 2012). In Africa, most of these tuberous roots were consumed locally as main food and very few were exported. In Asia, cassava is mainly used as raw material for feed and starch industry. The major cassava producers are Brazil in South America; Thailand, Indonesia, and India in Asia; and Nigeria and Congo in Africa. Thailand is the biggest exporter in the world. In developing countries, especially in sub-Saharan Africa, cassava plays a particularly important role in food security because of its high tolerance to poor soil and dry season; besides, it has a flexible harvesting schedule (Cock, 1984). The cassava root is rich in calcium and vitamin C and contains a significant quantity of thiamine, riboflavin, and nicotinic acid. Although cassava storage roots contain less protein, the protein content in cassava leaves are high and valuable because they are rich in essential amino acids such as methionine, cysteine, and cystine. Generally,

every part of cassava can be utilized, but the storage root is most commonly used in, for example, food, industry, and biofuels.

Cassava, like other foods, also has antinutritional and toxic factors such as the cyanogenic glucosides, which can release hydrocyanic acid (HCN) by hydrolysis. Cassava must be cooked first in order to detoxify it before it is eaten. However, cassava root is widely processed into variety of dishes and is consumed regionally, nationally, and sometimes ethnically. The soft-boiled and fried cassava root, having a flavor, can substitute for boiled potatoes as an accompaniment for meat dishes in some households. In Brazil, detoxified manioc is ground and cooked to a dry, often hard or crunchy, meal which is used as a condiment, toasted in butter, or eaten alone as a side dish.

Cassava leaves are used as vegetables in some regions of Africa. Overground part of cassava can be used for animal feed as well. The overground part, harvested approximately 30–45 cm at the three- or four-month stage and is dried for one or two days until it is classed as cassava hay. The cassava hay, containing high-level protein (25%) and condensed tannins, can be used as nutrient-rich roughage for animals.

In Thailand and China, cassava is mainly used as raw materials for extracting starch, which can be processed to various modified starches. Besides, cassava is also essential for energy security. Regionally, cassava becomes mostly a source for ethanol production. The increase in demand of cassava starch and nongain derived biofuels has boosted the expansion of cassava cultivation globally.

See also: Determining Functional Properties and Sources of Recently Identified Bioactive Food Components: Oligosaccharides, Glycolipids, Glycoproteins, and Peptides. Food Security: Development Strategies. Food Security, Market Processes, and the Role of Government Policy. Food Security: Yield Gap

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Rural Sociology

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Glossary

Adoption–diffusion of technology Process by which individual farmers (or other prospective users of technology) make decisions about the use or nonuse of a new technology.

Land grant universities Integrated system of teaching, research, and outreach created to modernize agriculture.

New Rural Sociology Conceptual approach to the sociology of agriculture that embraced critical perspectives of rural development.

Rural–urban continuum Notion that the nature of social structure, social relationships, and values vary systematically across rural and urban communities.

Sociology of agricultural science Study of the process through which scientists and scientific institutions discover new knowledge.

Sociology of agrifood studies Study of the sociology of agriculture and food that links agricultural production and food consumption to globalization and commodity systems.

Introduction

Rural sociology is historically defined as the sociological study of social organization and processes that are characteristic of rural societies and geographical areas where population densities are relatively low. In practice, modern rural sociology is considerably more comprehensive than the study of rural societies. As rural societies do not exist in isolation, rural sociology increasingly addresses the relationships between rural society and society as a whole and within the global economy and society. Vertical linkages to the macrosystem integrate rural areas into national and global social processes (Bonanno *et al.*, 1994; Warren, 1963).

Although rural sociology as a discipline originated in the United States in the early twentieth century, as part of decolonialization and modernization projects after World War II, it has diffused around the world where it is more often referred to as peasant studies, development studies, or village studies instead of rural sociology (Newby, 1980). Additionally, many of the foci of rural sociology are related closely to other social science disciplines including cultural geography, social anthropology, and agricultural economics.

The Roots of American Rural Sociology

Although the field of rural sociology has made major strides in understanding rural social processes, like the parent discipline of sociology, it still has strong roots in the nineteenth-century social thought. A central concern of nineteenth-century theorists was whether village and farm life was morally and socially superior to metropolitan life, and whether rural life would be resilient in the face of urban industrialism. Informed by the Enlightenment and Western rationalism, the classical sociologists Emile Durkheim (1858–1917) and Karl Marx (1818–83) both argued that urban–industrial capitalism and modern technologies and organizational practices were unavoidable and progressive social forces would eventually supplant the residual remnants of backward, preindustrial rural social forms. In contrast, Ferdinand Töennies (1855–1936) viewed urbanization and industrial capitalism that characterized gesellschaft societies as leading to the decline of the pastoral virtues and intimate communal bonds of rural gemeinschaft societies that are necessary for healthy social life. For Töennies and many early rural sociologists, the cities and social relations of industrial capitalism represented the degradation of civilization. Although Max Weber (1864–1920) recognized the dynamism of the social forces of bureaucratization, industrialization, and urbanization that were marginalizing traditional rural societies, he thought that bureaucratization and the industrial revolution, which he referred to as an iron cage, would lead to social movements, political ideologies, and other forms of resistance to these forces of rationalization and uniformity.

Throughout its history, rural sociology has engaged in these nineteenth-century debates over the desirability and resilience of traditional rural social organization. Two general positions have alternated over time and still exist: (1) the view that rural society, owing to its more intimate social bonds, lower incidence of social pathologies, and stronger religious institutions, is socially and morally superior to urban society and therefore deserves to be preserved and (2) the view that traditional rural beliefs, social structures, technologies, practices, and institutions are nostalgic anachronisms of the past and must be modernized for the quality of rural life to be enhanced. Both positions are embedded deeply in Western social thought and continue to inform the discipline and discourses of rural sociology.

The historical roots of rural sociology in America reside in the economic, political, and economic transformation brought about by the industrial revolution that occurred after the Civil War. Though the surge of industrial capitalism brought affluence to many regions in the United States, it also created poverty and inequality in many rural areas. A benchmark publication in the debate between these two views of rural society was Sorokin and Zimmerman's (1929) Principles of Rural–Urban Sociology, which synthesized rural sociological thought of the time and was the summative treatise in the field. Sorokin and Zimmerman's 'rural–urban continuum' perspective drew primarily on Töennies' analysis of how

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urbanization and industrial capitalism led to the undermining of the primary social bonds of community. Accordingly, the rural sociology research carried out before World War II was largely devoted to rural community studies and tended to present rural life as socially richer and morally superior to urban life.

Agrarian Politics and the Country Life Commission

America's agrarian politics also significantly shaped the trajectory of rural sociology. Though the term 'rural sociology' was not widely used until the 1920s, the first American rural sociological studies were conducted in the 1890s during a decade of populism and agrarian unrest. These pioneering rural sociological studies were initiated by DuBois (1898), a black sociologist on the staff of the US Department of Labor. DuBois' studies emphasized how the postbellum crop-lien system in southern plantation agriculture reinforced black poverty by tying black farmers to the plantation system and subordinating them to the power of the planter class. During this time, studies of agricultural communities in the northeast were also undertaken by F.H. Giddings and associates at Columbia University. In these early days, land grant universities had little or no presence in the scholarship now called rural sociology.

Although the populist critique of industrial capitalism swept through much of rural America during these years, populism did not directly influence early rural sociology. During the first full decade of American sociology, there was widespread suspicion among university administrators and their patrons that sociology should be scrutinized to ensure that it concerned itself with empirical research rather than populist politics. This political environment led most sociologists to distance themselves from radical social theories and movements. There is no indication that any American rural sociologists were active supporters of populism.

Populism's indirect influences on rural sociology, however, were important. The populists' mostly unsuccessful attempts to recruit black farmers into their movement contributed to the questioning of the sharecropping system, the structure of agriculture, and southern rural social structure. Populist radicalism was a major source of concern to urban industrialists who benefited from a socioeconomic system that provided a stable supply of cheap food for their workers. Although William Jennings Bryant's loss in the 1898 presidential election signaled the defeat of populism in electoral politics, fear of a resurgence of populist radicalism remained for more than a decade.

The aim of providing a moderate alternative to populism was integral to the establishment of the Country Life Movement (Danbom, 1979). Founded by industrial and other elites, the Country Life Movement maintained that, contrary to populist assertions, rural social problems were not owing to the negative impacts of industrial capitalism, but rather because of a lack of organization, poor infrastructure, and technological backwardness in rural areas. In 1908, President Theodore Roosevelt recognized this reform movement by appointing a Presidential Commission on County Life, chaired by Liberty Hyde Bailey, dean of Agriculture at Cornell University. The next six decades of American rural sociology were framed by the Country Life Commission Report published in 1909. The report did acknowledge many of the social problems of rural America (e.g., the inequities of the crop-lien system and widespread sharecropping), but its dominant message was that an expanded effort to modernize rural America technologically and socially was integral to improving rural society. The Country Life Commission recommended the establishment of what is now called the Cooperative Extension Service to speed the modernization of rural America. The Cooperative Extension Service (Smith–Lever Act of 1914) completed the land grant college modernization triangle of teaching (Morrell Act of 1862) and research (Hatch Act of 1887).

The Country Life Commission recommended the harnessing of the social sciences, particularly agricultural economics and rural sociology, to support the technological modernization of rural America. Rural sociological studies in land grant colleges of agriculture were critical in helping to remove social barriers to technological modernization and stabilize rural communities. The establishment of rural sociology, however, was slow and uneven, particularly compared with the field of agricultural economics. Only a few land grant colleges – generally the larger ones in the Northeast and Midwest – established major rural sociology programs. Moreover, it was not until the Purnell Act of 1925 that federal funds were available to support rural sociological research. For all practical purposes, the land grant colleges where rural sociology was present in the 1930s are the same 25 or so institutions where rural sociology existed in the early 1990s.

Institutionalizing Rural Sociology

Three other historical factors were crucial in shaping and institutionalizing rural sociology. First, the Great Depression and the New Deal opened up vast opportunities for rural sociological scholarship aimed at rural reform and relief. By the mid-1930s, sociologists in the United States Department of Agriculture (USDA) Bureau of Agricultural Economics (BAE) and other federal agencies had carried out an impressive program of empirical research on rural communities, rural population, and the structure of agriculture and had linked this research with an agenda for far-reaching rural reforms (e.g., reduction of the power of southern landlords, land tenure reform, and encouragement of cooperative forms of production). Second, the course of rural sociology was decisively shaped when in 1936–1937 rural sociologists broke from the American Sociological Society (later the American Sociological Association) to establish the Rural Sociological Society and started their own journal *Rural Sociology*. The organizational break from the larger discipline of sociology led rural sociology to become even more identified with and institutionalized within the land grant and USDA complex. Third, from the late-1930s through the mid-1940s the progressive reformism of the New Deal came under attack by conservative members of the Congress. The crackdown on reformist rural sociology (and agricultural economics) was completed when the BAE was disbanded in 1944. Seminal works on the relationship between the structure of agriculture and quality of life in rural areas carried out by Goldschmidt

(1947) working for the BAE were suppressed. For two decades after the dismantlement of the BAE, the new generations of rural sociologists were dissuaded from embracing the scholarly and political reform orientations of the New Deal rural sociologists. They were encouraged to embrace positivist social science and provide the basic descriptive information about rural people and rural society to help inform policies targeted to rural modernization.

As a result of these changes, the Töennies–Sorokin–Zimmerman perspective of the rural–urban continuum that favored rural over urban social forms declined in prominence as rural sociology was confronted with the Great Depression and rural squalor, and quickly embraced New Deal reformism. During the New Deal period, rural sociology adopted the modernist view that rural society needed the types of legal, social, and structural reforms that were underway in nonrural arenas, such as labor relations, state regulation of economy and society, old age assistance, and so on. This perspective questioned the romantic and nostalgic position that the traditional structures and practices of rural society were necessarily socially desirable. The rural–urban continuum perspective was also undermined empirically by studies showing that community-like primary social bonds persist even within large metropolitan places.

Rural sociology is a disciplinary product of these historical events interpreted from the two contradictory views of rural society grounded in social theory. The institutional separation from the parent discipline of sociology, the institutional housing of rural sociology programs in colleges of agriculture, and the structural linkages to the Extension Service shifted rural sociology from its original focus on preserving rural life in the face of industrial capitalism to facilitating technologically driven modernization. To survive in the institutional environment of the times, rural sociology embraced its function within the land grant college system by facilitating the modernization of rural society. As politicians and college of agriculture administrators pushed rural sociology to be useful in solving the practical problems of rural society, it lost its preservationist agenda informed by critical social theories. Research that contradicted the prevailing modernist agenda might threaten its institutional standing. By the 1940s, the function and practice of rural sociology was clear, to explicitly support the social policy of transforming rural society through enhanced adoption of modern technologies (Newby, 1980).

Modernist and Preservationist Perspectives

The modernist perspective dominated until the 1960s when rural sociologists and rural advocates began to document and criticize the negative impacts of unquestioned technological adoption as the only path that improved the rural quality of life. The rural–urban continuum perspective reappeared as advocates of rural society renewed their search for ways to preserve what they perceived to be the superior qualities of rural life in the face of the continued spread of industrial capitalism. Their concerns included community disintegration, rural out-migration, loss of local autonomy, family-farm decline, degradation of the rural landscape, and depletion of natural resources. Rural protagonists were informed by the Jeffersonian agrarian values of community, individualism, family-based businesses, and grass-roots democracy (Gilbert, 1982). As noted at the outset of this article, American rural sociology has oscillated between these polar views and agendas of (1) providing uncritical positivist science in support of modernizing backward remnants of preindustrial societies and (2) preserving the special aspects of rural society that support community well-being and enhanced quality of life. Many politicians, land grant university administrators, and advocates of technological innovations still view the preservationist agenda as a major barrier to progress for rural societies.

Though rural sociological research, teaching, and outreach are now undertaken in many nations with rural sociology professional societies on all continents, rural sociology is essentially an American phenomenon. The disciplinary category 'rural sociology' was created in association with the American land grant university system and even today most professional rural sociologists in the United States are still university faculty appointed in land grant colleges of agriculture. The land grant university system was created by the federal government to modernize agriculture and rural life. Though many other countries have a tradition of scholarship similar to rural sociology, the global spread of rural sociology was due mainly to the missionary zeal of rural sociologists from the 1940s through the 1960s, who embraced the modernization perspective. Mostly funded through the rapid expansion of American foreign aid in the post-World War II period, many famous American rural sociologists traveled extensively and diffused American-style rural sociology across a wide range of countries, often helping to create land grant-style systems. As late as the 1960s, rural sociology in other countries was very similar to the American variety.

Beginning in the 1970s, rural sociology became increasingly diverse. Today US rural sociology is not nearly so homogeneous or globally influential as it once was but increasingly borrows from the ideas of European and developing world scholars. Although the modernization perspective is still prominent, the reengagement with critical perspectives has expanded as positivist interpretations were found lacking in explaining social change. Continental and regional professional rural sociology societies, such as the Latin American Rural Sociological Association, European Society for Rural Sociology, Australia and Oceana Network, and Asia Rural Sociological Association as well as the International Rural Sociological Association have expanded. Rural sociologists are active in many of the research committees of the International Sociological Association. The dominance of the land grant university model in the United States has also waned. Owing to a combination of budget cuts, mission redefinition, and academic reorganizations, during the last two decades several rural sociology programs at land grant universities have closed or merged into broader social science programs. As a result, rural sociologists are increasingly employed in non-land grant university settings in the public and private sectors.

The Major Foci of Rural Sociology

Modern rural sociology has six major branches of study: rural population, rural community, rural social stratification,

natural resources and environment, agriculture and food, and science and technology. Following the dichotomous pattern presented in the Section Modernist and Preservationist Perspectives, some branches of study emerged and developed during the historical periods dominated by modernist perspectives and other branches during times informed by critical perspectives. In this article, principal attention is given to science and technology and agriculture and food. Before doing so, a brief description of each of the major specialties in American rural sociology is provided. This section concludes with a discussion on international rural sociology.

Population and Community

From the inception of rural sociology, sociological analysis of rural population and rural community dynamics through census and social survey data has been central to the field. DuBois' early work on black farming was largely based on population census data. As will be dealt in more depth later, the overarching frame of all early rural sociological research is the sociology of agriculture. Patterns of farming systems were studied to try to better understand the relationship between types of farming operations and quality of life in rural areas. Recall that DuBois' early work was on the implications of the Black tenant sharecroppers and planter landlords system of agriculture in the south. The methodology of these early studies was usually the community survey, which cemented the overlap between population and community studies. The Country Life Commission report noted the lack of and need for complete and accurate information regarding the conditions of rural life. The work of the Division of Farm Population and Rural Life of the BAE provided basic descriptive data about the rural population and established rural population studies as one of the pillars of the field. These early descriptive studies generated typologies of farming systems that were used to inform modernization programs carried out by the Cooperative Extension Service, which had an office in nearly every rural county in the United States. Major rural sociology programs included a specialist in rural population and rural community studies who analyzed census data for counties and rural places. Population studies still provide the important basic descriptive information used to inform the policies and programs designed to modernize rural society (Garkovich, 1989).

Rural population and community studies have become increasingly differentiated so that they are now seen as distinct specialties. Rural population research has followed demography in becoming more quantitative and descriptive. Studies that have moved past description into more sociological investigations tended to be guided by the human ecology perspective (Hawley, 1950). Although Hawley's systems model does incorporate the interplay between population, organization, environment, and technology variables and therefore allows for a more sophisticated evaluation than the empirical description of demography, its ability to integrate the spatial with the social aspects of rural society is limited. As population studies and demography generated a wealth of data on both rural and urban populations, it became possible to conduct statistical comparisons between the two groups and thereby test some of the preservationist propositions that population size and density influence social actions and organization; the greater the size and density the lower the social cohesion and quality of life. As noted in the Section The Roots of American Rural Sociology, this frame was first conceptualized as the Töennies–Sorokin–Zimmerman rural–urban continuum and later as the 'folk-urban continuum' (Redfield, 1947). The evidence of a linear relationship that shows decreased quality of life associated with increased population size and density has been mixed. Gemeinschaft relationships were discovered surviving within gesellschaft communities. As a result, the use of census data to document rural–urban differences has been discarded by most rural sociologists.

The rural sociological analysis of communities can be traced back to Galpin's (1915, 1918) pioneering holistic community studies. Galpin is known as the founder of rural sociology. At the University of Wisconsin, Galpin initiated rural life studies based on community studies. His study titled 'The Social Anatomy of an Agricultural Community' was the first Experimental Station bulletin in rural sociology. Galpin was also very active in the American Country Life Association, and later headed the Division of Farm Population and Rural Life in the BAE/USDA. Rural sociologists have conducted thousands of community studies in support of community developed policies and programs (Summers, 1986; Wilkinson, 1991).

By the 1960s, the criticisms of the rural–urban continuum approach for being weak methodologically and excessively descriptive had solidified (Bell and Newby, 1972). Community studies suffered from the advance of the mass-society thesis, which argued that local communities have been eclipsed by the macrosystem forces of industrialization, urbanization, and bureaucratization (Stein, 1964). Through increased vertical linkages, extralocal forces overwhelmed the horizontal linkages of local communities and rendered small rural communities powerless (Warren, 1963). Later research found that increased vertical linkages do not necessarily destroy horizontal linkages, which tempered the macrosystem dominance thesis (Summers, 1986). Much of the community studies work done today employs either the social capital perspective (Flora and Flora, 2008) or the interactional field perspective (Wilkinson, 1991).

Social Stratification

Throughout human history, there has been a tendency for poverty, disadvantage, and political subordination to be exhibited disproportionately among rural people. Preindustrial rural social structures (e.g., feudalism, the antebellum and postbellum Southern plantation systems in the United States, landlord-dominated rural economies in much of South and Southeast Asia, and the latifundia–minifundia complex of Latin America) tended to generate social inequality. In modern societies, rural people have tended to be poorer than urban people. The equation of rural with poverty and inequality has made analyses of rural social stratification and inequality an important dimension of rural sociology. The substantive area of rural social stratification has a long and controversial history

in rural sociology. DuBois' work on tenancy in the south revealed patterns of race-based institutional discrimination. Populist concerns over the power of the agribusiness trusts triggered a broad-based social movement critical of the impact of industrial capitalism on rural society. Cognizant of these expressed concerns regarding inequality, administrators of turn-of-the-century universities steered sociological attention away from controversial class and other inequalities and toward perspectives, such as population analysis and the rural–urban continuum. Thirty years later the New Deal climate of state-led reformism created space for rural sociological attention to social class, race, and poverty, though this space shrank as the New Deal was rolled back, the BAE was dismantled, and Cold War intensified.

Rural social stratification and related analyses enjoyed a renaissance during the Great Society Era and War on Poverty in the 1960s. The study of rural social stratification continues to be a lively and increasingly more diversified arena of inquiry. Studies of regional and labor market inequalities, rural gender inequality, and rural racial inequality have enriched the analysis of rural social inequality (Lobao *et al.*, 2007). These analyses have been extended to the global level and to metropolitan-corporate forces, such as international competition among private multinational agricultural input firms as part of the globalization of economy and society (Bonanno *et al.*, 1994; McMichael, 1994).

In the 1980s, rural labor market studies emerged to analyze the changing economic base and employment opportunities in rural America. Modernization and mechanization of agriculture and other extractive natural resource-based industries supported the steady decline of employment in the primary sector of the economy. From the modernization perspective, rural to urban migration was a natural outcome of the efficiencies gained when capital replaced labor. In the 1970s, rural areas experienced a manufacturing boom as industries migrated south from the rust belt in search of cheaper land, lower taxes, and nonunion workers. Although this trend continues as major manufacturing companies shop for rural locations to site their operations, service industries have emerged as the major source of employment growth. These shifts have contributed to uneven employment opportunities, high unemployment in many rural regions, the growth of temporary, part-time, and informal work, and often increases in poverty. Much of the research investigates the nature and extent of rural unemployment and underemployment, with a growing focus on the linkages of rural labor markets to the macroprocesses of national economic restructuring as part of the globalization of economy and society (Green, 2007; Tigges and Tootle, 1990).

Gender studies in rural sociology received little attention until the late twentieth century (Haney and Knowles, 1988). Since then numerous studies have been carried out that investigate how the institutions of capitalism and patriarchy influence the work roles of men and women in the home, on the farm, and in other rural labor markets. A major dimension of these studies is the nature of farm women's household, farm, and off-farm work (Sachs, 1996). Recent research has revealed the hidden and mostly unreported contributions of women to rural sociology (Zimmerman and Larson, 2010). Gender studies have also started to focus on the topic of farm men and issues of masculinity (Campbell *et al.*, 2006).

Natural Resources and Environment

There is an established tradition of rural sociological scholarship on the relations between people, communities, and natural resources. This scholarship is divided theoretically and methodologically into the sociology of natural resources (SNR) and environmental sociology (ES) camps (Buttel, 2002). These camps mostly followed the two perspectives noted in the Section Modernist and Preservationist Perspectives. The SNR camp is grounded in early twentieth-century discussions regarding conservationist (forester Gifford Pinchot) versus preservationist (ecologist John Muir) views of natural resources. It focuses on conservationist approaches regarding efficient management of nonrenewable and renewable resources with a strong applied and empirical orientation (Field and Burch, 1988). By the 1960s, the SNR was an established research area made up of a combination of (1) social scientists employed in government natural resource management agencies, such as the US Park Service, US Forest Service, Bureau of Land Management, and Corps of Engineers; (2) scholars working in the areas of leisure and recreation studies; and (3) rural sociologists working on resource-dependent community issues, such as the boomtown phenomenon of mining and forestry communities. In the 1970s, the field expanded to include the area of social impact assessment. Most SNR researchers are employed in private or public resource management agencies or natural resource-related academic departments, such as forestry, wildlife and range management, fisheries, or international development. SNR researchers are often members of the International Symposium on Society and Resource Management and publish in the flagship journal, *Society and Natural Resources*.

The substantive area of ES emerged in the 1960s and 1970s as part of the environmental movement (Buttel, 2002). Most early environmental sociologists were academics at liberal arts institutions with a substantive interest in environmentalism. Although some of the environmental sociologists had backgrounds in natural resource sociology and then expanded their research arena as environmental externalities and concerns manifested in the 1960s, most were younger academics with a strong commitment to environmentalism. The original research questions focused on the characteristics of environmentalism and the structure of the environmental movement, then expanded to the areas of pollution and resource scarcity owing to industrial production and consumption (Bell, 1998; Buttel, 1978; Catton and Dunlap, 1978; Schnaiberg and Gould, 1994).

ES approaches tend to be more critical and address the 'Environmental Question' regarding the relationship between modern agriculture and environmental quality. More radical neo-Marxist interpretations (O'Connor, 1998) argue that capitalism is inherently contradictory with ecological sustainability, whereas less radical perspectives such as reflexive modernization (Beck, 1992) support reformist agendas such as green technologies. In the past two decades, the field of political ecology, mostly advanced by critical geographers and development social scientists, emerged as a complement to ES (Peet and Watts, 1996). Rural sociology was at the leading edge of the larger subdiscipline of ES and continues to provide strong leadership in applied areas of ES (Freudenburg, 1986; Dunlap *et al.*, 2002).

International Rural Sociology

As noted earlier, many of the prominent American rural sociologists of the post-World War II period encouraged the global diffusion of rural sociology, particularly in the developing world. The impulse for diffusing international rural sociology (or the sociology of development) was partly the desire to promote a comparative approach to understanding rural social organization, but more importantly the post-War period was an emerging era of 'developmentalism,' based on a faith in the efficacy of scientifically planned social change and technological development in the decolonizing world. Rural sociologists thought they had a great deal to offer for improving the quality of life in the developing world. Rural sociologists trained in the adoption and diffusion of agricultural technology (see Section Rural Sociology and the Diffusion Era) were well represented among these early international rural sociologists. The Cold War dynamic accelerated the push to diffuse the technological answer to hunger and development and combat the spread of communism. Food aid such as PL480 was a major dimension of these development assistance programs. Modernizationist interpretations of PL480 viewed it as improving the Third World's diets, whereas critical interpretations viewed it as neocolonialism and cultural imperialism of Western diets (McMichael, 1996).

This modernizationist/developmentalist tradition of rural sociology held firm for nearly three decades, but ultimately was displaced intellectually by critiques for its lack of efficacy and of having ignored how development is constrained and blocked by the global and national dynamics of the international political economy, as well as the ethnocentrist imposition of one culture upon another. This early tradition of international rural sociology would be undermined, in particular, through critical assessments by rural sociologists regarding their participation and the role of rural sociology in the Green Revolution (Flora, 1990; Havens and Flinn, 1975).

The sociology of international rural development has contributed substantially to the development of rural sociology as a whole. International rural sociological studies have helped to temper the tendency for this discipline embedded in the land grant system to become parochial. International rural sociology scholarship has also contributed to important theoretical trends in the field. For example, the late 1970s is regarded as a period of ascendance of the 'New Rural Sociology,' whose principal theoretical underpinnings were grounded in the critique of international development programs and the role of developmentalist/modernizationist rural sociology in contributing to these programs (Buttle and Newby, 1980). This critical literature became known as the dependency theory (dependista) critique (Gunder Frank, 1969; Wallerstein, 1974) of the great modernization project (Parsons, 1966; Rostow, 1960). In the 1990s, the Wageningen School (Long and Long, 1992; Van der Ploeg, 1992) introduced actor–network theory (ANT) and a social anthropology approach to rural lifestyle studies. ANT provided an interpretive alternative to political economy perspectives, which dominated the New Rural Sociology in the United States.

In the early 1990s, three major social forces combined to alter the future of international rural sociology. First, land grant universities faced with growing fiscal pressures cut their international development program budgets. Second, a crisis of confidence in the ability of development intervention programs, such as the World Bank (WB), the International Monetary Fund (IMF), and the US Agency for International Development to make positive differences in the developing world ensued as the global recession of the 1980s, international mobility of finance and industry linked to the globalization of economy and society, and imposition of structural adjustment programs on debtor countries threatened the possibility of balanced growth in the developing world. The 1990s was the 'postdevelopmentalist' era in which the faith that meaningful planned development based on positivist approaches could occur waned as the harsh realities of globalization and fiscal austerity associated with the late twentieth century political economy became apparent. Third, the fiscal crisis of the state combined with the demise of the USSR as a global threat created a significant decline in the US development assistance programs, which had traditionally been the major source of funding for international development sociology (McMichael, 1996).

Rural Sociology and the Diffusion Era

Embracing the adoption and diffusion of technology perspective was a pivotal turn in the development of rural sociology (Fliegel, 1993). It dominated the rural sociological scholarship during the 1950s and 1960s. Before this shift the rural population, community studies, and rural–urban continuum traditions prevailed. Attention to technological change had been confined to a few studies, such as Williams' (1939) work on the impact of the mechanization of cotton production on field labor in the plantation systems of the south. Even during the height of diffusion research in rural sociology, the labor dislocations caused by mechanization of southern agriculture led many rural sociologists in the region to question the implications of new technologies.

The adoption–diffusion perspective is a social–psychological approach that explains why farmers adopt new technologies (Rogers, 1962). Farmers are social actors with different cognitive states due to variation in education and other factors and various value orientations, such as different levels of modernity, innovativeness, and risk-taking. Farmers respond to stimuli, such as the characteristics of new agricultural technologies, mass media messages, and influences from reference groups. Unlike the earlier traditions in which community was stressed, the adoption–diffusion perspective deemphasized the spatial aspect of rural society and focused on particular psychological traits of individuals (Fliegel, 1993).

The rise of the adoption–diffusion perspective was an outcome of many trends of the time. The rural–urban continuum perspective was exhausted and its role in data reconnaissance to support New Deal reforms had waned. In the 1940s, there was much excitement about hybrid corn and the pioneering adoption studies focused on this technology. It identified which farmers had the highest rates of adoption of hybrid corn and how the innovation was diffused to other farmers. The social climate of the time was conducive to shifting rural sociology to a focus on technologically driven

modernization of rural society as the best path to improved quality of life. Adoption–diffusion studies were also a strategic way to make rural sociological research useful to experiment station directors in the post-BAE climate. And in sociology at large, the 1940s was a period of increased emphasis on social psychology and survey research, which were integral to adoption–diffusion research. Adoption–diffusion advocates believed they had the answer to humanity's ills and the scientific method to diffuse the answer. In agriculture, the promise was to end hunger and generate development.

The adoption tradition produced a number of generalizations about the process of agricultural technology diffusion. For example, it was repeatedly found that plots of cumulative adoption over time took the form of a logistical growth (or 'S') curve where adoption by the innovators proceeded slowly, then accelerated through the early and late adopters, then decelerated again as some of the laggards finally adopted. Earlier adopters of new technology tended to be younger, have higher levels of education, and to have more 'modern' value orientations than do later or nonadopters. Research also revealed that correlations between farm size and farm household wealth and adoption of new commercial innovations tended to increase over time. Soon adoption–diffusion research spread to other innovations and countries as part of the modernization era (Fliegel, 1993).

Critics stressed that a shortcoming of adoption–diffusion was that it viewed new technologies as unambiguous improvements. Farmers who did not adopt were referred to as 'laggards.' Adoption researchers seldom considered how technologies might affect the structure of agriculture or the environment. Despite the utility of the adoption–diffusion perspective, its influence began to decline in the late 1960s and early 1970s in tandem with a growing skepticism toward modern agricultural technologies among sociologists and society at large. Although adoption–diffusion research no longer has the prominent position it once enjoyed, modified diffusion theories and methodologies still enhance the understanding of the processes of technological change.

The New Rural Sociology

By the 1960s, the critique of positivist frameworks that supported the unquestioned adoption of technology as the panacea for rural society was well established. Critical rural sociologists were concerned that social theory and research had been decoupled and that the uncritical empiricism of adoption–diffusion approaches generated unacceptable externalities for rural environments and rural people. Several rural sociologists with experience in adoption–diffusion programs internationally challenged the Western orthodoxy of the technological panacea by arguing that modernization served the interests of the wealthy elites and business interests to the detriment of peasants and poor people (Havens, 1972). In North America and Europe similar discontents emerged as social movements claimed that environmental degradation and institutional discrimination persisted. The normative and positivist conceptual frameworks that dominated for the previous 20 years could not explain the social unrest of the time. Rural social scientists turned to critical perspectives to better explain why the public policies and programs of the federally sponsored land grant university system which claimed to be improving the quality of life for rural people was working well for some groups but marginalizing other groups. This shift in theoretical focus generated what is called The New Rural Sociology (Buttle and Newby, 1980).

It was noted at the outset of this article that rural sociology's history has been one of alternating between opposing views regarding the distinctiveness of traditional rural social structures. Rural sociology came into its own during the post-World War II era. Post-War rural sociology tended to reject the rural romanticism of the 1920s and embraced the technological-modernizationist paradigm that traditional rural social structures were destined to disappear, that there was nothing intrinsic to rural America that was sufficiently socially or morally superior to make it worthy of preservation, and that technological modernization was the most desirable future for rural America. In the 1970s and early 1980s, the pendulum began to swing back toward the rural preservationist perspective. Emerging controversies over agricultural technologies and their social and environmental impacts tarnished the luster from the technological-modernizationist view. The 1970s were a period of 'rural renaissance' because of metro-to-nonmetro migration and a stabilization of the declines in farm numbers that characterized the post-War period.

The New Rural Sociology that emerged during the 1970s and 1980s was decisively shaped by several phenomena in the larger society. Five interrelated social movements are noteworthy: Hightower's (1973) critique of the land grant university system linked to mechanization technologies; the 1970s critique of the Green Revolution; public resistance to the rise of biotechnology in the 1980s; the sustainable agriculture movement in the 1980s; and the rise of global environmentalism in the 1980s. Social scientists placed emphasis on explaining the origins of these movements and how they shaped research policies and the content of new technologies. Most importantly, disagreements over new technologies in society at large prompted social scientists to ponder whether there are intellectually rigorous and socially constructive ways to take a neutral and detached position toward the practice of science and the development of new technologies.

These new realities of rural America combined with the growing popularity in sociology of critical theories led to the New Rural Sociology. Adoption–diffusion approaches grounded in positivistic assumptions of social change did not explain well the societal conflict in the times. These new theories ranged from various forms of neo-Marxism and neo-Weberianism to critical theories drawn from hermeneutics and related traditions. The coherence among these theories was their common critique of modernizationist rural sociology. The dominant theoretical underpinning of the New Rural Sociology drew heavily on neo-Marxist interpretations of the social differentiation in agriculture, including the central role of the state and powerful interest groups in maintaining the political-economic system. The farm/debt crisis of the 1980s provided the empirical setting to apply the New Rural Sociology framework. 'Save the Family Farm' was a familiar rallying cry for populist movements, such as Prairie Fire, the American Agriculture Movement, the Center for Rural Affairs (CRA, 2013), and the National Farmers' Union (NFU, 2013).

The critical New Rural Sociology first focused on the paradox of the persistence of a majority of small family-based producers that produced a small percentage of farm output combined with the growth of large, capitalist operations that accounted for large shares of production. The 'Agrarian Question' was rediscovered as rural sociologists asked, 'What is the relationship between the structure of agriculture and the quality of life in rural communities?' Goldschmidt's (1947) work from California on the negative relationship between community quality of life and industrial agriculture was rediscovered. The early discussions centered on how capitalist relations of production penetrated agriculture, including the barriers to agricultural industrialization. The sociology of agriculture emerged as a distinct substantive area within rural sociology (Buttel *et al.*, 1990).

At the international level, the New Rural Sociology represented a major shift away from positivist adoption–diffusion approaches to critical world systems and dependency conceptual frames. Much of the critique of adoption–diffusion came from those international rural social scientists who did research in the developing world and who realized its faults as a tool for understanding agricultural change in rural areas (Havens and Flinn, 1975; George, 1976; Lipton, 1977). Discussion centered on terms, such as Gunde Frank's (1969) 'the development of underdevelopment' and Wallerstein's (1974) 'world system' of core, semiperiphery, and periphery counties structured in unequal exchange relationships as a remnant of colonialism. In the 1990s, the New Rural Sociology combined the domestic and international foci to incorporate commodity systems (Friedland, 1984) and commodity chain analysis (Hopkins and Wallerstein, 1986), which documented the political-economic dimensions of globalization of agriculture and food systems (Bonanno *et al.*, 1994; McMichael, 1994; Goodman and Watts, 1997). Though the New Rural Sociology was most prominent in the sociology of agriculture literature (see Section Sociology of Agriculture and Food Studies), it had a major influence on the rural sociological study of agricultural science and technology as well.

The Sociology of Agricultural Science

In the post-Hightower period rural sociologists were unable to develop a distinctly sociological theory of technological change, so they build upon the 'treadmill of technology' concept from agricultural economist Cochrane (1979). Proceeding from an adoption–diffusion perspective, Cochrane's theory noted that earlier adopters received innovator's rents because of increased production combined with lower per unit production costs. However, because new technologies increase production and agricultural commodities have low price and income elasticities of demand, overproduction and declining commodity prices ensue. Depressed prices negate innovator's rent and force nonadopters to adopt, get on the treadmill, or go out of business. Nonadopter's lands were then consolidated into the early adopter's operations (cannibalism), increasing farm size. Cochrane commented that the treadmill was subsidized by government commodity programs, which placed a floor under commodity prices. These subsidies caused the benefits of new technologies to become capitalized in the farm asset values of the surviving large landowners.

Rural sociologists appropriated Cochrane's account of technological change but soon found it to be lacking for a number of reasons. The treadmill theory is more valid when analyzing family farming systems compared with large-scale industrial agriculture. It also exaggerates the structural nature of technological change in family-farm agricultures. As most family farmers have significant off-farm work, they have more autonomy concerning adoption decisions. The technology treadmill perspective's focus on mechanization technology applied better to the 1950s than the 1980s agriculture. Furthermore, treadmill of technology reasoning does not address the origins of new technologies, a limitation that was addressed by the development of a rural sociology of agricultural science.

As noted in the Section Agrarian Politics and the Country Life Commission, there were significant studies of technological change and labor displacement in southern plantation agriculture. The sociological study of the diffusion of agricultural innovations began during World War II. Until the late 1960s, the adoption–diffusion perspective was the most important area of rural sociological research. However, the diffusion tradition tended to ignore the social origins of science and technology and the social consequences of technology. The functionalist assumptions of adoption–diffusion approaches minimized the political–economic dimension of rural sociological research. Serious study of the processes by which agricultural science is practiced and new agricultural technologies are developed did not emerge until Lawrence Busch and William Lacy began to draw from the sociology of science to develop the field of the sociology of agricultural science. During the 1980s, a prominent group of rural sociologists, including Busch and Lacy (1983), Friedland (Friedland *et al.*, 1981), Geisler (Berardi and Geisler, 1984), and others created the sociological study of the social consequences of agricultural technology.

An important breakthrough in rural sociological thought occurred when Busch and Lacy grappled with how rural sociology could meaningfully engage public debates over agricultural research and technology. They recognized that critiques of technology needed to demonstrate that there are meaningful technological alternatives and that a change in the structure of research institutions or research policy can affect the content and impacts of new technology. To understand whether there are alternatives to existing or emerging technologies, science and research needs to be studied rather than just the social impacts of technology. Busch and Lacy pioneered the field of the sociology of agricultural science with their theoretical critique of the implicit sociology of science and knowledge within the adoption–diffusion tradition and the application of the sociological theory of influence on the research of agricultural scientists. Their seminal book, Science, Agriculture, and the Politics of Research (Busch and Lacy, 1983), demonstrated the important impacts that scientists' social backgrounds (e.g., farm vs. nonfarm) and institutional nexus (State Agricultural Experiment Stations vs. Agricultural Research Service) have on the research goals of scientists. It documented the fact that science is a social product, and that social factors help to determine which of the several alternative

priorities and approaches are stressed in scientific institutions. Their work provided a way for rural sociology to find some middle ground between unrealistic Hightower-style criticism of new technology on one hand, and uncompromising defense of land grant technology on the other. They contributed to a better understanding of how land grant and other public agricultural research institutions function and helped to galvanize rural sociological interest in contributing to public research policy.

It is notable that their work coincided with the growing interest in the conflict over agricultural biotechnology. They provided a general theoretical and empirical template for the numerous studies that would be done to explain the course of the development of agricultural biotechnology. Their own book on biotechnology provides an innovative theoretical position, which combines the insights of ANT from the sociology of science and induced innovation theory from economics (Busch *et al.*, 1991). Busch's work became increasingly informed by science and technology studies (Latour, 1987), which investigates the study of how science is made rather than the finished science. These interests led to his creation of the Michigan State University School of Agrifood Governance and Technoscience (Konefal and Hatanaka, 2010), where his students carried on this research agenda focusing on the scientific production of standards and resulting societal governance by standards. Following the ANT framework, standards are nonhuman actors that structure society in nondemocratic ways. Busch continues to be concerned with the negative impacts that scientism, statism, and marketism have for substantive forms of democracy (Busch, 2000, 2011).

Rural sociological studies of biotechnology are wide ranging. Some of these were aimed at placing modern biotechnology in a historical context of the changing division of labor between the state and private capital in developing and promoting new technology. Other scholars have stressed the new political–economic environment of biotechnology (e.g., new intellectual property restrictions, such as patents), the importance of intellectual competition in biotechnology, and how modern biotechnology could be expected to alter the dynamics of agrarian change in developed and developing countries (Buttel, 2005; Goodman *et al.*, 1987; Kloppenburg, 1988). The fierce controversy over GMO (genetically modified organism) food is a good example of the continuing tension between positivist and critical theoretical positions of the implications of agricultural technology (see the movie Food Inc. (Kenner, 2009)).

Rural sociologists have also pioneered in studies of several areas of agricultural science other than biotechnology, such as developing methodologies for 'commodity systems analysis' (Friedland, 1984). These studies have demonstrated that the forces that shape public and private agricultural research are, more often than not, relatively specific to the commodity sector involved. Another important area of research has concerned sustainable agriculture, which has included research aimed at facilitating agricultural sustainability as well as research on the origins and implications of the sustainable agriculture movement (Allen, 2005; Buttel, 1997). The sociology of agricultural science embraced a critical perspective to study the social significance of the research apparatus of the land grant university system itself, particularly as to whether it has essentially served as a state policy that helped to underwrite the growth of large-scale capitalist agriculture (Rudy *et al.*, 2007).

Sociology of Agriculture and Food Studies

The sociology of agriculture and food is the dominant substantive research area in rural sociology. As noted in the Section Modernist and Preservationist Perspectives, all of rural sociology can be contexted within the original concerns with the relationship between the structure of agriculture and the quality of life in rural communities. The New Rural Sociology represented a significant critical departure from the adoption–diffusion models that embraced positivist models of development. The initial and central problematic of the New Rural Sociology was the 'Agrarian Question' (Buttle and Newby, 1980), which centered on the subsumption/survival debate regarding how capitalism penetrates agriculture and the degree of farmer/peasant integration into industrial agricultural forms. National and international data not only revealed a steady depeasantization of rural areas but also showed that family-farm/peasant operations persisted in the face of industrialization. Rural sociologists were interested in whether family-farm/peasant agriculture would be subsumed into industrial models or if and why it might survive. Three perspectives emerged to explain this phenomenon: the seasonal nature of agriculture and associated biological constraints created barriers to capitalist penetration (Mann, 1990); detours around these barriers, such as debt, contract integration, market concentration, substitutionism, and appropriationism provide other avenues of penetration (Mooney, 1988; Goodman *et al.*, 1987); and petty-commodity producers survive through flexibility and self-exploitation (Friedmann, 1978). The outcome of this debate revealed that structuralist-Marxist interpretations of the demise of family/peasant agriculture were flawed due to particular configurations of family/peasant farming and that historical and spatial contingencies created alternative structures of agriculture (Marsden, 1989).

In the 1990s, the sociology of agriculture and food experienced two significant shifts: agroindustrial globalization and farming styles. The agroindustrial globalization approach argues that the primary drivers of agricultural change reside outside production agriculture and in the areas of national political–economic processes, the global economy, and geopolitics. In particular, the rising power of agribusiness transnational corporations (TNCs) and supranational forms of the state (e.g., IMF, WB, World Trade Organization) as major coordinators of the agrifood system became a crucial research arena. Friedmann and McMichael (1989) introduced the regimes approach from the French Regulationist School to interpret broad historical shifts in global agricultural arrangements. Regimes analysis looks at clusters of symbiotic factors that generate stable periods of capital accumulation interspersed with periods of crisis. The settler regime (Frontier) of the late 1800s dominated by the British Empire was replaced in the 1940s by the agricultural surplus regime (Fordist) dominated by the United States. Institutional crises of the 1970s prompted the end of the surplus regime and the nascent

emergence of the neoliberal regime (Post-Fordism) based on flexible accumulation strategies employed by TNCs who exercised global sourcing strategies to obtain the best factors of production, often to the detriment of subordinate groups and substantive forms of democracy (Bonanno and Constance, 2008; Burch and Lawrence, 2007; Campbell and Dixon, 2009; Heffernan, 2000; Magdoff *et al.*, 2000). The combination of food regimes theory with commodity systems analysis (Friedland, 1984) provided the terminology and framework that informed agrifood theory in the 1990s. Critiques of the neo-Marxist foundations of the agroindustrialization thesis (Goodman and Watts, 1994) grounded in social constructivist perspectives pushed agrifood theory beyond its structuralist and pessimistic outlook. As a result of these events, the sociology of agriculture expanded beyond production and the farm gate to include the global dimensions of complex commodity systems that linked global producers and consumers in shifting commodity chains.

The farming styles approach is often referred to as the Wageningen School based at Wageningen University in the Netherlands. The Wageningen School employs a neo-Weberian actor-oriented approach, which criticizes both functionalist and Marxist approaches for ignoring the relevance of social agency. From this social constructivist view, diverse rural cultures interact with diverse national environments and economies to create diverse farming styles. This diversity of farming styles based on locale-specific farming structures, technologies, rationalities, and practices mitigate the homogenizing forces of the globalization (Arce and Marsden, 1993; Long and Long, 1992; Van der Ploeg, 1992, 2009).

During the late 1990s, the 'Food Question' came to the fore and the substantive research area became known as the sociology of agrifood studies. The 'Food Question' investigates the relationship between the modern agrifood system and the quality of food. Commodity systems and globalization had taken the research beyond the farm gate to include how consumers were drivers of the agrifood system. Goodman's (2003) 'quality turn' captured the growing interest in alternative agrifood systems, such as food sheds (Kloppenburg *et al.*, 1996), regional food systems (Garrett and Feenstra, 1999), community-supported agriculture (DeLind, 2002), slow food (Miele and Murdoch, 2002), organics (Guthman, 2004), civic agriculture (Lyson, 2004), appellations (Barham, 2007), and agriculture of the middle (Lyson *et al.*, 2008). The legitimation crisis regarding both the environmental and socioeconomic externalities of conventional, chemical-intensive, monoculture agriculture, such as poor nutrition, obesity, *Escherichia coli*, *Salmonella*, pesticide contamination, confined animal feeding operations, animal welfare, and systematic rural depopulation had reached critical mass (Wright and Middendorf, 2008). Consumers were driving the agrifood system toward quality instead of commodity foods and researchers shifted their energies from the problems to the solutions of the agrifood system (Hinrichs and Lyson, 2007; The Meatrix (Fox and Sachs, 2003); Grocery Store Wars (Organic Trade Association (OTA) (2005)); King Corn (Woolf *et al.*, 2007); 3 Lies About Food You're Used to Hearing and Might Even Believe (Food Mythbusters and Lappe, 2013); Super Size Me (Spurlock, 2004); and Fast Food Nation (Schlosser, 2006)).

The newest focus of agrifood research addresses the 'Emancipatory Question.' It investigates the relationship between the structure of modern agriculture and the quality of civil rights for all participants. More specifically, it asks what kind of agrifood system might decrease injustice and inequality for farmers/ranchers/growers, farmworkers, food processing workers, and all consumers? How can we transform the agrifood system to be more socially, economically, and environmentally just (Allen, 2005; Hinrichs and Lyson, 2007; Thompson, 2010)? A central dimension of this research has been the discussion of the different position producers experience in commodity versus value chains. Commodity chains tend to be based on indirect sales of undifferentiated global commodities dominated by agribusiness TNCs, whereas value chains tend to be based on value-added dimensions of the chain (such as, organics) and attempts to share the value more equitably. Fair trade (Fair Trade International, 2013; Raynolds *et al.*, 2007) has emerged as an attempt to shift some of the profits along the value chain upstream toward the producers and avoid the power of the agribusiness TNCs that drive the conventional commodity chains. Agriculture of the middle (Lyson *et al.*, 2008) has emerged as an attempt to provide opportunities for those midsized producers who are too large for direct sales but too small to compete in global commodity markets by creating identity-preserved, value-added products. Food policy councils (Winne, 2008) have emerged to bring all stakeholders to the same table in an effort to create and sustain an equitable agrifood system. At the international level, organizations, such as La Via Campesina, are pushing back against the corporate domination of the agrifood system, especially regarding GMO foods, and arguing that food is a sovereign right (La Via Campesina, 2013; Wittman *et al.*, 2010). For many rural sociologists, alternative agriculture movements are viewed as the countervailing force to the corporate domination of the global agrifood system based on neoliberal restructuring that favors market-based governance over democratic institutions (Morgan *et al.*, 2006).

Summary

Rural sociology continues to be a diverse and vibrant field of study. Professional rural sociological associations span the globe. This article provides an overview of rural sociology with particular attention paid to the substantive areas of the sociology of agricultural science and the sociology of agrifood studies (see RSS (2013) for other historical sources). The social, economic, and environmental implications of the globalization of the agrifood system, including the alternative responses to the dominant model, create a rich environment for a long and interesting discourse in the field. A diverse array of social scientists including rural sociologists, agricultural economists, environmental sociologists, cultural geographers, cultural anthropologists, nutritionists, and others bring their particular disciplinary conceptual lenses to bear on the topic. The Four Questions framework (Constance, 2008) – Agrarian, Environmental, Food, and Emancipatory – spans disciplinary boundaries and is useful for organizing the ongoing discourse. Current issues, such as climate change, food sovereignty, land

grabs, governance, and genetically modified food occupy the cutting edge of new discourses. It is noteworthy that DuBois' original concerns regarding sharecropping and contract production are still salient today as agribusiness TNCs, in particular the dominant food retailers, create flexible commodity chains based on global sourcing. Recent research on the quality of life effects of industrial agriculture for rural people provides evidence in support of the critical perspective (Lobao and Stofferahn, 2008). Although the sociology of agrifood studies currently dominates the field of rural sociology, the historical foci of population and community studies, stratification studies, natural resource sociology, ES, and agricultural science studies continue to make theoretical and empirical contributions within those subareas. Similarly, although today the critical perspective enjoys some privilege over positivist approaches, both continue to inform social policy agendas and reflect divergent views of rural society. The issue of GMOs captures this point well. Although advocates invoke an adoption–diffusion perspective that presents GMOs as the answer to world hunger, opponents criticize GMOs as yet another example of industrial domination and marginalization of rural peoples.

Disclaimer

This article is an update of the original article written by Buttel (1994). The early sections of this article follow closely Buttel's original contribution and his later work (Summers and Buttel, 2000), whereas the later sections are informed by recent developments in the field.

See also: Agricultural Ethics and Social Justice. Agricultural Labor: Gender Issues. Agricultural Labor: Labor Market Operation. Changing Structure and Organization of US Agriculture. Ecoagriculture: Integrated Landscape Management for People, Food, and Nature. Food Chain: Farm to Market. Global Food Supply Chains. Government Agricultural Policy, United States. Industrialized Farming and Its Relationship to Community Well-Being. Linkages of the Agricultural Sector: Models and Precautions. Policy Frameworks for International Agricultural and Rural Development. Social Justice: Preservation of Cultures in Traditional Agriculture

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http://www.ca.uky.edu/snarl/rss/Publications.htm
Rural Sociological Association.

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Safety of Street Food: Indonesia's Experience

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Safety of Street Food

Statistic of Food Born Incidences in Indonesia

Food safety cases in Indonesia are more likely to be underreported. During 2001–09, for example, it was reported that the number of foodborne disease outbreaks per year was 122, involving 5808 cases and 36 fatalities as calculated from **Table 1** (Suratmono, 2010). Of the 109 outbreaks reported up to November in 2009, 36.7% was associated with microbiological hazards, 20.2% was due to chemical hazards, and approximately 40.4% could not be determined of their causes because of a lack of samples or inconclusive results (Suratmono, 2010). Although data were limited, a higher percentage of outbreaks associated with microbiological hazards have actually been identified in the past few years. However, no particular pathogens have been etiologically linked to most outbreaks.

Outbreaks investigation is carried out by the Indonesia National Agency for Drug and Food Control (NADFC) and Ministry of Health (MoH). In general, limited resources were the reason for limited reported data on the outbreaks; thus, preventive actions could not be established. No particular program has been established to improve the surveillance for foodborne outbreaks or their investigation. However, such programs exist for infectious diseases such as dengue fever, etc. Routine monitoring and inspections of food service establishment with regard to GMP implementation is carried out by NADFC and MoH; however, the coverage is low. A study by Susanti (2010) showed that only 15% of medium/large-scale food industries and 4% of home/small industries throughout the country are inspected routinely. The inspection results during 2005–08 suggested that 85% of the medium/large industry and 60% of small/home industry had implemented GMP satisfactorily

Based on the data that ready-to-eat food served at home or by food service industries were the most commonly cause of outbreaks (**Table 2**), several pathogens, especially those that form spores, could be suspected as the causative agent of the outbreaks. In addition, common practices to store ready-to-eat food at room temperature (danger zone) and large-scale cooking to cater for big parties by food service industries could actually allow some spore-forming bacteria such as *Clostridium perfringens* or *Bacillus cereus* to germinate and cause food poisoning. Another common problem with ready-to-eat food preparation is inadequate sanitation and hygiene implementation, which may introduce nonspore-forming bacterial pathogen such as *Salmonella* to food and cause infection. *Salmonella* is a very likely candidate because it is an important causative agent of foodborne illnesses worldwide. One example was the main cause of food export from Indonesia rejected by the US Food and Drug Administration (2004) and was isolated frequently in various food including shrimp (Dewanti-Hariyadi *et al.*, 2005). The problem with *Salmonella* often results in widespread typhoid fever, considered a major problem in certain areas in Indonesia. In certain endemic areas, a prevalence of 1400 typhoid cases per 100 000 populations has been reported (Suwandono *et al.*, (2005)).

Indonesia's Experience in Street Food Program

Study on street food vendors (data Food Technology Development Centre)

Indonesia has a long experience in improving safety of street food. During the period of 1988–92, the Indonesian Government worked together with the Netherlands' Ministry of Foreign Affairs to establish a program on the improvement of the wholesomeness of common people's food in Indonesia or well known as street food program. The program was designed to improve safety and quality of street food, to improve socioeconomic status of street food vendors, and to formulate policy for the proliferation of the program. The first phase of the program was basically a base line survey to map initial situation of the socioeconomic status of street food vendors, the quality and safety of street food, and street food handling.

In the early 1990s, the income per capita of those who are working on street food business is more than double of the minimum wages apart from the fact that they had rather limited educational background (67% of street food vendors had elementary school education or less). At the same time, street food business was able to provide jobs for 12.2% of workforce. Interestingly, 30% of food spending of household was for street food. Such a situation illustrates the importance of street food business and its impact on the community. Street food has significant roles in providing nutrition, to some extent, for the community. However, classical problems on safety of street food were also identified. The major food safety concerns are microbiological and chemical contamination. Poor food handling was also one of the major findings.

Table 1 Foodborne disease outbreaks in Indonesia during 2001–09

Year	*2001*	*2002*	*2003*	*2004*	*2005*	*2006*	*2007*	*2008*	*2009*[a]
Number of outbreaks	26	43	34	164	184	159	179	197	109
Number of cases	1955	3635	1843	7366	8949	8733	7471	8943	3050
Number of fatality	16	10	12	51	49	40	54	79	17

[a]Report till November, 2009.

Source: Reproduced with permission from Suratmono, 2010. Food safety in food service industry. Presented in "Safety of Food Service Industry." Jakarta: Kulinologi Indonesia Magazine, 18 March 2010 (in Bahasa Indonesia).

Table 2 Foods associated with outbreak in Indonesia in 2009

Type of food	*Percent (%)*
Homemade food	42
Food service food	27
Industrial processed food	15
Street food	13
Others	1

Source: Reproduced with permission from Suratmono, 2010. Food safety in food service industry. Presented in "Safety of Food Service Industry." Jakarta: Kulinologi Indonesia Magazine, 18 March 2010 (in Bahasa Indonesia).

Table 3 Potentially unsafe food sold in school canteens

No	*Food category*	*Number of sample*	*Potentially unsafe food (%)*
1	Iced drinks	332	48
2	Soft drinks	80	63
3	Cake	72	21
4	Fritters	67	18
5	Meat ball soup	66	24
6	Crackers	48	56
7	Puffed snacks	42	17
8	Chili and tomato Sauce	40	60
9	Jelly	10	40
10	Tofu	10	40
11	Noodle	8	50
12	Others	86	24

Source: Reproduced from NADFC, 2006.

The results obtained from the first phase were used to design the intervention programs which include general intervention, intervention on special product, pilot project, and mass media campaign. Intervention was done through involvement of the local government to ensure the smooth transfer of the idea and sustainability of the program. Task force for the intervention program consists of not only experts from universities but also local government officers, directly responsible to manage street food, and informal leaders in the community.

Study on school children's meals intake

In most cases, meals intake of school children in Indonesia is obtained from school canteen and/or street food vendors in the premises or immediate area of the school. Only a small fraction of school children bring their own meal from home. Therefore, the efforts to improve the safety and quality of food provided by school canteens are highly justified.

Even though the Republic of Indonesia Government regulation no. 19/2005 requires school to have at least one canteen, 40% of elementary schools have no school canteen. Unfortunately, 84.3% of the school canteens in elementary schools are below the minimum standard for sanitation and personal hygiene. Lack of proper school canteen forces school children to buy their school meals from street food vendors around the school, which are beyond the control of the school. In general, employees of school canteen and street food vendors have very limited knowledge of food safety and personal hygiene.

A report of NADFC indicated that in average approximately 38% of food sold in school canteen is potentially unsafe (NADFC, 2006). Percentage of potentially unsafe food for different food categories is presented in Table 3. The food is potentially unsafe because it may contain nonfood grade chemicals, contain food additive above its permitted level, may be contaminated by pathogen microbes, or may have extremely high microbial load. In addition, most of the foods sold in school canteens are snack foods and soft drinks which may result in imbalance of nutritional intake and or unhealthy diet.

This condition drove the ministry of education and culture of the Republic of Indonesia to launch Healthy Canteen program in 2009. The program was aimed to improve the facilities of the school canteen as well as improve the food safety there. Two main activities in the program were improvement of canteen facilities and capacity building. The program covered 288 school canteens in 2009 and it continued till 2011.

Remaining Challenges for Food Safety

Misuse of food additives

Food additives such as colorant, sweetener, and flavor enhancer are often misused in street food. They are frequently used in excessive amount, resulting in concentration above its maximum level. Street food vendors do not pay much attention to the label and instruction to use the additive. Another type of food additive misuse is its use not in accordance to its intended function. Classic example is the use of one of the famous flavor enhancer (monosodium glutamate) to provide salty taste instead of its intended *umami* flavor. As a result, they tend to use excessive amount of monosodium glutamate as it has to serve a different function.

Abuse of nonfood grade chemicals

A more classical problem of food safety in Indonesia is the abuse of certain nonfood grade chemicals in food processing. Formalin, a formaldehyde-containing solution, is often used to preserve fish, tofu, and wet noodles. Publication of the findings in 2006 had also caused a loss of some domestic trade, especially for the three aforementioned commodities. There were several reasons why the problem occurred. First, it was easy to access and obtain the chemical which was supposedly used for glue making and corpse preservation. Secondly, inadequate sanitation during production and lack of cold chain or refrigeration system has resulted in a short shelf life. The condition has prompted certain individuals to apply formalin to lengthen the shelf life without considering the risk of the hazard to human. The first problem was solved by a collaborative effort between NADFC and Ministry of Industry and Trade in a better management for the trade of hazardous chemicals. The second is handled through continuous education in food hygiene and sanitation process. Because refrigeration or cold chain has not been addressed adequately, the formalin problem has not been fully managed. The government routinely inspect presence of this chemical in foods, especially those that have previously been linked to the use of formalin. Sanctions for the abuse of hazardous chemicals use in food have actually been regulated in Law no. 7, 1996. The above incident has increased the law enforcement for such abuse.

Intervention to Improve Safety

Establishment of Street Food Pilot Project

Street food pilot project was first introduced in the city of Bogor under the street food program. The pilot project was designed as part of the street food program which was a collaborative program between the Government of Indonesia and the Government of Netherlands (Winarno, 1993). Street food pilot project was started in 1990. During the first year of the pilot project of the intervention (1990–91), all the activities were organized and executed without involvement of the local government. In the second year of the intervention, the local government was invited to actively be involved in the pilot project to secure the sustainability of the program. The active involvement of local government is realized in the formation of task forces involving government officer down to the village (*kelurahan*) level. The task force functions as facilitator as well as assessor. The local government contribution to the pilot project was also indicated by legalizing the activity of street food vendors in the pilot project zone. Before the pilot project, street food vendors were considered illegal and therefore would create insecurity for the vendors.

School Canteen Intervention

Selection of scope of study/target group

School canteen provides food for school children who are one of the most vulnerable groups of consumers. School canteens to receive intervention package were selected on the basis of several minimum requirements. A school must already have canteen with continuous and reliable supply of clean water. It is impossible to have a school canteen that is able to produce safe food without proper supply of clean water. Candidates for school canteens program were proposed by local government. A team from the ministry of national education directly inspects the proposed canteens to assess the suitability of the school canteens for the program. The canteen personnel, teachers, and school principals were invited to join capacity-building program as well as planning for facility improvement of the school canteen.

Capacity building

For school canteen management and employees

Healthy school canteen program targets to improve canteen facilities by providing significant amount of money. However, it is fully realized that the canteen facility improvement alone will not make significant difference without capacity building of those who are working daily in the canteen. Therefore, facility improvement and capacity building are given as one package to the target school.

Capacity building is given in the form of trainings on nutritionally balanced and healthy diet, food safety, good manufacturing and handling practices, and food sanitation and personal hygiene. The teaching materials are simplified to suit the need of school canteen employees. To ensure that the school canteen optimally use the money to improve the facilities, the trainer and the trainees discuss their plan in class. Such an approach stimulates fruitful discussion among trainees to optimally improve the canteen facilities within the provided budget. The discussion is also very useful for school canteen personnel to further improve the facilities in the future by developing list of priority for next facilities improvements.

For teachers and school principals

Capacity building of school canteen program targeted not only canteen personnel directly related to canteen operation but also teachers and school principals. The idea is to ensure that school canteen program is properly understood and fully supported by teachers and school principals. Capacity building of teachers and school principals is strategically important because of the authority that they have over the school canteens. Teachers are supplied with all the teaching materials used during the training. They are requested to share their knowledge with their students in order to create awareness among school children and to create high demand for safe food. The success of creating demand for safe and healthy food is highly dependent on the willingness of the teachers.

School principals are actively involved in the discussion of improvement of school facilities. It is important that they have field experience of implementing the knowledge obtained in the training class to practically solve their unique problem in their school.

Early food safety education to school children

School canteen program facilitates the improvement of school canteen in elementary school, junior high school, and senior high school. In 2009 alone, 288 schools which consist of 111 canteens in elementary school, 91 canteens in junior high school, and 80 canteens in senior high schools were involved in the program. School canteens are targeted because they cater food for the young generation as part of early food safety



Figure 1 Street food at Bina Marga Street, City of Bogor, Indonesia. Reproduced from Kementerian Koperasi dan, U.K.M., 2012. Final Report on Street Food Pilot Project (in Bahasa Indonesia).

education. This figure indicates that slightly higher proportion of canteen in elementary school is targeted in the program. The safety of street food from school canteens improved in 2012, the NADFC reported that the percentage of potentially unsafe food sold in school canteen decreased to only 23.1%.

Integrated Intervention of Street Food

Street foods are mostly provided by informal sector. Street food vendors often use public area and public facilities for their activities and consequently create social problems. However, informal sectors have also shown its significant contribution in providing jobs and economy. The incomes of those who are working in this informal sector are higher than regional minimum wage (UMR). Therefore, an integrated approach is required to minimize the negative social effect of street food, improve the safety and quality of street food, and maximize the economic contribution of street food.

Integrated intervention of street food includes activities to improve food safety, legal aspect of street food activities, financial support, and social engineering. The integrated approach was started in 2009 by ministry of cooperative and small and medium enterprises in collaboration with Bogor Agricultural University as a study to develop integrated model of street food vendors. The pilot project of intervention program started in 2011 and will continue till 2013 in Bogor. The integrated intervention program involves local governments, universities, nongovernment organizations, NADFC, and ministry of social affairs.

The first step in the integrated program is to legalize the activity of street food vendors through the establishment of 11 zones of street food vendors in Bogor. This was done through establishment of a decree by the city mayor. Four out of 11 zones are selected as pilot project for the integrated intervention. The selection was based on the number of vendors per zone, priority of local government, and availability of basic infrastructure such as water supply and electricity. Street food vendors are facilitated to form two cooperatives, namely cooperative *Selobang* and cooperative *Bhineka*. Capacity building on food safety includes several topics such as food additives (preservative, sweeteners, and colorant), food packaging, basic sanitation, and hygiene, which are all provided to street food vendors. Moreover, they are trained for simple accounting and business management. Financial support is given in the form of collective loan. The collective loan is aimed to form unity among cooperative members. Street food vendors are also facilitated to have business meetings with potential funding source such as banks and microfinance agencies. Local Government (City of Bogor) is fully supportive in rearranging and controlling the traffic in the intervention zone to minimize traffic jam and reducing air pollution/improving air quality. Cooperative office of the city is directly involved in the establishment of the cooperatives as well as mentoring and monitoring the activities of the cooperatives.

Evaluation of the program shows that business performance of street food vendor increases as indicated by the rise in total revenue (14–16%) and improvement in income (9–12%). (Kementerian Koperasi, 2012). The facilities and infrastructure of street food vendors in the intervention zone is significantly improved as shown in Figure 1. The improvement includes trash bins, sewage system, toilet, hand-washing facilities, cleaning area, and parking lot.

Lessons Learned

Long experience of Indonesia in improving safety of street food indicates that safety aspect of food is not independent of

other factors. Relatively low concern of food street vendors is mainly due to their lack of food safety knowledge and the absence for demand on safe and wholesome food from consumers. Therefore, efforts to improve safety of street food must come from both consumers and producers. Food safety education from the very early childhood is required to internalize food safety concept to the children.

Street food vendors have significant contribution to the local economy and are actually able to provide safe and good-quality food. However, they need capacity building in basic knowledge of food safety and business management. Intervention and facilitation from the Government are often required to link these microenterprises to commercial funding scheme in order to help them develop their business.

See also: Consumer-Oriented New Product Development. Food Law. Food Safety: Emerging Pathogens. Food Security: Development Strategies

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Sensory Science

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Glossary

Check-all-that-apply (CATA) A type of question, frequently used in survey questionnaires, that presents subjects with multiple response options to a single question. Participants are instructed to select as many of the response options that they perceive to be relevant. The list of answer options is not limited to product attributes and can relate to product usage, concept fit, or hedonic or emotional aspects.

Descriptive profiling/analysis Techniques that aim to generate quantitative data describing similarities and differences within a product set. While each approach is slightly different, the basic methodology is the same. The steps of descriptive analysis are selection of panel members, term generation, concept formation, testing of panel agreement, and finally, evaluation of products. Some of the techniques available include free choice profiling, the spectrum™ method, Quantitative Descriptive Analysis™, Flavor Profile method, texture profile method, Flash Profiling, and generic descriptive analysis.

Direct scaling A technique for estimating perceptual intensity proposed by S.S. Stevens that assumes individuals can directly generate a psychophysical function. Common direct scaling methods include magnitude estimation and the Labeled Magnitude Scale, and the general Labeled Magnitude Scale. This contrasts indirect methods based on signal detection theory.

Just Noticeable Difference (JND) A mathematical relationship defined as the smallest detectable difference between two levels of a sensory stimulus. Originally described by Ernst Weber and Gustav Fechner.

Method of limits One of the three traditional methods for testing subjects' perception, the other two are the method of constant stimulus, and the method of adjustment. The method of limits is a technique to determine thresholds, usually detection threshold. The technique can be performed as an ascending or descending method of limits. In the ascending method of limits there is some property of the stimulus (e.g., sweetness) that starts out at a level low enough that the property cannot be detected. The level of this attribute is slowly increased until the participant indicates that they can detect the attribute in the stimulus. The descending method of limits is conducted in the opposite order, decreasing until the participant indicates that they can no longer perceive the specific attribute.

Perceptual mapping A collection of techniques that can produce visual representations of perceived product relationships. These techniques, including pairwise comparisons, sorting, and mapping, are popular tools in market research as they can be used to evaluate product space within the market. Using these techniques, large datasets can be reduced to easily interpreted plots of a few dimensions. While it is not necessary to the techniques, these maps often also contain relevant product attributes, which lend interpretability to the map. Depending on type of data collection methods used, data from DA can be analyzed with principal component analysis, multidimensional scaling, multi-factor analysis, General Procrustes Analysis, and discriminant analysis.

Psychophysics A subdiscipline of psychology that qualitatively measures the relationship between physical stimuli and the sensations and perceptions evoked by these stimuli. The term 'psychophysics' encompasses the study of the stimulus-response relationships as well as the methods used for these studies.

Sensory evaluation An applied science focused on the study of product characteristics as they are perceived by human assessors via the senses.

Sensory science A discipline encompassing of fields of sensory evaluation, psychophysics, sensory and affective neuroscience, chemosensory biology, and genetics. The primary distinction between sensory evaluation and sensory science is that the former focuses primarily on methods used to study product characteristics while the latter includes study of the participant in addition to the product.

Signal Detection Theory (SDT) Used to measure decisions made under conditions of uncertainty. Signal detection theory assumes that any stimulus consists of a signal (audio tone) and noise (white noise). Using SDT based methods researchers can separate an individual's sensitivity from their response bias.

The general Labeled Magnitude Scale This scaling technique uses a line marked with empirically derived verbal anchors describing different sensation intensities (e.g., 'weak,' 'moderate,' 'strong'). This scale was developed as a way to evaluate perceptual differences in sensation intensity between participants, to avoid the rescaling problem in magnitude estimation.

Visual analog scale (VAS) A type of scale used frequently used to measure characteristics or attitudes that cannot be directly measured, such as how much someone likes/dislikes a product. When using the scale, panelists indicate their level of agreement to a statement by marking a point along a continuous line, somewhere between the two end points (e.g., 'strongest liking of any kind' and 'strongest disliking of any kind'). This scale is differentiated by discrete scales, such as a Likert scale, because of its continuous nature. This feature allows for a wider range of statistical techniques to be applied to data generated by a VAS though generally the sensitivity and reliability of the two types of scales (continuous vs. discrete) are very similar.

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Introduction

Sensory evaluation is defined by the US Institute of Food Technologists (IFT) as the "scientific discipline used to evoke, measure, analyze and interpret those reactions to those characteristics of foods and materials as they are perceived by the senses of sight, smell, touch, taste and hearing" (Stone and Siedel, 1985). As with any other scientific discipline, the keywords here are measure, analyze, and interpret. The traditional focus of sensory professionals has been the development of tools to make accurate, reproducible measurements with regard to food products. Originally, many of these approaches were empirical and atheoretical; sensory practitioners used what worked, and these approaches were codified into putative best practices. However, because the instruments used to make sensory measurements – human assessors – are inherently noisy, it can be difficult at times to separate the signal from the noise. Thus, a second major area of research has been the development of the experimental methods and statistical models needed to quantify and test human sensory data. In a similar vein, the modern sensory professional needs to be well versed in aspects of psychology and cognitive science in order to understand and ideally reduce potential biases when collecting data from human participants. At multiple points throughout the history of the field, the state of the science has been enhanced by fruitful collaborations and cross talk between applied sensory practitioners trained in food science, academic psychophysicists, and behavioral scientists trained in experimental and cognitive psychology.

The authors have intentionally chosen to title this article sensory science rather than sensory evaluation or sensory analysis, because they believe that the field of sensory evaluation is only one facet within a broader field of sensory science (i.e., the two disciplines are not entirely synonymous) and that the former is a subset of the latter. Sensory evaluation has classically focused on the product (as evidenced by the IFT definition above), whereas the broader field of sensory science also includes study of the person in their own right and how this influences their responses to products, that is, sensory science includes not only sensory evaluation but also psychophysics, sensory neuroscience, affective neuroscience, chemosensory biology, and genetics (Figure 1). Related but separate fields include ingestive behavior and flavor chemistry. As appropriate, aspects of some of these disciplines will be included in this article to provide insight into the sciences that underlie the applied aspects of sensory science.

Convergence of Sensory Evaluation and Experimental Psychology

Rose Marie Pangborn is generally acknowledged as the matriarch of a scientific sensory analysis in the US. During her tenure at the University of California, Davis, CA, USA, she published more than 180 scientific papers, mentored more than 40 graduate students, and coauthored one of the historic textbooks in the field (Amerine *et al.*, 1965). She cofounded the Association for Chemoreception Sciences and today, the biennial Pangborn Sensory Science Symposium, the premier international conference on applied sensory science, and an international scholarship for the doctoral training of academic sensory scientists bear her name. Many of today's senior sensory academics and practitioners internationally received their initial training under Prof. Pangborn.

Near the end of her career, Pangborn was asked why the literature on taste interactions in actual foods and beverages was so sparse and unsophisticated. In her reply, she made a sharp distinction between sensory analysts (trained in food science) and psychophysicists (trained in experimental psychology; Pangborn, 1987). Specifically, Pangborn called for more collaboration between food scientists and psychophysicists, noting that it was "unusual for sensory analysts to use

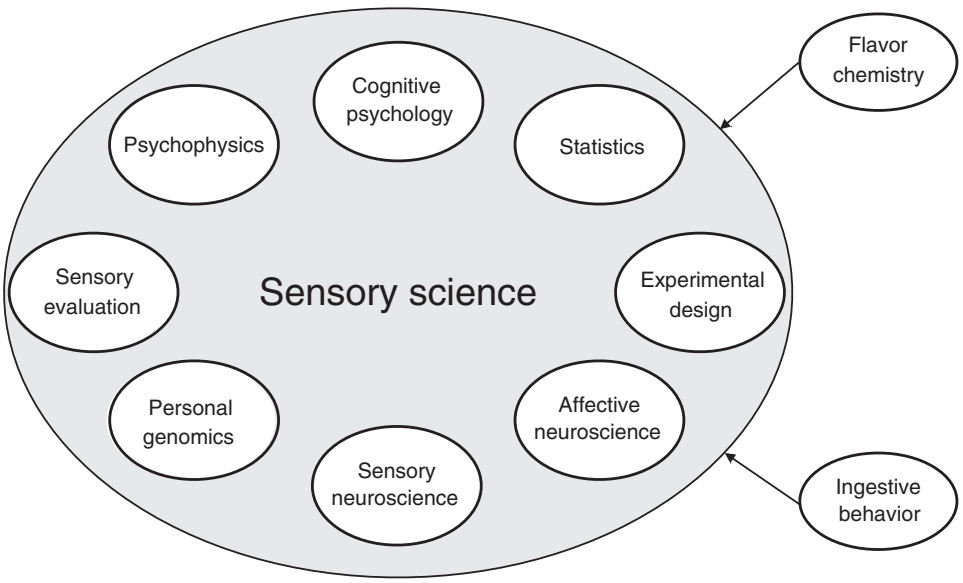


Figure 1 Schematic of contributing disciplines to sensory science.

good psychophysics and for psychophysicists to be well informed about the multiple functional properties of foods." Later, Lawless (1991) similarly lamented the substantial disconnect between basic research conducted by academic researchers and industrial practice.

It is no longer the case that psychophysics and sensory analysis are disconnected. For example, the authors of this article include an experimental psychologist formerly employed in both university food science and psychology departments and a food scientist trained in psychophysics and sensory neurobiology. Also, a key textbook on sensory evaluation in use today is coauthored by a wine scientist and a psychophysicist (Lawless and Heymann, 2010). Many active researchers in the field have strong training in both food science and psychology. Accordingly, it is not uncommon for articles in the modern sensory science literature to use strong psychophysics while drawing on methods from a variety of food science disciplines (e.g., Bakke and Vickers, 2008; Harwood *et al.*, 2012; Lucas *et al.*, 2011).

Much of the early cross-fertilization between sensory analysis and experimental psychology can be traced to the Behavioral Sciences Division at the US Army's Natick Laboratories under the leadership of Dr. Harry L. Jacobs (Meiselman and Schutz, 2003; Moskowitz, 2004). These laboratories have produced many of today's leading scientists in both basic and applied sensory research. As noted by Moskowitz (2003b), the normal pattern of practice following foundational science was reversed for sensory science, with practice coming well ahead of its theoretical framework. The pioneering work of the psychophysicists at Natick helped provide both a corpus of basic knowledge and academic credibility that moved sensory specialists beyond their traditional service function as 'taste testers' (Moskowitz and Gacula, 2003).

Notably, the cross-fertilization between psychology and food science was bidirectional. Psychologists like S.S. Stevens claimed that participants could only rate a single attribute in a session (Moskowitz *et al.*, 2003) when applied practitioners were regularly collecting such data during the course of descriptive profiling (Stone *et al.*, 1974). Only later did psychophysicists abandon the uniattribute rating paradigm (Moskowitz *et al.*, 2003) once it was shown that individuals could rate multiple attributes (Bartoshuk, 1975).

Collectively, bidirectional collaborations and cross-disciplinary conferences helped to infuse applied sensory practice with a theoretical foundation, both by influencing the training of future generations of sensory scientists and via collaboration among established researchers with domain expertise in different fields. A recent example of this collaborative approach is the application of modern psychophysical scaling methods, together with flavor chemistry and plant genetics to optimize tomato flavor (Tieman *et al.*, 2012). For additional discussions of how psychophysical thinking has helped to move sensory analysis from a set of measurement tools toward a mature discipline of study, the interested reader is referred to several reviews (Meiselman and Schutz, 2003; Moskowitz, 1993, 2003a).

Once the field was based on a theoretical foundation rather than revealed wisdom, it became possible for the sensory professional to move beyond simple dogma and 'break the rules' when appropriate, for example, asking naive, untrained panelists to rate intensity, not just liking (Moskowitz *et al.*, 2003). Nonetheless, even when working within a broader theoretical framework, 'the demand for practical testing is so great that the pursuit of causal mechanisms and general principles may be lost in the daily rush to solve immediate product development' (Cardello, 2005).

Distinctions between Sensory Science and Commodity Judging

Applications of sensory science represent a different historical and philosophical tradition from commodity judging. In commodity judging, the emphasis is placed on identification of standard defects by highly trained expert judges. Examples of this approach include coffee cupping (e.g., Specialty Coffee Association of America Q-grading), wine scoring (e.g., the University of California, Davis, CA, USA, 20-point scoring system), and dairy products judging (Clark and Costello, 2009). These approaches are fast and work reasonably well for narrowly defined systems with known defects – that is, in quality control settings. However, the necessary expertise and relevant attributes do not generalize outside the specific context of the individual commodity: a coffee Q-grader cannot be used to judge wine, and standard ballot items appropriate for pasteurized cow's milk may not apply to goat's milk.

Commodity judging has been criticized on the grounds that it focuses on causes rather than perceptions (e.g., 'light-struck' flavor), generates numbers that are not suitable for statistical analyses (ordinal vs. interval measurements; see Section Scaling), and lacks an underlying psychophysical model ('scoring is not scaling'). Additionally, it is important to remember that expert opinions may differ from those of consumers. For example, cork taint is a severe defect according to wine experts, but consumer testing indicates that the presence of low but detectable amounts of trichloroanisole (TCA) may not depress consumer acceptability (Prescott *et al.*, 2005). Finally, commodity judging assumes a singular purpose or appropriateness that does not match the multitude of ways packaged consumer goods are used (e.g., a can of mushroom soup can be used in a casserole or eaten as soup and may simultaneously be acceptable for one use but not the other).

Sensory Measurement

Classical Psychophysics

The origins of experimental psychology lie in efforts to understand the ways in which the information present in the world in the form of energy came to be translated into one's perceptions (the recommended reference for this section and the section to follow is Gescheider (1997)). Gustav Fechner, in his Elemente der Psychophysik (1860), approached this question by reducing the problem to meaningful and perceptually equivalent chunks known as just noticeable differences (JNDs). His measurements indicated that as stimulus energy (photons, sound pressure level, etc.) increased, a greater amount of this energy was required to produce a JND. Fechner

described the relationship between stimulus energy and perception mathematically, producing the first psychophysical function relating external stimuli and internal perceptions. He also attempted to operationalize the scaling of stimulus magnitude by promoting the idea of counting JNDs above threshold. Because JNDs are perceptually equal, any stimulus magnitude should be quantifiable as the sum of JNDs, producing in effect a type of magnitude scale.

The idea of JNDs was incorporated into attempts to measure discriminability between different stimuli. Ernst Weber, investigating the thresholds for perception of different weights, formulated what is known as Weber's Law (or Ratio). The law states that for a given sensory modality (salt taste, sound, weight, vibration, and so on), the change in intensity needed to produce a perceptible change (a JND) in sensation intensity is a constant fraction of the initial stimulus intensity. Hence, the absolute value of the JND may vary, but its value as a proportion of the stimulus energy does not. For example, the Weber ratio for saltiness has been estimated at 0.08, indicating that a minimum 8% increase in salt concentration (at least in water) will be apparent irrespective of the current salt concentration that is being increased.

These ideas have formed the basis for what is known as classical psychophysics and hence the basis of measurement of perception, whether in psychology or sensory science. From the concept of psychophysical functions comes the understanding of the relationship between a physical stimulus and the sensations evoked by that stimulus. In food sensory science this might be, for example, amount of salt and the impact of increasing the salt level on perceptions of saltiness. Ultimately, of course, determining such relationships helps one to understand consumer responses to salt (e.g., Hayes *et al.*, 2010). Psychophysical functions are almost always above or below unity – in other words, there is not a one-to-one linear relationship between stimulus magnitude and perceptual intensity. For instance, adding 20% more sucrose to a drink will not make it 20% sweeter.

Fechner described psychophysical functions as following a log relationship, but more recent research by Harvard psychologist S.S. Stevens has shown that the function is better fit by an exponent in an equation known as Steven's Power Law. This has provided a convenient way of describing psychophysical functions: so, the exponent for sweetness is 1.3, whereas that of coffee odor is 0.55. In effect, for every unit of increase of sucrose concentration, the intensity of sweetness is increased by 1.3 (log) units; conversely, a unit increase in coffee odorants leads to an increase of only 0.55 in coffee odor intensity.

The input of classical psychophysics into food sensory science has been invaluable in answering questions related to the perception of ingredients within foods as well as the effects of manufacturing processes, packaging, and storage. It is crucial, for example, to determine thresholds for ingredients that may have functional properties but which may adversely affect consumer preferences. Similarly, knowing whether an ingredient can be reduced or substituted, or a process changed will rely on determination of absolute threshold (that is, above some point below which a quality cannot be detected) or difference/discrimination thresholds, which are related to change. Answering these applied questions requires the estimation of JNDs at different points on the stimulus continuum.

In classical psychophysics, there are several approaches to determining absolute thresholds. The method of limits involves presenting a series of stimuli above and below the estimated threshold, in either (or both) ascending or descending series. Each 'yes' response (the stimulus is present) terminates the series and the threshold is taken as the average value over several such series either for an individual or across a group of individuals. In the staircase method, a series of stimuli ascends from below threshold until the stimulus is detected, and then reverses direction, descending until the stimulus is not detected. The threshold is the average of several (4–7) 'reversals.' The method of constant stimuli uses a set of 5–9 different values, from never detected to always detected, presented randomly, and the percentage of detections as function of stimulus intensity is determined. Here, threshold is the stimulus intensity for which the proportion of 'yes' responses is 50%.

Difference thresholds can be determined using similar methods except that on each trial there is a comparison between a reference sample and a different (more/less intense) sample. As an example, to a question such as "What change can I make in the sucrose content of an orange drink (10% sucrose) without a noticeable difference (JND)?" the stimuli might range from definitely less sweet (e.g., 3% sucrose) to definitely more sweet (e.g., 18% sucrose). In this version of the method of constant stimuli, a series of eight values between these two extremes would constitute the comparison stimuli. At each concentration of comparison stimulus, the panelist would be presented with a pair of stimuli (the reference stimulus plus one of the comparison stimuli) and asked to indicate which is the sweeter: the reference or the comparison? Clearly, if only 50% of the responses are that one stimulus is sweeter, it means that there is no discrimination from the reference. Similarly, 100% and 0% 'sweeter' mean perfect discrimination. Conventionally, the point at which discrimination occurs – the difference threshold – is taken as 25% (reference sweeter) and 75% (comparison sweeter), which is 50% of responses, adjusted for guessing.

This type of paired comparison test is in common usage for determining simple differences between samples (ISO5495, 2005). In this case, panelists are given two samples and asked to pick the one with the greater intensity. For example, given two sucrose solutions differing in concentration, a panelist would be asked to 'select the sweeter of the two.' The probability of guessing correctly by chance alone is 0.5, so a judgment on whether the samples are different relies on repeated trials with the same person or, more typically, across multiple panelists. Tables of binomial probabilities will indicate, for instance, that 21 out of 30 panelists correctly picking Sample A as the sweetest (when it has the higher concentration of sucrose) is significant at $p < .05$. The paired comparison test is an example of a directional test in which the quality of interest (in this case, sweetness) is specified.

A group of tests known as alternative forced choice (AFC) tests function is exactly the same way but are used with three (3-AFC) or more (n-AFC) samples (ISO13301, 2002). Hence, a panelist might be told that of the three sucrose solutions in

front of them "two are of the same sweetness, one is sweeter – pick the sweeter sample."

Nondirectional tests, which are generally less sensitive than directional tests (for a theoretical explanation of this, O'Mahony *et al.*, 1994), ask the panelist only to identify differences between samples, irrespective of quality. So, the duo–trio test (ISO10399, 2004) asks panelists to match one of the two unknown stimuli to a reference ("indicate which sample is the same as the reference"). The 'ABX' test is simply an inverted duo–trio, with two references and one unknown: panelists are asked to match the unknown (X) to reference A or B. The very commonly used triangle test requires a slightly different cognitive strategy: panelists are told that of three samples, "two are the same, one is different – pick the odd sample" (ISO4120, 2004). As with the paired comparison test, determining whether or not to accept a difference is based on binomial probability tables in relation to the guess rate (e.g., 0.33 for three samples). The cutoff for significance is not a fixed proportion because the confidence interval shrinks as the number of panelists increases: for example, with 60 panelists, 33 or more correct identifications (55% correct) are required for statistical significance, whereas only 58 correct identifications are required with 120 panelists (48%).

Most recently, there has been an increasing interest in the tetrad test, in which four samples are sorted in two groups of two, based on a perceived difference (Ennis and Jesionka, 2011). As noted above, there are differences in the sensitivity of discrimination tests such that the power of the tests to detect differences for a given number of panelists can be estimated. When this is done, the tetrad test can be shown to be far more sensitive than, for example, the triangle test. In practice, this means that far fewer panelists need to be used in this test in order to obtain the same likelihood of detecting a real difference.

Failure to find differences in a detection or discrimination test cannot, of course, be used as evidence that there is actually no difference between samples, as this will depend on the power of the test and the number of participants. There is always some risk of a failure to find a difference that is actually present (a Type-II error). However, in some applications, for example, product claim substantiation, there is a need to make statements about equivalence, and hence there have been developments in methods for such applications (Ennis and Ennis, 2010).

The A–Not-A test, in which the panelist indicates whether a sample is identical to a reference sample ("Is this sample the same as A (the reference) or not?") has also been commonly used (ISO8588, 1987). There is a crucial difference, however, between this test and those mentioned above. In the paired comparison, *n*-AFC, triangle, and tetrad tests, the panelist is told both that there are differences present among the samples and where more than two samples are judged, how many are the same and how many are different. By contrast, the A–not-A test introduces uncertainty about the presence of differences between the samples. The so-called forced choice tests, such as the triangle test, provide information that eliminates uncertainty about differences being present and in effect forces one to choose which sample is different/stronger. The importance of this distinction is covered in the Section Signal Detection Theory.

Signal Detection Theory

Because panelists may differ in how strict or lax they are in deciding whether a stimulus is present or that two stimuli are different, this may introduce a bias in estimating thresholds. This can be understood most easily by considering what is being measured when it is asked about differences or a threshold is tried to be determined. Thresholds are defined in terms of the stimulus – for example, a threshold of 0.01 M NaCl in water – but are based (as noted above) on the proportion of responses reporting presence of, or change in, the stimulus. The key question thus becomes one of how an individual makes a decision regarding the presence or absence of a stimulus (detection) or the occurrence of one type of event over another (discrimination). Green and Swets (1966) proposed that such decisions can best be understood by treating detection as a process determined by a combination of sensitivity to the signal and the tendency of the observer to report the presence of that signal. In their signal detection theory (SDT), they noted that a tendency to report the presence of a 'signal' could be influenced by external factors. These include such things as considering the implications ('payoffs') of reporting or not reporting a signal. As an obvious example, a simple desire to be seen as sensitive in the task being performed could bias a panelist in favor of reporting 'yes' on every trial in which a stimulus could be present in a threshold task. Thus, how often a person says 'yes' to a stimulus must be judged relative to how often they tend to say 'yes' on any trial, including trials on which the signal is absent (called noise trials), that is, the proportion correct must take into account the prevalence of 'false alarms (FA).'

As all detection or discrimination tasks take place in a context in which the presence of a stimulus or a stimulus difference is not obvious – that is, when uncertainty is present – the panelist is relying on how confident they are that a signal has occurred. At this point, even personality traits can be influential, that is, is the panelist a 'risk taker' or perhaps more judicious? If, in addition, there are financial or other consequences, a bias to respond can be present. In a case in which a panelist has to decide whether or not a taint has affected a batch of ice-cream, the decision takes place against a background of deciding what is worse: responding that 'yes' the taint is present and dumping the production run or deciding 'no' and possibly incurring the wrath of consumers. Being unclear about whether the taint is present allows both 'FA' and 'misses' (in addition to 'hits' and 'correct rejections (CR)'), and an imbalance in the consequences may push the decision toward one or the other.

Underpinning SDT is the realization that sensitivity to a stimulus or stimulus difference is not simply a case of 'stimulus absent' at a given stimulus magnitude and 'stimulus present' at some higher magnitude. For Fechner, a threshold stimulus was one that 'lifted the sensation or sensory difference over the threshold of consciousness,' implying a sharp boundary (a step function) between not detectable and detectable. In fact, data collected during threshold or difference tasks form a flattened S-shape curve (known as an ogive). This suggests that signals emerge into awareness gradually, reflecting points on the stimulus continuum during which the panelist is uncertain whether or not the signal has occurred.

One of the major theoretical contributions of SDT was to adopt the idea of signals and noise that were used in engineering contexts. In SDT, all threshold perceptual events consist of signal embedded in noise. The analogy is that of a weak radio signal that is heard against a background hiss or crackle and is hence unclear. In SDT, noise is always present – it can be neural or environmental, including actual noise, unwanted odors, a background or residual taste or flavor, or distracting thoughts. Hence, decisions about whether or not a signal is present are always about detecting the signal in the noise.

The major practical contribution of SDT to sensory science is that the panelist can be presented with simple task: Does this solution contain a salty taste or not? or Which of these two solutions contain the salty taste? As noted above, this allows uncertainty because a signal (saltiness) may or may not be present. This is dealt with in SDT by representing all responses as either noise trials (N; no signal present) or signal+noise trials (S+N; signal present). Both sorts of event over many signal values are represented as normal distributions of responses that overlap (**Figure 2**): the greater the overlap, the harder it is to distinguish S+N from N alone. In other words, it is difficult to detect the presence of the stimulus or stimulus difference. With these two distributions, all responses can be divided into hits (S present – 'yes'), misses (S present – 'no'), FA (S absent – 'yes'), and CR (S absent – 'no'). Critically, this allows the experimenter to separate response bias (lax or strict criterion for indicating a signal) from the unbiased sensitivity for a modality by comparing the correct 'yes' responses (hits) with the tendency to say 'yes' (hits+FA).

This comparison leads to a simple measure of sensitivity known as d' (d-prime), the difference between the means of the S+N and N distributions in standard deviation units. The values of d' range from 0 (complete overlap; signal impossible to detect) to >3 (effectively no overlap; signal easy to detect). Using d' provides an advantage over forced choice tests based on the binomial distribution in that the degree of discriminability is no longer based on proportions of responses, but rather can be given as a numeric value that is constant irrespective of sample size.

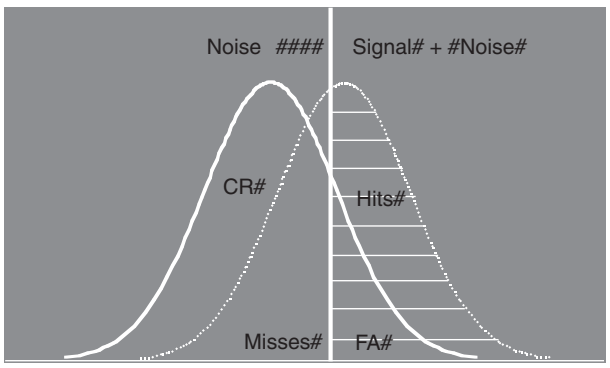


Figure 2 Schematic of overlapping distributions of noise and signal +noise. The difference between the means of these distributions is d', which will increase as the distributions separate, reflecting increased signal discriminability. Overlaid on these distributions are the areas under the curves that represent the proportion of hits, FA, CR for a given criterion, β (shown as the upright). Note that moving the criterion to the left (more liberal in saying 'yes,' a signal is present) or right (more conservative) will alter the relative proportions of these responses types but have no effect on the separation of the distributions themselves. Hits (S present – 'yes'); misses (S present – 'no'); FA (S absent – 'yes'); CR (S absent – 'no').

Of lesser interest in most cases is the fact that SDT approaches also provide a measure of response bias (β) that is independent of sensitivity. This is based on measures of where the panelist places their criterion. Panelists wishing to be seen as maximally sensitive, for example, will respond 'yes' with a lax criterion so that there will be few misses, but at the cost of increasing the number of FA. Alternatively, adopting a stricter or more conservative criterion ("I really want to be sure that the signal is present before I say 'yes'") means that there are few FA, but proportionally more misses. Note that these decisions occur against background of a constant degree of overlap of the distributions and hence a constant sensitivity.

Although SDT provides a strong theoretical framework for understanding of detection and discrimination processes, many sensory practitioners still rely on binomial tables to interpret forced choice results, rather than measuring directly. This is partly due to the need to run large numbers of trials to get stable and accurate estimates of d' and β and partly a result of the lack of training in theoretical psychophysics traditionally received by food scientists. Nevertheless, understanding the basis of SDT is crucial to understanding how humans behave when making decisions. This is reflected in some recent attempts to promote the conversion of proportions of discriminators, as the measure in routine discriminations tests into measures of discriminability such as d' (Jesionka *et al.*, 2014).

Scaling

As discussed in Section Classical Psychophysics, classical psychophysics was also initially concerned with questions of how to measure magnitude. Fechner's solution of measuring JNDs over a wide stimulus range is largely impractical because of the effort involved. Instead, the main approach has been to search for methods of direct scaling. At first glance, scaling seems to be deceptively simple and one is frequently asked to provide a number between 1 and 10 to describe an experience (How painful? and How much effort?). But, a deeper understanding of how numbers are used in scaling becomes crucial depending on the types of information that one is seeking.

The simplest form of measurement is ordinal and is reflected in the straightforward procedure of ranking two or more samples in order of intensity (ISO8587, 2006). This procedure, like any ordinal measurement, provides no information about the intensity of the quality on which the samples are ordered or the size of the differences between them. Ranking is a simple approach to determining whether samples are judged as differing in intensity and entirely appropriate if only this information is required. But, as the number of samples increase, the cognitive demands also rise sharply. Thus, ordering three samples requires only 3 comparisons between these samples, but ordering 10 samples requires 45 such comparisons.

Interval measurement allows statements to be made about degree of difference between those things being measured.

Hence, both Fahrenheit and Celsius temperature scales are interval measures because the difference between 40 and 60 °C is equivalent to the difference between 70 and 90 °C. In sensory evaluation, the most commonly employed scales are considered to have this property. Scales that have equal categories are widely used to measure intensity (see Section Hedonic Ranking and Rating for the most commonly used hedonic category scale). There is no universal standard for number of categories, and 5-, 7-, 9-, 11-, 15-, and 21-point scales are seen. More categories ought, in theory, to provide better discrimination between samples. Some category scales use adjective labels (very strong, moderately strong, etc.), whereas others do not, but it is argued that labels assist the panelist to use the numbers in a consistent way. Sometimes, standards for parts of the scale are provided to insure consistency of use. Thus, in some descriptive analysis methods, trained panels will use 15-point scales (sometimes on which half-point ratings are also allowed), for which prior standards for some or all points/half-points have been established (see Section Descriptive Profiling/Analysis).

Despite the fact that interval scale labels are converted into scores – for example, from 1 (extremely weak) to 7 (extremely strong), the absence of valid zero point means that the data from these scales do not have ratio properties. Hence, one cannot conclude that a product that receives a rating of 6 (very strong) is twice as strong as one that receives a rating of 3 (moderately weak). The data from this type of scale are typically summarized using a mean and analyzed using analysis of variance (ANOVA) despite the fact that there is no guarantee that such data are normally distributed (e.g., Lim *et al.*, 2009).

Scales that remove categories and most of the labels have also been popular. The so-called line scale or visual analog scale (VAS) typically has anchor labels at either end (e.g., extremely weak/extremely strong) and sometimes a center anchor, often unlabeled. There is no consistency in the anchor labels used and to some extent they depend on the range of samples used. Otherwise, as a featureless line, it essentially provides for a much greater spread of ratings than does a category scale. Its proponents argue, therefore, that it offers greater discrimination among multiple samples. There is no evidence that the length of the line is important.

It is obviously of benefit to be able to make statements about the relative magnitude of sample qualities. To express relationships as ratios requires that the scale has a true zero that acts as a reference point for all other values and effectively means a zero amount of whatever is measured. Harvard psychologist Stevens (1956) developed a method known as magnitude estimation (ME) (ISO11056, 1999), which was based on the assumption that one's use of numbers itself exhibits ratio properties. Hence, when asked to name a number twice as great as 25, 50 is the only answer. If these properties are then transferred to sensory qualities and a true zero is used, then ratio measurement ought to be the result. So, as ME is implemented, panelists are asked to attach numbers to sensory qualities in proportion to their perceived magnitude. For example, if sample B is twice as sweet as sample A, the author gives a score for sample B that is twice the score given to sample A. It does not matter what number the author gives to sample A (except that negative numbers are not permitted) as long as all subsequent samples are given numbers that are proportional: half, twice, thrice, and so on. Despite the fact that ME appears intuitive to use, and was a popular method among researchers in the 1960s and 1970s, its use in sensory evaluation generally has been limited. This is almost certainly due to the fact that some period of instruction and practice is needed for its reliable use (Moskowitz, 1977).

A more recent solution to generating data with ratio properties has been the use of the labeled magnitude scale (LMS). This was developed by taste and smell researchers at least partly in response to the problem of ceiling effects in interval scaling (Green *et al.*, 1993). Thus, a series of high-intensity stimuli might all be rated as extremely strong on a category scale, despite intensity differences, so that the ratings are compressed against the 'ceiling' of the scale. With the LMS, the scale's labels are common intensity terms, such as barely detectable, weak, moderate, strong, and very strong, whose position on the scale was determined by ratings of the relative magnitude of the words themselves. The resultant scale provides labels that are quasi-logarithmically spaced. In addition to the label spacing, the top end of the scale also distinguishes the LMS from standard category scales by using the term strongest imaginable (**Figure 3(b)**). Originally, this referred just to the domain of all tastes (if tastants were being rated), but subsequent modifications (Bartoshuk *et al.*, 2004) of the scale have meant that strongest imaginable now more commonly refers to sensations of any kind ever experienced (this is referred to as the general labeled magnitude scale; gLMS).

Again, this scale is, as yet, more accepted by sensory researchers than by practitioners in industry because some training in the scale's use is required, particularly in relation to the meaning of strongest imaginable. Without practice, inexperienced panelists will often place the strongest of a set of samples at or near the top of the LMS, even though on the gLMS, this point is meant to be outside (and more intense than) the samples currently being evaluated.

Time-Intensity Scaling

It has been recognized for some time that not all of the sensory information that is crucial for understanding product perceptions can be captured by a rating of an attribute at a single point in time. The release of flavors from foods happens over time, as do the interactions between the odors, tastes, and tactile properties of the foods. In particular, events such as swallowing can change the balance of the sensory in-mouth experience, as can the effects of temperature in the mouth (e.g., chocolate melting) or chewing. Aftertastes, too, can be the crucial determinant of acceptability of a food. As a result, time-intensity (TI) measures have been employed to reflect changes in sensory attributes that occur once a food or beverage is in the mouth until the demise of the sensations, typically following swallowing (Cliff and Heymann, 1993). Typically, via either repeated discrete ratings of an attribute at set intervals (e.g., every 5 s) or continuous ratings using a computer-interfaced device, such as a mouse, TI information is used to generate a curve of intensity across time (often a few minutes) (**Figure 4**). Although there is no consensus on the question of which measures extracted from these TI curves best predict consumer preferences, common parameters include

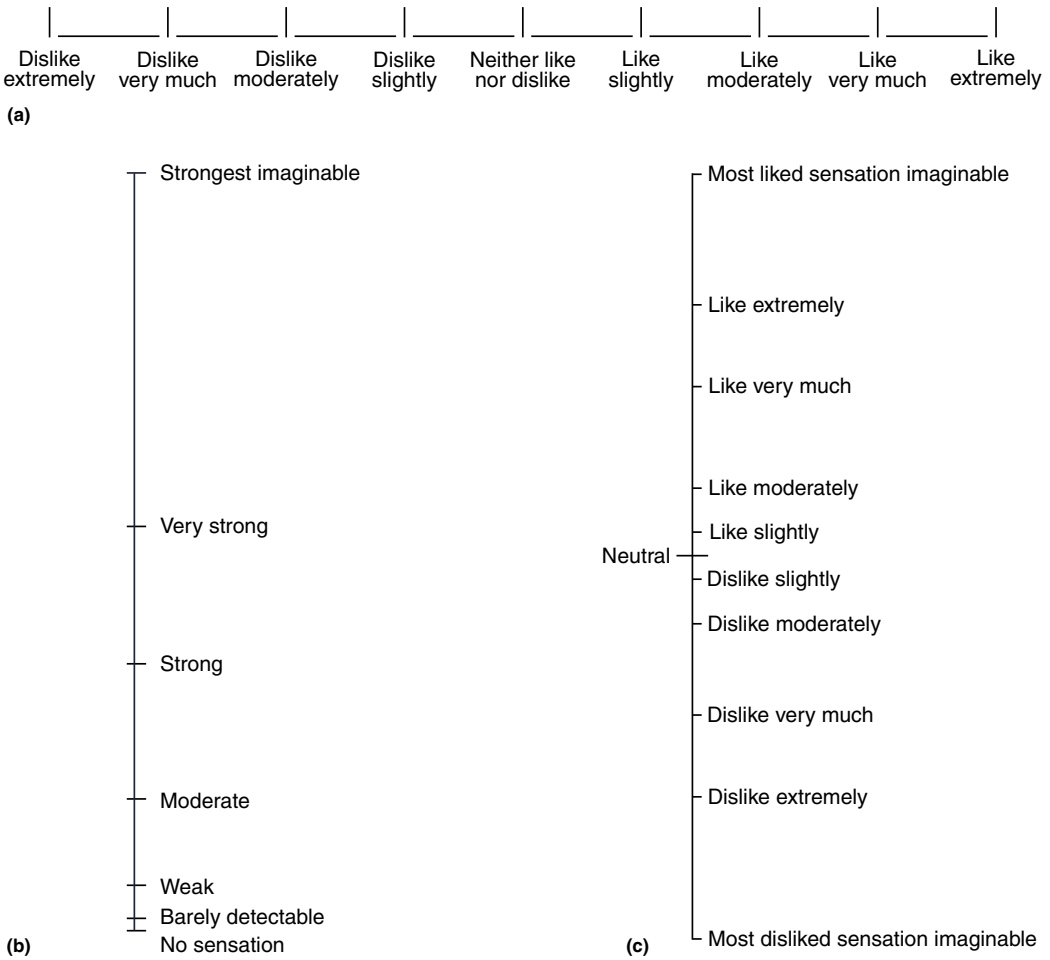


Figure 3 Intensity and hedonic scales. (a) The nine-point hedonic category scale. (b) The LMS. (c) The LHS.

maximum intensity, time to maximum intensity, total duration, rate of decline in intensity, and overall intensity (area under the curve). Also in use – but less widely than TI methods – are methods that directly assess the hedonic consequences of the time-course of sensory experience by measuring liking during the course of food consumption (Kremer *et al.*, 2013; Veldhuizen *et al.*, 2006).

Although providing valuable information, traditional TI methods are limited. The primary issue is that foods and beverages are inherently multisensory, whereas TI methods are typically useful for measuring only one of two attributes at a time. This means that a complete evaluation of a single complex product may take many sessions to complete. Moreover, TI methods do not provide any measure of the relative importance to the product experience of the attributes themselves.

In response to these drawbacks, several approaches have been used, including multiattribute TI (MATI) and temporal dominance of sensations (TDS) methods. In MATI, participants make ratings for multiple sensations repeatedly at discrete, fixed intervals, typically 15 or 30 s (e.g., Green and Hayes, 2003; Prescott and Stevenson, 1995). This approach

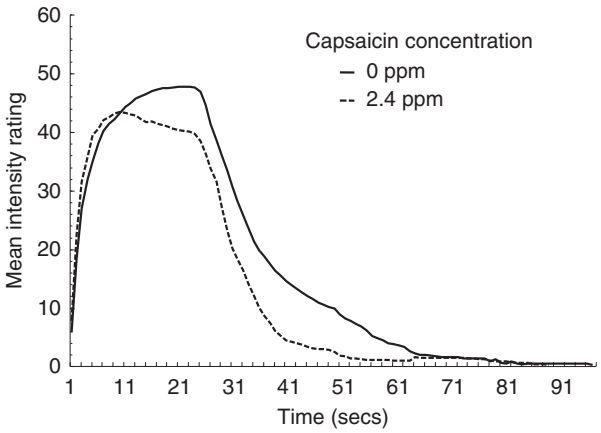


Figure 4 A tTI graph showing the impact of adding the pungent compound capsaicin to apple puree on ratings of apple flavor over time. Note that many of the effects are only evident at time periods that would not be captured by ratings made at a single time point. Of relevance also is the fact that these data were collected over two sessions, a limitation of traditional TI methods when compared with more recent techniques such as TDS (Prescott and Francis, 1997).

allows the sensory specialist to compare the relative intensity of different sensations with one another within a single test session. However, with a significant number of attributes, the temporal resolution may still be too coarse for the phenomenon of interest. Additionally, there is some evidence that participants may smear their ratings across multiple attributes (e.g., Bennett and Hayes, 2012). As an alternative, the TDS method was developed as a means of measuring the relative dominance (salience) of multiple sensory attributes over the duration of a single tasting/consumption session (Pineau *et al.*, 2009). The TDS method also allows for each sensation to be rated for intensity because it recognizes that an attribute may be dominant in other ways – for example, unusual, attention grabbing – rather than solely by its high relative intensity. The method presents all attributes (although a maximum of approximately 10 within each session is recognized) on a computer screen and the panelist is able to select, over the time-course of the sensation, which sensory attribute is dominant at that particular time point. Deciding that, overall, a particular attribute is dominant at a particular point (e.g., 5 s after swallowing) is based on calculating the proportion of times (taken over panelists and any replications) for which the given attribute was assessed as dominant at that point.

It has been recognized that TDS shares many similarities with conventional sensory profiling/descriptive analysis (see Section Descriptive Profiling/Analysis). Comparisons between the two methods have found that the methods tend to produce similar profiles, with those sensations that are dominant in TDS also being given high-intensity ratings in descriptive approaches (Dinnella *et al.*, 2012; Labbe *et al.*, 2009).

Descriptive Profiling/Analysis

Products can be defined in terms of a recipe of ingredients, but this is seldom adequate to reflect accurately the perceptions the product produces. Describing and measuring sensory attributes is a major activity within the food and other consumer goods industries as a way of understanding how product attributes influence preferences. The ultimate goal of such descriptive analysis is to generate quantitative profiles of a product or a series of products. Because instruments are not able to measure perceptions, this process involves using humans as sensors. Descriptive analysis may initially appear similar to focus group methods used in market research, but they are fundamentally different in that a large amount of effort is put into aligning and calibrating the language and the measurements that panelists use for consistency and precision. Also, once panelists undergo the calibration process, they are no longer considered representative of naive consumers, both because they use an analytic mindset and because they have been trained to attend to attributes of which naive consumers might be unaware. The dogma of the field holds that trained panelists should not be asked for affective or acceptability ratings (in contrast to the commodity-judging approaches mentioned in Section Issues of Good Sensory Practice). Accordingly, the phrase 'trained panels' is often used as shorthand to distinguish these individuals from other sensory methods. Finally, unlike focus groups that require the transcripts to be coded to identify qualitative themes, the data generated from descriptive profiling are inherently quantitative in nature.

Early approaches to profiling products quantitatively include the Flavor Profile® and the Texture Profile® developed, respectively, by Caul, Sjostrom, and Cairncross in the 1950s and by Szczesniak, Civille, and Liska in the 1960s. These approaches are not commonly used today, so they will not be discussed further. Interested, readers should see Lawless and Heymann (2010) and Moskowitz *et al.* (2003) for more information. By the end of the 1970s, two major methods had emerged to generate descriptive profiles: Spectrum Descriptive Analysis® and Quantitative Descriptive Analysis™. In spite of some key methodological and philosophical differences, these approaches are broadly similar in that both involve three key steps: (1) panelist training and lexicon development, (2) measurement of panelist reliability and calibration, and (3) evaluation of the test samples.

There is general agreement that a trained panel should consist of 8–12 motivated individuals who can be regularly and consistently available – panel training is typically intensive and can take months to achieve acceptable levels of performance (ISO13299, 2003). Some 'online' quality control panels use fewer members, but these panels are generally restricted to assessing a limited set of identical products (Munoz, 2002). The individuals are screened to exclude those with poor discriminative ability or lacking in verbal skills. This is commonly done using tests for ability to tell odor and taste qualities apart and to elicit a reasonable degree of descriptive ability for the qualities of the types of products being tested. Other exclusion criteria include ill health, especially if it affects the senses of taste and smell, smoking, and inadequate dentition. Age is not necessarily a key factor if other criteria are met (ISO8586, 2012).

Semantic error – assuming all participants attach the same meaning to the same word – can be a major source of variance if explicit steps are not taken to minimize it. For example, although most untrained consumers can probably rate 'sweetness' or 'bitterness,' they probably lack consensus on what is meant by 'creaminess' – it may be exclusively a textural attribute for some individuals, whereas for others, this term encompasses both mouthfeel and an olfactory dairy note. Accordingly, in both Spectrum and quantitative descriptive analysis (QDA), a large amount of emphasis is placed on concept formation and alignment among the participants during the initial training phase. This may be a top-down process, where the panel leader provides a list of descriptors, with definitions and physical references, as is done in the Spectrum method, or it may emerge from the group during the generation of a consensus, as occurs in the QDA method. Irrespective of which approach is used, the act of concept alignment is based on the psychological processes of abstraction and generalization, in which an individual learns to extract salient commonalities from a set of stimuli and then apply those abstractions to new stimuli.

In developing a lexicon, selecting appropriate terms (descriptors) is critical, as the panel leader must consider not only how the panelist perceives the product but also how they transmit this information. Lawless and Heymann (2010) identified criteria for selecting good descriptors: (1) they discriminate among products; (2) they are nonredundant

(i.e., little to no overlap); (3) they are simple, singular, and atomistic (i.e., not a combination of several other attributes); (4) there is consensus about their meaning; (5) they are unambiguous and easily recognizable in products; (6) they have communication value (i.e., not jargon and simply defined); (7) they relate to consumer acceptance/rejection; and (8) they relate to physical variables or instrumental measures. The use of physical references in the form of samples varying quantitatively and qualitatively is highly recommended, as they help a participant to decide what is or is not included within a concept. This is important when a concept has a poorly defined boundary. Also, use of reference stimuli helps to align concepts across panelists to ensure that they are using the same semantic label for the same underlying percept. For example, does the attribute lemon odor reflect the odor of lemonade, lemon juice, lemon peel, or artificial lemon flavoring?

A crucial aspect of all modern descriptive analysis techniques is training to achieve alignment between panelists of measurements of sensory qualities. In effect, this means that panelists learn to agree that a particular level of an attribute represents a particular value on the rating scale being used. So, even though all panelists may discriminate well between the samples/products being evaluated, at least initially they may use different parts of the scale in their ratings. To facilitate agreement between panelists on which parts of the scale to use, the panel trainer can provide reference samples to represent the scale extremes plus some intermediate points. However, there are also published references for scale values, especially in the evaluation of textural properties (e.g., Munoz, 1986).

The second step in descriptive profiling is to evaluate the reliability of the individual judges and the group as a whole (ISO11132, 2012). This is done by presenting actual products (not references) to panelists as if they are evaluating the final product. The sensory specialist can then analyze the data to see if all panelists are in agreement across multiple products. This process may identify problematic terms that require targeted retraining for the group as whole or it may identify a specific panelist who needs retraining to better align with the group. Traditionally, the sensory specialist would perform such analyses offline and debrief panelists at a later time. However, recent advances in computerized data collection and panelist training now allow the sensory specialist to provide immediate feedback to panelists (e.g., Findlay *et al.*, 2007). Use of instant feedback via software reportedly increases the salience of the feedback and decreases panel training time (Findlay *et al.*, 2006). Sophisticated statistical toolkits (e.g., *Panel Check*; *SensoMineR*) for measuring panel performance are also available as freeware.

The final step in descriptive profiling is to evaluate the product set of interest. Standard best practices – for example, blind presentation, appropriate portion sizes, counterbalanced presentation order, etc. – should be used (see Section Issues of Good Sensory Practice). Products are typically tested in at least triplicate to ensure a sufficient number of data points per attribute per product (i.e., 12 panelists × 3 replicates = 36 observations). Data are then analyzed via ANOVA to account for remaining panelist variability, and significant differences across products within attributes are tabulated or summarized graphically.

Descriptive analyses can produce product profiles consisting of tens of different sensory attributes. There is no guarantee either that all of these attributes are independent from one another or that they are equally important in discriminating the products. A common way of dealing with these issues is by determining the underlying dimensions of the sensory data using a technique such as principal components analysis (PCA; a type of factor analysis). The PCA summarizes the dataset by extracting a smaller number of independent dimensions (ideally, 2 or 3 that explain a high proportion of the variance in the data) than the number of attributes that are being measured. These dimensions (principal components; PCs) are linear combinations of correlated attributes. For example, measuring a set of attributes for desserts might produce a PC that is a combination of the ratings of vanilla odor, viscosity, and mouth coating. The PCA then correlates the original set of attributes with the dimensions as a way of describing what the dimension represents. So, each of these attributes will have high factor loading on PC1 (the component that explains the highest proportion of the data variance), a reasonable interpretation of which is that it represents creaminess.

Affective Consumer Methods

Ultimately, irrespective of the product, the aim of sensory science in an industrial context is most often to insure that consumer preferences are met. Although to some extent consumer sensory evaluation techniques emerged from those methods used to judge commodities such as wines and cheeses, they differ from these in that it is implicit within sensory evaluation that the best product is whatever the consumer says it is, rather than what an expert says is best. Although consumer evaluations are thought to measure liking, it is important to be aware that even though terms such as acceptability and preference are often used synonymously with liking, there can be subtle but important differences. For instance, are Brussels sprouts preferred to spinach? It may be easy enough to respond to this question, but the answer does not tell one the extent to which either vegetable is actually liked. Similarly, an individual may say that beer is a 'liked' beverage overall, but they only find it acceptable within specified contexts (e.g., not at 8 a.m.). As with any tool, appropriate usage is determined by the question being asked.

Interpretation of consumer data also requires an understanding of the nature of consumers' responses, how these are shaped by the test being administered, and what constraints are inherent in the method. It is a truism that consumer responses are subjective in nature. Scientists used to making measurements instrumentally rather than behaviorally often find this troubling. Specifically, 'subjectivity' becomes equated with variability, unreliability, and lack of veracity (see Section Individual Differences).

The practical way of dealing with variability in consumer data is to make sure that the test being used has sufficient power to detect differences between products. Although power is partly a function of the test itself and the size of any differences between products, sufficient power in consumer tests is typically established by using an appropriately large sample

of consumers. Certainly, if very large numbers of consumers are required to show differences between products, then the products are more likely to be equally liked for all practical purposes. A figure of 100 consumers is sometimes given as a realistic minimum. Although no single figure has universal validity, an analysis of the standard error of a set of similar studies, using conventional Type-I and -II error rates, gave an estimation of a sample size of 112 (Hough *et al.*, 2006). However, any subdivision of a sample of this size in terms of age, sex, etc. will rapidly diminish the power of the evaluation to show product differences (see Section How Many Participants?).

The variability of consumer data is often cited as one reason why consumers should not be used to generate product ratings of the sensory characteristics of products, as trained panels do (see Section Descriptive Profiling/Analysis). This problem can be exacerbated by potentially additional variability arising variations in understanding the meaning of sensory characteristics. Although it probably requires no training for consumers to be consistent about the meaning of sweetness or saltiness, the majority of sensory characteristics – and especially those related to texture – involve the learning of specific definitions of terms and concept alignment among participants. For example, an attribute such as 'creamy' has both a textural and an olfactory component, and consumers may differentially attend to each of these aspects when asked to rate 'creaminess.'

One way of looking at consumer perceptions is that they are both hedonic and global. Like one's own responses to food at mealtimes, consumer responses are typically not highly analytical, but rather a response to the whole flavor and the pleasure that it evokes. This is, of course, in contrast to how trained panelists in descriptive analysis respond, because their training involves a reliance on being analytical as well as treating the product as a collection of attributes, rather than as a whole flavor or food. Recently, it has been demonstrated that these contrasting styles of responding to products have measurable consequences. Inducing an analytical frame of mind in consumers during a product evaluation by simply listing a set of sensory attributes to be rated reduced the magnitude of an overall liking rating that was completed first (Prescott *et al.*, 2011).

All human measurement, unless guided by explicit points of reference in a defined context (which is what panel training hopes to achieve), is relative. One does not know, for example, whether an 18 °C day is cool or warm unless they know the season and the location. The situation is no different with consumer assessments of liking – they are always comparative. In the relatively rare situation, for example, that a single product was rated for liking, one would expect that the point of comparison was the consumer's prior experiences with that class of product (Walter and Boakes, 2009). In the more usual situation in which multiple products are compared within the same evaluation session, the products are compared relative to one another. One consequence of the influence of context in ratings is that a given product can be given a low or a high liking rating entirely as a function of what other products are in the evaluation (Schifferstein, 1995). Recent work suggests that the effects may be more subtle than simply being within a high or low context, as biased responses can also occur as a function of similarity to other products within the set (Hayes *et al.*, 2011a,b).

It is crucial to understand the implications of context effects if consumer data are not to be misused. Many companies have in the past, and to a lesser extent still today, relied on a fixed acceptability criterion. For example, on the standard 9-point hedonic scale (9PS) (see below), a mean rating of 7 in consumer testing may be required to launch the product. Because any given number on the rating scale can only be really understood in relation to the ratings given to other products, there is no validity to adopting such a value. Ironically, dogmatic reliance on such cutoff values is a key reason why there is resistance in industry to adopting new approaches to measurement.

Hedonic Ranking and Rating

Simple questions of preference – do I like version 1 or version 2 of a product most? – can be answered easily using paired preference (2 samples) or ranking (>2 samples) procedures. Like ranking based on intensity (see Section Scaling), these provide nonparametric ordinal data, which do not allow any inferences about the relative magnitude of liking, that is, degree of difference between the samples.

Hedonic scaling has adopted similar approaches to that of intensity scaling, using both multiple category and line (VAS) scales, the latter with endpoint descriptors (e.g., 'dislike very much'; 'like very much') only. The oldest and still most popular method of determining degree of liking is the 9PS developed by the well-known psychologist L.L. Thurstone, in the 1950s, for the use by the US Army at the Quartermaster Food and Container Institute in Chicago (Jones *et al.*, 1955). The scale, shown in **Figure 3(a)**, uses nine labeled categories. The developmental work by Thurstone and colleagues aimed to find labels that were judged as psychologically equidistant from one another. Hence, the degree of difference (or interval) between like moderately and like slightly is meant to be approximately the same as the distance between neither like nor dislike and like slightly. As noted earlier in relation to intensity scales, the absence of valid zero point in interval scales means that the scale does not have ratio properties, so one cannot conclude that a product that receives a rating of 8 (like very much) is twice as liked as one that receives a rating of 4 (slightly dislike). The fact of this scale's widespread and long-standing use in industry has generated considerable inertia in terms of resistance to adopting other scales that perhaps have advantages (Lim, 2011).

Most recently, scales that seek to emulate the apparent ratio properties of the labeled magnitude scale (LMS) of intensity (see Section Scaling) have been developed (Lim *et al.*, 2009; Schutz and Cardello, 2001). In principal, such ratio scales (**Figure 3(c)**) should allow statements about the relative degree of liking. Moreover, the fact that the data appear to be normally distributed removes objections about the use of parametric statistics for analysis. Lim *et al.* (2009) compared the labeled hedonic scale (LHS) with the 9PS, showing that for a range of products, the LHS data were normally distributed, whereas those of the 9PS were not. With products that were highly liked, the 9PS showed ceiling effects, with responses compressed at the upper scale end. When equated for scale

length, the LHS also gave a greater range of ratings for the same set of products, hence potentially improving hedonic discriminability. However, the LHS shares with its LMS cousin potential drawbacks in terms of ease of use. The first of these is the need to explain to consumers the meaning of the end labels most liked/disliked sensation imaginable and to firmly locate the context as all sensations and not just the category (e.g., sweet foods) being evaluated. A related issue is the need to include some form of practice using nonfood examples (e.g., 'most enjoyable film'), allowing both a check of the consumer's understanding of the scale and a measure that will allow a check against idiosyncratic scale usage. Whether or not these potential drawbacks will influence the uptake of the scale is still to be determined.

Special Populations

The rapid growth of the market for food aimed specifically at children has necessitated the development of hedonic methods that can be employed when the consumer has limited linguistic or cognitive skills. Even at a very young age, children's food preferences and choices are greatly influenced by what their peers eat (Birch, 1980), meaning that parental assessments of children's preferences are unlikely to be accurate once the child reaches (pre)school. There have been two general approaches to this problem (Chen *et al.*, 1996; Popper and Kroll, 2005). The first of these is to use ranking or rating procedures modified to fit the presumed cognitive sophistication of the child. This is usually accompanied by labels such as best, worst (ranking), or various versions of easily understandable hedonic terms such as really/super good, good, bad, 'OK,' and really/super bad attached to category scales. A presumption is that the younger the child, the fewer the categories that should be employed. Very young children are sometimes tested by making the procedures into a game, for example, by placing a ball into a 'bad' bucket if a sample is disliked or into a 'good' bucket if it is liked (e.g., Turnbull and Matisoo-Smith, 2002). An alternative approach has been to use emotional expressions as indicators of liking. This can mean either interpreting facial expressions while infants are sampling foods (e.g., Forestell and Mennella, 2007) or using the so-called smiley face scales, in which degrees of liking are represented as categories by depictions of facial expressions. The benefits of this latter approach are that no language skills are required. However, there are concerns about the extent to which facial expression can adequately discriminate subtle degrees of liking.

Globalization of the food industry in recent decades has created a demand for understanding consumer preferences cross-culturally. However, understanding food choice/preference in other cultures presents particular problems. There are a variety of issues here, including not only language barriers but also trying to understand both appropriate food types and flavors and food-related values and consumption habits that are culturally determined (Prescott, 1998; Prescott *et al.*, 2002). In terms of methods, given the ubiquity of the 9PS in industrial applications in the US and some other Western countries, cross-cultural studies have focused to some extent on the development of equivalent versions for other cultures (Chung and Han, 2013; Curia *et al.*, 2001; Daroub *et al.*, 2010). The use of hedonic scales, particularly those with multiple labeled categories, presents complex issues of translation. For example, a scale label such as 'like extremely' may be entirely inappropriate when dealing with food generally or specific types of foods. The degree of discrimination implied by the use of nine distinct categories also cannot be assumed. Consideration, too, needs to be given to scale-usage issues. Expressions of emotion, especially in public settings, may be modified by cultural norms. Such norms may underlie findings that consumers in some Asian countries (China, Korea, Japan, and Thailand) used fewer categories of the 9PS in ratings of the same samples than Americans did, often avoiding the emotionally intense end categories (Yao *et al.*, 2003; Yeh *et al.*, 1998). Overall, the same problems that beset the use of hedonic scales as predictors of food choices (see Section Hedonic Measurement: Limitations and New Approaches) are magnified when attempting to interpret their output for other cultures. Likewise, even within a common language, cultural differences may confound interpretation of hedonic labels. A not unreasonable translation of 'actually quite good' in British English is in American English, 'totally awesome!'

Consumers as Discriminators

It is generally believed that consumers are relatively insensitive to the presence of, or variations in, sensory qualities, at least when compared with trained panelists. This is often true. As a result, there has been a reluctance to use consumers to undertake discrimination tests. This practice, however, relies on two assumptions that are increasingly being tested. The first of these is that high levels of sensitivity to product variations or differences is always better. However, consumers may be entirely appropriate to use when making judgments about what other consumer might perceive in products. In some cases, there may be situations in which the judgment of a trained panel overestimates the effect of, for example, ingredient changes or the presence of taints or off-flavors on consumer preferences – perhaps with economic consequences. An appreciation that this might be happening in the wine industry with rejection of wines that had become contaminated with cork taint (trichloranisol; TCA) by highly sensitive trained panels led to the development of a technique known as the consumer rejection threshold (cRT; also referred to as the rejection threshold) (Prescott *et al.*, 2005). This technique was developed using presentation of pairs of wines that are identical except for the addition of increasing amounts of TCA. The consumers were asked simply to taste both wines and indicate which they preferred. The cRT reflected the point (that is, the TCA concentration) at which the wine without the added TCA became consistently preferred. This study produced a threshold value that was considerably higher than the detection threshold values commonly provided by trained panels, the implication being that batches of wine were being unnecessarily rejected for low levels of TCA, even though the (untrained/typical) wine drinker would find them quite acceptable.

The second assumption in relation to the discriminative abilities of consumers that is currently being challenged is the idea that an emotional response – typically, liking or

disliking – is necessarily at odds with perceptual sensitivity. A technique known as the Authenticity Test has shown that when judgments are based firmly in a strong emotional context, they can be highly sensitive. The approach, first reported by Köster (Mojet and Koster, 1986) and since then replicated in a variety of contexts (Boutrolle *et al.*, 2009; Chae *et al.*, 2010; Frandsen *et al.*, 2007), has demonstrated that consumers are highly sensitive to product variations when they are first emotionally primed. In the Authenticity Test, as the name suggests, this takes the form of a story about products with which the consumers have high involvement. The story typically sets up a contrast between the 'authentic' version of their product (essentially a standard) and another version that the consumer is told is to be made from inferior materials, is a foreign import, or is made by nontraditional means. In fact, this comparison product is simply different in some way (e.g., another brand).

The explanation for the increased sensitivity of consumers in such contexts runs contrary to predominant beliefs about perception and effective decision making – namely, that it is optimized by a rational, disinterested, and above all nonemotional approach. In fact, there is increasing indication that an overly analytical approach may actually impair decision making (Halberstadt and Hooton, 2008). The explanation for the sensitivity of the Authenticity Test may also be linked to what social psychologists refer to as the Mood As Information hypothesis. It is suggested that people interpret their emotions and make judgments based on those interpretations (e.g., Schwarz and Clore, 1983). This allows misattribution of current emotion to the object of any decision making. In particular, negative emotions can act as threat signals that provoke cognitive effort to search for causes of the emotion. In the case of product evaluations, a mindset of Something's wrong with my product! What is it?! leads to increased attention to details. Hence, emotion produces increased analysis and consequently increased discriminatory power.

Hedonic Measurement: Limitations and New Approaches

Despite widespread consumer testing by the food industry over many decades, the results of such tests have had very limited success in predicting which few products, out of the thousands released each year, will succeed. Hedonic ratings of different prototypes coming out of product development will, if done properly, eliminate those versions whose flavors are either too weird to succeed or just too unpalatable. Beyond this, however, ratings on hedonic scales are seldom good predictors of food choices or consumption (Levy and Koster, 1999; Tuorila *et al.*, 2008). Partly, this is a function of food choice being influenced by very many external factors not captured by a scale of liking for a food's sensory properties. Moreover, there are a variety of factors to consider that make hedonic testing a complex process. This list includes (1) whether products should be tested branded or unbranded and should they be tested in a central location, in the home, or other situations in which the product is consumed; (2) can a judgment based on a 10-ml sample reflect one that might occur following the amount usually consumed; and (3) does testing several versions of a product, as is commonly done, produce the same response as when a consumer selects and consumes one version on which a decision is made. To some extent, in each of these examples, experimental control versus ecological validity is balanced but unfortunately, there is no simple way to address any of these issues. Or put it another way, the answer is 'it depends' as a function of the specific goals of the project.

One approach to address the limitations of simple judgments of likes and dislikes has been to tap into consumer emotions in more extensive and elaborate ways. It is recognized that foods are consumed not just for the sake of sensory pleasure but also for potentially quite complex effects on other emotions and attitudes. One clear example is the concept of 'comfort food.' Research into accessing a more complete picture of emotions associated with products is in its early days, and it is safe to say that there is, as yet, no standard way of doing this. Although emotion checklists and questionnaire have a long history in clinical psychology and psychiatry, such methods are of limited value in sensory evaluation because they are meant to tap into pathological, largely negative, emotions such as anxiety and depression. More recently, several new questionnaires have been developed that balance the positive and negative emotions. For example, the EsSense™ Profile employs 39 emotional terms and asks consumers to read a food name and then rate how the food makes them feel on a 5-point intensity scale (King and Meiselman, 2010). Studies using this scale have established that different patterns and intensity of emotions discriminate both between product names and the taste of those products, including between different versions of similar products – for example, milk and dark chocolate (Cardello *et al.*, 2012).

Consistent with psychological concepts of emotions as both expressive and physiological states, attempts have been made to automatically code for facial expressions and to measure indices of autonomic nervous system activity. One recent study combined both approaches in eliciting responses from both adults and children to the sight, smell, or taste of liked and disliked foods (de Wijk *et al.*, 2012). Initial responses to the sight of the disliked foods were evident in both skin conductance (a measure of sweat gland activity indicative of autonomic nervous system arousal) and increased frequency of facial expressions typically associated with sadness, disgust, and anger. Finger temperature was also lower for disliked foods. Beyond these findings, however, there was little indication that these measures (including heart rate) could be used to consistently differentiate liked from disliked foods. Interpreting physiological measures, in particular, is problematical. What exactly, for example, does arousal in response to a disliked food mean? What sort of arousal is it – the kind associated with anger or the kind associated with excitement? For example, a hot chili may cause the same physiological arousal in two individuals, one of whom enjoys this state, whereas the other does not.

All measures of emotions – whether mood checklist or physiological indices – carry the same general limitations. First, there is not yet an agreed on set of emotions or emotional terms for use in all circumstances. Second, emotions and their expressions are both well known to be context and culture dependent (see classic experiment by Schachter and Singer, 1962). Nevertheless, this may be a potentially fertile

area for further basic research, which may, in turn, lead to methods that can be applied in industry.

Yet another approach in the search for better predictors of consumer preferences has been to adopt measures that do not require explicit ratings by the consumer. Eye-movement tracking has been used to identify the visual features of products and their packaging that are important. For example, a recent study measured fixation time for the features for jam jars that varied in shape, texture, and label type (Piqueras-Fiszman *et al.*, 2013) and found that the presence of a picture on the label, together with certain textural features, was associated with an increased willingness to buy. Another method that shows potential is the implicit association test (IAT). Borrowed from social psychology, where this has been employed to study implicit attitudes, the IAT allows assessment of the congruency of particular semantic associations with product characteristics. This method, therefore, provides a way of uncovering product perceptions that are perhaps difficult to show using methods that require explicit statements of associations. The IAT is derived from findings that it takes longer to react to pairings of information (such as a brand and a label) that are incongruent than it does to congruent pairings. A study of mouthwashes using the IAT, for example, was able to show that one brand was primarily associated with the word 'powerful,' whereas a competitor was associated with the word 'gentle' (Parise and Spence, 2012). The IAT may prove useful studying, for instance, the compatibility of sensory characteristics with brands or brand images.

Consumer Profiling

Integrating sensory information derived from trained panels and consumer information statistically is a common approach to understanding sensory factors underlying preferences (see Section Combining Consumer and Descriptive Data). Nevertheless, there is growth in other approaches in which consumers alone directly assess a range of products. One method, identified with Moskowitz (e.g., Moskowitz, 2001), utilizes the consumer at the product development stage, asking them to evaluate product prototypes that vary systematically on one or more ingredient dimensions. This approach uses factorial designs such that the ingredients vary independently of one another. So, for example, a prototype orange juice might vary over four concentrations of sucrose, three concentrations of citric acid, and four concentrations of orange flavor, giving a total of 48 prototypes to evaluate. This allows for not only the impact of each of the variables (sugar, citric acid, and orange flavor) to be evaluated but also the interactions between them. The burden of evaluating a large number of samples can be relieved by using incomplete designs in which consumers evaluate overlapping subset of the total number of samples (ISO29842, 2011). An advantage of this method is that regression equations can be used to link the values of the variables to consumer acceptability so that linear or quadratic relationships can point the way toward levels of the ingredients that optimize acceptability (or whatever measure is used). Additionally, the method can be used to study variations in production processes or the impact of changing/substituting ingredients.

'Diagnostic' scales

It is possible to collect reformulation guidance directly from consumers using 'Just-about-right' (JAR) scaling. JAR scales are bipolar, with semantic anchors at each end; instead of rating intensity or liking, participants are asked to report how much of an attribute is relative to their personal hedonic ideal. The midpoint is labeled 'JAR,' indicating the attribute is at an appropriate level, whereas the ends are some variation on too strong or too weak. Most researchers use five categories (e.g., 'much too small,' 'somewhat too small,' 'JAR,' 'somewhat too big,' and 'much too big'), although it is also possible to use continuous line scales with suitable end anchors (Rothman and Parker, 2009). JAR scales are popular for optimization because they are very rapid and generate data that appear easy to interpret. For example, if a majority of participants indicate that a fruit punch sample is 'somewhat too sweet' or 'much too sweet,' it is clear that it should be reformulated by reducing the sugar level.

Nonetheless, several caveats need to be considered when using JAR scales. First, the word usage and concept alignment issues raised in Section Descriptive Profiling/Analysis also apply to JAR scales: naive consumers can probably assess and diagnose simple attributes like sweetness or sourness while they may struggle with more complex descriptors. For example, if the group indicates a product is too astringent, are they referring to drying sensations or puckering sensations? Just because a group of consumers can generate data for an attribute does not mean that they are all using the term in the same way or that the data are meaningful. Second, JAR scales may be influenced by desirability biases. Consumers may indicate that a cookie always needs more chocolate chips, even if adding more would result in a cookie that simply falls apart and is messy to eat and too chocolatey. Finally, consumer recommendations may negatively influence other, unmeasured attributes if the relevant ingredient contributes to multiple aspects of the flavor profile. For example, adding more oregano to the pizza may not only improve the aroma intensity but also add undesirable bitterness. Accordingly, caution and professional judgment are needed to successfully interpret JAR data: the consumer is not always right.

Sorting, napping, and check all that apply

One of the recognized limitations of profiling of products by trained, analytical panels is that trained assessors may describe products using attributes that are irrelevant for consumers and that have an uncertain relationship with product preferences. Unfortunately, although consumers frequently have the ability to distinguish between samples, they do so without being able to provide a clear semantic label to describe the qualitative differences between them. Additionally, consumers may use words to describe samples that have vague, or multiple, meanings that may be dependent on the individual's prior experience with the product class. In some cases, English may inherently lack sufficient precision to describe the differences, resulting in awkward questions like "Is it too spicy hot or too hot?" whereas a Spanish speaker might ask "Is it too *picante* or too *caliente*?"

A range of techniques known as perceptual mapping based on sorting of samples can provide easy-to-interpret visual maps of perceptual spaces and products or stimuli within

those spaces. These maps are based on perceived similarities between samples, as determined by the participants, and unlike trained descriptive panels, the participant is not constrained to a specific set of *a priori* descriptors. Rather, the consensus space is based solely on reducing the stress for some measure of similarity (or dissimilarity) across stimuli using multivariate statistical methods.

Early mapping approaches used multidimensional scaling (MDS) to reduce similarity/dissimilarity matrices built from pairwise comparisons using semantic differential scales into visual maps (e.g., Schiffman *et al.*, 1979, 1980). However, such approaches were extremely labor intensive as the number of comparisons required rises rapidly with the number of samples involved. Subsequently, more efficient shortcuts like sorting greatly increased the utility of mapping techniques. In sorting-based MDS, participants need not make all of the possible comparisons; rather they simply group the stimuli into as many or as few groups as they need to organize the stimuli according to their own criteria. This also allows perceptual mapping to be used with highly fatiguing stimuli like odors or cheeses (Lawless and Glatter, 1990; Lawless *et al.*, 1995). The interpretability of perceptual maps can be further increased by adding a second step in the data collection process. Once participants have formed their groups, they can be asked to provide attributes (descriptors) for their groups. Mean data from frequency counts or attribute ratings for the most common descriptors can then be regressed into the perceptual maps. The resultant map thus contains both points for the individual stimuli as well as vectors for the relevant descriptors (**Figure 5**).

As an alternative to sorting-based MDS, a technique known as projective mapping or napping has been developed (Pagès, 2005). Although the participant task and the multivariate analysis are slightly different to sorting, the general goal is the same. The participant is provided a large two-dimensional (2-D) space (a *nappe*, French for tablecloth), and using their own criteria they are instructed to put similar items close together, with less similar items placed farther away. The x–y coordinates of the individual stimuli in this space are then reduced to a consensus perceptual map using multifactor analysis (MFA). Characteristics of the groups as generated by participants can be included as attributes and counts of descriptors can act as data that can be regressed into the space. This technique has been used with a variety of products, including apples, cheeses, citric juices, chocolates, and wine (Bershaw and Heymann, 2010; Kennedy and Heymann, 2009; Nestrud and Lawless, 2008, 2010). Notably, use of a 2-D space to collect data from participants does not restrict the solution

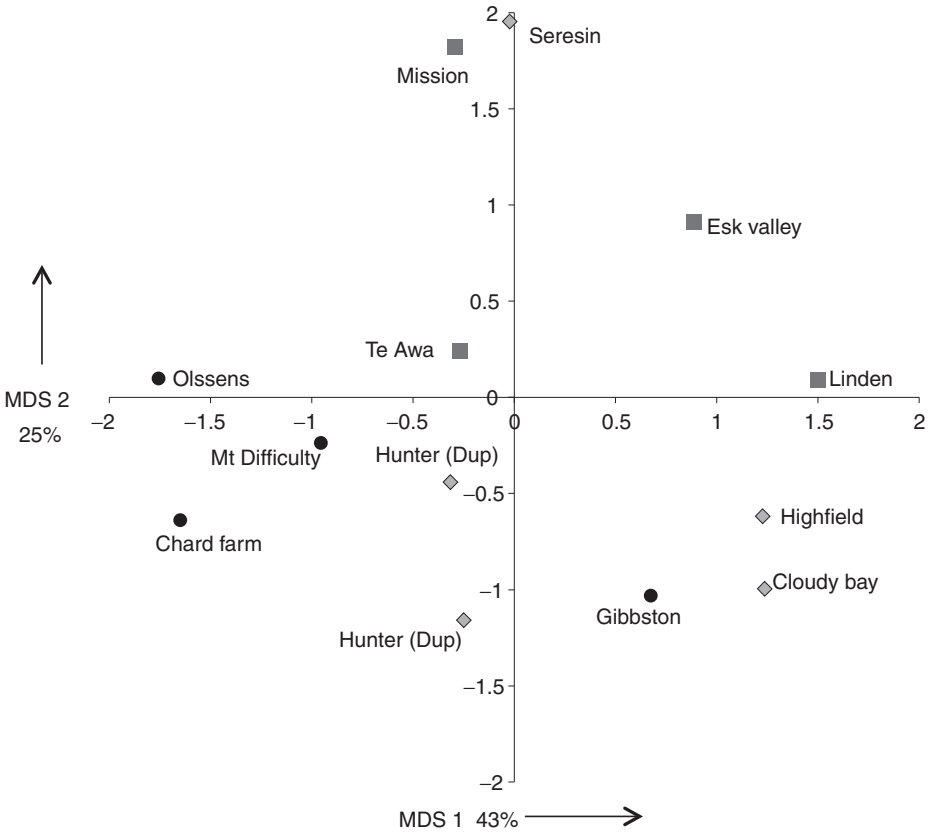


Figure 5 An example of a two-dimensional map based on sorting of 13 New Zealand Chardonnay wines based on similarity of flavor by a group of 27 wine experts/semiexperts, who also provided descriptors for the most prominent sensory characteristics. Physicochemical data for these wines were also provided by the winemakers. MDS 1, accounting for the largest share of variance, was found to be positively associated (right-hand side) with woody and caramel notes, volatile acidity, and negatively associated with pH. MDS 2 was positively associated with alcohol content and Brix (sugar content), whereas negatively associated with citrus notes. The different symbols represent different wine regions and the spread for each symbol suggests that region was not a significant determinant of how the wines were perceived by the panel (Springhall, 2002).

to two dimensions, as the analysis can successfully extract higher dimensionality from the data (Nestrud and Lawless, 2011). Open source tools to perform these analyses are available (Le and Husson, 2008).

Napping is considered a user-friendly procedure because little or no training is required. Moreover, relatively high numbers of samples (10–12) can be evaluated in each session. Although napping has the potential to uncover criteria that might be more relevant to consumers than those provided on an attribute list, there is a bias toward using hedonics as a major criterion. Hence, liked samples are typically positioned close to each other. In contrast, trained subjects tend to use nonhedonic criteria, which leads to better discrimination between samples.

Another recent approach to eliciting details of product attributes that are directly relevant to consumers is the check all that apply (CATA) method (Adams *et al.*, 2007). CATA allows consumers to decide which attributes from a list apply to the sample being assessed. The list itself can be generated by other consumers or a trained panel, but the selection process avoids any bias that might be inherent in having to respond to all attributes. As an example, a recent study used consumers to assess a series of milk desserts (Ares *et al.*, 2010). For each sample, consumers rated overall liking and selected from 17 hedonic and sensory attributes provided by a previous study in which consumers described vanilla milk desserts. The data consist of frequencies of the use of particular terms from the list: in this case, the most common terms were 'sweet,' 'soft,' 'yummy,' 'intense chocolate flavor,' and 'thick.' These counts were then submitted to factor analysis in order to determine which terms best discriminated between the different products.

A potential limitation of this approach is that the data appear to show only that any particular attribute is relevant to greater or lesser degrees. To what extent is this able to discriminate between products? A recent study compared CATA alone, CATA plus intensity ratings of the attributes, and Napping (Reinbach *et al.*, 2014). In fact, all methods produced a similar outcome and it was demonstrated that frequency of selecting a particular attribute provided a good estimate of its rated intensity, rendering the rating process unnecessary. Napping did produce a more varied and larger set of attributes because the consumers were not limited to a limited list of terms. The authors recommended that Napping was better suited to cases where unique, intuitive, or creative descriptors were needed (e.g., explorative studies) and that CATA was better able to increase awareness of certain attributes, in turn, aiding the consumer in performing the descriptive profile. Moreover, CATA is apparently more rapid to perform and hence better suited to studies with large numbers of consumers.

Combining Consumer and Descriptive Data

The outputs from descriptive analyses are often statistically combined and mapped together with consumer data as a means of providing explanations of consumer preferences in terms of sensory attributes. The so-called preference maps provide a relatively straightforward means of linking variation in attributes with variation in measures of acceptability (Greenhoff and Macfie, 1994; McEwan, 1996).

The maps can be constructed from sensory (or instrumental or product formulation) data onto which the consumer preference data are plotted, referred to as an external preference map. Internal preference maps, by contrast, map first the underlying dimensions of the preference data. The consumer data can be hedonic ratings or other types of data, for example, CATA counts. The rationale behind preference mapping is that if consumers like products to different degrees, then they must base this on different intensities of sensory attributes in the products, even if they are unable to describe these attributes. Thus, if one knows how products vary from the external data, they can infer the reasons for liking differences. Once the map is constructed by the external data, acceptance data for each individual are regressed against the product coordinates obtained from these data. The relationships between sensory attributes (and products) can be linear or quadratic, in the latter case reflecting an optimal sensory/ingredient level. An external map can be created by mapping all the relevant sensory or other attributes of the products (e.g., Daillant-Spinnler *et al.*, 1996; Prescott *et al.*, 2001). However, preference data can also be mapped onto the underlying dimensions of the sensory data derived using a technique such as PCA (see Section Descriptive Profiling/Analysis) (Menichelli *et al.*, 2012).

Mapping individual consumer data onto a space created by sensory data will facilitate the discovery of any consumer subgroup or cluster that perhaps views the products in different ways (e.g., Geel *et al.*, 2005). An average preference vector – essentially a direction of increasing preference – can also be derived from the individual ratings. Relating this vector to the product and their sensory attributes potentially allows an easy visualization of unoccupied 'spaces' on the map close to the point of maximum preference that could represent opportunities in terms of new products or improvements for existing products.

Individual Differences

As noted in Section Affective Consumer Methods, consumer responses are characterized by their high variability as well as their changeability from one test session to another. To some extent, this reflects the fact that consumers' decisions are complex, with preferences changing according to circumstances. Just as importantly, however, consumers themselves vary from one another in myriad ways. Certainly, consumer testing frequently stratifies participants according to sex, age, city/urban, and product usage, as these factors are recognizable sources of variation. In addition, however, there are potentially very many other variables that will have an impact on consumer preferences.

Just as some individuals are 'color blind,' it has been known for almost a century that some individuals may be 'taste blind' or 'smell blind' to specific compounds. This means that the same stimulus may differ in its fundamental perception across two individuals due to biological differences. Over the past 20 years, new research in taste biology and molecular genetics has provided new insight into the understanding of individual differences in chemosensation. These differences are not merely of academic interest, as emerging data indicate that they may be sufficient to influence food choice and dietary habits, at least in some contexts.

Recent research has identified, for example, consistent subgroups within populations that vary in terms of bitterness

sensitivity (Dinehart *et al.*, 2006) and liking of sweetness (Mennella *et al.*, 2011), both of which have been shown to relate to food preferences. A substantial minority of women in the USA are thought to be restrained eaters, that is, cognitive factors cause a disconnect between what they like and what they allow themselves to eat. Hence, understanding both food preferences and food choices is complex and nuanced. For example, variation in the bitter taste receptor TAS2R38 has been shown to predict differential intake of alcohol and vegetables (e.g., Duffy *et al.*, 2010; Hayes *et al.*, 2011a,b). Nor are these differences restricted to a single genetic variant in a single gene.

Other recent reports indicate the bitterness of the non-nutritive sweetener Acesulfame-K (Allen *et al.*, 2013), the grassy odor of cis-3-hexenal (Jaeger *et al.*, 2012), the meat defect boar taint (Keller *et al.*, 2007), and the creaminess of starch (Mandel *et al.*, 2010), which all differ across individuals as a function of genetic variation. So too does the intensity of food pungency and taste and one's ability to detect variations in tastes within products (Lee *et al.*, 2008; Prescott *et al.*, 2004a, b). This remains an active area of research and interested readers should see recent reviews (Hayes *et al.*, 2013; Prescott, 2006).

Other individual difference factors whose etiology is unknown have also come to light. The extent to which an individual responds to temperature changes on the tongue by perceiving tastes appears to predict not only responses to tastes themselves (Green and George, 2004) but also some food preferences (Bajec and Pickering, 2010). Patterns of hedonic responses over varying sweetener concentrations (Pangborn, 1970) may also be a good predictor of sweetness preferences within foods (Mennella *et al.*, 2011).This same factor, together with global bitterness sensitivity, has also been shown to influence the extent to one forms likes/dislikes for flavors when these are paired with sweet or bitter tastes, respectively (Yeomans *et al.*, 2009).

These academic studies have important implications for the practice of sensory science. They suggest that individual differences in consumer responses are not simply noise, but rather that one may be able to pin down the origins of a proportion of the variability in one's measures. Because many of the recent findings appear to be directly related to one's experience of foods, they may be better predictors of preferences than factors such as sex or age. In other words, should one be stratifying their consumer samples based on perceptual/preference segments? The food industry manufactures different product types for young and adult consumers. Do these recent findings from sensory science suggest that it would be appropriate to provide different sensory formulations based on different responses to sensory properties? Certainly, this may be happening already with some products. The fact that instant coffees come in different blends that vary in bitterness and flavor strength suggests an industry response to consumers who wish to self-select on the basis of their responses to these sensory qualities (Geel *et al.*, 2005).

Issues of Good Sensory Practice

Sensory science applications are first and foremost problem-solving exercises that require careful definition of the problem: What is the evaluation meant to achieve? To what use will the results be put? Once these questions are answered, the sensory specialist is able to define the method and then analyze and interpret results consistent with objectives and methods.

Lawless (e.g., Lawless and Heymann, 2010) has proposed a 'Central Dogma' that should guide sensory evaluation. The key aspects of this are that:

1. Test methods should match objectives. Analytical methods are for determining, describing, and measuring differences; hedonic measures are used to measure acceptability/liking.
2. Different people are used for different objectives. Trained/experienced panels are asked to ignore their 'gut response.' It is unimportant whether or not they like a product. Consumers are very poor at analyzing or describing. Therefore, do not mix analytical and hedonic measures with the same group.
3. As an extension of this last point, claims about acceptability ('the best product') should not be made if consumers have not been used.

Sensory Evaluation Facilities

Details of design specifications and ideal environmental conditions for panel training facilities, testing booths, and sample preparation areas can be found in the relevant standards (ISO8589, 2007) as well as in sensory evaluation texts (Lawless and Heymann, 2010). In general, however, the design and development of a sensory testing facility first requires consideration of its location within the larger building or complex in that it needs to be readily accessible to participants. If participants are not employees who are already on site, locating near an entrance adjacent to sufficient visitor parking is ideal. Test spaces should minimize distractions, such as noise and background odors; this means care should be given to isolate the testing facility away from smokehouses, bottling lines, cafeteria kitchens, machine shops, loading docks, etc. It is also important to consider the facility's location relative to mechanical systems such as air handlers, processing equipment, and cold storage units. Depending on the nature of materials being tested, it may be important to include oversized air handling to insure sufficient changeover in room air in order to eliminate background odors.

At its simplest, the evaluation area of a sensory testing facility can be a large multifunctional space. Many sensory tests place a strong emphasis on independent evaluations by the participant. However, there are other times when the participant needs to interact with the sensory professional and/or other participants (e.g., trained panels described in Section Descriptive Profiling/Analysis). Accordingly, most custom-built sensory facilities have two basic areas: individual booths and a group discussion room. Although permanent booths are preferable, effective participant isolation may be achieved in a multipurpose space with simple table-top dividers that collapse when they are not needed. Individual booths, whether temporary or permanent, are used when it is advantageous to keep panelists from interacting, as this could potentially introduce noise or bias. A discussion room is used most often for training panelists and other tasks where the interaction between the sensory professional and participants or between participants is encouraged. Critically, the evaluation area,

whether a booth or a large room, should be clean and uncluttered and should have easy access to the sample preparation area.

Ethical Issues

The vast majority of sensory tests do not represent risks beyond 'the ordinary risks of daily life' and may, therefore, be exempt from additional regulatory oversight. However, legal exemptions do not remove ethical responsibility from the sensory specialist. Specifically, participants need to be volunteers who are fully informed of the potential risks of participation, in accordance with the Declaration of Helsinki. In industrial settings, the potential for coercion is especially high when employees are used as participants. They may feel that they are expected to participate in tests and will be marginalized within the organization if they do not 'volunteer.' In academic settings, depending on the institutional review board, the sensory specialist may also need to get a signed copy of an informed consent form before participation. In some settings, implied consent, where participants read the consent form and then agree to move forward with the test, is acceptable.

The sensory specialist should not be complacent that they are 'just testing foods,' as improperly stored or prepared foods may present real risks to health to participants and potential financial losses to the company if injured parties take legal action. New products may also include novel or experimental ingredients that are not yet classified as generally recognized as safe – this needs to be disclosed to potential participants in order to allow them to make an informed decision about whether to participate. Also, the concept of risks does not include just physical harm – as sensory science continues to borrow and adapt tools from psychology to study emotion and personality, it is important to remember that harm may include potential emotional/psychological distress that may result from a focus on personal emotional responses or personality characteristics. Accordingly, a basic risk assessment is merited for all sensory tests. For additional guidance on these issues, see Kemp *et al.* (2009) or recent policy statements by the UK Institute of Food Science and Technology.

Participant Selection

The nature of the participant depends on the goal of the test. Different selection criteria can thus be applied to obtain appropriate participants for a given test. When individuals fail to meet screening criteria, tact is required to avoid offending the individual, as they may be appropriate for a future test. For hedonic tests, it is reasonable and common to select frequent users of the product, regardless of taste acuity. Consumer tests may also select on demographic criteria like age, sex, or income. For discrimination tests, one may screen participants to insure that they are not anosmic or ageusic for the compound of interest or for overall ability to discriminate between samples. Finally, there may be ethical considerations to consider. Regardless of self-reported use, testing certain products in those whose diets are restricted due to illness may not be advisable. Religious objections to some foods should also be considered.

How Many Participants?

The issue of typical numbers of panelists was raised in Sections Descriptive Profiling/Analysis and Affective Consumer Methods. In fact, in any sensory test, the number depends on a range of factors, specifically the actual degree of difference between samples as well as their degree of stability (batch-to-batch variation), the sensitivity of the participants, and the extent to which external factors that contribute to 'noise' (statistical error) can be controlled. Participant's sensitivity can be dramatically improved with training, which is why highly trained panels often contain only 10–12 individuals. Training, of course, produces panelists that are atypical of consumers. Although consumer tests are facilitated by insuring that participants are motivated and not subjected to fatiguing testing procedures, their inherent variability is dealt with by having much larger panel sizes. Having more panelists decreases the impact of factors that produce variability. In any sensory evaluation, 'noise' can be reduced via precise instructions and controlling any factor that might detract from the participant's focus on the samples being evaluated.

Each of these factors is an influence on the statistical power of the procedures (Cohen, 1988). A key concept underlying statistical power is that finding differences between treatments (in the case of sensory evaluation, products or samples) involves a trade-off between Type-I and -II errors. The former are produced when a statistical test tells one that a significant difference is present (at some probability level, usually 0.05) but that this is spurious – in fact, it was one of the 5 cases in 100 that shows up by chance. Type-II errors are the opposite: the test tells us that no differences have occurred when they may actually be evident if the test is done again, especially if either the statistical 'noise' is reduced or the number of participants is increased, or both. Increasing the alpha level above 0.05 would also reduce the Type-II error risk, but by convention this tends to be fixed.

Although increasing statistical power (and hence one's ability to detect differences) is very often desirable, it does raise other issues. In particular, it is important to know the pay off for detecting real differences versus detecting false differences. In other words, just how large a difference is needed to be shown? For instance, it might be shown with sufficient numbers a statistically significant difference between samples, even though, on average, they were rated only 3% of the scale length apart. Is such a significant result meaningful – will it reflect different patterns of food choice, for example?

Sample Preparation, Serving, and Tasting

Apparently mundane issues related to sample serving and presentation are critical for the execution of successful sensory tests. Seemingly trivial details, like the serving size or temperature, the order samples are presented, the timing of samples, or the protocol for rinsing between samples can have very large effects that swamp real differences across products.

Common pitfalls in sensory tests include variable serving sizes, serving temperature, and imprecise control over sample identity. Different sample sizes can influence not only the intensity of the sensation but also the rate at which samples cool or melt. This presumes that samples were presented at the same temperature initially, which may not be a valid assumption if the sensory specialist is not careful. Samples served at different temperatures may not only differ in aroma release or flavor intensity but also in appearance. So, although panelists are often tested blind to the brand of products, there are often sensory cues other than those being tested that distinguish samples. Commonly, samples are presented under red light to mask variations in appearance when this is irrelevant to the purpose of the test.

Instructions given to participants need to be pretested to remove ambiguity. Swallowing a sample produces different outcomes from expectorating the sample in many cases. But even when all panelists follow an instruction to swallow, care needs to be taken to insure that the sample amount remains the same. For example, Prinz and De Wijk (2007) instructed participants to take a single sip of vanilla custard via a large bore straw, and the mean volume ingested varied from 0.4 to 35 ml of sample. As might be expected, they also found sip size was significantly associated with differences in attribute ratings, and more importantly, the effect of sip size differed across attributes.

The number of samples to be served per testing session is a matter of judgment by the sensory specialist. This will depend on not only the flavor strength of the sample but also their pleasantness and the extent to which the sample qualities persist between samples. A key issue with the testing of samples with significant spiciness, for example, has been the fact that the heat of oral irritants such as chili may persist for 10 min or more once the sample has been swallowed or expectorated (Allison *et al.*, 1999). The length of time between samples can also influence ratings (e.g., Guinard *et al.*, 1986). Careful thought also needs to be given to the rinse agent and rinsing protocol between samples (Lee and Vickers, 2010).

Finally, the presentation order of samples is crucial, given the occurrence of contrast and context effects. Care should be taken, therefore, to insure that panelists receive samples according to appropriate randomization or counterbalancing protocols (Macfie *et al.*, 1989). Additional information on the issues presented in this section is provided in relevant sensory texts (Kemp *et al.*, 2009; Lawless and Heymann, 2010; Meilgaard *et al.*, 1987) and ASTM/ISO standards for sensory testing.

Conclusion

This article on sensory science covers only some of its basic issues and practices. The sophisticated analysis of sensory data from trained panels and consumers represents a large and growing part of the armory of sensory specialist, so much so that a new field – Sensometrics – has developed to meet the demand. The so-called objective measures of sensory perceptions and preferences, including brain scanning with functional magnetic resonance imaging techniques, are being explored academically and commercially, although there is nothing to suggest yet that these approaches will be better predicts of what consumers will choose to eat. Importantly, although neuroscience has begun in recent years to increasingly focus on human emotional states, it may bear fruit in time in terms of better understanding of what is measured. For those interested in understanding sensory science in greater depth, the following journals are the best reflection of current and future trends: *Food Quality and Preference*, *Journal of Sensory Studies*, *Appetite*, *Physiology and Behavior*, *Chemosensory Perception*, and *Chemical Senses*.

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Simulation Modeling: Applications in Cropping Systems

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Glossary

Climate change impact assessment Climate change impact assessments are using crop models to study the impact of projected climate change scenarios on agricultural production systems.

Crop models Crop models are a formal way to present mathematical algorithms that represent quantitative knowledge of crop growth in interaction with the environment.

Cropping systems analysis Cropping systems analysis combines crop modeling of atmosphere–crop–soil systems with field experimentation to increase the understanding of agricultural systems.

Dynamic simulation modeling Dynamic simulation modeling is the computer-assisted calculation of crop development and growth processes over time.

Phenotype simulations Phenotype simulations investigate crop trait impacts and are used to optimize crop characteristics for specific growing environments for agronomic and breeding support.

Simulated water-limited yield potential Simulated water-limited yield potential is a crop yield under rain-fed (water-limited) conditions in absence of pest, diseases, and weeds.

Simulated yield potential Simulated yield potential is a crop yield without water or nutrient limitations in absence of pest, diseases, and weeds.

Yield forecasting Yield forecasting combines dynamic simulation modeling with seasonal rainfall and temperature forecast to predict yield over a 39 month time frame.

Introduction

Crop modeling is a formal way to present mathematical algorithms that represent quantitative knowledge about how a crop grows in interaction with its environment. Crop models often simulate different aspects of a crop using daily weather information such as solar radiation, maximum and minimum temperatures, and rainfall. Other information needed for a crop simulation includes soil characteristics, initial soil conditions, cultivar characteristics, and crop management. Using these different data, the models can simulate the dynamics of crop development (or phenology), biomass accumulation, yield, water, and nutrient uptake (Table 1). Crop simulation models are a powerful means to capture the quantitative information of agronomy and physiology experiments in a way that can help explain and predict crop growth and development. These models have made a substantial contribution to agriculture. Crop models help explore dynamics between the atmosphere, crops, and the soil, and can be used to test quantitative hypotheses against reality. Also, they are valuable because researchers can use them to extrapolate data beyond field experimentations, assess the impacts of climate change, and test adaptation to climate change (Figure 1). Crop models are also a central part of decision support systems (DSS) for agriculture, which are computer models designed to assist farmers in making decisions for the season. Also, crop models are part of larger dynamic agricultural model systems that include economics and human behavior.

History of Crop Models

Crop simulation modeling started in the 1960s when scientists developed the first mathematical relationships between biomass growth and solar radiation (De Wit, 1965; Duncan *et al.*, 1967; Monteith, 1965). The first crop models were published

Table 1 List of processes commonly simulated in crop models. Models often incorporate these processes and their mathematical descriptions in various ways

Common processes in crop models	*External factors*
Phenological stages (anthesis, maturity, pod set, seed set, tuber initiation)	Temperature, day length
Crop growth (aboveground biomass, leaves, stems, pods, seeds or grain yield, tubers, roots, Harvest Index)	Solar radiation, temperature
Potential and actual evapotranspiration, crop transpiration or water uptake, soil evaporation	Solar radiation, temperature, rainfall, irrigation
Nutrient uptake (mostly nitrogen)	Nutrient supply
Stresses (water deficit, nitrogen deficit, low or high temperature stress)	Rainfall, temperature, nutrient supply

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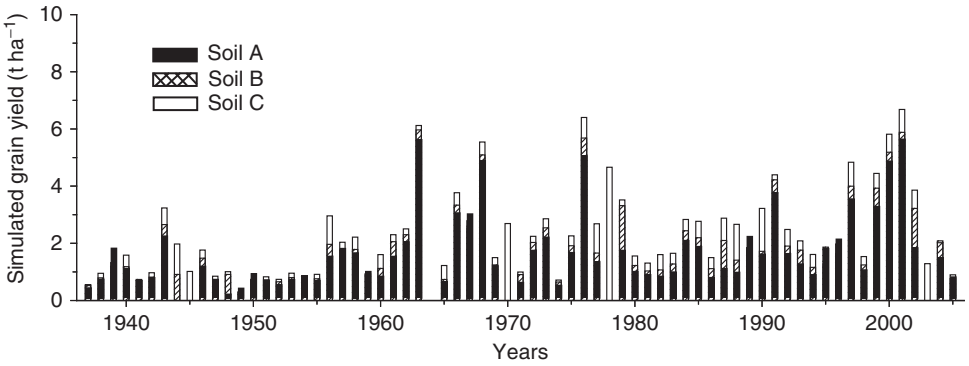


Figure 1 Simulated wheat grain yields to explore the wheat production potential of a current nonagricultural region. Simulations are from 1937 to 2005 for a location west of the current wheat-growing region of Argentina, which received increasing rainfall over the past 70 years, for three soils using a current modern cultivar and a summer fallow. The crops were sown every year on June 5, with a 100 kg N ha^{-a} fertilizer application. Simulations were reset each year; simulated yield variation and trend are because of rainfall variability and trend. Reproduced from Asseng, S., Travasso, M.I., Ludwig, F., Magrin, G.O., 2013. Has climate change opened new opportunities for wheat cropping in Argentina? Climate Change 117(1/2), 181–196, with permission from Springer.

in the 1970s (Loomis *et al.*, 1979). Monteith (1977) described a simple linear correlation of biomass and intercepted light, which led to further crop modeling in the 1980s and 1990s, and included the development of the crop models ARC-WHEAT1 (Porter, 1984), CERES-Wheat (Ritchie *et al.*, 1985), and the Dutch model Simple and Universal Crop Growth Simulator (van Laar *et al.*, 1992). Initial applications of crop models in agricultural research started in the early 1970s (Hesketh *et al.*, 1971). In the early 1980s, Farquhar *et al.* (1980) published a more detailed leaf photosynthesis model, which is still used in some crop models. Most crop models at that time concentrated on comparing models with experimental data to further improve the simulation of cropping systems. Crop models began to assess the impacts of climate change when researchers included data on the effects of atmospheric CO_2 in the models (Rosenzweig and Parry, 1994).

In the 1990s, crop models for various crops were merged into crop modeling platforms, including Decision Support System for Agrotechnology Transfer (DSSAT) (Jones *et al.*, 2003) (http://dssat.net/), Agricultural Production Systems Simulator (APSIM) (Keating *et al.*, 2003) (http://www.apsim.info/Wiki/), CropSyst (Stöckle *et al.*, 2003) (http://www.bsyse.wsu.edu/CS_Suite/CropSyst/), Wageningen crop models (van Ittersum *et al.*, 2003), Simulateur multidisciplinaire pour les Cultures Standard (STICS) (Brisson *et al.*, 2003) (http://www7.avignon.inra.fr/agroclim_stics_eng/), and Environmental Policy Integrated Climate model (EPIC) (Kiniry *et al.*, 1995). In the 2000s, researchers also further advanced single-crop models. For example, the SIRIUS model (Martre *et al.*, 2006) and WheatGrow model (Pan *et al.*, 2006) included grain quality simulations, and the RiceGrow model considered plant architecture (Zhu *et al.*, 2009). Over the past 10 years, researchers developed more crop models that vary in their approach and complexity, including System Approach to Land Use Sustainability (SALUS) (Basso *et al.*, 2001), AquaCrop (Steduto *et al.*, 2009) (http://www.fao.org/nr/water/aquacrop.html), HERMES (Kersebaum, 2007), Model of Nitrogen and Carbon Dynamics in Agro-ecosystems (Nendel *et al.*, 2011), and Lund-Potsdam-Jena Managed Land Dynamic Global Vegetation and Water Balance Model (Bondeau *et al.*, 2007) (http://www.pik-potsdam.de/research/projects/lpjweb). Today, at least 30 models exist for wheat, 19 for maize, and 13 for rice (www.agmip.org). Although crop model testing with field experimental data is still an important part of crop modeling to further improve the models (Asseng *et al.*, 2004), crop models are increasingly applied in simulation experiments.

Key Processes in Crop Models

Key processes simulated with crop models include crop development (phenology), biomass accumulation, yield, water, and nutrient uptake (**Table 1**).

Main Crop Model Systems

Based on the web of knowledge, the most cited crop models include DSSAT (Jones *et al.*, 2003), APSIM (Keating *et al.*, 2003), CropSyst (Stöckle *et al.*, 2003), models from Wageningen (van Ittersum *et al.*, 2003), and EPIC (Kiniry *et al.*, 1995). Most crop models have a modular structure, with crop modules for many different crops linked to soil water, soil nitrogen, and carbon modules. These crop models (a crop module linked with soil modules) have been extensively tested across field experiments and used in many applications.

Crop Model Links to Other Systems

Crop models are often integrated into other model systems, such as DSS (Hearn *et al.*, 1981), farm economic models (Stoorvogel *et al.*, 2004) and human-landscape interactive models (Matthews, 2006).

3-D Crop Models

In the 1980s, Prusinkiewicz and Hanan (1989) used theories ('rewriting rules') by Lindenmayer (1968) to start developing model simulations of dynamic plant architecture. Initially, these models described the 3-D architecture of plants without considering the plant physiological processes and interactions with

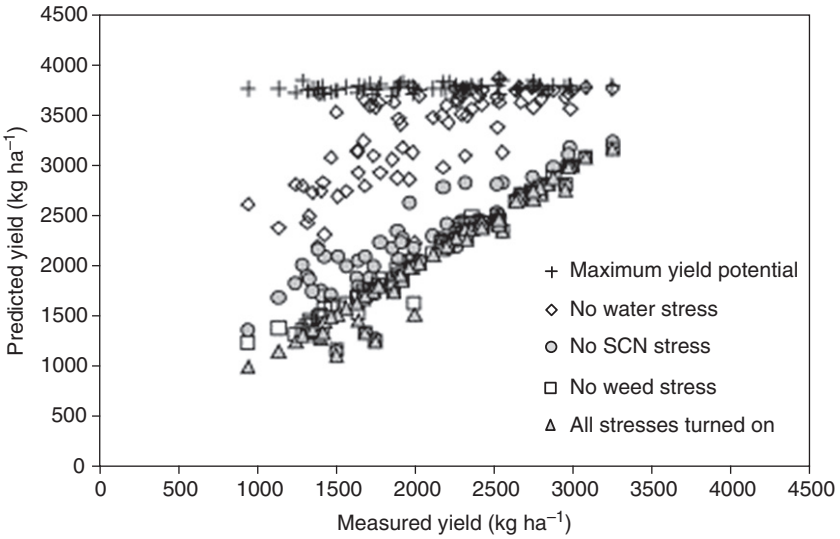


Figure 2 Maximum potential soybean yield, along with variations in predicted soybean yield as affected by soybean cyst nematode (SCN), weeds, and water stress. Reproduced from Batchelor, W.D., Basso, B., Paz, J.O., 2002. Examples of strategies to analyze spatial and temporal yield variability using crop models. European Journal of Agronomy 18(1–2), 141–158.

the environments. Recently, these 3-D architectural models are becoming connected with physiological algorithms from crop models to create functional-structural models (Vos *et al.*, 2007).

Crop Agronomy

Through the decades, agronomy has evolved from field management to an integrated discipline that includes genetics, plant physiology, agricultural meteorology, climatology, soil science, remote sensing, and computer science. As a consequence, scientists are increasingly applying mathematical, biological, chemical, and ecological principles in agronomy. Simulation models have become a tool that integrates different areas of agricultural research. In turn, the models help further research and provide information to assist farmers produce more food on less land and reduce the environmental impacts of agricultural practices.

Yield Gap

Crop yield potential is defined as the crop yield obtained when a crop is grown without limits on water or nutrients and in the absence of any pests, diseases, and weeds. Therefore, a crop's yield potential is a function of solar radiation, air temperature, and crop genetics at a specific location (van Ittersum *et al.*, 2003). In rain-fed environments (agricultural environments that must rely on rainfall for water), the potential yield concept is adjusted to a water-limited yield potential because crop growth and other factors affecting yield potential are defined by the water supply and soil characteristics (Lobell *et al.*, 2009). A crop's yield potential can be experimentally determined in a field or obtained from well-managed farmer fields. However, this is usually costly or hard to achieve (Lobell *et al.*, 2005). Crop models have been used to estimate yield potential and water-limited yield potential for specific fields, farms, and regions (Lobell *et al.*, 2009). In addition to quantifying a potential yield, crop models have been used to understand the reasons for a yield gap, or the difference between actual and potential yield. For example, Batchelor *et al.* (2002) used a crop model to attribute portions of a yield gap to disease, weeds, and water stress effects (**Figure 2**).

Nitrogen Management

Adequate nitrogen (N) management is an important challenge faced by researchers in agronomy. There is a need to produce more food with fewer inputs and minimal environmental impact. The nutrient needs of farmers' fields vary over time, and different areas of the field may need different levels of nutrients. Because of this temporal and spatial variability, studies must include information on multiple locations over a long time period. Using this information, researchers can develop nitrogen fertilization strategies specific to crops and the environment where they are grown.

Crop models can simulate the long-term effects of N on crop growth and yield and the interactions over time on daily crop growth and development (Batchelor *et al.*, 2002). Asseng *et al.* (2001a) used a crop simulation model to estimate the potential wheat crop response to N management over many locations using 80 years of historical weather data. The study showed that N use efficiency of a crop varies with rainfall zone, rainfall season, soil type, and initial soil water conditions. These results would have been difficult to estimate from field experiments alone. Although crop growth is affected by N fertilizer, grain quality also often depends on N supply. Several simulation studies have used crop models to understand the effects of N management practices on both crop growth and grain protein accumulation as a grain quality measure (Martre *et al.*, 2003).

Irrigation

Water is a main factor that limits crop growth and yield in many parts of the world. In these places, rain is insufficient to

meet crop demand. To help these areas, scientists need a better understanding of the crop water balance and crops' yield response to water (Steduto *et al.*, 2009). The crop water balance is complex and contains several processes, such as rainfall, irrigation, rainfall interception by crops, surface drainage and runoff, soil evaporation, transpiration, and root water uptake (Tang *et al.*, 2009). Most crop models include these components of a water balance, which allows them to be applied to manage irrigation of crops (Singh *et al.*, 2008). For example, a crop model helped maximize yields for a wheat crop in northern Africa in an area that only had access to limited supplementary irrigation (Heng *et al.*, 2007).

Sowing

The choices made when sowing a crop are some of farmer's key management options. These choices include determining the cultivar, planting density, and time of sowing. The optimum sowing practice to maximize economic return is often difficult to quantify. Many factors interact during a crop season, and new cultivars are continuously being developed. Crop simulation models have been used to generate yield response functions that can help to evaluate how different sowing strategies affect the economic response of crop yield. For example, Paz *et al.* (2001) used a crop simulation model to identify the best soybean variety for a specific location. Batchelor *et al.* (2002) used a crop simulation model to estimate the best variety that will maximize a farmer's economic return. Asseng *et al.* (2008) used a crop model to identify optimal sowing dates and yield penalties from delayed sowing in a variable rainfall environment.

Seasonal Variability

Variability in the amount of rainfall in rain-fed agriculture is a major source of variability in grain yields. Forecasting the season type (e.g., wet or dry) can allow farmers to adjust crop management. In dry, low-yielding seasons, producers can save input costs, whereas in wet, high-yielding seasons they can increase inputs for a higher yield potential. Crop models can simulate many management practices using long-term historical weather records, allowing producers to optimize management strategies for season types based on the seasonal forecast. Hammer *et al.* (1996) combined a seasonal forecast with multifactorial long-term simulation experiments and showed that profits could increase up to 20% when adjusting crop management to Southern Oscillation Index (SOI) phases in the Queensland wheat-belt. Similarly, using El Niño Southern Oscillation (ENSO)-based forecasts for maize management in the southern US and Argentina could increase profits by US\$13–15 ha^{-1} (Jones *et al.*, 2000). Asseng *et al.* (2012) linked crop simulations with a coupled ocean-atmosphere Global Circulation Model (GCM) to manage rainfall season types in the southern part of the wheat-belt of western Australia, yielding an extra profit of AU\$50 ha^{-1} from improved crop management.

Spatial Variability

Spatial variations of weather, soil water, nutrient supply, and crop management impact farmers' yield and may cause agricultural externalities (e.g., environmental consequences from nitrate leaching into water systems). Region-specific nitrogen fertilizer strategies have been developed by combining crop models with spatial field information (Basso *et al.*, 2011). In one instance, a crop model linked with regional soil and weather variability was used to quantify the potential water access of cropping systems as the main source of salinity in areas without irrigation (Pracilio *et al.*, 2003). Using remote sensing data (remote sensing in agriculture is using aerial sensor technology to gain information about crops) allows researchers to learn more about the spatial variability in farmers' fields. For example, combining crop simulation at points in a field with remote sensing at a regional scale can extend the simulation of temporal variability to spatial variability across a field or region (Wang *et al.*, 2012). Two methods used to integrate crop models with remote sensing data include driving methods and assimilation (Moulin *et al.*, 1998). Driving methods are updating variables in a crop model using remote sensing observations, and assimilation is creating new parameters in a crop model using remote sensing observations. Both of these methods can help to improve crop management of spatial variability.

Rotation

Crop rotation is the agronomic practice of growing crops on the same paddock in sequence. It has several benefits for soil and crop systems. Beneficial effects include lower incidence of weeds, insects, and plant diseases, as well as improvements of soil physical, chemical, and biological properties. Improvements in the soil physical properties include better water holding capacity and aggregate stability, whereas the improvements in the biological properties include an increase inorganic matter, which replenishes soil nitrogen (N) and carbon. Crops grown in rotation reduce greenhouse gas emissions because of the lower amount of N fertilizer added. For example, if cereal crops follow a leguminous crop, the rotation can fix atmospheric N through rhizobacteria. The selection of crops used in rotations is often determined by the crop's commodity price. Farmers often return to continuous cropping systems despite the numerous advantages provided by rotating crops, especially if the specific crop prices are high. This decision has been an error over the long term. Crop yields have declined in continuous cropping systems, and there have been increases in input demands, leading to lower overall farm profitability.

Agronomists have studied yield responses to crop rotation and tradeoff analysis between yield and input demand in field experiments. Yield responses often vary across these field experiments. Crop rotations are affected by various factors such as soil type and fertilizer input in interaction with seasonal rainfall variability. This means a system approach using crop models can help to evaluate the carryover effect of carbon, nitrogen, and water in a rotation to optimize crop rotations for a specific environment. Several crop models can simulate the effect of crop rotations on yield and soil properties. The most common models used to simulate crop rotations are DSSAT, EPIC, APSIM, CropSyst, STICS, SALUS, and root zone water quality model (RZWQM). Each of these models can simulate

Table 2 Dominant insect and herbivores on upland cotton, *Gossypium hirsutum,* in the western US, the structures they feed on, and the type of injury[a]

Herbivore	*Fruiting structures*	*Leaves*	*Stems*	*Roots*	*Meristem tissue*	*Feeding injury and its impact on the host crop*	*Plant feedback to the herbivore*
Aphids and whiteflies		●				Sucking produces excreta that support sooty mold, which restricts light and photosynthetic activity	Phloem 'N' content impacts aphid and whitefly fecundity and dispersal
Armyworms	•	●	●	●	●	Chewing reduces vascular transport and reduced photosynthesis when feeding on leaves	Plant vigor and/or available leaf area impacts feeding, which impacts aphid growth rate
Boll weevil	●					Chewing supports secondary fungal pathogens, which in bolls damages developing lint; fruit abscission prolongs vegetative development	Fruit availability in different age classes impacts what the larvae consume. 'N' in consumed fruiting structures impacts diapause
Fleahopper spp.	●				•	Sucking causes fruiting structure abscission	
Bollworm and budworm	●	•			•	Chewing; fruit abscission prolongs vegetative development	Fruit availability in different age classes impacts what the larvae consume. 'N' in consumed fruiting structures impacts diapause
Lygus spp.	●				•	Sucking can cause fruiting structure abscission and meristem death; fruit abscission prolongs vegetative development	
Pink bollworm	●					Chewing can cause fruiting structure abscission	Fruiting structure age impacts larval growth rates
Spider mite spp.		•				Sucking and phytotoxicity to surrounding cells	Leaf 'N' content impacts dispersal rates and fecundity
Thrips	•	•				Surface rasping can cause cell death and decreased cell expansion	

[a]The larger black circles represent organs pest species predominantly feed on, whereas the smaller black circles represent organs pest species less frequently feed on.

crop rotations, soil, water and nutrient dynamics, and management strategies over multiple years. The benefits of rotations have been simulated and tested for a corn-soybean rotation in comparison with continuous corn in the US using the RZWQM reproducing the higher corn yield under corn-soybean rotation than under continuous corn (Ma *et al.*, 2007).

Linkages with Pest and Diseases

Most crops are exposed to injury from a range of crop herbivores (e.g., insects, mites, plant pathogens, and nematodes). Capturing the dynamics of biomass accumulation, phenological development, and yield requires that crop models present how the crop is impacted by the physical environment and management inputs, as well as how it is impacted by dominant herbivores. Crop models need to have a structure that links each pest species to the plant organs that are directly impacted. The linkage (also referred to as 'coupling points') must allow the host crop to respond to the herbivore, as well as impact the development, fecundity (potential reproductive capacity), survivorship, and, in some cases, immigration/emigration of the pest species.

Interactions between pests and crops are quite varied as Table 2 illustrates for cotton, *Gossypium hirsutum.* In Table 2, the circle size represents the degree to which several insect and mite species feed on the plant organs. The two-way interaction between the crop and each of its dominant insect herbivores illustrates the dynamic nature of crop and pest interactions (Table 2).

The physical environment and the biological nature of the crop-pest interaction determine the manner in which a pest and its host crop are linked. Because interactions between pests and crops are complex, including these relationships in crop models requires many different physical factors of the crop and pest species. These physical factors include hourly canopy and soil temperature (pest species in general), the canopy vapor pressure/relative humidity gradients (surface inhabiting plant pathogens), photo flux density within the crop canopy and at the soil surface (weedy species), and water and nutrient availability within the soil (soil-dwelling insects, root-inhabiting nematodes, soil-borne plant pathogens).

Mapping these interactions in crop models also requires crop-based variables for each pest species. This data includes the density, mass, and nutrient content of each age class of each organ type (roots, stems, leaves, fruit) that serves as food for the pest. Other pest variables needed that are specific to the host plants include the type, density, age class, and mass of organs injured by each pest species, and the survivorship probabilities for injured organs. These variables allow feedback from the pest species to the host crop. For example, feeding by a leaf-chewing insect reduces the leaf area, which impacts light distribution throughout the canopy, photosynthesis by uninjured leaf tissue, and availability of metabolites for expansion of uninjured and injured leaves, and other crop structures. Each age class and type of leaf-feeding pest typically consume a predictable amount of mass. This

translates to the amount of leaf mass consumed changing dynamically with pest density and age class distribution, and the stage of crop growth during which the herbivore occurs.

A number of cropping systems have modeled the links between crop and pest species, including leaf spot on wheat and soybeans (Boote *et al.*, 1983), bollworm/budworm and spider mites on cotton (Ives *et al.*, 1984, Wilson *et al.*, 1991) rust and early leaf spot on peanuts (Savary *et al.*, 1990), and blast and water weevil on rice (Wu and Wilson, 1997).

Intercropping

Intercropping is defined as the agronomic practice of growing two or more crops on the same field at the same time. Crops selected for intercropping normally have different abilities to use the resources available for growth, which leads to yield advantages and increased stability compared to a single crop in a low input system. The use of high-yielding cultivars, increased mechanization, and increased fertilizer and pesticide use eliminated intercropping from most farming systems, with the exception of some regions in Africa and Asia (maize and cowpeas) or crops intercropped with agroforestry systems. The principles of crop models are also applied in intercropping models to show how different species combine and compete for light, water, and nutrients (Corre-Hellou *et al.*, 2009).

Kropff and van Laar (1993) described the ecophysiological model INTERCOM, which was one of the first models developed for competition between species. The model was mainly designed to evaluate the impact of weed infestation on crops. The model consists of a set of individual growth models (one for each competing species) that calculate the rates of growth and development for species based on environmental conditions. Under favorable conditions, light is the main factor determining the growth rate of the crop and its associated intercrop (i.e., weeds). The model calculated daily soil water balance accounting for plant-available water. If plant-available water dropped below a critical level, transpiration and growth rates of each species were reduced. Another example of an intercropping model is APSIM, which allows competition for resources (e.g., solar radiation, water, nitrogen) between two crops grown on the same field at the same time. Biological modules in APSIM compete on the daily time step through a set of allocation rules for resources. Adiku *et al.* (1998) used the APSIM model to compare a maize and cowpea intercropping system with these crops grown in monoculture for two savanna zones in Ghana. That study showed that for a sustainable production, intercropping maize and cowpea together with a modest fertilizer application was generally the better cropping system.

Natural Resources Management

When applied to agriculture, natural resources management (NRM) refers to the sustainable use of soil, rainfall, irrigation, and nutrients. Traditional crop management is aimed at increasing agricultural productivity alone. In the NMR framework, crop management to increase productivity is continued, but practices are adopted to maintain the long-term sustainability and integrity of agriculture systems. NRM has become increasingly important in the last decades as a result of soil degradation. Crop models can help farmers develop strategies to increase crop productivity without negatively impacting the basis of production and externalities. For example, a crop model has been used to identify optimal N fertilizer application rates for different management zones in a farmer's field (Basso *et al.*, 2011). The management zones were identified from long-term yield maps, remote sensing, and soil chemical and physical properties, which were then used as parameters for the crop model. The crop model simulated the cropping system for a range of N fertilizer applications. This helped to identify zone-specific N management strategies that result in the best yield with the least N leaching across the field (Basso *et al.*, 2011).

Soil Constraints

Although soil water and nitrogen effects on crop growth are included in most crop models, a number of other soil constraints are less commonly included (Probert and Keating, 2000). These include erosion, salinization, acidification, compaction, and water-logging, which are less understood. A range of erosion models have been developed that vary in complexity. Most of the erosion models are applied to environmental engineering, and a few have been included in crop models. For example, the EPIC model (Izaurralde *et al.*, 2006) and the APSIM model (Keating *et al.*, 2003) include routines that consider the impact of erosion on crop productivity. Some crop models consider the effects of soil compaction through a soil hospitality factor. For example, Wong and Asseng (2007) simulated the effect of deep tillage to overcome soil compaction on wheat productivity to quantify the potential benefits of deep tillage. These benefits ranged from positive to neutral to negative effects on yield, depending on soil type and seasonal rainfall. Tang *et al.* (2003) used the same soil hospitality factor as the basics to simulate the impact of various degrees of soil aluminum concentrations on root growth and subsequent grain yields in a low rainfall environment.

Salinity is a widespread soil constraint that can reduce crop growth and yield. Some salinity impact-routines, such as the function proposed by Van Genuchten (1987), have been used to relate water uptake to the average salt concentration in the root zone. For example, Dixit and Chen (2010) integrated the van Genuchten function into a spatially referenced water and nitrogen management model (WNMM) model (Li *et al.*, 2007) to understand the spatial yield variability because of salinity constraints. Other models consider the flow of water in the soil and use a mixing algorithm to simulate salt movements between soil layers. For example, this salinity algorithm has been included in APSIM to simulate the effects of irrigation water and chloride accumulation in soils (Snow *et al.*, 1999). Excess water or water-logging is another soil-related constraint that can limit crop growth. A simple water-logging routine has been included in the crop model APSIM-NWheat, which simulates the dynamics of a water table and its effects on root and crop growth (Asseng *et al.*, 1997).

Drainage

Drainage of water from the root zone occurs when the amount of rainfall is more than the soil can store. Drainage can be considered 'unproductive' water and causes dry-land salinity in some regions. Drainage is difficult to measure in the field and has spatial and temporal variability because of different soils and varying amounts of rainfall. Crop models are valuable to help quantify the potential of drainage across soils and regions (Asseng *et al.*, 2001b).

Nitrate Leaching

Groundwater pollution caused by excessive inorganic nitrogen (N) fertilization is a widespread environmental problem in many agricultural systems. N in the form of nitrate ($NO3^-$) is very mobile in the soil and can easily leach with moving water. Rainfall or irrigation can cause significant amounts of N leaching if large amounts of nitrate are present in the soil. N leaching can also cause soil acidification, another potential soil degradation that limits crop growth. As a consequence, regulators are attempting to restrict excess nitrate in soils. For example, the European Union (EU) Nitrates Directive (91/676/EEC) aims to preserve groundwater quality by promoting farming practices that increase N use efficiency of cropping systems (Basso *et al.*, 2010). Crop models have played a role in determining crop management and its impact on externalities, such as N leaching. For example, Asseng *et al.* (1998) used a crop model to show that on sandy soils and high rainfall, most of the initial soil N is lost to leaching before roots can take it up. Basso *et al.* (2012) used a crop model in a field study and showed that less N fertilizer can be used to reduce N leaching without causing reductions in economic return from the crop. Giola *et al.* (2012) quantified the nitrate leaching caused by mineral and organic fertilizer applications over 2 years of a maize-triticale rotation at a site in Italy with the SALUS model. The model showed nitrate leaching from slurry and manure was significantly reduced when applied without additional mineral N applications.

Soil Carbon

The amount of soil carbon and its dynamics play a crucial role in agricultural productivity and global climate stability. Numerous crop models that include soil carbon are currently available. These models differ in objectives, level of complexity, and relationship with other agricultural components. Most models present different fresh organic matter (metabolic litter: easily decomposable fresh residues; and structural litter: recalcitrant fresh residues such as lignin) and organic carbon pools. An active pool is based on material (sugars) with a mean residence time (MRT) <1 year. An intermediate pool is based on lignin and cell walls with a MRT of 30 years, and a resistant pool is formed mainly by inert material and stabilized microbial material. One of the most widely used soil carbon models, the CENTURY soil carbon model (Parton *et al.*, 1988), has been adapted for use in the DSSAT cropping system model (CSM) (Gijsman *et al.*, 2002). Senthilkumar *et al.* (2009) used the SALUS crop model to simulate soil carbon dynamics in a cropping system in Michigan under different tillage and fertilizer management strategies. The model predictions of soil C changes closely agreed with the observed results for the conventional tillage and no tillage fertilized treatments.

Breeding

Phenotypic Trait Expression

In the 1990s, crop models began to address the impact of phenotypic traits on cultivar performance and how trait values are gene based. White and Hoogenboom (1996) incorporated the effects of seven traits involving phenology, growth characteristics, and seed size for dry bean. Elings *et al.* (1997) used crop modeling to gain insight into how to increase maize yields in tropical environments. The authors concluded that yield was sink limited and could be improved by increasing the size of primary ears or by increasing plant density, which in turn increased the density of primary ears. The authors also concluded from the simulation analysis that yield can be increased under drought conditions by selecting for genotypes that have higher seed set.

Wilson *et al.* (1998) and Wu and Wilson (1998) simulated rice cultivar performance by incorporating primary phenotypic traits, which are described as being near invariant for a wide range of climatic and edaphic environments. A crop model was verified and validated across 13 crop data types for cultivars that exhibited a range of growth patterns. The authors proposed to use their model to identify which combinations of primary phenotypic traits to select to develop higher yielding cultivars. Wilson *et al.* (2000) presented simulation results supported by field data showing that rice yields can be drastically increased for the Texas Gulf Coast environment by selecting for genotypes that produce phytomers at a quicker rate and produce panicles at a slightly higher nodal position.

Genetics of Phenotypic Expressions

Hoogenboom and White (2003) categorized the degree to which different crop models incorporate genetic detail and concluded that most are at level three of a six-level scale. On the scale, level three means genetic differences are represented by cultivar-specific parameters, whereas level six means the generic model has no reference to species. Yin *et al.* (2003) combined crop modeling with quantitative trait locus (QTL) mapping. QTL mapping involves segments of DNA linked to the genes that underlie a crop phenotype. They did this by replacing measured input trait values with predictions from QTLs, and Messina *et al.* (2006) continued this in subsequent efforts. White *et al.* (2008) concluded that it is possible to use genetic data to estimate trait values, but that the estimates are not as accurate as those provide by directly measuring trait values and require more extensive genetic characterization. Chenu *et al.* (2009) studied the pleiotropic effects (a gene influences multiple phenotypic traits) on maize silk elongation. They illustrated the inability to interpret genetic control of yield by solely using additive effects of QTLs, but concluded that modeler/molecular biologist teams should use crop genotyping to improve the prediction of a cultivar's trait values.

This research suggests the current level of understanding of gene expression is not sufficient to accurately predict the majority of phenotypic traits from a cultivar's genotype or to allow accurate modeling.

Improvements in Cultivar Development

Although recent literature demonstrates the potential for using crop models to quantify the effects of phenotypic traits on cultivar performance, progress has been limited in using models to develop improved cultivars. Samonte *et al.* (2011) described progress with the Texas A&M marker- and model-assisted rice cultivar development program, where genotypes were selected based on two primary phenotypic traits and two secondary traits. The two primary traits were maximum mainstem node production rate and panicle node number, and the relatively easy to measure secondary traits were two primary phenotypic traits, potential leaf growth rate and maximum spikelets per panicle. This approach differs greatly from that of conventional inbred selection. In this approach, recombinant lines are selected based on primary phenotypic trait values and are not based primarily on yield. As a result, 22 (85%) of the 26 selected genotypes yielded more than the inbred control cultivar with the upper 5 (19%) producing an average of 23% greater yield. Consequently, the first rice cultivar was develop through marker- and model-assisted selection (**Figure 3**), which produced 7% greater yield than the best performing commercially available inbred cultivars (Tabien, personal communicaton, 2012).

Inbred breeding in the future will likely see the greatest initial strides in the use of model-assisted selection because cultivar selection programs for inbred genotypes are more straightforward than hybrid selection.



Figure 3 Panicles of rice cultivar 'Colorado' at the grain filling stage. Cultivar Colorado is a high-yielding semidwarf long-grain rice cultivar, and is the first rice cultivar developed using marker- and model-assisted selection. Colorado was developed by the Texas A&M AgriLife Research Center at Beaumont Texas (Photograph by R.E., Tabien).

Climate Change

Impact of Past Climate Trends

As the global climate has been changing and will continue to change (IPCC, 2007), crop models have played a key role in determining the impact of climate change in agriculture. A number of crop simulation studies have shown that past climate changes have affected cropping systems. For example, Ludwig *et al.* (2009) used a crop model to determine the impact of recent rainfall decline of up to 20% on crop yields and drainage. They showed that grain yields were not affected by rainfall decline, but drainage was significantly reduced. By using the model, they explained that limited soil water holding capacity and reductions of rainfall during the wettest part of the seasons were the reasons for these unexpected findings. Similarly, Liu *et al.* (2013) studied the effects of past climate change on crop phenology and production using a crop model for rice in China.

Impact of Future Climate Trends

Crop simulation models have been a key tool in assessing the impact of future climate change. A range of plausible projections (scenarios) of emissions from a number of general circulation model ensembles and various downscaling methods are usually employed together with single-crop models. Including these projections in crop models can help to assess possible impacts and explore management strategies to adapt to climate change. Many future climate change impact assessments have been carried out using crop models for specific locations (Semenov *et al.*, 1996), agricultural regions (Tao *et al.*, 2009), and at the global scale (Rosenzweig and Parry, 1994). Experts suggest including the uncertainty in crop models in such climate change assessments and multimodel applications. Including uncertainty ensures that crop models are used in a similar way to the multimodel approach in climate change science (Meehl *et al.*, 2007). The recently founded Agricultural Model Intercomparison and Improvement Project (AgMIP; www.agmip.org) is a major international collaborative effort to assess climate impacts on the agricultural sector. AgMIP incorporates state-of-the-art climate products as well as crop and agricultural trade model improvements in coordinated regional and global assessments of future climate impacts. Instead of using single-crop models, the project includes multiple models (**Figure 4**), scenarios, locations, crops, and participants to standardize climate change impact studies and define the uncertainty of impact assessments (Rosenzweig *et al.*, 2013).

Adaptation to Climate Change

As the global climate is changing, agriculture will need to adapt to the changes to maintain and improve crop production. Studies show that without adaptation, climate change may create considerable problems for agricultural production and communities in many regions of the world (Wall and Smit, 2005). Crop modeling has been used to determine the impact of climate change and to explore adaptation options (Luo *et al.*, 2009). These strategies included changes to sowing dates (Alexandrov *et al.*, 2002), irrigation (Chen *et al.*, 2012), nitrogen fertilizer input (Liu *et al.*, 2010), and cultivars (Butt *et al.*, 2005).

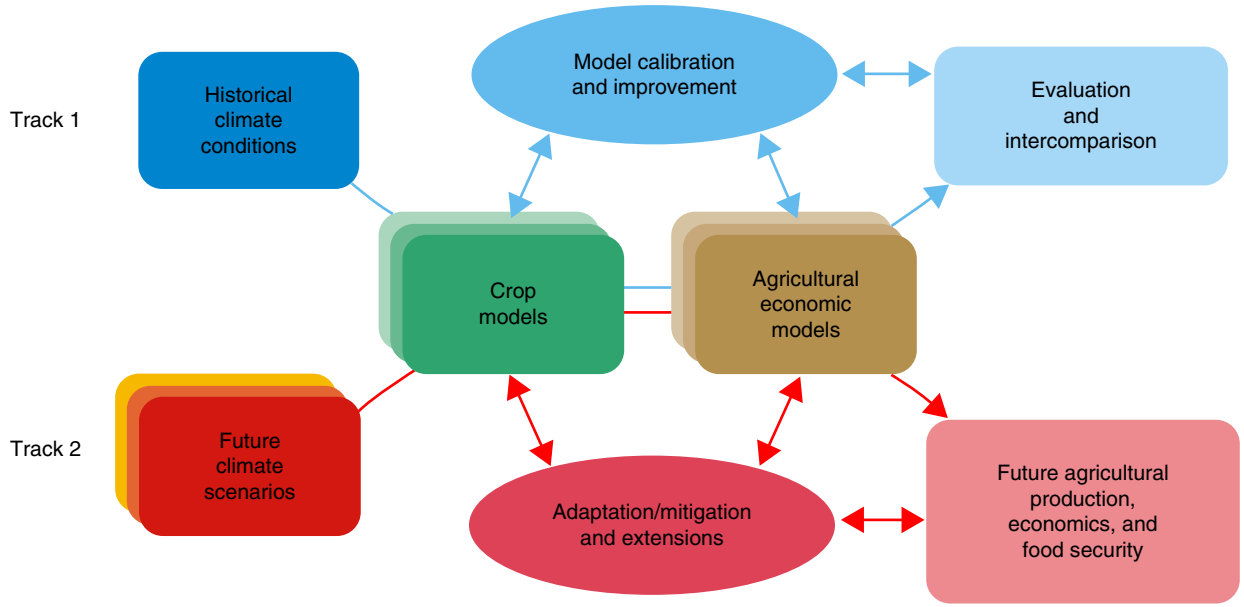


Figure 4 Two-track approach to AgMIP research activities. Track 1: model intercomparison and improvement; track 2: climate change multimodel assessment. Reproduced from Rosenzweig, C., *et al.*, 2013. The agricultural model intercomparison and improvement project (AgMIP): Protocols and pilot studies. Agricultural and Forest Meteorology 170, 166–182.

Mitigation

Agriculture can be of paramount importance for minimizing the impacts of climate change. Certain agricultural management practices allow for soil carbon sequestration, such as zero tillage and retaining residues on the soil surface, whereas others can help increase productivity and use less fertilizer. These practices will reduce greenhouse gas emissions such as CO_2 and N_2O, as these two gases are highly dependent on the level of soil organic carbon and the amount of nitrogen fertilizer added. Basso *et al.* (2012) demonstrated that through the use of crop modeling combined with precision agriculture technologies, the optimal amount of N fertilizer could be reduced, leading to lower N_2O emissions. In another study, a crop model was used to show that variable rate input (i.e., tillage, seeding, cultivars, fertilizer, irrigation, pesticides) can lower greenhouse gas emissions by more efficient use of products and energy reductions (Bertocco *et al.*, 2008). Also, crop models have helped increase yield by sequestering more carbon from the atmosphere (Basso and Ritchie, 2012).

See also: Climate Change: Agricultural Mitigation. Climate Change and Plant Disease. Climate Change: Cropping System Changes and Adaptations. Climate Change: New Breeding Pressures and Goals. Climate Change, Society, and Agriculture: An Economic and Policy Perspective. Computer Modeling: Applications to Environment and Food Security. Food Security: Yield Gap. Forage Crops. Organic Agricultural Production: Plants. Pathogen-Tested Planting Material. Plant Abiotic Stress: Temperature Extremes. Plant Abiotic Stress: Water. Plant Biotic Stress: Weeds. Plant Disease and Resistance. Precision Agriculture: Irrigation. Quantitative Methods in Agricultural Economics. Root and Tuber Crops. Soil: Carbon Sequestration in Agricultural Systems. Soil Fertility and Plant Nutrition. Soil: Nutrient Cycling. Sugar Crops. Weather Forecasting Applications in Agriculture

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Slum Livestock Agriculture

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Glossary

Animal husbandry The different aspects involved in raising animals in agricultural settings.
Cold chain The transport and storage of perishable products at appropriate cold temperatures to prolong the shelf life of the product.
Coprophagia Consumption of fecal matter; pigs are coprophagic.
Food safety The proper handling of food, preparation, and storage to avoid contamination that may cause illness to humans.
Food security The access of food, the availability, and the nutritional value of the food.
Goshala Protected shelter area for cattle, a sanctuary for animals due to their religious significance; for example, *goshalas* in India for cows, calves, and oxen.
Gray water Water contaminated with waste from household use that is recycled for other use such as irrigation and flushing toilets.
Production diseases Diseases of animals affecting the production capability; for example, mastitis affects milk yield.
Reportable diseases The occurrence of a disease requiring obligatory reporting due to the importance to human or animal health.
Zoonosis Diseases transmitted between animals and humans; the biological cycle may include one or more species and humans, humans could be an accident in the cycle.

Introduction

Slums are human settlements developing in peri- and urban areas. Often not recognized as part of planned urban environments, slums continue to grow in number and size around the world. There are now 800 million to a billion people living in slums, a large percent of the seven billion worldwide. Slums are difficult to define based on a single characteristic because they are not homogeneous within cities in a country or among countries; their unique milieu depends on the geographical location of the settlement, the socio-anthropological background of the dwellers, and the history of its development. Notwithstanding the sociocultural differences, slums have some common characteristics: poor housing, often illegitimately built on private or public land with poor drainage and unfit for agriculture; overcrowded conditions; limited access to potable water; poor sanitation and lack of sewage or waste removal; high numbers of domestic pets; and clandestine keeping of livestock.

Slums originate from the need of people for a place to live after displacement due to drought, famine, or wars, and migration from the countryside into the cities by the push of rural unemployment and the pull of urban opportunities. This migration from rural to urban areas populates informal settlements in the periphery of cities and towns in many countries (United Nations, 2011). Demographic information from slums is only as good as the reports governments make. Less than 100 countries report data on slum human population, and from those, 37 indicate they have more than 50% of the population living in slums. One country reported that 94% of the population lives in slum conditions (United Nations, 2007). In the 2013 census in India, 65 million people were identified as living in slums (Government of India, 2013), which is probably an underestimate.

In lesser developed countries, the increase in the urban population dating from the 1970s is parallel to the decrease of the rural population. Demographers expect that 60% of the world's population will live in urban areas by the year 2050 and 2 billion people will be living in slums (United Nations, 2011). In Africa, the population in urban areas increased sevenfold in 50 years. Population density in some slums has reached 200 000 people per square kilometer, as in Bangladesh (Huque, 2005). With one in every seven people living in a slum, ensuring sufficient food becomes a concern; slum livestock agriculture could be part of the solution to fulfill the nutritional needs of that many people (United Nations Human Settlements Programme, 2003).

Production of food in slums is clearly different from rural, peri-urban, or other types of urban agriculture developing in many industrial countries. Urban agriculture had been characterized as a decentralized supply system composed of small and scattered production units (Mougeot, 2000). There are other classifications of urban agriculture, only some of which include slum agriculture (Egbuna, 2008). Slum livestock keeping is especially difficult to classify. The lack of basic resources to maintain and exercise good agricultural practices coupled with unsanitary slaughter is likely to render slum livestock agricultural products unfit for human consumption. However, despite all the negatives, slum livestock agriculture is a means of securing food, earning income, and supporting livelihoods of slum dwellers. Slum agriculture benefits from a large market close at hand, low transportation costs, availability of production inputs, the ability to make use of waste foods and water, and low entry costs to setting up production (Food and Agriculture Organization, 2001).

Informal markets for real estate and goods develop in slums, including markets for processed and unprocessed animal products (Potsiou and Ioannidis, 2007). Peri-urban and urban

livestock agriculture is a complex and multifaceted activity developing in an environment often unfit for human habitation. Roaming chickens, pigs, and goats are a common sight in slums, and even cows and animals used for transportation or hauling such as donkeys and horses can be seen. In different regions of the world, different animal species are popular: goats and sheep are more common in Africa and Southeast Asia, and pigs are more common in Latin American slums. Food animals in slums are a public health concern due to their potential for transmitting zoonotic diseases, unsafe food products, the risk of physical injuries and traffic accidents, and environmental contamination. Animal products processed locally enter the general population food chain through peri-urban and urban food markets. Owing to the lack of a proper waste disposal, animal and human waste mixes in the streets with leftover water from household activities. Stagnant water and waste, garbage, and other contaminants develop a foul smell and attract vermin and insects. Untreated wastewater flows into local waterways and is drunk by roaming animals. This gray water is often used for urban vegetable or crop farming.

There are few estimates of the volume of animal or vegetable products originating from slums used to supplement the family diet or entering the food chain through peri-urban or urban markets. In Ghana, 95% of the lettuce consumed in Accra is produced in urban and peri-urban areas (Amoah *et al.*, 2007). In the Chimbote slum in Lima, Peru, where 400 000 people live, it has been estimated that there are 280 swine production units (Chimbotenlinea.com, 2014). That is approximately 25% of the households in the slum assuming there are four members per household.

Livestock Production in Slums

The Food and Agriculture Organization of the United Nations has conducted technical consultations and extensive studies on urban and peri-urban agriculture. Thirty percent of the meat and 70% of eggs produced in the world is associated with urban production (Food and Agriculture Organization, 1999). It is not clear if slum agriculture production is included in these estimates. Slum livestock keeping is typically smaller scale than the peri-urban and nonslum urban agriculture. However, slum agriculture has rarely been the focus of systematic evaluations and studies. The complexity of this type of slum livestock agriculture and its implications in the social and political arena is, however, getting recognition (International Livestock Research Institute, 2012; Lemma and Rao, 2013), and some evidence is emerging on scale and importance. In Maputo (1.2 million inhabitants), Mozambique, more than one in three households in urban areas raises livestock (International Livestock Research Institute, 2013). In Ibadan in southern Nigeria, one in three urban households kept livestock, whereas in Kaduna in northern Nigeria nearly half the households kept livestock (International Livestock Research Institute, 2013).

Species of Animals and Production and Scale

Livestock production in slums is typically small to medium scale and low technology. Chickens and pigs seem to be ubiquitous in Latin American slums, whereas goats and rabbits are favored in Africa and Southeast Asia. Cows are noticeable in India and Nepal where, for religious reasons, they cannot be slaughtered. Some animals in slums are allowed to roam and scavenge whereas others are confined in unsuitable small spaces shared with humans. The scale of this agricultural activity varies in type and size and it can range from subsistence to small- to medium-size commercial enterprises with hundreds of small animals. In more densely populated slums, fewer animals are kept and enterprises are likely to be small scale; where more land is available, livestock keeping is more common and on a larger scale (Box 1).

Smaller species: Chickens and rabbits

Chickens are animals most commonly raised in slums. One or two hens and one rooster roaming free with a few chicks is a common sight. It is not uncommon to find medium (10–30

Box 1 Livestock keeping in Dagoretti district, Nairobi, Kenya

Dagoretti District lies to the west of Nairobi city, 12 km from Nairobi city center. It is one of 8 urban districts in Nairobi and has around one-tenth of the total population. Most inhabitants live in tin-roofed timber houses with inadequate access to piped water, sanitation, and electricity. Unemployment (approximately 60%), human immunodeficiency virus-acquired immune deficiency syndrome, crime, and homelessness are persistent problems. Dagoretti was originally outside the city of Nairobi, but when the boundaries were extended in 1963, it became part of the city. Dagoretti district has both government and ancestral land. Some ancestral land has been sold to migrants, and government land has also been allocated to individuals. In some areas, squatters live on land temporarily leased out by landlords, a loose agreement, which can be revoked at any time. The population in the last available census was 240 509 up from 41 409 in 1969, a vivid illustration of the rapid growth of cities. Of the population, 42% are below 19 years of age, an age distribution that is also typical of developing countries.

A recent survey characterized livestock keeping in Dagoretti. More than half the households kept animals: in order of declining popularity: dogs (39%); poultry (39%); cats (37%); sheep and goats (14%); pigs (10%); and cattle (1%). A few households kept other animals including, rabbits, donkeys, doves, turkeys, ducks, and geese. Dogs were kept mainly for security, cats for vermin control, donkeys for work, geese for security and food production, and the other species were kept mainly for food production. In addition, cattle manure is a valuable by-product used for urban crop and vegetable production, and livestock are an easily liquidated asset that can be sold to meet urgent household needs or act as pledge enabling access to credit. Moreover, farmers report deriving social and psychological benefits from livestock keeping.

The study focused on dairy cattle kept by 1 in 80 households in Dagoretti. Farmers kept an average of three cattle. Nearly all households kept productive breeds, used artificial insemination, and zero grazing. Farms produced approximately 12 l of milk a day, and 88% of this was sold with the rest being consumed in the household. Most of the milk produced is sold in the community through informal markets. All sales of milk earn farmers in Dagoretti approximately US610 000 per year. Farmers reported that both demand and production are increasing.

chickens) to larger layer flocks (up to 100 chickens) in confined spaces. Chickens are the most versatile of poultry, given the value added of egg production and the worth of the animal, live or processed. In slums with limited electricity or where the cold chain is not available, chickens and eggs are a quick and easy source of protein and income generation. Chickens have an additional value because they are used in religious ceremonies and offerings (Alves *et al.*, 2009). The breeds of chickens vary from region to region and some commercial breeds are seen in slums. Scavenging chickens are fed in the morning with leftover food and possibly with added corn or poultry meal. During the day, chickens eat insects, garbage, and organic matter found in empty lots or by the side of the road. Housing is rudimentary and may consist of hay or rice husks arranged in cardboard or wooden boxes and placed off the ground for protection from dogs and predators mostly during the night. Raising chickens is considered an easy activity requiring minimal labor and is usually performed by women and children (Food and Agriculture Organization, 2001).

Backyard flocks requiring additional attention compete for space with humans and other animals and are more labor-intensive requiring feeding, watering, and pen cleaning. Noise levels and manure disposal become a problem with larger flocks and are a deterrent for keeping them in small and crowded spaces. Larger flocks are more common in peri-urban areas than slums, but broiler chickens keepers may have more than 100 birds, as in the case in the Mombasa slum in Bangladesh where a bird keeper is reported to have between 125 and 250 birds (Sabuni, 2010). Live chickens are transported in cages or burlap bags to nearby food markets. These markets are located at walking distance from the dwelling where the animals are raised, although sometimes birds are transported in cages on top of buses or trucks to other urban markets. Chickens are sold live or slaughtered on site at the buyer´s request. Eggs have a longer shelf life (lasting 3–4 weeks without refrigeration depending on environmental conditions) than poultry meat. Eggs are wrapped in newspaper and kept in the shade to prolong their shelf life. They may be sold to neighbors in small numbers, as needed, for income generation or in larger numbers at markets. Other poultry kept in slums include turkeys, geese, doves, pigeons, quail, and guinea fowl.

Rabbits are gaining popularity in slums in Africa. They can be kept in small spaces in crates, either individually or in small groups. Rabbit crates are easy to build and can be kept stacked up against each other or leaned against a wall to occupy less space. These animals require more attention than scavenging or backyard flocks of chickens for feeding, watering, and cage cleaning. However, it is a profitable and uncomplicated business as evidenced by the number of rabbits a person can keep. One resident in the Kahawa Soweto slum in Nairobi has more than 400 rabbits in a shed (Kelto, 2013). Rabbits are fed greens collected locally and supplemented with vegetable leftover from markets or pelleted food. This is a small species that can reach to 4 kg of weight and can easily be processed locally as chickens for sale or family consumption. In a space of 30×40 feet, slum residents can raise more than 500 rabbits of different breeds. More unusual animals are also kept: a survey in Nigeria reported snails, grass cutters, and antelope among a total of 14 species kept.

Monogastrics: Pigs

Pigs adapt easily to urban conditions. One sow can produce 6–12 piglets twice or three times a year if their reproductive cycle is timed properly (pregnancy lasts 3 months, 3 weeks, and 3 days). Selling the piglets before birth is not uncommon at certain times of the year for events or festivities where pork is commonly consumed. Pigs are considered a form of saving account because piglets can be sold for cash or given in exchange for the boar´s service (the piggy bank). Boars can grow tusks and become very large and aggressive, requiring confinement to protect people and other animals. This is why fewer people keep boars compared to sows. Rearing of pigs in slums in small numbers (one to five) is often done by women and larger herds by men (Food and Agriculture Organization, 2001). Piglets are easy to manage because they can roam during the day searching for food and come back to their home space at night. They can also be tethered and kept close to the dwelling, or housed in makeshift pens behind or in the confines of the human dwelling.

Nowadays pigs are ubiquitous to slums in Latin America and present even in countries with Muslim and Hindu population such as India and Nepal (Rajshekhar, 2004). It is difficult to establish the genetics of pigs commonly reared in slums. These are smaller and more adaptable to the local conditions than large commercial breeds. Pigs revert to wild type very quickly and grow hair and tusks adapting to the environment. However, pigs kept in confined spaces in and small numbers are usually larger commercial breeds requiring more attention and feeding.

The creole pig from Haiti was an example of a small hairy dark pig well adapted to the environment, eating garbage and fallen rotten fruit. They had sociocultural value and were considered to have an important role in recycling waste. Issues associated with swine fever in the late 1970s and early 1980s prompted the United States Department of Agriculture and other international organizations to develop and conduct an eradication program. The sociocultural value of these animals was not clearly understood. People were given large commercial breeds as substitutes for the creole pig and asked to pen the pigs. The larger breeds had to be fed and cared for and were not allowed to roam, which resulted in detrimental conditions of the environment in which people lived (Ebert, 1985).

Ruminants: Goats and cattle

Goats are adaptable to urban environments. They are known for eating almost anything, including bark from trees and shrubbery, garbage from streets and land fields, or clothes hanging to dry. These animals require attention, given their inquisitive nature and destructive eating habits. Usually people keep a couple of female goats for their milk with the offspring. In slums close to peri-urban areas people keep the goats in pens or house patios during the night and walk them to pasture at different locations during the day. In the urban environment, and in particular in slums, goats roam the streets in search of food, and it is common to see them searching for food with pigs (Diogo *et al.*, 2010). Goats can decimate green areas very quickly, causing damage to vegetables growing by the side of the roads or public open spaces. They require more attention than chickens or pigs and they need shelter from the

rain. Goats' milk is nutritious and can be easily transformed into yogurt and cheese to extend the shelf life of an otherwise perishable product. In some large slums such as in Delhi, India, slum goats' sightings have become a tourist attraction and are offered as part of city tours (News.com.au, 2013).

Mixed *Bos taurus taurus* and *Bos taurus indicus* cattle are let free in search of food or water or walked to pasture in the mornings and brought back at night. In countries with a predominantly Hindu population cows are sacred and only the milk is consumed. Oxens are mainly kept for draught power; they are used for plowing and also transport. Owing to religious reasons female cattle cannot be disposed of after their productive lives have ended. Older unproductive animals may be abandoned and may die of diseases, hunger, intoxication from garbage, or get involved in traffic accidents. There are also many *goshalas* in India where abandoned cattle are looked after. Milk is a valued product that contributes to food security in slums. But it is perishable and has to be consumed quickly or transformed into a variety of cheeses, yogurt, or sour milk. Naturally fermented sour milk is popular in East and West Africa; fermenting also removes lactose, which makes it easier to digest for populations that do not have lactase enzymes persisting in adulthood.

Tending larger animals is time consuming and may involve walking long distances to find a place to feed away from the city or to cut grass that can be brought back to the animal. This is easier to do when the slum is located in the periphery of a city compared to an urban-area slum. Often cattle are confined to a small space or their mobility may be limited by tethering them close to the dwelling. Studies of peri-urban dairying in East Africa found that nearly all cattle were 'zero grazed,' that is, kept inside all the time (**Figure 2**).

Cow dung in India is also a valuable fuel: it is collected, reshaped into cake-like forms, and dried. In India and elsewhere cattle dung is also used as a building material mixed with mud and other substances. Livestock value is more than monetary; it is a symbol of social status and social identity both individually and collective (Comaroff and Comaroff, 1990). The value of livestock and the production parameters used elsewhere (such as in the industrial countries) need to be revaluated because a cow or goat whose production is low may still be providing useful services (Dutta, 2003).

Production Challenges in Slums

In slums, an intricate relationship exists between poverty, food security, livestock keeping, and the environment. Enforcing livestock regulations becomes a difficult task when animal ownership is clandestine. In many countries regulations cover animal health and welfare issues, the disposal of dead animals, slaughter procedures, and environmental contamination, but in practice they are not enforced in slums. In other cases, regulations are used for 'rent-seeking' by authorities: that is police or other officials will confiscate animals and not give them back unless a bribe is paid. Keeping animals in cities undoubtedly creates environmental problems. For example, in Kisumu, Kenya, keeping animals is illegal. The city has six slums and enforcing animal farming law is a challenge. The dung of the animals becomes a problem when the rain washes it and contaminates the city water supply. The city lacks the infrastructure to recycle the dung and 75% of it is not utilized (New Agriculturist, 2006). Yet the Draconian response of banning livestock from cities may not be the most appropriate. In Kampala, Uganda, a process lasting several years has recently led to new City Ordinances that seek to support urban agriculture as an important economic activity, while regulating against the potential adverse effects.

Burden of Disease

Animals of the same or different species in slums are in proximity with each other and with humans. Contagious diseases can spread rapidly under these conditions. Additionally, slum-raised animals suffer from malnutrition coupled with an adverse environment that makes them more susceptible to disease or injury (Food and Agriculture Organizations, 2011). Some problems are associated with animals living in areas with poor waste disposal. Pigs and goats eat plastic bags and these are common findings at slaughter or necropsy. The bags fill the stomachs impeding food digestion and nutrient absorption. Rwanda banned nonbiodegradable plastic bags in 2008, an excellent example for other African countries where plastic waste is ubiquitous.

The health of animals in slums requires attention, but estimating disease and its impact is difficult. Both zoonotic (diseases transmitted from animals to people) and nonzoonotic animal diseases need to be considered. Reportable, zoonotic, and production diseases are discussed elsewhere in this encyclopedia. Some of these diseases are of national public health interest or are of international trade importance requiring immediate reporting through specific official public health channels and to the World Organisation for Animal Health, one of the three sisters of the World Trade Organization. Reportable diseases of animals are those with the potential to cause epidemics or pandemics that cause serious disease in people, as is the case of the severe acute respiratory syndrome known as SARS, the H5N1 (pathogenic avian), and H1N1 influenza virus (known as swine influenza) (Gauthier-Clerc *et al.*, 2007; Girad *et al.*, 2010). Public health resources and market inspections are deployed for some of these diseases, but control is often ineffective in poor countries. Determining the public health penetration of these programs in slums has been highlighted as a need (Unger and Riley, 2007). Risk communication in a crisis situation involving the livestock population in a slum may require additional resources and targeted programming. The lack of information of the size and location of the avian and swine population may impede the progress of disease control measures. Public awareness programs or the application of rigid standards for disease control without consideration of the sociocultural and economic value of the animals for people may also decrease compliance (**Box 2**). References to the 1920 flu pandemic are always brought to light in the media as the possible serious consequences of disease spread and death. However, public health crisis response is different today and includes emergency and disaster preparedness, first responders training programs, and damage mitigation and relief. Nonetheless robust economic estimates by the World Bank suggest that the

Box 2 The unanticipated effects of disease control

A pandemic of H1N1 influenza was declared in 2009. This disease originated in pigs but subsequently was maintained entirely by human to human transmission. In response to the pandemic, the government of Egypt ordered all of the country's pigs to be slaughtered. Because humans can only get the new flu from other humans this was not effective as a control response. It also had far-reaching and unintended consequences on the cities' waste management. Cairo's 30 000 garbage collectors used to feed the city's organic waste to pigs and their livelihood became endangered while the streets of the capital filled up with trash.

Source: Adapted from the *New York Times* article, Mona el-Naggar contributed reporting, 19 September 2009. Available at: http://www.nytimes.com/2009/09/20/world/africa/20cairo.html_r=2&scp=1&sq=michael%20slackman%20cairo%20pigs&st=cse& (accessed 30.01.14).



Figure 1 Cysticercus in pig muscle, Bolivia.

cost of an epidemic originating in animals could be a trillion dollars (World Bank, 2012).

There are approximately 1000 zoonoses or diseases transmitted from animals to humans. Disease transmission may be direct through contact with infected animals or its fluids, or through contaminated animal products, water, or objects contaminated with infectious material (Center for Disease Control and Prevention, CDC 24/7, 2011). Especially important for poor countries are the so-called neglected zoonoses often associated with poverty, poor hygiene, and poor understanding of disease transmission. The rest of the article discusses some neglected zoonoses that are known or likely to be a problem in slums.

Brucella melitensis, the cause of brucellosis, is very pathogenic to humans (Center for Disease Control and Prevention, 2012). It is transmitted from goats and sheep to humans through direct or indirect contact. Unpasteurized milk or contact with body fluids of infected animals are considered the most common transmission routes. There are other brucellae affecting swine, cattle, and dogs, but *melitensis* is associated with the more severe forms of the disease. Flaying and skinning sheep by blowing air through a cut in the skin exposes people to body fluids and inhalation of bacteria from infected animal, and hence is not recommended.

Cysticercosis is a disease caused by the larval stage of the tapeworm *Taenia solium*. The disease is sometimes wrongly known as the 'the pig tapeworm,' but humans are the definitive host for the adult form of the parasite, not the pig. The adult parasite releases segments daily containing thousands of eggs into the gut. These eggs pass into the environment with the feces. Humans and pigs become infected and develop cysticercosis by ingesting the parasite eggs. Pigs are coprophagic and human defecation in open spaces is one of the main forms of transmission of the disease from humans to pigs. When eaten by pigs, the eggs develop into cysts within the pig (**Figure 1**). If people eat meat containing viable cysts these can develop to tapeworms in the human host, thus completing its cycle. Human to human transmission occurs when people harboring the parasite contaminate food due to poor hand hygiene (Garcia *et al.*, 2001; Carrique-Mas *et al.*, 2001). Autoinfection can also occur following improper hand washing after a bowel movement. After humans consume eggs, cysts start to develop in any organ of the body, including the brain. When cysts develop in the brain, the disease is known as neurocysticercosis. It is considered as one of the most common infestations of the brain in humans. The main manifestation of the disease is epilepsy (Garcia *et al.*, 2001). Studies from a slum in India revealed that 25.5% of people in the studied sample who had active epilepsy had antibodies to *T. solium* (Singh *et al.*, 2012). Cysticercosis in pigs may reach 30% prevalence or more in some countries where pigs are allowed to roam and human defecation is done in the open (Carrique-Mas *et al.*, 2001; Fleury *et al.*, 2012; Flisser *et al.*, 2003). Even with low human taeniasis in the order of 1–2%, the prevalence of cysticercosis in pigs can be high. This is mainly due to the fact that only adult parasite can live in the intestine of the host for years and release thousands of eggs into the environment.

Hepatitis E virus is an enteric disease transmitted from different species of animals including pigs to humans; it can be transmitted between humans through contaminated water and food. The seroprevalence in the human population unexposed to swine is 2% whereas the seroprevalence in swine workers or other swine-exposed populations is 10% (Whithers *et al.*, 2002). Data from a study of a pediatric population in Karachi with access to municipal piped water and nonflush toilets in a slum in India showed a high seroprevalence for hepatitis E virus (Jafri *et al.*, 2013). The exposure to hepatitis E virus seems lower than hepatitis A (Mohanavalli *et al.*, 2003). Hepatitis E is a disease that can cause severe gastrointestinal symptoms and has been associated with high death rates of pregnant women in lesser developed countries. In some peri-urban farms pigs are raised close to ponds where fish are kept. The pig feces are washed down to the ponds for the fish to eat. The virus seems to be ubiquitous in swine populations and undistinguishable even in samples from different countries. This was the case in hepatitis E study in two farming communities (not slum conditions), in North Carolina and Costa Rica (Whithers *et al.*, 2002; Kase *et al.*, 2008). Hepatitis E is a zoonosis, but the importance of animals in its maintenance and transmission has not been fully established.



Figure 2 Zero grazed cattle, Kenya.

Cryptosporidium is associated with cattle and causes diarrheal disease in humans and cattle. Although extensively studied in developed countries, it has not been diagnosed until recently in slums. Surveyed households in the Nairobi´s Dagoretti district, Kenya, determined the extent of cattle keeping and the prevalence of cryptosporidiosis. With a prevalence of 20% in urban cattle, this parasite could be a major contaminant of water sources and disease that needs further consideration (International Livestock Research Institute, 2012) (**Figure 2**).

Antibiotics and other veterinary drugs administered to animals without proper veterinary supervision can have direct and indirect consequences for human health. After administration of an antibiotic there is a period of time when the animal product should not be consumed. This period known as the withdrawal period is to allow the drug in question to clear the animal's system because it may have harmful health effects if consumed by people who are allergic or sensitive to the drug. For example, Clenbuterol is commonly used as a growth promoter (often illegally), and several outbreaks of illness have occurred when people consume livestock products from animals treated with Clenbueterol. Of potentially greater importance than sickness as the result of consumption of residues is the risk of bacteria developing resistance to antibiotics because of their use in agriculture. As a result of these concerns, many countries require that antibiotics and some other animal health drugs should only be prescribed by veterinarians. However, this is not practicable in most slums. Veterinary services may be out of reach for many people in slums either because of distance or cost. In some cases, livestock owners may visit a veterinary office and explain the symptoms of the disease to the veterinarian, but without proper examination of the animal and the information received, the medicines may not be appropriately prescribed. The livestock owner may not fully understand how to administer the medicines and use a single dose of a medicament keeping the rest in case the animal does not improve. Getting advice from another family member or neighbors, purchasing a single dose of an antibiotic from a street vendor, or using leftover medicines from a previous case is not uncommon. Veterinary services are often expensive and out of reach of the poor (Ahuja *et al.*, 2003).

In addition, farmers may use drugs for nonhealth purposes. In Khartoum, the practice of adding antibiotic to milk to preserve it was reported, and this could have health consequences such as allergy in the people ingesting the product (Hassabo *et al.*, 2012). In China, melamine was added to milk so that it would appear to have higher protein levels. This lead to one of the largest food safety events of recent years resulting in the death of six infants; the children died from kidney stones and thousands were hospitalized as a result of drinking the contaminated milk (Wei and Liu, 2012).

Markets

Slum agriculture and associated markets are part of the informal sector of the economy. It is a business model based on necessity, mostly home-based, and often clandestine. When there is no proper access to water and refrigeration, meat and eggs must be consumed rapidly, processed, and sold close to the place of origin. Markets in slums are public places where vendors congregate. Products may also be sold by hawkers moving from door-to-door or as requested. In many cities in developing countries milk is sold in this way. It is not uncommon to sell products from homes through modified window sills, from makeshift sale racks in corridors between houses, or on top of blankets or plastic sheets in the floor in open spaces. Slum dwellers acquire knowledge of who produces and sell different items. Prices vary based on perceived notions of quality, hygiene, or availability. The exchange of money is not always the norm for payment and people engage in bartering or exchanging products for services. Agricultural markets in slums differ from municipal markets where there is an operational legal framework and the state is responsible for the enforcement of public health and food safety regulations. However, the great majority of food sold in municipal markets lack any structured sanitary inspection. This does not mean that the markets in slums lack internal form of self-regulation, they have a *sui generis* operational business model. Although these markets are outside the purview of state regulation and disease control and preventative measures, the prevailing food-safety actions are based on accepted cultural norms. These norms are developed by the people who live, sell, and purchase products under these conditions or based on religious beliefs or restrictions (Rheinländer, 2006).

The number, identification of species, and location and ownership of animals in a slum is not usually performed. The lack of census data and owner identification poses a challenge for the implementation of national disease control or eradication programs. Required reporting of diseases and animal or product traceability to origin may be impossible in case of a food-related outbreak. This is contrary to the application of the Sanitary and Phtyo-Sanitary Measures of the World Trade Organization. Most countries agree to adhere to these measures when they join the World Trade Organization. Conducting an animal census in a slum is challenging but without knowing how many animals there are, vaccine campaigns or eradication programs cannot be conducted. However, the legally ambiguous position of livestock in slums mean owners are reluctant to incur official notice.

Slaughter

The inspection of animal facilities and product transformation industries destined for human consumption is highly regulated. Although in many developing countries animals must be processed in municipal slaughterhouses, at home and clandestine slaughter are common. In Bolivia, some of the municipal slaughterhouses are rudimentary and managed by the local communities. The official veterinarian is allowed to inspect the animals preslaughter and outside the facility. The inspection concerns mostly reportable diseases of national importance. Inside the slaughterhouse, skilled butchers castrate male pigs, and these and other animals bleed on the floor as part of the exsanguination process. Once the internal organs are removed the carcass is hung on a wall hook and employees rub the pigs´ canal with a rag. The same rag and water stored in a bucket is used to wash several carcasses. An inquiry into the practice revealed the employees neither understood why they were doing the cleaning nor how it was supposed to be done (Correa *et al.*, 2003). In Ibadan, Nigeria facilities are even less developed. Approximately 250–300 cattle are slaughtered daily; more are slaughtered on weekends, and fewer during Muslim holidays. Cattle are kept in pens, then moved to the slaughter slab. They are tied down at the slab and killed by cutting the throat. The dead cattle are then dragged on the ground to the abattoir area. This is simply a shed with a concrete floor and open sides. Removal of the intestines and quartering is done on the floor. Portions of the carcass are then carried to the adjacent butchers' stalls where they are sold. The abattoir is under municipal management and officers collect tax and tariffs on each cow amounting to US$1 per animal. The role of environmental sanitary officers is to inspect slaughter slabs and the general environment and ensure the area is clean. However, the filthy conditions of the market witness the challenges they face in carrying out their work. The veterinary department is supposed to check animals before slaughtering and inspect meat after slaughter, but many animals escape inspection, and even when problems are found veterinarians find it difficult to ensure condemned meat is discarded. Most butchers kill only one animal a day, and if this is condemned by veterinarians as unfit for human consumption they lose their entire day's earnings. Hence, they strongly resist attempts to condemn meat (Grace *et al.*, 2012).

Slaughter practices are probably clearly specified in pertinent regulations, but without oversight or evaluation by competent authorities, wrongly learned and applied practices may never be corrected. New employees learn from other employees and the practice is passed down, transformed, and perpetuated. The 'Trichina inspectors' in livestock markets in Bolivia are lay people trained by other people to inspect the tongue of pigs in order to detect cysts associated with cysticercosis. Trichina is a different parasite and the tongue inspection is not associated with this parasite, but *T. solium*. The wrong parasite reference has prevailed and the practice continues unchecked for efficiency in preslaughter diagnosis of cysticercosis in pigs. In Ecuador´s countryside, a traveling butcher works at the community slaughterhouses at scheduled days and times of the week and processes the carcasses of mainly large species at the municipal facility. This is a trained person who can condemn carcasses from sick animals and has an important food safety role. However, the most predominant form of slaughter in slums is the one done at home, in the streets, between or behind buildings. Usually for smaller species the head is removed using a sharp knife or axe against a hard surface like a piece of wood or the stump of a tree. The internal organs are removed swiftly; sometimes the esophagus and the rectum are tied to avoid intestinal content spillage and contamination. Animals processed in this manner are not properly exsanguinated. Raw offal may attract dogs and vermin. The meat, without refrigeration must be consumed immediately or it is left to dry on racks. Meat maybe carried to markets in small carts, buckets, or burlap bags and sold in small pieces or cut by the client´s request. The meat is not inspected when sold in the slums to neighbors or at smaller slum markets. In Nepal, animal parts are sold with other identifiable body parts like a hoof or horns in order to guarantee that the species being sold is the actual species. In many cases the meat is covered in turmeric, reported to be done to decrease contamination (oral tradition reported to authors by street vendors). Interestingly, homeopathy studies suggest that turmeric can help combat bacterial infections (Krup *et al.*, 2013; Vasavda *et al.*, 2013).

Conclusions

Slum livestock agriculture interweaves its existence with the geographic location and culture of the population. People take advantage of their new environment and recreate a way of living based on their upbringing, including raising and processing livestock. The main motivations for this activity are family subsistence, income generation, and social status. Slum livestock agriculture activities range from subsistence to semicommercial production. It plays a role in the livelihood of millions of people providing animal protein and generating income. However, it lacks technical sophistication and typically operates outside regulatory purview, and its practice overlooked and tolerated by local authorities. Animals pose a risk to human health and other animals, are a public nuisance, and contribute to the waste accumulating on streets and the run off contaminating the environment and water sources. Livestock products, raw or processed are sold in street markets and may enter the urban food chain. Animal ownership is difficult to establish in slums and livestock population difficult to determine. Under these circumstances, veterinary services and disease-control programs may be hard to implement. Good hygiene, good manufacturing practices, and animal slaughter inspection turn into an impossible task to implement and enforce. Disaster and white-coat diplomacy practices combined with information and communication technologies should be considered in the planning and implementation of public awareness and outreach programs (Lemery, 2010; Lin and Heffernan, 2010).

The elimination of the slums is not feasible. The magnitude of the animal population in slums is unknown, but its food security importance is getting recognition from public and private organizations. There is a need for a community-led approach in collaboration with private and public institutions, academic, international, and nongovernmental organizations to find sustainable solutions.

See also: Agricultural Ethics and Social Justice. Animal Health: Ectoparasites. Animal Health: Foot-and-Mouth Disease. Beef Cattle. Critical Tracking Events Approach to Food Traceability. Dairy Animals. Emerging Zoonoses in Domesticated Livestock of Southeast Asia. Food Chain: Farm to Market. Food Security: Food Defense and Biosecurity. Poultry and Avian Diseases. Regulatory Conventions and Institutions that Govern Global Agricultural Trade. Small Ruminants in Smallholder Integrated Production Systems. Swine Diseases and Disorders. Zoonotic Helminths of Livestock

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World Trade Organization.

Small Ruminants in Smallholder Integrated Production Systems

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Glossary

Agropastoralists Producers who practice sedentary farming as well as temporary migration with livestock.
Caprinae Of or relating to goats.
Fat-tail or fat-rump sheep Domestic breeds of sheep found in North Africa, the Middle East, East and Central Asia; fat stored in the rump and tail is reserve source of energy during periods of sheeps nutritional stress; also used as food for humans.
Hair sheep Breeds found in hot, arid regions; hair fibers outnumber amount of wool fiber, resulting in shorter and smoother hair coat.
Mitochondrial deoxyribonucleic acid (mtDNA) The genetic material (DNA) contained cell structures important for creating energy; mtDNA is inherited only from females.
Pastoralism Pastoralists migrate in set patterns taking with them their flocks as well as family members.
Phylogenetic Relating to the development or evolution of a particular group of organisms.
Phylogeographic Relating to study of the processes controlling geographic distribution of lineages by constructing the genealogies of populations and genetics.
Urial Subspecies of wild sheep; most notable feature is the enormous curling horns on the rams.
Zoonotic diseases Diseases that can be passed from humans to animals and vice versa; tuberculosis is an example.

Origins of Small Ruminants

Evolution and Genetic Diversity

Studies of the earliest known existence of sheep and goats are based on Eurasian fossils 15–18 million years ago. During the late Miocene period, Caprinae evolved rapidly. It is one of the bovid subfamilies and species within it can be found across most of the world. Owing to its evolution in Eurasian mountainous regions, Caprinae species can tolerate temperature extremes occurring in such ecoregions (Estes, 1991; Hernandez-Fernandez and Vrba, 2005; Vrba and Schaller, 2000).

Lines of descent and ancestries between wild and domestic goats are clearer than those between wild and domestic sheep. Mitochondrial deoxyribonucleic acid (mtDNA) research has been used to track the domestication of both species. Such studies have revealed differences between diverse wild goat species and domesticated ones. Because there is no mtDNA recombination in females, genetic studies of samples revealed three ancestral lines with each having one set of chromosomes different from the other. Using these studies, researchers deduced that female Bezoar goats, the major contributor of modern goats, were captured during three separate times in three geographically separate locations, each one contributing to the formation of the early domestic populations. Even after thousands of years of interbreeding, mtDNA sequences from diverse wild species remain phylogenetically distinct (MacHugh and Bradley, 2001; Luikart *et al.*, 2001). Further research concluded that there are six lineages in Europe and Asia (Sardina *et al.*, 2006).

Where wild and domestic sheep are located within the same region, they can also interbreed, but unlike goats, sheep usually do not revert to a feral state. Moreover, unlike goats, researchers have not yet defined a precise lineage from wild to domestic sheep (Hiendleder *et al.*, 2002), although three major and distinct lineages were defined by DNA and mtDNA studies using European, African, and Asian domestic sheep (Pedrosa *et al.*, 2005).

Lineages were classified as Type A (Asian), Type B (European), and Type C (from modern sheep of Turkey or China). Another study determined that a Bronze Age sheep in China was Type B, leading researchers to conclude that it may have been introduced sometime in the fifth millennium (Guo *et al.*, 2005).

Scientists believe that these lineages descended from a different wild species of the genus *Ovis* (*Ovis gmelini* spp.) in the Fertile Crescent. This genus is highly polymorphic and includes several Eurasian wild sheep that may be ancestors of domestic breeds. There are several hypotheses about domestic sheep descending from wild ancestors. Origins include the European and Western Asian mouflon, the Asian urial, and the Asian argali. Asiatic mouflon continue to live in Asia Minor and Southern Iran, whereas European mouflon can be found on the Mediterranean islands of Sardinia and Corsica.

Although the urial had been considered to be the progenitor of the majority of current domestic sheep breeds, including the hair sheep of Africa and Asia, domestic sheep of India and the Far East are more closely related to the argali; both urial and argali were found to differ from other *Ovis* species in their number of chromosomes. This conflicts with the hypothesis of direct relationships, and further phylogenetic studies confirmed the absence of such evidence (Hiendleder *et al.*, 2002). In addition, more research showed major differences between the genetics leading to two possible explanations. One is the possibility that a heretofore unknown species or subspecies of wild sheep influenced the subsequent evolution of domestic breeds (Hiendleder *et al.*, 2007). Another conjecture relates domestic sheep breeds with multiple captures of wild mouflon over time (Meadows *et al.*, 2007).

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Phylogenetic studies have led researchers to conclude that the Asiatic (*Ovis orientalis*) species of mouflon is the progenitor of *Ovis aries*. The original geographic range of wild sheep is the Middle East or Central or Western Asia (Williams). This has led to the theory that the European mouflon could be one of the ancient sheep breeds that reverted to the feral state, rather than a wild sheep that became domesticated (Ensminger and Parker, 1986). Past literature often cites the mouflon as the ancestor.

Climate, specifically temperature and level of precipitation, most likely influenced the regions where small ruminants evolved. In comparison with sheep, goats are more adapted to a harsher environment with conditions of greater aridity, lower quality forages, and less water availability.

History of Domestication

The earliest known domestication of small ruminants occurred in the Near East approximately 11 000 years ago during the Neolithic era (Zeder, 2008), although it is posited that some domestication began before this period based on archeological findings in different locations. Evidence of animal domestication dates to the last glacial period when humans began to practice settled agriculture, including animal production for meat and milk. Sheep are reputedly the first species to be domesticated for meat consumption.

Researchers conclude that during the early Neolithic period, when animal domestication emerged as an agricultural practice, there were different animal management strategies specific to geographic and sociocultural practices. Zoo archeological analyses of ancient caprine bones and teeth have been used to differentiate animals that were domesticated versus those of wild animals that might have been hunted (Arbuckle, 2008). Goats can revert to feral conditions if the chance permits, which provides a way to document genetic changes.

As human populations expanded, people began to migrate, taking livestock with them westward from Mesopotamia (the Fertile Crescent) into Eurasia. Tracing the routes from the Neolithic period when the earliest evidence arises, human migration flowed into Europe along two major routes – the Mediterranean and the Danubian (Hiendleder *et al.*, 2007).

Sheep

Archeological, genetic, and phylogeographic research provide evidence that most sheep domestication occurred approximately 10 500 years ago in Western Asia and that the species most likely was domesticated three separate times in the Fertile Crescent (Western Iran and Turkey) – in Syria and Iraq. It has been posited that dogs, the first animals to be domesticated, most likely factored into the sheep domestication process. Ancestral species of wild sheep can be found extending from China to Western Europe and by 3500 BC several breeds had been established in ancient Mesopotamia and Egypt (Budiansky, 1999).

After domestication in Western Asia, humans migrated with sheep through the Sinai into Northern Africa. Artifacts show that sheep were kept in ancient Egyptian society seven to eight thousand years ago (Blench and MacDonald, 1999). However, different environments between North and South interrupted or prevented the gene flow.

The dispersal across Eurasia and Africa happened by separate migratory paths. The first migration period included the mouflon and other primitive breeds, whereas the second migration period included animals with more productive traits. It is most likely that these sheep shaped the majority of current breeds (Chessa *et al.*, 2009). However, between the early and the late Bronze Age periods (3000–1200 BC), sheep breeds evolved and spread through the Western Asian region (Ensminger and Parker, 1986). Four ancestral species of wild sheep have been identified. They are: the mouflon of Europe, the Middle East (Asia Minor), and Western Iran; the urial of Western Asia and Afghanistan; the argali of Central Asia; and the bighorn of Northern Asia and North America (Pereira *et al.*, 2009).

As sheep became more domesticated and raised under containment, morphological changes occurred; body size decreased, females lacked horns, and there were larger percentages of young animals indicating planned breeding. The characteristics of wild species, such as lack of aggression and high reproduction rates, were considered of merit (Budiansky, 1999). Economically important traits, such as wool type and milk production, became selection factors. Selection for wool might have begun approximately 6000 BC (Ensminger and Parker, 1986; Weaver, 2005) according to archeological evidence from statues found at sites in Iran (Hyams, 1972), although there is a lack of evidence that wool was used for clothing at that early date (Smith *et al.*, 1997).

Archeological sites with early evidence for sheep domestication include Iran (Ali Kosh, Tepe Sarab, and Ganj Dareh, which is one of the earliest settlements in the Middle East), Iraq (Shanidar, Zawi Chemi Shanidar, and Jarmo), Turkey (Cayonu, Asikli Hoyuk, and Catalhoyuk, which is one of the oldest civilizations on record), and China (Dashanqian).

Goats

The earliest evidence of goat domestication is recorded at 10 000–11 000 years ago. They were adapted from a wild species, *Capra aegargus*, by Neolithic farmers. Like sheep, they were valued for milk, meat, hair, bone, and sinew for clothing as well as manure used for fuel. Goat remains have been found at archeological sites in Western Asia, such as Palestine (Jericho), Russia (Choga), Turkmenistan (Djeitun), and Turkey (Cayonu), which allows domestication of the goats to be dated at between 6000 and 7000 BC.

Unlike sheep, tracing the lineage of goats by mtDNA research has been more definite. Recent research has proposed that all current goat breeds can be traced to a small number of wild animals and then domesticated in two primary regions – Turkey's Euphrates River valley during 11 000 before present (bp) and Iran's Zagros Mountains during 10 000 bp (Zeder and Hesse, 2000). Other domestication sites include Pakistan's Indus Basin (9000 bp), Turkey (Cayonu – 8500–8000 BC), Syria (8000–7400 BC), Israel (Jericho – 7500 BC), and Jordan (Ain Ghazal – 7600–7500 BC) (Fernández *et al.*, 2006).

Goats were reportedly introduced into Northern Africa with human migration from the Near East, although questions arose over time regarding their origins. To genetically characterize the indigenous goat population, one study combined

mtDNA and Y chromosome loci from a population on the northwestern fringe. Sequence analyses coupled with 2000 published mtDNA sequences showed a striking level of maternal and paternal lineage diversity. Further studies concluded that there was a strong genetic relationship between Northwest African and Near Eastern goat populations (Pereira *et al.*, 2009). Crossbreeding over time has resulted in several hundred goat breeds today ranging from high-altitude mountains to arid and semiarid deserts.

Animal Population Densities

Based on the FAO's Statistical database (United Nations, 2010), the total number of small ruminants globally equaled 1 987 453 552. Of this total, sheep numbered 1 077 762 456 and goats numbered 909 691 096. The Asian region as a whole contained 50% of the world total. Of the 50% of the world total, 59% were goats and 42% were sheep. Within Asia, the subregion of Southern Asia had the highest percentage of animals (24%), of which 33.5% were goats and 16% were sheep. Africa held 31% of the world total (34% goats and 28% sheep) and within Africa, the subregion of Western Africa had 10.9% of total small ruminants, of which 8.6% were sheep followed by Northern Africa subregion with total of 8.6% small ruminants, of which 10% were sheep. Goats predominated in three of five regions in both Asia and Africa where the mixed crop–livestock production system prevails. The following list delineates total numbers and percentages.

World – 1 987 453 552 total small ruminants
- Sheep = 1 077 762 456 (54% of total)
- Goats = 909 691 096 (46% of total)

Asia – 994 069 195 (50% of world total)
- Sheep = 454 703 708 (42% of world total sheep)
- Goats = 539 365 487 (59% of world total goats)

Eastern Asia – 317 086 887 (16% of world total)
- Sheep = 148 682 613 (13.8%)
- Goats = 168 404 274 (18.5%)

Southern Asia – 477 368 749 (24% of world total)
- Sheep = 171 718 980 (16%)
- Goats = 305 659 769 (33.5%)

Southeast Asia – 38 188 990 (1.92% of world total)
- Sheep = 11 715 175 (1.1%)
- Goats = 26 473 815 (2.9%)

Central Asia – 57 123 723 (2.9% of world total)
- Sheep = 46 817 000 (4.3%)
- Goats = 10 306 723 (1.1%)

West Asia and the Middle East – 104 300 846 (5% of world total)
- Sheep = 75 769 940 (7%)
- Goats = 28 530 906 (3.1%)

Africa – 609 022 313 (31% of world total)
- Sheep = 299 031 760 (28%)
- Goats = 310 890 553 (34%)

Northern Africa – 171 368 910 (8.6% of world total)
- Sheep = 110 021 270 (10%)
- Goats = 23 254 000 (2.6%)

Eastern Africa – 150 324 039 (7.6% of world total)
- Sheep = 58 775 230 (5.5%)
- Goats = 91 548 809 (10%)

Southern Africa – 40 324 744 (2% of world total)
- Sheep = 28 716 710 (2.77%)
- Goats = 11 626 034 (1.3%)

Western Africa – 215 749 920 (10.9% of world total)
- Sheep = 92 635 850 (8.6%)
- Goats = 2 114 070 (1.3%)

Central Africa – 32 136 700 (1.6% of world total)
- Sheep = 8 882 700 (0.01%)
- Goats = 23 254 000 (2.6%)

(United Nations, 2010).

Predominant Breeds

Native breeds of small ruminants most predominant in the geographic regions where they are found are also known by local names and may be found in more than one region. Uses of the breeds are for meat, milk, and fiber, listed in parentheses after the breed names. The countries that are included in these regions are based on the United Nations Food and Agriculture Organization FAOSTAT website list, and details of specific breeds can be found in the list of relevant websites section at the end of the article.

East Asia – Cambodia, China, Mongolia, North Korea, South Korea, and Taiwan
- Sheep – Altay (meat); Karakul and Kazakh (meat and fiber); and Khalka (meat, wool, and milk)
- Goats – Dagris, Baladi, and Shami (meat)

Central Asia – Azerbaijan, Kazakhstan, Kyrgyzstan, the Republic of Georgia, Russian Federation, Turkmenistan, Tajikistan, and Uzbekistan
- Sheep – Akhar Merino, Sargin (wool); Adal (meat and wool)
- Goats – Orenburg, Altay (mohair); Adal (meat and fiber)

Southeast Asia – Bangladesh, Bhutan, East Timor, India, Indonesia, Laos, Nepal, Pakistan, Malaysia, Myanmar (Burma), the Philippine Islands, Sri Lanka, Thailand, and Vietnam
- Sheep – Arabi, Balkhi, Araghi, Baluchi dumda, and Karakul (meat and wool); Kandahar Gadik and local Javanese thin tailed; Priangan of West Java; and fat-tailed sheep of East Java (meat)
- Goats – Barbari, Boer, Jamnapuri, Kabuli, Kandahari, Tahiki, Watani, and Zaraby (meat and milk)

Western Asia and the Middle East – Bahrain, Iran, Iraq, Israel, Jordan, Lebanon, Oman, Pakistan, Qatar, Saudi Arabia, Syria, Turkey, the United Arab Emirates, and Yemen
- Sheep – fat-tail – Arabi; Awassi (milk); Baluchi; Ghezel; Karakul; Taleshi, (wool); thin tail – Damani (meat, milk, and wool); Waziri (meat and wool); Assaf (meat and milk); and Balki (meat)
- Goats – Baluchi, Baladi, and Damascus (Shami) (meat)

Northern Africa – Algeria, Egypt, Libya, Morocco, South Sudan, the Sudan, Tunisia, and Western Sahara
- Sheep – Algerian Arabi; Uda; the Sudan; Tunisian Barbary – hair sheep (meat); Rahmani (meat, milk, and wool)
- Goats – Nubian (meat and milk)

Southern Africa – Botswana, Lesotho, Namibia, South Africa, and Swaziland

- Sheep – fat tailed – Blackhead Persian; Danakil (Adal); Damara; Dorper; Meatmaster; Pedi; Van Rooy; Zulu (meat); Dohne Merino; South African Meat Merino (meat and wool); Namaqua Afrikaner; and Ronderib Afrikaner (Cape fat tail) (meat and pelts)
- Goats – Boer; White Savannah; Nguni; Pedi (meat); and Angora (mohair)

Eastern Africa – Burundi, Djibouti, Eritrea, Ethiopia, Kenya, Madagascar, Malawi, Mauritius, Mozambique, Reunion, Rwanda, Seychelles, Somalia, Uganda, the United Republic of Tanzania, Zambia, and Zimbabwe

- Sheep – Adal; Berbera Blackhead; Danakil; Masai (Red Masai); Tanganyika Short tailed; East African Fat-tailed type – hair sheep (meat)
- Goats – East African (meat); Galla (Bora and Somali) (milk); Kenyan dual purpose goat (meat and milk); Nubian (meat, milk, and hides)

Western Africa – Benin, Burkina Faso, Cape Verde, cote d'Ivoire, Gambia, Ghana, Guinea, Guinea-Bissau, Liberia, Mali, Mauritania, Niger, Nigeria, and Senegal

- Sheep – Uda; Cameroon Sheep – hair sheep (meat); Peul; Bali-Bali; Maure; Guinea Long legged; West African Long legged – hair sheep (meat and milk)
- Goats – Djallonké (African, West African Dwarf, and African Pygmy); Chevre Naine, Chevre de Casamance, Hausa, Kosi, Mossi, Cameroon Grassland, Kirdi, and Kirdimi (meat); Boer; Guinean goats (meat); Sahelian (Fulani and Tuareg) (milk, meat, and skins)

Characteristics and Species Differences

Environmental changes over the centuries have influenced human and animal movements as well as adaptation and coping strategies. Many morphological differences of small ruminants evolved with their domestication as breeding for specific traits became important. Hair or wool sheep, fat- or thin-tail sheep, and fat-rumped sheep are examples as are breeds of goats that produce dairy, meat, or specialized fiber, such as cashmere or mohair.

In tropical regions of Africa and Southeastern Asia, hair sheep are most common.

As all sheep have a mix of hair and wool fibers, the difference between hair and wool sheep is the ratio between the two kinds of fibers the animal contains. This ratio depends on the origin and the climate in which the stock is produced. In more arid and hotter regions, hair fibers outnumber the amount of wool fibers, resulting in a shorter and smoother hair coat with very little wool. In colder climates, the opposite ratio occurs, producing a greater number of wool fibers versus hair fibers. Difference in management relates to labor required for shearing (wool sheep) versus combing or natural shedding (hair sheep). There are also differences in traits and characteristics of hair versus wool sheep, for example, hair sheep have lower reproduction efficiency but higher tolerance for arid climatic conditions without major loss of productivity and survival ability when feeds are limited or of low nutritional value (Bradford and Fitzhugh, 1983).

In extremely arid regions, such as Mongolia, Northern India, Pakistan, Western China, Central Asia, the Near East, the Middle East, and Southern and Eastern Africa, some sheep breeds have survived since 2400 BC. The unusual characteristic is the high level of fat stored in the rump and tail, which is a reserve source of energy during periods of nutritional stress for the sheep as well as a food product for human use. For this reason, fat-tail sheep are rapidly replacing the native thin-tail breeds in Indonesia, especially on the island of Java.

As with sheep, goats in arid/semiarid climates or other extreme environments exhibit characteristics that enable them to survive and thrive where temperate climate breeds might not. In pastoral societies where livestock are produced on rangelands of variable forage quantity and quality, goats can survive in harsh or degraded environments by maintaining body condition during feed or water shortages. They are able to walk for very long distances in search of food and exhibit ability to find and assimilate browse that sheep or cattle cannot use. Females have low abortion and stillbirth rates, produce strong kids at birth that aids in survival rates, and produce good yields of milk. A combination of such traits provides a level of protection against other risks in the production system (Fitzhugh and Bradford, 1989).

Although most domestic goats are produced at lower altitudes, a few breeds produced for fiber, specifically pashmina or cashmere, are raised at high altitudes where extremely cold winters prevail. The high Himalayas and the Gobi desert in both Inner Mongolia and Mongolia are such regions. The Pashmina or Changra breed thrives in this environment. The inner wool (cashmere) grows in the winter and is shed in the spring when it is collected and spun. One characteristic of this breed that is different from sheep and other goat breeds is that it eats both grass and grass roots. As a result, mismanaged grazing of large herds can produce significant environmental damage.

Behavior

One common behavioral difference between goats and most sheep breeds is the instinct for sheep to bunch together for mutual protection. Sheep are more clannish than goats due to a strong gregarious tendency and innate need for protection where natural predators can be found. If cornered, sheep may try to escape or maintain an aggressive behavior posture. Goats are more inquisitive than sheep and explore their surroundings independently rather than as a herd. They display a more assertive behavior than sheep and are less likely to run from apparent danger.

Feeding habits

Most breeds of sheep are selective grazers due to their anatomical split-lip structure that enables them to thrive in environments that have variable forages. Taste buds develop in the fetal stage and the lamb begins to nibble available feeds soon after birth. Depending on the production system, the availability of forage or feed varieties may be limited, thus reducing the choices sheep have. However, some breeds, such as Dorper, Meatmaster, and Blackhead Persian, are nonselective and tend to browse like goats. This enables them to access a higher level of nutrition than other breeds and be productive in environments where other breeds might not survive.

Sheep thrive in monoculture pastures, whereas goats require forage variety. Hence, they browse to select a diet that includes tree or shrub leaves, twigs, grasses, weeds, and roughages, often climbing up trees to access the leaves or standing on hind legs to reach lower hanging branches. They tolerate bitter tasting plants better than sheep (which may account for browsing forages more bitter than grasses) as well as reject urine or feces-tainted forages. Like camels, goats can tolerate limited water intakes, whereas sheep require a more consistent supply. When temperatures reach the 100 °F mark (38 °C), goats pant less than sheep, thus reducing moisture loss through sweating as well as feces and urine elimination (Devendra, 1989).

Genetics

Tropical ruminant breeds vary in genetic potential for a variety of traits. Positive traits include heat tolerance, disease, and parasite resistance. Some examples include the Red Masai sheep, which is genetically resistant or less prone to infestation with intestinal worms; Uda sheep of Northern Nigeria, which are much less susceptible to foot rot; and the Dorper, the second most common breed in South Africa, has low susceptibility to internal and external parasites. The West African Dwarf goat, the predominant breed of the humid tropics from southern West Africa through Central Africa, is trypanotolerant. The Savanna goat is heat and pest tolerant, adapts to mixed climates, needs little management, and has a natural resistance to tick-borne diseases, such as heartwater and other external parasites. Similarly, the Djallonké breed is trypanotolerant and resistant to parasitic diseases.

As noted, fat-tail sheep breeds are tolerant of extreme aridity, whereas cashmere breeds of goats are adapted to an extremely cold environment.

Smallholder Production Systems

Classification of Systems

In developing countries, the term 'smallholder' is used to describe producers with limited resources, i.e., resource-poor or subsistence farmers. This definition may differ among countries and agroecological zones as economic strata exist within all production systems (Dixon *et al.*, 2004). In terms of agricultural systems, the three most basic resources are land, labor, and capital. Access to inputs and supplies are additional necessities.

Pastoralists could be classified as resource-poor producers as they provide labor for raising livestock but rarely own the land their livestock graze on. However, not all pastoralists are resource poor. Livestock are their capital and have been termed a living savings account. This section applies the resource-poor or smallholder producer definition to pastoralists as well as to nonpastoralists, given that the majority of them fit the definition.

Livestock production systems in developing countries are commonly described by the ecosystem conditions in which the animals are raised. Several production systems can be found within the same country depending on the environment, ecology, and human population size as well as on economic and sociocultural factors that promote or inhibit specific livestock species from being produced. Management practices, including gender roles, differ according to system as does the nutrition of livestock, reproduction rates, and health challenges. Climate change is impacting traditional systems, and the interactions among livestock and environmental and human health (including human nutrition) is dynamic. Production systems are changing as producers adapt to climatic changes or adopt coping methods to preserve their traditional practices as best as they can.

Regional environmental conditions are used to define livestock production systems.

The primary livestock production systems and the environments in which they are found are:

- pastoralism/agropastoralism (extensive, rangeland based/partially settled) – arid and semiarid zones;
- integrated mixed crop–livestock (crop-based) – humid/subhumid zones;
- intensive (large numbers of animals in confined conditions) – temperate zones; and
- periurban/urban (around or in cities or slums) – humid/subhumid zones and temperate zones.

The geographic regions where these environmental zonal systems are located are:

- arid/semiarid zone – North and West Africa, East Asia (Mongolia), South America (Andean Mountain range or Altiplano), Western USA, and Northern Australia;
- humid/subhumid zone – parts of Africa (coastal zones and southern region), South and Latin America (northern Andean mountain range), and South Asia; and
- temperate zone – Americas, Europe/Eastern Europe, and New Zealand.

The focus of this section is on smallholder production systems in the arid/semiarid zones of North and West Africa and of East Asia and the humid/subhumid zones of coastal zones and southern region of Africa and of South, Southeast, and Central Asia extending into parts of the Middle East.

Each of the production systems includes sheep and goats, although populations vary depending on culture, uses for their products (meat, milk, fiber or skins, manure, generation of household income, or barter), climate, input availability including service delivery (such as animal health), and availability of labor. Because many breeds are adapted to harsh environmental conditions and can convert lower quality forages into usable products, the species fill an important need in developing country smallholder production systems. They are used to diversify risk from failing crop harvests or lack of feed for large ruminants due to drought or floods or from economic shocks resulting from low prices for crops. Because they reproduce more quickly than cattle, they provide a quick return to investment (Gutierrez, 1985).

The two most commonly found systems in developing countries of the Asian and African regions are pastoralism/agropastoralism or mixed crop–livestock systems in the humid/subhumid zones. Pastoralism involves grazing larger size herds or flocks than mixed crop–livestock systems where animals most commonly are confined (Safilios, 1983).

Pastoralism/Agropastoralism

Extensive, rangeland based/partially settled – arid/semiarid climate

Description of system

Both the northern and southern hemispheres contain arid and semiarid desert climates. These are defined as areas with short growing seasons where rainfall ranges from 0–300 mm to 300–600 mm, respectively. Owing to intense dry heat and light winds moisture evaporates quickly. Average air temperature is 16 °C. Arid deserts cover 12% of the Earth's land surface (Lohmann *et al.*, 1993).

A semiarid climate predominates in regions between the arid deserts and more humid climates. Average temperatures are 24 °C (43 °F) and annual precipitation varies from less than 10 cm (4 in.) (Lohmann *et al.*, 1993) in the driest regions to 50 cm (20 in.) in the moister grassland steppes of Eurasia in the Ukraine and east into Russia. Semiarid conditions also exist in colder highland climates, such as the Andean Mountain range in South America, Mount Kilimanjaro in Africa, and the Tibetan Himalayas.

Seasonal migration is an important characteristic of pastoralism because it enables access to forage as well as breaks up crusted soils as herds/flocks transit the land. Small ruminants are combined with large ruminants (cattle or camels depending on location) to diversify risk. However, sheep may compete with cattle or wild sheep or other herbivores for limited grazing resources.

Air temperature and rainfall determine the ecology of arid and semiarid ecosystems and thus influence the use of the land. Intense heat, low levels of readily available water often at great distance between sources, and lack of forage or grasses affect the smallholder's choices of species and breeds of small ruminants that can be raised in the region. A producer's lack of access to higher quality feed, animal health supplies, technical advice, and availability of markets for the livestock influence decision making, adoption of new practices, or adaptation to situations unfavorable to increasing numbers of animals or improved genetics.

Pastoralism is an important production system in the drylands – nearly half of the land area of sub-Saharan Africa and one-third of the world's land surface. It contributes significantly to food security in the Horn of Africa and a source of livelihood for approximately 200 million people worldwide (Nori *et al.*, 2005).

Although there is no annual census of global pastoral/agropastoral populations, it has been estimated that approximately 120 million produce livestock worldwide, of which approximately 42% reside in sub-Saharan Africa. The Sudan, Somalia, and Ethiopia contain the largest populations. However, in some countries pastoralists represent the majority of the population (Rass, 2006). The number of animals raised by these populations varies with climate, the availability of water, and forage. As of 2010, Western Africa had a larger number and proportion of small ruminants than Eastern Africa (United Nations, 2010).

Geographic location, social organization, national government policies, national economic status, and evolutionary history of people and animals combine as parameters that influence production practices. Pastoralists migrate in set patterns taking with them their flocks as well as family members, moveable shelters, and food. Agropastoralists are partially settled and produce a small amount of crops to feed the family members that remain at the household while other members migrate.

Livestock management practices

Pastoralist managerial practices include movement and migration with livestock; supplementing livestock with feeds when necessary and if feeds are available; coping or adapting to extreme weather variations; determining whether to sell animals during crises; and disease management if technical assistance or supplies are available, accessible, and affordable. Sociocultural practices of pastoral communities serve to bond related families and provide a foundation for protection or compromise when others compete for rangeland forage and water.

Gender roles are well defined irrespective of whether they are pastoralists or agropastoralists. An agropastoralist family divides during specific seasons, leaving the women and young children at the residence, whereas men and older boys migrate with flocks in search of forage and water. Women and young children often raise a few sheep and goats within the household area. Social norms in pastoral societies confer small ruminant management as well as milking, milk processing and sales, and use of milk for domestic consumption on women. Women may also be traders or marketers of small ruminants, although this depends on their level of business knowledge and the latitude of societal norms in their subculture. These might include whether or not they are allowed to own or have access to livestock assets, their status as single or married women, whether or not they head the household due to absence of a spouse, and the predominant roles of the men in their subculture (Sikana *et al.*, 1993; Ridgewell and Flintan, 2007; Aklilu and Catley, 2009).

Livestock nutrition

Zonal ecology determines primary feeds or forage that varies by location. Both sheep and goats shift preference from forage classes and grasses in the wet season to browse in the dry season. Trees, shrubs, subshrubs and grass, moist, broad leaf, wooded savannah, and dry thornbush scrub are among forage browsed by goats in this agroclimate. As grazers, sheep are more limited in forage selection depending on the geographic areas and ecosystem in which they are raised. Seasonality and the availability of grasses or browse may influence a pastoralist's mix of species in the herd (Sidahmed, 1996).

Livestock reproduction

Pastoralists are extremely familiar with the animals in their herds/flocks and employ identification systems similar to large-scale producers in nonpastoral systems. Selection factors include animal body size, level of milk production, drought tolerance, and parent and grandparent features. One study in Northern Kenya documented the intricate memory system some producer groups used (Mbuku *et al.*, 2010). Record keeping also includes dates of birth, castration, new stock, weaning, culling, performance, and health (Ayantunde *et al.*, 2007). Ear notching and coat color are two physical means of identification.

Certain groups select animals for breeding based on body size and milk yield, whereas drought tolerance, fertility, mothering ability, and prolificacy are less important. Other producer groups consider large body size, drought tolerance, and offspring quality as important but fertility, meat or milk production, and mothering ability as less significant. Therefore, although producers may use similar criteria for selecting breeding stock, they differ in which traits are most important for individual consideration. A high level of productivity, although important, is not always the most significant factor. Some breeds or types are recognized for specific products and are selected primarily to produce meat (e.g., South African Boer, Galla, and East African goats), milk (e.g., Somali and Jamunapari), or fiber (cashmere). One important drawback to selecting for high productivity traits is that such animals may exhibit lower resistance to disease or adaptability to long droughts and decreased availability of water or forage.

Livestock health challenges

In this production system, primary health challenges are: Peste de petite ruminant (PPR), brucellosis (primarily in goats), circling disease, helminths, Q fever, contagious caprine pleuropneumonia (CCPP – a major disease of goats), capripox, ticks and tick-borne diseases, tsetse flies and trypanosomiasis, anaplasmosis, babesiosis, and cowdriosis. Vaccines and medications are in use for many of the diseases, but pastoralists may not be able to access or afford them. Weather events, such as prolonged and more frequent droughts, aberrant rainfall, or flooding, are occurring more frequently and unexpectedly, resulting in higher numbers of livestock displacements, sickness, and death. These events are creating microenvironments that are optimal for disease pathogens or vectors to occur where they have not been found before, forcing livestock and producers to confront greater health challenges than in the past.

Integrated Mixed Crop–Livestock and Periurban Production Systems

Crop-based – Humid/subhumid climate

Description of systems

Humid and subhumid climatic zones include tropical forests and savannas, where seasonal changes result in very wet and very dry seasons, and boreal and deciduous forests. Temperatures range from 16–18 °C (60–64 °F) in the savannas and rainforests to 31 °C (56 °F) in deciduous forests. Although boreal forests are considered to be humid, one exception is Western Siberia where precipitation is low, thus creating a subhumid or semiarid climate type. There is a wide swing in temperature through the year with lows of −25 °C (−14 °F) and highs of 16 °C (60 °F). Referencing the Koppen–Geiger climate classification system, annual precipitation varies widely depending on geographic location and ecosystem from a high of 262 cm (103 in.) in rainforests to 0.25 cm (0.1 in.) in savannas.

The Amazon Basin, Congo Basin of equatorial Africa, and the East Indies from Sumatra to New Guinea are all classified as humid/subhumid tropical rainforests. Savannas are found in India, Indochina, West Africa, Southern Africa, South America, and the north coast of Australia. Northern China and Central and Eastern Europe contain deciduous forests. Boreal forest climates are in Central and Western Alaska, Canada, from the Yukon Territory to Labrador, and in Eurasia, from Northern Europe across all of Siberia to the Pacific Ocean. Small ruminants can be found in all of these regions.

Increasing urbanization has led to income inequities, economic insecurity, and urban poverty, forcing some smallholder producers to earn income from off-farm labor, although opportunities may be limited. To supplement such income smallholder producers may raise small ruminants as a secondary activity for household food security. Because of their small sizes and lower cost of production than cattle, sheep and goats fit the limited resource base of urban and periurban households (Waters-Bayer, 1995). Smallholders prefer to raise goats because they require less management and are hardier than sheep. Because they are browsers, goats forage widely and are able to meet their nutritive needs, albeit at suboptimum levels at times (Wilson, 1991). A common reason that households often need cash is to pay school fees, healthcare, or unanticipated emergencies. In some societies, small ruminants are kept for religious or social reasons. For example, Muslims prefer sheep for religious festivals when rams are slaughtered to provide meat for the household. Other social occasions include naming ceremonies and birthday celebrations.

Like other production systems, urban/periurban livestock producers face economic sociocultural and institutional constraints. Availability, access to, and affordability of inputs, supplies, and technical services may constrain smallholder producers scaling up their enterprises. Other important factors are land tenure, access to markets, lack of credit or working capital, and other forms of assistance when needed.

Credit is very often a major limiting factor for building or improving infrastructure for animals, for purchasing additional numbers of animals, or for buying routinely used animal health products. Unless rural banks are established and are accessible by community members, producers often lack collateral required by financial institutions. In addition, producers may encounter difficulties in repaying loans due to low rates of return on their investments.

Livestock management practices

The importance of small ruminants in this production system is similar to the pastoral/agropastoral system. However, management practices differ in that the flocks/herds are much smaller due to the land base on which they are raised; the greater availability of water and forage, including crop by-products; and their affordability compared with a large ruminant. However, there is still competition with other farm undertakings for land, capital, and labor (Gutierrez, 1985). If tethered or confined there is a need to bring fresh grasses or legumes to the animals, thus requiring an individual who has time, energy, and strength to do so. This work often falls on women and children. The alternative is to use a controlled grazing system that also requires a shepherd who often is a child (Coop, 1986).

Because dairy goats are easy to handle, women and children assume their management. Management duties that women perform include milking animals, sale of dairy

products, castrating, delivery and attending to the newborn, and animal sanitation, including housing if used. In some societies, women sell the animals and use the returns for household needs, although the purchase of new stock remains the responsibility of the male in the household.

Owing to raising a small number of animals often in confinement, the cut-and-carry system for forage is a relatively common practice in periurban/urban systems but requires extra nonfamily labor that may fluctuate seasonally if family members cannot meet the need. Animal and human population density in the locality, cost of animal housing, availability of marginal lands for grazing or foraging, and whether natural pasture is available factor into the level of confinement under which small ruminants are raised. Similar to the mixed crop–livestock system, management decisions are made by the head of the household, usually the man, or if the animals are owned by an absentee landlord, by the owners themselves. Women or children are responsible for sanitation of animals, feeding troughs, and animal housing, but hired labor or family members of lower social status may also be employed.

Livestock nutrition

Mixed crop–livestock and periurban/urban production are traditional systems in the humid/subhumid tropics. Different patterns of crop production as well as the type of crops, including trees such as palm oil, coconuts, or rubber, enable producers to use crop residues and stubbles while providing organic fertilizer (dung and urine) to the land. In Southeast Asia, grazing animals under tree crops in association with tropical legumes adds value by increasing soil fertility, controlling waste herbage thereby decreasing the need for herbicides, and adding a second profitable element to the system (Devendra, 1986).

Many households keep only a few animals; thus, feeding is more labor intensive. Animals may be tethered in areas of intensive crop cultivation or confined to the household and fed various crop residues when available, in addition to grasses or shrub/tree leaves that are cut and carried to them (Devendra, 1986). Where families have access to grazing, for example, along roadsides or marginal field areas, more extensive grazing is practiced. Families may combine their flocks/herds during the day under management of an unpaid family member or shepherd who returns them to the households in the evening.

Cereal cultivation of maize, rice, and wheat provides stubble, and other residues may include sweet potato vines or sugarcane tops, although the level of nutrition is general. Supplementing the diet with tree leaves, pods, and seeds, especially leguminous ones like leucaena, cassava, jackfruit, acacia species, sesbania, and gliricidia, adds additional nutrients (Devendra, 1983; Hutagalong, 1981).

Livestock reproduction

Because producers in mixed crop–livestock systems rely on both crops and livestock for household income generation, raising small ruminants that are highly productive is important to management decisions. The type of species, cost of animals, products derived from the species, access to markets, consumer demand for the products, availability of labor, availability and access to technical services, and inputs all contribute to a producer's ability to maintain a viable farming enterprise. Sheep and goats fill an economic niche but must be productively profitable. This requires breeding stock that can add value to a household herd or flock as well as a level of technical understanding about livestock nutrition and health.

In the periurban/urban system, the primary source of household income is off-farm work. Small ruminants act as a repository for rural capital ('living savings bank') and provide a high return on investment (often more than 10%). In poor households, livestock – especially small ruminants – are a key means of managing risk, protecting savings, and offer insurance against drought and crop failure due to changes of climate patterns. Successfully breeding the household's limited stock serves to reduce the expense of purchasing replacement animals.

Livestock health challenges

The humid/subhumid climate in which these production systems occur is ideal for parasite and disease vector multiplication and spread. High ambient temperature and humidity create an environment conducive to internal and external parasites, bacteria, fungi, mosquitoes, and flies that act as disease vectors. Genetic characteristics often limit disease resistance and weak management practices can provoke disease transmission.

Small ruminants are subject to a daunting list of diseases and parasites. Viral and bacterial diseases include: PPR, CCPP, Rift Valley fever, sheep pox, salmonellosis, brucellosis, anthrax, hemorrhagic septicemia, heartwater, schistosomasis, Nairobi sheep disease, enzootic abortion of ewes, foot-and-mouth disease, bluetongue, Crimean–Congo hemorrhagic fever, pneumonic pasteurellosis, contagious pustular dermatitis, coccidiosis, tetanus, black quarter (*Clostridium chauvoei*), botulism, enterotoxemia, contagious ecthyma, caseous lymphadenitis, hypocalcemia, mastitis, transit tetany, foot rot, and trypanosomiasis. Some indigenous breeds are tolerant of trypanosomiasis, such as the West African dwarf sheep and goats and East African goats (OIE Documents Database).

Internal parasites include helminths that cause Haemonchus contortus, liver fluke, roundworms, lung worms, tapeworms, nasal bot, and bloat. Common external parasites are ticks, fleas, lice, and mites.

In periurban/urban production systems, zoonotic diseases become more significant when livestock are raised close to household premises, or within the household dwelling itself. Lack of food safety standards also exacerbate human health threats. Traditional producers are aware of the role of management in disease avoidance and control but may lack the ability to prevent their occurrence (Ntifo-Siaw and Ghartey, 1988). Zoonotic diseases are particularly important, especially brucellosis, tuberculosis, animal-sourced foodborne gastroenteritis, *Tenia solium* neurocysticercosis, and *Mycobacterium bovis* tuberculosis. The *Fasciola*, *Entamoeba*, and *Giardia* species and *Balantidium coli* are especially significant in these systems (Kagira and Kanyari, 2001). Both humans and livestock are vulnerable to the diseases these parasites transmit (Harper and Penzhorn, 1999; Kanyari *et al.*, 2009).

Values of Small Ruminants

Livestock represent diversified values – sociocultural, environmental, economic, and nutritional – and not all of these

can be measured in hard numbers. Nor can one value be equated with another, particularly across cultures and ecosystems. Livestock serve as critical components for poverty alleviation, for conflict mitigation, prevention, and resolution. In some societies animals represent social value, for example, status in the community often based on the number of animals a household owns. Instead of a dowry payment by the bride's family, a practice once widespread in the West, some cultures use cattle, sheep, and goats as bride price. Payment is made by the groom's family to secure the woman's hand in marriage.

But they also serve as a valuable entry point for promoting gender equity in rural areas. Women play an important role in livestock management through animal genetic selection, milking, processing, and marketing as care providers, feed gatherers, and birth attendants. Identifying and supporting women's roles as livestock owners, processors, and users of livestock products and strengthening their decision-making power and capabilities are key aspects of promoting women's economic and social empowerment.

Smallholder producers benefit at various economic levels by keeping small ruminants. Small ruminants produce meat, milk, fiber, and hides. The levels of production and economic importance of these products vary among regions, especially in the developing countries. Sheep and goats are often cited as a hedge against natural disasters, economic shocks, and rising food prices, particularly in situations of small or failed crop harvests. They fill nutritional and economic gaps and are a coping mechanism until the next cropping season. Dairy sheep and goats can produce enough milk for household use as well as supply local markets, and the nutritional values are almost equivalent to cow milk, although compositions vary by breed, animal, and point in the lactation period. However, sheep milk is higher in fat, energy, sugars (lactose), and calcium and slightly lower in water (U.S. Department of Agriculture, 2012). Small ruminants produce meat, milk, fiber, and hides. The levels of production and economic importance of these products vary among regions, especially in the developing countries.

Production trends in the developing countries parallel consumption trends. The FAO estimated that in 2010 developing countries would produce 143 million tons of meat. Of this volume, 45% would be pork, 25% poultry, 23% beef, and 7% mutton or lamb and goat meat. Yet, as a group, developing countries were expected to increase net meat imports twentyfold, amounting to 11.5 million tons in 2020. Of net meat imports, beef was expected to constitute 46%, poultry 30%, pig meat 13%, and sheep and goat meat 11%.

Total sheep and goat milk production globally amounted to 27 465 619 ton in 2010 (United Nations, 2010). Of this total, 49% was produced in the Asian region and 44% in the African region. Global sheep and goat meat production during the same period totaled 60 285 054 ton, of which Asian region countries produced 7.5% and African region countries produced 4.7%. The top five countries producing these products were located in Asia and Africa and the majority, if not all, of the milk and meat was produced by smallholders.

Positive environmental values, especially those of raising livestock on the range and grasslands, include mineral and nutrient cycling; enabling soil conditions for storing soil carbon, water cycling and/storage (grass/vegetative cover can capture 50–80% more water than bare ground), and improving the diversity of grasses by dispersing seeds and breaking up the soil crust. In pastoral societies, livestock consume forage on lands that cannot produce crops, thus changing these areas into food-producing landscapes. Sixty-five percent of global dryland area is grassland used for livestock production by 800 M people (Mortimore *et al.*, 2009).

Pastoralists graze livestock on lands that cannot produce crops, thus turning them into food-producing landscapes. Grasslands represent major terrestrial carbon stock, are approximately half the emerged ice-free world, and represent approximately 70% of world's agricultural area. Good land management results in reduced risk of drought and floods, greater permeability, and increased water-holding capacity in soils, both of which are examples of direct benefits up- and downstream. In fragile environments as are found in arid/semiarid ecoregions, goats add value to the grazing system due to their ability to browse forage species, including weeds, that other species do not.

Nutritional value

Animal source foods (ASF) reinforce household food security. One of the most difficult and least accounted values of livestock is the nutritional merit of ASF. From the early 1970s to the 1990s, meat and milk consumption in developing countries grew by more than twice the increase seen in developed countries and more than half as large as the increase in cereal consumption resulting from the Green Revolution. Developing countries now consume close to half of the global meat supply.

On a global basis, foods of animal (including fish) origin provide approximately 17% of the energy and more than 35% of the dietary protein for humans. In rural areas of developing countries, diets of children are primarily crop based and often deficient in vitamin A, vitamin B_{12}, riboflavin, calcium, iron, and zinc. ASF contain more bioavailable levels of essential minerals and vitamins and provide concentrated sources of energy and fat, vitamin B_{12}, riboflavin, vitamin A, vitamin E, iron, zinc, calcium, and vitamin D. Vitamin A in its usable form and vitamin B_{12} is present only in animal source foods. Animal proteins are 20–30% more digestible than plant proteins (96–98% vs. 65–70%) and contain higher, more bioavailable levels of essential minerals and vitamins. Vitamin A in its usable form and vitamin B_{12} are present only in ASF. Vitamin A is an important micronutrient for the cognitive and physical development of children (Murphy and Allen, 2003).

See also: Slum Livestock Agriculture

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Social Justice: Preservation of Cultures in Traditional Agriculture

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Glossary

Coevolution People, animals, plants, and the land changed over time together in complementary ways.
Fictive kin Individuals included in a family unit through ceremonies, such as baptism and weddings, which involved mutual obligation of those serving in the ceremonies.
Hegemony The ability of one group to enforce its way of valuing people, actions, and things on another.
Land titling Granting title to a land previously held in common, by the state or a large landlord.
Pastoralists People who herd animals from place to place, depending on the season and availability of pasture.
Verticality Farming at different altitudes.

Introduction

Culture determines the way humans see the world, including how they link the seen and the unseen. It emerges as humans interact with each other and their environments. As a result, culture both shapes and justifies behavior, human interactions, and collective identity, including those related to food, water, and fiber production, processing, procurement, and consumption. Traditional agriculture is a way of preserving culture – an important anchor in an ever more chaotic world of globalization and climate change.

When traditional agriculture is destroyed, so is the culture and the people's relation to the land and to each other. Social justice is denied when traditional agriculture and the societies it supports and support it are destroyed in the name of progress.

Cultural Capital and Traditional Agriculture

Traditional agriculture coevolved with people who practiced it in different ecosystems, contributing to human health in terms of food and diet. Food and the ceremonies surrounding food are an important part of traditional agriculture and the well-being of the groups that practice it.

Cultural capital links the seen and the unseen. In Northern countries, it is referred to as 'world view' or *Weltanschauung*. In Spanish America, it is best referred to as cosmovision. It includes symbols, a sense of place (or lack thereof), ways of knowing, language and history, ways of acting, and what is believed to be possible to change.

A keen awareness of the land and its characteristics (WinklerPrins and Barrera-Bassols, 2004) was part of the cultural capital of precolonial societies in Mesoamerica and the Andes (Williams, 1975; Barrera-Bassols *et al.*, 2006), as well as other parts of the world. Rituals and ceremonies honored the Earth and human mindfulness of it (Bolin, 1998). But settled societies and colonization separated cultural capital and agriculture, separating people from the land and from each other.

The cultures of traditional agriculturalists define how they relate to each other, to the ecosystem, as well as what and how they produce and consume. Hegemony is the ability of one group to impose its culture – the beliefs about what should be and what is possible to change – on others. Thus for dominant cultures, their values reinforce the primacy of increasing production to generate money, and other values are viewed as sentimentality and blocking progress. These hegemonic values are then translated into laws that often deprive indigenous people of their land (Alden Wiley, 2012).

For smallholders, in particular, cultural capital includes the way soil and water are classified, the uses for which it is deemed most suitable, and the things that must be done to maintain its fertility and purity, including terraces, crop rotations, soil amendments, ceremonies, and prayers. The cultural aspects of maintaining soil and water were inseparable from traditional agriculture and herding.

Some smallholders, often members of specific ethnic groups, have been in a place hundreds of years to develop a culture of land and water and how to use them. They classify and protect soils and water sources based on observation and generations of experience (Williams, 1975). Other smallholders are driven to marginal lands as mining (including petroleum exploration) and industrial agriculture forces them off their ancestral lands. Particularly, as smallholders moved onto marginal lands, few believe they can do much to improve the soil on their new, often degraded, land. They may seek to grow crops they traditionally grew, whether adapted to the new ecosystem or not. The practices that worked in the context they came from are often not transferable to the new setting. They do not understand local hydrology or seasonal variations in precipitation that are unlike where they came from.

The 'chacra' in Latin America is the place where one grows or cultivates plants of human interest (Rengifo, 2004). A 'chacra' is not only defined and delimited by humans, but also by the nature and gods. The traditional 'chacra' serves multiple purposes in human livelihoods, serving to reproduce not only the human body by producing food, but also collective identity in reproducing spirituality.

Rengifo (2004) identified three important cultural aspects of the Andean farm field (chacra):

1. the relation between cultivators and their crops is personal,

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2. agricultural practices are performed as rituals, and
3. a fine and detailed conversation with nature is necessary to undertake agricultural work at a proper time, in a proper place, and in a proper way.

Revilla (2006) shows that the effect is most important than rationality, communal sentiment predominates over individualism, and humans continue to be part of nature, rather than seeking to control it.

In 1990, there were more than 460 different ethnic groups in Latin America that still managed local ecosystems with indigenous technologies (Altieri and Hecht, 1990). The ethnoecological knowledge of some of these groups is impressive. For example, the Mayans recognize approximately 908 botanical taxa and the Huastecos of Mexico, approximately 861 (Toledo, 1992). This indigenous knowledge has led to management systems now considered sustainable and, therefore, proper to guide modern resource management. Sustainable traditional farming systems still in existence include the *chinampas* (small rectangular areas of fertile arable land to grow crops on shallow lake beds) of Mexico, the *waru waru* raised bed cultivation in the Andean *altiplano*, and the agroforestry systems of several Amazonian tribes. These small landholders use a very diverse array of traditional slope, water, soil, pest, and vegetation management techniques, which include composting, rotations, polycultures, agroforestry, and watershed management systems (Altieri, 1987; Wilken, 1987; Altieri and Masera, 1993).

Similar intersections of culture and microecosystems occur around the world. For example, in oasis agriculture in North Africa, pastoralism in combination with intensive fruit and vegetable production is carried out only on the most fertile land (Ilahiane, 2004). Such cultural and farming systems have coevolved according to environmental conditions that are often ethnically specific and determined by intracommunal notions of change and community (Ilahiane, 1999).

Most traditional agricultural systems seek to minimize risk, both long term and short term (Rist and San Martin, 1993). In many steep regions, households traditionally farmed at various altitudes to capture the specific soil and climate conditions necessary for optimal production over time. However, the move to land privatization (usually done through titling contiguous land parcels) and large machinery has made such soil protection strategies socially difficult, and also mechanically impossible, as the traditional plots were small and intensively farmed. Diversification and verticality have both been diminished by modernization projects. Such practices were stigmatized or considered obsolete, causing the loss of some of the knowledge necessary to preserve soil quality.

Gender division of labor is an important part of smallholder agriculture, although those traditions are challenged as more and more men migrate to seek wage labor. Traditionally, men and women perform separate tasks within the same enterprise, suggesting that each gender can appreciate and enhance different aspects of soil quality. Often, men in Latin American smallholder households are in charge of plowing, women in charge of seed selection, both do planting and harvesting, men do tilling, and women do postharvest processing. In smallholders of Africa, there are women's crops (usually for household consumption or local sale) and men's crops (generally for an expanded market).

Cultural capital either values or denigrates social organization. It is social organization that has made smallholders in the Andes capable of overcoming the limitations of the verticality based in the community (Mayer, 1989), as traditional organizations have aided responses to drought and flood in other parts of the world. Shared cultural capital collectively maintains traditional agriculture. Managing the verticality means the community is concerned and acts in ways that maintain the soil and reduce risk from weather.

A major component of social capital, which is reinforced by cultural capital, is reciprocity. In many Andean communities, reciprocity is not an individual reciprocity only. Reciprocity has various forms (*humarapa*, *ayrí*, *mink'a*, and *waqui*) related to space and time and energy and mass. There are various types of reciprocity: work for a product, work for work, and work for food and party. Although in some reciprocity, it is individual to individual, in others it means that the group will act to support the group based on mutual commitment or that the individual will give to the group when there is a need in the understanding that they will receive help when they need it.

The *umaraqa* form of reciprocity in peasant communities has three categories of reciprocity: harvesting agricultural products, conserving soil, and in rituals, festivals, and fictive kin relationships (*compradazgo*). *Ayni* is another form of reciprocity that shares daily household work and tools. This tends to be more individual to individual reciprocity, generally among blood or fictive kin. *Mink'a* involves providing a service in return for a similar service, food, or the product produced by the work. *Waki* is where one person offers the field, the other the seed, and both work on the land from land preparation to seeding, weeding, and harvest. All of these forms of reciprocity depend on cultural capital and traditional patterns of farming.

Timing of planting of complex rotations was very important in the precolonial era. Fiestas and rituals marked the beginning and end of each phase of the agricultural cycle, which also helped to provide the family and labor needed. In some smallholder areas, these continued, although climate change has reduced their coincidence with appropriate soil moisture and soil temperature. As Bolin (1998) indicates, the rituals surrounding soil conservation and other farming activities, which still continue in some smallholder communities, enhance respect for the land, for its products, and for the members of the community.

The normative principle of precolonial agriculture was not the maximization of production but the management, conservation, and improvement of the fertility of soils over the long term, with social relations formed to meet the collective needs of the society within the limits of each vernacular ecosystem (Rist and San Martin, 1993). Social and cultural capital were critical for traditional agriculture and the rituals and ceremonies that supported it.

Relationship skills are important for building social capital. For many smallholders, building relationships with their neighbors is a part of their cultural capital. It involves mutual trust, in that smallholders know they can count on their neighbors when mutual action is needed. Reciprocity is a critical part of this – in some smallholder communities, participating in the *minga* (collective work for the community, including building roads and terraces to prevent soil erosion)

is critical for each smallholder contributing to the collective good. Mutual trust is established when different institutions and individuals can both give and receive. When mutual trust, reciprocity, and working in groups exist, a collective identity emerges and that collective identity can be embedded in the land.

Communal cooperation is necessary to conserve and rebuild the degraded soils. Building on existing social capital is critical, as such efforts require considerable collective investments of all the community capitals. Bridging social capital is necessary not only to bring in external knowledge, equipment, and funds, but also to help local people recreate what their ancestors did to protect the soil to provide continuous livelihoods.

Early Colonization and Separation of Agriculture and Culture

The Spanish colonists to the Americas brought with them the extensive agriculture of Spain, in contrast to the intensive agriculture of the indigenous populations. The kings of Spain rewarded the *conquistadores* with land concessions, called land grants, which included the labor of the indigenous people on the land, further stigmatizing the indigenous ways of farming and eating.

Although under the indigenous empires of the Inca, Maya, and others, agriculture was organized in ways that maintained the soil in place and covered and paid close attention to climate and precipitation. Under colonization, European forms of farming – which had depleted soils there – were introduced and indigenous farmers were left on the least productive and most marginal soils with less access to water.

Yet, through communal management of those lands, communities maintained soil fertility through rotations, fallowing the land (which facilitated the growth of cover crops), and judicious herding of animals with small soft hooves to maintain multilevel production systems for hundreds of year. The Spanish introduced new cultivars, particularly cereal grains, and livestock with small, hard hooves (sheep and goats) and large hard hooves (horses and cattle). They also introduced new agricultural technology, including plowing with animal traction, deforestation, and burning. All these technologies had negative impacts on soil carbon levels. To utilize animal traction efficiently, they abandoned the system of cultivation characterized by many small distributed fields at different altitudes that reduced risk by utilizing a variety of microclimates. They favored leveling the land and creating much larger fields in flatter areas, seeking greater efficiency in working the land. The hard-hooved animals, with their habits of eating entire plants, replaced the soft-hooved animals that had coevolved with the fragile ecosystems of the Andean plains, further degrading the soil and leaving it without cover. In the Andes, overgrazing affected the ecology of the main source of fuel, *taquia*, a low growing bush, causing a shift to wood for fuel, further destroying some of the natural protection for soils.

Rist and San Martin (1993) reported that the substitution of bread for potatoes as the mainstay of the peasant diet was extremely inefficient in terms of the comparative calories produced per unit of land – a factor of approximately four to one. Planting enough wheat to feed the population required clearing land that then quickly eroded. By the twenty-first century, much of the land was seriously degraded. Land degradation and the loss of traditional agriculture contributed to the decline in cultural capital as well as human capital, as families sent members out to earn income in other places. Under these colonially based systems, people kept their land, but not their traditional agriculture.

Separating People from Their Land, Their Agriculture, and Their Culture

Development Projects

Generally, the dominant group defines such imposition of new agricultural practices as 'progress' or 'development.' Many studies document the negative results of cultural deprivation in Australia (Hill, 1995), Africa (Kusiluka *et al.*, 2011), Asia (Colchester *et al.*, 2006), and the Americas. The impacts include decline in human health and well-being (human capital), income and wealth (financial capital), human interactions and social group support (social capital), and the ability of groups to express their norms and values to form policies (political capital) (Flora and Flora, 2013). When hegemonic norms and values deny the value of traditional cultures, but block access to fulfilling those of the dominant class, a sense of isolation and anomie can result in actions that degrade natural and built capital. For example, with initial colonization, dietary staples (principally wheat and meat) were transferred to settled states from the Americas, Australia, New Zealand, Asia, and Africa to provide low-cost wage foods in the rapidly industrializing colonial states (Friedmann and McMichael, 1989). The impact on traditional agricultures, the food they produced, and the health of the previous producers were simply unimportant under the new set of extractive values.

In the 1970s and the early 1980s, substantial international development resources were invested to 'improve' African pastoral system period. Some of the investments made no impact, while others were actually harmful to the environment and the pastoralists. (Park, 1992). Ellis and Swift (1988), based on long-term research in northern Kenya, argued that assumptions of development agencies that African pastoral systems with potentially stable (equilibrial) biotic feedback mechanisms (assumptions not based on research) have resulted in severely misdirected development programs. "[C]hanges in land tenure systems and existing institutions are assumed to be desirable and are therefore undertaken without consideration of what may be useful or valuable in the existing systems" (Ellis and Swift, 1988). Changes in these tenure systems, which influence land access for traditional agriculture systems, destroy cultural capital. Ellis and Swift showed that pastoralist systems in a variety of settings are persistent rather than equilibrial. The question then is how to aid persistence in an environment controlled by abiotic, chaotic forces, and not how to manage the equilibrium of the system with group ranches or grazing blocks. In this view, far from being irrational mismanagers, traditional pastoralists tend to be decidedly rational in reinventing survival systems in response to human-induced and natural ecosystem changes.

The cultural capital that governs norms and behavior in such systems is critical for the survival of the community as well as the ecosystem.

Spatial diffusion in northern Europe, Latin America, Africa, and Asia allowed pastoralists to persist relatively free of famine. However, demands for the land along their routes for grazing, logging, roads, tourism, sedentary agriculture, and mining have decreased use of this risk reduction strategy that is part of their culture (as are fights over land access). Because, no matter how remote, pastoralists are increasingly influenced by external human forces, and simply leaving them alone is not an option. "A cautious approach to pastoral development is to ask if intervention strategies can be formulated which will build on the best aspects of traditional systems, rather than imposing wholesale alterations on them" (Ellis and Swift, 1988).

Deliberate Attempts to Destroy Culture

There have been specific times in human history when overt attempts to destroy culture, by separating people from their land, had serious impacts on people, place, and biodiversity. Generally, removal from the land (often defined as 'civilizing savages') opened up the land for settlers and investors.

Earlier, US policy toward its indigenous inhabitants was conquest and removal. Indeed, at one point only one vote in the US Congress kept the policy from becoming one of total annihilation. The dominant culture, as represented by the Federal government in the 1820s, viewed indigenous cultures, varied as those cultures were among more than 600 separate tribal nations, as something to extinguish for the well-being of the United States. One way of extinguishing them was by removing the people from their land and changing that land by giving it to new settlers.

The US government practiced cultural annihilation by separation of cultures from the lands that nurtured them. Mechanisms for separation included military incursions and Indian wars (up to the presidency of Ulysses S. Grant), movement of nations to reservations, often far from the lands that gave rise to their culture (from 1870 to 1930s), and assimilation (attempted through boarding schools and through movement to urban areas). In addition, many European settlers used economic mechanisms and force to remove Indians from potentially valuable lands.

American Indian Boarding schools in the US were designed to 'get the red out' (Adams, 1995; Davis, 2001). The 'red' was the culture that resisted domination and land alienation. Culture included specific ways of hunting, gathering, and farming that allowed for survival of people in terms of the linkages between body and soul (Flora and Emery, 2011). This was attempted by removing Native American children from all symbols of their culture – their names, hair, food, clothing, religion, language, place, and extended families.

Stated in positive form (but equally devastating to the young people and their families), boarding schools were meant to 'civilize' Native American children. Boarding schools sought to replace indigenous ways of seeing, knowing, and being with English, Christianity, athletic activities, and a ritual calendar intended to further patriotic citizenship. All this was done under militaristic regimentation and discipline (Adams, 1995). Because they would no longer have the survival skills taught by their parents, the girls were taught how to cook and clean in European homes and the boys were taught to be mechanics and farmers, all skills irrelevant for most reservations where the indigenous adults were forced to live. They instructed students in the industrial and domestic skills considered appropriate to European American gender roles and taught them manual skills appropriate for an industrializing economy. For many Indian children, this cultural assault led to confusion and alienation, homesickness, and resentment (Adams, 1995; Davis, 2001). Traditional agriculture, which in its practices, linked people to each other and the land was denigrated (Grinder, 2004). Both traditional food and traditional agriculture, and the cultural links between them and the people, were denied.

Although separation from traditional agriculture was a deliberate attempt to change culture, there was another motive. The 'vacant' land became open for agriculture linked to industrial development.

Current Separations of People from Land, Traditional Agriculture, and Culture

More recent removal of people from traditional agriculture is less based on a perceived justification of taming the savage (Gasteyer and Flora, 2000) and more on a conviction that traditional agriculture does not have the financial promise that other land uses have, such as mining, reservoirs, plantations, and export crops. These changes in land use require changes in property rights that are referred to as development or as land grabs, depending on one's values and analytical approach (Kugelman and Levenstein, 2012). Because much of the land in traditional agriculture is untitled, the seemingly progressive move to title lands leads to massive displacement (Alden Wiley, 2012).

Many governments around the world are implementing what Brazilian economist Bresser-Pereira (2007, 2010) has named the New Developmentalism. That approach to modernization privileges generating financial capital through public–private partnerships (rather than relying mainly on the state under developmentalism, or the market, as under neoliberalism) in order to reach the other goals. But, as with neoliberal approaches, the new developmentalism is often accompanied by degradation of natural and human capital, disregard of cultural capital, and deteriorating social capital when the state does not act to check the market (Rodríguez-Garavito, 2011). Under this model, a new set of actors clustered around the financial sector – banks, both private and public; investment consultants and deal makers, etc. – have vested interests in changing land use (White and White, 2012).

Cultural hegemony – when the world view of a dominant group determines the actions of marginalized people – that discounts soil and traditional ways of caring for it came with the conquest, but continued well into the twentieth and even twenty-first century. It comes in part from the emphasis on short-term profit maximization as a major individual and household goal. Its impacts can be seen when Latin American smallholders turn to monocropping and high-input agriculture, which increases their financial risk and risk to soil

health. Often returning to ancestral ways of managing soils resolves risks to all the capitals.

Although there has been hegemonic pressures to use 'modern' agriculture, many of the processes that guided traditional practices have persisted and can be observed being implemented by smallholders in traditional communities around Latin America and elsewhere around the world (Wilken, 1987; Toledo, 1992; Rist and San Martin, 1993; Faust, 1998; WinklerPrins and Barrera-Bassols, 2004).

Political capital is the ability of a group, such as smallholders in an area, to translate their norms and values into standards that are then turned into rules and regulations and enforced. Those regulations often determine the distribution of resources, including access to natural resources, and how they are used.

In traditional agricultural communities, much land was controlled in common, with village leaders assigning land use on a year-by-year basis. In this system, women had access to land through traditional use rights. Privatizing land was thought to be a more efficient way of land management by modernizing elites. As land became titled and later sold, it was almost always titled in the name of the man in the household rather than the man and woman. The new private plots in the reformed areas and in new colonization and transmigration areas favored men's crops. There was seldom land left for the women's gardens, which were often vital for household nutrition and even survival. Women's collective production efforts were eliminated entirely. Often the animals that women would pasture, such as small ruminants, also were not allocated land for grazing. And in this process, communal ways of managing land, particularly through fallow, was eliminated.

Land reform was often necessary due to political unrest in response to inequality, the poverty induced by land concentration, and the lack of concern for the soil by absentee *latifundistas* (landlords). But in many places these reforms were unsuccessful in promoting rural well-being and ecosystem health. In part, the failure was due to superimposing new structures, rather than utilizing the traditional forms of social organization. Political decisions made from national capitals tended to impose a single model for the entire countryside, rather than considering the varied social and natural contexts.

In parts of Latin America, few export crops were planted until the era of land reform, beginning in the early 1960s. Most land reforms propagated during that period were intended to make land more productive, as measured through the market, not to redistribute land. Under the threat of expropriation, many large landowners shifted from extensive agricultural systems to more intensive ones, including soybeans, cotton, and even more sugarcane – all crops aimed for foreign markets. As a result, local populations, who had farmed the land as part of their usufruct rights, were displaced. Many moved to the cities, whereas others moved to less-desirable highland areas where they found that the traditional practices that worked well on flat ground tended to seriously erode hillside lands. Others moved to jungle and rain forest areas, with equally disastrous results.

The diversity of agricultural activities in traditional smallholder systems constitutes a livelihood strategy for many traditional agricultural communities, where the scarcity of agricultural land is a major limiting factor. Genetic conservation *in situ*, from the point of view of smallholders, guarantees at least minimal food security and guarantees that the household can obtain food without going to market, although they acknowledge the importance of markets in their overall strategy (Cuba *et al.*, 2006). In smallholder households, expenditure reduction, which is aided when soil quality is maintained, is often preferred over income increases, as the volatility of markets has been experienced by many smallholders in rural development projects in earlier eras.

The need for financial capital for purchased inputs, food, clothing, school, and taxes has encouraged many members of smallholder households to migrate to engage in wage labor. Such immigration may be long term or circular (Flora, 2006). Because such migration streams are predominantly of men, this leaves women with the agricultural tasks, leaving little or no labor for communal work that contributes to soil retention and fertility (Collins, 1988).

Land Grabs, Traditional Agriculture, and Culture

Increasingly, land is taken from smallholders and export crops, such as palm oil, are planted. The impacts are felt differentially by men and women. Men often see themselves as benefitting from the wage labor that comes on a seasonal basis, whereas women lose their opportunities to use traditional agriculture to provide for their households. These communities' experience of coercion, exploitation, intimidation, consent, and resistance is highly gendered, as women are more affected – and often more willing to resist – than are men (White and White, 2012). Land is being shifted from communal or smallholder ownership to governments and corporations, both national and international as part of the new developmentalism (German *et al.*, 2013).

Although 'modernizing' land tenure laws privatized some smallholdings in Africa and Asia (Alden Wiley, 2012), generally land held in common makes it extremely difficult to establish exact limits that meet surveyors' standards, although all in the community know what the limits are by natural indicators, such as trees, rivers, and rock formations. This makes defense of these communal lands almost impossible (Silva Castañeda, 2012).

The magnitude of this current wave of land deals is unprecedented: A World Bank (2010) study of 464 projects found land deals accounting for 46.6 million ha in 203 projects in 81 countries, with information on areas unavailable in the rest. This has increased substantially, since then, as countries see the possibility of public–private partnerships around resource extraction as good ways to enhance the public treasury and provide subsidies to the poor, including the poor that are displaced (German *et al.*, 2013).

Although there is much community protest and attempts to block projects, such as mining and dams, and protect traditional agriculture and cultures, these protests are generally ineffectual (Behrman *et al.*, 2012). Smallholders are pushed off the land and seek new areas to set up farming. Those areas are often marginal, and the practices brought, such as burning forests and turning them into pasture, further degrades the soil

and sets in motion a pattern of permanent migration that harms both natural and social capital.

The impact on transhuman cultures, such as the Sami in northern Scandinavia and Russia (Minority Rights Group International, 2012), or the Mapuche in southern Argentina and Chile (Bendini, 2001), is enormous. The link between the animals and the land needed for them to graze from season to season sets up conflicts with those who do not share their culture.

Conservation Land Grabs

Often conservation is used as the mechanism of separating ethnic groups from traditional agriculture – and their land (Chatty and Colchester, 2002). For example, in Belize the government informed the Mopan Maya that they were destroying the forest through their swidden agriculture (which they had used for thousands of years) and needed to vacate the forest. The targeted area has been referred to as the 'cultural hearth' of Mopan Maya (Wilk, 1997). The Maya, whose collective title to the land was affirmed by Belize's Supreme Court but still not recognized by the government of Belize, replied that they had used the system for thousands of years and the forest was flourishing. The Belize government denied their claims.

Sophisticated longitudinal analysis by scientists from the Ohio State University supported the Mayans: they were not decreasing forest cover, as they left ample time for regrowth. However, that did not stop the plan of removal of the Maya from their land, their agriculture, and their culture that included living with the land for a long time horizon (Wainwright *et al.*, 2013).

The government of Belize did not reveal the pending public–private partnership with a major logging company to use that same land (Servindi, 2013). It appears that the 'conservation' rhetoric against the Mopan Maya worked to allow the Belize government to change land use by finessing 'prior consultation,' a key concern for the Organization of American States' InterAmerican Commission on Human Rights (OAS/CIDH, 2004, 2009).

As Maasai leader Martin Sanin'o put in the 2004 World Conservation Congress, "We were the original conservationist. We don't want to be like you. We want you to be like us. We are here to change your minds. You cannot accomplish conservation without us." Over one hundred thousand Maasi 'conservation refugee' have been displaced from southern Kenya and the Serengeti Plains of Tanzania (Dowie, 2005).

Using Culture to Defend Traditional Agriculture

Culture determines what human groups declare to be 'fair' and 'just.' Many traditional societies are being deprived of their culture as they are removed from the land that sustained them for generations. Worldwide indigenous groups are responding to that removal by protesting and blocking attempts to drastically change their landscape and thus their culture.

Some of the movements defending indigenous lands and water as the basis for traditional agriculture and culture has received international attention, such as the case of Rio Blanco in Honduras. The Honduran-owned and foreign-financed company has been attempting to build a dam on the sacred Gualcarque River in the Lenca community of Rio Blanco. Community members have blocked the road against the company, thwarting the dam's construction, for more than 5 months. While the leaders of the movement against the dam are in prison, the company destroyed fields of corn, beans, coffee, and bananas (Bell and Fields, 2013). In the Philippines, indigenous people in Palawan united to demand a moratorium on the expansion of oil palm. As in the many cases, the pressures to expand come from the government in the form of public–private partnerships (Colchester *et al.*, 2006).

The movement among smallholders and indigenous people supporting *vivir bien* or *buen vivir* (living well) is an important reaffirmation of precolonial values and modern rights and responsibilities that support such positive change (Plataforma de co-partes de tierra de hombres, 2013). It has gained political saliency in Bolivia, where on 15 October 2012, the government passed Law 33, Law of the Framework of Mother Earth and Integrated Development to live well. The goal of the law and the movements promoted it to once again unite cultural capital, earth, and way by guaranteeing the continuity of the regenerative capacity of the components and system of life of Mother Earth, recuperating and strengthening local and ancestral knowledge, recognizing the complementarity of rights, obligations, and responsibilities (Delgado Burgoa, 2013).

Conclusions

Culture has linked humans to their environment for millennia. Agriculture and herding required that attention be paid to land and water, which were in turn honored as sacred and needed human attention, just as humans needed water, land, and animals to survive. Modernization has broken that link, sometimes by willfully destroying cultures in the name of civilization, but more often in order to get access to the natural resources the culture honored. Resistance to the loss of land and water is now being led by a call to return to cultures of solidarity with one's community and the Earth. Although there is little chance to return to traditional agriculture in many places, the link between traditional agriculture and cultures can provide alternatives in an increasingly changing environment.

See also: Agricultural Ethics and Social Justice. Agricultural Law. Changing Structure and Organization of US Agriculture. Global Food Supply Chains. Rural Sociology

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Soil: Carbon Sequestration in Agricultural Systems

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Glossary

Greenhouse gases (GHG) Trace gases found in the atmosphere that absorb and emit infrared radiation, resulting in the greenhouse effect. These gases include naturally occurring gases, such as carbon dioxide (CO_2), methane (CH_4), nitrous oxide (N_2O), water vapor (H_2O), and ozone (O_3), and several man-made gases, such as chlorofluorocarbons (CFCs), hydrofluorocarbons (HFCs), perfluorocarbons (PFCs), and sulfur hexafluoride (SF_6).

Histosols Soils that contain more than 12–20% organic C (depending on clay content), which are formed under inundated conditions in which minimal decomposition of plant residues occurs.

Leakage In the context of GHG mitigation, leakage is the increase in GHG emissions that occurs outside the boundary of a mitigation project or program, due to the mitigation activities undertaken inside the project/program boundary.

Mean residence time The average time for which a defined entity of matter (e.g., type of atom or molecule) remains within a defined state (e.g., soil organic matter pool) under steady state conditions.

Mineral soils Soils in which the dry mass is made up predominantly of mineral particles. Any soils that are not classified as histosols are considered mineral soils.

No-till A method of soil management in which physical disturbance and mixing of soils is excluded or nearly excluded and seeds or plants are sown in a narrow slot opened in the soil. Herbicides or nontillage mechanical means are used for weed control.

Organic soils Soils with high organic matter content, with at least 12–20% (depending on clay content) organic C by mass, to a minimum of 20 cm depth. These soils are typically formed under inundated conditions in which minimal decomposition of plant residues occurs.

Permanence Refers to the longevity that CO_2 removals by sinks (in this instance in soils) can be maintained without being reemitted to the atmosphere and the relative risk of loss of the sink integrity.

Radiative forcing Externally imposed perturbations of the earth's radiative energy balance because of secular changes in factors such as concentrations of greenhouse gases and aerosols, changes in incident solar irradiance, and changes in the radiative energy absorbed by the earth's surface.

Introduction

The challenges in dealing with global climate change are by now widely recognized among scientists, policy makers, and much of the general public. However, the role of land management and agriculture in particular, in both helping to mitigate and adapting to climate change, is much less well known. Changes in the concentration of greenhouse gases (GHGs) (e.g., carbon dioxide, CO_2; methane, CH_4; and nitrous oxide, N_2O) in the earth's atmosphere, which affect the net energy retained from the sun (referred to as radiative forcing), are the primary drivers of contemporary (and near future) climate change, and the use of fossil fuel is the dominant source of GHG emissions. What is less widely known – certainly by the general public – is that land-use activities currently account for approximately one-third of the human-induced warming from GHG increases (IPCC, 2007). Much of those land-use activities are directly or indirectly linked to agriculture and include multiple sources and different gases, for example, CO_2 emissions from deforestation and vegetation removal from ecosystems converted into agricultural use; CO_2, CH_4, and N_2O from managed soils; CO_2, CH_4, and N_2O from biomass, grassland, and crop residue burning; CH_4 and N_2O emissions from livestock husbandry; and a number of other minor sources (IPCC, 2007). Thus, agriculture has an important role to play in helping reduce these emissions and contribute to mitigation of GHG increases in the atmosphere.

One of the ways in which agriculture can contribute to GHG and climate change mitigation is through a process commonly referred to as carbon (C) sequestration. Broadly speaking, and in the context of GHG mitigation, carbon sequestration entails removing CO_2 from the atmosphere and storing it elsewhere, thus reducing the concentration of atmospheric CO_2 and its contribution to radiative forcing. A variety of pathways for carbon sequestration exist, including capturing CO_2 from large point source emissions and injecting it into deep geologic formations (known as carbon capture and storage) as well as enhancing natural biotic uptake of CO_2 by plants and then retaining more of that fixed C in biotic sinks or 'pools' including vegetation and soils. This latter process, taking advantage of the uptake of CO_2 from the atmosphere by plant photosynthesis and then increasing the storage of that fixed carbon in the soil, is referred to as soil C sequestration. This article focuses specifically on soil carbon sequestration on land managed for agricultural use, i.e., croplands and grazed grasslands.

In this article, basic principles and controlling mechanisms involved in soil carbon sequestration are presented, along with key concepts such as soil carbon equilibrium, saturation, and mean residence time. This is followed by a discussion of the agricultural practices that can be employed to increase soil C sequestration and an overview of the rates and amounts of soil C sequestration associated with different management practices, derived from long-term field experiments and other analyses. The article is then concluded by a section on science

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and policy-related issues that have a bearing on the successful implementation of soil carbon sequestration as a GHG mitigation option.

Basics of Soil Carbon Sequestration

Globally, soils contain approximately 1500 Pg of organic C to a depth of 1 m (Batjes, 1996); of this total, approximately 45% is found in soils under agricultural use (~130 Pg C in croplands and 550 Pg C in grassland used for grazing; IPCC, 2000). In most cases, cropland soils are depleted in C relative to the native ecosystems (e.g., forest and grasslands) from which they were derived, largely due to the legacy of historical land use, including reduced net primary production, intensive soil disturbance, erosion, and export of crop residues as contributing factors (Paustian *et al.*, 1997a,b). It is estimated that cropland land use has reduced C stocks in the topsoil by 30–50% relative to their native condition (Davidson and Ackermann, 1993; Mann, 1986). In contrast, grassland soils managed for grazing may or may not have suffered C losses relative to their native state, depending on how they have been managed. In general, grassland soils that have been overgrazed and poorly managed are likely to be depleted in soil C, whereas well-managed grasslands may have C stocks equal to or exceeding their original native condition (Conant and Paustian, 2002a; Ogle *et al.*, 2004).

The carbon content of agricultural soils varies considerably as a function of climate, soil texture, drainage, and other biophysical factors. Most agricultural soils fall into a range of <0.5–5% C by mass in the top 10–20 cm, and the C content usually decreases sharply with depth. Although the highest concentration and most dynamic C stocks are found in the top 20–30 cm of the soil, significant amounts of soil organic carbon (SOC) can be found through the full depth of the root zone and below. Soils that have developed under restricted drainage (and therefore prone to waterlogging) can have much higher C contents, due to the reduced decomposition of plant litter under anoxic conditions. Soils in which much of the total mass consists of organic matter (i.e., peat and muck soils) comprise a special class of soils referred to as histosols and can contain very large amounts of C, in some cases up to several meters in depth. Although histosols are used as both cropland and grazing land, the vast majority of agricultural lands are on the so-called mineral soils in which organic C makes up a few percent of the total soil mass. Finally, in addition to C in organic forms, some soils contain significant amounts of inorganic C in the form of carbonate minerals (typically Ca/$MgCO_3$). Soils with high inorganic carbon contents include those formed from carbonate-containing parent material (e.g., limestone) as well as soils in arid and semiarid environments in which secondary pedogenic carbonates (e.g., caliche) are formed from the reaction of bicarbonate (derived from CO_2 in the soil) with base cations, which can then be precipitated in subsoil layers (Nordt *et al.*, 2000). However, in most cases changes in inorganic C stocks are slow and are not amenable to traditional soil management practices. Thus, further discussion of soil C sequestration in this article is restricted to organic C stocks.

The organic carbon content of soils is mainly governed by the balance between the emissions of CO_2 from decomposition processes (i.e., heterotrophic soil respiration) and the amount of carbon added to soils as plant residues and manures. Other processes such as leaching of dissolved organic C can affect the soil C balance, but in most soils leaching is a minor or insignificant C-loss process. Soil erosion can also have a significant impact on C stocks at a given location, by removing soil mass (including associated organic matter) from the soil surface. However, erosion is primarily a transport process so that materials removed from one area are subsequently deposited elsewhere. Thus, whether soil erosion contributes to a net emission of CO_2 to the atmosphere (a source) or it represents a C sink through the deposition and burial of C-rich sediments depends on landscape level dynamics of erosion and deposition (van Oost *et al.*, 2007). Although minimizing erosion is an important agricultural management objective, given the uncertainty about erosion impacts on soil C stocks at landscape and regional scales (Harden *et al.*, 2008), subsequent discussion of management impacts on soil C are made under the assumption of negligible soil erosion rates.

Given that soil C stocks are the result of a dynamic balance of C inputs and losses, increased SOC stocks can be achieved by increasing C inputs to soils and decreasing the specific rate of decomposition of organic matter already in the soil. Conversely, decreasing C additions and increasing the specific rate of decay will decrease soil C stocks. Over time, in the absence of major disturbances or changes in climate, soil C stocks tend toward an equilibrium in which the rate of C additions to soil and the rate of C losses from soil are approximately equal and soil C stocks remain roughly constant. The fundamental reason for this equilibrium behavior of soil organic matter is that decomposition rates for a given soil tend to be proportional to the amount of organic matter that is available for decomposition by soil organisms. This proportional relationship between decomposition rates and the amount of decomposable organic matter is referred to as first-order kinetics.

This simplified soil C balance can be shown as,

$$dC/dt = I - kC \quad [1]$$

in which the rate of soil C change (dC/dt) is given by the difference between the rate of C addition (I) and the rate of C loss via decomposition (kC), where k is the specific rate of decomposition and C is carbon content of the soil. The rate of C addition (I) is closely related to plant productivity and plant dry matter partitioning (i.e., between roots, leaves, fruits, etc.), which, in turn, are largely a function of climate, vegetation type, and soil fertility and water relationships. Similarly k, the specific decomposition rate, is influenced by climate and soil characteristics that determine the activity rate of decomposing organisms in soil.

In a young developing soil with low organic matter contents, 'I' initially exceeds 'kC' and hence SOC levels (C) initially increase, but as SOC accumulates, losses through decomposition rise and the SOC content eventually plateaus at a level where C additions are offset by decomposition losses and the rate of change equals 0, viz.,

$$dC/dt = 0 = I - kC \quad [2]$$

$$I = kC$$
$$C^* = I/k \quad [3]$$

where C^* is the equilibrium (or 'steady state') SOC level. Another useful concept is that of the mean residence time (MRT), which at steady state is defined as $MRT = 1/k$ and represents the average duration of C atoms in the SOC pool. From this simple model of the soil C balance, it is readily apparent that the equilibrium SOC level is directly proportional to the C input rate and inversely proportional to the specific decomposition rate. Most operational models of soil C dynamics conceptualize soil organic matter not as a single homogeneous entity (as implied in eqn [1]), but rather as a number of fractions or pools that vary distinctly in their relative rates of decay. However, it can be shown that even for models with multiple pools, provided that individual pools decay according to first-order kinetics, the overall equilibrium relationship shown in eqn [3] still holds (Paustian *et al.*, 1997a).

From eqn [3], it is clear that for a mature soil at an equilibrium SOC level, either an increase in the rate of C input or a decrease in the specific rate of SOC decay will provoke an increase to a new higher equilibrium SOC level. However, the rate of increase will be finite and within a few decades (depending on the SOC MRT) SOC levels will approach the new equilibrium level and the rate of change will go toward zero. **Figure 1** shows an idealized time history of SOC stocks, beginning with a substantial initial loss of C following conversion of a native ecosystem to annually cropped land, with a subsequent trend over time toward a lower equilibrium carbon level. Adoption of improved management practices on cropland can increase SOC stocks toward new equilibrium levels depending on the attributes of those systems.

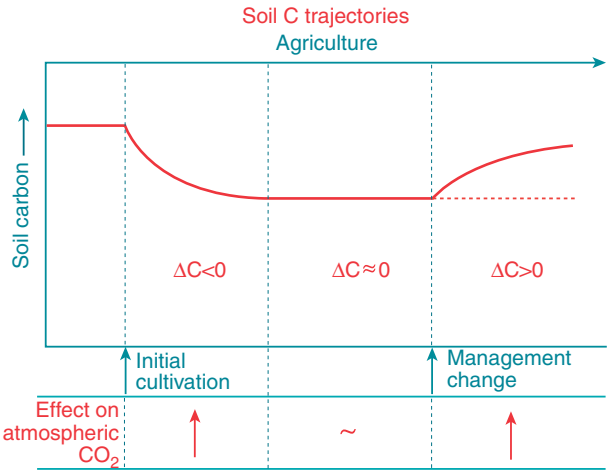


Figure 1 Idealized changes in soil organic carbon (SOC) over time as a function of ecosystem management. Conversion of native ecosystems to annual cropland leads to an initial loss of SOC (with net CO_2 emissions going to the atmosphere) that eventually tends toward new equilibrium where the net exchange of CO_2 with the atmosphere is near zero. Adoption of management practices that promote C sequestration results in an increase in SOC stocks with a net uptake of CO_2 from the atmosphere. Under the new practice, SOC stocks will again tend toward new equilibrium so that the rate of net CO_2 uptake diminishes over time. Reprinted with permission from Council for Agricultural Science and Technology (CAST), 2011. Carbon Sequestration and Greenhouse Gas Fluxes in Agriculture: Challenges and Opportunities. CAST Task Force Report 142. Ames, Iowa: CAST.

One implication of this model of soil C balance is that as C inputs increase, SOC stocks at equilibrium increase in direct proportion. Although there is good evidence that many agricultural soils exhibit this behavior over a limited range of C input levels (Paustian *et al.*, 1997b; Huggins *et al.*, 1998), a model assuming first-order kinetics implies that there is no upper limit to SOC storage and that stocks can always be increased by further increasing input rates (I; eqn [3]; see **Figures 2(a)** and **(b)**). Several lines of evidence suggest that there is an effective upper limit for the amount of SOC that can be stored in mineral soils, and the concept of soil C sequestration has been proposed as a modifier of the first-order model (Hassink and Whitmore, 1997; Six *et al.*, 2002). It is widely recognized that one of the main ways in which a portion of soil organic matter can persist for very long periods (centuries to millennia) is through interactions with soil mineral particles, in which organic matter bound on clay mineral surfaces and encapsulated within stabile microaggregates may be largely protected from decomposition by soil microorganisms (von Lützow *et al.*, 2006). As there is a finite amount of mineral surface area for a given soil, there would also be a limit to the amount of organic matter that could be physically protected against decomposition, and above this 'saturation limit' additional organic matter inputs would be subject to rapid decomposition and would be released as CO_2 (Six *et al.*, 2002; Stewart *et al.*, 2007; **Figures 2(c)** and **(d)**). The amount and type of clay minerals determine the amount of surface area and binding capacity for organic materials and thus soil texture and mineralogy are major determinants of the soil saturation capacity. Several recent experiments support this revised model of SOC balance (Stewart *et al.*, 2008; Chung *et al.*, 2010; Huang *et al.*, 2012; O'Brien and Jastrow, 2013).

The implications of saturation for soil C sequestration as a CO_2 mitigation strategy is that the soils (layers) which already have high organic matter contents may not be responsive to practices designed to further increase SOC stocks. Conversely, soils with C contents well below saturation (i.e., a large saturation deficit) will have greater capacity to stabilize more organic matter (**Figure 2(d)**) in SOC pools having long residence times and will show the greatest impacts of C-sequestering practices. Finally, it should be noted that this saturation concept applies to mineral soils only. For organic soils (i.e., histosols), decomposition dynamics are dominated by limited aeration due to a high and persistent water table that inhibits oxygen diffusion into the soil. Thus, SOC storage capacity under these conditions will be limited mainly by the depths to which organic matter can accumulate in the saturated zone, which is mainly controlled by underlying topography and hydrology.

Practices to Promote Soil Carbon Sequestration

As discussed in Section Basics of Soil Carbon Sequestration, many agricultural soils have lost a substantial portion of their original carbon stocks following conversion from native

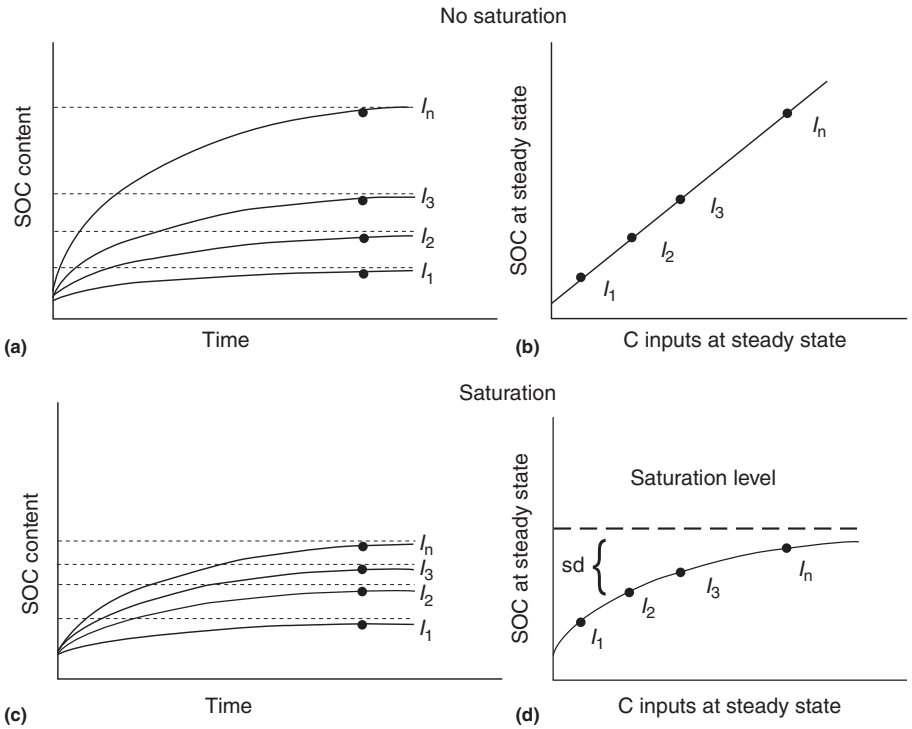


Figure 2 Illustration of differences in C dynamics and effects of C input rate on equilibrium soil organic carbon (SOC) stocks. Assuming first-order kinetics, increases in C input rates cause an increase over time in SOC stocks (a) toward a new equilibrium state, where equilibrium (i.e., steady state) SOC stocks are proportional to C input rate (b). Under saturation kinetics, increases in C input act to increase SOC stocks that also tend toward a new steady state over time (c), but the increase in the steady state SOC per unit of C input decreases as SOC stocks approach a saturation limit (d). The difference between SOC stocks and the maximum level at saturation is termed the saturation deficit (see (d)). Reprinted with permission from Figure 1 in Stewart, C.E., Paustian, K., Conant, R.T., Plante, A.F., Six, J., 2007. Soil carbon saturation: Concept, evidence and evaluation. Biogeochemistry 86, 19–31, with permission from Springer Science + Business Media B.V.

ecosystems. Land managed for annual crops in particular tends to be depleted in SOC as a consequence of historical land management practices. There are a number of different reasons for the loss of SOC following conversion to cropland. First, perennial native vegetation, which typically has a high fraction of C allocated below ground, was replaced by annual crops that were bred for maximum aboveground production and harvest offtake, thus minimizing crop residue return. Secondly, intensive soil tillage practices were typically used for weed control and for preparing a uniform seedbed. Conventional intensive soil tillage tends to break down soil structure and stimulates organic matter mineralization. In other cases, artificial drainage of wet soils (particularly histosols) and liming of acid soils, in order to improve conditions for annual crop production, resulted in accelerated organic matter mineralization, depleting SOC stocks. In contrast, agricultural lands managed for grazing (pasture and rangeland) are less likely to have a large SOC deficit relative to their native state, given the maintenance of perennial grass-dominated vegetation and thus high C allocation to roots and the lack of tillage disturbance. However, substantial management-induced C losses can occur, especially with overgrazing or poor grazing management in which plant production is degraded, thereby reducing C inputs from plant residues. Also, pastures established on organic (e.g., peat) soils typically involve drainage and other practices (e.g., liming and fertilization) that can greatly stimulate decomposition rates resulting in large decreases in SOC stocks.

Given these impacts of past conventional management practices, there is a clear potential to recover previously lost carbon with the adoption of improved practices. In many cases, SOC stocks under native vegetation do not represent a maximum or saturation limit for SOC contents, so at least theoretically it may be possible to sequester more SOC than under conditions of the native ecosystem.

The main practices that can contribute to an increase in carbon stocks in soils are well known from numerous field experiments and comparative field observations. Table 1 lists several classes of practices, classified according to their main mode of action in either increasing C inputs or reducing C losses emissions.

Increased Productivity and Residue Retention

Numerous long-term field experiments in which crop rotation or residue retention is the main treatment variable show a roughly linear relationship between the rate of C return in residues and changes in SOC stocks (e.g., Paustian *et al.*, 1997a; Huggins *et al.*, 1998). Annual crops that produce large amounts of residues, such as corn and sorghum, typically result in higher soil carbon levels than many other crops.

Table 1 Agricultural management actions that can increase organic carbon storage and promote a net removal of CO_2 from the atmosphere

Management practice	*Increased C inputs*	*Reduced C losses*
Increased productivity and residue retention	✓	
Conversion to perennial grasses and legumes	✓	✓
Manure and compost addition	✓	
Biochar addition	✓	
No-tillage and other conservation tillage		✓
Rewetting organic (i.e., peat and muck) soils		✓
Improved grazing land management	✓	

For example, long-term experiments at two sites in Ohio (Dick *et al.*, 1998) show approximately 10 Mg C ha^{-1} more soil carbon after 30 years under continuous corn crops or with corn–oat–hay rotations than in the conventional corn–soybean rotations, equal to an average gain of 0.3 Mg C ha^{-1} $year^{-1}$. Soybeans typically produce approximately one-third as much residue as corn (and also much less than hay crops), and this lower C input rate accounts for the lower SOC levels.

Conventional annual crop production in temperate climates often entails crop production only over the main growing season (summer) such that the soil is bare for half or more of the year (during the winter fallow period). If favorable moisture and temperature conditions exist, winter cover crops (e.g., annual grasses, legumes, and root crops) can be grown outside of the main cropping season, supplying additional residue inputs. Another option to both lengthen the total vegetated period during a crop rotation and incorporate crops that have higher C inputs is to combine annual crops with short-duration (2–4 year) perennial grasses and legumes that are used for forage production. Such mixed annual/perennial crop rotations were the dominant practice on cropland in much of Europe and North America before the widespread use of chemical fertilizers and the replacement of animal traction by machinery.

Similarly, in many semiarid regions (e.g., Great Plains of the United States and Canada, parts of the Australian wheat belt, and parts of Europe, Africa, and the Middle East), cereals may be grown in a 'summer fallow' rotation in which one crop (e.g., winter wheat) is grown only every other year. This is primarily done to store additional soil water during the long fallow period to help ensure a successful grain harvest from the planted crop; however, it results in the soil being bare for as much as 18 months during a 2-year period. However, by using no-till practices (see Section No-Till and Conservation Tillage Practices) and more drought-resistant crops, it is possible to add additional crops to the rotation and substantially reduce or eliminate the bare fallow period, thus increasing the amount of plant residues added to soil (Peterson *et al.*, 1998; Alvaro-Fuentes *et al.*, 2008).

Several reviews have been made of long-term field experiments with different crop treatments that relate to the amount of crop residues returned to the soil. In a majority of field studies reviewed by Ogle *et al.* (2005), rotations with high C inputs (i.e., use of winter cover crops, green manures, irrigation, high residue crop varieties, or annual crop rotations that have one or more years of hay) increased SOC storage relative to conventional crop rotations (e.g., continuous cereals) by 7–11% over a 20-year period. In a more recent review of US studies (Eagle *et al.*, 2012), the authors reported average C sequestration rates of 0.27 Mg C ha^{-1} $year^{-1}$ for winter cover crops and 0.16 Mg C ha^{-1} $year^{-1}$ for more diversified crop rotations. Including perennial crops in the rotation and full conversion to perennial crops resulted in average sequestration rates of 0.16 and 0.62 Mg C ha^{-1} $year^{-1}$, respectively. In semiarid systems, intensifying crop rotations by eliminating or reducing summer fallow has been found to increase soil C stock when converting into no-till practices (Campbell *et al.*, 2005). It is likely that the key factor involved is the additional water storage occurring under no-till, enabling greater total crop production over the rotation and hence greater C inputs to the soil (Peterson *et al.*, 1998). The C sequestration potential of eliminating summer fallow in the United States and Canada has been estimated to be 0.1–0.2 Mg C ha^{-1} $year^{-1}$ (Eagle *et al.*, 2012).

In addition to altering or intensifying crop rotations, practices that promote the more efficient use of inputs, such as fertilizer and irrigation, will generally yield the best results for GHG mitigation (Paustian *et al.*, 1998). Efficiency in this context is defined as maximizing crop production per unit of input. Where fertilizer and irrigation inputs are used in excess, there is risk of increases in other GHG emissions, particularly nitrous oxide, which can offset part or all of the gains in soil carbon. Tailoring fertilizer and irrigation applications to match crop nitrogen demands, so that less nitrogen is left behind in the soil, can reduce nitrous oxide emissions while building soil carbon stocks. Efficient use of irrigation water will similarly reduce nitrogen losses, including nitrous oxide, and minimize CO_2 emissions from energy use for pumping while maintaining high yields and crop residue production.

Conversion of Annual Cropland to Perennial Grasses and Legumes

In some instances, marginal croplands that are susceptible to high erosion rates, flooding, or have otherwise unsuitable soils have been allowed to revert to natural vegetation or replanted to perennial vegetation as a soil conservation measure. Examples of land-use policies to set aside such marginal lands include the Conservation Reserve Program (CRP) in the United States and similar set-aside programs in other industrialized countries. In addition to governmental policies, reversion of annual cropland for wildlife conservation is being explored by private organizations (Ducks Unlimited, 2013). Such cropland set-asides can result in significant C sequestration

benefits, due to the greater root C inputs and elimination of soil tillage with conversion into perennial vegetation. Other practices involving small-scale land cover conversion, such as adding grass buffer strips along cropland field margins, can additionally sequester C by the perennial vegetation as well as trap sediment from agricultural runoff. In reviewing studies involving conversion of annual cropland to grassland as a conservation set-aside, Ogle *et al.* (2005) found a restoration of SOC levels ranging from 82 to 93% (for the top 30 cm) of native grassland levels after 20 years. A global literature review by Post and Kwon (2000) estimated average C sequestration rates for conversion of agricultural land into perennial forest and grassland at 0.34 and 0.33 Mg C ha^{-1} $year^{-1}$, respectively. Overall, conversions of cropland tended to yield somewhat higher SOC gains in subtropical compared with temperate regions. Studies of SOC accumulation rates on CRP land in the United States by Follet *et al.* (2001) yielded average increases of 0.9 Mg C ha^{-1} $year^{-1}$ (in the 0–20 cm depth). A more recent review of published studies on set-aside lands in the United States estimated an average C sequestration rate of 0.68 Mg C ha^{-1} $year^{-1}$ (Eagle *et al.*, 2012). The potential of set-aside land to sequester C greatly depends on the vegetation, former land use, soil type, and climate. Another important factor to consider is the duration of the set-aside practice. In many instances, set-asides are later returned to annual cropland use, and thus much of the soil C accumulated during the set-aside may be lost following reversion to annual cropping. Thus, permanent set-asides for conservation purposes are needed to preserve the C sequestration benefits over the long term.

Manure and Compost Addition

Soil organic matter typically increases much more with manure or compost additions than for an equivalent amount of C added as crop residues or green manure. As manure and compost consist of plant matter that has already been partially decomposed (i.e., in animal digestive tracts and subsequently in manure storage or composting systems), the residual organic matter decomposes more slowly than fresh plant material and thus promotes a greater increase SOC per unit of C addition (Paustian *et al.*, 1997b). Changes in SOC stocks from application of animal manure, and to a lesser degree compost, have been studied extensively in long-term field experiments (e.g., Paustian *et al.*, 1997a,b; Ogle *et al.*, 2005; Eagle *et al.*, 2012). In a global meta-analysis, Ogle *et al.* (2005) found that manure additions were among the crop management practices yielding the greatest increases in SOC, with an average increase of approximately 35% in SOC in the top 30 cm compared with reference cropping systems with no manure addition. Based on European studies, Freibauer *et al.* (2004) estimated an average rate of SOC increase of 0.4 Mg C ha^{-1} $year^{-1}$ with application of farmyard manure on cropland. One issue in considering organic amendments (manure and compost) as a soil carbon sequestration activity is that the organic matter in the manure often originates from off-site locations (i.e., as purchased livestock feed). Thus, a full net accounting of the impact of manure additions on soil C (and other GHGs) requires that the C 'cost' associated with the production of the livestock feed itself be included in the calculation (Smith and Powlson, 2000).

Biochar Addition

Biochar has received attention as a soil amendment for C sequestration that can also enhance soil fertility and crop productivity (Lehmann *et al.*, 2006; Lehmann, 2007; Verheijen *et al.*, 2009). Biochar is essentially the same substance as charcoal, but the term biochar is typically used to denote its intended use as a soil amendment rather than as a fuel (charcoal). Biochar is formed from the heating of biomass (300–1000 °C) in the absence of oxygen and is a coproduct of pyrolysis and gasification processes used to produce liquid and gaseous fuels. Biochar is the solid residue remaining in which O and H have been preferentially removed with the more volatile biomass components, and thus the residue consists of C-rich and highly aromatic molecules and ash (i.e., K, Ca, and Mg). In general, the higher the treatment temperature, the more the O and H are removed and the solid residual takes on more of a graphite-like structure that consists of sheets of hexagonally arranged carbon atoms (graphene). In addition to temperature, the duration of the heating as well as the properties of the original biomass contributes to chemical and physical variation of the biochar (Verheijen *et al.*, 2009).

Owing to its recalcitrant chemical structure, the graphene-like biochar molecules are not readily decomposed by microorganisms and thus can remain in soils for hundreds or thousands of years. Thus, biochar produced from renewable biomass stocks (or from waste biomass) as a coproduct of biofuel production offers a potential means to sequester large amounts of C in soils. Modern interest in biochar as a soil amendment stems from studies of prehistoric 'anthropomorphic' soils in the Amazon region – the so-called Terra Preta – which are believed to have been formed from additions of charcoal and various household waste and plant residues over many years (Glaser *et al.*, 2001). These soils are dark in color, rich in organic matter, and more fertile than the native highly weathered acidic soils. There is considerable interest and ongoing research on how biochar affects plant productivity and various soil properties (e.g., pH, water-holding capacity, cation exchange capacity, nitrogen dynamics, trace gas emissions, and microbial communities). Although much of the research to date suggests that biochar additions can be beneficial to many soils (particularly for old and highly weather acidic soils in tropical climates), the irreversible nature of biochar additions to soil has led to calls for more research to determine optimal amounts of biochar additions and how different types of biochar (i.e., type of plant material, heating temperature and duration, etc.) impact the plant–soil system. In addition, the economic and full life cycle implications of large-scale production and use of biochar in agricultural systems are just beginning to be assessed (Field *et al.*, 2013).

Rewetting of Organic Soils

Cultivated organic soils represent another land restoration opportunity. These lands are a significant source of agricultural CO_2 emissions with high rates up to 10–20 Mg C ha^{-1} $year^{-1}$

(Ogle *et al.*, 2005). Hence, wetland restoration may be a mitigation option. However, restored wetlands may emit methane, which would need to be considered in assessing the overall mitigation potential of wetland restoration.

No-Till and Conservation Tillage Practices

The use of no-till and other conservation tillage practices have been adopted increasingly over the past 20 years. No-tillage eliminates the turning and mixing of the soil by using herbicides for weed control and planting seed directly into the soil at the desired depth with no other soil disturbance. Typically, aboveground residues are left in place on the surface. Other so-called conservation tillage practices (e.g., mulch tillage and ridge tillage) still involve some physical disturbance of the soil with tillage implements, although to a shallower depth or less intense mixing of the soil compared with conventional tillage using a moldboard plow or deep-disk tillage.

It is well recognized that intensive soil tillage tends to accelerate organic matter decomposition – resulting in oxidation of carbon to CO_2 – by warming the soil, breaking up residues and soil aggregates, and placing surface residues into the moister environment within the soil (Reicosky *et al.*, 1995; Six *et al.*, 2000). Hence, reducing the frequency and intensity of this physical soil disturbance helps to preserve the natural soil structure and enhances the stabilization (i.e., decreased susceptibility to decomposition) of organic matter within soil aggregate structures (Denef *et al.*, 2004).

Several reviews of long-term field studies with varying tillage treatments have summarized findings on SOC sequestration rates following conversion to reduced or no-till. More consistent soil C sequestration rates are typically found for conversions to no-till than to reduced-till systems, probably reflecting the greater stabilization of organic matter with the near complete absence of mechanical disturbance with no-till (Six *et al.*, 2000; West and Post, 2002). Using a global dataset of 67 long-term agricultural experiments, West and Post (2002) reported SOC sequestration with adoption of no-till averaging 0.48 Mg C ha^{-1} $year^{-1}$ over a mean duration of 15 years. Ogle *et al.* (2005) analyzed data from 126 studies worldwide and estimated that soil carbon stocks in surface soil layers (to 30 cm depth) increased by an average of 10–20% over a 20-year time period under no-till compared with intensive tillage practices. The relative increases in SOC were higher under humid than dry climates and higher under tropical than temperate temperature regimes. For the Southeastern United States, Franzluebbers (2010) estimated SOC sequestration with conservation tillage at 0.45 Mg C ha^{-1} $year^{-1}$ and Johnson *et al.* (2005) found a similar average gain of 0.48 Mg C ha^{-1} $year^{-1}$ in the Central United States. Lower average rates have been reported for the Southwestern (0.30 Mg C ha^{-1} $year^{-1}$, Martens *et al.*, 2005) and Northwestern United States (0.27 Mg C ha^{-1} $year^{-1}$, Liebig *et al.*, 2005). For the entire United States, a recent review (Eagle *et al.*, 2012) estimated mean C sequestration rates of 0.3 Mg ha^{-1} $year^{-1}$ for conservation tillage and no-till systems, similar to earlier estimates by West and Marland (2002) for no-till systems in the United States (0.34 Mg ha^{-1} $year^{-1}$).

The impact of tillage practices on SOC stocks appears to depend heavily on climate (Ogle *et al.*, 2005; Six *et al.*, 2004) as well as soil type (Dumanski *et al.*, 1998) and initial soil organic C content (Franzluebbers, 2010). A lack of C sequestration following no-till adoption, or even C losses relative to intensive tillage, has also been reported for some cool, moist environments and on heavy textured soils (e.g., Angers and Eriksen-Hamel, 2007). Reduced rates of residue C inputs under no-till for corn and wheat, predominately in cooler, wetter regions (upper Midwest), may explain part of the reduced C sequestration performance of no-till under these conditions (Ogle *et al.*, 2012). Also, soils in cool, wet environments often have already high surface organic matter contents and thus may be closer to a C 'saturation level' and hence less of the residue added at the soil surface under no-till can be effectively stabilized (Stewart *et al.*, 2007; Gregorich *et al.*, 2009).

Improved Grazing Land Management

Permanent grasslands can maintain large SOC stocks due to several characteristics. Perennial grasses allocate a high proportion of photosynthetically fixed carbon below ground, maintain plant cover year-round, and promote formation of stable soil aggregates. However, the potential for increasing SOC stocks in grazing lands is highly dependent on past management and the extent to which plant productivity and carbon inputs can be enhanced through management improvements (Conant *et al.*, 2001). Grassland systems that have been degraded in the past or maintained under suboptimal management conditions are most conducive for sequestering additional carbon.

A commonly used differentiation of grazing land is between pastures and rangelands, where pastures are more intensively managed grazing lands, often with nonnative (introduced) plant species, located in mesic (humid and subhumid) environments, compared with rangelands that are more extensively managed, with predominantly native plant species, in semiarid and arid environments. These differences in climatic conditions and management intensity largely align with the type of management interventions that are possible to enhance SOC sequestration. Pasture systems with their higher productivity offer a diverse set of management options, for example, selection of improved grass species, overseeding with legumes, improved fertilizer management, water management, liming, and improved grazing systems. In contrast, most rangeland systems have relatively low plant productivity and therefore practices such as fertilization are unlikely to be financially viable. In rangelands, management activities are mostly restricted to manipulating grazing practices (density, duration, and timing of livestock grazing) and vegetation manipulations, such as burning and mechanical removal/control of woody shrubs.

Conant *et al.* (2001) summarized more than 115 studies of management effects on grassland SOC and estimated rates of C increase averaging between 0.1 and 3 Mg C ha^{-1} $year^{-1}$ for different management improvements. The highest rates occurred with introduction of deep-rooted African grasses in South American savannas (Fisher *et al.*, 1994), whereas most of the higher rates for temperate grasslands showed gains of approximately 1 Mg C ha^{-1} $year^{-1}$. Average rates of SOC

increase were approximately 0.3 Mg C ha^{-1} $year^{-1}$ for fertilization and improved grazing systems and approximately 0.7 Mg C ha^{-1} $year^{-1}$ for introduction of legumes.

Appropriate grazing strategies are important to maintain grassland health, productivity, and SOC stocks, although it is difficult to generalize the effects of stocking rates and grazing intensity across the great diversity of pasture/range systems. Overgrazing, where grassland productivity and plant cover are significantly diminished, generally decreases soil (and plant) C stocks (Ogle *et al.*, 2004), whereas low to moderate grazing intensities tend to promote higher C storage (Ogle *et al.*, 2004; Franzluebbers and Stuedemann, 2009), compared with either ungrazed or heavily grazed systems. More intensively managed grazing systems – often referred to as rotational grazing, mob grazing, or multipaddock grazing – can be effective by promoting efficient use of available forage while allowing an optimal 'rest and recovery' period for regrowth (Conant *et al.*, 2003). However, many whole-system grazing approaches are difficult to generalize because grazing practices are often site specific and involve a suite of different management activities. Some studies suggest that rotational grazing can increase soil C stocks in humid and subhumid environments (Conant *et al.*, 2003; Sanjari *et al.*, 2008; Teague *et al.*, 2010), relative to conventional continuous grazing. In tallgrass prairie systems in the United States, Teague *et al.* (2010) found that rotational grazing increased soil organic matter by 50% relative to heavy continuous grazing and 11% relative to light continuous grazing. However, in a review of grazing systems focusing mainly on semiarid rangelands in the United States, rotational grazing systems did not appear to significantly improve the grassland productivity, soil C stocks, or animal performance, relative to continuous grazing systems, at the same stocking rates (Derner and Hart, 2007; Briske *et al.*, 2011). In these systems, the dominant controls on soil C stocks, independent of grazing system, appear to be total animal stocking rate and precipitation (Derner and Schuman, 2007).

Overall Soil Carbon Sequestration Potential

A variety of estimates of soil C sequestration potential on agricultural lands have been made at national as well as global scales (e.g., Paustian *et al.*, 1998; IPCC, 2000; Lal, 2004; Smith *et al.*, 2007). These estimates build on regionally averaged gains in soil C for various management interventions and assumptions of the land area available for implementation and potential rates of adoption of C-sequestering practices. Such estimates are referred to as technical potentials in that they do not consider economic or policy constraints on the actual amounts of mitigation that might be achieved. Technical potentials can be regarded as a theoretical upper limit with present technologies in the absence of economic or other constraints on implementation. Thus, the expected mitigation potential that could realistically occur would be much lower.

Currently, the most comprehensive and spatially and temporary refined estimates of global soil C sequestration are those given in the Intergovernmental Panel on Climate Change fourth assessment report (IPCC, 2007; Smith *et al.*, 2007). The analysis stratifies global agricultural land area by economic/development zones as well as major climatic and land-use type. Their analysis also considers economic constraints on achievable mitigation by using regionally modeled marginal cost curves for implementing new practices and various levels of C offset pricing to estimate how much adoption of mitigation practices would be incentivized at a given monetary value for GHG reductions achieved (Figure 3).

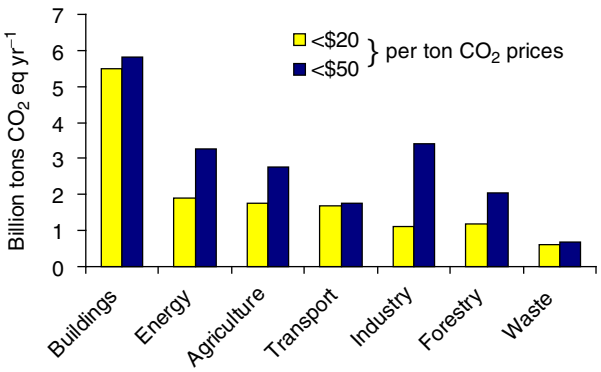


Figure 3 Estimates of potential GHG mitigation by major sectors of the global economy for two putative marginal carbon prices (<20 and <50 US$), reproduced with permission from Smith, P., Martino, D., Cai, Z., *et al.*, 2007. Greenhouse gas mitigation in agriculture. Philosophical Transactions of the Royal Society, B 363 (1492), 789–813. Estimates are in billion MT CO_2 equivalent per year. Estimates include mitigation for all gases (CO_2, CH_4, and N_2O) and emission sources but carbon sequestration constitutes ~90% of total mitigation potential for the agricultural sector (Smith *et al.*, 2007).

Although there are still many uncertainties with such an analysis, it provides a useful first approximation of what mitigation might be achieved through improved agricultural practices if a significant economic value were placed on emission reductions as part of mandatory GHG reduction policies. This analysis (Figure 3) also suggests that agricultural mitigation options have the potential to be a significant contributor to overall reductions in GHG emission as the agricultural potential in total is similar to the mitigation potential for other major sectors of the global economy.

Implementation of Soil Carbon Sequestration – Challenges and Opportunities

For soil carbon sequestration to become a significant GHG mitigation strategy, a number of technical and policy-related barriers need to be overcome. For the vast majority of agricultural soils, increasing and maintaining SOC stocks is a highly desirable objective for improved productivity and sustainability. Thus, some adoption of improved management practices that promote C sequestration will undoubtedly occur independent of climate change concerns. However, to qualify as a mitigation practice, actions need to be in addition to 'business as usual' activities (i.e., activities that would have taken place in the absence of mitigation policies). This principle is referred to as 'additionality' and it is a widely recognized concept for climate mitigation policies at both national and international levels. Thus, agricultural GHG mitigation, including soil C sequestration, will involve incentivizing farmers to adopt practices beyond what they might do anyway. There can be a variety of reasons – including economic,

technical, social, and cultural barriers – why farmers might not otherwise adopt C sequestering without additional incentives (Antle *et al.*, 2003). Incentives might come in the form of government payments or other support for adopting conservation practices. Another approach is to allow agricultural producers to generate the so-called carbon offsets, which then have value in a cap-and-trade emission reductions system. With a cap-and-trade policy, emissions from large industrial sources are subject to mandatory limits (caps) that then decrease over time. To comply with the specified emission reductions, industries that are subject to the cap either can undertake mitigation activities for the capped sources or may purchase unused emission allowances or offsets from elsewhere within the system, for example, from agricultural mitigation projects.

To date, soil C sequestration has not been included in many major GHG mitigation policies, such as the Kyoto Protocol and the Clean Development Mechanism (CDM). However, there is broader interest in including soil C sequestration as a part of future international agreements, in part because of the added benefits from encouraging soil improvements generally and helping to buffer vulnerable agriculture soils against climate change impacts (Smith and Olesen, 2010). In addition, outside of formal regulatory agreements, there is a growing voluntary market for GHG mitigation activities and several soil C sequestration projects have been initiated in which farmers and land owners can receive financial incentives to undertake improved management practices through the production and sale of C offsets for the voluntary market.

In the remainder of this chapter, a brief discussion is provided about some of the technical and policy-related issues with respect to soil C sequestration. Because GHG mitigation activities can span all sectors of the global economy and a wide variety of emission sources, any one mitigation strategy (including soil C sequestration) must be competitive with other mitigation actions. Thus, a key issue is providing confidence to policy makers and potential emission offset buyers that soil C sequestration from agricultural practices is 'real' (i.e., actually benefits the atmosphere), can be measured and verified, and that the emission reductions are long lasting ('permanent').

Quantifying Soil C Sequestration

Accurately quantifying changes in soil C stocks is the key to ensuring that C sequestration resulting from improved land use and management practices is real and verifiable. Compared with many other emission sources, for example, CO_2 emissions from fuel consumption, quantifying soil C stock changes is more complex and difficult. Soils differ from point emission sources in that emissions and sinks (C uptake) are distributed widely across a varying and heterogeneous landscape. In addition, soil C dynamics are driven by a complex and interacting set of factors, many of which vary at fine spatial scales. Thus, soil responses to the same set of practices can often vary significantly across the landscape and even within the same field (Paustian *et al.*, 2011). This makes accurate local-scale quantification of soil C stock changes, as for a specific mitigation project, challenging. Two main options are described: (1) direct measurements of C stock changes and (2) practice-based approaches using empirical or process-based models, although in practice a combination of the two options might also be used.

Direct measurement of soil carbon changes

Estimating the net flux of CO_2 between soils and the atmosphere can, in principle, be done with direct flux measurements, such as eddy covariance (Hollinger *et al.*, 2005). However, these techniques are largely confined to research applications and are not practical for routine measurement and monitoring of mitigation projects. Instead, the main direct measurement approach involves tracking changes in SOC stocks over time. This C-balance approach assumes that the primary C flows that affect SOC stocks are the addition of C from plant/animal residues (representing CO_2 uptake) and the losses of CO_2 via decomposition and mineralization of organic matter in the soil. Thus, measurement of SOC stock changes at the same location at two or more points in time, or measurements of contrasting management treatments (preferably in a randomized field experiment) that have been in place for a known period of time, can be used to estimate net CO_2 emissions or removals by soils.

Accurate methods to measure SOC content (i.e., g C g^{-1} soil) and soil bulk density (i.e., g soil cm^{-3} soil), which are the two values needed to compute SOC stocks on an area basis and to a defined depth, have been developed and routinely applied for many decades. Automated dry combustion soil C analyzers are highly accurate and currently constitute the 'gold standard' for measuring C concentration in soils. Mid- and near-infrared spectroscopy (and other spectroscopic methods) are being used more widely as a way to reduce analysis costs and increase sample throughput (Shepherd *et al.*, 2003; Brown *et al.*, 2006; Janik *et al.*, 2007), although they require careful calibration for different soil types to attain high accuracy and precision. Bulk density is easily measured gravimetrically from a known sample volume but requires care in sampling and handling (e.g., avoiding compaction).

Thus, the challenge in measuring SOC stock changes is not in the measurement technology per se but rather in designing an efficient and cost-effective sampling regime. The spatial variability of SOC is often high (Robertson *et al.*, 1997) and the rate of C stock change is typically low relative to the amount of C already present in the soil; thus, there is a low 'signal-to-noise' ratio. Hence, a 5–10-years period between measurements is typically needed to adequately detect the cumulative change (Conant and Paustian, 2002b; Smith, 2004). Depending on the degree of spatial heterogeneity and the amount of change relative to the background level, detecting significant changes at field scales can require a relatively large number (e.g., 15–100) of samples (Garten and Wullschleger, 1999). However, sampling designs configured for precisely relocatable points for repeated measurement over time (e.g., Conant *et al.*, 2003; Lark, 2009; Spencer *et al.*, 2011) can reduce sample requirements compared with simple random or stratified random sampling designs. Because the sample size requirements (per unit area) decrease greatly as the area of inference increases in size (Conant and Paustian, 2002b), direct measurements – although expensive – can be feasible for large project areas (Mooney *et al.*, 2004).

Model-based approaches

Models provide a means to integrate the effects of different land-use and management practices, as well as soil and climate effects, on SOC stocks. The models use data on land management practices, i.e., 'activity data,' together with information on environmental variables, such as climate and soil type, to predict soil C stocks and C stock changes for project-level accounting (Paustian *et al.*, 2011). As part of an activity or 'practice-based' approach, models provide a means of estimating outcomes (i.e., C stock change) for specified actions (i.e., adoption of prescribed conservation practices). In a broad sense, models of SOC change can be characterized as empirical models, which are based on statistical relationships estimated from field measurements, and process-based models, in which the model algorithms are based on more basic scientific principles as well as parameterization and testing against field measurements. Most process-based models strive to achieve a more general description of the processes and controls on SOC dynamics in order to better represent the complex interactions between these controls. A key requirement for model-based approaches is that they have demonstrated acceptable predictive capacity for the conditions for which they are being applied, typically by validation against long-term field experiment data.

A variety of process-based models (e.g., Century (Parton *et al.*, 1994), DayCent (Del Grosso *et al.*, 2002), DNDC (Li *et al.*, 1992), EPIC (Williams, 1995), and RothC (Coleman and Jenkinson, 1996), among others) that were developed originally as research tools have been utilized to varying degrees for soil C and GHG inventory and accounting purposes. Further discussion of the details of these and other models of soil C dynamics is beyond the scope of this article. Recent reviews of these model-based approaches for soil C accounting can be found in Denef *et al.* (2012) and Paustian *et al.* (2011).

One limitation of process-based model approaches for quantifying soil C dynamics is that most of these models – because they were originally designed for research purposes – are difficult to use without specialized training. To make such models more accessible to project managers, developers, and natural resource management personnel – as well as farmers themselves – several soil C and GHG estimation support tools have been developed in recent years. Reviews and information about obtaining and using user-friendly calculators for estimating soil C sequestration and GHG emissions from agriculture are provided by Denef *et al.* (2012).

Other Policy-Related Issues Relevant to Soil C Sequestration

Full GHG accounting

The use of soils as a C sink for removal of CO_2 from the atmosphere is only one of a number of processes and GHG gas species that are affected by agricultural management practices. As detailed elsewhere in this volume, soils are also sources of two other biogenic GHGs, namely, nitrous oxide (N_2O) and methane (CH_4). Thus, an important consideration when promoting soil C sequestration for GHG mitigation is the various interactions between soil C dynamics and processes involved in N_2O and CH_4 emissions. In some cases management practices that could increase soil C storage could have impacts on these other emission processes, such that the benefits of additional CO_2 removal and storage are reduced or eliminated by increased emissions of these other gases. Examples of such counteracting outcomes include increased N fertilizer or manure additions that could not only induce soil C increases but also stimulate N_2O emissions; similarly, increased straw residue retention in flooded rice systems could not only benefit soil C storage but also promote higher soil CH_4 emissions. Because soil C and N cycles are closely linked, there are numerous interactions of importance for the net greenhouse balance of a particular management system. Hence, design and implementation of soil C sequestration projects should consider the impacts of any practices on all three gases and have the capability to perform full net GHG accounting.

Permanence

The issue of permanence in the context of GHG mitigation is specifically applicable to C sinks. Current mitigation policies define reductions in emissions as permanent in the sense that the act of reducing emissions in the present should not increase the risk for increased emissions at some point in the future. For carbon sinks, whereby actions are taken to remove CO_2 from the atmosphere and store it elsewhere (e.g., in soils), there is a risk that the stored C could be reemitted at a later time if the integrity of the C sink is compromised. Thus, the benefits to the atmosphere would be much less as CO_2 was only temporarily removed. Because C in soil organic matter (as well as C in biomass and other biotic-derived pools) is part of an active C cycle with the atmosphere, these C stocks are not permanent in a strict sense. However, if a C sink (i.e., an increase in SOC storage) can be maintained over a long period of time, then the net removal of CO_2 from the atmosphere can meet the permanence requirement. Thus, for implementation of policy, mechanisms are needed to minimize sink reversals and impacts of unplanned events that could result in loss of the stored carbon and to provide for replacement of any losses. In the case of SOC sequestration activities, there might be either intentional or 'forced' reversals in which the C sequestering practices are temporarily or permanently reversed. Examples of temporary reversals could include tillage needed for controlling weed infestation or failure of establishing a cover crop. Nontemporary or 'permanent' reversion could include plow out of perennial grass set aside and reversion to annual cropping for economic reasons.

Various ways have been proposed to deal with the risk of nonpermanence, including requiring long project periods so that C-sequestering practices are maintained even after net increases in SOC are nil, as the soil reaches a new equilibrium. However, many land managers may be reluctant to commit to a specific management regime for a long period of time, given the uncertainties of markets, weather, pest infestations, changes in land ownership, etc. An alternative gaining acceptance in the voluntary market system is the use of a permanence buffer system, in which a carbon registry that certifies C offsets for sale withholds a certain percentage of C offset credits as a hedge against unanticipated losses of stored carbon – in effect the buffer acts as a kind of insurance policy. This type of system has been pioneered by Verified Carbon System (VCS), which is the largest registry in the

voluntary GHG mitigation market. In the VCS system, the size of the buffer required for an individual mitigation project varies according to different risk factors, so that the buffer withholding is greater for projects deemed as having a greater risk of nonpermanence. With increased project longevity and mitigation of risk factors the percentage of credits withheld in the buffer can decrease over time. In the VCS, there is a pooled permanence buffer encompassing all projects within the registry, so that permanence in issued credits is maintained even if one or more projects fail, resulting in the release of previously stored carbon.

Leakage

Because GHG emissions are a global-scale perturbation in terms of their effect on climate, it is how much is emitted, and not where the emissions occur, that matters. Thus, it is important that actions taken in one location to reduce emissions do not lead to an increase in emissions elsewhere, thereby reducing or negating the intended mitigation activity. This phenomenon is commonly termed 'leakage' and is defined as an unintended or indirect increase in emissions occurring outside of the boundaries of a mitigation project, due to the implementation of the project. Leakage can be the result of a direct displacement of emission-causing activities from a project area to areas that are not subject to the same emission reduction requirements. For example, if cropland is converted into set-aside land for conservation purposes and GHG reductions, this could cause the crop production activities to move to other noncropland areas (e.g., native forest or grassland). Subsequent land clearance and conversion into cropland production could cause equal or greater total GHG emissions than the reductions occurring on the set-aside land. Leakage can also occur if the project mitigation activities cause an increase in other, nontargeted emission sources within the project boundaries. The other main source of leakage is a more indirect displacement of emissions due to effects on commodity production and supply and demand of products, often referred to as market-based leakage. Market-based leakage is very difficult to precisely quantify due to the fact that many different factors (including ones unrelated to mitigation activities) can influence land-use and management choices.

Leakage associated with soil carbon sequestration practices is likely to be negligible for most practices that do not involve land-use change, such as cropland set-asides (e.g., conversion to perennial grass cover). Changes in tillage practices, crop rotations, winter cover crops, etc. are unlikely to have a significant aggregate impact on commodity production and in some cases, for example, reduction in summer fallow, could positively impact commodity production. For instances where mitigation activities involve land-use change, such as set aside cropland or grazing land as conservation reserves, leakage can be minimized if more marginal agricultural lands are targeted.

See also: Dust Pollution from Agriculture. Soil Fertility and Plant Nutrition. Soil Greenhouse Gas Emissions and Their Mitigation

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Soil: Conservation Practices

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Glossary

Avalanching The cumulative effect of saltation and surface creep to disintegrate soil aggregates and increase movement of soil grains with increasing field length to produce greater wind erosion impact.
Interrill or sheet erosion Uniform soil particle detachment by the action of rainfall and runoff as a result of raindrop impact and slaking, which remove thin layers of soil from the land surface.
Rill erosion Soil removal in small, generally parallel channels formed by runoff water.
Saltation Discontinuous wind transport of 0.1–0.5-mm soil particles in a bouncing motion, usually within 300 mm of the soil surface, which is exacerbated by the impact of other saltating soil grains.
Surface creep Movement of 0.5–1.0-mm soil particles that are rolled along the soil surface by wind.
Suspension Wind transport of soil particles <0.1 mm after entering wind streams of varying elevations that may exceed thousands of meters for distances spanning continents.
Threshold velocity The minimum wind velocity required to initiate soil movement from an unprotected surface condition.

Introduction

Soil conservation practices are those farming operations and management strategies conducted with the goal to control soil erosion by preventing or limiting soil particle detachment and transport in water or air. Although some aspects of soil conservation practices may relate to water conservation, and although soil and water conservations are strongly linked, the authors concentrate herein on soil conservation. The objective of this article is to describe soil erosion mechanics and relate that to both traditional and innovative management practices for preventing soil erosion driven by either water or wind. Persuasive arguments depicting an apparent global climate change characterized by extreme weather events, including drought, has spawned a growing concern about soil susceptibility to erosion and fears of reliving the historic North American 'Dust Bowl.' These fears may be assuaged by a more complete knowledge of the array of soil management practices routinely implemented in conventional production agriculture for the purpose of conserving soil resources. This routine application of soil conservation practices followed a developing soil conservation ethic or commitment to land stewardship and greater understanding of both climate and appropriate farming practices.

The westward Euro-American settlement of the US is replete with examples of land degradation and soil erosion. Dabney *et al.* (2012) described water-driven soil erosion problems extending from the US southeastern coastal plain that began with clearing land of virgin timber for agriculture during the 1830s and, for an example, resulted in what was later described in 1910 as the badlands of Mississippi. The native range of the North American bison that includes the southern Great Plains, previously labeled the 'Great American Desert' by explorer Stephen Long in 1820 (Price and Rathjen, 1986), similarly entered agricultural production at the beginning of the 1900s with the encouragement of railroads and land speculators (Egan, 2006; Campbell, 1907). Fueling this migration to the Great Plains was an early claim of anthropogenical climate change that 'rain follows the plow' as professed with certainty by Cyrus Thomas who served as agriculturalist and naturalist for the 1871 Hayden expedition (Bartlett, 1980). The ensuing cultivation implemented the widely adopted farming practices from Campbell's 'A Complete Guide to Scientific Agriculture as Adapted to the Semiarid Regions' (1907) that promoted frequent residue-burying tillage using implements intended for maximum pulverizing of soil. That soil condition was intended to increase rain infiltration plus provide an evaporation-limiting dust mulch and an 'ideal seedbed.' However, some 16 million hectares of potentially erodible soil were exposed and eventually became the Dust Bowl of the 1930s.

The 1909 Bureau of Soils Bulletin 55 provided an impressively extensive survey of the US soil resource prefaced by recent investigations containing the notable claim that the soil was an 'indestructible, immutable asset' (Whitney, 1909). Nevertheless, the Great Plains' agriculture dependency on overgrazing and 'excessive plowing' to produce a dust mulch contributed significantly to wind-driven soil erosion as identified in a 1936 report to President Roosevelt by the drought area committee of Cooke *et al.* (1936). Soil conservation began with the commitment to protect an ecology from agricultural production using largely untested technology that failed to conform the natural requirements of the land. The evolving land degradation could only be understood by determining whether the causes were natural or consequences of unwise use (Tanner, 2012). Hugh H. Bennett, director of the newly established Soil Erosion Service in 1933, indicted Americans as "the greatest destroyers of the land" (Egan, 2006) as illustrated by dust storms resulting from ignorance of and need for improved farming practices. Soil conservation ultimately requires efforts to 'adjust men and machines to land' to reverse what Aldo Leopold referred to as land pathology (Tanner, 2012). The expanding commitment to land stewardship reflected Aldo

Leopold's land ethic that exemplifies a shift from conquering the land-community to becoming a citizen.

Soil Erosion Service director Hugh H. Bennett contributed both the insight and leadership necessary to developing, distributing, and implementing soil conservation practices to control catastrophic soil erosion. To develop soil conservation practices for implementing his insight, Bennett recruited Howard Finnell from the Oklahoma Panhandle in 1934 to conduct a research and demonstration program at Dalhart, TX, USA that featured techniques for increased precipitation capture by minimizing runoff with terraces and contour farming (Duncan and Burns, 2012). Conservation practices of retaining crop residue cover on the soil surface and listing deeper furrows to produce soil clods too large to erode and provide ridges to capture eroding sand were also investigated. Bennett's leadership as a practical tactician was consummately demonstrated during the week following 'Black Sunday,' 14 April 1935, when he delayed his testimony before a US Senate hearing to coincide with the arriving catastrophic dust storm that he heralded by stating "This, gentlemen, is what I'm talking about" (Egan, 2006). This convincing tactic dramatically illustrated the necessity of soil conservation contained within the pending Soil Conservation Act, Public Law 46, which passed without a dissenting vote (Cook, 2003).

Soil conservation during the Dust Bowl faced skeptics that questioned success when the simplest solution of increased rain was unattainable. Bennett observed that "One man cannot stop the soil from blowing, but one man can start it" (Egan, 2006), which suggests guidance on soil conservation practices avoided management mistakes of exposing bare soil to wind or water. Conservation practices sought farming methods that were compatible with the land or reversed the effects of incompatible management for more extreme erosion cases. Practical knowledge of soil destabilization, entrainment, transport, and deposition could lead to attainable solutions for conserving soil.

Soil Erosion Mechanics

Understanding the factors and processes governing soil erosion is important to implementing control practices for managing accelerated erosion. Soil erosion mechanics involve fluid (water/wind) detachment or entrainment followed by transport of soil particles and subsequent deposition as soil sediment. Although erosion processes are important contributors to soil formation, erosion becomes problematic when it is accelerated.

The integrated fluid pressures exerted on soil grains that overcome the soil shear resistance during entrainment were described as three types in a review article by Chepil and Woodruff (1963). Fluid pressure exerted directly against the soil grain is called the impact or velocity pressure and varies with the fluid velocity and density that is applied to the cross sectional area of the soil grain normal to the direction of the flow. The second complementary force is the tractive pressure applied on the lee side of the grain depending additionally on fluid viscosity, and sums with the impact pressure to provide the total drag force applied to the soil grain. The third pressure is the one that exerts an upward tractive force transverse to the fluid direction as a result of the Bernoulli Effect that relates lift to the fluid velocity traveling over the soil grain. These forces have been described in relation to fluid with simple uniform velocities; however, nonuniform fluid velocity facilitates soil movement through turbulent flow that can maximize particle lift and drag impulses.

Soil movement by wind begins when the minimum drag and lift forces exceed the threshold required to move soil grains. Movement can increase with increasing fluid velocity to the maximal threshold velocity that is capable of dislodging all erodible soil fractions. The threshold friction velocity varies as a function of square root of both particle diameter and the ratio of the particle and fluid density. For wind, these drag and lift forces combine to cause soil particles, approximately 0.1–0.5-mm diameter size, to bounce along the surface, striking other soil particles in a process known as 'Saltation' (**Figure 1**). Soil particles in saltation repeatedly impact the soil surface and may briefly dislodge larger soil particles, approximately 0.5 to <0.84-mm diameter, to roll along the surface as 'Surface creep' until stopped by larger soil particles and aggregates or areas protected from wind, including furrows, fence rows, and ditches. Saltating soil may also strike particles <0.1 mm, ejecting them into the windstream for sustained transport in

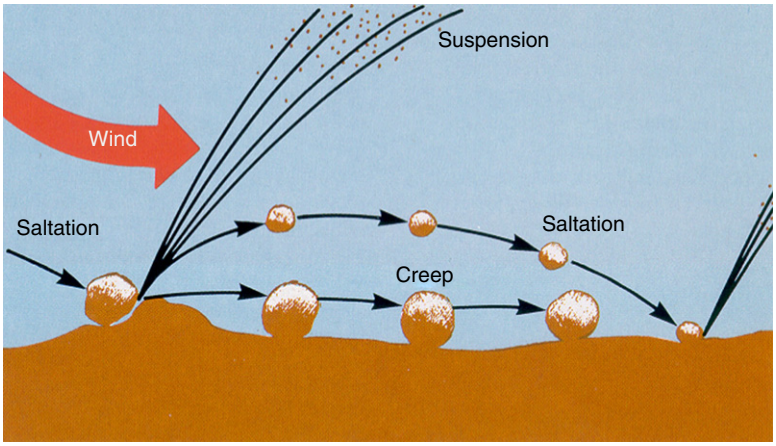


Figure 1 Diagram showing types of wind-driven soil particle movement including saltation that can promote surface creep, suspension, or continued saltation. Graphic courtesy of USDA-ARS Engineering and Wind Erosion Research Unit.

'Suspension.' Suspension also results from erosion of loose particles and the fracture of larger particles during the saltation process. Of these soil movement types, saltation is responsible for between 50% and 75% of the eroding soil mass with 3–40% carried in suspension and from 5% to 25% moved as surface creep. The cumulative effect of saltation on soil aggregates and grains increases with field length for greater erosion or the 'Avalanching Effect.' Because soil movement in saltation promotes both surface creep of coarse grains and suspension of dust, the most effective conservation practices are provided by limiting factors and conditions resulting in saltation.

Soil movement by water often starts when a raindrop impacts the soil surface and initiates splash erosion, i.e., raindrops break aggregates into finer soil particles, displacing those particles and aggregates to create depressions in the soil surface. The splashed soil particles clog the pores during rain infiltration to form less conductive surface seals that increasingly decrease rainwater infiltration. Water that does not infiltrate into the soil flows over the field surface and can entrain sediment. The declining capacity of the soil to absorb rainwater increases the volume of runoff available for interill water erosion. Water erosion depends on rainfall intensity, soil erodibility, and field slope among other factors.

Splashed soil particles are prone to rapid removal by interrill and rill erosion; thus interconnecting these erosion processes. Interrill erosion, also known as sheet erosion, occurs as uniform surface flow, whereas rill erosion occurs when runoff concentrates in small and shallow depressions. Interrill and rill erosions are the most dominant forms of water erosion; however, increased runoff transport capacity coupled with high runoff volume leads to the more catastrophic gully erosion. Sloping fields with little or no vegetative cover are prone to gully erosion that may be temporarily erased with tillage operations, but growing ephemeral gullies often require mechanical structures or changes in land cover and use to reduce erosion and prevent permanent gullies. Mechanical structures and agronomical or biological practices may be used to manage and control water erosion. In other words, accelerated soil erosion is an avoidable process.

Soil susceptibility to erosion processes will increase with the prevalence of soil destabilization factors that depress durability and particle cohesiveness. For example, the combined effects of limited precipitation and high air temperatures commonly experienced during drought may decrease the soil organic matter effective in stabilizing aggregates as well as the benefits of water films to improve soil particle cohesion noted for damp soil. Chepil and Woodruff (1963) illustrate this point for silt loam soil erosion rates that increased by over one order of magnitude at 11.6 m s^{-1} wind velocity when soil water content equivalent at −1.5 MPa water potential decreased by 75%. The finer grains of dry soil are more susceptible to wind erosion, a condition that persists after 2 years of drought and is only reversed by more than 2 years with favorable moisture and vegetation growth. Sustained drought can displace microbial communities in favor of those capable of tolerating desiccation or radiation such as *Bacteriodetes* that survive in ecological soil niches normally associated with erodible fine soil grains (Gardner *et al.*, 2012). Displaced communities include the *Proteobacteria* that promote C and N cycling and are associated with less erodible coarse soil particles.

In the absence of residue cover, structural breakdown of soil aggregates becomes problematic due to weathering or frequent tillage. The weathered or excessively tilled soil forms a smooth surface that promotes greater wind velocity and produces fine soil grains that are susceptible to wind or water erosion. Saltation, surface creep, and suspension often sort soil grains prone to movement on the leeward side of small aggregates. This soil movement also provides for abrasion of any aggregates or stable rain-formed crusts, which are also sorted and further supplement the supply of erodible soil grains. Soil deposition by sedimentation or trapping in deep cross-ridges and large aggregates prevents or stops continued soil movement and the erosion process. Reduced tillage and improved cropping practices can increase residue retention and preserve soil aggregation.

Integrating Wind Erosion Factors

Early efforts to estimate wind-driven soil erosion resulted in the 'Wind Erosion Equation' (WEQ) developed by W. S. Chepil and published by Woodruff and Siddoway (1965). The WEQ functional form:

$$E = f(I, C, K, L, V)$$

estimates the mean annual soil loss by wind (E) from agricultural fields depending on soil erodibility (I) as adjusted for the effects of ridge roughness (K), length (L) along the prevailing wind erosion direction, climatic factor (C), and vegetative factor (V). Empirically combining these factors to estimate soil erosion permitted potential interaction of factor-contributions for controlling erosion and possible conservation practices.

The soil erodibility I-factor is based on a wide, smooth, and unsheltered bare field with erosion loss being controlled by various fractions of erodible aggregates <0.84 mm. Increasing the percentage of erodible soil particles or aggregates also increases I. The effects of wind velocity and soil moisture on erosion are, generally, independent climate C-factors, but permit adjustments for adapting calculations to multiple regions. Soil roughness, K-factor, combined with field L-factor related to orientation and length, represent less adaptable management inputs available to limit exposure of erodible soil or trap saltating soil. The vegetative V-factor characterizes both quantity and type of crop residue that can reduce wind velocity and, consequently, erosion. The empirical WEQ was revised to the RWEQ (Fryrear *et al.*, 2000), which more completely represented the factors governing wind erosion for improved annual soil loss estimates and fostered the development of a more comprehensive process-based wind erosion prediction system (WEPS); Hagen *et al.*, 1999).

On a daily time step, WEPS integrates climate, soil properties, management practices, and crop residue input data with governing transport relationships as summarized by Chepil and Woodruff (1963) to calculate soil erosion. Thus, when the threshold friction velocity is exceeded, movement of soil including PM-10 is estimated from interacting saltation, surface creep, and suspension processes for a specified region. Soil

surface roughness conditions are updated to reflect dynamic detachment and deposition processes that modify aggregation and residue status and the related susceptibility of soil to erosion. As reported by Hagen (2004), these more accurate estimates of soil erosion in response to the combined effects of soil crust and residue cover, aggregate size and stability, and ridge height and random roughness can improve the coordinated application of conservation practices.

Integrating Water Erosion Factors

Empirical soil erosion estimation methods have resulted from research characterizing water-driven erosion as moderated by potential conservation practices. Various factors affecting soil erosion, including soil slope and length or supporting control practices like contour rows, strip cropping, and terrace systems, were recognized as independent factors influencing soil erosion by their inclusion in regional soil-loss equations beginning in 1940 (Wischmeier and Smith, 1978). Eventually, a national committee's effort to predict soil erosion proposed a universal soil loss equation (USLE) that retained field length and slope (LS), crop cover and management (C), and support practices (P). This new relationship estimated annual soil erosion amounts (A) as mass per unit area independently of regional soil and climate differences with the addition of terms describing the combined rainfall and runoff erosivity (R) and soil erodibility (K) or susceptibility to erosion. The resulting soil loss equation is:

$$A = RKLSCP$$

The rainfall and runoff or R factor is a spatial erosion index (energy·rain-depth/area·hr·year) that increases from <20 in western USA to 550 along the southeastern US Gulf coast and reflects both the amount of rain and its energy, which increases with rain intensity and increasing drop size and terminal velocity. Soil erodibility indexes soil loss potential in relation to texture and percent organic matter as a first approximation for K (mass·area·h/energy·rain-depth) that ranges from <0.1 to 0.7. The K value is further refined by considering soil structure and profile permeability to characterize potential infiltration and internal drainage, which can further influence runoff and soil movement. The soil LS topographical factor compares slope angle and field length contributions to runoff energy from fields in contrast to a standard uniform 9% slope and approximately 22-m length. Varying field slope from 9% affects runoff energy that is cumulative with length resulting in dimensionless LS values that vary from <0.1 to approximately 12.9. The crop cover and management C factor is a dimensionless time-weighted index characterizing soil cover due to residue management and crop canopy condition as a percentage compared with clean till (bare) fallow. Lastly, the supporting dimensionless conservation practice P-factor indexes potential soil loss of various conservation practices such as contour rows, strip cropping, and terrace systems to up-and-down slope straight-row farming. The P-factor revisits, somewhat, field length and slope effects on soil erosion as managed using agricultural practices.

Efforts to estimate soil erosion have steadily evolved from empirical methods to the process-based mechanistic computer simulation approach of the water erosion prediction project (WEPP) as summarized by Nearing *et al.* (1989). The primary erosion processes of detachment, transport, and deposition as modified by residue cover or the cover of a growing crop canopy were based on the quantified fundamental erosion agents of rain infiltration, surface runoff, plant growth, residue decomposition, and soil management. The advantage of a mechanistic model is its design to accommodate spatial variability of topography, surface roughness, and soil properties in addition to variable hydrology and land-use application.

The WEPP process-based estimate of soil loss employs a continuity equation that relates sediment load in the runoff to the distance downslope as a function of the interrill and rill erosion rates calculated on a daily time step. Interrill erosion is the process of sediment delivery to more concentrated flow in rills, but rill erosion depends on the potential detachment capacity as limited by the sediment transport capacity of runoff in the rill. Rill and interill runoff must produce a hydraulic flow shear stress sufficient to exceed the minimum shear stress required to detach soil, depending on the soil erodibility. In contrast to soil erosion, deposition is calculated when sediment load exceeds the sediment transport capacity. The hydrological factors driving these processes are rainfall intensity and runoff rate and duration, which govern flow volume in the rill and combine with other factors such as slope gradient and friction in determining flow shear stress.

Field interill erosion model estimates in WEPP combine the base soil erodibility and erosion agents with spatial varying factors such as rill frequency and width. Modeled temporal variations in soil erodibility replicate decomposing residue cover, soil consolidation for reduced roughness, and crop factors. Temporally dynamic crop canopy height and cover that varies due to plant growth also directly modifies the soil-water balance and related rain infiltration. The growing crop further complicates erosion estimates by interactions with temporal varying seasonal rain and the factors for adjusted soil erodibility. The resulting mechanistic soil erosion calculations permit useful comparisons of conservation practices by incorporating climatic details and interacting seasonal crop growth.

Conservation Practices – Wind Erosion

Conservation practices implemented to control wind erosion act directly to: (1) increase the size of exposed soil aggregates in excess of the wind entrainment capacity, (2) reduce wind velocity sufficiently to prevent sediment entrainment, and (3) provide a barrier between the soil and wind. An indirect wind erosion control can act by reducing evaporation, thereby leading to increased soil water content that improves soil cohesiveness. Conservation practices may exhibit a common mode of action like reducing wind velocity to similarly control erosion, but at different scales ranging from crop-row spacing to field width. Conservation practices often provide two or more modes of action such as residue mulches that reduce evaporation of soil water to promote soil particle cohesiveness, increase overall crop biomass productivity, and provide a protective barrier for greater erosion control. Many conservation practices represent mature technologies, including

management of standing residues from previous crops to decrease wind velocity and control erosion (Woodruff *et al.*, 1972), but innovative approaches to residue management such as the application of new weed control chemistries for converting cover crops into dry mulches modernize that technology.

Emergency Tillage

Tillage alternatives are necessitated by the absence of adequate crop residue to form a barrier that prevents soil erosion. Drought often prevents crop growth sufficient to form adequate residue cover. Emergency tillage roughens the soil surface to conserve soil by producing large clods or aggregates. Examples include cultivation by primary tillage practices and specific purpose implements like the 'sand fighter' (**Figure 2**). The resulting aggregates are larger than can be transported by the wind and temporarily stabilize the exposed soil until saltating grains cause clods to disintegrate. Tillage can be used to stop an ongoing erosion process from an involved field and is applied beginning along the upwind edge of the eroding field using a chisel or lister plow to expose coarse subsoil aggregates. Chisel plows are often preferred because they preserve available crop residue. In contrast, disk plows or harrows are generally not suitable for emergency tillage because the soil is pulverized, which may contribute to the saltating grains in the erosion process.

This tillage practice should, ideally, disrupt the soil surface in tilled strips that are perpendicular to the direction of the wind. The tilled soil strips may be roughened or ridged to reduce wind velocity at the soil surface, but should provide a surface with nonerodible soil aggregates >0.84 mm and, preferably, larger clods capable of trapping the saltating soil particles. Tillage strip frequency may be governed by operational requirements of the machinery and, occasionally, will require additional emergency tillage between strips to control movement of saltating grains. The tilled strip spacing will vary with soil texture from approximately 30 m for sandy loam soils to approximately 120 m for clay loams. Nevertheless, the on-going saltation and surface-creep erosion processes dictate that emergency tillage is a temporary conservation measure of last resort, remaining effective only until clods disintegrate.

Crosswind Ridges, Terraces, and Contours

Crosswind ridges consist of tall listed seed beds that are formed over the entire field or as trap strips with an orientation perpendicular to a required prevailing wind direction (**Figure 3**). Although not an emergency conservation practice, crosswind ridges also exploit the larger soil aggregates present after lister tillage and the much increased roughness that reduces near-surface wind velocity to limit soil erosion. In addition to the decreased wind velocity that reduces the transport capacity of the wind, much of the wind erosion control results from between-bed interception or surface clod trapping of soil grains moving in saltation and surface creep. Crosswind ridges realize greater success for soils capable of producing large stable aggregates compared with sandy soils.

The formation of an earthen embankment along a common elevation contour produces an elevated terrace structure that can directly reduce wind erosion by potential reduction in wind velocity and interception of saltating soil grains. Permanent tall grass vegetation or annual forage and cereal cropping as a strip on the terrace can augment trapping of soil grains and further reduce wind velocity. Indirect wind erosion control benefits of terraces and the related contour tillage and cropping practices expand overall crop grain and residue productivity by controlling runoff for increased water storage in the soil (Duncan and Burns, 2012).

Wind Breaks – Shelterbelts

One of the more aesthetically pleasing and permanent conservation practices for controlling wind erosion includes agroforestry shelterbelts or windbreaks (**Figure 4**). Windbreaks may contain single or multiple rows of evergreen and/or deciduous trees supplemented with shrubs or grasses that are planted in linear strips perpendicular to the prevailing wind (Brandle *et al.*, 2004). A windbreak serves as a barrier with the purpose of deflecting air flow and reducing the leeward wind



Figure 2 Emergency tillage with a 'sand fighter' implement to control surface abrasion by wind-driven soil particles and produce nonerodible coarse aggregates. Photo courtesy of USDA NRCS, TX, USA.



Figure 3 Land bedded for crosswind ridges that control wind erosion by trapping and intercepting saltating soil particles and by reducing surface wind velocity. Image courtesy of USDA-ARS Engineering and Wind Erosion Research Unit.



Figure 4 Tree rows planted as windbreaks, shelterbelts, to reduce wind velocity at the soil surface and control erosion (NRCSND99001). Photo courtesy of USDA NRCS.

velocity, which varies with windbreak height, spacing frequency, and porosity. Windbreaks control wind erosion by reducing surface wind velocity below the minimum threshold for soil movement and remain effective during drought when other conservation practices fail. These barriers can also reduce wind velocity sufficiently to decrease its soil-carrying capacity, resulting in soil deposition and possible dune formation.

The success of shelterbelts to effectively reduce wind velocity, albeit limited depending on porosity to distances from the belt of 5–12 times the tree height, combines with improved wildlife habitat and livestock protection to encourage the application of this conservation practice. The wind erosion control benefit is not, however, immediately available with this conservation practice and, depending on the tree growth rate, will be delayed by several years. Actively growing trees also compete for space and water resources with nearby cropped land, resulting in tree root exploration that can extend some 2.5 times the tree height (Chepil, 1965). Alternatively, Brandle *et al.* (2004) observed windbreak effects to reduce air flow also resulted in a beneficial distribution of snow and a general reduction in evaporation that benefited nearby crops. These contrasting crop responses to windbreaks may reflect spatial differences in potential crop water stress indicated by the ratio of precipitation to the potential evapotranspiration that, in the continental US, increases when proceeding from south to north or west to east (Follett *et al.*, 2012). Similarly, the historical 1935–42 shelterbelt establishment in the eastern Great Plains and the ongoing shelterbelt renovation in the northern Great Plains appear in less arid regions. The availability of irrigation makes this conservation practice viable in a difficult environment.

Strip Cropping

Crops may be cultured in strips perpendicular to the prevailing wind where field orientation is not restricted as a means to reduce the near surface wind velocity (Chepil, 1965; Woodruff *et al.*, 1972). Cross-wind strips typically subdivide fields with alternately planted erosion-controlling crops and erosion-susceptible crops or fields. These strips effectively reduce the field width and limit downwind soil avalanching. The design distances between strips vary with soil erodibility, ranging from approximately 30 m for a sandy loam soil to 100 m for clay loam, but are further complicated by the required compatibility with farm machinery. Nevertheless, cross-wind strip cropping typically accommodates most crop rotations with only limited impact on net production.



Figure 5 Cimarron County, Oklahoma, site of the Arthur Coble farmstead, in April 1936 (inset) and present day, revegetated with various grass species after enrolling in the Conservation Reserve Program (CRP) to prevent wind erosion. Inset photograph by Arthur Rothstein (Library of Congress), present day photograph courtesy of Cimarron County NRCS.

The strip cropping conservation practice is broadly accommodating of variable width crop strips and interstrip widths, depending on crop tolerance to eroding soil or potential to trap saltating soil grains. This adaptation of strip cropping for trapping saltation does impose a width requirement of 5–8 m depending on the height limitations of the strip crop. Relatively narrow two-row strips can be cropped using sudangrass or grain and forage sorghum to reduce near-surface wind velocity and control soil grain movement as a herbaceous wind barrier. Taller perennial grasses can provide similar erosion control in semiarid regions where crop establishment and growth are unpredictable.

Rangeland and Permanent Cover

Erosion is possible when soil grains susceptible to movement by saltation are exposed through some destabilization process, including excessive tillage or grazing (Chepil and Woodruff, 1963). Effective soil conservation practices thus include avoiding soil disturbance for crop production on marginal lands. The economics driving agricultural production that firmly entrench areas for permanent range management may, however, alternately encourage or discourage sustainable stocking rates as a result of market volatility. Some marginal lands have been designated as highly erodible and were to some extent returned to permanent cover management under the US federal government's 'Conservation Reserve Program' included in the 1985 Farm Bill. Various tall-grass species are cultured on marginal lands with no grazing as a means to remediate the soil of an eroded site (**Figure 5**).

The protective value of a residue cover is functionally related to residue mass, stem density, and orientation, but is expressed as an equivalent of a small-grain crop reference that is 25-cm long flattened wheat residue cultured in rows 25 cm apart and parallel to the wind direction (USDA-NRCS, 2002). Undisturbed crop covers are more effective at preventing soil movement when residues are standing, perpendicular to the wind, and have numerous stems. For example, flat randomly oriented wheat straw provides the same protection as 1.6 times the reference straw mass. Standing wheat residue oriented perpendicular to the wind is 3.5 times more effective than the reference for protecting soil from wind erosion. An example of poor protective value of crops with large stem size and reduced number is reflected by the 0.225 small grain-equivalent reference mass for standing sunflowers, meaning that 1.1 Mg ha^{-1} of sunflower residue provides soil protection equal to only 0.25 Mg ha^{-1} of flat wheat residue.

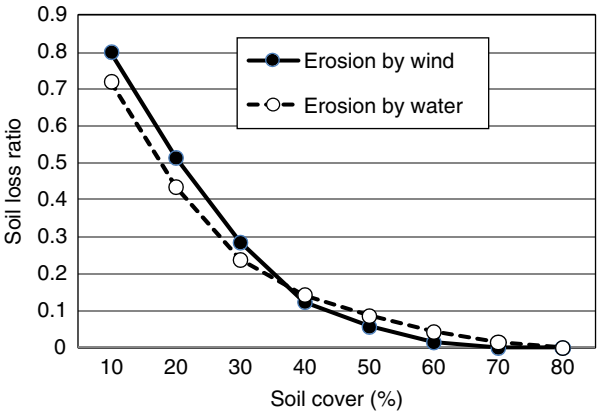


Figure 6 Relationship between soil loss ratio (soil loss with cover divided by loss from bare soil) and percentage of surface cover by residue for erosion by wind and water. Reproduced from Papendick, R.I., Parr, J.F., Meyer, R.E., 1990. Managing crop residues to optimize crop/livestock production systems for dryland agriculture. Advances in Soil Science 13, 253–272.

Residue Management

Residue management generally is the preferred control method for wind erosion for most crops and climates (Fryrear and Skidmore, 1985). It comprises various tillage practices that maintain residue from a previously harvested crop as a surface cover to prevent soil erosion. Protection is by providing a barrier that reduces wind velocity below the threshold for erosion. Ideally, standing crop residues are retained to reduce the velocities or deflect near-surface winds so that insufficient force is available to entrain and transport soil particles. Flat crop residue, although less effective for reducing wind velocity, still provides a critical barrier that shields soil aggregates from abrasion by saltating soil grains and disintegration to an erodible size. Residue management also maintains mulches, either standing or flat, to intercept soil grains by trapping their movement to reduce saltation, surface creep, or suspended soil movement for wind erosion control. Harvesting residue to supply bioenergy is, however, one management consideration that varies with the crop and resulted in unsustainable wind erosion (modeled with WEQ) after removing 10–30% of dryland corn stover and 80% wheat straw under no-till (Miner *et al.*, 2013).

Although control of soil erosion by wind or water varies with residue cover as shown in **Figure 6**, that cover must exceed approximately 30% to minimize soil loss (Papendick *et al.*, 1990) and meet conservation compliance. Conservation tillage includes strip-till, stubble-mulch till, and no-till practices that eliminate the more disruptive and potentially pulverizing inversion tillage that incorporates crop residue, providing less than the 30% minimum soil cover. In contrast with no-till retention of all residue at the soil surface, inversion-type primary tillage implements such as moldboard or disk plows eliminate, on average, 95% of the residue cover compared with crop residue incorporation of 10–40% for stubble-mulch tillage sweep plows and from 20% to 40% with chisel tillage (Unger *et al.*, 2012). Leaving residue from the previous crop on the soil surface has the added benefit of improved soil water storage, regardless of runoff-controlling contours, by increasing rain infiltration and decreasing evaporation. Greater soil water contributes to soil cohesiveness and reduces the fraction of erodible particles. But, improving soil water storage with residue management increases crop productivity for greater potential soil cover and stabilizing organic matter.

Cover Crops

The cover crops conservation practice describes the culturing of a crop primarily for the purpose of controlling erosion. Cover crops are necessary for erosion control when principal crops produce insufficient or unsuitable residue for more conventional residue management-based erosion control. For example, a cotton monoculture does not provide adequate residue to provide >30% ground cover to prevent soil loss or add organic matter to maintain soil stability. Yet, favorable cotton production economics encourages this monoculture in semiarid regions despite the expectation of intense spring winds eroding susceptible bare-tilled and dry soils. With irrigation, one solution has been to plant cereal crops, including winter wheat, rye, or oats after cotton harvest exclusively for temporary prevention of wind erosion during the idle period before planting cotton again (Keeling *et al.*, 1989). In addition to wind erosion control, a herbicide-killed wheat cover crop provided residue for increased rain infiltration and reduced evaporation that improved subsequent crop growth.

Dryland cover crop production in the semiarid western Great Plains competes for limited precipitation and frequently results in inconsistent crop establishment and production results. For this reason, Baumhardt and Lascano (1999) concluded that establishing dryland cotton after a wheat cover crop was problematic and contributed to production risk. Where precipitation is adequate, cover crops like field peas can supplement the wind erosion control benefit from residue cover with the addition of fixing nitrogen and preventing weed establishment or competition for water.

Soil Amendments

Using soil amendments as a conservation practice for wind erosion control is almost exclusively applied to small vulnerable

locations, 'blowouts' or knolls, to prevent saltation erosion from spreading to other fields (Woodruff *et al.*, 1972). Natural soil amendments include crop residue in the form of straw or hay and crop-processing byproducts such as corncobs or cotton gin trash that are typically anchored by shallow tillage operations with a rotary hoe or mulch treader. The applied plant biomass functions primarily as a mulch barrier to prevent abrasion and to trap saltating soil grains, but can act to reduce soil surface wind velocity. Similar to plant materials, livestock manure functions to intercept and trap saltating soil grains and depress wind velocity at the soil surface; however, manure nutrients must be managed for the benefit of crops.

Synthetic amendments functioning as adhesives for binding soil grains are applied to temporarily stabilize eroding soil affecting high-value crops (Armbrust and Lyles, 1975). These materials include resins, asphalt, latex, polymers, and polyvinyls, but may not be compatible or effective with all crops or soils. Treatment efficacy preventing soil erosion can be lost after any postapplication rain event, abrasion by saltating soil grains from adjacent fields, or use of cultivation. More recent investigation of wind erosion control using various formulations and application rates of polyacrylamide (PAM) indicated this amendment was ineffective (Armbrust, 1999).

Conservation Practices – Water Erosion

Mechanical Structures

Various mechanical or engineering structures can be used for control of water erosion. Among these are terraces, drop structures, spillways, culverts, gabions, ripraps, and ditches. Mechanical erosion control practices reduce runoff velocity, store runoff water, and convey runoff at nonerosive velocities. There are also mechanical structures for harvesting rainwater that is stored for immediate or later use. These structures control water erosion by reducing rainwater available for runoff. Some of the common water-harvesting structures are farm ponds, storage tanks (underground or aboveground), and check dams. Mechanical structures are important companion practices to biological or agronomical practices such as conservation tillage (i.e., no-till and reduced till), residue mulching, cover crops, and conservation buffers. Mechanical practices are especially needed to reduce concentrated flow and gullying when biological practices alone can be insufficient.

Terracing is the most common mechanical practice to reduce runoff velocity and safely divert runoff to an outlet. Terraces reduce the slope length by splitting large fields into smaller strips and can be more effective than biological practices for reducing water erosion in sloping soils. In soils with steep slopes, residue mulching and cover crops can fail to control concentrated runoff flow and gully formation but are effective at controlling interrill and rill erosion. Terraces are practices similar in their function to other cultural practices such as contour farming and strip cropping.

Use of silt fences and surface mats are also important methods to control water erosion. Silt fences and surface mats are often used as temporary measures in disturbed lands or construction sites until permanent structures and conservation practices are established. Silt fences are vertical synthetic fabric barriers that reduce runoff velocity, filter sediment, and reduce off-site transport of sediment. Silt fences can reduce approximately 80% of total suspended sediment in runoff (Barrett *et al.*, 1998). Surface mats can buffer raindrop impacts, hold the soil in place, reduce surface sealing and crusting, enhance vegetation establishment, filter sediment in runoff, and stabilize disturbed soils. Silt fences and surface mats may be made of geotextiles or appropriate plant by-products such as straw, straw bales, coir, paper waste with binders, and wood chips, for example. Mechanical structures and practices should be used in combination with agronomical or biological practices.

Agronomical or Biological Practices

Agronomical practices such as conservation tillage, residue mulching, and cover cropping are soil conservation practices, whereas mechanical structures are typically water-control practices. Biological practices such as residue mulching and cover crops keep the soil in place. In contrast, mechanical engineering structures are effective practices for intercepting and redirecting runoff, promoting sedimentation, and reducing off-site transport of sediment. Biological practices maintain a permanent vegetative or surface cover to reduce erosion and are preferable over mechanical practices, especially in soils with gentle or moderate slopes. Well-established and site-specific agronomical practices can effectively reduce runoff, increase water infiltration, and reduce soil loss.

Conservation tillage has been defined as any tillage system that leaves at least 30% of residue on the soil surface. It includes a number of tillage systems such as no-till, minimum tillage, mulch tillage, strip tillage, vertical tillage, and ridge tillage. In the US, the Dust Bowl in the 1930s heightened the interest in conservation tillage practices. Development of preemergent herbicides in the 1960s further enhanced the use of conservation tillage practices such as no-till. The potential of conservation tillage to reduce water erosion is widely recognized. Indeed, conservation tillage was conceived to reduce soil erosion from croplands. Its increased use has reduced the need for mechanical structures (i.e., terraces), particularly in moderately sloping soils.

No-till is an effective conservation tillage system to reduce soil erosion that succeeds by maintaining a near constant residue mulch cover. No-till soils with complete residue cover may completely eliminate soil loss. As a result, no-till performance depends on the amount of residue left on the soil surface after harvest. If residues are grazed, baled, or burned, or crops are harvested for silage or to produce ethanol, surface cover decreases and can rapidly diminish the ability of no-till soils to reduce soil erosion. Similar to plowed soils, no-till soils may create surface seals and erode when residue cover is insufficient. In semiarid regions, limited residue production under no-till may limit the potential of no-till to effectively control water erosion. Surface residue mulch is more effective at reducing splash, interrill, and rill erosion than at controlling concentrated runoff or gully erosion.

Crop residues intercept the erosive energy of raindrop impacts and reduce near-surface aggregate detachment, aggregate slaking, and surface sealing (**Figure 7**). When raindrops impact bare soils, surface seals develop and rainwater infiltration



Figure 7 No-till irrigated corn near Colby, KS, with corn stover retained (top) or removed (bottom). In the absence of residue to intercept water drops, a soil crust formed with the potential to restrict seedling emergence.



Figure 8 No-till sorghum fields near Hays, KS, retain declining residue cover with increasing time since harvest, showing that no-till soils can become progressively more erodible.

rapidly decreases; but when raindrops impact residue mulch, rain loses its kinetic or erosive energy, water moves through the residues, and water infiltration is less affected by surface sealing. Crop residues also reduce the erosivity of incoming runoff by intercepting runoff and reducing its velocity. By intercepting runoff, residues increase the opportunity time for infiltration and filter sediments in runoff. Residue cover increases time to runoff (the time between the beginning of precipitation and beginning of runoff) because of increased water infiltration, which concomitantly reduces runoff amount and reduces the number of precipitation events that result in runoff.

Baling or removal of crop residue exposes soil surface to raindrop impacts and reduces surface roughness to intercept runoff. As the amount of residue removal increases, water infiltration decreases and water erosion increases. Percentage of soil covered with residues is a critical factor that affects water infiltration and the amount of water that runs off the field (Figure 8). Between 60% and 80% of rainwater is lost as runoff from bare soils compared with residue mulched soils. Leaving a soil bare is a recipe for increased soil loss. No-till management combined with residue mulching and cover crops is the most effective strategy to prevent and control water erosion.

No-till with residue mulch provides a dual function. It reduces both erosivity of raindrops and soil erodibility due to residue cover and organic matter input. This combined action of no-till decreases soil-erosion risks compared with other tillage practices that disturb soil and bury crop residues. No-till reduces soil erodibility by improving near-surface soil structural properties. For example, soil aggregates under no-till are more stable than under conventional till. Residue-derived soil organic C combined with microbial activity under no-till promotes soil aggregation. Soil organic matter has organic binding agents that enmesh and bind soil particles into stable aggregates. Soil aggregate stability is strongly and positively correlated with management-induced increase in soil organic carbon.

Improved soil aggregation results in greater macroporosity and water infiltration and lower runoff rates. In some environments, soil aggregates and macropores under no-till remain practically undisturbed. No-till soils may also have abundant earthworms, which increase water infiltration and reduce the amount of water available for runoff. Earthworm channels and biopores can increase water flow by as much as 100 times compared with soils without biopores (Edwards *et al.*, 1990). Soil macropores open to the atmosphere are protected by the residue cover. In semiarid environments, however, soil water content may be too small to support abundant soil fauna and microbiota, reducing the beneficial macropore formation and soil aggregation typically found in more humid environments. Some semiarid soils consolidate under no-till practice, forming relatively dense and impermeable surface layers. In such environments, judicious use of limited tillage systems may improve infiltration while leaving surface plant residues relatively undisturbed.

No-tilled soils also have greater critical shear stress than soils under conventional till. This means, no-till soils are harder to shear than plowed or loose soils. Thus, under similar runoff transport capacity and hydraulic-shear stress, plowed soils have greater risks of developing rills and gullies. No-tilled soils also have lower erodibility than conventional tilled soils

because of the higher critical shear stress. Soil erodibility and critical shear stress parameters are important to understanding the soil's resistance to concentrated flow erosion.

No-till can reduce soil loss by as much as 90% compared with conventional till. No-till is more effective at reducing sediment loss than runoff. It may not always reduce runoff compared with conventional till, but its effectiveness for reducing soil loss is far superior. Soil surface consolidation may increase runoff in no-till compared with conventional till in some soils. This can be particularly true in clayey and flat soils (Rhoton *et al.*, 2002). It is important to note, however, that runoff leaving no-till soils is typically cleaner and has less sediment than from conventionally tilled soils. Residue mulch filters sediment particles in suspension.

Some of the site-specific challenges with no-till management include soil compaction, stratification of soil organic carbon and nutrients near the soil surface, and others, but its effectiveness for controlling water erosion is unparalleled among all tillage systems. No-till benefits for reducing soil erodibility are more clearly observed in the long term as soil structural properties (i.e., macroporosity, aggregate stability, and infiltration) and organic matter content increases. Depending on the extent of soil disturbance and amount of residue left on the soil surface, reduced tillage, stubble-mulch tillage, strip tillage, and ridge tillage also reduce soil loss more than conventional till but less than no-till management.

Conservation Buffers

Conservation buffers include vegetative filter strips, grass barriers, grass waterways, and riparian buffers. These buffers are designed to intercept runoff flow and reduce runoff velocity and transport of sediment and sediment-bound nutrients, thereby reducing risks of nonpoint source water pollution. Buffers spread the incoming runoff, filter sediment, and promote sedimentation. Debris or plant residues mixed with buffers help to trap sediments and nutrients. Buffers can also stabilize soil and promote water infiltration through their roots. Conservation buffers can trap $>70\%$ of sediments and $>50\%$ of nutrients, depending on the type of buffer, plant species, management, rainfall intensity, and soil slope. These practices can differ in design, vegetative species, and management.

Vegetative filter strips: These are 5–15-m wide strips of vegetation established at the bottom perimeter of croplands. Filter strips are often planted to cool-season grasses including tall fescue, Kentucky bluegrass, orchard grass, smooth bromegrass, and others. Filter strips are a common conservation practice to reduce off-site sediment and nutrient transport in croplands. Filter strips of approximately 10-m wide can reduce sediment loss by 90% in moderately sloping soils.

Grass hedges: These hedges are 0.75–1.2 m-wide strips of stiff, perennial, and tall grass established at short intervals (<15 m) within croplands perpendicular to the main field slope. Grass hedges are grown parallel to row crops on the contour. Grass hedges are commonly planted to warm-season grass species such as switchgrass (Kemper *et al.*, 1992). Other perennial warm-season grasses include eastern gamagrass, indiangrass and big bluestem. In tropical environments with hilly terrains, vetiver grass (elephant grass), a perennial and stiff-stemmed species, is used as hedges to control erosion. Vetiver grass can grow on steep terrains (30% and 60% slope) and can be used like bench terraces. Various Andropogon species are also used for erosion control, being grown on terraces in, for example, Burkina Faso.

Grass hedges differ from vegetative filter strips because they have stiff stems and are often planted to perennial and native warm-season grass species. Grass hedges intercept and pond runoff above hedges, increase infiltration, promote sediment deposition, and form natural terraces upslope of the hedges with time. Grass hedges are well suited to moderately sloping soils to reduce interrill and rill erosion. On steep sloping soils, effectiveness of grass buffers for reducing concentrated flow and gully formation may be limited.

The aboveground biomass of grass hedges intercepts runoff and promotes sediment deposition, whereas the belowground biomass with extensive and deep roots stabilizes the soil, promotes soil aggregation, and improves water-transmission characteristics. Soils within grass hedges often have greater aggregate stability, water infiltration, saturated hydraulic conductivity, macroporosity, organic matter content, and lower bulk density compared with rows without hedges (Rachman *et al.*, 2003).

Riparian buffer strips: These consist of 5–30-m wide strips of mixture of grasses, trees, and shrubs planted between croplands and streams. Riparian buffers have been used more commonly than grass hedges to control water erosion. These buffers not only slow runoff flow and filter sediment but also can improve wildlife habitat and diversity and provide numerous additional ecosystem services. Riparian buffers can reduce runoff and sediment transport by at least 30% (Sheridan *et al.*, 1999). Water infiltration rates under riparian buffers are often higher than under annual row crops. Buffers consisting of sparse trees may not be as effective as those mixed with grasses for reducing incoming runoff and filtering sediment and nutrients.

Grass waterways: Another common conservation practice, grass waterways are natural or constructed channels under perennial grass established along the sides and lower perimeter of fields to convey runoff at nonerosive velocities from terraces, field outlets, and diversion systems on moderately sloping fields ($<5\%$). Dense grass species in grass waterways can filter runoff, reduce sediment and nutrient transport in runoff, and prevent gully formation. The grass waterways can also trap and biodegrade pollutants such as herbicides in runoff. These practices can be combined with drop structures (dam, embankment, and weir) established perpendicular to the main slope at different points within the waterway.

Cover Crops

Cover crops are another effective soil conservation practice to reduce runoff and water erosion. Cover crops are not a new practice, but there is renewed interest in using cover crops to conserve soil and improve soil productivity. Benefits of cover crops for reducing soil erosion are well recognized. Cover crops provide permanent surface cover between growing seasons of main crops. After termination, residues from cover crops continue to protect the soil from erosion. Incorporating cover crops into the soil as green manure reduces their benefits

to soil erosion control as opposed to leaving cover crop mulch on the soil surface. Therefore, cover crops are a potential companion practice to no-till and intensified cropping systems (Figure 9).

These crops also provide many other ecosystem services including improvement in soil properties, soil fertility, biological diversity, and water quality. Cover crops perform a dual function because they protect the soil surface and improve soil properties. Cover crops increase infiltration, create macropores (i.e., earthworm burrows), improve aggregate stability, and increase soil organic matter content and soil microbial biomass. Roots and microbial processes provide labile C to contribute to aggregate formation and stabilization. Improved soil aggregate stability leads to increased water infiltration and reduced soil's susceptibility to erosion.

Surface canopy and residue cover provided by cover crops buffer against the erosive energy of raindrops. It also intercepts upstream runoff and promotes water infiltration. Cover crops also increase the amount of below ground biomass. Cover crop roots under no-till interact with the soil to reduce soil erodibility. Plant roots can strengthen the soil aggregates and anchor the whole soil. Cover crops may also reduce concentrated flow erosion due to the presence of roots even when surface cover is reduced such as during winter. Root density among cover crops differs. Cover crops with fine and extensive roots such as rye and oats can prevent concentrated flow erosion.

Cover crops are becoming a part of intensified cropping systems under conservation tillage in semihumid or humid regions. Cover crops can be grown in winter after summer crops or in summer or fall after winter crops such as winter wheat. Their adoption in semiarid or water-limited regions is limited because cover crops may reduce plant-available water for the main crops. Proper management including early termination and species selection are strategies to grow cover crops in water-limited regions. Although establishment and management can be a challenge in some soils, cover crops provide many soil and environmental benefits.



Figure 9 Example cover crops, including sun hemp (background) and off-season soybean (foreground) compared with declining residue of the uncropped control; photo by M. Claassen, Professor (ret.) Kansas State University.

Soil Conditioners

Soil conditioners are products that are applied to control water erosion and improve soil properties. Some of the conditioners used to reduce water erosion include PAMs, phosphogypsum, and flue gas desulfurization (FGD) gypsum. These conditioners have not been widely used in agricultural lands although they are receiving increased attention as potential erosion control practices. Phosphogypsum and FGD are by-products of phosphate fertilizer manufacturing and generation of electricity from coal-fired power plants, respectively. These two conditioners have similar properties to gypsum and can be used in combination with PAM for soil erosion control. Phosphogypsum and FGD are applied to soil in larger quantities than PAM to achieve similar results. The FGD is a relatively new by-product that is being evaluated for erosion control.

PAMs come in different formulation types (dry granular beads, blocks, powders, and liquid). PAMs have been used in construction sites or disturbed soils, and in furrow- and sprinkler-irrigated soils. Application rates of PAM can vary depending on the soil-specific conditions (i.e., soil slope and texture), but application at 10 or 20 kg ha^{-1} can significantly reduce soil erosion in gently sloping soils. PAMs can reduce soil loss by as much as 90% and increase the infiltration rates by as much as 50% in furrow-irrigated croplands (Sojka *et al.*, 2004).

PAMs applied to the soil surface reduce water erosion by stabilizing exposed soil aggregates, maintaining the integrity of soil macropores, reducing surface sealing and crusting, and promoting flocculation of suspended sediment. These mechanisms increase water infiltration, reduce runoff and soil loss, and reduce turbidity in runoff water resulting from rain or irrigation. Application of PAM is more effective at reducing soil loss than runoff as it stabilizes aggregates and reduces their detachment. PAMs may not improve soil structure or aggregation like organic amendments (e.g., green manures, crop residues, and compost) do, but they stabilize the exposed soil.

Performance of PAM will depend on soil properties and companion management practices (Flanagan *et al.*, 2002). Soils with low clay and organic matter concentration may respond better to PAM application as PAM particles may interact more with fine particles. PAM's effectiveness and longevity decrease with increasing soil slopes and rainfall intensities because of greater concentrated flow and high runoff transport capacity. Combined application of PAM with phosphogypsum, FGD, and other conditioners may reduce water erosion more than the application of each product alone.

Phosphogypsum, gypsum, and FGD can complement PAM functions. Application of PAM stabilizes soil aggregates but conditioners, such as phosphogypsum, gypsum, and FGD, which have electrolytes, can chemically react with soil particles and promote soil aggregation. Recent studies across a wide range of soil types and climates have shown that application of phosphogypsum, PAM, and FGD can reduce runoff and soil loss (Cochrane *et al.*, 2005; Truman *et al.*, 2010; Rhoton and McChesney, 2011). These studies suggest that FGD application can be recycled into agricultural fields for erosion control. However, although the erosion control potential of FGD appears high, possible presence of trace elements (Hg and As) and their associated risks should be investigated more (Rhoton and McChesney, 2011).

Conditioners are not a substitute to soil conservation practices but should be used as companions to other practices. For example, PAM can be used as temporary stabilization practices in disturbed soils until a permanent surface cover is established. Cost of PAM technology for controlling soil erosion can be lower than that of construction of mechanical structures (e.g., sediment retention basins), but repeated PAM applications may increase the total cost.

Summary and Concluding Statements

The soil erosion process of sediment entrainment resulting from fluid pressures acting to detach and transport erodible soil particles has been extensively investigated for both wind and water. The resulting knowledge relating soil erosion mechanisms to fluid volume and velocity sufficient to exert the threshold energy for overcoming soil shear resistance has led to management practices for controlling erosion. Many contributing factors were linked to the overall complex soil erosion process using both empirical and mechanistic approaches. The resulting integration of those factors describes soil erodibility, wind or water erosivity, and potential soil and crop management avenues for controlling soil erosion.

Controlling soil erosion by management is generally directed at decreasing the energy of wind or water by limiting their velocity through decreased soil slope for water and through barriers for intercepting wind and raindrop impact. The erosive effects of both wind and water are cumulative with increasing distance because of greater transport capacity of increasing runoff water volumes or the intensifying downwind soil saltation and surface creep that produces soil avalanching. Soil stabilization reduces erosion through management practices resulting in aggregates that resist water degradation and transport or exceed the particle size transportable by wind. Soil protection prevents erosion through crop management practices that promote, for example, residue barriers to intercept the impact of saltating soil grains and raindrops. The common characteristics of soil entrainment and any countering management for both wind and water erosion agents often use common conservation practices.

Successful conservation practices include modifying field features, using tillage, and managing crop rotations for cover or residue retention. For example, fields are managed with terraces on a contour to reduce runoff that transports soil; however, reducing runoff also increases available soil water for greater potential crop biomass production that can be directed to increasing soil organic carbon. Tillage practices for wind erosion control produce large aggregates to resist surface erosion or crosswind ridges to trap saltating soil grains. Similar ridges formed along an elevation contour effectively control water erosion by redirecting runoff water movement along almost negligible slopes to prevent rill formation. Cover crops or residue management simply provide a barrier at the soil surface to intercept the impact of raindrops or saltating soil grains and disrupt seal formation or abrasion resulting in greater runoff or erosion susceptibility. These examples of conservation practices represent only a fraction of the available management technology that has matured since the catastrophic erosion conditions when soil conservation in the US was first investigated. The mature erosion-control technology limits the risk of similar erosion reoccurring.

Soil erosion processes are essentially unchanged and can be managed successfully using established conservation practices so that risks of resuming soil erosion at the catastrophic rates are unlikely. One significant caveat related to recurring soil erosion is the impact of potential climate change whether a natural, but infrequent, occurrence or an anthropogenical result. Climate change affecting temperature and precipitation will necessarily stabilize or destabilize the soil through modified soil properties. For example, soil organic matter content that improves aggregation is inversely related to increasing soil temperature, which suggests greater potential erodibility in the event of prolonged warming trends. Alternatively, the amount of precipitation is directly related to soil organic matter and would also shift soil erodibility in a corresponding manner. Climatic temperature and precipitation conditions are interrelated as is their potential impact on soil conservation.

Severe drought can limit or prevent vegetative growth but, as observed by Chepil and Woodruff (1963), drought was not exclusively responsible for severe wind erosion. Erosion events combined the effects of drought-limited vegetative growth with various destabilizing soil disturbances, including grazing and tillage. The resulting soil condition featured critically depleted organic carbon or destroyed residue cover that increased soil erodibility. Nevertheless, soil erodibility does increase with the duration of drought and diminishes only after a minimum of two consecutive years of favorable precipitation and vegetative growth. Recent investigations characterizing more erodible fine soil material found microbial communities capable of tolerating the extreme ecological conditions of desiccation or radiation consistent with drought conditions in lieu of those important to C and N cycling, which are found in less erodible coarse soil particles (Gardner *et al.*, 2012). Although the knowledge of effective soil conservation practices is unaffected by climatic concerns and mature soil erosion control technologies will follow best known management applications, concern for the risk of recurrent catastrophic erosion cannot be disregarded.

Acknowledgment

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See also: Climate Change: Cropping System Changes and Adaptations. Dust Pollution from Agriculture. Edaphic Soil Science, Introduction to. Farm Management. From Foraging to Agriculture

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Soil Fertility and Plant Nutrition

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Glossary

Chlorosis Yellowing or lighter shade of green.
Immobile nutrient The immobile elements cannot translocate within the plant to meet need and therefore their deficiency typically occurs in the younger leaves first.
Internode The distance on the stem between leaves.
Interveinal Between the leaf veins.
Meristem The growing point of a plant.
Mobile nutrient A mobile element is able to translocate to areas of the plant with the most need. Typically, mobile elements move from the older or lower leaves to the upper or younger leaves to support new growth.
Necrosis Browning or dying of plant tissue.

Introduction

Soil fertility and plant nutrition encompasses the management of essential elements necessary for plant growth, typically to achieve selected management objectives. Although soil fertility plays a vital role in natural systems, the scope of this article is limited to plant production for human uses (e.g., food, feed, fiber, energy, and landscape esthetics). An element is considered essential if it is required for plant metabolism and for completion of the plant's life cycle (Epstein and Bloom, 2005; Havlin *et al.*, 2005). Typically, 17 elements are considered to meet these criteria and they are divided into macro- and micronutrients (Table 1). This division is based on their relative abundance in plant tissue rather than on their necessity for plant growth. Macronutrients are generally present in plant tissue at concentrations above 0.2%, whereas micronutrients are present below 0.01% (dry weight basis). Carbon (C), hydrogen (H), and oxygen (O) are derived from carbon dioxide (CO_2) and water (H_2O), which are transformed through photosynthesis to produce carbohydrates and are, therefore, present in the highest concentrations of any element in plant tissue. They are not, however, considered mineral elements and are almost always available in amounts necessary for their direct use in complete plant metabolism.

The essential mineral macronutrients can be divided into primary macronutrients, which include nitrogen (N), potassium (K), and phosphorus (P), and secondary macronutrients, calcium (Ca), magnesium (Mg), and sulfur (S). The eight micronutrients are copper (Cu), manganese (Mn), iron (Fe), boron (B), nickel (Ni), molybdenum (Mo), chlorine (Cl), and zinc (Zn). Other mineral elements may be essential for some plants or benefit crop quality or growth, although not being essential for metabolic processes or completion of the plant's life cycle; often these elements are referred to as 'beneficial elements.' Beneficial elements include cobalt (Co), sodium (Na), silicon (Si), selenium (Se), and vanadium (V). Silicon is present in concentrations on the order of some of the macronutrients in many plant tissues and has beneficial properties but is not generally considered essential to metabolic processes or the life cycle of any plants outside the family Equisetaceae (Epstein, 1994). However, there is an emerging school within the soil fertility research community that believes it may be more essential than previously thought.

Many other elements are taken up by plants in varying degrees but are not considered essential as defined above. Both essential and nonessential elements may be toxic to plants if accumulated at high enough concentrations to interfere with metabolic functions. Therefore, soil fertility and plant nutrition as a discipline encompasses management of these essential elements in the soil to provide them in adequate or sufficient amounts for plant metabolic processes and reproductive activities to be completed. Optimum soil fertility requires not only adequate quantities of the essential elements but also that they be in a form and location available for plant uptake and therefore optimum plant nutrition.

Soil Fertility Management

History of Soil Fertility and Plant Nutrition

Actively managing soil nutrients to provide optimum plant nutrition has been a core practice of agricultural production throughout human history. For many centuries agricultural production relied on recycling of organic residuals, such as manure and crop residues. Industrialization and population growth of the nineteenth century demanded increased agricultural production and coincided with the development of commercially produced P fertilizers. Providing adequate P fertilization allowed the true potential of N fertilization to be realized, and industrial production of inorganic N fertilizer soon followed with the development of the Haber–Bosch process in 1909. Stewart *et al.* (2005) estimated that N, P, and K fertilizers likely account for 40–60% of yield in the United States and England and much higher in the tropics. Industrially fixed N fertilizer has been estimated to account for 40–48% of the world's protein supply (Erisman *et al.*, 2008).

In a macrosense, the relationship between the development of commercial P and N fertilizers reflects one of the guiding premises of soil fertility explicitly stated as the theory of the minimum developed by Carl Sprengel in 1828 and popularized as 'Liebig's law of the minimum,' which states that

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Table 1 Essential nutrients and beneficial elements, their ionic plant-available forms, and their role in plant growth and development

	Element(s)	*Form taken up by plants*	*Role*
Nonmineral macronutrients	Carbon (C)	CO_2	Directly involved in photosynthesis
	Hydrogen (H)	H^+, OH^-, and H_2O	
	Oxygen (O)	O_2	
Mineral primary macronutrients	Nitrogen (N)	NH_4^+ and NO_3^-	Found in chlorophyll, nucleic acids, and amino acids. Major component of proteins and enzymes controlling most biological processes
	Phosphorus (P)	HPO_4^{2-} and $H_2PO_4^-$	Component of adenosine di- and triphosphate (ADP and ATP), which is essential for energy storage and transfer. Essential component of deoxyribonucleic acid (DNA) and ribonucleic acid (RNA). Important for most plant development processes and component of plant tissues, particularly concentrated in seeds
	Potassium (K)	K^+	Not incorporated in cell structure. Found in ionic form. Regulates water usage and provides disease resistance and stem strength. Involved in photosynthesis, drought tolerance, winter hardiness, and protein synthesis
Mineral secondary macronutrients	Calcium (Ca)	Ca^{2+}	Essential for cell elongation and division. Required for root and leaf development and function and formation of cell membranes and walls (e.g., Ca pectate). Involved in activation of enzymes
	Magnesium (Mg)	Mg^{2+}	Primary component of chlorophyll and important to photosynthesis. Component of ribosomes required for protein synthesis. Involved in phosphate metabolism, respiration, and enzyme activity
	Sulfur (S)	SO_4^{2-}	Required for synthesis of and contained in amino acids, which are essential for protein formation. Promotes nodulation in legumes. Involved in development of enzymes, seed production, and chlorophyll formation
Mineral micronutrients	Copper (Cu)	Cu^{2+}	Enzyme catalyst and required for chlorophyll formation
	Manganese (Mn)	Mn^{2+} and Mn^{4+}	Involved as catalyst and in activation for enzyme systems. Serves as a catalyst in chlorophyll synthesis
	Iron (Fe)	Fe^{2+} and Fe^{3+}	Catalyst in chlorophyll synthesis. Involved in oxidation and reduction reactions during respiration and photosynthesis
	Boron (B)	H_3BO_3, BO_3^-, and $B_4O_7^{2-}$	Essential for germination of pollen, growth of pollen tubes, seed and cell wall formation, and development and growth of new cells in meristematic tissue. Associated with translocation of sugars, starches, N, and P
	Nickel (Ni)	Ni^{2+}	Component of the urease enzyme. Essential for plants supplied with urea and for those in which ureides are important in N metabolism
	Molybdenum (Mo)	MoO_4^{2-}	Required for synthesis and activity of the enzyme system that reduces NO_3^- to NH_4^+ in plants (nitrate reductase). Essential for N fixation by rhizobia
	Chlorine (Cl)	Cl^-	Involved in plant energy reactions, plant–water relationships, regulation of stomata guard cells, drought and disease resistance, enzyme activation, and cation transport in plants
	Zinc (Zn)	Zn^{2+}	Involved in the synthesis of plant growth compounds and the enzyme system. Necessary for the production of chlorophyll, carbohydrates, and growth hormones
Beneficial elements	Cobalt (Co)	Co^{2+}	Complexes with N and synthesis of vitamin B_{12}
	Sodium (Na)	Na^{2+}	Essential for halophytic plants partially replacing K^+
	Silicon (Si)	H_4SiO_4	Possibly photosynthesis regulation enzyme activity
	Selenium (Se)	SeO_3^{2-} and SeO_4^{2-}	Not essential to plants but required by animals
	Vanadium (V)	VO_3^-	May be involved in fixation by rhizobia or biological oxidation–reduction reactions

production is limited by the amount of the most limited nutrient relative to the plant's need (Jungk, 2009). In other words, regardless of how much N is added, yield would be limited if P were not available in sufficient quantities. Once adequate P was provided through fertilization, after the development of P fertilizers, only then could additional yield be attained through N fertilization. Through the rigorous application of the scientific method, Sprengel and his contemporaries launched the discipline of soil fertility and plant nutrition to meet the world's growing demand for food. Perhaps Sprengel's greatest contribution was the understanding that mineral nutrients external to the plant were required for

plant growth. Identifying the essential elements and understanding that they must be provided external to the plant was a fundamental shift in agricultural production. Before Sprengel's work, some nutrients were supplied through recycling of crop residues and manures, and N could be provided through N-fixing crops in rotation; however, the majority of nutrients were lost from the system (due to system inefficiencies) and crop production was limited and agricultural lands were often depleted after a few years of cropping. Daniel Webster understood the importance of conservation of matter to this system when he stated "it is upon this fundamental idea of constant production without exhaustion, that the system of English cultivation, and indeed, of all good cultivation is founded" in his lecture 'On the Agriculture of England' presented 13 January 1840 (Webster and Everett, 1851).

The development of the concepts of soil fertility and plant nutrition and the realization that nutrients had to be supplied externally through fertilization to avoid the 'exhaustion' of the soil in the early nineteenth century by a new breed of soil chemists and agronomists helped to avoid the Malthusian Catastrophe, predicted in 1798 by Thomas Robert Malthus. These principles underpinned the 'Green Revolution' of the twentieth century. Tilman *et al.* (2002) estimated that, between 1960 and 2000, global cereal production doubled while global N use increased sevenfold and P use increased three and one-half fold. However, this increase in production and concomitant increase in fertilizer use has not come without cost. There are questions regarding the environmental sustainability of continuing to fix N and mine P for fertilizer, both due to resource availability (of energy and the mined minerals) and concerns about the impact of N and P losses from agriculture to surface and groundwaters (Cordell *et al.*, 2009; Dawson and Hilton, 2011). As a result, although managing soil nutrients for optimum plant nutrition and yield continues to be a pressing concern in light of global population growth, the management of nutrients in an efficient manner to protect resources is an important component of any discussion of soil fertility and plant nutrition.

Soil Fertility Evaluation

Modern soil fertility management integrates the disciplines of soil chemistry, soil biology, soil physics, and plant science to develop practices that provide the essential elements required for plant growth in sufficient quantities to maximize production while providing for environmental protection. In agricultural systems, this may mean optimizing production for economic return, whereas in other systems, such as phytoremediation or landscaping, there may be other goals that should be accounted for when planning a soil fertility strategy (e.g., rapid stand establishment, sufficient ground cover, or species biodiversity). Beyond management of soil nutrients, soil fertility must also address factors contributing to the soil's ability to supply nutrients and the plant's ability to efficiently utilize nutrients present. Optimum soil nutrient status alone will not provide for optimum system performance as numerous other factors influence plant nutritional status. Factors such as soil pH, moisture status, salinity, and physical condition as well as biotic stressors have a profound effect on a plant's interaction with nutrients. These factors are covered elsewhere in this encyclopedia and should be considered integral to comprehensive soil fertility and plant nutrition management. Most soil fertility management strategies have three key components: soil fertility assessment, nutrient recommendations, and performance evaluation to inform future decisions.

The goal of any soil fertility and plant nutrition program is to holistically address the factors influencing crop nutrient utilization in order to maximize plant performance. Therefore, the ultimate goal is to have each of the essential nutrients present in plant tissue at a sufficient concentration to support metabolic functions of the plant. For each essential element, there is a critical concentration within plant tissue above which added nutrients will not increase plant performance but may increase tissue concentrations of that nutrient. Below the critical concentration, plant performance will likely suffer due to a deficiency of that nutrient. Beyond the sufficiency range, concentrations of certain essential elements in plant tissue may be toxic and decrease plant performance; this range is often referred to as excessive or toxic range. Figure 1 shows an idealized response curve with the critical concentration and the deficient, sufficient, and excessive or toxic ranges identified. The actual concentrations for each nutrient will vary withplant species, plant part, and growth stage.

Soil fertility assessment is a critical component to soil fertility management. The traditional goal of this assessment has been to evaluate the ability of a soil to supply the essential nutrients for optimum crop performance. Performance may be determined by yield, crop quality, or some other metric depending on management goals. Beyond quantifying essential elements present, soil fertility assessment should also evaluate other factors that might influence the soil nutrient supply to the plant, such as pH or compaction. Increasingly, modern soil fertility assessment also accounts for the potential

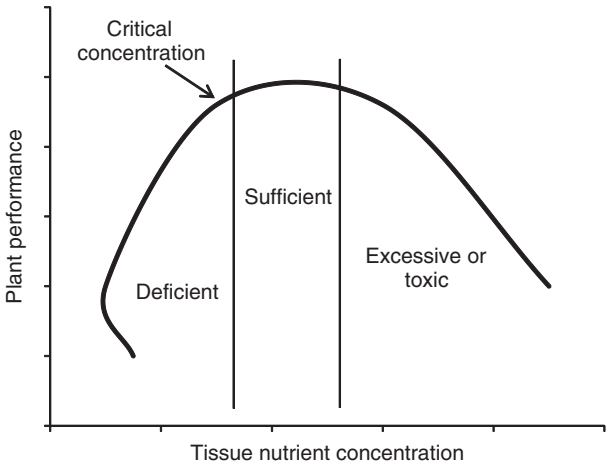


Figure 1 Nutrient concentration in plant tissues as it relates to plant performance. Below the critical range plants are considered deficient. The range where nutrient concentration in the tissue increases, but performance does not, is considered the sufficient range. At some point beyond the sufficiency range, excessive nutrient concentrations can limit plant performance and this is considered the excessive or toxic range.

environmental impact of soil nutrients. There is a wide range of techniques used to assess soil fertility. Generally, soil fertility assessment can fall into three broad categories: direct assessment of soil physical or chemical characteristics; quantification of essential elements in plant tissue; or evaluation of plant response to soil nutrient status. A key component of any soil fertility assessment is the interpretation of results to generate fertilizer recommendations. Typically, one analyzes the nutrient content of soil or tissue samples or evaluates the expression of deficiency or sufficiency in plants and then interprets these findings to recommend rates of nutrient to apply to avoid or correct deficiencies.

Soil analysis

The first broad category of soil fertility evaluation is soil testing or the chemical extraction of soil nutrients to estimate their plant availability. Research in soil testing began in the nineteenth century following Sprengel's work, but systematic research into soil testing and plant nutrient status began in earnest in the 1920s. With the development of more advanced analytical capabilities, organized soil testing programs were established in the United States in the 1940s. Peck and Soltanpour (1990) defined soil testing as "…rapid chemical analyses to assess the plant-available nutrient status, salinity, and elemental toxicity of a soil…a program that includes interpretation, evaluation, fertilizer and amendment recommendations based on results of chemical analyses and other considerations." This definition identifies four key components of a soil fertility assessment. The first is an assessment of the soil nutrient status, typically through a chemical extraction of soil or plant tissue. However, the other three components are equally important: the results of the nutrient quantification must be interpreted to provide an index of the relative proportion of the nutrient present that is available for plant use; they must then be evaluated in the context of potential plant response to fertilizer; and finally they must be translated into a recommendation for the amount, form, placement, and timing of a fertilizer application to provide optimum nutrient status for crop growth.

The soil test typically extracts a portion of the total amount of the element present. The amount extracted is proportional to the amount that is available for plant uptake. A response curve is then defined, typically through empirical laboratory, greenhouse, or field experiments, which predicts the potential for crop response to added fertilizer. Therefore, a soil test provides a relative index of potential responsiveness that forms the basis of a fertilizer or lime amendment. Interpretation of soil test results follows closely the definition provided previously for plant nutrition sufficiency (**Figure 1**). An idealized soil testing response curve is provided in **Figure 2**. Generally, no response to added fertilizer is expected above the critical soil test level identified in **Figure 2**. The relative index of soil nutrient supply capacity varies according to recommendations system, but generally the scale is divided into areas, 'below optimum,' 'optimum,' and 'above optimum' or 'excessive' nutrient concentration. A yield response to added fertilizer is expected when soil test levels are below optimum (i.e., below the critical threshold). Starter or maintenance levels of fertilizer may be recommended in the optimum range. Some nutrients may cause environmental risk or plant toxicity above the optimum range.

Nutrient recommendations are determined by soil test results; however, even when two labs use the same methods and generate equivalent results, their nutrient recommendations may differ. These disparities arise due to differences in soil test interpretation and recommendation philosophies. Over the years, three basic philosophies have emerged. These include the sufficiency approach, the build and maintain approach, and the base cation saturation ratio (BCSR) theory. Both the sufficiency approach and the build and maintain approach

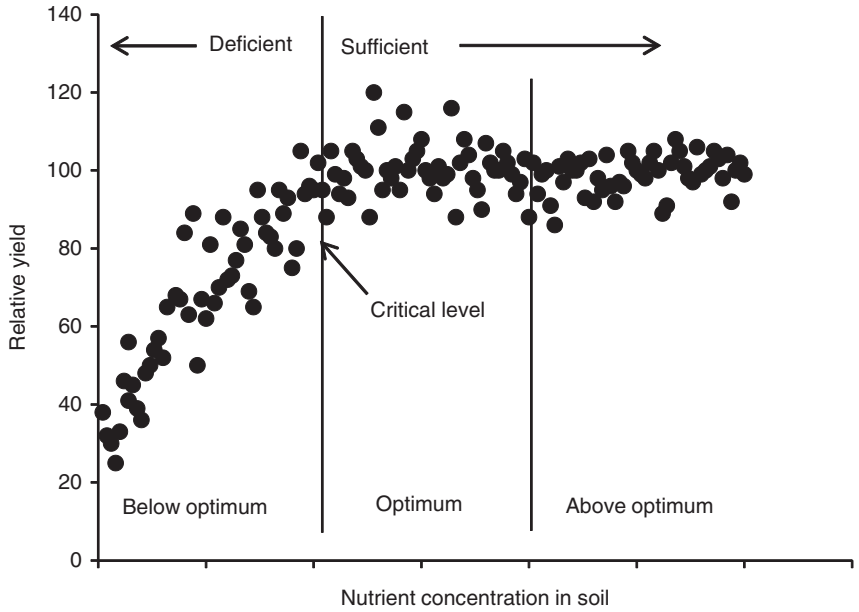


Figure 2 Empirical relationships are defined between soil nutrient concentrations and yield response. As the soil concentration increases less fertilizer is required to optimize yield.

follow the general concept that there are definable critical levels of nutrients in soil and that below this level crops are likely to respond to additional applied nutrients. When nutrient concentrations are in the optimum range, just above the critical level, there is a low probability of crop response with further addition of that nutrient. With the build and maintain approach, fertilizer recommendations are made with the goal of building the soil's nutrient levels into the optimum range, then maintaining these levels by applying nutrients at rates that approximate crop removal. The sufficiency approach is a more conservative philosophy where nutrient recommendations are intended to only meet crop needs and not build soil fertility. No nutrients are recommended above the critical soil test level. The sufficiency approach is designed to 'feed the crop,' whereas the build and maintain approach is designed more to 'feed the soil.' In theory, the sufficiency approach is a more profitable system because fertilizer is applied only when there is likely to be an economic return. However, in practice the sufficiency approach is also more risky due to the inherent uncertainty associated with soil testing.

The third philosophy, the BCSR theory, promotes the idea that maximum yields can only be achieved by creating a balanced ratio of Ca, Mg, and K in the soil. The concept is rooted in the work conducted by Dr. Firman Bear and his colleagues at the New Jersey Agricultural Experiment Station in the 1940s (Bear and Prince, 1945; Bear and Toth, 1948). Bear's work showed that the luxury consumption of costly fertilizer K by alfalfa could be reduced by applying high rates of relatively low-cost Ca (as ground gypsum or calcitic lime). As an aside, Bear also pointed out that another effective strategy to reduce luxury consumption of K by alfalfa was to use split applications of moderate doses of fertilizer K rather than infrequent high rates (a best management practice still recommended today). Bear and his colleagues suggested that there were ideal ratios of Ca, Mg, and K; however, they provided no data to support these claims, so it is unclear how they were developed.

Around the same time, Dr. William Albrecht and his colleagues at the University of Missouri began to investigate the BCSR theory. This work and its findings are summarized in the Albrecht Papers (Albrecht and Walters, 1996). They conducted a series of experiments on soils and soil minerals amended to achieve a wide range of Ca:Mg:K ratios. Based on this work, Albrecht suggested that a balanced soil should have a cation saturation of 60–75% Ca, 10–20% Mg, and 2–5% K. It is unclear how Albrecht derived these values; in fact, much of the data Albrecht and his colleagues published illustrated that optimum yields occurred over a wide range of Ca, Mg, and K ratios. Further, careful evaluation of the work a number of years later revealed several fundamental flaws in the methods Albrecht and his colleagues used. Over the years, a number of soil scientists have evaluated the BCSR theory (see review by Kopittke and Menzies, 2007). This work has failed to support claims of BCSR theory and has illustrated that using it to manage soil fertility results in inefficient use of both capital and natural resources. Nonetheless, the importance of attaining an ideal BCSR, especially pertaining to the importance of very specific Ca:Mg ratios, continues to be promoted. These claims include the following: improved soil structure, reduced weed pressure, increased resistance to insect and disease, and reduced leaching of other nutrients. There are no research data that support these claims.

Most of the guidelines developed by US Land Grant Universities and used by both public and private soil test labs follow a combination of the sufficiency and build and maintain approaches, the goal being to provide adequate, but not excessive, levels of essential nutrients to promote healthy plant growth. The nutrient guidelines are intended to help growers optimize crop yield and quality, maximize return on fertilizer investment, and minimize nutrient losses to the environment.

Plant tissue analysis

Soil fertility evaluation does not rely on soil testing alone. Visual diagnosis of plant nutrient deficiencies, in-field measurements of plant nutrient status, laboratory analysis of tissue nutrient concentrations, and remote sensing of plants can all be valuable tools in identifying plant nutrient deficiencies, so that they can be corrected or prevented. Soil testing can be used before planting or in season to guide nutrient applications. Plant tissue analysis can be used in season to identify or confirm visually observed nutrient deficiencies (Table 1). When combined with a soil testing program, plant tissue sampling and testing or analysis can be very useful in determining the cause of visual deficiency symptoms. There are many tools available for in-field plant analysis, including the leaf chlorophyll meter that measures light absorption at specific wavelengths and handheld or equipment-mounted photometers that measure light reflectance. These tools are often used to calculate various vegetative indexes based on the ratio of light reflectance at different wavelengths to estimate sufficiency or predict nutrient need through more advanced algorithms. However, these types of diagnostic tools are beyond the scope of this article, which is limited to traditional visual diagnosis and plant tissue analysis.

It is important to take a holistic approach to soil fertility management and interpret tissue test results in the context of soil test results, field conditions, plant health, and other potential plant stresses. Many factors can influence relative nutrient availability or the ability of a plant to take up available nutrients, causing a nutrient deficiency to be expressed visually or in tissue nutrient concentrations. For example, a grower may visually identify P deficiency in a corn field due to the presence of stunted, purple-colored plants. If only a tissue sample was collected and it showed P deficiency, the grower may then conclude that additional P is required. However, a soil sample may reveal that there was adequate P in the soil, but that the pH was low, limiting P availability, evaluation of the whole plant could reveal that a root disease, such as Pythium root rot, induced the above-ground P deficiency symptoms. In either case P fertilizer was not truly required, even though a tissue test alone would have indicated that it was. There are many examples where soil nutrient concentration is not the culprit of a deficiency identified visually or through tissue analysis, so caution should be applied when interpreting plant tissue concentrations. A valuable application of tissue testing is to confirm nutrient deficiencies within problem areas observed in a field. For example, many nutrient deficiencies result in plants exhibiting interveinal chlorosis. If the symptom is exhibited sporadically across the field, tissue samples can be collected from within the affected regions and

compared with results from samples collected from unaffected regions. This comparison along with soil test results from both areas can be used to narrow which specific nutrient might be causing the symptoms. However, it is important to remember that it is not enough to identify a nutrient deficiency, the cause must also be determined before corrective action can be taken. It does no good to apply a nutrient that is deficient if soil compaction, pH, root disease, or other problems are limiting uptake of that nutrient by the crop.

The results of tissue analysis are highly dependent on how and when the sample was collected. Some of the essential elements are considered mobile nutrients within plants because they can be translocated from mature plant parts to the areas of the plant that are actively growing (meristem), so that deficiencies will occur initially in the older parts of the plant. Conversely, immobile nutrients cannot translocate and therefore deficiency symptoms are typically exhibited initially in the youngest part of the plant. **Table 2** provides a list of the essential mineral elements, their relative mobility within the plant, relative and average concentration in plant tissue, and typical deficiency symptoms. The relative concentrations presented in **Table 2** are provided to give perspective on the relative proportion of each nutrient in plants, where the average concentration presented for each nutrient is divided by the average concentration of Mo in plant tissues (Havlin *et al.*, 2005). As the sufficiency range for nutrient concentrations varies greatly between plants, the part of the plant sampled, and the timing of sample collection, it is best to refer to optimum ranges supplied by local soil and plant tissue testing laboratories.

Most laboratories that provide soil and plant tissue testing services provide instructions on which part of the plant should be sampled and the appropriate timing for tissue sampling. For example, when sampling corn seedlings ($<$ 12 in. tall), the entire plant should be sampled by cutting it off approximately 1 in. above the soil surface; for vegetative growth stages the uppermost collared leaf should be sampled, and at tasseling the ear leaf should be sampled. Once the plant enters reproductive stages, some essential nutrients begin to move to the seed or fruit from other parts of the plant and therefore a tissue sample taken after initial flowering may not accurately represent nutrient uptake and availability. Similarly, tissue sampling and tissue test results are often used inappropriately to determine fertilizer need. In corn, for example, during the first two vegetative growth stages (up to V2 or two fully collared leaves) the plant utilizes very little soil N and relies primarily on N provided by the seed. Therefore, tissue samples collected at this time provide very little value in terms of determining additional N need. Once the plant reaches the rapid growth stage ($\approx$V4 – tasseling), tissue N concentrations fluctuate

Table 2 Essential elements, their mobility, relative and average concentration in plants, and common deficiency symptoms

Essential element	*Mobility*	*Concentration in plants*[a]		*Common deficiency symptoms*
		Relative	*Average*	
Nitrogen	Mobile	1 000 000	1.5%	Stunted chlorotic plants with increased susceptibility to stress. Early maturity
Phosphorus	Mobile	30 000	0.2%	Overall stunted plant and poor root development with purple to reddish color
Potassium	Mobile	400 000	1.0%	Scorching or firing along leaf edge. Deficient plants grow slowly with poor root development. Weak stalks with lodging common and small seed or fruit. Low stress tolerance
Calcium	Immobile	200 000	0.5%	Poor root growth with roots often turning black and rotting. Failure of terminal buds and apical tips of roots to develop
Magnesium	Mobile	100 000	0.2%	Leaves show a yellowish, bronze, or reddish color while leaf veins remain green
Sulfur	Somewhat mobile	30 000	0.2%	Chlorosis of longer leaves or chlorotic stunted plants. Resembles N deficiency; however, upper leaves tend to show deficiency first
Copper	Immobile	100	6 ppm	Reduced leaf size. Uniformly pale yellow leaves. Leaves lack turgor and may develop bluish green color, become chlorotic, and curl. Flower production fails
Manganese	Immobile	1 000	50 ppm	Interveinal chlorosis. Appearance of brownish black specks
Iron	Immobile	2 000	100 ppm	Interveinal chlorosis. In the case of severe deficiency the entire leaf may turn white
Boron	Immobile	2 000	20 ppm	Reduced leaf size and deformation of new leaves. Interveinal chlorosis if deficiency is severe. Possibly distorted stems. May cause flower or fruit abortion, poor grain fill, and stunted growth
Nickel	Mobile	0.1	0.01 ppm	Limited information available on deficiency symptoms
Molybdenum	Immobile	1	0.1 ppm	Interveinal chlorosis, wilting, and marginal necrosis of upper leaves
Chlorine	Mobile	3 000	100 ppm	Chlorosis of upper leaves and overall wilting of plant. Deficiencies may show in upper leaves, even though mobile
Zinc	Immobile	300	20 ppm	Shortened internodes between new leaves, death of meristematic tissue, deformed new leaves, and interveinal chlorosis

[a]Relative nutrient concentrations are expressed on the basis of their concentration relative to molybdenum. Concentrations are expressed on a dry matter mass basis and adapted from Havlin, J.L., Beaton, J.D., Tisdale, S.L., 2005. Soil Fertility and Fertilizers: An Introduction to Nutrient Management. Upper Saddle River, NJ: Pearson Prentice Hall.

wildly due to the rapid growth of the plant and variation in uptake relative to tissue development. Therefore, recommendations based on tissue samples collected at this time may be highly unreliable. Owing to the many factors that influence nutrient concentrations in tissues, great caution should be taken when interpreting tissue sample results and trying to formulate fertility recommendations. Their best utility is in comparing 'good' and 'bad' areas within the same field as they were exposed to the same growing and management conditions.

A unique tissue test that has gained popularity recently is the corn stalk nitrate test (CSNT). The CSNT is an end-of-season test that provides a retrospective assessment of the season's nitrogen management. Corn plants show no visual evidence of overfertilization. The CSNT can provide this information, allowing producers to know when a field received more nitrogen than needed for maximum yield. After pollination, nitrogen from the leaves and stalk is mobilized and transported into the developing grain. During this process and after black layer, nitrate uptake from the soil into the plant also continues. If more nitrogen is available to the plant than needed for maximum yield, nitrate accumulates in the stalk, particularly the lower stalk. The CSNT is a robust test that is able to identify when N was available in excess of crop need and along with other information on N management it can be used to fine tune N management in future growing seasons (Binford *et al.*, 1990). However, the range of stalk nitrate concentrations is very narrow in the optimum and below optimum ranges and therefore of limited utility in accurately identifying when very little N is available.

Soil Characteristics Contributing to Nutrient Supply

Soil Mineralogy

Soil mineralogy is one of the dominant soil properties controlling the amount of nutrients present in the root zone and the rate at which they are made available to plants. Nutrient supply is simply the quantity of nutrients held onto the soil particle surface, either as a result of natural geologic parent material or anthropogenic activity (i.e., fertilization). A simple but important concept regarding the role of soil mineralogy in soil fertility and plant nutrition is the notion that plants can take up nutrients only from solution. The focus is often on the amount or 'quantity' of nutrients present in the soil, but the ability of a soil to supply nutrients is also determined by the soil's ability to potentially release those nutrients into the soil solution where they are then available to the plants. The concentration of the nutrient that is found in or easily dissolves or desorbs into solution is known as the 'intensity.' The quantity–intensity relationship for a given soil is a measure of the soil's buffering capacity with respect to that nutrient. An example of quantity–intensity relationship is shown in Figure 3.

In general, the quantity is some measure of the total nutrient supply that is not necessarily 100% labile. This could be the nutrient concentration determined by a total digestion under strong acid and heat, or some other type of harsh extraction. However, the intensity is the concentration of that same nutrient that is labile or in solution, often estimated with

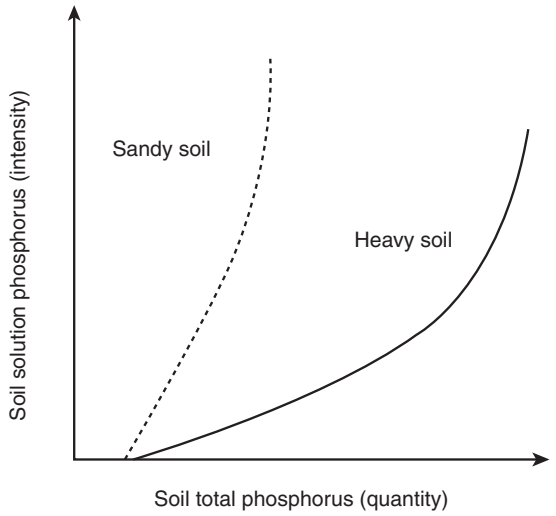


Figure 3 Example of quantity–intensity (Q/I) curves for soil phosphorus for sandy and 'heavy' (high clay content) soils.

ion-exchange membranes or water extraction analysis. The quantity–intensity curve varies depending on the nutrient and chemical characteristics of the soil, particularly the mineralogy and pH. Essentially, the quantity–intensity curve describes the ability of the soil to supply the solution with the nutrient. As it is not feasible to determine the quantity–intensity relationship in every case where a nutrient recommendation is required, it is the goal of agronomic soil testing to provide some of this information using rapid and affordable techniques.

The slope of the quantity–intensity curve is considered to be the buffering capacity for the specific nutrient and soil depicted. In general, as the soil quantity (i.e., supply) of the nutrient increases, the ability of that nutrient to be released into solution increases. However, note that the slope of this curve is not generally constant; this is especially true for certain nutrients that are strongly bound to the soil, such as trace metals or P onto Fe oxide minerals. In such cases, the soil shows a limited capacity to release the nutrient into solution when the quantity is low, but as the quantity becomes larger, a given increase in quantity will result in a greater increase in intensity, or solution concentration, compared with the case where the quantity is lower. In other words, at higher quantity concentrations, further increases in the quantity through fertilization will yield more efficient release of the nutrient into solution. This is why for certain soils it is important to 'build up' P concentrations so that plants can have access to soil P.

Permanent-charge versus variable-charge minerals

As previously mentioned, soil mineralogy can have a profound impact on the quantity–intensity relationship. With regard to the mechanism by which soil minerals retain nutrients, minerals can be classified into two different groups: permanent-charge (or variable potential) minerals and variable-charge minerals. Permanent-charge minerals retain a constant negative charge regardless of solution conditions (i.e., pH and ionic strength). Permanent-charge minerals obtain their inner-layer charge from isomorphous substitution occurring in 2:1 clay minerals. In addition to possessing negative charge, for a

mineral to sorb a cation nutrient from solution, the negative charge must be physically accessible to cations in solution. Thus, it is found that some minerals with high levels of permanent negative charge are unable to sorb many cation nutrients from solution, such as illite and biotite, as their inner layer is mostly clamped shut with K ions holding the layers together tightly. Instead, it is mostly vermiculite and montmorillonite that possess a permanent negative charge which is accessible to solution cations. In addition to vermiculite and montmorillonite, there are amorphous 2:1 minerals that possess accessible permanent negative charge; such minerals are most common in recently developed volcanic (Andic) soils. Zeolites (tectosilicates) are a group of soil minerals that possesses a large amount of accessible permanent negative charge but are not 2:1 minerals.

Permanent-charge minerals can retain only cation nutrients from solution, such as Ca^{2+}, Mg^{2+}, Ni^{2+}, K^{+}, Cu^{2+}, etc. However, variable-charge minerals can become positively charged depending on solution pH, which allows them to sorb anion nutrients, such as PO_4^{3-} and SO_4^{2-}. This variable charge occurs mostly on the terminal hydroxide groups located on the edges of 1:1 minerals (such as kaolinite) and Fe, Al, and Mn oxides or hydroxides (such as goethite and gibbsite). Although not a mineral, soil organic matter contains numerous variable-charged functional groups that behave similarly. Similar to the 2:1 minerals, there exists both crystalline and amorphous 1:1, oxide, and hydroxide minerals. Equations [1 and 2] show generic reactions where charge development occurs due to protonation or deprotonation of hydroxide groups.

Protonation of a metal hydroxide mineral resulting in a positively charged surface site (eqn [1]).

$$FeOH^0 + H^+ \leftrightarrow FeOH_2^+ \quad [1]$$

Deprotonation of a metal hydroxide mineral resulting in a negatively charged surface site (eqn [2]).

$$FeOH^0 \leftrightarrow FeO^- + H^+ \quad [2]$$

Note that the degree of each reaction can be quantified by a specific *k* value (i.e., reaction constant) for each mineral. Thus, as pH increases, the negative charge on the mineral surface increases, whereas the positive charge decreases, and when pH decreases the negative charge decreases and positive charge increases. For example, if the surface functional groups shown in eqns [1] and [2] were located on goethite, the *k* value would equal to $10^{6.2}$ and $10^{-11.8}$, respectively. As you would expect, this change in charge can impact the ability of the surface of variable-charge minerals to retain anion and cation nutrients. Each variable-charge mineral possesses a unique point of zero charge (PZC), which is the pH at which the net charge equals zero. When the pH is greater than the PZC of the mineral, the net charge on the mineral is negative. Note that this does not necessarily mean that there is no longer any positive charge; it simply means that there is more negatively charged sites than positively charged sites.

Ion-exchange reactions (nonspecific sorption)

Nutrient ions are attracted to sites of opposite charge located on minerals and organic matter, either permanent or variable charge. When ions bind to the mineral sites by weak electrostatic attraction (i.e., no direct contact with the surface), this is known as ion exchange. Ion exchange is characterized by a weak and reversible bond known as nonspecific sorption. Ions that bind by this mechanism can be easily and rapidly displaced by other ions of the same charge. This reversible nature of ion exchange is extremely important to both agronomic production and environmental quality. Specifically, if bonds retaining nutrient ions are excessively strong then there is less potential for them to be released into solution for subsequent nutrient uptake or transport. Yet the reversible nature of the ion-exchange reaction is still strong enough to prevent all nutrients from simply passing through the soil and directly to groundwater and surface water, being lost from the agroecosystem and having potentially negative implications.

Other characteristics of ion exchange include charge balance and selectivity. All ion-exchange reactions are charge balanced; for example, one mole of Ca^{2+} can exchange with 2 mol of K^{+}. This is why ion exchange and soil charge are typically quantified in units of equivalents, which is the same as a mole of charge (i.e., molecular weight normalized for valence of the ion). The selectivity of ion-exchange reactions has several implications. At equal concentrations, ions with a greater charge density are preferred over ions of lesser charge density. For example, Al^{3+} is preferred over Ca^{2+}, which is preferred over K^{+}. Similarly, K^{+} is preferred over Na^{+} because K^{+} has a greater charge density; although the two ions possess the same charge, K^{+} is a smaller ion due to a lower degree of hydration. Although ions of greater charge density are selectively sorbed over ions of lesser charge density, this is somewhat concentration dependent due to the fact that ion-exchange reactions are subject to Le Chatelier's principle (the equilibrium law that states if a system at equilibrium undergoes a shift in concentration the system will adjust to try and counteract the shift in equilibrium). For example, consider a soil system where K^{+} ions are sorbed to the clay surfaces and Ca^{2+} is added to the soil solution. For each mole of Ca^{2+} added to the system, two moles of K^{+} will be replaced and moved to the soil solution.

Although Ca^{2+} is selectively sorbed over K^{+} at equal concentrations, if the concentration of K^{+} becomes large enough, it can displace the Ca^{2+} at the surface (i.e., reverse reaction). Note that ion-exchange reactions are subject to the laws of thermodynamics and are quantified by the reaction constant *k*. As a result, if the concentration on one side of the reaction becomes much greater than the concentrations on the opposite side, the reaction will proceed toward the side with lower concentrations in order to equilibrate the system to maintain the reaction constant (Le Chatelier's principle). Thus, as a plant depletes the soil solution of nutrients, this offsets the balance between ions sorbed onto the surface and ions in solution, and Le Chatelier's principle tells that the ions sorbed onto the surface will desorb into solution in order to maintain equilibrium between the surface and solution. In this way, the soil serves as a 'nutrient warehouse' that acts to supply the solution for plants; one of the challenges of nutrient management is to resupply the warehouse when it becomes depleted.

The sum of all cation charges (equivalents) that are held onto the soil by the ion-exchange mechanism is the cation-exchange capacity (CEC). Likewise, the sum of all anion

Table 3 General description of the ability of cations and anions to bind by specific sorption, nonspecific sorption, or both

	Specific sorption (ligand exchange or chemisorption)	*Nonspecific sorption only (ion exchange)*	*Both specific and nonspecific sorption*
Anion	OH^- PO_4^{3-}, AsO_4^{3-}, SeO_3^{2-}, and F^-	CO_3^{2-}, Cl^-, Br^-, I^-, NO_3^-, and $B(OH)^{4-}$	MoO_4^{2-}, SeO_4^{2-}, SO_4^{2-}, and CrO_4^{2-}
Cation	Ni^{2+}, Co^{2+}, Cu^{2+}, Zn^{2+}, Pb^{2+}, Mn^{2+}, and Ag^+	Ca^{2+}, Mg^{2+}, Li^+, Na^+, Ba^{2+}, and NH_4^+	K^+, Cd^{2+}, and Hg^{2+}

Note: Ions listed under specific sorption can also bind by nonspecific sorption, but those listed under nonspecific sorption never bind by specific sorption. Those listed under 'both' have only a weak ability to bind by specific sorption mechanisms.

charges held onto the soil by the ion-exchange mechanism is the anion-exchange capacity (AEC). In general, the composition of nutrients on the ion-exchange sites is proportional to the solution composition of ions. For example, if the soil CEC contains 20% Al^{3+}, 40% Ca^{2+}, 10% K^+, 10% Na^+, 10% H^+, and 10% Mg^{2+}, then the solution will contain those ions in a similar ratio.

Ligand-exchange and chemisorption (specific sorption) reactions

Ligand exchange and chemisorption are the names given to the 'specific' sorption reactions for anions and cations, respectively. Specific sorption differs from ion exchange (nonspecific sorption) in that the reaction results in a strong covalent bond, because the ion is bound directly to the surface with no water molecule in between. As a result, nutrients held by specific sorption are bound somewhat irreversibly, that is, a portion of nutrients that are sorbed by this mechanism will not completely desorb (i.e., hysteresis). In addition, specific sorption occurs dominantly on edge terminal hydroxide groups among variable-charge minerals as opposed to permanent-charge minerals, which mostly retain nutrients by weak ion-exchange reactions. Another difference between ion exchange is that specific sorption reactions can occur on positive, negative, or neutral surfaces; this is due to the fact that the bound nutrient actually becomes somewhat part of the surface (known as the Stern layer) of the variable-charge mineral. Thus, there is a general trend that specific sorption of anions can increase the negative charge (i.e., increase CEC) and sorption of cations can increase positive charge (i.e., increase AEC).

Soil pH has an impact on specific sorption due to the increased competition with H^+ at low pH and OH^- with increasing pH. Particularly, specific sorption of cations (i.e., chemisorption) decreases with a decrease in pH as the cation must compete with protons that have a strong affinity for the surface of variable-charge minerals. Likewise, specific sorption of anions (i.e., ligand exchange) is lessened with increasing pH due to competition with OH^-, as OH^- is itself a ligand. Cations that can potentially bind strongly via chemisorption are those that easily hydrolyze, which are mostly transition metals, such as the micronutrients Zn^{2+} and Cu^{2+}. In general, 'base cation' nutrients, which consist of the alkali and alkali earth metal nutrients (Ca^{2+}, Mg^{2+}, and K^+), bind only by ion-exchange reactions, although there are several exceptions discussed%% later. Anions that can potentially bind by ligand-exchange to variable-charge sites are typically oxyanions, such as phosphate and molybdenate. Anions that can bind strongly by ligand exchange (such as phosphate) will outcompete anions that can only bind by the weak ion-exchange mechanism (such as nitrate) and anions that can bind by ligand exchange with less strength (such as sulfate). Table 3 shows which ions are capable of binding by specific sorption.

Precipitation and dissolution

Precipitation and dissolution make up the third category of reaction mechanism that enables soils to both bind and release ions into solution, making them available for plant uptake or mobile for water transport. Precipitation theory states that as the concentration of an ion in solution increases, precipitation of a new solid phase does not occur until the solubility product of that phase has been exceeded.

Generic reaction showing the precipitation of a reaction product from an anion and a cation (eqn [3]).

$$A_n^- + C_{at}^+ \leftrightarrow P_r;\ k = X \qquad [3]$$

Equation [3] provides a general reaction where an anion (A_n^-) and cation (C_{at}^+) react with each other to form a solid precipitant or mineral (P_r). The ions on the left side of the reaction are the reactants, and the solid mineral on the right side is the product. There is equilibrium between the reactants and products that is quantified by the reaction constant k, which is unique to each mineral. This concept of equilibrium is the same as was described for specific and nonspecific sorption except that the product is a solid mineral. Le Chatelier's principle also applies to precipitation reactions and their reverse reaction, dissolution of the mineral back into the soil solution. Depending on the ion concentrations in solution and the potential presence of a solid mineral, the ions may react with each other to form a solid mineral, thereby leaving the solution where they cannot be taken up by a plant, or conversely the solid may dissolve to resupply the solution with the ions where they can be taken up by a plant.

Many plant nutrients are subject to precipitation and dissolution reactions that can impact nutrient availability. Those most affected ones include P, Ca, Mg, and trace metals. Because most precipitation and dissolution reactions involve OH^- or H^+, nutrient availability of such ions tend to be highly pH dependent. The impact of pH on nutrient availability is discussed in the Section pH and Soil Fertility.

Soil Type

Soil type plays a profound role in soil fertility because mineralogy partly dictates soil type and mineralogy controls the capacity and strength in which nutrients are retained. For this

discussion, the term 'soil type' will be relegated to the most broad soil taxonomic category, soil order (based on US Department of Agriculture soil taxonomic classification system).

Because soil orders are classified partly due to their mineralogy, and as mineralogy partly dictates fertility, knowledge of the soil order can provide useful information regarding fertility. As discussed in the Section Permanent-charge versus variable-charge minerals, 2:1 minerals that possess accessible permanent negative charge have the highest CEC among soil minerals and therefore the greatest capacity to retain base cations, such as K^+, Ca^{2+}, Mg^{2+}, and NH_4^+. Typically, these include the soil clay minerals montmorillonite and vermiculite. However, these minerals possess very little AEC as they have little to no variable charge. Because variable-charge minerals have the ability to strongly sorb nutrients by ligand exchange and chemisorption, soils dominated with variable-charge minerals tend to 'fix' ions (i.e., prevent them from entering solution) that are highly susceptible to such reactions (Table 3) and are considered infertile. Another reason variable-charge minerals are typically considered infertile is because they generally have a low CEC. However, soils dominated with variable-charge minerals have the ability to prevent excessive runoff and leaching losses of P and trace metals, thereby preventing a potentially negative environmental impact in cases when excessive nutrients are applied.

As a general rule, 'younger' soils are more fertile than 'older' ones as the former is dominated by permanently charged 2:1 minerals, whereas the latter is dominated with variable-charge 1:1 and metal oxide or hydroxide minerals. In this context, 'younger' and 'older' refers to soil development as impacted by the five soil-forming factors (parent material, climate, organisms, topography, and time). The five soil-forming factors generally transform minerals from primary minerals to high-layer charge 2:1 minerals (i.e., mica and illite), lower-layer charge 2:1 minerals (i.e., montmorillonite and vermiculite), 1:1 minerals, and finally metal hydroxides.

Some of the least developed soil orders, which include Entisols and Inceptisols, do not necessarily fit this general rule because the mineralogy of these soil orders are mostly a function of their parent geologic material. Aridisols are characterized by a high level of primary minerals, mainly sulfates and carbonates. These soils develop in areas of low rainfall and often possess naturally high amounts of K, Ca, Mg, and S but a low CEC and AEC due to the lack of more developed minerals. One of the least developed and most fertile soil orders, Andisols, are derived from relatively recently deposited volcanic materials and are, therefore, rich in amorphous 2:1 minerals with high CEC. Similarly, Vertisols are dominated by montmorillonite and therefore are considered to be highly fertile. As soils weather and 2:1 minerals begin to give way to 1:1 minerals, Mollisols and Alfisols are formed. The former is distinguished by higher levels of organic carbon, making it more fertile than Alfisols, but both soil orders are characterized as having 'high' base cation saturation ($>35\%$). With continued development, Ultisols are formed, which contain less 2:1 minerals and more 1:1 and metal oxides and hydroxides, which results in a lower base cation saturation ($<35\%$) and therefore a decreased CEC. Still, the most developed soil order is the Oxisol, which has very little CEC and is dominated by 1:1 minerals and metals oxides and hydroxides.

pH and Soil Fertility

Soil pH is considered the 'master variable' in soil fertility for several reasons. Soil pH often has a large impact on (1) precipitation and dissolution of primary minerals, (2) the degree of CEC and AEC on variable-charge minerals, (3) the degree of ion-exchange, ligand-exchange, and chemisorption reactions, (4) microbial activity that impacts nutrient cycling, and (5) the solubility of Al. The general change in nutrient availability with changes in pH is shown in Figure 4. One of the most important aspects of the impact of pH on soil fertility is percent base cation saturation of the CEC. Percent base saturation is quantified as the amount of exchangeable base cations divided by the soil CEC and multiplied by 100%. Soils with low percent base saturation are considered infertile, whereas those with high saturation are fertile. Soils with low-base saturation are dominated by H^+ and Al^{3+}, contributing to acidity and Al^{3+} toxicity in plants. Indeed, it is the increased solution concentrations of Al^{3+} and Mn^{4+} that are often most detrimental to plant growth under acidic pH conditions. The influence of soil pH on nutrient availability to plants varies with nutrient and soil mineralogy. Details on the interaction between soil pH and nutrient availability is covered in more detail in the following Section Nutrient Cycling and Plant Nutritional Roles of Essential Elements.

pH management

Most weathered soils in humid regions act as weak acid systems where the total acidity is much greater than the active acidity and therefore the potential acidity is great. Soil systems become more acidic as H^+ ions are released into solution through the dissociation or ionization of acids. Many soil processes can contribute to soil acidity, including the dissolution of CO_2 gas (originating from organic matter decomposition or soil microbial respiration) into water to form carbonic acid (H_2CO_3), clay structure mutations, hydrolysis of Al, acid rain, leaching or weathering of soils, plant uptake of base cations, and oxidation of S. One of the principle farming practices that contributes to soil acidity is the use of ammoniacal fertilizers, such as ammonium nitrate, which produces acidity as ammonium is oxidized during the nitrification process. As a result of the various natural processes and anthropogenic activities that contribute to soil acidity, many soils require the addition of acid-neutralizing materials, generally called 'liming materials,' to increase the pH and optimize plant performance. Liming materials contain an anion that removes H^+ from solution and precipitates Al^{3+} into a solid mineral, thereby reducing acidity. Most liming materials are oxides, hydroxides, carbonates, or silicates of Ca or Mg, or both. The standard liming material is Ca carbonate ($CaCO_3$), found as the mineral calcite, or some mixture of Ca and Mg carbonate ($CaMg(CO_3)_2$; dolomite). Other common materials include burned lime (CaO and MgO), hydrated lime ($Ca(OH)_2$ and $Mg(OH)_2$), and certain byproducts of manufacturing processes. Many manures or biosolids contain appreciable amounts of carbonates and can raise soil pH. The neutralizing power of a potential liming material is expressed by its Ca carbonate equivalent (CCE), which is a normalization of neutralizing power relative to pure calcium carbonate. The higher the CCE, the more potent the liming material is on a

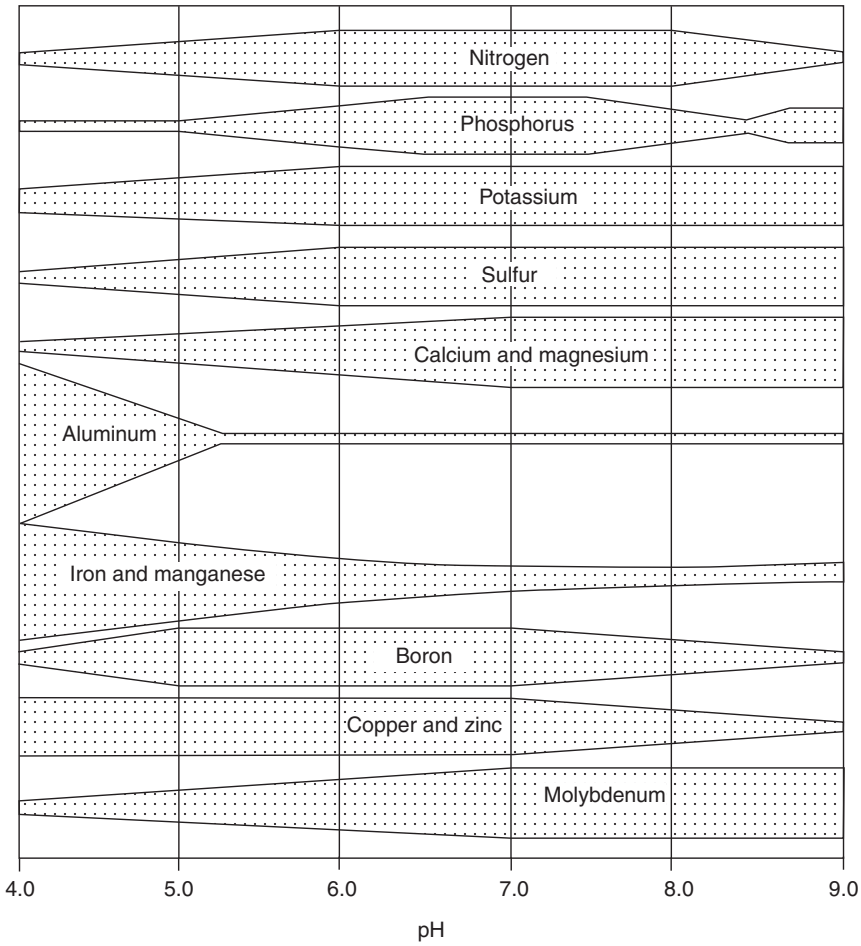


Figure 4 The relative availability of the essential plant nutrients varies with pH. In this classic figure, the width of the bar indicates relative nutrient availability; as bar width increases, the nutrient availability increases as well. Adapted from Truog, E., 1947. Soil reaction influence on availability of plant nutrients. Soil Science Society of American Journal 11, 305–308.

mass basis. Equation [4] presents the generalized lime reaction for calcium carbonate as a two-step process.

Generalized lime reaction using calcium carbonate as the liming material (eqn [4]).

$$\begin{aligned}&\text{Step 1: } CaCO_3 + H_2O \rightarrow Ca^{2+} + HCO_3^- + OH^-\\&\text{Step 2: } OH^- + H^+ \rightarrow H_2O\end{aligned} \quad [4]$$

Lime requirement is defined as the quantity of limestone or other basic material required to raise the pH of the soil to the desired value that is needed on the basis of the intended use of the soil. The amount of liming material applied must be sufficient to not only neutralize the H^+ and Al^{3+} in solution (active acidity) but also neutralize much of the exchangeable and nonexchangeable acidity (or potential acidity). The exchangeable and nonexchangeable acidity is the H^+ and Al^{3+} associated with the solid phase, and the two are distinguished from each other through an operational definition: exchangeable acidity is extractable with a 1 M KCl solution. It is this solid phase H^+ and Al^{3+} bound to soil organic matter and clay minerals that buffers the soil solution. Thus, as the solution acidity is neutralized, the exchangeable acidity pool resupplies the solution with H^+ and Al^{3+}, and then the nonexchangeable pool resupplies the exchangeable pool. Soils that can retain more H^+ and Al^{3+} are more buffered and typically have higher amounts of clay and organic matter. These well-buffered soils require a greater amount of liming material to neutralize acidity, but the soils also remain near neutral for a greater period of time. Conversely, sandy soils with low organic matter require little liming material to neutralize soil acidity but require more frequent liming. Overall, factors that affect lime requirement include initial soil pH, desired soil pH, and soil buffer capacity. Although there are many methods of estimating lime requirement, most soil testing labs utilize some type of calibrated buffer solution, such as the Adams–Evans, Shoemaker–McLean–Pratt (SMP), or Mehlich buffers.

There are some soils that have excessively basic soil pH, and in some instances it is economically feasible to acidify them. This is especially true of high-pH soils that display micronutrient deficiencies; a decrease in pH often alleviates the deficiency. Basic soils are usually treated with elemental sulfur, Fe or Al sulfate, ammonium-containing fertilizers, or sulfuric acid. Although elemental sulfur is often the most economical treatment, it requires microbial activity to be reduced to sulfate, and therefore time, before the pH is decreased. Fe or Al

sulfates or NH_4SO_4 do not decrease pH due to the sulfate, but through the hydrolysis of Fe^{3+} and Al^{3+} that is released from these highly soluble minerals or nitrification of NH_4. Sulfuric acid can be injected into irrigation systems and works very rapidly but requires special handling due to its caustic nature. A general acid-producing reaction from application of Al sulfate is shown in eqn [5], which results in the precipitation of an amorphous Al hydroxide mineral.

Acidifying reaction resulting from the application of aluminum sulfate (eqn [5]).

$$Al_2(SO_4)_3 + 6H_2O \leftrightarrow 2Al(OH)_3 + 6H^+ + 3SO_4^{2-} \quad [5]$$

Nutrient Cycling and Plant Nutritional Roles of Essential Elements

As described in the Section Soil Characteristics Contributing to Nutrient Supply, the macro- and micronutrients are present in varying degrees in soil and their availability is dependent on soil mineralogy and soil chemical and physical characteristics. Understanding how the essential elements cycle in the soil and are utilized by plants is critical to understanding how to manage them to optimize plant performance. Table 2 provides a brief overview of each of the essential elements and their functions in plants. The following sections briefly describe management of each of the essential elements in regard to their plant–soil cycle. In essence, applied soil fertility and plant nutrition revolves around the management of the plant–soil nutrient cycle to provide these nutrients in adequate amounts for optimum plant performance.

Primary Macronutrients

Nitrogen

Nitrogen is present in plant tissue at the highest relative abundance of the essential mineral nutrients that comprise from 1% to 5% of plant dry matter. Plants use N to form amino acids, which are subsequently incorporated into proteins and nucleic acids (DNA and RNA). Nitrogen is also an integral component of chlorophyll, the light-absorbing pigment needed for photosynthesis. Because of the high N requirement of most crops and its mobility in the environment, it is also commonly the most limiting nutrient in both managed and natural ecosystems. As a result, N is typically the nutrient that receives the most attention.

Nitrogen behavior is arguably more dynamic than any of the other essential mineral elements (Figure 5). The ultimate source of most plant-available N is N_2, which comprises 78% of the earth's atmosphere. However, most plants can only utilize NO_3^- or NH_4^+ from the soil solution, referred to as plant-available forms. Conversion of N_2 to plant-available N is called fixation and is a very energy-intensive process as it requires breaking the strong triple bonds of the thermodynamically stable N_2 molecule. Legumes have symbiotic relationships with rhizobia bacteria that can fix N_2 from the soil atmosphere. Biological N_2 fixation (BNF) is catalyzed in the presence of the nitrogenase enzyme produced by these bacteria (eqn [6]). For nonleguminous plants, N sources include N fixed from atmospheric N_2 introduced to the soil system by nonsymbiotic soil microorganisms capable of BNF, atmospheric deposition of N oxides formed either through electrical discharges or through high temperature combustion, and the application of industrially fixed N fertilizers. Natural processes (e.g., lightning and volcanic activity) as well as human activities (e.g., operation of internal combustion engines and industrial fixation of N to make inorganic fertilizer) convert N_2 to NH_3 through thermal fixation, as described in eqn [7].

BNF (eqn [6]).

$$N_2 + 8H^+ + 8e^- + 16ATP \xrightarrow{\text{nitrogenase}} 2NH_3 + H_2 + 16ADP + 16P_i \quad [6]$$

Thermal nitrogen fixation (eqn [7]).

$$N_2 + 3H_2 \rightarrow 2NH_3 \quad [7]$$

The soil N cycle is very complex because it varies greatly, both in space and time, due to the influence of biotic and abiotic transformations. The total N content of the surface 20 cm of mineral soils is generally within the range of 0.05 to 0.5%. Soil N can be generally classified as organic or inorganic. Soil N resides in soil solution, soil organic matter, clay mineral surfaces (typically residing in the interlayer of 2:1 clays), or in the soil atmosphere (although this is typically transitive in nature). Forms of inorganic N include exchangeable NH_4^+, fixed or nonexchangeable NH_4^+, NH_3, NO_3^-, N_2, N_2O, and N oxides. Inorganic N generally represents less than 5% of the total soil N. Organic N forms include amino acids or proteins, amino sugars, and a large pool of unidentified compounds. Organic N is a component of soil organic matter, including microbial biomass and organic residues from plants and animals. The major N transformations that dominate the soil N cycle include N_2 fixation, nitrification, mineralization, biological immobilization, chemical immobilization, deprotonation of NH_4 to NH_3, and denitrification.

The interrelationship and transformation of N between the inorganic and organic pools is the most central aspect of the N cycle and dominates the management of N for crop production. Nitrogen mineralization is the conversion of organic N into inorganic forms, both NH_4^+ and NO_3^-, whereas N immobilization refers to the transformation of inorganic N into organic forms. Typically, N immobilization is used to refer to biological processes, such as assimilation by microorganisms; however, NH_4^+ can also be immobilized by direct adsorption and incorporation into soil organic matter. Furthermore, some microorganisms can directly assimilate NO_3^-; however, this is typically explicitly referred to as NO_3^- assimilation. Mineralization typically involves three steps and results in the production of both NH_4 and NO_3^-. In the first step, aminization, heterotrophic soil organisms decompose complex proteins into simple amines and amino acids (R–NH_2). During the second step, ammonification, the amines and amino acids are further decomposed by other heterotrophs, releasing NH_4 (eqn [8]). Finally, ammonium can be converted to nitrate through nitrification (eqns [9] and [10]). Nitrification itself is a two-step process where obligate autotrophic *Nitrosomonas* bacteria first oxidize NH_4^+ to NO_2^- (eqn [9]) then the obligate autotrophic *Nitrobacter* oxidize NO_2^- to NO_3^- (eqn [10]).

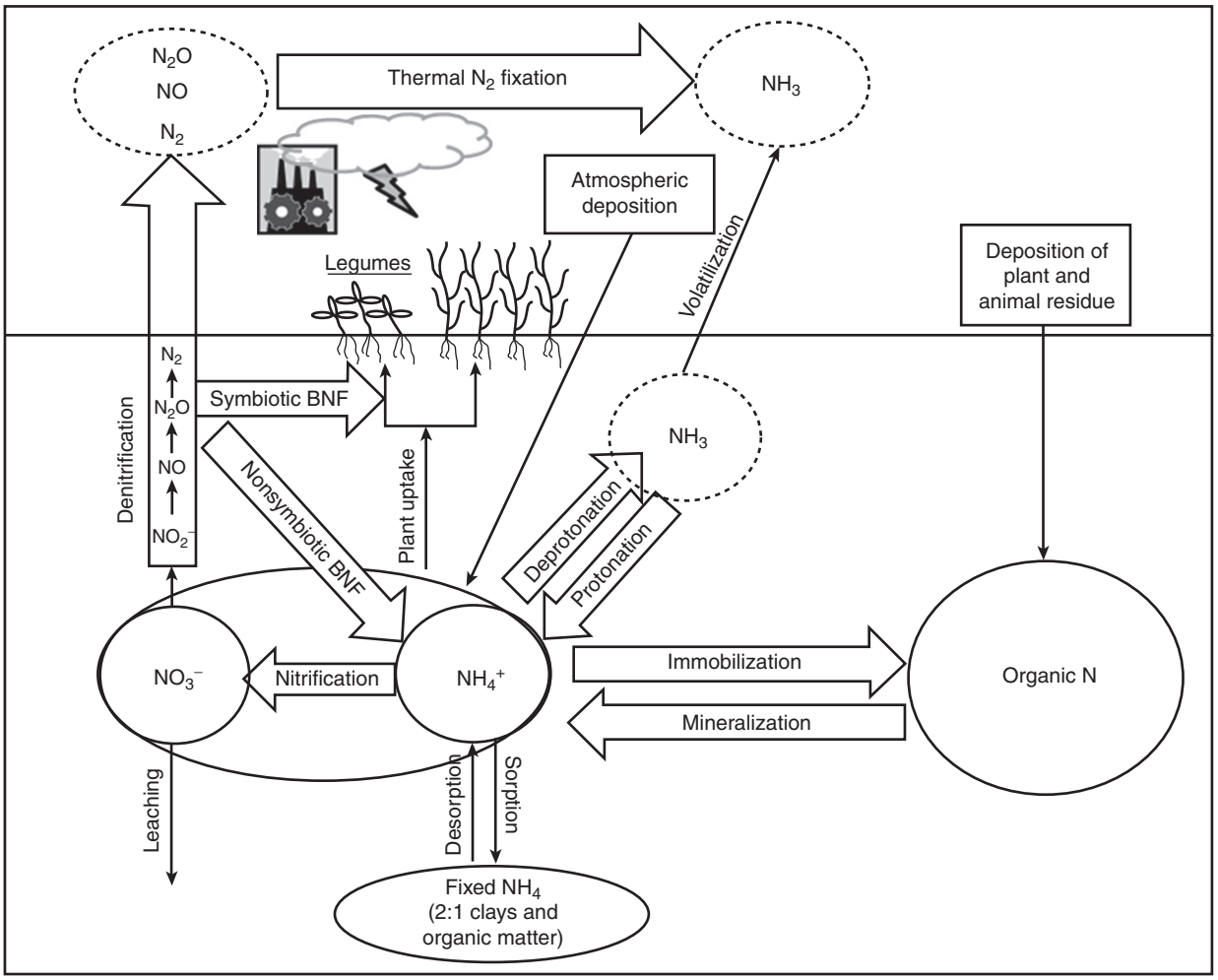


Figure 5 The soil nitrogen cycle, with major transformations (block arrows), pools (ovals), and movement into, out of, and through the soil system identified.

Ammonification (eqn [8]).

$$R-NH_2 + H_2O \rightarrow NH_3 + R-OH + \text{energy} \quad [8]$$

Oxidation of ammonium by *Nitrosomonas* (eqn [9]).

$$2NH_4^+ + 3O_2 \rightarrow 2NO_2^- + 2H_2O + 4H^+ \quad [9]$$

Oxidation of nitrite by *Nitrobacter* (eqn [10]).

$$2NO_2^- + O_2 \rightarrow 2NO_3^- \quad [10]$$

Nitrogen transport and transformation processes are inextricably linked within the soil system because the form of N present is influenced by both, and they determine storage or loss patterns. The loss of N from the soil system has significant implications for both crop production and environmental quality. The vast majority of industrially fixed N applied as fertilizer is as NH_4^+ or forms that release NH_4^+ when applied, such as urea ($CO(NH_2)_2$). Once in the soil, NH_4^+ can be rapidly deprotonated to form NH_3, particularly in neutral or alkaline soils, and lost to the atmosphere through volatilization (eqn [11]). Urea accounts for approximately half of the ammoniacal fertilizer applied. Urea is rapidly converted to NH_4^+ through urea hydrolysis, an enzymatic reaction where urea and water react in the presence of urease to form NH_4^+ and HCO_3^-. When urea fertilizers are surface applied or incorporated into low CEC soils (particularly if incorporated to shallow depths), this reaction often continues to form NH_3 and CO_2. The two ammoniacal forms, NH_4^+ and NH_3, are in equilibrium in the soil and the partitioning between the two is highly dependent on pH.

The deprotonation of ammonium produces ammonia gas that can volatilize to the atmosphere (eqn [11]).

$$NH_4^+ \leftrightarrow NH_3 + H^+;\ pK_a = 9.25 \quad [11]$$

Retention of N in the soil as NH_4^+ is important to crop production as this form provides favorable energy balance to crops in regard to N utilization and because NH_4^+ is held by the soil CEC, it is less susceptible to loss. Nitrification is an important process in the soil N cycle because it is assumed that in most systems the majority of N is lost through NO_3^-

leaching. Nitrate is a poorly held anion, easily transported out of the soil system through leaching or runoff.

Biological denitrification is the reduction of nitrogen oxides under anaerobic conditions. It can be a major N loss pathway from agricultural soils, particularly when they are periodically inundated with water. It is important to the global N cycle because it is the principle pathway by which inorganic N in soil or surface water returns to the atmospheric N pool as N_2, N_2O, or NO, the latter two contributing to greenhouse gases and ozone depletion, respectively.

Nitrogen fertilizer efficiency or N use efficiency are terms generally used to quantify how much of the applied N fertilizer makes it into the target plant or the harvested portion of the crop. There are many ways to calculate N use efficiency (see Section Relevant Websites – Oklahoma State University's NUE website). Nitrogen's mobility in the environment, and specifically the plant–soil system, contributes to low global N use efficiency. For example, Raun and Johnson (1999) estimated N use efficiency in global cereal production at approximately 33% in 1996. One of the most critical steps to increase N use efficiency is determining the correct amount of N required to optimize crop performance. Nitrogen's mobility makes predicting the correct amount of N needed for optimum plant performance very difficult. Most recommendation systems rely on a mass balance approach, as detailed by Stanford (1973). Fundamentally, the mass balance approach accounts for the N requirement of the crop, the amount of N supplied by the soil through mineralization of organic N or residual mineral N present in soil, externally supplied N (e.g., through precipitation), and N lost through various pathways. The difference between N supplied and N required is then determined to be the amount needed through fertilization. Through repeated plot trials, agronomists have developed region-specific, empirical relationships between applied N rate and yield based on Stanford's equation. Some recommendation systems also included economic factors and may be grouped by soil type, rather than relying on estimated yield alone; however, these recommendations are still based on empirical results from N rate response trials (Sawyer *et al.*, 2006). Regardless of how recommendations are generated, the objective is to maximize return on N fertilizer investment by optimize plant performance and minimizing residual reactive N that can be lost to the environment. Beyond determining the optimum rate, increasing N fertilizer use efficiency is also highly dependent on timing of N fertilizer application. Because N is so mobile in the environment, applied N that is not immediately taken up by plants is at constant risk for transport out of the soil system. One way to mitigate this is to time N applications to match the temporal plant uptake patterns as closely as possible. This can be accomplished by splitting the total amount of N fertilizer thought to be required among multiple applications in an attempt to match the timing of plant uptake. Another method to increase N fertilizer efficiency is the use of 'slow-release' fertilizers designed to release N slowly over time, in the hope that plants then take up the N as it is released, minimizing the time that mobile forms of N are in the soil system and at risk for loss to the environment. Similarly, certain formulations of N or chemical treatments of N fertilizers attempt to disrupt N transformations to limit its mobility in the environment. Nitrification and urease inhibitors fall into this category. Finally, N fertilizer efficiency can be manipulated by where the fertilizer is placed. For example, as described above, urea fertilizer can rapidly hydrolyze to form NH_4, which can deprotonate and then volatilize, being lost to the atmosphere as NH_3. However, simply incorporating urea fertilizer below the soil surface can significantly reduce NH_3 gaseous losses. Overall, soil fertility managers must focus on rate, timing, form, and placement of N fertilizer in order to maximize the efficiency of applied fertilizers.

Phosphorus

Phosphorus is essential for all forms of life on the earth. It is typically less abundant in the soil than N or K, with total P concentrations in soil ranging from 50 to 1500 mg kg^{-1}. Likewise, typical total P concentrations in plant tissue are approximately an order of magnitude less than N or K concentrations, averaging 0.2% (dry weight basis; **Table 2**). Phosphorus is involved in almost every metabolic and reproductive process in plants and is most often associated with vigorous growth, development of reproductive parts, and energy transfer. Phosphorus is important in the storage and transfer of energy in plants, as a basic building block of ADP and ATP. Sugar phosphates are an essential structural component of DNA and RNA, which contain the genetic coding responsible for plant growth, development, and metabolism. Phospholipids and phosphoproteins are important structural components of membrane chemistry.

Phosphorus occurs in many forms in the soil. It resides in and moves between three major pools: organic P, inorganic P, and soil solution P as part of the soil P cycle (**Figure 6**). Plants can absorb phosphate from the soil solution as either dihydrogen phosphate ($H_2PO_4^-$) or hydrogen phosphate (HPO_4^{2-}), depending on soil pH. To a more limited extent, plants can also absorb low molecular weight, soluble organic compounds, such as phytin and nucleic acid, from the soil solution; however, these dissolved organic P compounds are considered a negligible source of P for higher order plants. Inorganic P can be found in forms that are readily available, slowly available, or very stable. The degradation of organic compounds to release phosphate or soluble organic P to solution is referred to as mineralization. Solution P can be fixed through adsorption to clay and mineral surfaces or precipitation of secondary minerals. Phosphate can be released to the soil solution from secondary minerals and primary minerals through dissolution and from clay and mineral surfaces through desorption. Easily mineralized organic P, readily desorbable inorganic P, and soluble P are all forms of P readily available for plant uptake and are often referred to as labile P. Generally, organic P that is more recalcitrant and primary or secondary mineral P are considered nonlabile. The quantity–intensity relationship described in the Soil Mineralogy Section and **Figure 3** depicts the relationship between labile P and solution P. As plants remove phosphate from soil solution, labile P replenishes the solution pool. This relationship is highly dependent on soil mineralogy and pH.

Soil P differs from N and K in that it can bind somewhat irreversibly to variable-charge minerals by ligand-exchange (specific sorption) mechanisms. For example, as pH decreases below 6 (**Figure 4**), phosphate has less competition with OH^-

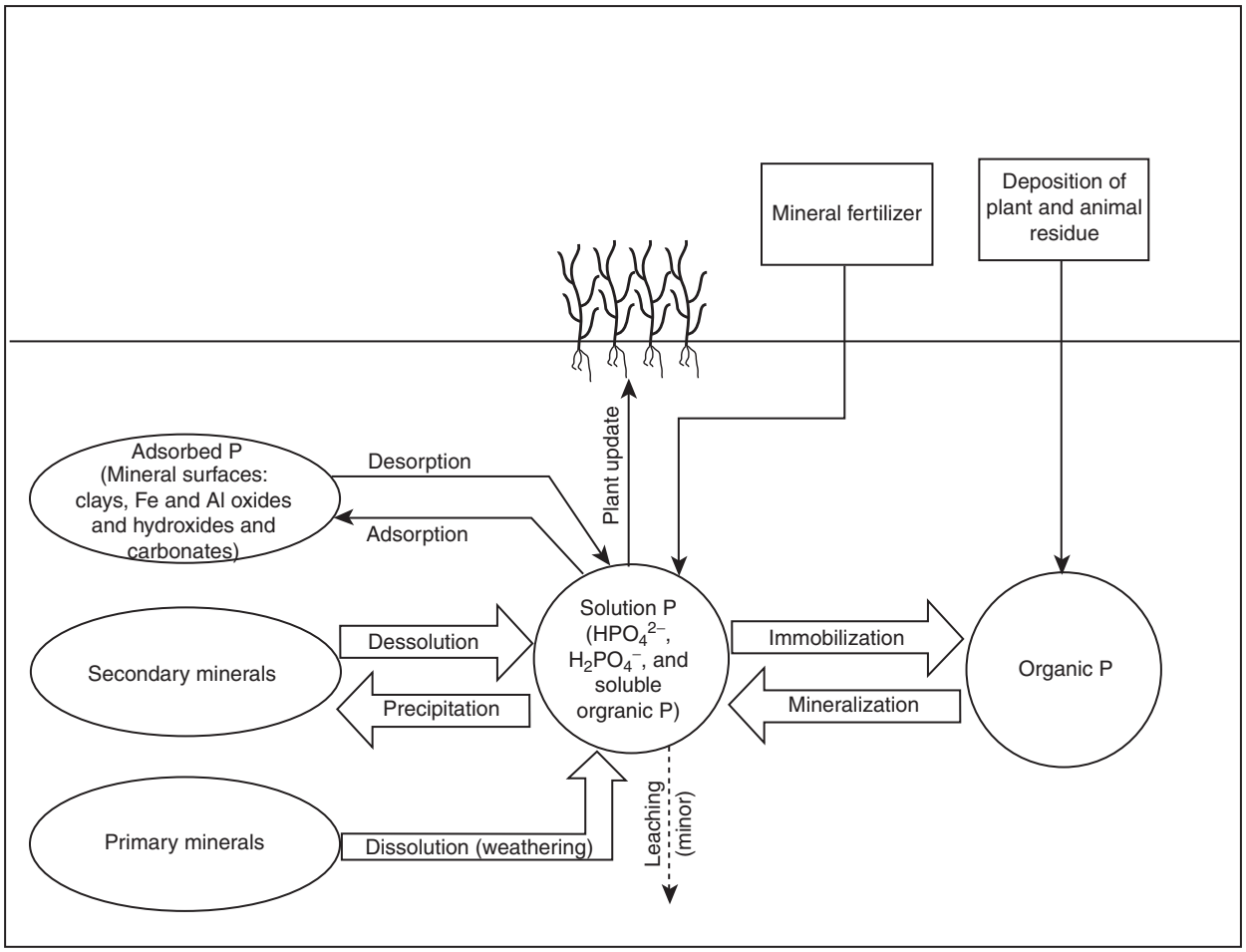


Figure 6 The soil phosphorus cycle, with major transformations (block arrows), pools (ovals), and movement into, out of, and through the soil system identified.

and the mineral surfaces become more positively charged, which together results in a strong ligand-exchange reaction on the surface. The problem is that the phosphate is often held so strongly that it cannot desorb back into solution until the pH appreciably increases. This is most common in Ultisols and Oxisols because they are rich in Fe and Al oxides and hydroxides. Another way in which P availability differs from N and K is that P is extremely susceptible to precipitation reactions with Al, Fe, Mg, and Ca. At pH below 6, P begins to precipitate as a solid Al or Fe phosphate mineral, which is also a common problem in Ultisols and Oxisols. In addition, as pH increases above 7, P begins to precipitate as a solid Mg and Ca phosphate until the pH reaches approximately 8.2 (**Figure 4**). Because of the impact of pH on ligand-exchange and precipitation reactions, optimum P availability is assumed to be approximately pH 6.5.

Organic P accounts for less than 50% of P found in surface soils. Plant material and organic wastes supply organic P to soils. These organic materials are typically deposited on the surface, and as P is not easily transported downward through soil, the largest portion of the organic P pool is contained in the topsoil. Most of the soil organic P occurs as stable, organic compounds not readily available for plant uptake. Nonetheless, mineralization of organic P through microbial activity can provide labile organic P for crop use, albeit at a very slow rate.

Inorganic P in acidic soils not taken up by plants can be fixed or sorbed by iron (Fe) and aluminum (Al) oxides, organic matter, and clay minerals or precipitate as Fe and Al minerals. In alkaline soils, calcium (Ca) phosphates rather than Fe or Al phosphates are the dominant minerals controlling P fixation (Lookman *et al.*, 1996; Van der Zee and van Riemsdijk, 1988). Most inorganic forms of P in the soil are sparingly soluble. Desorption of P from metal oxides, clays, and organic matter or dissolution of Ca, Fe, and Al minerals replenishes soluble P removed by plant uptake or runoff.

Mineralization of organic P and dissolution (or weathering) of stable P minerals are natural processes that provide labile P to crops. However, in soils that have low to medium soil test P values, these processes typically proceed too slowly to supply sufficient available P for plant growth. Therefore, it is often necessary to provide P to crops through fertilization. Organic and inorganic fertilizers are most commonly used to build soil P fertility to the optimum concentrations that can replenish soil solution P for production of crops.

Organic fertilizers, such as manures and biosolids, provide essential nutrients, such as P and N, and add organic matter,

which can improve soil fertility. Best management practices, such as immediate incorporation of manure after application, can reduce the potential for environmental impacts resulting from manure use. When properly managed, manures and other organic P sources can provide nutrients with no more environmental consequences than well-managed commercial fertilizers. However, use of manures as fertilizers can complicate nutrient management because of the unpredictability of organic nutrient mineralization and the fact that many constituents are present inorganic fertilizers at varying and often unknown concentrations.

Inorganic fertilizers can be easier to manage than organic fertilizers. The primary advantages of inorganic fertilizer over organic fertilizer, from an environmental standpoint, are: (1) that the application of a specific nutrient is independent of other nutrients; (2) the P content of inorganic fertilizers is known and uniform, permitting the user to apply the desired amount of P accurately; (3) inorganic fertilizers are homogeneous in composition, produced in granular, pelletized, or liquid forms, allowing more even distribution; and (4) dissolution of inorganic fertilizers is more predictable than organic fertilizers, so that timing and rate of application can be accurately determined. Good management practices, such as band application and fertilizer incorporation, can further enhance fertilizer efficiency. Band application of fertilizer increases the concentration of nutrients near the root zone, improving the plant's ability to utilize the nutrients. Furthermore, incorporating or injecting fertilizers reduces fertilizer loss in runoff and erosion (Baker and Laflen, 1982).

Potassium

Potassium is adsorbed by plants more and is present in plant tissue at higher concentrations than any other essential nutrient except for N (Table 2). It is responsible for water relations and charge balance in plant cells and is highly mobile within the plant. The primary nutrients, N, P, and K, are typically lacking in the soil due to the natural geologic material. However, soils rich in micas (biotite and muscovite), illite, or vermiculite tend to contain naturally adequate levels of K. As the K is bound up as part of the minerals, it requires the influence of the five soil-forming factors to weather the mineral and release K^+ to solution for plants. Older or highly weathered soils or soils in areas with high rainfall are more prone to exhibiting K deficiency due to leaching of K^+. Potassium is one of the base cation nutrients (along with Ca^{2+} and Mg^{2+}) that typically only bind by ion exchange reactions discussed in the Section Ion-exchange reactions (nonspecific sorption). When K^+ is not bound tightly by the aforementioned minerals or located in solution, it can bind to the soil CEC through nonspecific sorption where it can be easily displaced into solution by another cation. Thus, it is found that K^+ availability decreases when the soil pH decreases below 6 because the soil CEC resulting from variable-charge minerals decreases. Another reason for the decrease in K^+ availability in acid soils is because of increased competition from Al^{3+} and H^+ ions. Specifically, Al^{3+} concentrations or, more specifically activity, increase in acidic soils due to the dissolution of Al hydroxide minerals (eqn [12]).

Al hydroxide minerals can dissolve, releasing Al^{3+} to solution, decreasing K^+ activity, which allows K^+ to leach out of the root zone (eqn [12]).

$$Al(OH)_3 + 3H^+ \leftrightarrow Al^{3+} + 3H_2O \quad [12]$$

This reaction occurs for a variety of Al oxide and hydroxide minerals, and the net result is that soil Al tends to buffer the pH at approximately 5.5. The increased concentration of Al^{3+} causes the activity of Al^{3+} to increase and the activity of K^+ to decrease. Thus, the soil CEC and solution becomes dominated with Al^{3+} and K^+ is then able to leach out of the soil along with other base cations.

Soil K resides in five primary pools: organic matter, primary minerals (feldspars and micas), nonexchangeable K^+ (retained in the inner layer of 2:1 minerals), exchangeable K^+ (sorbed on the surface of 2:1 minerals), and soil solution K^+ that is available for plant uptake. Potassium in soil organic matter comes from the deposition of plant and animal materials, which can be quite high in K content. Unlike other nutrients, K is not a structural component of plant tissue; rather it exists as an ion in solution or bound to charges on tissue surfaces. Therefore, decomposition of organic matter can rapidly and directly contribute K^+ to the soil solution pool. The soil solution pool can also be replenished rapidly through desorption of K^+ from 2:1 clay mineral surfaces. Because exchangeable K^+ is in equilibrium with the solution pool, it can be replenished through adsorption from the solution pool. By contrast, nonexchangeable K+ held tightly in the inner layer of 2:1 minerals equilibrates very slowly, releasing K^+ to the exchangeable and solution pools over long periods of time and at not a fast enough rate to supply crop needs. The nonexchangeable pool primarily originates from the weathering of soil minerals or the fixation of exchangeable K^+. Potassium can be lost from the soil system through leaching or plant uptake, adsorbed as K^+.

Secondary Macronutrients

Calcium and magnesium

Calcium and Mg are often found in soil minerals originating from geologic parent material, and therefore their plant availability is usually a function of the solubility of those minerals. Plants require approximately the same amount of Mg as they do P, with Ca requirement approximately double of that (Table 2). Soils rich in Ca- and Mg-containing minerals are often found in arid and semiarid areas or are younger soils formed from recently deposited parent material. The source of Ca and Mg are typically carbonate minerals that dissolve with decreases in pH that occur with normal agricultural activities and rainfall. As a result, it is typically not required to fertilize for Ca and Mg in these soils. However, assuming that Ca and Mg are present in the soil, Figure 4 shows that their availability decreases as the pH drops below 6. This is because Ca and Mg are base cations that are held onto the CEC by ion exchange reactions if they are not precipitated as a solid mineral. Therefore, acid pH allows Al^{3+} to dominate the CEC and solution, thereby decreasing Ca and Mg activity and allowing them to potentially leach. Course-textured soils in humid areas are generally very low in Ca; however, the application of agricultural lime to manage soil acidity in these soils typically provides sufficient Ca and Mg for optimum

plant growth. As soil pH increases above pH 8, Ca and Mg availability decreases as a result of precipitation with carbonates.

The soil cycles for Ca and Mg are very similar to the soil K cycle. Plants adsorb Ca^{2+} and Mg^{2+} from the soil solution, which is in equilibrium with mineral forms of the two elements and exchangeable forms sorbed to clay mineral surfaces. The processes of desorption and adsorption maintain the equilibrium between the soil solution and exchangeable Ca^{2+} and Mg^{2+}. Both Ca^{2+} and Mg^{2+} in solution can precipitate to form secondary minerals, which can dissolve to replace solution Ca or Mg that has leached out or been removed by plant uptake. Organic residues also contain Mg and Ca that can feed the soil solution pool, but the soil cycle is by far dominated by inorganic cycling.

Plants obtain Ca^{2+} and Mg^{2+} from the soil solution through mass flow and root interception. Calcium is a principle component of cell wall structures and important to cell wall permeability. Because of its importance to cell structure, Ca^{2+} is essential for development of terminal buds and shoots and the apical tips of roots and is also involved in the translocation of nutrients and carbohydrates produced through photosynthesis (Tables 1 and 2). As a result, inhibition of new leaf development, root growth, or storage components are common symptoms of Ca deficiency. Even though Ca^{2+} is essential for translocation of elements in the plants, it moves through the xylem and not the phloem; therefore, Ca is considered an immobile nutrient with deficiency appearing in new growth first. Magnesium is a principal component of chlorophyll, a structural component of ribosomes, and is required for phosphate transfer from ATP. Although Mg^{2+} moves through the soil and into the plant in much the same way as Ca^{2+}, it behaves quite differently in the plant. Deficiency symptoms associated with Mg^{2+} appear in older leaves first, as it is mobile within the plant (Table 2). Because of its role in chlorophyll and protein synthesis, Mg^{2+} deficiency appears similar to N deficiency resulting in chlorotic plants, although this symptom typically first appears as interveinal chlorosis and only causing complete chlorosis in cases of extreme deficiency.

Sulfur

Similar to Ca and Mg, S is often found in large quantities in soil depending primarily on parent material and climate. However, S differs from Ca and Mg in that it can exist as an anion (SO_4^{2-}). Sulfate retention on the soil is, therefore, impacted by the abundance of variable-charge minerals that increase the soil's AEC as pH decreases. Sulfur is similar to N in that organic matter is an important pool in most soils. More than 90% of the S present in noncalcareous soils resides in the organic pool. Therefore, cycling of organic S is a key component of the soil S cycle. Like N, the cycling of S by microorganisms is reduced under acidic conditions. Plant-available S is present as adsorbed and solution SO_4^{2-}. Historically, sulfur deficiency has been considered rare due to high sulfur deposition rates from the burning of fossil fuels. The decline in S deposition due to reduced S emissions has increased the incidence of S deficiency, particularly in high-yielding crops grown on deep sandy soils with low organic matter contents or on soils that developed from parent materials low in S. Plants primarily absorb SO_4^{2-} from the soil solution; however, they can also absorb thiosulfate ($S_2O_3^{2-}$) from the soil solution or absorb very small quantities of sulfur dioxide (SO_2) through their leaves. Sulfur is contained in and required for synthesis of amino acids, which are essential in protein formation. Sulfur is also required for the formation of chlorophyll. In legumes S promotes nodulation. Because of its role in chlorophyll and amino acid formation, S deficiency closely resembles N deficiency; however, S is not as mobile as N in the plant and therefore symptoms should be exhibited in younger tissue first.

Concentrations of SO_4-S in the soil solution of most temperate zone soils ranged from 5 to 20 mg SO_4-S per liter, higher than the 3–5 mg SO_4-S per liter required for the optimum growth of most plants. However, recent S deficiencies have been reported globally due to a combination of factors, the primary factor being a marked decrease in S deposition due to air pollution-control measures. Sulfate deposition has clearly decreased over the past 20 years as indicated by the National Atmospheric Deposition Program. For example, the average total wet deposition of sulfate at the Huntington Wildlife Station in Essex County, NY, USA was 22 kg ha^{-1} for the period of 1979–83 and decreased by 43% to 14 kg ha^{-1} for the period of 2003–07(NADP, 2008). This decrease in atmospheric deposition combined with increased crop yields and decreased agronomic S inputs is expected to contribute to increasing S deficiencies in crops (McGrath and Zhao, 1995). These predictions have been supported by recent studies showing increased yield responses to S fertilization in previously nonresponsive soils (Chen *et al.*, 2008).

Micronutrients

The eight essential micronutrient elements are just as important to plant nutrition as the macronutrients; they simply are required in very small, or trace, amounts by plants. The role of each of the essential micronutrient elements in plant nutrition is summarized in Table 1. A deficiency of any of the essential micronutrients results in similar reductions in plant health and vigor as a deficiency of any of the macronutrient elements. Unlike the macronutrients, the range between deficient and toxic levels for many of the micronutrients is generally narrow. Toxic levels of available nutrients may result from over application of fertilizer materials (e.g., B and Mo), or waste residuals such as biosolids (e.g., Cu and Zn). Toxic levels of some micronutrients may also result from soil conditions, such as low pH (e.g., Mn and Fe) or water-logged conditions (e.g., Mn).

Like the macronutrients, micronutrient elements may occur in soil as constituents of primary and secondary minerals or organic matter, adsorbed on mineral and organic matter surfaces, and in soil solution. The importance of any of these solid phases to the supply or buffering of plant-available ionic forms in soil solution depends on the micronutrient and the soil's condition. The ionic form of each of the essential micronutrient elements taken up by plants, summarized in Table 1, provides important information about their behavior in soil. The available forms of Cu, Mn, Fe, Ni, and Zn are metallic cations, whereas B, Mo, and Cl are anions.

As the micronutrients are needed by plants in such small amounts, most soils contain sufficient quantities to satisfy plant needs; however, the amount of available micronutrients in soil solution can be significantly affected by several factors, most notably soil pH (Figure 4). For example, Fe comprises approximately 4% of the earth's crust and is, on average, the fourth most abundant element in soil. It is a constituent of numerous common primary and secondary soil minerals, including olivine, siderite, hematite, goethite, and ferrihydrite. However, the solubility of these common Fe minerals is exceedingly low, resulting in very low concentrations of plant-available Fe^{2+} and Fe^{3+} in soil solution, and deficiencies commonly occur in soils with abundant levels of total Fe, especially where soil pH exceeds 6.5.

Similar to Fe, the other transition metal micronutrients Cu, Mn, Ni, and Zn are extremely sensitive to pH. At high pH all of these metals precipitate as insoluble carbonates and hydroxides. In addition, Cu and Zn are known to bind strongly to variable-charge minerals via chemisorption (specific sorption). For these reasons, Cu, Fe, Mn, Ni, and Zn availability decreases with increasing pH and are commonly deficient above pH 8. However, very acidic soils can have excessive availability to the point of plant toxicity. Molybdenum is the only trace metal micronutrient that becomes more available with an increase in pH above 6 (Figure 4).

There are several other factors or soil properties that govern processes of micronutrient sorption and desorption. These include soil organic matter content, soil texture, CEC, and soil aeration. The influence of soil organic matter, soil texture, and CEC on micronutrient behavior was discussed in the Section Soil Characteristics Contributing to Nutrient Supply. Soil aeration influences metallic micronutrient availability by favoring specific oxidation states of these elements. For example, in water-logged soils the concentration of dissolved oxygen in soil solution is depleted by microbial oxidation of soil organic matter. Under these conditions, the lower valence state, or reduced form, of the metallic micronutrients is favored. In general, the reduced form of the metallic micronutrients is more soluble and available, including Fe, Mn, and Cu.

Another important mechanism responsible for maintaining adequate levels of the metallic micronutrient elements to support plant growth in soil solution is called 'chelation.' Numerous organic molecules in soil can form organometallic complexes with these micronutrients. Chelation protects metallic ions from precipitation and specific sorption and increases micronutrient availability. The chelation of Fe, Cu, Zn, Mn, and Ni increases their concentration in soil solution and movement to plant roots by mass flow or diffusion. There are a number of naturally occurring chelating agents in soil formed from root and microbial exudates, including oxalic and citric acids. A number of synthetic chelates have also been used to enhance micronutrient availability, including ethylenediaminetetraacetic acid (EDTA), ethylenediamine bis (2-hydroxyphenyl)acetic acid (EDDHA), and hydroxy-2-ethylenediaminetriacetic acid (HEEDTA).

Molybdenum is the only trace metal micronutrient that becomes less available with a decrease in pH below 6 (Figure 4). The explanation for this is that Mo exists as an anion in solution (molybdate) that is somewhat susceptible to strong ligand-exchange reactions similar to P. For this reason, it is observed that Mo availability decreases with decreasing pH due to ligand-exchange reactions onto variable-charge minerals.

Like all micronutrients, B is found in geologic materials and organic matter and is typically slowly released via dissolution, desorption, and mineralization. As B often exists as an anion, it is usually bound to the soil AEC of variable-charge minerals. As a result, increases in pH that precipitate Al hydroxide minerals provide a surface for B to sorb onto, thereby decreasing B availability. The range between sufficient and toxic levels of available B is quite narrow, and certain crops are especially sensitive to excessive B, whereas others are more sensitive to B deficiencies. For example, most cereal crops, cotton, and soybean have low tolerance to high levels of available B, whereas most of the Brassicaceae family crops, alfalfa, and apples tend to be more sensitive to B deficiencies.

Among micronutrients, Cl is unique in that it exists primarily in soil solution, with only small quantities in mineral and organic soil fractions. Adsorption of Cl^- to mineral surfaces is negligible; therefore, it is extremely mobile in soils. The principle source of soil Cl is salts in the soil parent material and atmospheric deposition from volcanic emissions or marine aerosols in coastal areas. Chloride is also a principle component of the most common K fertilizer KCl.

Micronutrient fertilizer sources and practices

In most arable soils, adequate levels of available micronutrients can be achieved by managing the soil conditions that influence their supply to plants, such as soil acidity, aeration, and soil organic matter. However, in very coarse textured or highly weathered soils where large quantities of plant biomass are harvested and the supply of micronutrients is low, the soil supply may need to be supplemented through the use of fertilizers in order to optimize crop yield and plant health. As micronutrients are needed in such small quantities and due to their potential toxicity at high levels, very low (e.g., 0.5–5 $kg\,ha^{-1}$) and uniform applications are required. Micronutrient fertilizers are commonly applied to soil by blending with macronutrient fertilizers to improve handling and increase uniformity of application. Micronutrient fertilizers are commonly soluble salts or, in the case of the metallic micronutrients, synthetic chelates. In some cases, foliar applications may be used effectively to apply micronutrients to address a deficiency where soil applications are not convenient or possible (i.e., in-season application to annual crops or perennial fruit crops) or where soil conditions (e.g., high pH) may render soil-applied nutrients unavailable.

Summary

As a discipline, soil fertility and plant nutrition encompasses management of the soil environment to provide the essential nutrients in the required amounts to plants for optimum performance. Essential nutrients are those elements that play a vital role in plant growth, development, reproduction, or metabolic functions. Each nutrient is required at a specific concentration in plant tissue, below which normal plant functions are restricted. Carl Sprengel's theory of the minimum is a foundational principle in soil fertility, stating that if any of the essential nutrients are present below their critical

concentration then that nutrient is limiting, regardless of the amount of other nutrients present. Therefore, soil fertility evaluation to quantify the amount of available essential nutrients present is the basis for any soil fertility and plant nutrition management program. Multiple factors beyond just nutrient concentration in the soil influence the ability of the soil to supply nutrients to the plant and also the ability of the plant to take up and utilize those nutrients. The chemical, biological, and physical soil properties and processes influence plant nutrient utilization as well as other environmental factors such as pest pressure, climate, and crop management practices. Therefore, soil fertility and plant nutrition is an applied science that integrates all of the soil and crop management disciplines to provide optimum nutrient supply to plants for a specific goal (e.g., plant production for food, fiber, energy, or landscape esthetics) while protecting natural resources and environmental quality.

See also: Air: Greenhouse Gases from Agriculture. Edaphic Soil Science, Introduction to. Mineral Nutrition and Suppression of Plant Disease. Precision Agriculture: Irrigation. Soil: Nutrient Cycling. Water: Water Quality and Challenges from Agriculture

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Soil Greenhouse Gas Emissions and Their Mitigation

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Glossary

Carbon sequestration Carbon storage in soil and plants.

Climate forcing The difference between solar energy reaching the earth's surface and energy (both light and heat) radiated back to space. A positive forcing warms the biosphere.

Gas flux The movement of a gas molecule into or out of an ecosystem.

Life cycle assessment A full accounting of the environmental consequences of a product from creation to disposal.

Mitigation Reducing the emission of greenhouse gases to alleviate the severity of climate change harm.

Radiative energy Energy transmitted by electromagnetic waves.

Sources and sinks Places within the biosphere where carbon, nitrous oxide, and other molecules are either released (source) or stored (sink).

Introduction

Greenhouse gases (GHGs) make up a tiny proportion of today's atmosphere but make life on earth possible. In their absence, the light absorbed by the earth's surface and re-emitted as long-wave radiation (heat) would be immediately lost to space. Instead, a substantial fraction of the 161 W m^{-2} absorbed and reemitted by the earth's surface is temporarily held in the atmosphere, warming the biosphere to an inhabitable temperature. In the absence of GHGs the earth's surface would be frozen with an average surface temperature of −18 °C (Ramanathan, 1988).

It thus stands to reason that changes in atmospheric GHG concentrations will lead to changes in the earth's surface temperature, and, although radiative feedbacks make the story more complex, in general this is in fact the case. As GHG concentrations have increased in the atmosphere, the biosphere has correspondingly warmed (IPCC, 2007). Almost all of the recent increase in global surface temperatures can be attributed to increases in GHG concentrations (IPCC, 2007).

In what way has agriculture played a role in GHG changes? Of the six major radiative sources of climate forcing since 1750 (**Figure 1**), agriculture has directly influenced five: carbon dioxide (CO_2), methane (CH_4), nitrous oxide (N_2O), tropospheric ozone (O_3), and black carbon (IPCC, 2001). These sources are together responsible for approximately 80% of contemporary climate forcing, and agricultural activities affect some GHGs more than others. Overall, agriculture is estimated to directly contribute 10–14% of total global anthropogenic GHG emissions annually (Smith *et al.*, 2007; Barker *et al.*, 2007). This includes N_2O emissions from soil (38% of agriculture's direct contribution) and manure (7%), enteric emissions of CH_4 from ruminant animals (32%), and N_2O and CH_4 from biomass burning (12%).

Not included in this estimate are GHGs from land-cover change due to agricultural expansion; the manufacture of agricultural inputs such as fertilizer and pesticides; or post-harvest activities such as processing, transport, refrigeration, and food management. Land-cover change emits both CO_2 and N_2O to the atmosphere, and in total is responsible for another 12–17% of global GHG emissions (Barker *et al.*, 2007; van der Werf *et al.*, 2009). The manufacture of nitrogen fertilizers and pesticides together adds another 0.6–1.5% to agriculture's global GHG footprint (calculated from Vermeulen *et al.*, 2012), and postproduction activities add at a minimum another 3% (Vermeulen *et al.*, 2012). Including these sources brings agriculture's GHG footprint to 26–36% of all anthropogenic GHG emissions.

The purpose of this article is to describe the ways that agricultural soils have contributed to the GHG burden of the atmosphere, and – as importantly – to show how future agricultural management might mitigate the GHG build-up and thereby contribute to climate stabilization.

In the pages that follow are descriptions of agricultural sources and sinks of the major GHGs affected by agriculture and potential mitigation strategies related to soil management. Because agriculture is a systems enterprise in that all of its parts are interconnected, mitigation must also be approached from a systems and not just a soils standpoint. The penultimate section presents the case for a life cycle assessment of entire agricultural systems in the context of a Midwest US

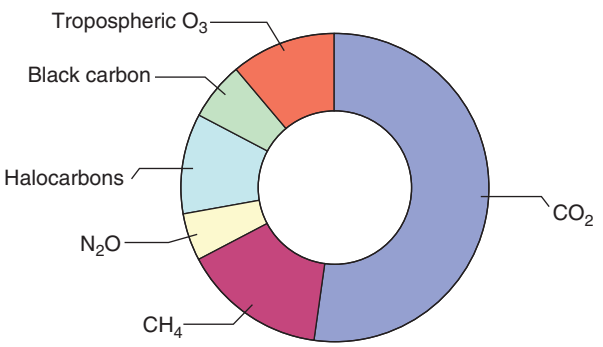


Figure 1 Global sources of atmospheric radiative forcing over the period 1750–2005. Drawn from data in IPCC, 2007. Climate change 2007: The physical science basis. In: Solomon, S., Qin, D., Manning, M., *et al.* (Eds.), Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. New York, NY: Cambridge University Press.

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Table 1 Global warming potentials (GWPs) for the major greenhouse gases affected by agriculture

Greenhouse gas[a]	*Atmospheric lifetime (years)*	*GWP*		
		20 Years	*100 Years*	*500 Years*
Carbon dioxide (CO_2)	Variable	1	1	1
Methane (CH_4)	12	72	25	8
Nitrous oxide (N_2O)	114	289	298	153

[a]Short-lived and heterogeneously distributed gases such as tropospheric ozone and water vapor are too variable to be calculated.
Source: Data extracted from IPCC, 2007. Climate change 2007: The physical science basis. In: Solomon, S., Qin, D., Manning, M., *et al.* (Eds.), Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. New York, NY: Cambridge University Press.

cropping system. Finally, future mitigation is discussed in the context of biofuels and carbon capture and sequestration technologies.

Nitrous Oxide

The significance of N_2O stems not from its atmospheric mass, which is small, but from its high global warming potential (GWP). GWP is a measure of the capacity of a well-mixed gas to trap heat once emitted to the atmosphere (IPCC, 2001). Its value is relative to a reference gas, by convention CO_2, and its magnitude depends on both its efficiency as a GHG and its atmospheric lifetime – long-lived gases will have high GWPs even if their heat trapping efficiency is relatively low. Nitrous oxide has a GWP of approximately 300 over a 100-year time horizon (Table 1), meaning that it traps heat in the atmosphere 300 time more effectively than CO_2. Thus, a kilogram of N_2O emitted to the atmosphere is equivalent to approximately 300 kg of CO_2 emitted at the same time. Conversely, avoiding the emission of 1 kg of N_2O is equivalent to sequestering approximately 300 kg of CO_2.

Sources and Sinks of Nitrous Oxide in Agricultural Soils

Agriculture is responsible for approximately 84% of the global anthropogenic N_2O flux of 8.1 Tg yr^{-1} and approximately 38% of the total global flux (anthropogenic+natural sources) of 17.7 Tg yr^{-1} (**Figure 2(a)**; Mosier *et al.*, 1998a; Robertson, 2004). A small portion (0.5 Tg yr^{-1}) of the N_2O flux is due to biomass burning, primarily in the tropics and subtropics when crop residues are burned and when new land is cleared for row crops and pastures. A larger amount (2.1 Tg yr^{-1}) is associated with microbial activity during animal waste treatment. Nitrification and denitrification, the primary microbial pathways for N_2O production, occur readily in manure and other animal waste products when conditions are right. A still larger source of anthropogenic N_2O is agricultural soils, which emit approximately 4.2 Tg N_2O per year globally or approximately 52% of the total anthropogenic N_2O source. Nitrification and denitrification also occur readily in soils, where their rates are stimulated by the abundant nitrogen that cycles rapidly in virtually all cropped ecosystems.

During nitrification, ammonium (NH_4^+) added as fertilizer or mineralized from soil organic matter, crop residues, or other organic inputs is oxidized by nitrifiers to nitrite (NO_2^-) and eventually to nitrate (NO_3^-) in a series of reactions that can also produce N_2O.

$$\begin{array}{ccccccc} & & N_2O & & N_2O & & \\ & & \uparrow & & \uparrow & & \\ NH_4^+ & \longrightarrow & NH_2OH & \longrightarrow & NO_2^- & \longrightarrow & NO_3^- \end{array} \quad [1]$$

Some N_2O is produced from the chemical decomposition of hydroxylamine (NH_2OH), an intermediate formed during the oxidation of NH_4^+ to NO_2^-. Significantly more N_2O is produced by nitrifiers under low oxygen conditions, when they use NO_2^- as an electron acceptor, a pathway they have in common with denitrifiers (Robertson and Groffman, 2007).

Denitrifiers use NO_3^- and other oxidized forms of nitrogen as an electron acceptor during cellular respiration when oxygen is in limited supply. Nitrous oxide is an intermediate product that can either escape to the atmosphere or be further reduced to N_2 gas by the enzyme N_2O reductase, thereby closing the global nitrogen cycle.

$$\begin{array}{ccccccccc} 2NO_3^- & \longrightarrow & 2NO_2^- & \longrightarrow & 2NO & \longrightarrow & N_2O & \longrightarrow & N_2 \\ & & & & \uparrow & & \uparrow & & \uparrow \end{array} \quad [2]$$

Each transformation step is mediated by a specific inducible enzyme, such that delays in the production of one enzyme can lead to the accumulation and release to the environment of its substrate: N_2O in the case of delays in N_2O reductase formation (Bergsma *et al.*, 2002; Robertson and Groffman, 2007). Theoretically, atmospheric N_2O can also diffuse into cells and be reduced directly to N_2, though in practice this appears to be a negligible global sink for N_2O: rarely are negative soil N_2O fluxes detected.

Soil N_2O fluxes are thus largely controlled by the same environmental factors that control nitrification and denitrification: Soil temperature and moisture as they affect microbial activity in general and the diffusion of oxygen to microsites where nitrification and denitrification occur; soil carbon as it affects the availability of electron donors to heterotrophic denitrifiers as well as the consumption of oxygen in soil microsites; and the availability of soil inorganic nitrogen (NH_4^+ for nitrifiers and NO_3^- for denitrifiers). Soil inorganic nitrogen is derived from the mineralization of soil organic matter and from the addition of synthetic or organic fertilizers and animal manure. Soil structure also plays an important role in N_2O production in that sandy or otherwise poorly structured soils have fewer

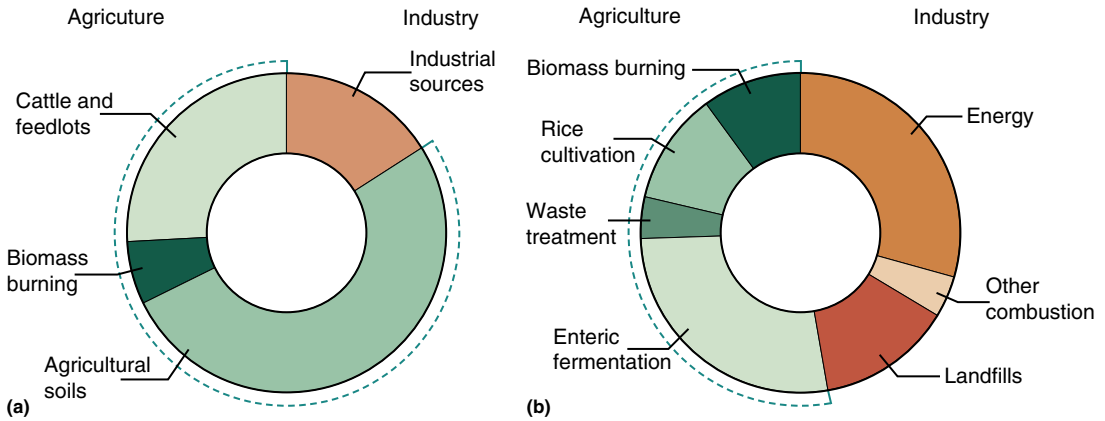


Figure 2 Anthropogenic sources of (a) nitrous oxide and (b) methane. Redrawn from Robertson, G.P., 2004. Abatement of nitrous oxide, methane, and the other non-CO_2 greenhouse gases: The need for a systems approach. In: Field, C.B., Raupach, M.R. (Eds.), The Global Carbon Cycle. Washington, DC: Island Press, pp. 493–506 and based primarily on data in IPCC, 2001. Climate change 2001: The scientific basis. In: Houghton, J.T., Ding, Y., Griggs, D.J., *et al.* (Eds.), Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. New York, NY: Cambridge University Press.

anaerobic microsites than well-structured or heavier soils with higher clay content.

In upland soils, denitrification occurs primarily within soil aggregates (Sexstone *et al.*, 1985) or within soil organic matter particles (Parkin, 1987) where ample carbon fuels oxygen consumption at rates greater than oxygen can be immediately replaced via diffusion from the bulk soil atmosphere. Diffusion of oxygen is substantially inhibited by the water film that surrounds biologically active soil aggregates and particles. Denitrification also occurs in submerged low-oxygen wetland soils, riparian zones, and stream and lake sediments, and insofar as these habitats receive nitrate leached from cropped soils, agriculture is also a major source of N_2O from these environments (Ostrom *et al.*, 2002; Whitmire and Hamilton, 2005; Beaulieu *et al.*, 2011).

It is not surprising, then, that arable soils, managed to cycle carbon and nitrogen rapidly in order to support high crop productivity, produce large quantities of N_2O particularly in mesic or irrigated environments. That for any given cropping system N_2O fluxes are directly related to nitrogen inputs should also come as no surprise: typically fluxes are highest following fertilization (**Figure 3**) or the incorporation of nitrogen-rich residues such as leguminous cover crops into soil. Production of nitrous oxide during these periods can dominate the annual soil flux. Moreover, the rate of nitrogen fertilizer addition is generally the best predictor of N_2O flux in both cropped and pasture systems: On average, approximately 1% of the nitrogen applied to cropland is emitted as N_2O–N (Bouwman *et al.*, 2002) and this emission factor is the basis for the Intergovernmental Panel on Climate Change (IPCC) GHG inventory estimates of N_2O flux from cropped soils (De Klein *et al.*, 2006). Recent evidence suggests that this value will be high for nitrogen fertilizer levels that exceed crop nitrogen needs (McSwiney and Robertson, 2005; Hoben *et al.*, 2011) – in these cases the excess nitrogen available to nitrifiers and denitrifiers will result in still higher N_2O fluxes.

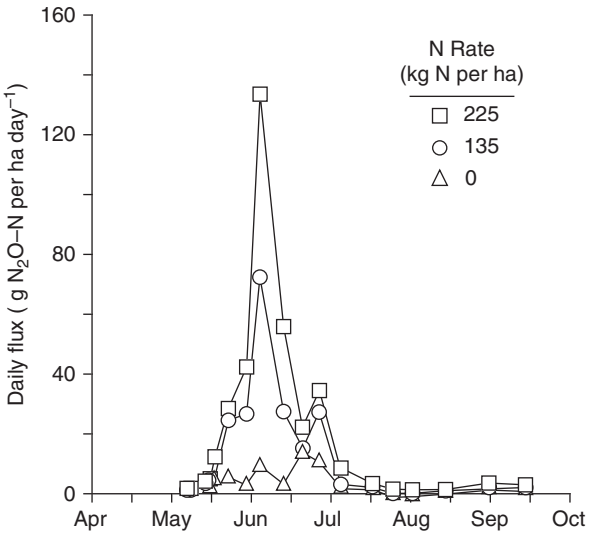


Figure 3 Nitrous oxide (N_2O) flux response to fertilizer addition. Reproduced from Hoben, J.P., Gehl, R.J., Millar, N., Grace, P.R., Robertson, G.P., 2011. Nonlinear nitrous oxide (N_2O) response to nitrogen fertilizer in on-farm corn crops of the US Midwest. Global Change Biology 17, 1140–1152.

Mitigation of Nitrous Oxide in Agricultural Soils

Because there are no significant environmental sinks for N_2O, mitigation is best pursued by avoiding or attenuating known N_2O sources. For agriculture, this means slowing the microbial conversion of inorganic nitrogen (NH_4^+, NO_3^-) to N_2O by altering one or more of the environmental factors that affect the conversion – carbon, oxygen, and soil nitrogen – or by biochemically inhibiting these pathways using soil additives.

Nitrification, for example, can be managed to reduce N_2O production during manure handling by creating an anaerobic environment that suppresses nitrifier metabolism. By storing

manure in anaerobic lagoons, nitrification will be inhibited by the lack of oxygen. Although anaerobic conditions typically promote denitrification, without the nitrate provided by nitrifiers this pathway will be substrate-limited and denitrifiers will produce less N_2O.

In soils, N_2O mitigation is more complex. Nitrification is necessary in order to provide nitrate to plants, and generally occurs very quickly in arable soils (Robertson and Groffman, 2007) whether the source of ammonium is mineralized soil organic matter, manure, or ammonium-based fertilizers such as urea or anhydrous ammonia. In some soils, nitrification can be inhibited with commercial chemical additives such as nitrapyrin and dicyandiamide. These compounds slow ammonium oxidation and thus mitigation is achieved both by reducing nitrifier-derived N_2O and reducing the nitrate supply to denitrifiers. Field experiments suggest that N_2O fluxes can be reduced by inhibitors to 40% in some soils (Akiyama *et al.*, 2010; Halvorson *et al.*, 2010), though very little in others (e.g., Parkin and Hatfield, 2010). In some cases, the reduction may be simply delayed production – nitrification is inhibited, not prevented, such that added ammonium will eventually be nitrified and hence available for N_2O production. But if less fertilizer is applied because plant fertilizer-use efficiency is improved, then the avoided N_2O loss will be permanent. Likewise, theory suggests that urease inhibitors ought also to be effective for reducing N_2O fluxes by slowing the conversion of urea to ammonium, but results of field trials are even more mixed than those for nitrification inhibitors (Akiyama *et al.*, 2010; cf. Halvorson *et al.*, 2010).

A more direct means for N_2O mitigation in agricultural soils is more precise nitrogen fertilizer management (Millar *et al.*, 2010), i.e., reducing the availability of excess inorganic nitrogen to nitrifiers and denitrifiers. Because the best predictor of N_2O fluxes from soils is nitrogen availability, it makes sense that the most effective mitigation strategy is to reduce fertilizer additions to the lowest levels necessary to ensure optimal crop yields. Millar *et al.* (2010) suggested that N_2O fluxes from agricultural soils could be reduced 50% if farmers adopted more conservative fertilizer practices.

How can fertilizers be used more conservatively? Four factors contribute most importantly to fertilizer-use efficiency: fertilizer rate, placement, timing, and formulation. Rates of fertilizer application vary widely across the globe even for the same crop. In China, rates are exceedingly high (Vitousek *et al.*, 2009) and not much based on expected yields. In North America, nitrogen fertilizer rates are typically based on a yield-goal approach wherein a projected yield is multiplied by a standard factor to provide a recommended nitrogen rate, sometimes debited for nitrogen credits provided by a preceding legume crop, manure application, or soil nitrogen tests. However, even this approach is not very conservative. A more robust Maximum Return to Nitrogen (MRTN) approach (Sawyer *et al.*, 2006) is instead based on nitrogen field trails, fertilizer costs, and commodity prices. Recommended rates for a particular region are based on the asymptotic response of that crop to incremental nitrogen additions. Data from hundreds of field trials are used to identify the nitrogen rate at which the cost of further nitrogen fertilizer additions is not paid for by the economic return of additional yield. Though MRTN is now the university-recommended approach for corn in seven Midwest US states, it is not yet widely adopted (Stuart *et al.*, 2012). Quantitative crop models such as Adapt-N (Melkonian *et al.*, 2007) and Maize-N (Setiyono *et al.*, 2011) can provide even more precise nitrogen recommendations based on still more localized climate and soils information.

Fertilizer placement refers to putting nitrogen fertilizer where it is most likely to be taken up by nearby plants or kept from volatilizing to the atmosphere as ammonia (NH_3). Subsurface banding, for example, can achieve higher fertilizer-use efficiencies, as can nitrogen application calibrated to the spatial distribution of crop nitrogen needs across a field. This spatial pattern of nitrogen needs can be estimated from the spatial patterns of prior crop yields across the field – readily provided by yield monitors on modern grain combines. Or nitrogen needs can be estimated in real time during the growing season using spectral sensors that indicate a growing crop's nitrogen stress based on leaf chlorophyll content (Raun *et al.*, 2002; Gehl and Boring, 2011). The optimal placement of fertilizer nitrogen across a cropped field can substantially reduce nitrogen fertilizer rates without affecting crop yields (e.g., Scharf *et al.*, 2005; Mamo *et al.*, 2003).

The timing of nitrogen fertilizer application can also affect nitrogen fertilizer-use efficiency and, by inference, N_2O fluxes. Adding nitrogen closer to the time of plant nitrogen need will leave less nitrogen available in the soil for N_2O production. This can be achieved by avoiding fall fertilization of spring planted crops, by splitting fertilizer applications into smaller portions added more frequently (e.g., some at planting and the remainder after the plants are growing), or by adding fertilizer to irrigation water.

Fertilizer formulation can also affect N_2O fluxes, though the effects are not consistent among the major fertilizer types such as anhydrous ammonia, urea, manure, or urea ammonium nitrate. For this reason, the IPCC GHG inventory methods make no distinctions among fertilizer types (De Klein *et al.*, 2006), nor do other mitigation protocols (Millar *et al.*, 2010, 2012; CAR, 2012). Slow-release formulations, however, are designed to delay the release of nitrogen to the soil solution by coating fertilizer particles with sulfur, polymers, or other temperature- or moisture-sensitive compounds, and to the extent that they can improve fertilizer-use efficiency – and thereby reduce fertilizer rates for the same yield – they ought to reduce N_2O fluxes. There are currently too few successful N_2O field trials to judge their effectiveness.

Mitigation of N_2O through carbon market cap and trade programs has only recently become available with the 2012 approvals of nitrogen management protocols by the major carbon registries. The American Carbon Registry (ACR), Verified Carbon Standard (VCS), and Climate Action Reserve (CAR) have approved methodologies that allow payments to farmers for reducing N_2O emissions by changing fertilizer practices. In one of ACR's methods, the protocol is based on the application of a complex quantitative N_2O model not thoroughly field tested. In other cases (ACR, CAR, and VCS), the method is based on fertilizer rate reductions by whatever means a farmer chooses to use – by more precisely predicting fertilizer need (e.g., using the MRTN rather than yield-goal fertilizer estimators), or the use of precision application technologies, nitrification inhibitors, slow-release formulations, or other strategies that reduce nitrogen fertilizer use without

affecting crop yield. Avoided N_2O emissions are credited using the relationships between nitrogen fertilizer use and N_2O emission noted above – either linear as for the IPCC methodology (De Klein *et al.*, 2006) or nonlinear as for more recent analyses (Millar *et al.*, 2010). Avoided N_2O, determined as the difference between estimated past emissions during a 5-year baseline period and estimated emissions during the credit period, is multiplied by its GWP (298) to provide a saleable CO_2 credit that can then be traded on carbon markets (Millar *et al.*, 2010).

Methane

Globally, agriculture is responsible for approximately 53% of the total anthropogenic CH_4 flux of 344 Tg CH_4 per year (**Figure 2(b)**), itself approximately 58% of the total global CH_4 flux of 598 Tg CH_4 per year (Mosier *et al.*, 1998b; Sass *et al.*, 1999; IPCC, 2001; Robertson, 2004). Agricultural sources of CH_4 include enteric fermentation by anaerobic bacteria within ruminant animals such as cattle and sheep, which accounts for approximately 52% of agricultural emissions; methanogenesis by anaerobic bacteria in submerged soils during rice cultivation (approximately 19% of agricultural emissions); biomass burning when crop residues are burned or land is cleared for agricultural production (approximately 19% of agricultural emissions); and methanogenesis during the handling and treatment of animal wastes (approximately 10%).

Sources and Sinks of Methane in Agricultural Soils

Biological CH_4 production is the result of methanogenesis carried out by methanogens – a class of microbes that inhabit anaerobic environments such as submerged soils and cow rumens and derive their energy from substrates formed during fermentation or from fermentation derivatives (McGill, 2007). In lowland rice, much of the CH_4 produced depends on the plant itself, which provides both photosynthate to methanogens inhabiting the rhizosphere and a pipeline to the atmosphere. While some CH_4 exits rice sediments via ebullition – bubbles formed on the accumulation of sufficient gas that float to the surface – much also exits through the rice plant itself: some portion of the CH_4 produced near its roots passes from sediments through aerenchyma in the rice stem and out open stomata to the atmosphere.

In well-aerated soils everywhere, CH_4 is not produced but rather consumed. Methane consumption is performed by methanotrophs, a class of microbes with the capacity to oxidize CH_4 to CO_2 for energy. In so doing, methanotrophs provide an important ecosystem service: globally, they remove from the atmosphere approximately 30 Tg CH_4 per year. Although it is not a large sink relative to the total global flux of 598 Tg CH_4 per year, it is nevertheless equivalent to the annual loading rate for CH_4 in the atmosphere; without methanotrophs, the atmosphere would be accumulating CH_4 at approximately twice today's rate. Thus, the fact that land conversion to agriculture reduces CH_4 oxidation by 60–90% in most soils (Mosier *et al.*, 1991; Smith *et al.*, 2000) is significant.

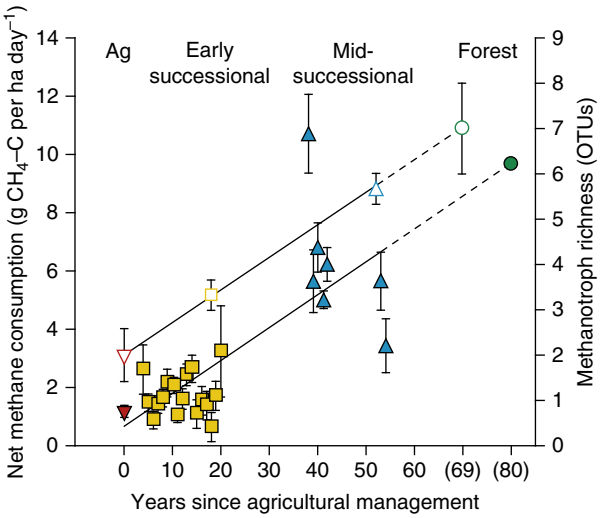


Figure 4 The simultaneous recovery of methanotroph diversity (in operational taxonomic units or OTUs; open symbols) and methane consumption (closed symbols) in ecological succession from row-crop fields (Ag, green) through early (yellow) and mid-successional (blue) fields to mature forest (orange) at a site in southwest Michigan, USA. Reproduced from Levine, U., Teal, T.K., Robertson, G.P., Schmidt, T.M., 2011. Agriculture's impact on microbial diversity and associated fluxes of carbon dioxide and methane. ISME Journal 5, 1683–1691.

Reduced CH_4 oxidation capacity may be related to faster nitrogen cycling in arable soils (Hütsch *et al.*, 1993) – ammonium, either mineralized from crop residues or added as fertilizer, appears to competitively inhibit the enzymes involved in CH_4 oxidation (Gulledge and Schimel, 1998). Agronomic management of the soil environment, such as tillage, appears to have little effect on CH_4 oxidation (Burke *et al.*, 1999; Suwanwaree and Robertson, 2005). Recent results suggest that microbial diversity may also influence the CH_4 oxidation capacity of soils. Levine *et al.* (2011) found a remarkable positive association between CH_4 oxidation and methanotroph diversity along a 100+-year successional gradient (**Figure 4**).

Mitigation of Methane Fluxes in Agricultural Soils

Rice management provides a ready means to attenuate CH_4 production in paddy rice fields. High-yielding varieties tend to have substantially lower CH_4 emissions (Corton *et al.*, 2000; van der Gon *et al.*, 2002) owing to more efficient photosynthate use – higher-yielding plants allocate more fixed carbon to biomass and transmit less to methanotrophs in the rhizosphere.

Residue management and drainage also affects CH_4 fluxes in lowland rice. Encouraging the decomposition of residues before flooding through tillage or composting can substantially diminish CH_4 emissions after flooding (Wassmann *et al.*, 1993). Likewise, drainage for several-day periods during the growing season can also markedly reduce seasonal emissions (Lu *et al.*, 2000) due to accelerated organic matter decomposition as soils become aerated during drainage periods.

Recovering the lost oxidation potential of agricultural soils represents another potential mitigation opportunity. To date,

however, no management practices have been identified that can enhance CH_4 oxidation in cropped soils. Only after abandoning cropland to secondary succession (e.g., Robertson *et al.*, 2000) does soil CH_4 oxidation return, although new insights into the role of microbial community composition (Levine *et al.*, 2011) may eventually provide some new management insights as well.

Reactive Nitrogen Oxides

Oxides of nitrogen, most notably nitric oxide (NO), are also emitted from agricultural systems. Because NO oxidizes quickly in the atmosphere to form NO_2 and other compounds, most fluxes of reactive oxidized N are reported collectively as nitrogen oxides (NO_x), the sum of all such forms. NO_x is not itself radiatively active and is therefore not explicitly a GHG. Nevertheless, emitted NO_x leads to the formation of tropospheric ozone (O_3), which is both a GHG (**Figure 1**) and toxic to crops and humans.

Agriculture is responsible for approximately 25% of the global anthropogenic NO_x flux, which itself represents approximately 80% of the total terrestrial NO_x flux (Galloway *et al.*, 2004). Of the agricultural flux, Galloway *et al.* (2004) estimated that approximately 30% is derived from agricultural soils, with the remainder from the burning of crop residue (27%) and native vegetation as land is cleared for agriculture (44%). Davidson and Kingerlee (1997) estimated that agricultural soils worldwide are responsible for 5.5 Tg of NO_x–N emissions annually, approximately twice the estimate made by Galloway *et al.* (2004). Jaeglé *et al.* (2005) used top-down atmospheric modeling to estimate 2.5–4.5 Tg NO_x–N per year from fertilized agricultural soils.

The role of NO_x in tropospheric photochemistry is substantial: elevated NO_x leads to the oxidation of atmospheric hydrocarbons and carbon monoxide, which leads in turn to O_3 production. Conversely, low NO_x concentrations lead to O_3 consumption (Chameides *et al.*, 1992).

Sources and Sinks of Nitrogen Oxides in Agricultural Soils

Soil-derived NO_x is from NO produced during nitrification and denitrification (Robertson and Groffman, 2007). When hydroxylamine (NH_2OH in eqn [1]) is oxidized to nitrite (NO_2^-) during nitrification, intermediary compounds can result in the formation of NO (as well as N_2O) that then escapes to the atmosphere. In denitrification, NO is formed by the enzyme nitrite reductase (nir) and is either further reduced to nitrous oxide via nitric oxide reductase (nor) or escapes to the atmosphere. Because denitrifier enzymes are induced sequentially, there is often a lag between the production of NO and its subsequent reduction to N_2O in soil, leading to a substantial opportunity for NO escape in environments where denitrification occurs sporadically following wetting events. This is the case in most arable soils, where NO_x fluxes can for short periods equal or exceed N_2O fluxes (e.g., Matson *et al.*, 1998). In general, however, annual global NO_x–N fluxes from cropland soils are approximately half the magnitude of N_2O–N emissions from cropland soils (Stehfest and Bouwman, 2006).

Mitigation of Nitrogen Oxides from Agricultural Soils

Because NO emitted from soils is formed during nitrification and denitrification, NO emissions are affected by the same environmental and management factors discussed earlier for N_2O. These include fertilizer rate, placement, timing, and formulation. There is evidence that some management factors such as no-till may have a different effect for NO than for N_2O (e.g., Liu *et al.*, 2006) but in general effects are consistently similar based on available data.

Carbon Dioxide

By mass, CO_2 is by far the largest source of radiative forcing in the atmosphere, responsible for >50% of the greenhouse warming that has occurred since 1750 (**Figure 1**). Most of this, of course, is from fossil fuel use, but a substantial portion is from the net release of CO_2 from soils when forests and grasslands are first cleared for agriculture. Before 1900, agricultural expansion in North America, Australia, Southern Africa, and Eastern Europe may have released as much as 100 Pg C from soils (Wilson, 1978), contributing as much as 25% of the increase in atmospheric CO_2 at that time (Paustian *et al.*, 1995). Today, approximately 16% of the global CO_2 flux is from deforestation (Canadell *et al.*, 2007), mostly in South America and Southeast Asia.

In well-established croplands, CO_2 emissions are largely confined to the use of fossil fuel during the manufacture and transport of fertilizers, pesticides, and other agrochemicals, as well as from changes in soil organic carbon (SOC) as affected by various management practices.

Sources and Sinks of Carbon Dioxide in Agricultural Soils

Soil carbon in agricultural lands can represent a net sink or source of CO_2 depending on cropping history and contemporary management. As described in Paustian *et al.* (1995), soil carbon stores typically decline 40–60% in the first 40–60 years following conversion to agriculture. The decline happens faster in the humid tropics and is even more abrupt in high-organic matter soils such as drained wetlands, but in general soils reach an equilibrium carbon content that is relatively stable for a given soil type and climate. Deviations from equilibrium values indicate CO_2 uptake from or release to the atmosphere, and occur due to management and climate change.

Net carbon storage in soils results from changes in carbon inputs, changes in decomposition rates, or both. Carbon enters soil primarily as plant residues – aboveground leaves, stems, and other tissues as well as belowground roots and their exudates. The rate at which this material decomposes largely determines whether soil carbon will accumulate: If more organic carbon enters the soil pool than can be readily oxidized by microbes and invertebrates, soil carbon stores will increase and the soil will become a net sink of CO_2. If biomass that enters the soil is readily decomposed, then there will be no net change in carbon stores. If decomposers oxidize soil organic matter faster than it is replaced by new biomass, then carbon stores will decline.

Decomposition is affected both by the quality of organic matter – the degree to which its chemical constituents are

readily metabolized by soil organisms – and the soil microclimate. Biomass with a high carbon:nitrogen ratio such as senesced leaves and stems and biomass with a high lignin content such as corn stalks and wood will decompose relatively slowly. Biomass with low carbon:nitrogen and lignin content such as legume leaves and stems will decompose rapidly.

Likewise, tillage accelerates decomposition by breaking apart soil aggregates that would otherwise delay decomposition of the carbon they contain by restricting the supply of oxygen to microbes within the aggregates (Sexstone *et al.*, 1985). Exposing this otherwise protected carbon to air leads to its rapid oxidation (Six *et al.*, 2000; Grandy and Robertson, 2007). Plowing also leads to higher soil surface temperatures as residue that would normally shade the soil from direct insolation is instead buried, further accelerating decomposition. Thus, management that affects the quantity and quality of organic matter inputs or the microenvironment where decomposition occurs can have profound effects on soil CO_2 emissions. In the absence of erosion, any change in organic soil carbon from year to year represents a net annual flux of soil CO_2.

Erosion presents a special case. Although erosion removes carbon from a particular location, it usually deposits carbon elsewhere in the landscape rather than oxidize it directly to CO_2. Often these locations are in toe-slope positions where the added soil can serve to bury existing carbon and thereby slow its decomposition, or particles can be washed into waterways or surface waters where they can accumulate in anaerobic sediments. Perversely, erosion can result in a carbon sink as decomposition slows in areas of deposition and carbon is replaced on the eroded sites (Harden *et al.*, 2008). Quine and van Oost (2007) estimated a sink capacity of approximately 26% for eroded soil.

Energy inputs and soil amendments can also represent sources of agricultural CO_2. Fossil fuel, usually diesel, is used to power equipment used for tilling, planting, and harvesting and for applying fertilizers, herbicides, and other inputs, and this fuel is emitted as CO_2 on use. Likewise, the fossil fuel used to manufacture herbicides and synthetic fertilizers represents a CO_2 cost of agriculture. As will be seen in the Section Synthesis: System-Wide Global Warming Impact, these costs are small but significant. The CO_2 cost of atrazine, for example, is 2.3 kg CO_2 per kg of active ingredient (750 g l^{-1}) (Gelfand *et al.*, 2013) and the CO_2 cost of nitrogen fertilizer manufacture – which uses CH_4 as a feedstock in addition to using fossil fuel to meet its temperature and pressure requirements – is 4.5 kg CO_2 per kg of N applied (Schlesinger, 1999).

Agricultural lime is another special case. Lime, as crushed limestone ($CaCO_3$) and dolomite ($CaMg(CO_3)_2$), is commonly applied to agricultural land to counteract the acidity caused by nitrogen fertilizers and the removal of base cations in harvested biomass. The carbonate (CO_3^{-2}) in lime weathers to CO_2 or bicarbonate (HCO_3^-) depending on the strength of the weathering agent (Hamilton *et al.*, 2007). If the weathering agent is nitric acid, produced by nitrifying bacteria, then the carbon in lime is dissolved and released to the atmosphere directly, as in the equation:

$$CaCO_3 + 2HNO_3 \rightarrow Ca^{2+} + 2NO_3^- + H_2O + CO_2 \qquad [3]$$

If, however, the weathering agent is the weaker carbonic acid, produced by the dissolution of CO_2 from root and microbial respiration in soil solution, then the lime is transformed to bicarbonate, as in the equation:

$$CaCO_3 + H_2O + CO_2 \rightarrow Ca^{2+} + 2HCO_3^- \qquad [4]$$

Interestingly, the latter reaction consumes an additional mole of CO_2 from the atmosphere for every mole of $CaCO_3$ dissolved. Thus, lime dissolved by strong acid becomes a source of CO_2 whereas lime dissolved by weak acid becomes a CO_2 sink. Current evidence suggests that more lime is dissolved by carbonic than by nitric acid (West and McBride, 2005; Oh and Raymond, 2006; Hamilton *et al.*, 2007), resulting in sequestration equivalent to approximately 33% of the lime's carbon content. This is counterbalanced, however, by emissions from fossil fuel use during the mining and transport of lime (West and Marland, 2002), which is more than sufficient to offset its sequestration potential. Agricultural lime use may thus be largely neutral with respect to CO_2.

The growth of perennial vegetation represents a sink for CO_2 as carbon is captured in growing biomass both above and belowground. And because perennial crops are rarely tilled, CO_2 is also sequestered as SOC, which, because of persistent roots, can build soil carbon at even faster rates than can annual crops managed with no-till practices. For example, successional vegetation on abandoned farmland and perennial grasses planted as part of set-aside programs such as the US Department of Agriculture's Conservation Reserve Program (CRP) can sequester soil carbon at rates twice those of no-till annual crops (Robertson *et al.*, 2000; Gelfand *et al.*, 2011). However, replanting practices can have a major impact on the persistence of this stored carbon. Syswerda *et al.* (2011), for example, found that a large portion of the soil carbon stored by a 12-year-old hybrid poplar plantation was lost during harvest and reestablishment, due apparently to warmer and moister soils during early reestablishment that stimulated decomposition rates. Likewise, converting perennial cropland back to annual cropping – for example, the return of CRP lands to corn-soybean production – can release large amounts of CO_2 (and N_2O) even when conversion involves no-till management (Zenone *et al.*, 2011; Gelfand *et al.*, 2011), but especially when the soil is plowed (Grandy and Robertson, 2006; Ruan and Robertson, 2013).

Mitigation of Soil Carbon Dioxide Fluxes in Agricultural Soils

Mitigation of soil CO_2 fluxes generally involves increasing SOC stores. This can be accomplished by increasing the inputs of biomass carbon to soil, by reducing soil decomposition rates or both (CAST, 2011). Crops that produce abundant residue will sequester more soil carbon than those that do not; corn, for example, will produce 2–3 times more biomass than soybean and, if not harvested, corn residue will contribute more than soybean to building or maintaining SOC. Thus, continuous corn rotations will build soil carbon faster than corn–soybean rotations. Likewise, cover crops can help to build soil carbon by increasing the quantity or biochemical complexity of residue carbon inputs (Syswerda *et al.*, 2011).

The reduction of soil decomposition rates is generally accomplished through tillage management. No-till practices are one of the most widespread and effective ways to sequester soil carbon in most soils. Other forms of conservation tillage – strip tillage and shallow tillage, for example – can provide some of the benefit of no-till, but not as much (CAST, 2011).

However, no-till is not effective at storing soil carbon in all soils, and some have suggested that increased storage in the surface layers of many soils may be offset by lost carbon deeper in the profile (Baker *et al.*, 2007). Others (Kravchenko and Robertson, 2011) have pointed out that a failure to detect whole-profile carbon change with no-till is a consequence of low statistical power rather than the absence of effects, and the fact that most no-till soils show an increased surface soil carbon content is ample evidence for no-till carbon gain. No studies to date have shown statistically significant carbon declines below the A horizon of no-till soils.

Evidence to date suggests that all cropping system soils – unless continuously amended by exogenous inputs such as manure, biochar, or sewage sludge – will equilibrate at some soil carbon content less than that in the native ecosystem that existed before cultivation (Six *et al.*, 2002; Stewart *et al.*, 2007). Quantitative models suggest that this will occur within 60–100 years of management in most temperate region soils.

Evidence also suggests that carbon thus stored is at significant risk of re-release (CAST, 2011). Grandy and Robertson (2006), for example, showed that a substantial fraction of the soil carbon stored in a native never-plowed soil was released after a single plowing, which immediately destabilized soil aggregates to the same degree as in an adjacent field that had been plowed for >100 years. Permanent no-till is by far the preferred mitigation approach (Grandy *et al.*, 2006); although occasional light tillage may permit the persistence of some stored carbon, there is too little evidence to date to judge its effectiveness.

Synthesis: System-Wide Global Warming Impact

The balance of all GHG sources and sinks in a given cropping system for a particular year is termed the net GHG balance or net global warming impact (GWI). The GWI is calculated by summing all GHG fluxes (whether positive or negative) after first converting each to a CO_2-equivalent (CO_2e) basis. For N_2O and CH_4, this is performed by multiplying each by its respective 100 year GWP (Table 1; 298 for N_2O and 25 for CH_4). For N_2O (g CO_2e per ha day^{-1}) the equation is:

$$CO_2e\ (N_2O) = \frac{x_1\ \text{g}\ N_2O\text{–}N}{\text{ha} \times \text{day}} \times \frac{44\ \text{g}\ N_2O}{28\ \text{g}\ N_2O\text{–}N} \times \frac{365\ \text{days}}{1\ \text{year}} \times \frac{1\ \text{ha}}{10^4\ \text{m}^2} \times \frac{298\ \text{g}\ CO_2}{1\ \text{g}\ N_2O} \quad [5]$$

where x_1 is the average daily N_2O emission rate (g N per ha day^{-1}). For CH_4 the equation is similar but the mole ratio 44:28 for N_2O:N becomes 16:12 for CH_4:C and the GWP term for CH_4 (25) substitutes for N_2O's (298).

The energy used for field operations must also be determined, usually by standard tables to calculate annual diesel use, which is then converted into CO_2e.

$$CO_2e\ (\text{diesel}) = \frac{x_1\ \text{l}\ C_{16}H_{34}}{\text{ha} \times \text{year}} \times \frac{832\ \text{g}\ C_{16}H_{34}}{1\ \text{l}\ C_{16}H_{34}} \times \frac{192\ \text{g C}}{226\ \text{g}\ C_{16}H_{34}} \times \frac{44\ \text{g}\ CO_2}{12\ \text{g C}} \times \frac{1\ \text{ha}}{10^4\ \text{m}^2} \quad [6]$$

where x_1 is the average annual diesel use for the field. Likewise, the CO_2e costs of other agronomic inputs such as fertilizer and pesticides must be calculated on the basis of actual use and their embedded CO_2e costs (e.g., Gelfand *et al.*, 2013).

Annual SOC change is calculated as:

$$CO_2e\ (\text{SOC})\ \ \text{g}\ CO_2 \times \text{m}^{-2}\ \text{yr}^{-1} = \frac{(x_1 - x_2)\ \text{kg C}}{\text{m}^2 \times x_3\ \ \text{year}} \times \frac{44\ \text{kg}\ CO_2}{12\ \text{kg C}} \times \frac{10^3\ \text{g}\ CO_2}{1\ \text{kg}\ CO_2} \quad [7]$$

where x_1 is the current soil carbon content of the target system (in kg C per m^2), x_2 is the original soil carbon content, and x_3 is the period of carbon accumulation (the difference in years between current and original).

Once calculated, the overall balance for a given system can be tallied as in Table 2, which shows results of a GWI analysis

Table 2 Global warming impacts (GWIs) for four cropping systems and a field abandoned from agriculture and undergoing ecological succession[a]

Cropping System	*Soil C*	*N_2O*	*CH_4*	*Farming input*							*Net GWI*
				N	*P*	*K*	*Lime*	*Fuel*	*Seeds*	*Pesticides*	
				(g CO_2e per m^2 yr^{-1})							
C–S–W conventional	0 (31)	34 (6)	−0.8 (0.1)	32.7	0.4	1	3	13	7	7	98 (31)
C–S–W no-till	−122 (31)	35 (4)	−0.8 (0.1)	32.7	0.3	1	4	9	7	16	−18 (31)
Alfalfa	−122 (92)	33 (3)	−1.0 (0.1)	0	0.3	4	14	11	6	3	−52 (92)
Hybrid poplar	61 (153)	17 (3)	−0.8 (0.0)	3.3	0	0	0	1	0	2	84 (153)
Successional	−397 (31)	11 (1)	−1.1 (0.1)	0	0	0	0	0	0	0	−383 (31)

[a]GWIs are based on annual greenhouse gas emissions of cropping systems of the Kellogg Biological Station Long-term Ecological Research site in southwest Michigan, USA for the period 1989–2009. Values are means±SE (n=4–6 replicate blocks). C–S–W=corn–soybean–wheat rotation.

Source: Reproduced from Gelfand, I., Sahajpal, R., Zhang, X., *et al.*, 2013. Sustainable bioenergy production from marginal lands in the US Midwest. Nature 493, 514–517.

for five different cropping systems in Southwest Michigan, USA (Gelfand *et al.*, 2013). Here, for example, one can see that for a conventionally managed corn–soybean–wheat rotation the greatest GHG cost over a 20 year period was from N_2O emissions at 34 g CO_2e per m^2 yr^{-1}, followed closely by nitrogen fertilizer manufacture (33 g CO_2e per m^2 yr^{-1}). The cost of fuel, seeds, and pesticides summed to 27 g CO_2e per m^2 yr^{-1}, for a total cost of 98 g CO_2e per m^2 yr^{-1}. The no-till system, otherwise identical but for tillage, in contrast had a net cost of −20 g CO_2e per m^2 yr^{-1} – indicating net mitigation – on account of substantial soil carbon sequestration. Figure 5 provides a graphical illustration of the net balances: in the top part of the figure is the net GWI for each system broken out by component. The bottom graph shows clearly those systems that are net GHG sources versus net GHG mitigators.

Such a comparison has at least two purposes. First, one can identify the practices within each system that contribute the greatest GHG burden (or conversely, the least) and target mitigation efforts toward those practices with the greatest payout. Second, one can use such comparisons as a basis for crediting systems on a GHG market. If the conventional system is considered business as usual, the conversion of this system to another ought to generate carbon credits as the difference between business as usual and the alternative system. Converting to no-till, for example, would generate 118 g CO_2e credits per year on average, whereas retiring the land to successional vegetation would generate 481 CO_2e credits (see Table 2). If the products of these systems were used to generate biofuels, then the respective fossil fuel offset credits could be added in as well (Gelfand *et al.*, 2013) – assuming management changes do not create indirect carbon costs by displacing lost food production to lands newly converted to agriculture elsewhere (Searchinger *et al.*, 2008). This also assumes that net soil carbon gains are permanent.

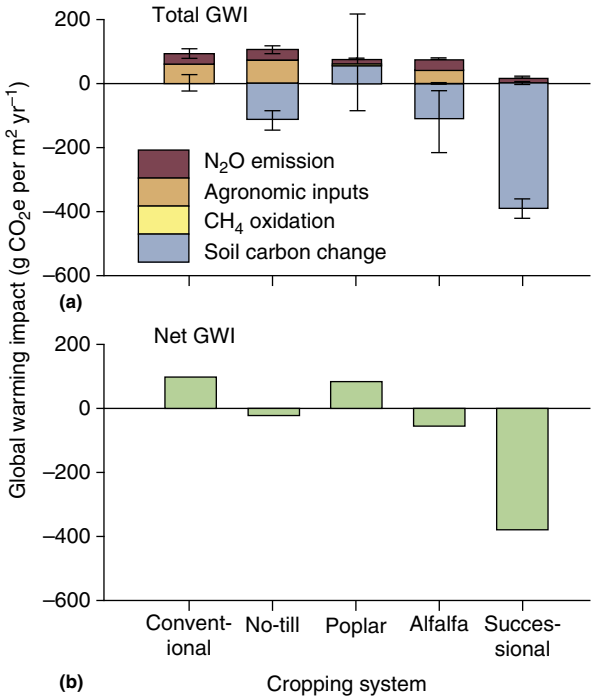


Figure 5 (a) Total and (b) net GWI for four cropping systems and a field abandoned from agriculture and undergoing ecological succession at the W.K. Kellogg Biological Station Long-term Ecological Research site in southwest Michigan, USA for a 20-year period ending in 2009. Conventional and no-till systems are corn-soybean-wheat rotations. Reproduced from Gelfand, I., Sahajpal, R., Zhang, X., *et al.*, 2013. Sustainable bioenergy production from marginal lands in the US Midwest. Nature 493, 514–517.

Not yet included in these analyses is the GWI of changes in NO_x fluxes. This is because of spatial variability in the regional conversion of NO_x to tropospheric ozone and the complexity of ozone's subsequent effect on radiative forcing. The short lifetime of ozone in the atmosphere (hours to days) precludes the calculation of a meaningful GWP for ozone (IPCC, 2007).

This type of systems approach is crucial for fully evaluating the total GHG effects of different agricultural practices. Otherwise it is difficult to know, for example, that the additional herbicides needed for no-till offset the fuel savings or carbon sequestration relative to conventional practices (Table 2). These sorts of trade-offs must be evaluated at the systems level.

Future Mitigation Potentials via Soil Management: Cropping Systems and Biofuels

Our current understanding of agriculture's impact on the atmosphere's GHG burden reveals many opportunities for mitigation, almost none of which have been implemented to date. Designing effective mitigation practices for soil management requires a systems approach because some practices are incompatible with one another and others involve trade offs. The CO_2e costs of each consequence must be evaluated, in turn, to show that no-till management does, indeed, provide a net GWI benefit, i.e., net mitigation (see Figure 5).

The design of future climate-benefiting systems can be best informed by existing whole-system studies (e.g., Robertson *et al.*, 2000; Robertson and Grace, 2004; Mosier *et al.*, 2005, 2006; Adviento-Borbe *et al.*, 2007; Piva *et al.*, 2012; Sainju *et al.*, 2012; Ma *et al.*, 2013). A number of mitigation practices can be implemented to significantly reduce GHG emissions from agricultural soils. Among those most important across most types of annual cropping systems are:

- more precise fertilizer nitrogen management to reduce N_2O emissions;
- permanent no-till management to maximize soil carbon gain and reduce fuel use;
- irrigation management to minimize the need for electricity and fuel to pump water;
- leguminous cover crops to maximize soil carbon gain and reduce the need for synthetic nitrogen fertilizers; and
- diverse rotations that include perennial crops such as alfalfa and high-biomass crops such as corn to build soil carbon and reduce the need for pesticides.

Many of these practices can be combined such that it is possible to not just reduce cropping system GHG costs to nil but to make the system net negative, thereby providing a valuable ecosystem service beyond the farm boundary.

An additional, emerging mitigation opportunity is cellulosic biofuels (Perlack *et al.*, 2005; Robertson *et al.*, 2008). Biofuels made from cellulosic feedstocks – crop residues and purpose-grown lignocellulose biomass – can offset fossil fuel use and thereby provide a climate benefit substantially greater than that of the cropping system itself (NRC, 2009; Gelfand *et al.*, 2013).

The environmental hazards of grain-based biofuels are well known (Crutzen *et al.*, 2008; Donner and Kucharik, 2008; Landis *et al.*, 2008; Robertson *et al.*, 2011) and can be largely avoided by the use of perennial feedstocks that require little soil disturbance after planting but for harvest and perhaps fertilizer applications. Perennial cellulosic feedstocks use little fossil fuel to plant and maintain, require few inputs, and have a correspondingly high energy return on investment (Farrell *et al.*, 2006), which can translate into high climate benefit.

However, the climate benefits of biofuels are conditional. First, the CO_2 captured and used to offset fossil fuel use must be greater than the CO_2e costs of establishment (Fargione *et al.*, 2008), which can create a so-called carbon debt that can take decades to a century or more to repay (Gelfand *et al.*, 2011). Almost all of this debt is related to soil processes. Second, the establishment of a new biofuel crop must not result in the creation of new cropland elsewhere to replace food production that was displaced by the new biofuel crop (Searchinger *et al.*, 2008). Indirect land use change with its associated soil- and vegetation-related GHG costs can discount a substantial fraction of the local crop's CO_2e benefit (Plevin and Kammen, 2013). And third, the CO_2e benefit of the new crop must be discounted by the expected CO_2e benefit of the existing ecosystem (Searchinger *et al.*, 2009). For example, a growing forest sequesters substantial carbon in its soil and biomass. To achieve a climate benefit, the carbon capture of a replacement crop must exceed both the current and future expected rate of carbon capture by the forest vegetation and soil (Field *et al.*, 2008). Soil carbon storage and fluxes of N_2O and CH_4 play a large role in the GHG balance of biofuel cropping systems.

Worth noting overall is that although soil GHG emissions from agriculture can be substantial, and are the single greatest contributors to the GHG footprint of agriculture, emissions can be managed. Purposeful changes to cropping practices and careful consideration of their GHG impacts can substantially reduce and even reverse their climate impacts.

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See also: Climate Change: Agricultural Mitigation. Energy and Greenhouse Gases Footprint of Food Processing. Soil: Carbon Sequestration in Agricultural Systems. Soil: Nutrient Cycling. Soil Fertility and Plant Nutrition

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US Cropland Greenhouse Gas Calculator.
www.v-c-s.org
Verified Carbon Standard.

Soil: Nutrient Cycling

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Glossary

Ammonification Release of ammonium from organic forms of N by soil organisms.
Chemodenitrification Chemical reaction between high concentrations of nitrite at alkaline soil pH which results in losses of gaseous forms of N.
Denitrification Microbe-induced losses of gaseous forms of N from nitrate under low soil concentrations of oxygen.
Eutrophication Low concentrations of oxygen in aquatic environments that result from the decay of dense algal growth induced by an abundant supply of nutrients.
Immobilization Incorporation of nutrients during growth by soil microbes.
Macronutrients Nutrients that are required in large amounts to support plant growth.
Micronutrients Nutrients that are required in very small amounts to support plant growth.
Mineralization Microbe-mediated release of inorganic nutrients from organic matter.
Nitrification Conversion of ammonium to nitrite and nitrate by soil organisms.
Symbioses Mutually beneficial relationships between microorganisms and plants.

Introduction

Nutrients Required by Plants

Some soil nutrients such as nitrogen (N), phosphorus (P), potassium (K), sulfur (S), magnesium (Mg), and calcium (Ca) are key components of organic compounds in plants, such as proteins and nucleic acids, or contribute to the internal control of cellular pH and osmotic potential. These elements are collectively described as macronutrients. Micronutrients such as molybdenum (Mo), iron (Fe), and zinc (Zn) are constituents of enzymes and are thus required by plants in very small amounts. Although the concentrations of macro- and micronutrients detected in plant shoots can vary considerably depending on plant species, plant age and stage of development and the general differences in function between macro- and micronutrients are usually reflected in the average concentrations of mineral nutrients observed in actively growing plants (Table 1).

Table 1 Example of concentrations of mineral nutrients detected in plant shoot dry matter

Element	*Symbol*	*%*	*mg kg^{-1} (ppm)*
Nitrogen	N	1.5	15 000
Potassium	K	1.0	10 000
Calcium	Ca	0.5	5 000
Magnesium	Mg	0.2	2 000
Phosphorus	P	0.2	2 000
Sulfur	S	0.1	1 000
Chloride	Cl	0.01	100
Iron	Fe	0.01	100
Manganese	Mn	0.005	50
Zinc	Zn	0.002	20
Boron	B	0.002	20
Copper	Cu	0.000 6	6
Molybdenum	Mo	0.000 01	0.1

Source: Adapted from information presented by Marschner, H., 1986. Mineral Nutrition of Higher Plants. London: Academic Press.

Sources of Plant Nutrients

Many nutrients present in soil originate from weathering of the parent rock through the action of water, acidity, and frost. Much of the soil N, however, would originally have been derived from biological N_2 fixation (see the N cycle section). However, regardless of their origin, large amounts of nutrients are often present in soil organic matter, which includes both the active (labile) fractions associated with the microbial biomass, or fresh and partially decomposed plant and animal residues having turnover times in the order of months to years, and the more stable forms such as humus, which can take decades to turnover. Approximately 90–95% of the soil N, 40% of the soil P, and 90% of the soil S can be present in soil organic matter, which typically has a carbon (C):N:P:S ratio of 100:8:2:1.4 (Kirkby *et al.*, 2011). In agricultural soils, approximately 2% of the nutrients in soil organic matter are made available to plants each year as a result of microbe-mediated mineralization processes and this provides a significant source of macronutrients such as N and S to satisfy plant requirements. In the case of P, its availability to plants is more commonly controlled by soil chemistry and chemical transformations, although soil organic matter can also be an important source of P for plant uptake in certain circumstances.

The Influence of Water on Nutrient Availability and Uptake

Water is a key factor that influences nutrient availability for plants. Soil water content is an important determinant of microbial activity, which can have either positive or negative implications for the cycling of nutrients and/or in influencing the plant's capacity to capture and utilize nutrients (Table 2). Microbial activity and the release of nutrients tend to be greatest in warm soil when it is near field capacity (i.e., the water content of soil a few days after rain has saturated the soil and free drainage has ceased). As soils dry, microbial activity also declines and nutrient release from organic matter slows.

Table 2 Examples of interactions between soil biology and plants that can affect either availability of nutrients from soil or the capacity of plants to capture or utilize nutrients

Positive	*Negative*
Inputs of N via symbiotic and free-living N_2 fixation.	N losses via denitrification in waterlogged soils.
Microbe-mediated release (mineralization) of nutrients from soil and plant organic matter.	Incorporation (immobilization) of nutrients during growth by the soil microbial biomass.
Phosphate solubilization increasing P availability.	Direct competition with plants for available forms of nutrients.
Mycorrhizal enhancement of P and Zn uptake by plants.	
Plant growth-promoting bacteria and disease-suppressive organisms enhancing plant growth potential.	Deleterious bacteria, root pathogens, and pests impacting on root vigor, plant health, and growth potential.
Biochelation of toxic materials.	Release of phytotoxic metabolites.

At the other extreme, nutrient loss processes generally prevail if soils become waterlogged and air is displaced from soil pore spaces by water so that soil oxygen levels become exceptionally low (Peoples *et al.*, 2009b).

Water is also the medium by which nutrients move through the soil to plant roots. Soluble and abundant nutrients such as N, Ca, Mg, and S are transported to the root surface by mass flow, whereby nutrients move with the water flow as the plant roots absorb water for transpiration. Micronutrients, P, and K, which are often present in low concentrations in soil solution, however, tend to be supplied to plant roots by diffusion as they move from areas of high concentration in soil to areas of low concentration in the plant rhizosphere. Plant nutrients are usually most readily available when the soil is near field capacity. Soil water is held as a film around soil particles; the thickness of this film of water decreases and the water becomes progressively more difficult for plant roots to extract as the soil water content declines under dryland (rainfed) conditions. Consequently, nutrient availability will be lowest when the soil water content approaches permanent wilting point when plant roots can no longer extract water from the soil. As the soil water content diminishes, diffusion path lengths in the thin film of water around soil particles become longer, thus slowing the rate of nutrient supply to roots. Some less-soluble nutrients may precipitate out of the soil solution and become unavailable to plants. However, these minerals will dissolve and become available again as the soil is rewetted. Changes in redox potential under waterlogged conditions can result in toxic levels of Mn accumulating in soil. The reduction of sulfate ($SO4^{-}$) to hydrogen sulfide (H_2S) under prolonged periods of waterlogging also decreases the solubility of Fe, Zn, and other heavy metals, which can result in deficiency symptoms in plants (Marschner, 1986).

Nutrient Cycling

The subsequent discussion on aspects of nutrient cycling will focus on just N and P. The availability of either of these two particular macronutrients frequently constrains plant productivity, but they differ markedly in cycling processes in the soil. The following will describe how N and P is added (inputs) to terrestrial ecosystems and then either cycled through or removed (losses) from the soil–plant–animal continuum.

The Nitrogen Cycle

The N cycle comprises soil, plant, and animal pools that contain relatively small quantities of biologically active N, in comparison with the large pools of relatively inert N in the lithosphere and atmosphere. Despite their small size, these active pools exert a substantial influence on the global biogeochemical N cycle. After C (~40% of plant dry matter) and oxygen (O,~45%), N is the next most abundant element in plants, commonly representing 1–2% of the plant dry weight in grasses and forbs, 2–3% in legumes, and ≤0.5% in woody tissue and ≤2% in leaves of woody perennials. The N concentrations of plant roots have been less intensively investigated than shoots but are typically at the lower end of the range recorded for the above-ground components of the species.

Nitrogen is a key component of plant amino and nucleic acids as well as chlorophyll and provides the basis for the dietary N (protein) of all animals including humans. The total amounts of N taken up by plants are a reflection of ecosystem productivity and N supply. For example, the N uptake by irrigated cereals in highly productive agricultural systems may be as much as 450 kg N ha^{-1} per year, whereas in low rainfall (<300 mm per annum) environments, crop N uptake is generally <100 kg N ha^{-1}. The major food crops grown for human consumption, for example, wheat, maize, and rice require 20, 15, and 12 kg N, respectively, for every Mg (tonne, 10^6 g) of grain harvested. Grain generally represents >50% of the above-ground plant N and equates to the global removal of approximately 31 Tg N (million tonnes; 10^{12} g) from soil each year in these three cereal crops alone (Peoples *et al.*, 2009b). By contrast, most of the N in plant material in pasture and forestry ecosystems eventually returns to the soil surface as litter (in the absence of fire) or via excreta from grazing animals. Although there is considerable information on above-ground fluxes of plant N, there is a paucity of data for N accumulated in roots, and thus it is difficult to accurately quantify total returns of N to soil as plant residues (McNeill and Unkovich, 2007).

Nitrogen cycling occurs via the decomposition of organic matter in soil, which provides available forms of N for plant and microbial uptake. Nitrogen subsequently returns to the soil organic N pool following death or via dung or urine from grazing animals (**Figure 1**). Decomposition of organic matter is mediated by the microbial biomass, which, despite being a very small component within soil organic matter, is a critical

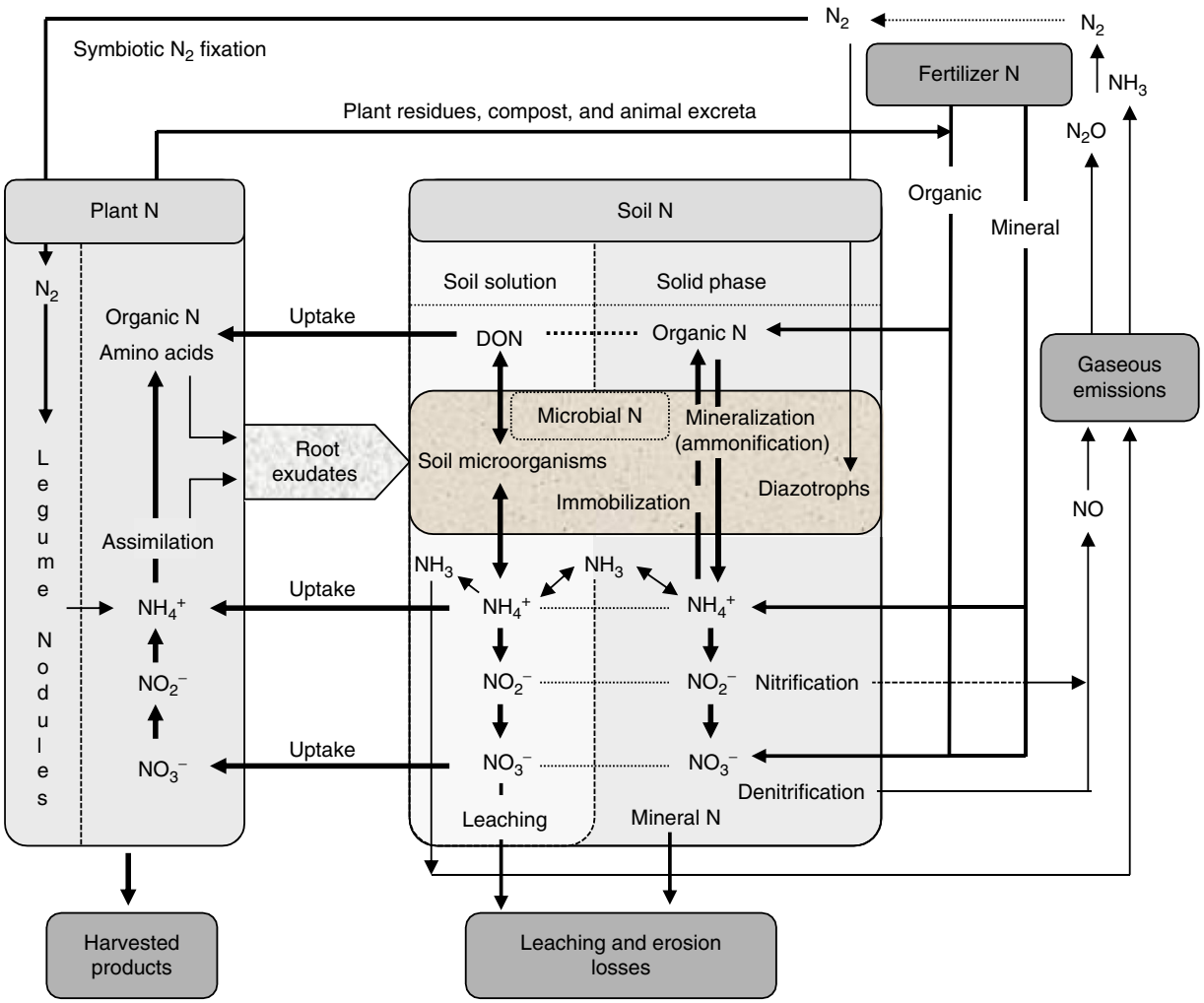


Figure 1 Schematic representation of the soil–plant N cycle showing major pools of N, points of input and output, and major transformation pathways (DON, dissolved organic N).

nutrient pool, with the living microbial biomass providing the enzymes for decomposition of organic matter, whereas the dead microbial biomass represents a labile pool of soil N for mineralization.

Nitrogen inputs

Atmospheric N deposition

Nitrogen inputs through deposition of dust (dry deposition) or in rain (wet deposition) are often overlooked. The relative importance of dust or N contained in rainfall depends on the extent of climatic conditions and atmospheric pollution. Organic N deposition, in the form of amine aerosols, organic nitrates, and particulate N (dust, pollen, and bacteria) in the atmosphere, can make up ~30% of N inputs in some ecosystems. Ammonia (NH_3) released to the atmosphere tends to return to the plant–soil system relatively rapidly either redeposited near the source of emission or, because it is highly water soluble, dissolved in atmospheric water. Nitrous oxides can return to terrestrial ecosystems as nitric acid (HNO3; acid rain), which has serious implications for soil and atmospheric chemistry (Mosier, 2001).

Deposition tends to be greatest adjacent to urban and industrial areas but can be particularly high in areas surrounding livestock production facilities. For example, NH_3 evolved from a cattle feedlot provided the equivalent of 50 kg N ha^{-1} to soils within a few km of the feedlot (Mosier, 2001). The annual contribution of deposited N to cereal crops in the UK has been reported to be in the order of 20–45 kg N ha^{-1}, but elsewhere in the world where inputs of N to the atmosphere from intensive livestock facilities and industry are smaller, and where rainfall and ecosystem productivity are lower, deposition is predominantly as dust and rates are more likely to be <5 kg N ha^{-1} per year (McNeill and Unkovich, 2007). Terrestrial atmospheric N deposition has been estimated to be 20–23 Tg N annually, approximately half of this occurring on agricultural lands, with a further 16 Tg N being deposited in oceans (Mosier, 2001; Smil, 2001).

Biological N_2 fixation

Although dinitrogen gas (N_2) represents almost 80% of the earth's atmosphere, it is not a source of N that is readily available to plants. However, a number of procaryotic

microorganisms utilize the enzyme nitrogenase to reduce atmospheric N_2 to NH_3, which is subsequently converted into amino acids or other forms of N to be used to support their growth. Biological N_2 fixation by some diazotrophs can occur in a free-living state. This includes the photosynthetic cyanobacteria (previously known as blue-green algae) and a number of species of bacteria that rely on decomposition of plant residues as an energy source. Other N_2-fixing microbes require habitats abundant in C and tend to fix N_2 in various associations with plants. The diversity of types of N_2 fixation have arisen from the multiple modes with which bacteria and eukaryotes have coevolved to meet the rather exacting demands of active N_2 fixation. Relationships between prokaryotes and plants range from rather loose associations of free-living heterotrophic bacteria with plant roots or endophytic N_2-fixing bacteria present in the vascular tissues of C_4-photosynthetic pathway graminaceous plants such as sugarcane, to highly evolved symbioses that involve complex morphological differentiation of both microbe and plant in specialized root structures such as nodules. Symbioses between N_2-fixing bacteria and eukaryotes include: (a) Cyanobacteria with fungi in lichens, cycads, and *Gunnera*; (b) Actinomycetes (generally placed in the genus *Frankia*) with a range of angiosperms such as Alders and Casuarinas; and (c) the soil bacteria, rhizobia, with legumes (and a single nonlegume genus *Parasponia*).

There is quantitative evidence that indicates that nonsymbiotic diazotrophs have the potential to provide a useful source of N for agricultural production in some tropical and subtropical environments, but a number of researchers argue that annual inputs of fixed N from such sources are more likely to be <5–10 kg N ha^{-1} in temperate agriculture (Unkovich and Baldock, 2008). Although N_2 fixation by a legume–rhizobia symbiosis in any particular farming system can be greatly influenced by specific management practices and a range of abiotic or biotic stresses, the amounts fixed are generally closely related to legume biomass production. Measures of N_2 fixation for legumes from around the world suggest that N inputs can often be in the order of 100–200 kg shoot-N per year or growing season for both crop and forage legumes (Carlsson and Huss-Danell, 2003; Peoples *et al.*, 2009a).

Although calculations of global inputs of fixed N are subject to gross approximations, estimates suggest that crop legumes such as soybean, peanut, common bean and field peas, and forage legumes such as alfalfa (lucerne) and clovers could all be contributing between 33 and 46 Tg of N each year to agriculture, with the combined contributions from free-living N_2-fixing bacteria and endophytic, associative, and other nonlegume symbiotic relationships providing a further 17–24 Tg N fixed (Herridge *et al.*, 2008).

Fertilizer N

Before the advent of N fertilizers, 25–50% of a farm was typically maintained in a legume-rich pasture or cover crop, and it has been estimated that in some farming systems in the 1950s, as much as 50% of all available N may have originated directly from leguminous food, forage, and green manure crops. However, most farmers around the world progressively replaced legume rotations and organic sources of N fertility with synthetic N fertilizers over the following 3–4 decades, so that by the end of the twentieth century the US agriculture derived almost half of its total N supply from fertilizers and two-thirds of all N in China's food originated from the industrial synthesis of NH_3 by the energy-intensive Haber–Bosch process (Smil, 2001). The rapid adoption of N fertilizers occurred in parallel with the increasing availability of fossil energy, and annual global fertilizer consumption increased from 11 Tg N in 1960 to 80 Tg N in the 1990s and has remained between 80 and 100 Tg N ever since. Urea is the most widely used form of N fertilizer applied in agriculture and represented 67% of total fertilizer N consumed in 2007 (Peoples *et al.*, 2009b). Average rates of N fertilizer applied by farmers vary widely across geographic region and crop and can range from 30 to 250 kg N ha^{-1} (Smil, 2001).

Nitrogen returns via grazing livestock

Grazing animals exert substantial direct influence on N cycling through their return of ingested N in plant material to the soil in highly concentrated patches as urine and dung, thus providing nutrient-rich sites which can have positive and negative influences on subsequent plant growth and other N cycle processes. Indirect effects of grazing on the N cycle can also occur as plants are defoliated, changing their internal N economies and N dynamics in the rhizosphere, as well as impacting on plant community structure. Of the dietary N consumed by domestic livestock, $<30\%$ is retained as live weight gain, milk, or wool, with the remainder being excreted. Annual returns of excreta from grazing animals can represent from 130 to 240 kg N ha^{-1} for steers or sheep grazing clover/grass pastures to 300–450 kg N ha^{-1} for dairy herds on heavily N-fertilized grasslands. Urinary N constitutes between 40% and 80% of the total N excreted and increases with increasing concentrations of N in the diet. Urine is deposited in localized areas of pasture at rates equivalent to 100–500 kg N ha^{-1} and 600–1200 kg N ha^{-1} for sheep and cattle, respectively (Ledgard, 2001).

Nitrogen transformations in soil

The largest N pool in the plant root zone is in the soil organic matter, but this is mostly unavailable to plants. Decomposition of organic matter is a complex process that occurs, to differing extents, with a continuum of organic materials of varying ages, stages of decay, and degrees of recalcitrance that includes newly added plant residues (above and below ground), animal waste products, root exudates, and rhizodeposits as well as various existing or 'native' soil organic matter pools.

The process of microbial decomposition and ammonification of organic N into available inorganic forms commences with the breakdown of organic compounds to provide the soil microbes with a C source for respiration and growth (Fillery, 2001). Much of the simple organic N released is rapidly assimilated (immobilized) by the soil microbial population. Mineral N for uptake by plants becomes available when the amounts of N released from the organic residues exceed the microbial requirement for N for growth (i.e., when ammonification of N exceeds microbial immobilization processes). This is more likely to occur with leguminous material than with the residues of cereals or grasses because legume organic matter has a higher N content and lower C:N ratio.

Field data collected from rainfed systems suggest that peak rates of ammonification of organic matter of approximately 1 kg N ha^{-1} per day can occur in spring or summer when both soil water and temperatures are favorable for microbial activity. Rates of ammonification are considerably reduced in winter due to low temperatures and essentially fall to zero in a dry soil. Ammonification processes are known to be very responsive to rainfall, particularly when a seasonally dry soil is rewet (e.g., Sparling *et al.*, 1995). Collectively, the experimental data indicate that between 0.1 and 0.9 kg N ha^{-1} can be accumulated in the soil profile per millimeter rainfall, depending on the timing and the amount of rainfall, previous cropping history, the relative water-holding capacity of the soil, and its susceptibility to leaching losses. The wide diversity of organisms in soil that use organic C as an energy source minimizes the effect of soil pH on rates of ammonification of organic N.

During the ammonification process, released ammonium (NH_4^+) is typically used as an energy source by two distinct groups of soil organisms. It has been long understood that a small group of bacteria, with the majority belonging to the betaproteobacteria, oxidizes NH_3 to produce nitrite (NO_2^-; Paul and Clark, 1996). The recent discovery that Archaea have the genetic material to produce NH_3 monooxygenase, the enzyme responsible for catalyzing the conversion of NH_3 to NO_2^-, implies that Archaea also nitrify (Schauss *et al.*, 2009). Evidence is accumulating that shows that nitrifying Archaea are widespread in soil and in many soils are numerically more dominant than bacterial nitrifiers. Nitrite N produced by ammonia oxidizers is, in turn, converted into nitrate (NO_3^-) by nitrite-oxidizing bacteria (Paul and Clark, 1996). Both ammonium and nitrate can be used for growth, but plants generally prefer nitrate.

Soil pH through its effect on the concentration of NH_3, the substrate for ammonia oxidizers, has a major effect on the conversion of ammonium to nitrate by nitrifying bacteria, with little activity below pH 4, optimum activity at slightly acidic to neutral pH, and evidence of a decline in activity above pH 8 (Paul and Clark, 1996). In contrast, Archeal nitrifiers appear to be favored over bacterial nitifiers at lower soil pH (O'Sullivan *et al.*, 2011) and at alkaline soil pH (Shen *et al.*, 2008), suggesting that Archaea nitrifiers may be better adapted to extremes in soil pH than bacterial nitrifers. Evidence is mixed as to whether Archaea have a higher affinity for low NH_3, a trait that would enable Archaea to operate more effectively, at least at low soil pH.

Once urea, either applied as fertilizer or excreted in urine by animals, comes in contact with soil, it is rapidly hydrolyzed to CO_2 and NH_3 by the enzyme urease. NH_3, in turn, is oxidized and nitrified to NH_4^+ and NO_3^- as described above. The addition of alkalinity during the hydrolysis of urine and urea fertilizer increases soil pH in the zone of placement with the increase in pH dependent on rate of N application and soil pH buffering capacity. Where alkaline soil pH results, losses of NH_3 can occur from soil zones in contact with urea granules and from urine patches (Thompson and Fillery, 1998).

Plant utilization of nitrogen

Plant roots assimilate available forms of N from the soil either released directly from N fertilizers or arising from N mineralized from (a) soil organic matter, (b) plant residues, or (c) animal urine or feces. Legumes have an added capacity of accessing atmospheric N_2 for growth through symbiotic relationships with soil bacteria (see biological N_2 fixation section).

The soil layers explored by crop roots commonly contain between 5000 and 12 000 kg of soil organic N per hectare. Approximately 2% of this is typically mineralized each year. As the conversion of organic N in plant residues into inorganic N is dependent on microbial activity, only a portion of the N contributed to soil by legumes or other plant material will become available for root uptake in the short term. A number of studies indicate that generally $<30\%$ of the legume N is directly taken up by a subsequent crop (Peoples *et al.*, 2009a). The low recovery of legume N (10–15% on average) is usually much lower than uptake of fertilizer N (30–40% average recovery of the N applied depending on the form of fertilizer used, crop, and farming system; Crews and Peoples, 2005). A notable feature of legume residues is that, although a lower proportion of the legume N is recovered by a subsequent crop than from fertilizer, less legume N tends to be lost through leaching or denitrification than from fertilizer N, so that considerably more legume N remains in the soil system at the end of the growing season (on average, 60% of the applied legume N) compared with fertilizer sources (30%; Crews and Peoples, 2005). After a period of time, the subsequent rate of mineralization of the legume N remaining in soil can be quite slow, so that the legume N that was not mineralized during the first cropping season becomes available only very slowly thereafter for successive crops (usually $<10\%$ per year). Consequently, one of the main contributions of legumes is in the maintenance of the long-term organic fertility of the soil (Fillery, 2001).

The high localized level of N excreted by grazing animals can suppress N_2 fixation by legumes in the immediate vicinity of the urine patch (Ledgard, 2001) but stimulates the growth of surrounding grasses and may provide a small contribution of N to following crops (Thompson and Fillery, 1998).

Factors that contribute to N loss processes

Nitrogen can be lost from soil through wind or water erosion, runoff, leaching of nitrate or dissolved forms of organic N, or via gaseous releases to the atmosphere in (a) the form of NH_3 as the result of volatilization from ammonia-based fertilizers and animal urine patches; (b) nitrous oxide (N_2O) and other nitrogen oxides (NO and NO_2) released during nitrification; and (c) the same nitrogen oxides and N_2 as the result of denitrification (**Figure 1**).

The amount of ammonium N in soil at the interface with the atmosphere, specifically the concentration of NH_3 in soil solution, determines the potential for NH_3 loss. It is accepted that NH_3 loss only occurs from alkaline soil. In the case of urea-based fertilizer, anhydrous NH_3 and animal urine, soil pH increases after N application. The extent of pH change is dependent on the soil pH buffering capacity, which is largely determined by soil texture. Other factors influencing NH_3 loss include soil temperature, soil water content, wind speed, and the presence of a plant canopy. In contrast to other mechanisms of N loss, NH_3 emissions typically occur 7–14 days after fertilizer application or urine deposition. Small rainfall events can increase NH_3 loss from urea-based fertilizers and

urine by increasing the activity of the urease enzyme that mediates hydrolysis. Large rainfall events or irrigation that moves ammonium N into the soil reduces the potential for NH_3 loss (Sommer *et al.*, 2004).

Denitrification occurs when a soil has restricted supply of oxygen which triggers microbial use of nitrate, nitrite, and nitrogen oxides as terminal electron acceptors in place of oxygen. Extensive knowledge of the denitrification process exists, including the diversity of microorganisms that denitrify, the biochemical pathways linked to each step in the reduction chain between nitrate and N_2 gas, substrate kinetics, and soil and environmental factors that impact on rate of denitrification, with most of this information derived from controlled environment studies (see Aulakh *et al.*, 1992 for a review of early literature). The classical view of denitrification is that nitrate is first reduced to nitrite and subsequently to nitric oxide, then to N_2O, and finally to N_2 gas. However, intermediate products of denitrification can react with other N constituents, for example, one atom from NO or N_2O can combine with one atom of another N-containing source, resulting in two molecules of N_2O being produced for every nitrate molecule reduced in a process termed codenitrification (Baggs, 2011). Nitrite in high concentration at alkaline soil pH can react chemically to produce gaseous N compounds in a process termed chemodenitrifcation (Chalk and Smith, 1983). In this case, inhibition of nitrite oxidation, but not NH_3 oxidation during nitrification, results in accumulation of nitrite, as observed after band application of urea or anhydrous NH_3. Percentage water-filled pore space (WFPS) in soil, quantities of readily respirable carbon, soil temperature, and the supply of nitrate are key factors that determine amounts of N that are denitrified.

It has been known for some time that N_2O is released during the process of nitrification. Recent work indicates that betaproteobacteria ammonia oxidizers can also produce N_2O in periods of oxygen limitation in the denitrification process (Baggs, 2011). Percentage WFPS in soil appears to be a key driver as to whether nitrification or denitrification are the key sources of N_2O with denitrification the major contributor at 70% WFPS and nitrification the key source when soil is kept between 35% and 60% WFPS in a silt loam (Bateman and Baggs, 2005).

Managing denitrification in soil and other man-made environments has assumed prominence in recent decades largely to reduce the release of N_2O, NO, and NO_2, which are directly or indirectly linked to global warming (Mosier *et al.*, 2002). However, the proportion released as N_2O is typically small in comparison with the portion released as N_2 gas. This conversion of nitrate into the environmentally harmless N_2 gas represents reduced efficiency of utilization of applied or plant-available N. The need to apply fertilizer N produced in energy-consumptive industries to overcome N deficiencies caused by denitrification impacts on the C-footprint for agriculture, highlighting the need for strategies for minimizing denitrification (Mosier *et al.*, 2002).

Leaching of nitrate is dependent on transport of water through soil and the concentration of nitrate in soil solution and typically occurs when water inputs into the soil system exceed short-term evapotranspiration demands (Fillery, 1999). Leaching of nitrate is more prevalent in sandy-textured soils that have higher hydraulic conductivity than in loams or clays. Strategies for reducing nitrate leaching are discussed in detail by Meisinger and Degado (2002).

Table 3 provides a summary of the complexity of factors involved in these various N loss processes. The influencing factors can be divided into environmental variables, which are largely uncontrollable, and the impacts of human activity where there is some ability to manage losses. The relative importance of the different loss processes will vary considerably across different regions based on climate, soils, dominant land use, and the amount and source of N applied (Peoples *et al.*, 2009b). One of the main factors that influence both the efficiency of N use and the extent of N losses is the degree to which the rates of supply of mineral N match rates of plant N requirements. This will be true regardless of whether the mineral N originated from fertilizer or organic sources. High rates of localized N applications in animal urine patches in pastures are one example where concentrations of mineral N are more likely to exceed plant need and to result in volatile or leaching losses of N. Indeed, it has been calculated that almost 75% of the NH_3 emitted from Western Europe might be derived from livestock compared with just 12% from fertilizer applications (Mosier, 2001).

It is when N supply (via fertilizer applications or mineralization of plant and soil organic matter) exceeds plant demand for N that there is the potential for mineral N to accumulate in soils and there is a risk of losses of N from the system (**Figure 1**; Crews and Peoples, 2005). Maintaining N in the ammonium form in soil can be a key management strategy to improve efficiency of use of applied N. Nitrification inhibitors have been developed and some marketed as soil amendments to control the process of nitrification. These consistently retard nitrification when tested under controlled environments in laboratories. However, the effectiveness of commercial nitrification inhibitors is less apparent when examined under field conditions for a range of crops (Wolt, 2004). Microbial degradation of nitrification inhibitors in soil along with displacement from the zone of fertilizer placement are explanations for the indifferent performance of nitrification inhibitors under field conditions. The uncertain return from investment together with high input cost has discouraged the use of commercial inhibitors in broad-scale agriculture. The recent demonstration that a tropical grass, *Brachiaria humidicol*a, releases compounds from roots that reduce the activity of nitrifying bacteria, the so-called biological nitrification inhibition, offers a less costly approach to managing nitrification if the same function can be introduced into important food crops and pasture species (Fillery, 2007).

The extent of annual global losses of N from soils has been calculated to be 20 Tg N via erosion and 17 Tg N in leaching (Smil, 2001), 11–31 Tg N as NH_3 from animal excreta and fertilizer, 6–8 Tg N as N_2O, NO, and NO_2, and 14 Tg N as N_2 (Mosier, 2001); however, there are large uncertainties around these estimates. All these different forms for N loss, with the important exception of N_2, either have important implications for human health or contribute to one or more of the many contemporary environmental problems associated with the increased N availability in the biosphere (Peoples *et al.*, 2009b). However, it should be acknowledged that a portion of

Table 3 Summary of key processes and factors influencing N losses from soil

Factors	*Pathway of N loss*			
	Denitrification	*NH_3 volatilization*	*Leaching*	*Runoff/erosion*
Environmental variables				
Soil water content/supply	xxx	–	xxx	xxx
Soil pH	x	xxx	–	–
Topsoil texture	xxx	xx	xxx	xxx
Soil aeration	xxx	–	–	–
Microbial activity	xxx	–	–	–
Available C	xxx	–	–	x
Temperature	xx	xx	–	–
Topography/slope	xx	–	–	xxx
Impact of human activity				
N fertilizer				
Type	xx	xxx	xxx	–
Amount	xxx	xxx	xxx	xxx
Placement	xx	xxx	x	xx
Timing	xx	xx	xx	xx
Legume species	x	–	xxx	xx
Legume residues				
Quality	xx	x	xxx	xx
Amount	xxx	xxx	xxx	xxx
Tillage	xx	x	x	xxx
Soil compaction	xxx	–	x	xxx
Drainage	xxx	x	xxx	xx
Irrigation	xxx	xx	xxx	xxx
Stocking rate	xx	xxx	xxx	xx
Land use change	xxx	xxx	xxx	xxx

Note: Each factor is ranked against each process according to its relative importance in controlling that process. The number of 'x' represents: small (x), medium (xx), high (xxx), little or no (–) importance. These rankings include both positive and negative effects. Available C is not just an environmental variable but is also influenced by human activity.
Source: Modified from Peoples, M.B., Hauggaard-Nielsen, H., Jensen, E.S., 2009b. The potential environmental benefits and risks derived from legumes in rotations. In: Emerich, D. W., Krishnan, H.B. (Eds.), Nitrogen Fixation in Crop Production, Agronomy Monograph, vol. 52. Madison: American Society of Agronomy, Crop Science Society of America, Soil Science Society of America, pp. 349–385.

the volatile losses will be ultimately redeposited on soil to reenter the terrestrial N cycle (Mosier, 2001).

The Phosphorus Cycle

Phosphorus is an essential nutrient for plant growth and cellular function and typically constitutes between 2 and 5 g P kg^{-1} of tissue dry weight in agricultural plants. It is required for the structure and function of nucleic acids, integrity of lipid membranes, and for the maintenance of cellular energy systems. For animals, P is also an important component of teeth and bones. The P concentration of a mature sheep or cow is approximately 7–8 g P kg^{-1} of liveweight; approximately 80% of the P is found in the skeleton and teeth.

Most topsoils contain a large amount of total P (range: 0.2–3 g P kg^{-1} soil; Harrison, 1987) in both organic and inorganic P forms (**Figure 2**). By comparison, annual crop requirements and fertilizer inputs are typically only approximately 10–30 kg P ha^{-1} per year (i.e., approximately equivalent to adding only 8–24 mg of P kg^{-1} soil to the top 10 cm of the soil profile). Crop and pasture plants take up P from soil in the form of orthophosphate (HPO_4^{2-} and $H_2PO_4^{1-}$) via their roots.

Plants are responsive to P supply from soil and adapt their root systems to enable better exploration of soil when P is in low supply. Internally, P is also recycled from older and senescing leaves to functionally active tissues. Herbivores normally obtain their P by consuming plants (omnivores by consuming plants and animals and carnivores by consuming other animals). The supply of P is particularly important for growing animals because they accumulate P in muscle and bones and for lactating animals because they excrete relatively large amounts of P in milk. By contrast, nonlactating, mature animals do not accumulate P and will excrete P in feces and urine in amounts equivalent to the amount they consume. P is often one of the primary nutrient limitations for plant growth on farms and when this is the case, soil P levels can be increased by application of P fertilizers to increase plant production. In agriculture practiced on very low P soils and where fertilizer use is unaffordable or unprofitable, P can also be a primary limitation for animal production. This is more likely to be the case only at particular times of the year because energy and other nutrients are also limiting constraints in these systems. On farms, P is most often returned to soil in both inorganic (orthophosphate) and organic P forms as feces, urine, and as dead or trampled plant material. Phosphorus is also returned as a consequence of animal death. Organic P is hydrolyzed by soil microorganisms, and P entering the soil by this route is ultimately released as orthophosphate, the form that plants can access.

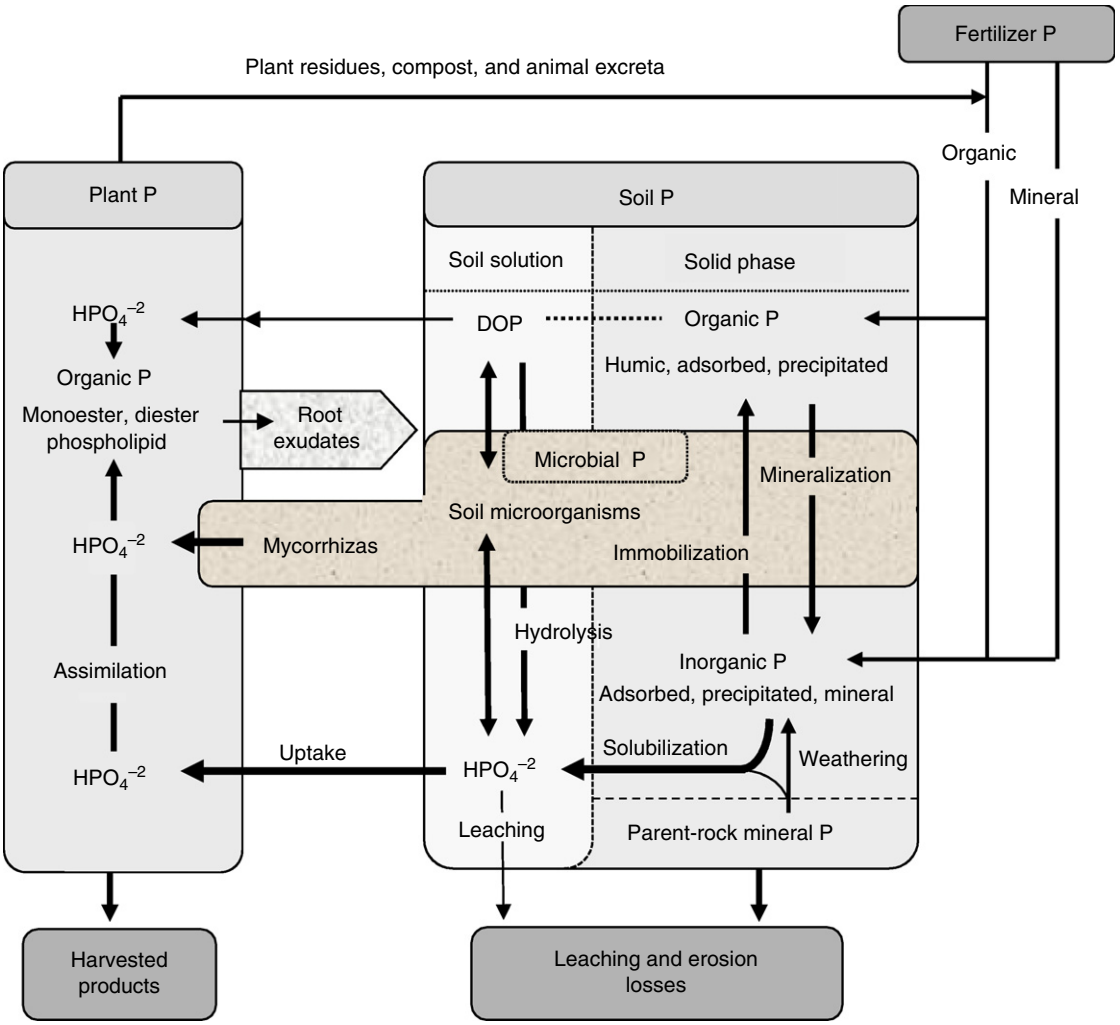


Figure 2 Schematic representation of the soil–plant P cycle showing major pools of P, points of input and output, and major transformation pathways (DOP, dissolved organic P).

Human interventions in the P cycle have significant impacts. Nutrient foraging is often practiced in subsistence and organic-based agriculture. P is collected in the form of waste materials and excreta from animals grazing over large areas and is applied to crops on a smaller area to enhance soil P availability and crop yields. In modern intensive agriculture, excreta combined with fertilizers derived from mined phosphate rocks are used to improve soil P availability and crop yields. A significant proportion of the inorganic and organic P in soil is slowly converted into sparingly available forms of inorganic and organic P, which constitute the majority of the reserve of total P that exist in soils. Relatively small proportions of total soil P are lost continually from the terrestrial landscape to streams and ultimately to the oceans. These losses can be accelerated by poor agricultural practices, and if streams, lakes, and inshore marine environments become enriched with P, eutrophication and algal blooms can occur. Phosphorus in agricultural products is transported to cities and is channeled into effluent. Some of this is recycled in the terrestrial environment and a small component is reused for agriculture, but a substantial proportion is transferred to oceans where it reenters the slowest part of the global P cycle (Cordell *et al.*, 2011). The P entering the oceans accumulates as insoluble sedimentary deposits which are normally only able to reenter the terrestrial P cycle after major geological events that bring submerged rock strata to the surface (timeframe is millions of years).

Unlike soil N, where significant inputs of nutrient occur from atmospheric sources (i.e., biological N_2 fixation and to a small extent by atmospheric deposition), soil P is only replenished by weathering of parent rock materials and through fertilizer applications with relatively small inputs from the atmosphere (usually in the form of windblown dust) (Smil, 2000).

Phosphorus inputs

Although weathering of parent materials is the initial source of P in soil, analyses of soils from chronosequences show that there is a decline in total soil P as soils age after their initial genesis. Systems with young soils may initially have high P content and are N-limited, but they become severely P limited and N enriched (due to biological inputs) over time. Soil genesis is also associated with a shift in the relative

contribution of organic P to total P content, with organic P generally becoming a more predominant component with time (Walker and Syers, 1976; Crews *et al.*, 1995).

Phosphorus fertilizers are used routinely to overcome soil P deficiency and improve agricultural production. Currently, some 18 Tg of P as fertilizer are used annually throughout the world (Cordell and White, 2011), with considerable disparity in usage across continents and within different agricultural systems. P-based fertilizers of inorganic origin are essentially derived from deposits of rock phosphate with some ~15 Tg of P being mined as phosphate rock (~160 Tg of mineral in total) per annum (Van Kauwenbergh, 2010). Crushed phosphate rock may be applied directly to soil as a fertilizer but its effectiveness depends on the P content of the rock, its reactivity with soil and the farming system in which it is being used. More commonly, phosphate rocks are processed to produce soluble, high-analysis fertilizers. The manufacture of phosphate fertilizers dictates that P is usually applied in combination with other mineral nutrients, for example, Ca (when applied as triple superphosphate), Ca and S (as superphosphate), and N (as mono- (MAP) and diammonium phosphate (DAP)). This is used to advantage in agriculture, enabling appropriate mixtures of nutrients in fertilizers to address specific soil and crop requirements. Further treatments of mineral P fertilizers can be used to add other essential nutrients as required (e.g., micronutrients such Mo, Zn, etc.). Organic forms of P fertilizer and organic-based products are also widely used in different farming systems. Organic-based P fertilizers are derived predominantly from animal manures that are used either directly or after composting. This may account for a further 8–17 Tg P applied to agriculture per year (Cordell *et al.*, 2009; Bouwman *et al.*, 2011) Organic P from other recycled forms of animal and plant biomass is also used, along with P collected from industrial waste streams. The forms and amounts of P fertilizer that are used as inputs to farming systems across the world vary considerably and are governed by the specific nutrient requirements of each farming system, socioeconomic issues, access to product, and affordability.

Forms of phosphorus in soil and availability to plants

Phosphorus that is contained in parent rock is not available to plants. Plant-available P occurs as orthophosphate anions in soil solution, which are replenished by exchange with orthophosphate that is adsorbed to soil constituents such as clay minerals or by rapid mineralization of labile forms of organic P. Less available forms of P occur as components of sesquioxides (amorphous oxides of Fe and Al), as poorly soluble or precipitated forms of P (primarily associated with Ca in alkaline soils and with Fe and Al in acidic soils), and as a component of organic matter. Reactions of orthophosphate with soil minerals are complex, time dependent, and are influenced by factors such as the orthophosphate concentration of soil solution, moisture, mineralogy, soil pH, and microbial activity (McLaughlin *et al.*, 2011). Here, the reactions involving plant-available phosphate are distinguished (orthophosphate-adsorption and desorption reactions) from the continuing reactions of phosphate with soil that lead to phosphate accumulations in various forms that are only sparingly available to plants, by referring to the latter as P-sorption reactions. The balance between adsorption/desorption and the rates of P-sorption differ markedly between soils, depending on their chemistry, intrinsic P content, and their history of fertilizer P additions (Barrow *et al.*, 1998). These reactions influence the availability of P to plants, the need or otherwise for P fertilizer, and the efficiency with which P fertilizers are used.

Organic forms of P typically account for between 30% and 80% of the total soil P with higher predominance in grassland soils and native systems as compared with cropping soils. A large proportion (approximately 50%) of the organic P remains poorly identified and exists as high molecular weight material that is associated with the humic fraction of soil organic matter. Identified forms of organic P in soil include monoesters and diesters, with lesser amounts of teichoic acids and phosphonates (Condron *et al.*, 1990). Monoester P occurs predominantly as cation derivatives of inositol hexakisphosphates (mainly as phytate) and its lower order derivatives (typically up to 30%; Turner *et al.*, 2002), whereas sugar phosphates and diester P (e.g., nucleic acids and phospholipids) constitute a smaller (approximately 5%) component. Organic P compounds in soil similarly undergo adsorption (desorption) and precipitation reactions and are associated with soil minerals or as part of the soil organic matter (Anderson, 1980).

Utilization of soil P by plants

Only a small proportion (generally less than 1%) of the large amount of P in a soil is immediately available to plants. Roots take up P as orthophosphate anions from the soil solution that is held as a film around soil particles. However, the concentration of orthophosphate in solution is often very low (typically less than 5 μM; Conyers and Moody, 2009). Phosphate uptake by plant roots readily creates a concentration gradient between the 'bulk' soil and the root surface. Unlike NO_3^-, which is very soluble and can be moved to plant roots by mass flow of soil water, orthophosphate anions are relatively immobile in soil and movement toward the root occurs by diffusion (Barber, 1984). In any particular soil, the rate of P diffusion to the root is determined by the size of the concentration gradient and the ability of the soil to replenish orthophosphate removed from the soil solution. If the rate of supply of orthophosphate to a plant is less than the rate of uptake needed for maximum growth, the soil is defined as P-deficient for plant growth. Under these circumstances in agriculture, the concentration of orthophosphate in soil solution and its concentration-dependent rate of diffusion may be increased by application of fertilizer.

Plants are well adapted to obtain P from soil and use a wide range of mechanisms to increase access to soil P or increase the availability of orthophosphate (Richardson *et al.*, 2009). Characteristics of roots that assist exploration of soil and acquisition of P include: high root mass and rate of root elongation, high specific root length (length per unit root mass), long and dense root hairs that significantly increase root–soil contact, and, in some cases, the development of specialized root structures (e.g., proteoid roots in white lupins). Mobilization of P from soil pools can also be increased by root exudates. For example, acidification of the rhizosphere and release of organic anions may enhance phosphate desorption and increase the solubilization of

precipitated P, and release of phosphatase enzymes potentially increase the hydrolysis (mineralization) of organic P.

Role of microorganisms in soil and biological transformations of P

Microorganisms play a critical role in the transformation of soil P between inorganic and organic P pools and in mediating the availability of P to plants (**Figure 2**). Microorganisms increase P availability though mechanisms that include solubilization and mineralization of orthophosphate from soil inorganic and organic P, direct enhancement of uptake through extending the root system (e.g., mycorrhizal associations; Smith and Read, 2008), and by stimulation of root growth through phytohormones (Richardson *et al.*, 2009). The microbial biomass also contains a substantial pool of immobilized P, which accounts for approximately 2–5% of total soil P (Oberson and Joner, 2005). Although microorganisms readily immobilize P from applied fertilizer and organic residues (McLaughlin *et al.*, 1988), they also release significant quantities of P back to soil solution through turnover as either orthophosphate (and polyphosphates) or organic forms that are readily mineralized (e.g., nucleic acids) and thus potentially available to plants (Seeling and Zasoski, 1993). Turnover of P within the microbial biomass is rapid and can be independent of any net change in the size of the microbial pool (Oberson and Joner, 2005). Higher rates of turnover have been observed in unfertilized soils and in soils amended with organic inputs. The capacity for microorganisms to mobilize P from sparingly available pools of soil P and provide orthophosphate to plants is increased considerably within the rhizosphere where there is a large supply of root-released C (Richardson and Simpson, 2011). However, the relative importance of microbial processes to P mobilization as compared with direct plant mechanisms remains poorly understood.

The role of mycorrhizal fungi and their contribution to the uptake of soil P by agricultural plants is likewise not clear. It is well established that agricultural plants show varying dependency on mycorrhizal infection (i.e., arbuscular mycorrhizas; AM) and the extent of host infection is influenced strongly by plant species, plant P status, and the availability of soil P. In conventional agricultural systems, which operate at high levels of plant-available soil P, the reliance of plants on mycorrhizas for P uptake is, therefore, often reduced. In contrast, in many organically managed (Mäder *et al.*, 2000) and biodynamic farming systems (Ryan *et al.*, 2000), mycorrhizal fungi (both AM and ectomycorrhizas) are considered to play a greater role in the P nutrition of plants, primarily as a function of lower soil P status.

Management of soil P fertility

Despite the large amounts of total P found in soil, plant growth is restricted by P deficiency in many soils throughout the world, with plant growth affected on more than 30% of the world's arable land (Vance *et al.*, 2003). Some agriculture is practiced in P-deficient landscapes. This includes situations where: (a) constraints on achievable yields imposed by other more limiting resources (e.g., extensive, water-limited grazing systems in northern Australia; McIvor *et al.*, 2011) are more substantial than P limitations and make use of P fertilizers uneconomic, (b) socioeconomic circumstances do not allow applications of P fertilizer (e.g., low-input agriculture in some developing economies of Africa; Sánchez, 2010), or (c) 'rule-based' agricultural production philosophies which restrict sources of P that may be used as an input (e.g., 'biodynamic' farm enterprises; Burkitt *et al.*, 2007). These systems typically have low productive capacity and may only require small inputs of P to balance P removal in products (e.g., McIvor *et al.*, 2011). However, 'plant-available' P declines when P inputs are low or absent and net extraction of soil P can occur as a result of P export in products and other losses (e.g., soil erosion; **Table 4**). Depletion of P from low-P soils is not sustainable in the longer term and can ultimately lead to nutrient exhaustion and declining production over time. Examples of this have been observed during colonial agriculture in Australia (Kirkegaard and Hunt, 2010), modern low-input farming (e.g., Burkitt *et al.*, 2007), and in subsistence agriculture in Africa (Sánchez, 2010). For production in a farming system to be sustainable, a minimum requirement is that exported P should be replaced by P inputs.

More commonly, P fertilizers are applied to agricultural crops either when an increase in the level of 'plant-available' P in the soil will deliver higher crop yields or to maintain soil fertility when levels are already adequate for high productivity. Crops are typically fertilized to achieve 'critical' soil P fertility levels, usually defined as the plant-available orthophosphate concentration of the soil that will support near-maximum crop yield (Peverill *et al.*, 1999). Various extractable-P soil tests are used to estimate plant-available P. The 'critical' soil test level for a crop–soil system reflects both the P requirement of the crop species and the P supply characteristics of the soil in which it is growing.

The amount of P that must be applied each year to achieve and then maintain soil fertility includes a component of P to build soil fertility if it is below the required level of plant-available P and another to hold soil fertility at the target level. Because soils vary considerably in their rates of P-sorption and desorption, and in their potential for P losses (erosion, runoff, and/or leaching), the amount of P applied to maintain soil P fertility can sometimes greatly exceed the export of P in products (**Table 4**).

Phosphorus-use efficiency and the P balance of farming systems

Phosphorus inputs are required for agriculture to be both sustainable and productive. In contrast to N, where N_2-fixing legumes provide an alternative to fertilizers, maintenance of soil P fertility is dependent on P inputs from external sources along with efficient recycling of P within the soil–plant–animal system (**Figure 2**). Global P 'reserves' (high-quality phosphate rock deposits) and P 'resources' (phosphate rock deposits of lower quality or harder to access; not currently economic to mine) are extensive (Van Kauwenbergh, 2010). However, the high-quality phosphate rock reserves are effectively a finite resource because lower grade resources will be more costly to extract. Although it has been estimated that the world's known P reserves could supply P for 300–400 years at current rates of use (Van Kauwenbergh, 2010), issues concerning P scarcity, inequitable distribution of available P resources, and the reliability of global supply have been raised in relation to long-term global food security (Cordell and White, 2011). Consequently, there are many reasons why it is

Table 4 Factors that determine the amount of fertilizer P to be applied to a crop or pasture

Factor	*Determinants*
Amount of P required to lift the plant-available P concentration of the soil to the target for soil fertility management	If a soil is below the target soil fertility required to achieve the production goal for the crop, extra P must be applied to increase the plant-available P concentration of the soil to the target level. The amount of P varies depending on the P-sorption capacity of the soil (Burkitt *et al.*, 2001) and will be lower for soils with low P-sorption capacity (e.g., sandy soils or soils where P-sorption sites are nearly saturated as a result of naturally high P fertility or previous fertilizer applications). The soil test target for soil P management may or may not be the 'critical' P level determined for the crop–soil system, but it should not exceed this level as no further increase in production would be achieved.
Amount of P exported in the agricultural product	Examples: *Animal liveweight* – P concentration is approximately 7–8 g kg^{-1} liveweight for a mature cow or sheep (SCA, 1990); thus, if a 50 kg mature sheep is removed from a field that is being grazed continuously and is replaced by a 25 kg weaner sheep, approximately 0.2 kg of P would be exported from the field. *Milk* – Average P concentration of cows' milk varies between approximately 0.9 and 1.4 g kg^{-1}, depending on breed (SCA, 1990); a Friesian cow producing 20 kg milk per day with a P concentration of 0.9 g P kg^{-1} would result in 18 g of P being exported from a dairy farm per cow each day. *Cereal grain* – if P concentration of the grain is 3.5 g kg^{-1} DM, ~3.5 kg of P will be exported per tonne of grain yield.
The amount of P that accumulates annually in the agricultural field	(a) P may be immobilized in soil organic matter fractions that resist degradation (Dalal 1977; Anderson, 1980) (b) Phosphate may accumulate in sparingly available soil pools due to sorption or precipitation reactions of inorganic P (Barrow, 1983; McLaughlin *et al.*, 2011). Soils with high P-sorption capacity will accumulate more phosphate in this way. (c) P may become ineffective for plant growth in grazed fields through uneven dispersal of animal excreta (Williams and Haynes, 1992). Although uneven distribution represents no 'net' change in the amount of P returned to a grazed field, it results in localized area with excessively high P concentrations and increases the amount that must be applied to achieve target soil fertility levels in the rest of the field (Simpson *et al.*, 2011).
Losses due to soil erosion, leaching, and/or in runoff	P losses due to erosion and surface runoff occur because of the close association of P with soil particles (i.e., P adsorbed to clay surfaces, P associated with soil minerals, or P contained within organic matter, including animal manures) but can be minimized by soil conservation and fertilizer management practices (Hart and Cornish, 2012). Loss of P due to leaching varies considerably with soil type. On soils with moderate to high P-sorption capacity is generally considered to be relatively small (i.e., less than 5% of applied P; Melland *et al.*, 2008). However, on low P-sorbing soils losses of phosphate due to leaching can be significant and require specific management interventions; for example, through the use of less-soluble forms of fertilizer. Organic forms of P in soil leachate and in runoff may also be a significant source of P loss due to greater mobility of organic P in soil solution compared with phosphate anions (Toor *et al.*, 2003).

important to achieve high efficiency in the use of P resources. There will also be an increasing need to close the more rapid terrestrial component of the P cycle by recovering more P from waste streams for use as fertilizer. At present, the extent of P recovery is determined by the need to reduce waste streams and pollution associated with them and is constrained by the high cost of P recovery compared with fertilizer manufactured from phosphate rock. In developing economies, improved P use efficiency can mean development of farming systems that are more productive at low P availability because fertilizer is already a relatively expensive input. Ultimately, these systems are more likely to migrate to increasing use of P fertilizers to ensure improved food security (Sánchez, 2010). By contrast, in more intensive agriculture, there is often a need to minimize inefficient use of P inputs and to reduce potential loss of P to the environment (Sharpley *et al.*, 2001; Schröder *et al.*, 2011).

The most efficient use of P fertilizer occurs when P fertilizer inputs are approximately equal to the quantity of P exported in agricultural products (i.e., P balance efficiency ($100*P_{output}/P_{input}$) = 100%: Helyar, 1998). This can sometimes be achieved in low-input farming systems (e.g., McIvor *et al.*, 2011), but these systems will have characteristically low production. When P is the major limitation to potential production, low P inputs may also result in low land, water, and other resource-use efficiencies. In more intensive agriculture, P-balance efficiency is determined largely by the P-sorption capacity of the soil. Agriculture practiced on low P-sorbing soils (where P-buffering capacity is low because sorption sites for P are close to saturation and soil P fertility is relatively high) can

achieve relatively high P-balance efficiencies. For example, greater than 90% P-balance efficiency has been reported for cereal production using appropriate rates of P input to maintain fertility on soil with a long fertilizer history (Johnston and Syers, 2009). However, in P-deficient soils with moderate to high P-sorption capacity, P-balance efficiencies are commonly approximately 10–30% and 45–60% for grazing and cropping systems, respectively (Simpson *et al.*, 2011; Weaver and Wong, 2011). In these cases, P inefficiency is mainly associated with unavoidable accumulation of P in the soil (McLaughlin *et al.*, 2011; Simpson *et al.*, 2011). Analysis of western European farming systems by Sattari *et al.* (2012) similarly indicates that in the period from 1965 to 2007, inputs of P fertilizer to crops exceeded on average that removed in product by approximately three-fold. The application rates of P in Europe have declined since the 1980s; however, there has been no accompanying reduction in plant P uptake, indicating that soils (on average) have been fertilized to levels in excess of crop requirements and that plant assimilation of P is being sustained by utilization of soil reserves. However, where the P-sorption capacity of the soil is low, such imbalances in P use are also more likely to be indicative of P losses to the wider environment where they can cause substantial environmental problems (Schröder *et al.*, 2011). This scenario is mirrored in other parts of the world where there is high use of P fertilizers (e.g., USA, Sharpley *et al.*, 2001; China, Li *et al.*, 2011).

Conclusion

The productive capacity of agricultural land is largely dependent on the access by plant roots to available forms of key essential nutrients in soil. The current global demand for food now exceeds the ability of natural soil processes to supply sufficient N and P without human intervention supplying additional external inputs to accelerate the flux of N and P through their respective nutrient cycles (Smil, 2001). There are strong economic and environmental incentives to improve the efficiency of both N and P use in farming systems.

Different approaches to improve the efficiency of use of soil and fertilizer N and to minimize N losses from the plant–soil system aim to either:

1. Increase plant N demand through choice of plant species and/or genetic selection to enhance the efficiency of acquisition or recovery of N from soil, or improve the internal efficiency with which N is used to produce biomass. Plant N demand can also be increased through management by applying good agronomic practices to address factors that would otherwise restrict plant growth such as disease, weeds, pests, and soil constraints to root growth (Crews and Peoples, 2005),
2. Manipulate N supply to better match plant N demand through presowing soil testing of soil mineral N status, N-budgets and decision-support tools, the timing, placement, rate, and form of N input applied, or the use of technologies to slow the release of plant-available forms of N (Crews and Peoples, 2005), or
3. Capture excess inorganic N before it can be lost by planting cover ('catch') crops during periods of fallow between crops, or interplanting annual crops with perennials (perennial polyculture).

The options for achieving more efficient use of P are similar irrespective of whether the aim is to develop crops that yield more in low-P soils, crops that will yield well when supplied only the P that will be exported in products, or farming systems that are less prone to P losses to the wider environment. These include:

1. Targeting fertilizer use to ensure that crops are only fertilized to their 'critical' P requirement, and better use must be made of the P that has been accumulated in agricultural soils throughout the world (Sattari *et al.*, 2012; Stutter *et al.*, 2012),
2. Application of fertilizer technologies to minimize P losses from low P-sorbing soils or fertilizers that avoid reactions in soils that lead to accumulations of sparingly available P (McLaughlin *et al.*, 2011).
3. The use of crops with lower critical P requirements and improved yield in low P soils as this will lead to more efficient use of the P that is applied as fertilizer and will lessen the opportunities for nutrient leakage (Simpson *et al.*, 2011).
4. Development of plant genotypes, agronomic management, and microbial options that improve access by crops to sparingly available and accumulating pools of P in soil (Richardson *et al.*, 2011).

See also: Air: Greenhouse Gases from Agriculture. Ecoagriculture: Integrated Landscape Management for People, Food, and Nature. Food Security: Yield Gap. Organic Agricultural Production: Plants. Soil Fertility and Plant Nutrition. Soil Greenhouse Gas Emissions and Their Mitigation

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Relevant Website

http://www.csiro.au/pi
Plant Industry, Commonwealth Scientific and Industrial Research Organisation, Australia.

Spices and Aromatics

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Glossary

Convergent breeding A breeding method involving the reciprocal addition to each of two inbred lines of the dominant favorable genes lacking in one line and present in the other.

Dioecious Having the male and female reproductive structures on separate plants.

Geitonogamy Pollination, by pollen falling from upper flowers to the lower flowers by gravitational pull.

Orthotropic The vegetative propagule assumes an upright or normal tree form.

Patch budding Plant budding in which a small rectangle of bark bearing a scion bud is fitted into a corresponding opening in the stock.

Plagiotropic Branches that arise from the axils of leaves of the orthotropic shoots.

Polygamodioecious Plants bearing bisexual as well as either male or female flowers.

Protogyny The female phase preceding the male phase a few days to weeks.

Schizocarp A dry fruit that, when mature, splits up into mericarps.

Introduction

Spices are a part of history, associated with wars and romance. 'King of Spices' (black pepper) and 'Queen of Spices' (small cardamom) reign supreme in the global flavors and food industry. In search of spices, Columbus discovered the New World, whereas Vasco da Gama, a Portuguese navigator, with the same pursuit landed at Calicut on the Malabar Coast of India on 20 May 1498. This changed the history of India and the world at large. Spices were known as early as 2100–2600 BC and were well known in Greek civilization. Spice crops are mainly confined to Southeast Asia, some parts of Africa, and South America. The crops are highly location specific and are grown in certain agroclimatic conditions that vary according to the crop.

There are no precise data on the area and production of spices at the global level. It has been estimated that globally these crops are grown on an area of 8 million ha contributing to 31.6 million tons of spices annually. India's share to world spices production is 6 million tones amounting to 19% (DASD, 2014). The global spice industry amounts to 1.1 million metric tons, accounting for US$ 3.475 billion in value. India's share at the global level is 0.575 million metric tons, accounting for US$ 2.037 billion i.e., 52% in volume and 58.6% in value (see Spices Board of India website).

During the period from 1994 to 2004, the value of spice imports increased on an average by 6.8% per year, whereas the volume increased by 5.9% during that time. In 2004, world import in spices consisted of 1.547 million tons valued at US$ 2.97 billion (ITC, 1999). In the period 2000–02, world import volumes of spices grew at an annual average rate of 7%, whereas import values decreased, on average, by 5% annually. This negative growth in value is attributed to dramatic decreases in the value for whole pepper during 2000/01 – by approximately 40% and a further 18% in 2002/03. Although import volumes stabilized from 2003 to 2004, that of values grew by 4.6%. This upward value trend is mainly attributed to higher market prices for major commodities, such as capsicum, vanilla, ginger, bay leaves, and spice mixtures. There was a growing trend toward the trade of processed spices, which bring higher prices. The growing demand for value-added processing of spices, such as capsicum and ginger, offers business opportunities for the food and extraction industries in international markets. The major markets in the global spice trade are the US, the European Union, Japan, Singapore, Saudi Arabia, and Malaysia. The principal supplying countries are China, India, Madagascar, Indonesia, Vietnam, Brazil, Spain, Guatemala, and Sri Lanka.

Spices are aromatic plants that are used mainly for imparting flavor, aroma, and pungency and for seasoning food. Many of them are also used in medicines and perfumery. The International Standards Organization lists approximately 109 plant species as spices. India is considered the magical land of spices. From the Indian subcontinent, many major spices spread over to most of the tropical part of the world. Peninsular India is a rich repository of spices, and more than 100 species of spices and herbs are grown on approximately 3.47 million ha with an annual production of 6.33 million tons and accounts for approximately 52% of the global trade. Black pepper, cardamom, ginger, turmeric, capsicum, cinnamon, clove, nutmeg, tamarind, and vanilla constitute the major spices. Seed spices like coriander, cumin, fennel, fenugreek, dill, caraway, anise and herbal spices like saffron, lavender, thyme, oregano, celery, anise, sage, and basil are also important. The spices are cultivated in many countries in a wide variety of geographical regions. Each country has its own traditional cultivars/races/types of these spices.

Black Pepper (*Piper nigrum* L.)

Black pepper is considered the King of Spices and is the most widely used spice in the world. Mature berries (fruit), harvested and dried, are the black pepper of commerce. Ripe berries are harvested and decorticated for production of white pepper. It is valued for its characteristic pungency and flavor, the former due mainly to the alkaloid piperine and the later due to a volatile oil. Black pepper has multiple uses in the

processed food industry, the kitchen, in perfumery, traditional medicines and in beauty care.

Black pepper is mainly grown in tropical regions of the world, such as India, Indonesia, Malaysia, Sri Lanka, Thailand, China, Vietnam, Cambodia, Brazil, Mexico, and Guatemala. The estimated production of black pepper (including long pepper) in the world is approximately 409 899 ton on an approximate area of 583 897 ha. The International Pepper Community members namely India, Brazil, Malaysia, Indonesia, Vietnam, and Sri Lanka are the main suppliers to the world market. Major importers of Indian pepper include USA, Russia, Canada, Germany, Italy, Netherlands, France, Japan, Morocco, Poland, UK, Canada, and Saudi Arabia. Black pepper accounts for approximately 6.2%.of the total spices traded internationally. Demand for black pepper and its products in the world market are increasing at the rate of 3.2% annually in volume and 8% in value.

The genus *Piper* comprises around 1200 species, approximately 60% of which occur in Central and Northern South America. The Malabar Coast of South West India is the traditional home of black pepper, grown from almost sea level to approximately 1500 m. Black pepper was the first oriental spice to be introduced into the western world.

Black pepper is a perennial woody climber. Under cultivation, pepper vines are trailed on either living or other nonliving supports, as columns 5–10 m tall (**Figure 1**). The climbing woody stems have swollen nodes with roots at each node anchoring the vine to the support. Pepper plants exhibit two types of branches: the main stem and orthotropic vegetative climbing shoots that adhere to the support with short adventitious roots at nodes; and flowering or plagiotropic (sympodial habit of growth) branches that arise from the axils of leaves of the orthotropic shoots. The pepper plant has mostly surface-feeding root system. The flowers are minute, white to light green, arranged spirally on fleshy peduncles. The cultivated pepper is self-pollinated, and pollination is by pollen falling from upper flowers to the lower flowers by gravitational pull, a process called 'geitonogamy.' The fruit (berry) is a single-seeded drupe with a fleshy pericarp and hard endocarp, pungent and red when ripe, black when dried. White pepper is the dried berries after removing the pericarp (**Figure 1**).

Wild populations of *P. nigrum* are found extensively distributed in many forest areas. Wild forms are usually dioecious but most cultivated ones are bisexual. It is thought that the bisexual forms might have evolved due to unconscious selection for high-yielding types during domestication. Many cultivated types exhibit protogyny with the female phase preceding the male phase a few days to weeks.

Black pepper is cultivated either as a pure crop on wooden poles in Indonesia, Malaysia, Vietnam, Brazil, and on live supports like *Erythrina indica*, *Glyricidia*, Jack trees, Silver oak, etc. in India and Sri Lanka or as a mixed crop along with a wide variety of plantation crops, such as coffee, tea, coconut, and arecanut (**Figure 1**).

More than 100 cultivars of black pepper are known but only some of them are popular. Cultivar diversity is richest in the Indian state of Kerala. The cultivar Karimunda is popular and gives consistent yields under varying agroclimatic conditions. Kottanadan, Kumbhakodi, and Aimpirian are cultivars with high contents of oleoresin and essential oils and hence give high-quality pepper. Others such as Neelamundi, Balankotta, Chumalakodi, Narayakodi, Kalluvally, Kuthiravally, Malligesara, and Thommankodi are popular in certain locations. The hybrid Panniyur-1 is the most preferred variety and is spreading throughout the world. Cultivars Kuching, Lampung Daun Kocil, Belantung are popular varieties in Malaysia and Indonesia and Vinh Linh is another popular variety from Vietnam (**Figure 1**). Mutation breeding and polyploidy breeding methods were attempted in Sri Lanka and India. No resistance was observed in cultivated black pepper for all the three major diseases or pests viz. Phytophthora foot rot (*Phytophthora capsici*), burrowing nematode (*Radopholus similis*), and pollu beetle (*Longitarsus nigripennis*; Sarma, 2010). *Piper colubrinum*, a distant relative from Brazil, was found to be resistant to all three of these pathogens and pests. Efforts are underway to bring these characters into cultivated black pepper using interspecific hybridization and also through biotechnological approaches (Ravindran and Kallupurackal, 2000).

The best collection of black pepper genetic resources is conserved at the Indian Institute of Spices Resources, Kozhikode, India with more than 2900 varieties in the collection. They are conserved in clonal field repositories. Considerable variability exists among cultivars with respect to morphology, yield, and quality, but variability for resistance to biotic and abiotic stresses is limited. Much of the germplasm has been evaluated for genetic variability with respect to yield, quality, and reaction to biotic and abiotic stresses, and promising clones have been identified.

Seedling progenies are never used for propagation as they segregate. Instead, runner shoots or top orthotropic shoots are typically used as vegetative planting materials. These shoots are cut into two to three node bits and planted in polybags housed in humid thatched nursery sheds. This method results in a success rate of 70–80% rooting. Alternatively, these shoots are allowed to grow either on polybags filled with potting mixture or on bamboo splits with coconut pith for multiplication (**Figure 2**).

Pepper, being a climber, requires a support (standard) for its growth and yield. In India, it is mostly cultivated in homestead gardens as a mixed crop on existing support trees. In Brazil, Indonesia, Vietnam, Malaysia (Sarawak), and Thailand pepper vines are usually supported on dead standards. Usually, the trees selected for support are raised for trailing pepper vines. A live support should be fast-growing with few branches, should tolerate periodical pruning, should not compete with other crops for resources and should not produce allelopathic chemicals.

Pepper can be grown as a companion crop, such as coconut, arecanut, or mango/jack. Pepper is also grown with perennial crops, such as coffee, cardamom, tea, and clove, utilizing the shade trees. The coffee/pepper cropping system is very profitable. In coffee plantations the silver oak tree (used as shade tree) is ideal for growing pepper with less competition for light and nutrients (**Figure 1**).

Bush Pepper

Pepper can also be raised in bush form. The fruiting lateral branches of any cultivar can be rooted and the resultant plant grown like a small bush, which flowers in the same year



Figure 1 (a) Black pepper – pure crop on wooden supports; (b) coffee – pepper cropping system; (c) tea-pepper cropping system; (d) variation in spike characters; (e) high-yielding variety 'Subhakara', a Karimunda cultivar from India; (f) high-yielding hybrid 'Panniyur-1' from India; (g) variety 'Vinh Linh' from Vietnam; (h) *Phytophthora*-tolerant variety 'Shakti'; (i) dried black pepper; and (j) dried white (top), ripened (left), and fresh green (right) pepper.



Figure 2 Left to right: Healthy black pepper nursery with rooted cuttings, multiplication using serpentine method and multiplication using the bamboo method.



Figure 3 Bush pepper in a pot and in the field.

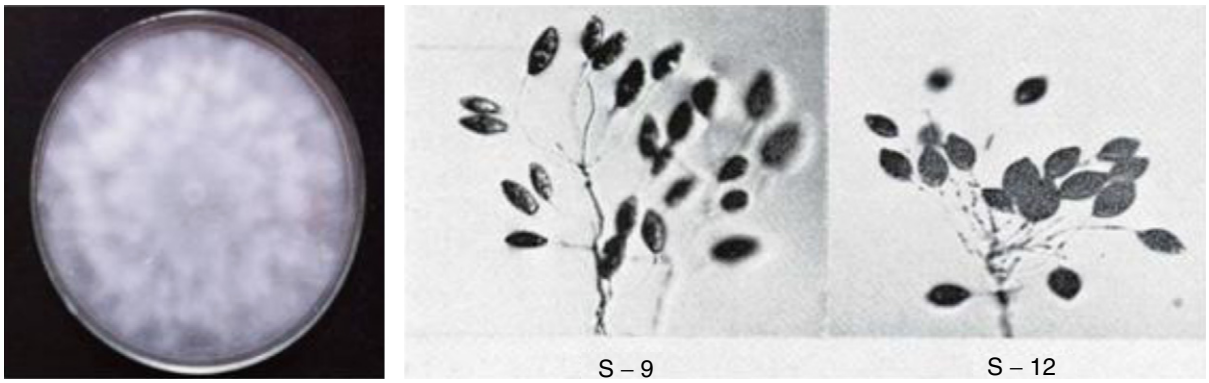


Figure 4 *Phythophthora capsici* in culture (left), as umbellate sporangiophore (center), and sympodial sporangiophore with zoosponagia (right).

and continues to yield throughout the year under irrigation (Figure 3).

These bush peppers can be accommodated well in homes and terrace gardens. The crop tolerates temperatures between 10 and 40 °C although above 32–34 °C is not conducive for productivity.

Pepper plants take 6–8 months from flower to harvest depending on the cultivar and rains. Whole spikes are hand-picked when a few berries in the spikes turn orange red. Harvesting is also done based on processing requirements. Harvested spikes are kept overnight for easy despiking. Berries are separated from spikes manually or mechanically using threshers. To give a uniformly lustrous black color and to prevent moldiness, the separated berries are dipped in boiling water for 1 min before drying. Drying is done both by sunlight for 7–10 days or using mechanical dryers to a moisture content of 10–12%. Dried pepper is cleaned to remove extraneous matter and graded according to size before packing.

Approximately 20 diseases have been described worldwide for black pepper. However, Phytophthora foot rot caused by *P. capsici* (Figures 4 and 5), slow decline caused by the nematode *R. similis*, (Figure 6), anthracnose and stunted disease complex caused by a virus (Figure 7) are the most serious ones (Holliday and Mowat, 1963; Sarma and Nambiar, 1982; Anandaraj, 1997; Sarma *et al.*, 2013). The spectrum of diseases in all the pepper-growing countries is



Figure 5 Phytophthora foot and root rot showing root symptoms (left), foliar wilting (center), and foliar lesions (right).



Figure 6 Black pepper showing (left) root symptoms of the knot nematode, *M. incognita*; (center) symptoms of root necrosis/rot by the nematode, *R. similis*; and (right) vines showing symptoms of slow decline caused by *R. similis*.



Figure 7 Black pepper showing symptoms (a) anthracnose leaf infection; (b) spike infection; (c) cucumber mosaic virus foliar infection; and (d) pepper yellow mottle mosaic virus infection.

very similar, particularly in the cases of stunted disease complex and Phytophthora foot rot. This would indicate a common origin of these diseases, probably India from where this crop has gone to other countries through planting material. Quarantine regulations have never existed between these countries. Nematodes, pollu beetle, mealy bugs, shoot borer, scale insects, leaf gall thrips, burrowing and root knot nematodes (*Meloidogyne incognita* and *R. similis*), and root



Figure 8 Biological control of Phytophthora foot and root rot of black pepper with *Trichoderma harzianum* formulation Left, nontreated plot; right, treated plot, showing dark green foliage.

mealy bugs (*Planococcus* spp.) are the major pests limiting productivity of pepper.

Solarized or nonsolarized soil mixes fortified with effective biocontrol agents, such as *Glomus fasciculatum* (vesicular arbuscular mycorrhiza fungus), *Trichoderma harzianum* or *Trichoderma viride* (**Figure 8**), and *Pseudomonas fluorescens*, *Pochonia chlamydosporia*, or *Paecilomyces lilacinus* and filled into polybags meant for raising rooted cuttings (Sarma, 2006; Sarma *et al.*, 2014). This method reduces root infection and ensures robust root-rot free planting material. Production of disease-free planting materials is imperative in establishing a healthy plantation.

Research work on isolation, cloning, and validation of full-length genes of pepper is in progress. Resistance gene candidates encoding the defense-related proteins, such as osmotin and β-1,3-glucanase, were cloned and sequenced from black pepper and *P. colubrinum*. Transcriptome sequencing of *P. colubrinum* and *P. nigrum* leaf samples challenge inoculated with *P. capsici* revealed the expression of many genes similar to those involved in secondary metabolism, metabolic processes, response to stress, flower development, and fruit ripening. Sequences similar to regulatory genes were also found (Nirmal Babu *et al.*, 2011).

Small Cardamom (*Elettaria cardamomum* Maton)

Small cardamom, the 'Queen of Spices,' is commonly cultivated beneath the evergreen forest trees of Western Ghats of South India, Sri Lanka, and Guatemala. Guatemala, where cardamom is grown largely on plantation scale, is the world's premier producer and exporter followed by India. The major consumers of cardamom are India, Saudi Arabia, other Arab countries, Europe, and Japan.

The most significant component of cardamom, as a spice, is the volatile oil with its characteristic aroma, described generally as camphory, sweet, and aromatic spicy. This is due to the presence of 1,8 cineole, di-terphenol, terpinyl acetate, limonene, sabinene, and borneol, which makes cardamom oil unique (Lewis *et al.*, 1966).

The evergreen forests of Western Ghats in India where natural populations of cardamom still exist is considered the native home of small cardamom. The genus *Elettaria* consists of seven species distributed in India, Sri Lanka, Malaysia, and Indonesia; of these, only *E. cardamomum* is economically important (Holttum, 1950). In India, the genus *Elettaria* is represented only by one species, *E. cardamomum*.

Cardamom is a herbaceous perennial (2–5 m in height) having underground (subterranean) rhizomes with aerial leafy stems (tillers) made of leaf sheaths (**Figure 9**). The suckers grow for approximately 10–18 months before flowering (Madhusoodanan *et al.*, 2002). The growth habit of the panicles and the shape as well as the size of the capsules varies in different cultivars/types of cardamom. Flowers are arranged in clusters known as *cincinni*, are bisexual, and occur from May to October. Bisexual flowers are self-compatible but cross-pollination is the rule. Honey bees contribute for more than 90% of pollination. Cardamom is a shade-loving plant that thrives well at elevations of 600–1200 m above sea level under an average annual rainfall of 1500–4000 mm and temperature range of 10–35 °C.

Cardamom germplasm is maintained as clonal field repositories in India with more than 1500 accessions. The main focus of cardamom breeding, in addition to high yield, bold capsules, and quality attributes, are resistance to viral and fungal diseases, and drought. The main breeding strategies are selection and hybridization. Convergent breeding programs designed to bring multiple resistance are in progress (Madhusoodanan *et al.*, 2002).

Cardamom is propagated both through seedlings and vegetatively through suckers. Clonal multiplication of cardamom ensures genetically uniform true-to-type planting material. Seedlings are raised in a nursery under partial shade using seeds from ripe capsules collected from high-yielding and healthy clumps. Cardamom seed has a hard seed coat, and scarification of seed with 25% nitric acid for 10 min followed by thorough washing in water before sowing assures above 80% germination. Soil solarization of seedbeds in cardamom nurseries enhances germination by 25%, reduces weed growth by 82%, and suppresses pest and disease incidence.

Small cardamom (**Figure 9**) requires a warm and humid climate fairly well distributed annual rainfall of 1500–5000 mm. Cardamom is a surface feeder; 70% roots are at a depth of 15 cm and hence availability of moisture at the root zone is important for good growth and yield. It is also susceptible to wind damage. Cardamom thrives well in moderate shade (50–60% light).

The crop starts flowering during early monsoon showers in India and comes to bearing during July–August, with harvest

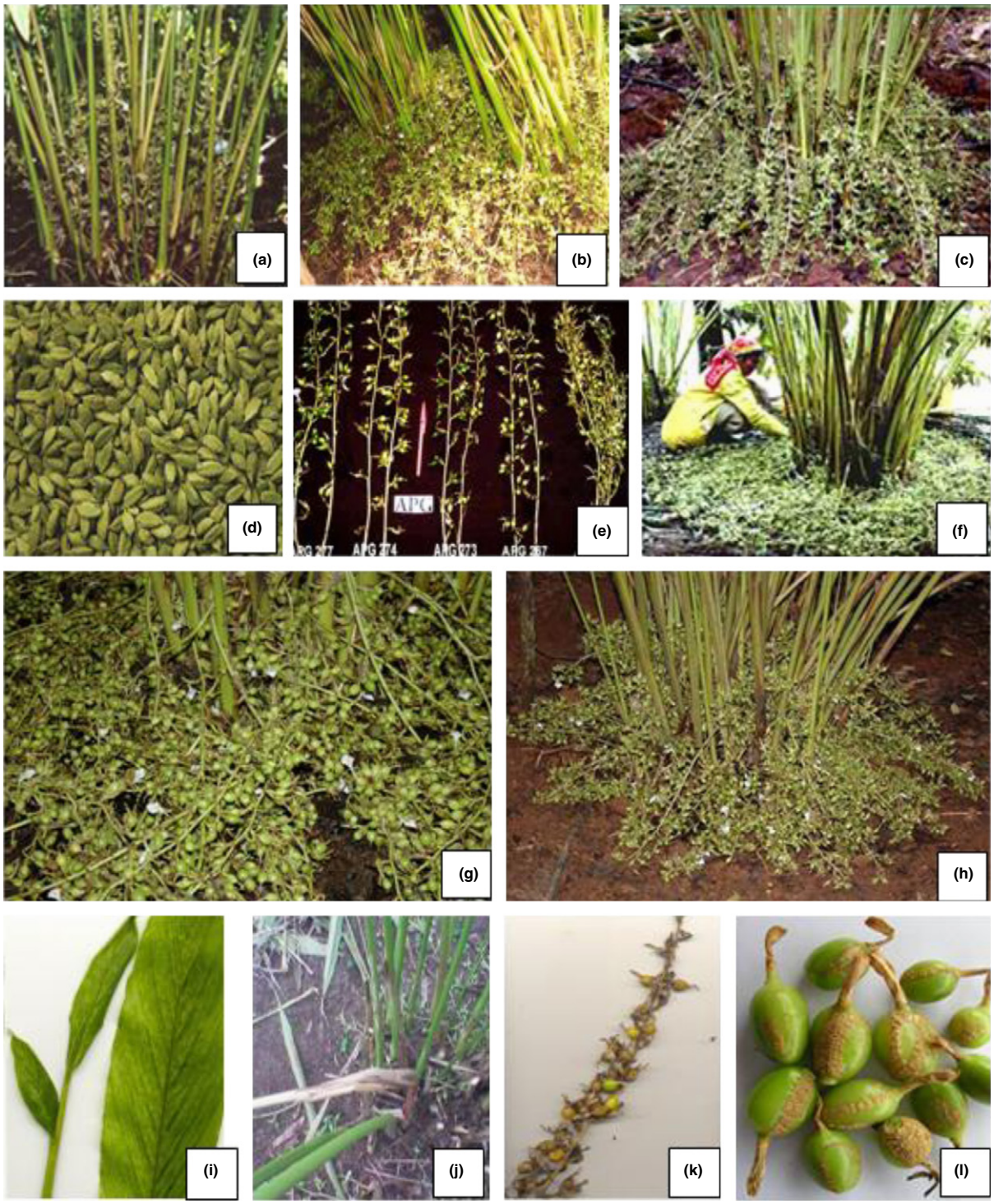


Figure 9 Small cardamom (a) Mysore type; (b) Malabar type; (c) Vazhuka type; (d) dried cardamom; (e) variation in panicle branching patterns; (f) high-yielding variety 'Mudigere1'; (g) high-yielding high-quality variety 'Kodagu Suvasini' suitable for high-density planting; (h) high-yielding katte-resistant variety 'Vijetha'; (i) symptoms of katte virus; (j) rhizome rot; (k) capsule rot; and (l) thrips infestation.

generally completed by October–November. This highly humid warm climate so congenial to growth and productivity is also congenial for fungal diseases; among them are capsule rot caused by *Phytophthora meadii*/*P. nicotiana* and clump rot caused by a *Pythium–Fusarium* complex. The root knot nematode *M. incognita* is another serious soil-borne pest. Three viral diseases are important, namely, katte or mosaic disease (Figure 9), kokke kandu, and banana bract mosaic virus. A minor viral disease, nilgiri necrosis virus (Naidu and Thomas, 1994) has also been reported (Siljo *et al.*, 2013).

Katte virus is a Potyvirus transmitted by the banana aphid *Pentalonia nigronervosa*. The disease is not fatal but results in a gradual decline in the vigor and productivity of the affected clumps (Venugopal and Naidu, 1984; Naidu and Thomas, 1994). The disease starts as chlorotic spindle-shaped streaks that later merge to produce a mosaic pattern of the disease (Figure 17). Studies on the coat protein and 3′ untranslated sequence of a Karnataka (Sakleshpur) isolate indicated that the virus is a new member of the genus, *Macluravirus*, family Potyviridae (Jacob and Usha, 2001). At least six distinct strains of the virus have been reported (Jacob *et al.*, 2003). Both serological and reverse transcription polymerase chain reaction methods are available for the detection of the virus in plants.

Cardamom plants start bearing fruits (capsules) in the second year after planting and satisfactory yield is obtained starting in the third year. It takes 110 days from flowering to fruit maturity. Time and duration of harvest depend on the climate, varietal differences, and irrigation. Fruits are hand-picked just before fully ripe to get maximum green color during curing. Capsules are processed within a day after harvest. Processing consists of washing, curing (drying), cleaning, polishing, sorting, grading, and packing. Capsules immediately after harvest are washed in clean water to remove adhering soil. Sometimes capsules are treated with 2% washing soda (sodium carbonate) for 10 min to stabilize the chlorophyll and impart a grass better green color. After washing capsules are dried to a moisture content of 7–20%, in drying houses by heat radiation. Dried capsules are rubbed with coir mat/gunny cloth/steel mesh and sieved to remove the plant debris, and graded according to size and color.

Large Cardamom (*Amomum subulatum* Roxb.)

Large cardamom (Figure 10) is one of the main cash crops cultivated mainly in India, Nepal, and Bhutan. It is also grown to some extent in Thailand, Laos, Cambodia, and China. The major importing countries are China, Arab countries, Pakistan, Vietnam, Korea, and Japan. It is used as a spice in Ayurvedic preparations. It contains 2–3% essential oil and possesses medicinal properties as carminative for stomach ache, diuretic, cardiac stimulant, and antiemetic.

Large cardamom is a perennial herb having subterranean rhizomes that give rise to leafy shoots (pseudostem) and spikes. Mature plants range in height from 1.5 to 3.0 m. The inflorescence is a dense spike on a short peduncle bearing 40–50 flower buds in an acropetal sequence. The fruit is a trilocular many seeded capsule. The capsule wall is reddish brown to dark pink. Large cardamom is essentially a cross-pollinated crop. Flowering is completed in 75–125 days from April to June at lower altitudes and from May to July at higher altitudes, depending on the weather conditions and the cultivar. The flowers remain viable for approximately 14 h after opening. Bumble bees (*Bumbus* sp.) are the main pollinators due to their compatible size followed by honey bees (*Apis dorsata*).

India has the largest collection of large cardamom with more than 300 accessions. There are several cultivars, such as Ramsey, Golsey, Sawney, Ramla, Chivey Ramsey, Garday Seto Ramsey, Seto Golsey, Ramnag, Madhusay, Red Sawney, Green Sawney, Mingney, and Barlanga (Gyatso *et al.*, 1980; Subba, 1984). Ramsey, Sawney, Golsey, Ramla, and Varlanga are the most popular with Seremna gaining importance in lower altitudes. Bebo is another cultivar from Arunachal Pradesh. Barlanga, Ramsey, and Ramla are well suited to higher altitudes, Golsey for lower altitudes, and Sawney with bold capsules is widely adaptable to different elevations. Varlanga is a high-yielding cultivar suitable to low, medium, and high altitudes. Most cultivars are susceptible to the viral diseases 'chirkey' and 'foorkey', but Golsey is relatively tolerant to chirkey. Ramla with bold dark pinkish capsules is moderately tolerant to chirkey. Leaf blight and leaf streak are the other two important fungal diseases in Large cardamom (Figure 10).

Large cardamom is propagated using either seeds or suckers. Although seed propagation reduces spread of viruses, clonal propagation with adequate precaution ensures genetic purity and high productivity. Efficient micropropagation technology for virus-free clonal propagation of large cardamom is also available. The crop grows well under the shade of trees at altitudes ranging from 1000 to 2000 m above sea level. For successful cultivation of this crop, the mean minimum and maximum temperature requirements are 6 °C during winter months and 25 °C during warm months. Well-drained loamy soils are rich in organic matter and nitrogen, low in phosphorus and medium in potash with a pH range 4.5–6.0 are ideally suited for large cardamom cultivation.

It takes approximately 4 months for the fruits to mature. Harvesting is done once a year by collecting spikes containing ripe fruits with the help of a special chisel-shaped narrow knife made especially for this purpose. The individual capsules are separated by hand, cleaned, and dried before marketing. The quality of large cardamom depends mainly on external appearance, i.e., color, uniformity in size, shape, consistency, texture, and flavor. 1,8 Cineole contributes to pungency, whereas α-terpinyl acetate adds a pleasant aroma.

Ginger (*Zingiber officinale* Rosc.)

Ginger an underground rhizome (Figure 11) is used as spice and condiment. In Indian and Chinese systems of medicines, it is also used to treat liver complaints, flatulence, anemia, rheumatism, piles, and jaundice. The main areas of ginger cultivation are India, China, Nigeria, Indonesia, Jamaica, Taiwan, Sierra Leone, Fiji, Mauritius, Brazil, Costa Rica, Ghana, Japan, Malaysia, Bangladesh, Philippines, Sri Lanka, Solomon Islands, Thailand, Trinidad and Tobago, Uganda, Hawaii, Guatemala, and many Pacific Ocean islands. India is the largest producer of dry ginger in the world contributing approximately 30% of the world's production.

The genus *Zingiber* consisting of approximately 150 species is widely distributed in tropical and subtropical Asia. It is thought to have originated in Southeast Asia, but was under cultivation from ancient times in India. The other important taxa of this genus are turmeric, cardamom, large cardamom, and several other species having economic and medicinal importance. Ginger is not found in the truly wild state.

Ginger contains 2–3% protein, 0.9% fat, 1.2% minerals, 2.4% fiber, and 12.3% carbohydrate and is a good source of calcium, phosphorous, iron, and vitamins. The volatile oils (lisabolene, cinol, phellandrene, citrol, borneol, cibonellol,



Figure 10 Large cardamom (a) field view; (b) flowers; (c) fruits; (d) frost injury; (e) 'chirkey' (mosaic) disease; (f) 'foorkey' disease, showing extensive tillering and sprouting of stunted shoots; (g) leaf blight (*Colletotrichum*); and (h) leaf streak (*Pestalotia*) disease.

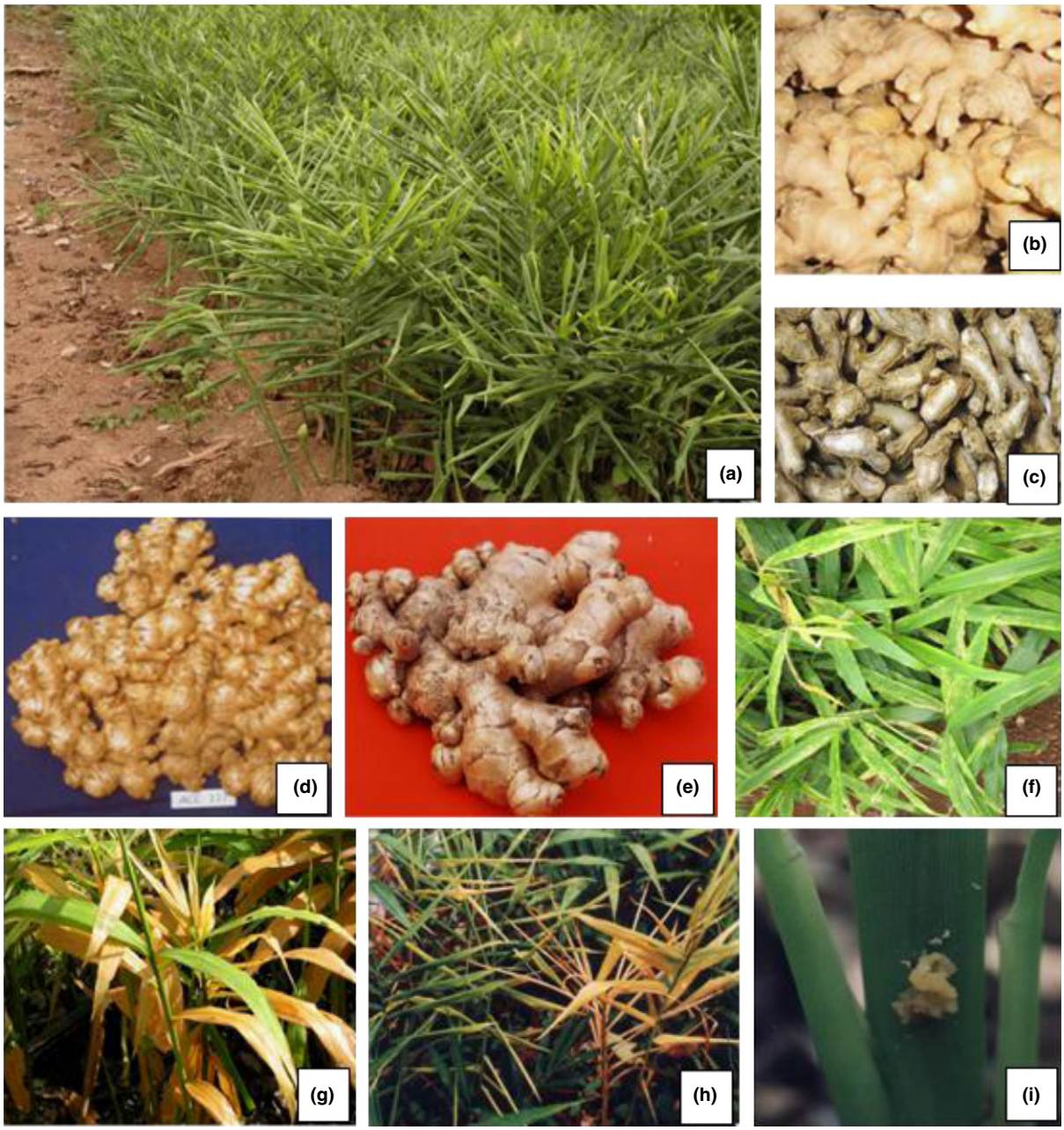


Figure 11 Ginger (a) field view; (b) fresh ginger; (c) dried ginger; (d) 'Mahima' a high-yielding extra bold variety; (e) 'Bhaise' a high-yielding vegetable-type ginger suitable for temperate regions; (f) symptoms of leaf spot; (g) symptoms of rhizome rot; (h) symptoms of bacterial wilt; and (i) damage caused by shoot borer.

geranial, linaloal, limoline, zingiberol, zingiberene, and camphenes), oleoresin (gingenol and shogaol), phenols (gingeol and zingerone), proteolytic enzyme (zingibain), vitamin B_6, vitamin C, calcium, magnesium, phosphorus, potassium, and linoleic acid are important constituents of ginger. The pungency of ginger is due to gingerol, whereas the aroma is due to the volatile oils lisabolene, zingiberene, and zingiberol.

Ginger is a herbaceous perennial but is usually cultivated as an annual (Figure 11) for its underground branched rhizome. Adventitious roots and storage roots arise from the nodes of these rhizomes. The ancillary buds shoot up as leafy stems known as pseudostems, which die out annually, whereas the plant continues to live through its rhizome. Flowers are borne on a spike produced in a peduncle different from the aerial leafy stem and arising directly from the rhizome. Ginger is not known to set seeds (Purseglove *et al.*, 1981; Ravindran and Nirmal Babu, 2005; Ravindran *et al.*, 2005; Nirmal Babu *et al.*, 2012a).

Though there is no natural seed set in ginger, reasonable variability exists for yield and quality attributes. Cultivar diversity is richest in China followed by India where many distinctly different morphotypes have been identified. A good

germplasm collection of ginger with more than 1000 accessions is maintained in India. A few high-yielding exotic cultivars, such as 'Rio-de-Janeiro' with a bold rhizome, fair skin, pungent, flavored, and less fibrous; 'China' with bold rhizome, yellowish-white skin, highly pungent, flavored and fibrous; 'Jamaica' with bold rhizomes, white skin, moderately pungent, highly flavored, and fibrous; 'Sierra-Leone' with slender rhizomes, buff skin, pungent, with good flavor. Collections are also available from Nepal, Nigeria, USA, New Zealand, and Fiji. The germplasm is maintained as clonal repositories.

Ginger is location specific and the agroclimatic conditions have a great role in creating variability in the qualitative as well as in the quantitative attributes. The crop improvement in ginger is aimed at developing high-yielding cultivars with wide adoption, high-quality parameters (oil and oleoresins), and low fiber, besides resistant to major pests and diseases. The main approach to crop improvement is by selection, with some mutation breeding and polyploidy breeding. Each location has its own high-yielding cultivars (**Figure 11**).

Ginger is propagated vegetatively using rhizome pieces with at least two growing buds. The seed rhizomes from the previous harvest are to be stored properly in pits under shade in layers along with dry sand or sawdust to provide adequate aeration for better germination. Ginger is planted either on raised beds of approximately 1-m width and convenient length or in ridges and furrows. Technology for *in-vitro* induction of microrhizomes in ginger for use as planting material is available. Ginger grows well in warm humid climates, from sea level to an altitude of 1500 m above sea level. It can be grown under both rain-fed and irrigated conditions.

Ginger production benefits greatly from applications of organic manure, including compost and farm-yard manure applied at the time of bed preparation, together with applications of Nitrogen, Phosphorus, and Potassium in three split doses. Mulching with green leaves at the time of planting and again at the time of subsequent fertilization is recommended to prevent erosion of soil due to heavy rain. Studies also confirmed that application of green manure; farm-yard manure, and groundnut cake/sesame oil cake/cotton cake are good for boosting yields. Being a soil-exhaustive crop, it is not desirable to grow ginger in the same site year after year.

The crop is ready for harvest 7–9 months after planting when the leaves start drying up. Harvesting is done by carefully uprooting the underground rhizome without causing injury or damage using either manual or mechanical means. The rhizomes are separated from the dried up leaves. For green ginger, the crop is harvested in 5–6 months after planting. For curing, the rhizomes are soaked in water for 6–7 h and washed to remove soil particles, then rubbed well, the outer skin removed, dried in sun for a week, and then stored in a cool and dry place. Average yield ranges from 15 to 30 ton ha^{-1}, with the yield of dry ginger being 20–25% of the yield of green ginger, depending on the variety.

Turmeric (*Curcuma longa* L. *Syn. Curcuma domestica* Val.)

Commercial turmeric is the dried underground rhizome of the perennial herb *C. longa* L. (Syn: *C. domestica* Val.) (**Figure 12**). Turmeric is used for medicinal and culinary purposes and also as a cosmetic and a natural dye. Turmeric is also credited with religious and magical rites in India and certain Southeast Asian countries. It is geographically distributed in Cambodia, China, India, Indonesia, Lao People's Democratic Republic, Madagascar, Malaysia, the Philippines, and Vietnam. It is extensively cultivated in China, India, Indonesia, and Thailand and throughout the tropics, including tropical regions of Africa, South America, and Australia. The major items of export are dry rhizome and powder. India is the single largest producer, consumer, and exporter of turmeric in the world (Purseglove *et al.*, 1981; Ravindran *et al.*, 2007; Nirmal Babu *et al.*, 2012b). The major markets are USA, Iran, Japan, UK, Bangladesh, Sri Lanka, South Africa, Germany, and the Netherlands.

The past few decades have witnessed extensive research interests worldwide in the biological activity of turmeric and its compounds. Thus, turmeric is gaining importance all over the world as a cure to combat a variety of human ailments because of its antiinflammatory, hypocholesterolemic, choleratic, antimicrobial, antirheumatic, antifibrotic, antivenomous, antiviral, antidiabetic, antihepatotoxic, antioxidant, and anticancerous properties as well as insect repellent activity (Chempakam and Parthasarathy, 2008). The rhizomes contain curcuminoids (2.5–6%) and are responsible for the yellow color. Curcumin (diferuloylmethane) comprises curcumin I (curcumin), curcumin II (demethoxycurcumin), and curcumin III (bisdemethoxycurcumin), which are found to be natural antioxidants. A new curcuminoid, cyclocurcumin, has been isolated from a nematocidally active fraction of turmeric. The fresh rhizomes also contain two new natural phenolics with antioxidant and antiinflammatory activities, and also two new pigments. The essential oil (5.8%) obtained by steam distillation of rhizomes has α-phellandrene (1%), sabinene (0.6%), cineol (1%), borneol (0.5%), zingiberene (25%), and sesquiterpenes (53%).

Turmeric grows well in the tropics of Asia, Africa, and Australia from sea level to an altitude of 2000 m above sea level (Ravindran *et al.*, 2007; Skornickova *et al.*, 2010; Skornickova *et al.*, 2007). Many species of *Curcuma* are economically valuable, and different species are cultivated in different countries. The country of origin of cultivated turmeric (*C. longa*) is presumed to be Southeast Asia.

Turmeric is an erect perennial herb with underground rhizomes but is grown as an annual under cultivation. Rhizomes are fleshy at the base of each shoot and consist of a mother rhizome ringed with the bases of old scale leaves bearing a succession of horizontal or curved rhizomes known as primary, secondary, and tertiary fingers, the whole forming a dense clump (Figure 12). The rhizomes show a deep orange-colored inner core and yellowish orange on the outer side and are rich in curcumin. The inflorescence is terminal and borne in between the leaf sheaths and are pale yellow. Fruiting is rare.

Flowering in turmeric takes place between 109 and 155 days after planting when mother rhizomes or bigger primary rhizomes are planted and depend on the cultivars, climatic conditions, and cultivation practices. Turmeric is a triploid with a chromosome number of $2n = 63$, 84 (Holttum, 1950; Nazeem *et al.*, 1993; Ramachandran, 1969; Nambiar *et al.*, 1982).

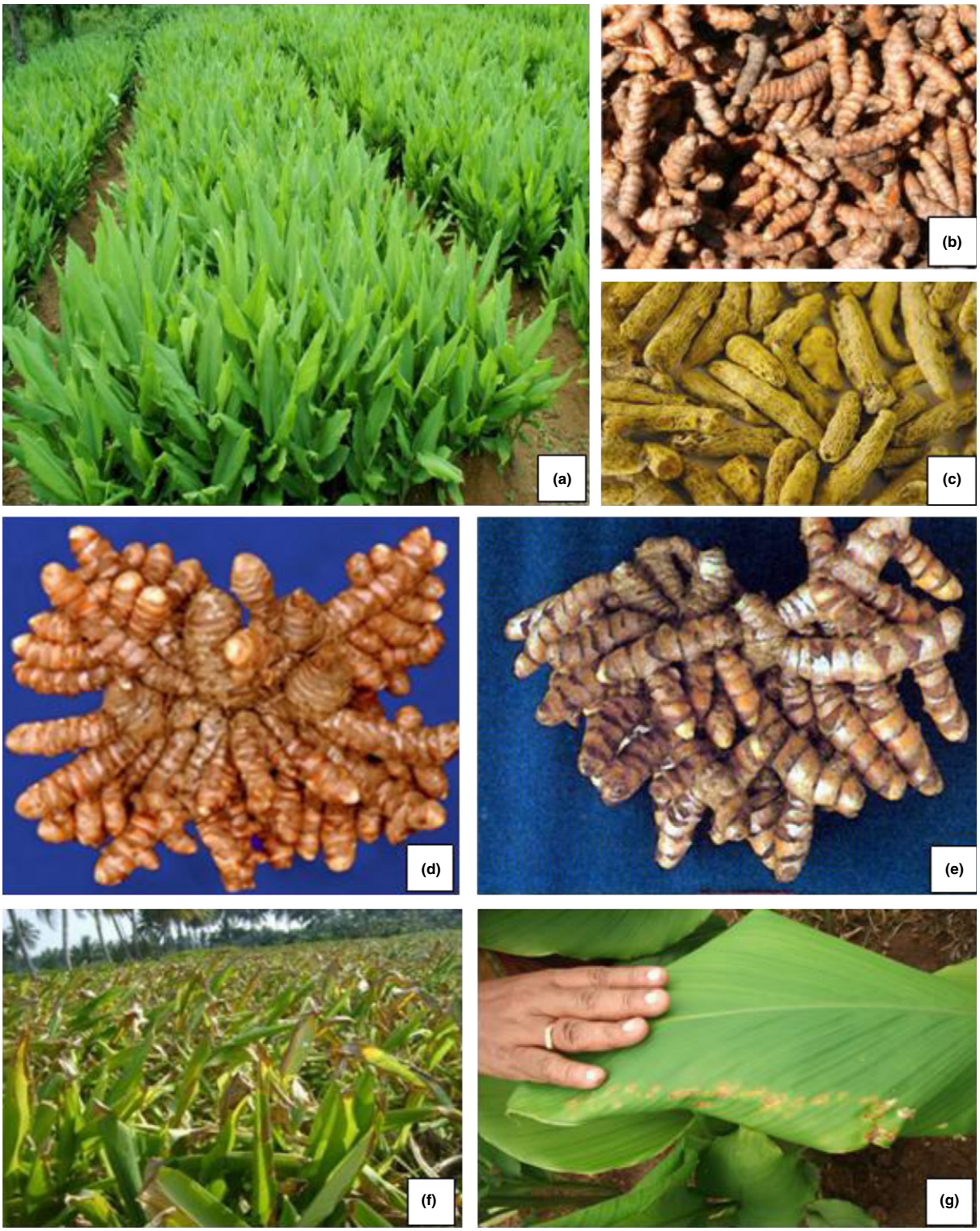


Figure 12 Turmeric (a) field view; (b) fresh primary rhizomes of turmeric; (c) dried and polished turmeric; (d) high-yielding turmeric variety 'Kedaram'; (e) high-yielding rhizome-rot-tolerant short-duration variety 'Suguna'; (f) leaf blotch disease; and (g) leaf spot disease.

The genus *Curcuma* consists of more than 117 species distributed chiefly in South and Southeast Asia of which approximately 40 species are reported from India. In addition to *C. longa*, the other economically important species of the genus are *Curcuma aromatica*, used in medicine and in toiletry articles; *Curcuma kwangsiensis*, *Curcuma ochrorhiza*, *Curcuma pierreana*, *Curcuma zedoaria*, and *Curcuma caesia* used in folk medicines of the South and Southeast Asian nations; *Curcuma*

alismatifolia, *Curcuma elata*, and *Curcuma roscoeana* with floricultural importance; *Curcuma amada* (mango ginger) used as medicine and in a variety of culinary preparations, pickles, and salads; and *C. zedoaria*, *Curcuma pseudomontana*, *Curcuma montana*, *Curcuma angustifolia*, *Curcuma rubescens*, *Curcuma haritha*, and *Curcuma caulina* all used in manufacturing arrowroot powder. The other species of minor importance are *Curcuma purpurascens*, *Curcuma mangga*, *Curcuma heyneana*, *Curcuma zanthorrhiza*, *Curcuma phaeocaulis*, and *Curcuma petiolata* (Skornickova *et al.*, 2007).

Though vegetatively propagated because of rare seed set, there is considerable variability in cultivated turmeric. More than 70 popular turmeric types belonging to both *C. longa* and *C. aromatic* are under cultivation in India. India has good diversity in turmeric cultivars, and a germplasm collection of more than 2000 accessions are maintained in clonal repositories. Wide variability exists among the cultivars with respect to growth parameters, yield attributes, resistance to biotic and abiotic stresses, and quality characters (Govindarajan, 1980; Mohanty, 1979; Ratnambal *et al.*, 1986; Rao *et al.*, 1975; Ravindran *et al.*, 2007). Crop-improvement programs on turmeric in India have been limited to identifying superior turmeric genotypes with high yield, high dry recovery, and high curcumin content. Mutation breeding has also been used; of 24 improved varieties of turmeric (Figure 20) four are induced mutants.

Turmeric is propagated vegetatively through rhizome bits with one or two buds, using mother and finger rhizomes with the larger, rhizomes promoting greater seedling vigor, earlier growth, and higher yield (Rao *et al.*, 2006). Micropropagation and microtuber technology is also available for large-scale multiplication of pathogen-free planting materials (Nirmal Babu *et al.*, 2007). Planting is done in raised beds or ridges with the onset of rains under either rain-fed or irrigated conditions. Turmeric is cultivated either as a single crop or intercropped with other crops, such as maize, castor, and also among coconut plants for increased and diversified income. It grows well in warm humid climates and is widely grown in the tropics of Asia, Africa, and Australia from sea level to an altitude of 2000 m above sea level.

Turmeric can neither stand water logging nor drought and hence is grown under irrigation in major producing areas. It emerges and grows well under partial shade and hence it is recommended as an intercrop in coconut and arecanut gardens. Mixed cropping is also practiced with short-duration crops, such as bhindi, small onion, black gram, green gram, french bean, soybean, or horse gram. It is a heavy feeder and requires a higher level of nutrients and responds well to large quantities of organic manures in the form of farm-yard manure, oil cakes, and green leaves (mulch) (Rethinam *et al.*, 1994).

Turmeric is usually harvested 6–9 months after planting depending on the cultivar, location, and irrigation facilities. Short-duration cultivars mature in 6–7 months, medium-duration cultivars in 7–8 months and long-duration cultivars in 8–9 months. Processing of turmeric consists of cleaning, boiling, drying, polishing, and coloring of raw turmeric rhizomes. Boiling (for 45–60 min) is done to kill the cells as well as to get uniform color throughout the rhizome. Use of sodium bicarbonate in the boiling water (0.1%) gives a deeper color to the final product.

Vanilla (*Vanilla planifolia* Andrews, *Syn. Vanilla fragrans* Salisb.)

Vanilla (Figure 13) is the natural source of the natural flavor compound vanillin, which is the world's most popular flavor. A lower-quality vanilla is obtained from *Vanilla pompano* (Pompan vanilla) and *Vanilla tahitensis* (Tahiti vanilla). It is indigenous to Mexico and Central America and is cultivated in many parts of the world. The main producers are Madagascar, Mexico, Solomon Islands, Indonesia, Seychelles, and Reunion Islands, and the major importing countries are USA, Canada, France, Germany, Japan, Switzerland, UK, Netherlands, Ireland, Denmark, Saudi Arabia, Botswana, Australia, and other European Union countries. Vanilla beans are used for flavoring numerous sweetened foods. Only a small portion of vanilla beans are consumed directly with almost 95% of the beans processed into vanilla extract. The dairy industry is the largest consumer.

Vanilla is a climbing orchid having a stout and succulent green stem and leaves (Figure 13). When the aerial velamin roots reach soil they grow as normal roots and spread in the humus layer. Flowers are large, pale greenish yellow, have short stalks, mature from base to the apex, and last only for a day. Owing to the presence of the rostellum, natural self-pollination is generally impossible. Fruits (capsules, commonly called the beans) contain thousands of minute seeds that are liberated at maturity by longitudinal splitting of the capsule. Under cultivation, the capsules are harvested before they are fully ripe. The seeds do not germinate under natural conditions. Vanillin is extracted from cured beans and is used for flavoring ice creams, chocolate, beverages, cakes, puddings, custards, etc.

Efforts toward crop improvement are confined to the selection of genotypes that perform well under local conditions. Interspecific hybridization is being attempted to bring disease and pest resistance from wild to cultivated vanilla (Minoo *et al.*, 2006a,b, 2008, 2010).

Vanilla is commercially propagated vegetatively through stem cuttings collected from vigorously growing healthy plants. For direct planting in the field, usually 60–120 cm-long cuttings each with 10–20 nods are used as planting material, using extreme care to avoid virus-infected plants. Fresh cuttings after collection should be kept under shade for a week before planting. Such a partial desiccation is essential for good rooting. Micropropagation technology is also available for commercial multiplication of vanilla (Minoo and Nirmal Babu, 2009; Minoo *et al.*, 2010). Being a climber, vanilla requires a standard for support, usually a trellis or low branches of support trees. *Gliricidia maculata*, *Plumaria alba*, *Casuarina equisetifolia*, Mulberry, *Erythrina lithosperma* are used as support trees.

Vanilla grows well in tropical warm humid climates and can be grown between 10° and 20° North and South latitudes from sea level to more than 1000 m above sea level, at temperatures ranging from 25 to 32 °C (average 27 °C). A dry period of approximately 2 months just before flowering is necessary to restrict vegetative growth and induce flowering. Vanilla is a shallow-rooted surface feeder with root growth confined to the decayed organic matter (humus layer) applied around the plant base. A thick layer of humus is required for



Figure 13 Vanilla (a) vine with beans; (b) flowers; (c) processed vanilla beans; (d) *Phytophthora* bunch infection; (e) Fusarium rot; (f) blight; (g) wilt; and (h) virus-affected vines.

its proper growth. Vanilla requires partial shade as leaves get scorched in direct sunlight.

Under good management practice, vanilla flowers by the third year after planting, but it depends on the length and physiology of the original cutting used for planting. The flowering season is from October to March depending on the climate and takes approximately 45–60 days from initiation of inflorescence to flower opening. The flowers begin to open during midnight and last only from early morning to late evening. Natural pollination of vanilla only occurs in the place of origin – Mexico. The natural pollinators are *Melapona* bees and humming birds. Elsewhere in the world commercial fruit production is through hand pollination. A trained worker can pollinate approximately 1000 flowers a day with more than 80% success. It is advisable to pollinate only the first produced 8–10 flowers in a bunch and only 10–12 inflorescences in a vine to get beans of good size.

Stem rot caused by *Fusarium oxysporum* and bunch rot caused by *Phytophthora meadii* (**Figure 13**) and viral diseases are the major production constraints (Sarma *et al.*, 2010).

Vanilla beans take 9–11 months to reach full maturity after flowering. Delay in harvesting leads to splitting of beans and scattering of the seeds. The harvested beans are 'killed' by immersion in hot water at 63–65 °C for 3 min to initiate the enzymatic action that leads to the formation of vanillin. The hot beans are then covered in a blanket and stored in wooden boxes, a process called sweating. The beans are then dried in closed boxes for approximately 3 months at ambient temperature (30–40 °C) until the beans have reached approximately one-third of the original weight and developed various fragrance substances (Sudharsan, 2002). Beans stored at lower temperatures lead to 'frosting' (deposition of vanilla crystals on the beans). The important attributes of cured vanilla beans for grading purposes are length of beans, aroma, and color flexibility, luster and free from mold and insect infestation. Properly cured beans will yield 2–2.5% vanillin.

Tree Spices

There are 17 trees used as sources of spices and grown in humid tropical forests of India, South and Southeast Asia, Australia, Pacific Islands, and Tropical America. Among them cinnamon, clove, nutmeg, tamarind, garcinia/kokam, curry leaf, and allspice are the most important (Nybe *et al.*, 2007).

Cinnamon (*Cinnamomum verum* Bercht and Presl. Syn. *Cinnamomum zeylanicum*, Blume)

Cinnamon (**Figures 14(a)** and **(b)**) is obtained from various sources, including *C. cassia* (syn. *C. aromaticum*) (Chinese cassia), *C. burmannii* (Indonesian cassia), *C. loureirii* (Saigin cassia), and *C. tamala* (Indian bay leaf). The genus, a native of Southwestern tropical India and Sri Lanka, consist of more than 250 species distributed in Southeast Asia, China, and Australia. Seychelles and Malagay Republic are the major cinnamon-producing countries besides Sri Lanka.

True cinnamon comes from the dried bark of *C. verum*. In addition, oil can be obtained from the bark (bark oil), leaves (leaf oil), roots (root bark oil), and seeds (seed oil). The main constituent of leaf oil is eugenol (75–80%) and that of bark oil is cinnamaldehyde (65%). The bark, oil, and oleoresin are the economically important products. Bark either as a small piece or as powder is extensively used as spice or condiment in food and confectionary. In the ground form, it is used in curry powders and in the preparation of various preserves. It is also used in the manufacture of soaps, dental preparations, and perfumes.

Cinnamon is said to have carminative, astringent, simulative, and antiseptic properties. It is prescribed in powder and infusion but is usually combined with other medicines and claimed to check vomiting and relieve flatulence and gastric disabilities. It has a high germicidal and fungicidal activity but the irritant nature prevents its use as such.

Cinnamomum verum is a medium-sized evergreen tree, reaching a height of 15–20 m in 25–30 years, but generally coppiced for the enhancement of side shoots. The cinnamon germplasm collection in India has 500 accessions, 35 wild species, and 14 exotic accessions. There is wide variability in the cinnamon germplasm for various yield-attributing characters, such as number of peeler shoots per plant, plant height, plant girth, and tree spread, and quality characters. Crop improvement for the production of cinnamon is confined to selection and popularization of elite types from the germplasm for better regeneration capacity, yield of dry bark, and quality of the bark (Haldankar *et al.*, 1994; Krishnamoorthy *et al.*, 1996; Ravindran *et al.*, 2004). So far, seven high-yielding improved selections were released for cultivation from India.

Cinnamon is commonly propagated through seeds extracted from ripe fruits from mother trees with desirable characters, such as smooth bark, erect stem, easy pealing of bark, vigorous growth, free from pests and diseases, and having good qualities, such as sweetness, pungency, and flavor. The seeds are sown immediately after collection; otherwise viability is reduced. Under normal conditions, seeds germinate within 20 days. Seedlings are transplanted from beds to polythene bags for better growth. Ten- to twelve-month-old seedlings are suitable for planting (Krishnamoorthy and Rema,1988). Cinnamon is also propagated using hard and semihard wood cuttings.

Cinnamon is a hardy plant that tolerates a wide range of climatic conditions. The crop performs well from 300 to 350 m above sea level and thrives up to 1000 m. It flourishes in places with an annual rainfall of 150–250 cm with an average temperature of 27 °C. A hot and moist climate is highly suited for its cultivation but prolonged spells of dry weather are not conducive for its growth. In general, cinnamon is free from serious pests and diseases.

Coppicing is practiced from the fourth or fifth year depending on the availability of peeler shoots. Stems are cut during rains to facilitate peeling. Best time for peeling (**Figure 14(b)**) is when new flushes and leaves are hardened after a rainy season. The side shoots are also cut so that the plant assumes the shape of a low bush and a bunch of canes suitable for peeling are subsequently available. The best quality is obtained from the thin bark of shoots in the center



Figure 14 Tree spices (a) cinnamon flowering branches; (b) harvesting of cinnamon quills and bark chippings (inset); (c) clove flower buds ready for harvest and dried flower buds (inset); (d) nutmeg fruits ready for harvest; (e) variability in nutmeg fruit, mace (including yellow mace and nut characters); (f) nutmeg nuts; (g) nutmeg aril; (h) anthracnose (*Colletotrichum* sp.) in nutmeg leaves; and (i) thread blight in nutmeg.

from the middle portion of shoots. Fully developed cinnamon shoots of 1.5–3.0 cm diameter harvested during the rainy season gives good quality bark and high yield (Pruthy *et al.*, 1978). After scraping the outer skin, the peeling of the bark is done carefully by piercing the bark with a sharp knife. The tube-like barks thus obtained in lengths of 6–8 in. are placed one inside the other to form a tube of length 1 m called quills and dried. Barks that cannot be taken out like tubes are called

'quillings' and the scraped pieces are called 'featherings.' Approximately 70–100 kg of quills and 30 kg of quillings and featherings are obtained from an acre of cinnamon after 4 years.

Clove (*Syzygium aromaticum* (L) Merr. and Perry)

The clove of commerce is the dried, unopened flower buds (Figure 14(c)) of the evergreen tree, *Syzygium aromaticum* (L), of the family Myrtaceae. It is native to the Moluccas. The major clove-producing countries are Indonesia, Zanzibar, and Madagascar. The importing countries are India, USA, Germany, France, and Singapore. The world production is estimated to be 63 700 ton and Indonesia alone accounts for 66% of the world production.

India grows two morphological variants of clove, one with bolder flower buds (king clove) and the other a smaller spreading plant type (dwarf clove). Crop improvement in clove is confined to selection of high-yielding mother cloves. Propagation of these trees is through seeds. The clove is a slender, evergreen tree reaching a height of 10–15 m. The fruit is a one-seeded drupe popularly known as mother clove. It contains one oblong seed 1.5 cm long. Clove flowers are bisexual and inbreeding is common. The variability in clove is very limited, with the present-day population in India reported to have been originated from a few trees with a narrow genetic base originally introduced into India. Self-pollination also limits the scope for variability.

Propagation of clove is through seeds collected from healthy regular-bearing trees. Seed viability is short and hence they are to be sown immediately after collection. One- to two-year-old seedlings are suited for main field planting. Clove requires a humid climate and grows at 600–1000 m above sea level with a rainfall of 1500–2000 mm and a mean temperature of 20–30° C. Clove is a shade-loving plant and is successfully cultivated under coconut plantations aged more than 20 years.

Clove trees start flowering from the forth year after planting under good management conditions. Full-bearing stage is reached only after 15 years. Flowering season ranges from October to December. Flower buds are harvested when they turn pink. The harvested flower buds are separated from the clusters by hand and are dried for 4–5 days. On an average 3–4 kg of dried buds can be harvested from 15-year-old clove trees. The dried buds yield 14–21% oil, which contains 70–90% eugenol and 5–12% eugenol acetate.

Nutmeg (*Myristica fragrans* Houtt.)

Nutmeg (Figures 14(d)–(i)) includes two distinct spices: nutmeg (seed) and mace (aril). Native of Indonesia (Moluccas Islands), the nutmeg tree grows there abundantly and is now naturalized in West Indies, Sri Lanka, India, Philippines, Tropical America, and Pacific Islands. It is also grown in a small scale in Sri Lanka, Trinidad, China, India, Tobago, Zanzibar, and Mauritius.

Nutmeg is an evergreen aromatic tree usually 10–20 m tall with spreading branches. The fruit is pyriform and yellow in color (Figure 14(d)). The pericarp is fleshy when the fruit matures; it splits into two, exposing the scarlet-colored net like aril covering the dark brown seed (Purseglove *et al.*, 1981; Verghese, 2000; Krishnamoorthy, 2000). The principal constituents of nutmeg are fixed oil (fat), volatile oil, and starch. The flavor and therapeutic action are due to the volatile oil whose content varies from 6% to 16% based on the origin and quality of nutmeg (Lewis *et al.*, 1966). Nutmeg fat contains eight fatty acids, the most important of them being myristic acid. Nutmeg and mace are used as a stimulant, carminative, astringent, aphrodisiac, and hallucinogen. Oil of nutmeg or mace is employed for flavoring food products and liquors, soaps, tobacco, dental creams, and perfumery products. The fleshy pericarp of the fruit is used for making pickles and jelly.

The genus *Myristica* consists of approximately 120 species. A high amount of variability has been reported in growth rate, productivity, size and shape of the leaf, flower size and shape and size of the fruit and nut, and the amount of mace in nutmeg (Krishnamoorthy and Rema, 1991; Haldankar *et al.*, 1999). Crop improvement in nutmeg is confined to selection and multiplication of elite lines. So far, three improved varieties were released in nutmeg.

The general method of propagation of nutmeg is through seeds collected from regular-bearing and high-yielding trees. The seeds have low viability and hence are to be sown immediately after collection. Germination commences from about the 40th day and lasts for up to 90 days after sowing. The germinated sprouts must be transferred to polythene bags (30 cm×15 cm) containing a potting mixture. After 1 year in a nursery the seedlings can be field planted. Nutmeg, being a dioecious crop, requires that the proper ratio of female and male plants (10:1) be maintained in the plantation. Vegetative propagation techniques, such as approach grafting, softwood grafting, epicotyl grafting, budding, and top working in nutmeg are commonly used, with epicotyls grafting being the best (Mathew, 1985; Haldankar *et al.*, 1999; Rema *et al.*, 2000).

Nutmeg requires a hot humid climate with no pronounced dry season and is a shade-loving plant. It can be grown up to approximately 900 m above sea level. In India, nutmeg is planted as an intercrop in coconut plantations. Fruiting commences from 6 to 9 years depending on the climate and planting materials used. Optimum productivity is attained in approximately 15 years. Fruits are collected periodically from the tree by hand or with hooked sticks or allowed to fall naturally on the ground. All three parts of the fruit, viz. the pericarp, aril (mace), and seed (nutmeg) are separated carefully and sun dried or are dried by mechanical means. Aflatoxin is a serious post-harvest problem in the mace and nuts.

Garcinia (*Garcinia cambogia* Desr (Syn. *Garcinia gummi-gutta, L.*) and Kokam (*Garcinia indica* Chiosy)

Garcinia (Figure 15) and Kokam are two potential underexploited tree spices, currently gaining much agricultural, commercial, industrial, and medicinal importance. Cambodge, the product of commerce, is the dried pericarp lobe used in the preparation of Indian dishes. Fruits are edible but too acidic to be eaten raw. They are valued for the processed and dried pericarp used as condiment for flavoring curries, as a very popular spice used in cooking, as a major ingredient in



Figure 15 The spice tree, *G. cambogia* (left); dried rinds of comboge (center); ripe fruits of *G. indica* (right).

many dishes as a substitute for tamarind. They are also used in the pharmaceutical industry as a source of hydroxy citric acid (HCA), an antiobesity compound, and as an ingredient in herbal medicines. The reddish rind of kokum is used for the preparation of a refreshing, attractive drink. The fruit has excellent therapeutic value against obesity and is used for ailments, such as rheumatism, rickets, and enlargement of spleen. The fruit, being rich in acids, also possesses antiseptic properties. The fruit rind of kokum after drying and mixing with sugar sirup is used to control hyperacidity. Garcinia rind is the richest known natural source of HCA, the derivatives of which are potent metabolic regulators of obesity. The unique acid lowers the blood lipids, such as cholesterol and triglycerides, by triggering fatty acid oxidation in the liver via thermogenesis.

Garcinia and Kokam are both found naturally in the Western Ghats and in the evergreen forests of North Eastern India and Southeast Asia. In India, Garcinia has two centers of distribution: the Western Ghats and the North East region. *G. cambogia* and *G. indica* occur in the Western Ghats of Kerala.

Garcinia is a moderate sized (18–20 m) evergreen tree with an oval-shaped crown. It has separate male and bisexual trees and it is a cross-pollinated species. Flowers are solitary or in groups of 2–3 in bisexual trees and in clusters of 3–5 in male trees. Fruit are ovoid, weighing 50–180 g, and are yellow or reddish yellow at maturity. Kokam is a small slender evergreen tree growing up to 18 m tall with drooping branches that attain a pyramidal shape. It is a dioecious tree with spherical fruit each having 5–8 seeds compressed in an acid pulp.

Immediately after harvest the fruit is cut into two halves. Seeds along with the pulpy mass are removed and the cleaned rind is either sun-dried or smoke-dried for 3–7 days to keep a moisture level of 15–20%. Cambodge and kokam concentrate are produced from dried or fresh rind.

Garcinia is mostly collected from the wild or from home gardens; commercial cultivation of garcinia is yet to pick up. Propagation is through seeds with the seedlings segregated into productive bisexual and unproductive male trees.



Figure 16 The fruit of tamarind.

Vegetative propagation through softwood grafting/side grafting is commonly practiced. A hardy tropical tree crop, it can be grown in tropical and subtropical climates from seashore to an elevation of 1200 m. It is adaptable to a wide range of climatic and soil conditions.

Tamarind (*Tamarindus indica* Linn.)

Tamarind (Figure 16) is one of the most important tree spices. Originated in Madagascar, it is now cultivated in India, Thailand, Mexico, the Middle East, Africa, Southeast Asia, the Caribbean, Bangladesh, Myanmar, Malaysia, Sri Lanka, Central Africa, Australia, and Central and South America. It is one of the most common trees in most parts of India and the source of one of the most commonly used spices in the Indian kitchen. The fruit pulp, the useful part of tamarind, is a rich source of tartaric and ascorbic acids. India exports tamarind pulp to the UK, Iraq, Oman, Germany, and some countries in the Pacific.

Tamarind is a slow-growing evergreen tree with a height of up to 25 m. It prefers a warm climate, withstands drought, but is sensitive to frost. The tree flowers between April and June and the fruit ripens by winter. Tamarind flowers are bisexual and produced in small terminal racemes. Pollination is by bees. Fruit is a pod, 10–15 cm long and 2–3 cm wide, 3–10 seeds each, and is strap shaped. The pods begin to ripen from February to April. Annual fresh yield is in the range of 150–500 kg per tree.

All the plantations in India originated from seedlings and hence there is immense scope for selection of desirable traits. A germplasm bank with more than 500 collections is maintained in India. Twelve elite types were short listed from the germplasm for multiplication and distribution. The variety Periakulam-1, an early-bearing line, was released for cultivation in India. Two more high-yielding cultivars, viz. Prathisthan and No. 263 selection, were also released. In Thailand, a very sweet tamarind type is reported to be grown. Local cultivars, such as Cumbum or Lower Camp and Urigam, are popular in the Cumbum area of Tamil Nadu, India. On the basis of color and taste of pulp, tamarind is classified as the sweet and red types. The red-fleshed type is known as 'yogeswari.'

Tamarind is a highly adaptive evergreen tree that can thrive well at temperatures in the range of 30–40 °C and an annual rain fall of 500–2000 mm. Tamarind is suited for growing in semiarid areas. It does well in poor soils. In India, tamarind grows well in almost all areas, except under high elevations. It can be propagated by seed or clonally. Approach grafting and softwood grafting are also used in addition to patch budding for large-scale multiplication.

Fruits contain approximately 30% pulp, 40% seed, and 30% hull. When fruits are ripe, the pulp is rust-colored and its water content is approximately 38%. It is rich in pectin and reducing sugars and contains a significant amount of organic acids, 98% of which is tartaric acid. The main flavor compound of the pulp is 2-acetylfuran.

The fruits are harvested when fully ripe and the fruit shell is almost dry. The ripe fruits are shelled, the seeds and pulp are removed, and the separated pulp is dried for a day or two in sun and then mixed with approximately 10% of common salt. The pulp has a sharp, sweet, sour, fruity taste, and a sweetish brown aroma. The fruit pulp is the chief agent for sour curries, sauces, chutneys, and certain beverages throughout the greater part of India. Tamarind fruit is reported to be used as a raw material for the preparation of wine-like beverages.

Curry Leaf (*Murraya koenigii* Linn.)

Curry leaf (Figure 17) is cultivated for its aromatic leaves and is widely used in Asian cooking as an essential flavoring in most Indian food preparations. Leaves, roots, and seeds of the plant all contain the active principles and essential oil of medical value and extensively used in many Ayurvedic preparations. Leaves are used internally against dysentery, diarrhea, and also to check vomiting. Leaf paste is applied externally for curing bruises and bites of poisonous animals.

Thought to have originated in India and Sri Lanka, *M. koenigii* is grown from South and East Asia to Australia. It occurs widely in India, Myanmar, Java, Laos, Bangladesh, Madagascar, Sri Lanka, Malaysia, and the Pacific Islands. It also



Figure 17 Fresh curry leaves.

grows wild and is found almost throughout India up to an altitude of 1500 m, including in the forest along the foot of Himalayas to Sikkim and Assam, Chitagong, upper and lower Burma, and Andaman.

A small tree reaching a height of 6–8 m under cultivation, it is maintained as a bush by periodical coppicing. Flowers are white and fragrant; berries are purplish-black when mature. The stem and branches are covered with brownish bark and have a pleasant aroma but pungent taste. Curry leaf plants are broadly classified into the broad-leaved and narrow-leaved types. The broad-leaved varieties are used for commercial cultivation, whereas narrow-leaved varieties are grown for home use.

Curry leaf is propagated by its seeds that germinate in 3–4 weeks under partial shade. Seedlings can be raised in individual polybags, which after 1 year can be directly planted in the field. Curry leaf can also be propagated by root suckers. Being a hardy crop, curry leaf grows under varying climatic and soil conditions, including at altitudes of 60–1200 m above sea level and at temperatures of 16–37 °C.

Commercial harvesting of leaves can start at 3-month intervals when the trees are of 3–4 years old. The average yield is approximately 20 ton ha^{-1}. Fresh leaves contain up to 2.6% essential oil. The important aroma components are β-caryophyllene, β-gurjunene, β-elemene, β-phellandrene, β-thujene, α-selinene, β-bisabolene, limonene, β-*trans*-ocimene, and β-cadinene. Fresh leaves on steam distillation yield approximately 2.6% of a volatile oil (curry leaf oil). The oil contains DL-α-phellandrene, D-sabinene, D-α-pinene, dipentene, D-α-terpineol, caryophyllene, safrol, cadinene, cadinol, lauric acid, and palmitic acid.

Pimento (Allspice) (*Pimenta dioica* L. Merr.)

Pimento of commerce is the dried unripe fruits of *P. dioica* L. Merr., an evergreen tree that grows to a height of 8–12 m and belonging to the family Myrtaceae. Pimento is the major spice of Jamaica contributing 70% of the world's production. It is grown to a certain extent in Mexico, Honduras, Guatemala, Cuba, Haiti, and Costa Rica, besides a few West Indian islands. The dried immature berry combines the odors and flavors of four spices, namely, nutmeg, clove, cinnamon, and black pepper, hence the name 'allspice.' Allspice is an aromatic,

stimulant, digestive, and carminative. Powdered fruits are used against flatulence, dyspepsia, and diarrhea and are used in the preparation of tonics and purgatives. It is used in many culinary preparations, such as soups, sauces, ketchup, pickles, meat, curry powder confectionary, and in liquor as a flavoring.

Allspice is polygamodioecious in nature, which makes it difficult to identify functional male and female trees until they begin to bear fruit. The common method of propagation is by seeds collected from high-yielding and regular-bearing trees. The trees start flowering in 5–6 years under good management. Fully developed greenish berries are harvested, dried, and used as spice.

Seed Spices

Coriander, cumin, fennel, and fenugreek are the major seed spices of commerce.

Coriander (*Coriandrum sativum* L.)

Coriander (Figures 18(a)–(d)) is grown extensively in India, Russia, Morocco, Romania, Bulgaria, Mexico, France, Spain, Italy, Holland, Argentina, China, Egypt, North Africa, Hungary, Yugoslavia Poland, Czechoslovakia, Guatemala, USA, Middle



Figure 18 Coriander and cumin (a) coriander seed; (b) coriander field view; (c) powdery mildew on coriander foliage; (d) coriander as an intercrop in young black pepper plantation in Brazil; (e) cumin field view; (f) cumin wilt; and (g) powdery mildew on cumin.

East, and South Asia. India is the major producer where it is cultivated for its leaves and seeds. Malaysia, Singapore, South Africa, UAE, UK, USA, Saudi Arabia, and Indonesia are the major importing countries. It is native to Eastern Mediterranean region and Southern Europe and is widespread as both cultivated and naturalized weedy species throughout the warmer regions of the world.

Coriander is a short-season annual, semierect to erect herb cultivated for its dried aromatic fruits and tender leaves. The fruit consists of two mericarps, almost round, 3–4 mm in diameter. The leaves have a totally different flavor and are used fresh or dried in cooking. All parts of the plant-tender stem, leaves, flowers, and fruits have characteristic pleasant aromatic odor. The seed has a very pleasant odor and taste due to the presence of essential oil varying from 0.1% to 1.7% on dry weight basis. The composition of oil varies depending on the country of origin and climatic conditions where it is grown. The content of essential oil is generally more when grown in colder regions and at higher altitudes. Thus, the volatile oil content is higher in the Russian and European coriander varieties and the fruits are smaller than the Indian coriander. The Russian varieties have small spherical fruits and are considered superior to Indian and Moroccan due to their higher essential oil content. The leaf contains approximately 4% volatiles on a wet leaf basis. The principal component of the oil is D-linalool, also known as coriandrol (60–70%), an important starting material for the production of a variety of aroma chemicals. Other compounds present are D-pinenes, terpinenes, geraniol, and borneol.

The crop-improvement programs in coriander are essentially selections from open pollinated or controlled crosses. Approximately 24 improved cultivars were released for cultivation in India. A few tolerant/resistant lines against wilt and stem gall have been developed. A dry and moderately cool weather condition favors high seed formation as well as quality of the produce. Sowing is done by broadcasting on plowed and leveled land or using seed drills. Coriander is grown both as a rain-fed and irrigated crop. The crop is ready for harvest in approximately 90–120 days after sowing for grains and 40 days for greens depending on the varieties and growing season. Leaf plucking to the extent of 50% of the foliage, 60–75 days after sowing, gives an economical return. Fruits ripen progressively on the plant; harvesting is done when fruits are fully mature, i.e., when the green color has changed slightly to yellow. Bundles are dried under shade to avoid breakage of seeds and loss of volatile oil. After drying, plants are mildly threshed and grains are separated. Seeds can shatter if harvesting is delayed (Singhania *et al.*, 2005).

Cumin (*Cuminum cyminum* L.)

Cumin (**Figures 18(e)–(g)**) of commerce is the dried fruit of the annual herb, *C. cyminum* L., and belonging to the family Apiaceae. Cumin seeds are small, elongated, yellowish brown, aromatic, and spicy, having a bitter taste and strong flavor. The main ingredient of cumin is cuminaldehyde (cuminic aldehyde) present in the volatile oil. Cumin finds worldwide use in foods, beverages, liquors, medicines, toiletries, and perfumery. Seeds are extensively used in a variety of culinary preparations. Cumin is also an important ingredient of curry powder and spice mixture; for flavoring soups, vegetables, sausages, pickles, and a variety of curries; and for preparing cold/soft drinks like Jal-jeera. The aromatic oil is used for flavoring curries, liquors, cordials, and also in perfumery. It is also used as a fungicide, insecticide, and as a veterinary medicine.

Cumin is a small, slender, herbaceous bushy annual plant with a much branched stem and long finely dissected narrow, deep-green leaves. The plant grows to a height of approximately 15–60 cm, with many branches. Flowers are small, rose, or white. The plant comes to bearing in 60–90 days from sowing. The elongated grayish (yellowish brown) bristly fruit (schizocarp) are approximately 6 mm long, tapering toward both ends, laterally compressed with a short stalk. Seeds contain 2–5% volatile oil of which 40–65% is cuminaldehyde.

Cumin is grown in Egypt, Syria, Turkistan and in the Eastern Mediterranean region, Iran, China, Mexico, Indonesia, Japan, Pakistan, Italy, Afghanistan, Germany, whereas UAE, UK, USA, Singapore, Nepal, Malaysia, Japan, Bangladesh, and Brazil are the major importers. India is the largest producer.

Cumin is mainly a tropical plant and thrives well in tropical and subtropical climates. A moderately cool dry climate is best for cumin cultivation and hence it is grown as a winter crop. The crop matures in 130–150 days after sowing when the leaves turn yellow and is ready for harvesting by the beginning of summer. The crop is vulnerable to frost damage. Five high-yielding high-quality cultivars have been released for cultivation in India (Patel *et al.*, 2005).

Harvesting, usually done in the morning hours to avoid shedding losses, is by uprooting the whole plant or cutting the plant with a sickle. The harvested plants are bundled and stacked for 2 days and subsequently spread out on the threshing floor to dry in the sun. Threshing is either by beating with stick or by rubbing the plants with hands in to gunny bags. Seeds are cleaned by mechanical winnowing, and are packed and stored under ambient conditions.

Fennel (*Foeniculam vulgare* Miller)

Fennel (**Figures 19(a)–(b)**), the dried fruit of an aromatic herb, *F. vulgare* Miller, belonging to the family Apiaceae, is a native of Europe and the Mediterranean region and is cultivated in temperate regions around the world. The main fennel-producing countries are India, Egypt, China, Romania, Russia, Germany, France, Italy, Japan, Argentina, USA, Indonesia, and Pakistan. Morocco, Spain, and Southern Europe. The main importing countries are Canada, Malaysia, UAE, UK, Japan, Malaysia, Singapore, Saudi Arabia, USA, Bangladesh, South Africa, Bahrain, and Holland.

The feathery fragrant leaves are used as a herb and the seed as spice. The leaves are also used for garnishing. Fennel seed is used for flavoring meats, vegetable products, fish sauces, soups, salad dressings, stews, breads, pastries, and alcoholic beverages. Fennel contains 1–3% of a volatile oil composed of approximately 50–60% anethole and 20% de-fenchone. Other compounds present in fennel are D-α-pinene, D-α-phellandrene, dipentene, methyl chavicol, feniculum, anisaldehyde,



Figure 19 Fennel and fenugreek (a) field view of fennel; (b) mature seeds of fennel; (c) fenugreek seeds; (d) field view of leafy type of fenugreek; (e) root rot on fenugreek; and (f) powdery mildew on fenugreek foliage.

and anisic acid. The volatile oil of fennel is used in favoring medicines; to scent soaps and perfumes; flavor beverages, baked foods, condiments, ice creams, and liquors and season meats and sausages. Fennel is used in Ayurvedic or domestic medicines. The plant is pleasantly aromatic and used as a potted herb; leaf stalks are used in salads and vegetables (Singhania and Singh, 2005).

Fennel can be grown in all types of well-drained soils except sandy soil. It requires a fairly mild climate and is grown as a cold-weather crop in North India as well as in higher elevations in South India.

When the fruiting umbels turn brown they are ready for harvest. As the umbels do not mature uniformly, several harvests are necessary to maximize yield. For good quality fennel, the umbels should be picked when seed development is completed and before full maturity when seeds start turning yellow. After harvesting, umbels are dried in sunlight for 1–2 days, followed by further drying in shade to retain the color.

For producing the chewing-type fennel, umbels are harvested at 30–40 days after pollination when seed size is just half of fully developed seeds.

Fenugreek (*Trigonella foenum-graecum* L.)

Fenugreek (**Figures 19(c)–(f)**) is the dried seed of a slender annual strongly scented herb, *T. foenum-graecum* L. and belongs to the family Fabaceae. It is a native of Europe and Asia (Eastern Mediterranean) and is now cultivated in India, Pakistan, France, Morocco, Greece, Lebanon, Germany, Argentina, and USA. Bahrain, UAE, Holland, Saudi Arabia, USA, and UK are the major importing countries, whereas Argentina, Algeria, Egypt, France, Moroco, Ethiopia, Lebanon, Australia, and Pakistan are the major producing countries.

The seed has a strong aroma and bitter taste and is used as a spice in the preparation of a variety of dishes and pickles. Fresh green leaves are used as a vegetable and whole plants as fodder. Ground seed is used in curry powders, spice blends, pickling spice, mayonnaise, etc. The seed or extracts are commonly used in sirups, pickles, baked foods, condiments, chewing gums, and meat seasoning and as an emollient and flavoring agent in pharmacy. Diosgenin, an important steroid, is present in seeds. Most of the product is consumed domestically. Because of its high nutritive contents, it is an important ingredient in vegetable dishes. Fresh or dried leaves are widely used in Indian cooking and are often combined with vegetables.

Flowers are small whitish and yellow. The crop flowers in 50 days after sowing and it takes 80–90 days to reach maturity after flowering. Fenugreek grows well in subtropical climates, with a moderately cool climate being required for proper growth and good yield. It is generally grown as irrigated crop (Singhania *et al.*, 2005).

The ground seed has a very strong spicy but bitter flavor. The volatile oil content is extremely odorous and fixed oil has a very bitter taste. The volatile oil content of fenugreek is very small (less than 0.02%). It also contains fixed oils (fat) at 5–7%. They contain the alkaloids trigonelline and choline. It is rich in proteins, minerals, and vitamins.

See also: Analyses of Total Phenolics, Total Flavonoids, and Total Antioxidant Activities in Foods and Dietary Supplements. Breeding: Plants, Modern. Crop Pollination. Genebanks: Past, Present, and Optimistic Future. Pathogen-Tested Planting Material. Plant Disease and Resistance

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Stem Cells

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Introduction

At the time of their discovery in 1981 by Sir Martin Evans and his colleagues at Cambridge University, embryonic stem cells (ESCs) were defined as pluripotential cells that could be maintained in culture and could retain the ability to contribute to all of the somatic lineages and the germline. At the time, the field was aligned with an agricultural interest in splitting embryos at early stages (e.g., 4 and 8 cell embryos) to propagate genetically identical animals (i.e., cloning), a desire to insert specific modifications into the genome of animals and the field of tumorigenesis. The hope of many was that pluripotential cell lines would be found and propagated with the ease of transformed cells derived from tumors. Speculation during this era also predicted that these cell lines would be genetically modified using emerging recombinant DNA technologies. Furthermore, it was the hope of many that whole animals could be derived from these pluripotential cell lines in the same way that whole plants could be propagated from callus tissues.

In spite of enormous effort, very few of the predictions of the 1980s have been realized as they were envisaged. Nevertheless, the objectives of accessing cloning technologies and developing genetic engineering tools have been achieved. The equivalent of murine ESCs has not been found for any other animal but the need for these cell lines has been greatly diminished by the development of somatic cell nuclear transfer (SCNT), which shifted the focus from stem cells to reprogramming of somatic cells.

Murine Embryonic Stem Cells Are the Gold Standard

Murine ESCs remain the gold standard against which all other pluripotential cell lines are measured (Figure 1). They can be maintained in culture for extended periods, they can be genetically modified using a variety of technologies and they will contribute to both somatic tissues and the germline. To date, thousands of mutations have been inserted into the murine germline using a variety of sophisticated genetic engineering approaches. Although most of these mutants have been created to advance biomedical research (e.g., see the Jackson Laboratories and Taconic catalogs), some of these mice have been used to create many of the human therapeutic antibodies marketed in the past decade (Lonberg, 2008).

The Murine Embryonic Stem Cells Phenotype

Although morphology and gene expression are used as surrogates for the ESC phenotype (see Sections Morphology and Culture Conditions for Murine Embryonic Stem Cells; Gene Expression Profile of Murine Embryonic Stem Cells), the ultimate property defining ESCs is their ability to contribute to somatic tissues and the germline following their return to an embryonic environment. In mice, a few ESCs are injected into the inner cell mass to form a G0 chimera comprised of endogenous cells and ESC-derived cells. Ideally, the ratio of endogenous cells to ESC-derived cells should be very low and technologies to entirely eliminate the contribution of the recipient murine embryos have been developed (Nagy *et al.*, 1993). From a theoretical perspective, the recipient embryo serves only to organize the donor ESCs into an embryonic template. Practically, the contribution of ESCs to somatic tissues can be evaluated using visual markers such as coat color or introduced genes such as green fluorescent protein (GFP). Quantitation of the contribution of ESCs to the germline requires mating the G0 chimera to obtain G1 offspring. Typically, the G0 gonad contains both ESC-derived and endogenous sperm or eggs and the ratio of donor-derived to endogenous offspring (i.e., the rate of germline transmission) varies from 0 to 100%. For mice, *in vivo* evaluation of the rate of germline transmission by breeding can be achieved within a few months. However, the long generation times of agriculturally relevant animals makes *in vivo* evaluation of putative ESCs time consuming and expensive. Hence, morphology, behavior of the cells *in vitro*, the culture conditions, and gene expression profiles are used as indirect measures of the ESC phenotype (see Sections Morphology and Culture Conditions for Murine Embryonic Stem Cells; Gene Expression Profile of Murine Embryonic Stem Cells).

Morphology and Culture Conditions for Murine Embryonic Stem Cells

Murine ESCs require the presence of Leukemia Inhibitory Factor (LIF) in the media to maintain ESC morphology and

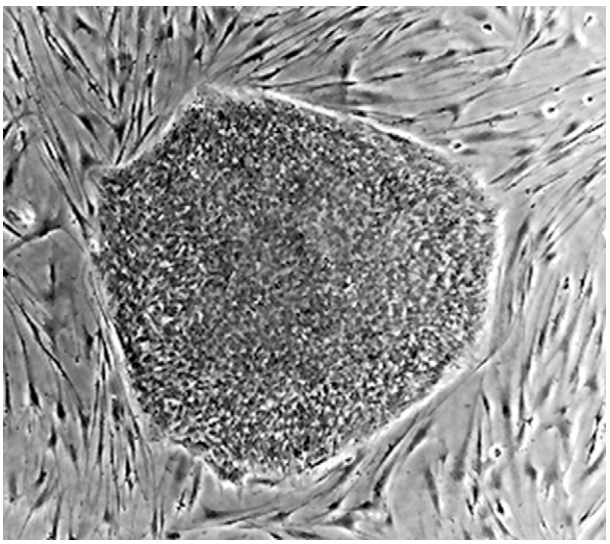


Figure 1 Murine embryonic stem cells growing on a layer of murine embryonic fibroblasts. Reproduced from Adamo, L., García-Cardeña, G., 2011. Directed stem cell differentiation by fluid mechanical forces. Antioxidants and Redox Signaling 15 (5), 1463–1473.

 doi:10.1016/B978-0-444-52512-3.00239-4

functionality. Typically they are cultured in Dulbecco's Modified Eagle's Medium supplemented with 10–20% fetal bovine serum, glutamine, nonessential amino acids, β-mercaptoethanol, and 1000–2000 units of LIF in the presence of a feeder layer comprised of inactivated murine embryonic fibroblasts (see Section Relevant Website). Alternatively, murine ESCs can be grown without feeders on gelatin coated plates. Murine ESCs are small cells attached to the feeder layer with a large nucleus and small amounts of cytoplasm.

Gene Expression Profile of Murine Embryonic Stem Cells

It is self-evident that cells within tissues express genes encoding their specific function and gene expression profiling has been applied by many in an attempt to define the gene expression profile of pluripotential cells. Murine ESCs are distinguished by expression of Nanog, Oct4, Sox2, and telomerase. Expression of these genes, however, does not necessarily confer all of the properties of murine ESCs, even in the mouse (see Section *In Vitro* and *In Vivo* Evaluation of Murine Embryonic Stem Cells). Characterization of the gene expression profile that confers the ability of cells to contribute to both somatic tissues and the germline has been used as a surrogate in the search for ESCs in other animals, but to date, cells with expression profiles that resemble those of murine ESCs have failed to yield practical contributions to either somatic tissues or the germline. These data underscore the empirical nature of the stem cell research which to date, relies primarily on a functional definition to define the phenotype of these cells.

In Vitro and *In Vivo* Evaluation of Murine Embryonic Stem Cells

In the absence of feeder cells or a substitute substrate, murine ESCs form embryoid bodies. These cystic structures differentiate into many different cell types in the somatic lineages and, therefore, provide evidence that the ESCs are pluripotential (Martin, 1981). Putative ESCs can also be evaluated by injection into the peritoneal cavity of mice, where they form teratocarcinomas. Like embryoid bodies, teratocarcinomas include cells from the endoderm, mesoderm, and ectodermal lineages indicating that they are pluripotential. Construction of embryoid bodies and the formation of teratocarcinomas have been employed as surrogates for pluripotency in the evaluation of putative ESCs from other animals. Although embryoid bodies and teratocarcinomas are reasonable surrogates for contributions to the somatic tissues of chimeras, equivalent surrogates for germline transmission in chimeras are not available.

Non-Murine Embryonic Stem Cells

The elusive search for non-murine ESCs may be attributed to their absence during embryogenesis. Although it is clear that ESCs share many of the attributes of inner mass cells in the blastocyst, it remains unclear if ESCs and inner cell mass cells are identical. The murine ESC phenotype might be created by the conditions of the cell culture system or it may be a transient cell type during embryogenesis that is held in a static state *in vitro*. It is also unclear if there is sufficient homology between the inner cell mass of murine and non-murine blastocysts to extrapolate to other species although the failure to find non-rodent ESCs suggests that conditions that support inner cell mass cells in other mammals are different from those that support murine ESCs.

The close phylogenetic relationship between rats and mice suggests that culture conditions supporting murine ESCs might also support isolation and propagation of inner cell mass cells from rats. However, 25 years of empirical tweaking of the culture conditions were required before conditions for the culture of rat ESCs were described (Meek *et al.*, 2010). As the phylogenetic distance increases to rabbits, the ability to isolate ESCs diminishes. To date, rabbit ESCs with *in vitro* characteristics that resemble those of murine ESCs have been reported but none make significant contributions to somatic tissues and the germline of chimeras (Tancos *et al.*, 2012).

In mice, ESC-like cells can be isolated from the epiblast of post implantation embryos. Although these ESC-like cells share morphological features and several *in vitro* characteristics with mouse ESCs, there are some important differences. For example, they grow more slowly, they do not respond to LIF, and they require fibroblast growth factor. Functionally, germline chimeras cannot be created from these ESC-like cell lines. Stem cell cultures from ungulate embryos share many of the properties of murine epiblast derived ESC-like cells. In some cases, ESC-like cultures from ungulate embryos have expressed genes such as Nanog, Sox2, or telomerase, and formed embryoid bodies *in vitro* and contributed to teratomas *in vivo*. To date, however, none have demonstrated the capacity to make either significant contributions to somatic tissues or contribute to the germline when injected into recipient embryos. The details of the *in vivo* and *in vitro* characteristics of embryo derived cell cultures from livestock are presented in excellent reviews by Blomberg and Telugu (2012) and Gandolfi *et al.* (2012).

Avian Pluripotential Cell Lines

Two pluripotential cell lines with unique attributes have been isolated from chicken embryos. One of the cell lines is referred to as an ESC because it is morphologically similar to murine ESCs (**Figure 2**) and it shares many of the gene expression profiles of its murine counterpart (van de Lavoir *et al.*, 2006a; Jean *et al.*, 2012). In spite of their morphological similarity, however, chicken ESCs contribute only to somatic tissues when returned to an embryonic environment. Chicken ESCs can be genetically modified and the genetic modifications are expressed in a tissue-specific and developmentally regulated manner (Zhu *et al.*, 2005). The contribution of ESC-derived tissues in chimeras can be altered by compromising the recipient embryo using irradiation, time, and temperature to produce chicks that appear to be completely derived from the donor ESCs (van de Lavoir *et al.*, 2006a). Unlike their murine counterparts, however, unequivocal contributions to the germline have never been reported even in the presence of extensive contributions to somatic tissues.

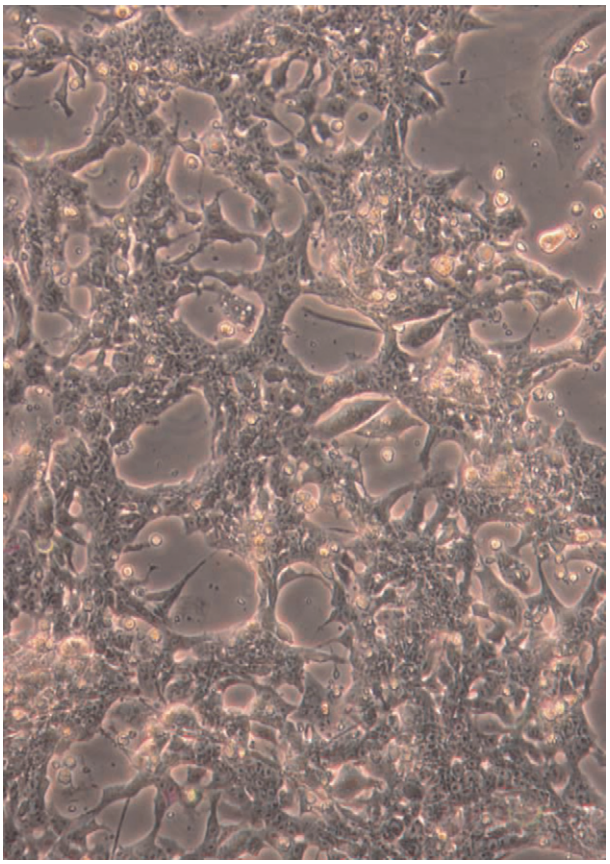


Figure 2 Chicken embryonic stem cells are characterized by their small size, large nucleus, and prominent nucleolus. Reproduced from van de Lavoir, M., *et al.*, 2006b. High-grade transgenic somatic chimeras from chicken ESCs. Mechanisms of Development 123 (1), 31–41.

The second pluripotential cell line isolated from chicken embryos is derived from the primordial germ (PG) cell lineage. In culture, these cells retain the morphology and non-adherent features of their *in vivo* counterparts (**Figure 3**). The media contains a buffalo rat liver (BRL) feeder layer and BRL conditioned media. When injected into the vasculature of Stage 13–17 (H&H) recipient embryos, avian PG cells migrate to the developing gonad and colonize the germline of G0 chimeras. Some of the G0 chimeras will transmit the PG cell-derived genotype to their G1 offspring and several lines of chickens expressing GFP have been produced using this technology (van de Lavoir *et al.*, 2006b; Macdonald *et al.*, 2010; Kim *et al.*, 2010; Macdonald *et al.*, 2012; van de Lavoir *et al.*, 2012). In addition, chickens with specific modifications in the heavy and light chain immunoglobulin genes are being produced as part of a novel discovery platform for therapeutic antibodies (see Section Relevant Websites).

Stem Cells as Vehicles for Creating Transgenic Animals

One of the compelling reasons to identify culture conditions that support the propagation of pluripotential stem cells is the introduction of genetic modifications to create 'transgenic' or

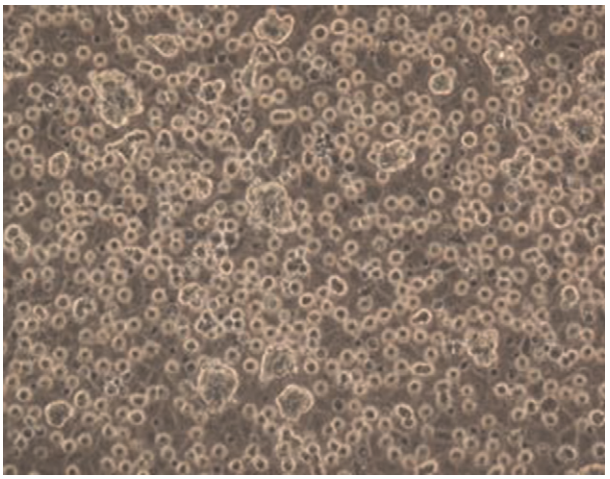


Figure 3 Chicken primordial germ cells are non-adherent, large, single cells with abundant cytoplasm. Reproduced from Song, Y., Duraisamy, S., Ali, J., *et al.*, 2014. Characteristics of long-term cultures of avian primordial germ cells and gonocytes. Biology of Reproduction 90 (1), 15, 1–8.

'genetically modified' animals. This utilitarian objective imposes parameters on the culture conditions that separate experimental protocols from robust procedures. Typically, introduction of genetic modifications into the genome occurs at a frequency between 10^{-5} and 10^{-8}. Hence, a culture must contain at least 10^5–10^8 cells to support a reasonable expectation that the desired genetic modification can be recovered. Typically, the likelihood that murine ESCs or chicken PG cells will contribute to the germline declines as their duration in culture increases. Therefore, the cells must propagate at a sufficient rate to obtain 10^5–10^8 cells in a period of several weeks. Because the genetic modifications are inserted into the genome at a low frequency, the culture used for injections into embryos is derived from a single founder cell, which must be expanded to 10^5–10^6 cells for evaluation, injection, and storage. These constraints of growth rate, efficiency of genetic modification, and a general decline in the ability of cells to contribute to the germline as the culture ages require a cell cycle that is completed within 24–36 h. When cell division occurs at longer intervals, the facilities, time, and cost of creating transgenic animals become prohibitive.

The long gestation periods of domestic mammals and consequent significant interval between injection of a putative ESC and recovery of the genotype in G1 offspring could be overcome by using ESC nuclei in SCNT. This idea receives support from studies in mice showing that the efficiency of nuclear transfer is greater when the donor nucleus is derived from an ESC (Hochedlinger and Jaenisch, 2002). Nevertheless, the overall rate of production of animals by SCNT is typically less than 3% of all reconstructed oocytes.

Induced Pluripotential stem Cells

In 2006, Takahashi and Yamanaka reported that adult mouse fibroblasts could be reprogrammed into an ESC-like state by introducing Oct4, Sox2, Klf4, and c-Myc (Takahashi and

Yamanaka, 2006). This remarkable discovery sparked an intense debate about the equivalency of ESCs and induced pluripotential stem cells (iPSC), which now appears to be resolved. In general, there is as much variation between lines of murine iPS cells and murine ESCs as there is within lines of these two cell types. Although there is considerable variation in the ability of both cell types to contribute to the germline of recipient embryos, some cell lines of each type can give rise to viable mice that are completely derived from both ESC lines and iPSC lines (Nagy *et al.*, 1993; Boland *et al.*, 2009). In principle, therefore, iPSC could be derived from all classes of livestock and used directly as ESCs or indirectly as nuclear donors for SCNT. The advent of induced pluripotential cells in mice has provided insights into the molecular events that occur as somatic cells acquire an ESC-like phenotype and these data may be applicable to reprogramming of somatic cells from livestock species (Buganim *et al.*, 2013). To date, however, none of the putative iPSC lines from livestock or poultry, which express some of the *in vitro* characteristics of murine ESC, have demonstrated significant contributions to somatic tissues or the germline.

Lineage-Specific Stem Cells

Research with stem cells in livestock and poultry has primarily focussed on pluripotent cell lines and their application to cloning and genetic engineering. In horses, however, mesenchymal stem cells derived from adipose tissue or bone marrow have been used in the treatment of tendinopathies (Muttini *et al.*, 2012). To date, this novel approach to the difficult problem of treating tendinopathies in horses has not been used in a sufficient number of clinical situations to evaluate effectiveness. As the field of stem cell biology matures, the utility of tissue-specific stem cell treatments might gain wider acceptance if they deliver both short- and long-term benefits.

Stem Cells and Genetic Engineering

Applications of stem cell technology in domestic animals are frequently associated with the introduction of modifications to the genome and this application is often used as the rationale for developing pluripotential cell lines (Etches, 2006; Petitte *et al.*, 2004; Sang, 2004; Park and Han, 2012). In chickens, the stem cell approach has provided a route to make both random (van de Lavoir *et al.*, 2006b; Macdonald *et al.*, 2010; Kim *et al.*, 2010; Macdonald *et al.*, 2012; van de Lavoir *et al.*, 2012) and site-specific (Schusser *et al.*, 2013) modifications to the chicken genome. By contrast, genetic engineering in domestic mammals has been achieved using SCNT and cloning. It is reasonable to ask, therefore, if stem cell technologies continue to be relevant to the livestock industries. From a biological perspective, an understanding of the molecular mechanisms that confer a stem cell phenotype to embryonic cells derived from early embryos would reveal fundamentally important information about pluripotentiality. Extrapolation from mouse experiments suggests that SCNT using a pluripotential stem cell as the nuclear donor would increase the proportion of embryos carrying the desired genotype and therefore a concerted effort to isolate cells with an ES phenotype is warranted. In addition, tissue-specific and lineage-specific stem cells could have important roles in veterinary medicine and could be important models as stem cell therapies are developed in human medicine.

See also: Cloning Animals by Somatic Cell Nuclear Transplantation. Transgenic Methodologies – Plants

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ATCC.
http://www.crystalbioscience.com/
Crystal Bioscience.
http://www.jax.com/
JAX Inc.
http://www.Taconic.com
Taconic.

Sugar Crops

SR Kaffka, University of California, Davis, CA, USA
DA Grantz, University of California, Riverside, CA, USA

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Glossary

Bagasse Fibrous material remaining after crushing and extracting juice from sugarcane stalks.
Biomass Dry matter produced by plants.
Bolting The formation of seed stalks by sugar beet.
C3 Photosynthetic system of most plants of temperate regions.
C4 Photosynthetic system of many important tropical crop plants, including grasses, such as maize, sorghum, and sugarcane.
Evapotranspiration The loss of water from a given area by evaporation from the soil surface and by transpiration from plants.
Mega grams per ha (Mg ha^{-1}) An equivalent to metric tons per ha; when multiplied by 0.446 equals short tons (2000 pounds) per acre.
Photosynthesis The process by which green plants utilize the sun's energy to produce carbohydrate from carbon dioxide and water.
Photosynthetically active radiation The spectral range of solar radiation from 400 to 700 nm used by plants for phtotosynthesis.
Stand The number and distribution of plants after emergence from seed or vegetative cuttings.
Sucrose ($C_{12}H_{22}O_{11}$) The sugar of world commerce.
Ton 2000 lb, when multiplied by 1.102 equals 1 MT (mg).

Overview

Sucrose, the common sugar of commerce, is synthesized in most plants as a temporary storage product for photosynthetically reduced carbon, and it is the principal form of carbon transported in plants. Sucrose is typically converted into starch for long-term storage, especially in the seeds of plants, but accumulates to an exceptional degree in unmodified form in sugar beet (*Beta vulgaris* L.) and sugarcane (*Saccharum officinarum* L.). These two crops produce nearly all of the world's supply of sucrose, the 'sugar' of commerce. Small amounts of sucrose and alternative sweeteners are produced from sorghum, agave, stevia, and other sources of natural sweeteners; from high fructose syrup derived from maize grain; and increasingly from noncaloric synthetic sweeteners. Sugar production is a global, agroindustrial enterprise, with 123 countries producing sugar (43 beet, 71 cane, and 9 both, Figure 1). In 2013, approximately 20% of the world's sugar supply was derived from beets and nearly 80% from sugarcane (FAOSTAT, 2013). The most recent estimate for world sugar (sucrose) production is 160 million metric tons. Sugar consumption has been growing at roughly the same rate as world population or 2% per year. There are substantial differences in per capita sugar consumption among nations worldwide. It is highest in Europe and lowest in China and Africa. Sucrose from cane and beets is also converted into ethanol and a wide range of consumer products and feedstock chemicals, substituting for nonrenewable petroleum.

Sugarcane is a perennial tropical grass with highly efficient C4 photosynthesis, high yields, and the ability to provide harvests for several years without replanting. It is suitable for low-technology hand planting and harvest as well as amenable to automation. Production is heavily concentrated in the countries of South America and Asia (Table 1). Brazil has the largest area devoted to sugarcane production for both sugar and ethanol and dominates world sugarcane production. A crop of temperate and Mediterranean regions (Figure 1), sugar beet is a biennial crop grown as an annual. For the most part, it is intensively farmed and is one of the most efficient crop plants. Over time, production technology has come to include a long list of innovations in plant breeding, mechanization, pest management, and fertilizer practice. Sugar beet-producing regions lie north and south of the 30th parallels. It must be grown in rotation with other complimentary crops. Most sugar beet and sugarcane production is rain fed, but in Mediterranean to arid regions, irrigation is necessary.

Origin and History of Sugar Crops

Sugar Beets

Sugar beet (*B. vulgaris* spp. *vulgaris,* L.), a genus of the family Amaranthaceae (formerly Chenopodiaceae), is one of the diverse and useful group of cultivars from the same species that includes Swiss chard, fodder beet, and red beet (McGrath, 2011). The first modern sugar beets originated as selections made in the middle of the eighteenth century from fodder beets grown in then German Silesia, but food and medicinal uses of the genus are much older. A precursor is known to have been used as food as early as dynastic times in ancient Egypt. In 1747 a German chemist, Andreas Marggraf, demonstrated that the crystals formed after a crude extraction from pulverized roots were identical to sugarcane crystals (sucrose). Attempts to derive sugar from beets, and the beet sugar industry itself, originated from this work. His student Karl Achard developed processing methods for sugar extraction from beet and made the first selections of higher sugar-type beets. The blockade of shipments of cane sugar to Europe by the British during the Napoleonic wars stimulated the industrialization of sugar production from

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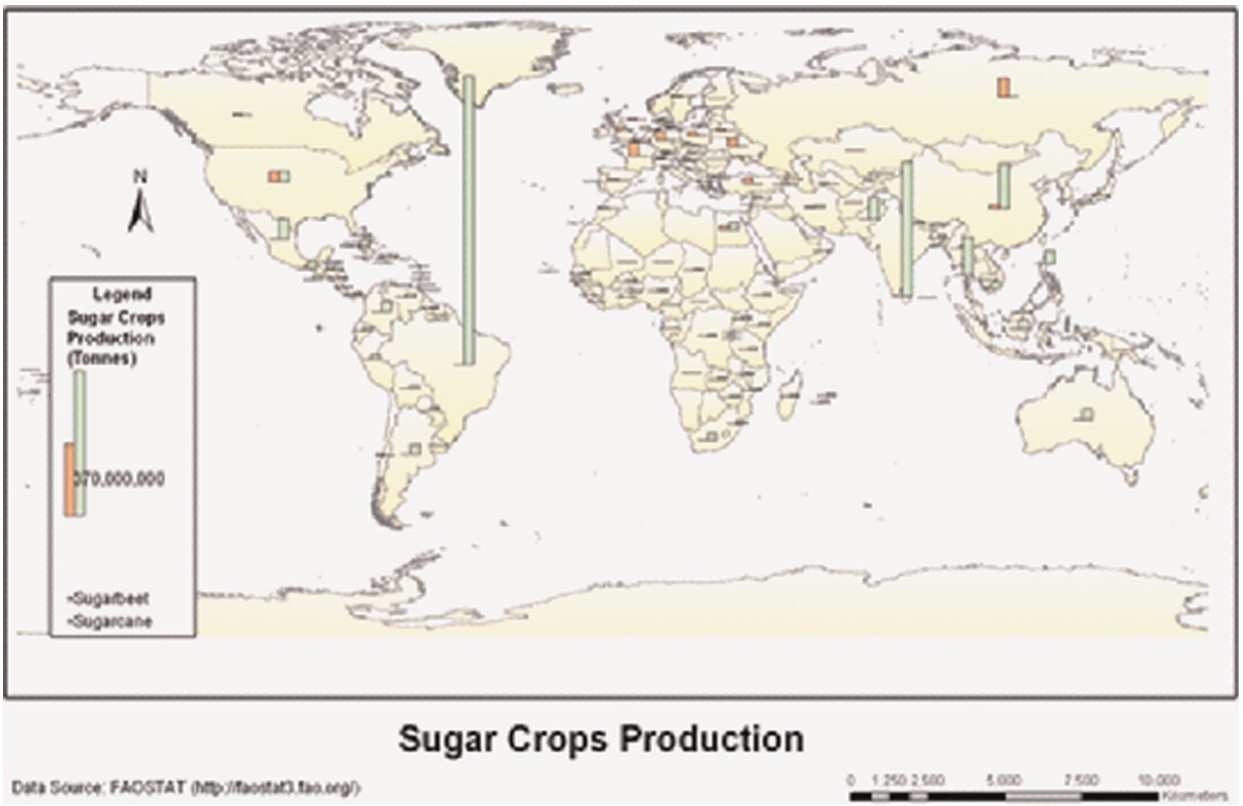


Figure 1 Sugar production from sugarcane and sugar beet by country. Reproduced from FAOSTAT, 2013. Food and Agriculture Organization of the United Nations. Available at: http://faostat.fao.org/default.aspx (accessed 18.02.14).

Table 1 Top 20 countries ranked by sugarcane production during the period 2001–12. Yields of recoverable sugar are approximately 8–12% of these fresh cane yields

Country	*Area harvested (ha)*	*Cane production (ton)*	*Cane yield (tons ha^{-1} year^{-1})*
	Average 2001–11	*Average 2001–11*	*Average 2001–11*
Brazil	6 715 370	507 308 916	74.7
India	4 417 324	296 284 500	66.9
China	1 496 251	98 746 750	65.6
Thailand	1 008 002	64 130 700	63.3
Pakistan	1 020 691	50 762 858	49.7
Mexico	669 208	49 023 541	73.3
Colombia	362 281	35 358 300	99.6
Australia	407 179	33 548 691	82.3
Philippines	389 918	31 078 416	79.9
United States of America	377 878	29 764 208	78.5
Indonesia	380 629	26 013 750	68.9
Argentina	313 960	23 055 833	73.4
Cuba	615 858	20 130 000	32.5
South Africa	315 416	19 962 458	63.2
Guatemala	211 612	19 213 150	91.3
Vietnam	287 233	16 147 566	56.4
Egypt	135 577	16 098 700	118.7
Venezuela	127 957	9 135 769	71.6
Peru	69 807	8 518 708	121.9
Myanmar	148 384	8 027 825	53.9

Source: Reproduced from FAOSTAT (http://faostat.fao.org/default.aspx).

beets, especially in France, through a more intensive search for sweeter beets, an innovative plant breeding program, and the construction of many crude factories in France and elsewhere in Europe. After the battle of Waterloo (1815) and the lifting of the British blockade, the incipient sugar beet industry in France declined for a time, but effectively a new crop had been created and the efficacy of sugar extraction from the beet had been demonstrated. The beet industry not only continued to expand in Europe, which remains the center of the industry, but also developed in other countries in the Middle East and North Africa; Central Asia and Japan; and North and South America. The first successful commercial factory in the United States was constructed by E. H. Dyer Alvarado, in California, in 1879. Soon after, sugar beet culture and factories expanded in many states.

Sugarcane

In contrast to sugar beet, sugarcane has been used as a sweetener in India and China for nearly three millennia. An early ancestor of commercial sugarcane spread from Asia into Papua New Guinea, which became a center of diversity and a major site of domestication. Selected sugarcanes spread throughout the Pacific Basin from around CE 8000, with eventual reintroduction of domesticated clonal materials to South and Southeast Asia. Domesticated clones spread throughout the Pacific islands with exploration and migration, reaching Hawaii by CE 750 (Barnes, 1974). Sugarcane was introduced to Europe from India in the fourth century CE by Alexander the Great and again from the Middle East by returning Crusaders in the Middle Ages. It came to the Americas with Columbus in CE 1493. Successful production was established in Haiti and the Dominican Republic (formerly Hispañola) in 1506, in Puerto Rico in 1515, and in Mexico by 1520 (Barnes, 1974; James, 2004).

Sugar was a luxury in European economies until extensive cultivation of sugarcane began in the Caribbean islands and Central and South America (James, 2004; Galloway, 1989). This allowed a more than hundred-fold increase in English sugar consumption between the mid-1600s and mid-1900s. Sugar use increased along with the Industrial Revolution and the broad appeal of inexpensive and rapidly prepared calories to support urban factory workers who no longer produced their own food. Per capita consumption was also fostered by the increased availability of newly introduced beverages, including coffee, cocoa, and, in England especially, tea, all typically consumed with sugar. Sugarcane provided nearly all sugar in world commerce until the commercialization of sugar beet in the nineteenth century.

Impacts of sugarcane production had substantial impacts on the global labor force. The development of a global sugar market based on sugarcane was closely associated with development of a global market in slave and later indentured labor. Sugarcane production throughout the Americas was dependent on importation of African slaves beginning in the early sixteenth century (James, 2004). By the eighteenth century a major component of international commerce was the exchange of slaves for sugar, molasses, and rum. Slavery was abolished over a prolonged period, ending in the British colonies by 1838, in United States' sugarcane-producing areas in 1863, and in Brazil by 1888. With the abolition of slavery, and advent of wage labor, production in many areas declined precipitously.

This situation was addressed in many production systems by institution of indentured contract labor, fostering immigration of large numbers of workers, especially from China and India. Some of these laborers were eventually repatriated, but most remained as settlers after their period of indentured servitude. These social and economic forces had substantial impact on the demographics of sugarcane-producing countries, contributing to large present day communities of African, Indian, and Chinese descent in many current and former sugarcane-producing countries. More recently, labor in sugarcane enterprises has been on a more conventional wage basis, or by small holders working their own or leased plots.

Production Environments

Sugar Beets

Cultivated sugar beet is a crop of temperate and Mediterranean regions predominantly and has a C_3 photosynthetic system. It is biennial and when the growing plant undergoes prolonged exposure to cold temperatures (approximately 90 days at 5–7 °C, followed by warmer temperatures and longer days), seed stalk production ('bolting') takes place. Wild beet relatives (*B. vulgaris*, spp. *maritima*) do not require vernalization to flower, only increasing day length. Sugar beet seed will germinate and emerge at low soil temperatures (4–5 °C), but emergence is much greater at temperatures greater than 10 °C. Mature plants tolerate modest freezing temperatures, but extended exposure to temperatures below approximately −4 to −5 °C results in cell disruption and death leading to rotting, requiring harvest and storage before severely freezing temperatures occur. These limits affect the length of the growing season of beets in northern latitudes with cold winters. The farthest northern production regions with sugar industries are located in Finland and Sweden in Europe. In Mediterranean locations, like California's central valley and parts of Turkey, Egypt, and Morocco, sugar beets grow year round, but overwintered crops must be harvested by late spring to prevent vernalization-induced flowering from occurring. In arid desert regions with irrigation, like California's Imperial Valley and parts of the Middle East, extremely hot temperatures increase the susceptibility of roots to pathogens like root rots and insect pressures and reduce water-use efficiency, creating other seasonal limits to efficient production. Where successful sugar beet-based industries have developed, diverse adjustments to these effective physiological limits to crop growth have been made. In addition, pest and disease management issues, like the threat of insect-vectored virus diseases, interact with the crop's agroecological requirements in locally diverse ways to set other practical limits to crop production that are regionally specific (Section Crop Management). These factors result in a large number of different cropping patterns worldwide.

Sugarcane

Sugarcane is a tropical plant with a highly efficient nicotinamide adenine dinucleotide phosphate-malic enzyme type C_4

Table 2 Top 10 countries ranked by yield of sugarcane per land area during the period 2001–12. Yields of recoverable sugar are approximately 8–12% of these fresh cane yields

Country	*Area harvested (ha)*	*Cane production (ton)*	*Cane yield (ton ha^{-1} year^{-1})*
Peru	69 807	8 518 708	121.9
Egypt	135 577	16 098 700	118.7
Senegal	7 307	837 038	114.6
Ethiopia	21 775	2 399 600	112.1
Malawi	22 041	2 370 833	107.5
United Republic of Tanzania	20 125	2 113 750	104.8
Zambia	23 875	2 498 333	104.6
Burkina Faso	4 458	445 833	100.0
Colombia	362 281	35 358 300	99.6
Chad	3 797	376 916	99.2

Source: Reproduced from FAOSTAT (http://faostat.fao.org/default.aspx).

photosynthetic pathway. This photosynthetic pathway is generally associated with adaptation to high temperature and high light environments, and to efficient use of water as well as light, while maintaining high productivity (Sage and Kubien, 2007). The optimal environment for cultivation of sugarcane was described as one having a "long warm growing season with adequate rainfall, fairly dry and cool but frost-free ripening and harvesting season, [and] freedom from tropical storms" (Mangelsdorf, 1950). However, with irrigation this ideal changes to one with an absence of clouds, and diurnal and seasonal gradients in temperature, but still free from frost or hurricanes. These requirements are met primarily in lowland subtropical areas and in the tropical highlands, and the highest yields per land area are achieved in such environments (**Table 2**), with high irradiance, irrigation, and a cool dry season to stimulate sugar accumulation, known as ripening.

A major limitation to the expansion of sugarcane as a sugar or biofuel crop is its natural limitation to the latitudes where native *Palmaceae* (palm trees) are found (**Figure 1**). This palm zone, approximately 30° N to 30° S, accommodates the limited cold tolerance of commercial sugarcane clones and avoids the occurrence of freezing night temperatures (Ming *et al.*, 2001) that absolutely limit the current production region. Visible cold damage is not generally observed above 0 °C (Irvine, 1983), when cold chlorosis may be observed as bleached stripes across the leaf lamina. In Louisiana and Florida, risk of freezing nights dictates short growing seasons of approximately 9 months, compared with 12 months in tropical and subtropical environments. A large number of producing countries experience freezing temperatures during the off-season.

Even in the mild, subtropical, marine environment of Hawaii, sugarcane exhibits a strongly bimodal growth pattern, with substantial reduction in the cool (but not cold) winters. Physiological acclimation to progressively cooling temperatures may extend this range. Even moderate chilling may be deleterious (Moore, 1987). In sugarcane fields in Hawaii, excursions below average nocturnal temperatures of only a few degrees Celsius were sufficient to depress stomatal conductance and to substantially inhibit photosynthesis for several days (Grantz, 1989). Chilling effects on mesophyll function dominated these responses, and conductance and photosynthesis were uncoupled. This was most pronounced in summer when rates were greatest and least acclimated to chilling. The effect was also observed in spring, but not in winter, although rates were lower in winter relative to their levels in spring or summer. Extreme heat may also limit production. Sugarcane trials in the low desert of California, where summer temperatures exceed 45 °C, resulted in mid-summer bleaching of leaves in some clones. At both high and low temperatures, stomatal control of water loss may be disrupted (Grantz, 2014).

Under production conditions, flowering of sugarcane is to be avoided as it reduces growth, consumes sugar, and reduces yield. Most modern commercial clones are not heavily flowering in their adapted production environments. Flowering is required for traditional breeding but is often difficult to induce. Shortening days are required, but not sufficient. Conditions with photoperiods just exceeding 12 h, moderate day and night temperatures, and reduced fertility and water supply have been considered essential (James, 1980). For example, in Hawaii, a breeding station on the windward side of the island of Oahu provided a far more favorable environment for flowering than locations at the same latitude on the leeward side.

The Sugar beet Crop

Sugar Beet Breeding and Genetics

In countries with intensive agriculture, hybrid varieties are used for production. Hybrid creation in sugar beets is complex and is made difficult by both physiological and genetic characteristics particularly associated with sugar beets (Bosemark, 2006). These have to do with the crop's biennial character, self-incompatibility, multigerm seed formation in the Beta genome, and the wide range of environments, pest, and diseases affecting the crop in diverse production regions. Creating a new hybrid is a multiyear process. Sugar beets are self-sterile, but mating between close genetic relatives is possible. Cytoplasmic male sterility is found commonly in the Beta genome (Owen, 1945) and is used for hybrid production. However, to obtain offspring from male sterile plants that are themselves male sterile, maintainer lines (called O-types) must be produced as part of the hybrid development process, adding to the complexity of hybrid creation and plant breeding in general. In 1950, Savitsky (1952) laboriously identified a few

plants that formed single embryos (monogerms) which have become the basis for the seed industry worldwide outside of Russia, where separate lines were identified. All commercial hybrid seeds are monogerm.

In both Europe and the United States, sugar beet variety improvement and seed production are carried out primarily by private companies. However, the US Department of Agriculture (USDA) developed most of the varieties grown in the first half of the twentieth century in the United States and current variety development often uses genetic lines derived from USDA research (Panella *et al.*, 2013). Both diploid ($n=9$) and triploid hybrids are available, but increasingly, diploid hybrids are being developed due to greater ease and better adaptability to rapid incorporation of new traits (Bosemark, 2006), most recently resistance to a virus disease (Beet necrotic yellow vein virus) called rhizomania (vectored by *Polymyxa betae*) that spread rapidly to all growing regions of the world in the 1980s (Wisler and Duffus, 2000). Plant biotechnology, such as marker-assisted selection, has been used to assist the development of new sugar beet hybrids (Panella *et al.*, 2013; McGrath *et al.*, 2007). In North America, herbicide-tolerant sugar beets are now grown commercially, but their adoption in other parts of the world has been delayed by regulatory restrictions.

For most of the world, sugar beet seed is produced in narrow latitudinal ranges (44°–46° N) in northern Mediterranean areas in Italy and Southern France that have appropriate day length conditions and mild winter temperatures for seed production. Similarly in the United States, sugar beet seed is produced most efficiently in the Willamette Valley of Oregon at similar latitude. In all these locations, winter temperatures are low, but the roots do not freeze, allowing seed producers to manipulate the plant's biennial habit, and day-length conditions support selection of types less likely to flower ('bolt') during the growing season.

Most countries have a variety of testing programs to ensure the use of cultivars that are productive and well adapted to local conditions. Sugar beet breeding, together with improvements in agronomic and pest management practices, has allowed continuous yield and efficiency improvements over time (especially root yield, (**Figure 2**; Panella *et al.*, 2013; Jaggard *et al.*, 2012; Zimmerman and Zeddies, 2000). In countries with less intensive agriculture or where larger numbers of small-scale producers grow beets using less than optimal technology, yields have not risen as much indicating that there is substantial room for yield increases if supporting conditions are established.

Sugar Beet Industry Organization

Worldwide, sugar beet production, sugar processing, and marketing are carefully integrated. In North America, all the companies are grower-owned cooperatives. In other regions, either privately held or state-owned companies are found. Of necessity, there is a closer and more cooperative relationship among growers and companies than is found with many other agronomic commodities, which results in careful organization of all aspects of production from area planted, scheduling of harvest of individual fields, and through sale of the final product. Commonly, contracts between sugar processors and growers contain quality incentives (see Section Sugar Beet Growth and Management; **Figure 8**).

Sugar beet root yields (**Figure 2**) and sucrose concentrations vary widely. This variance is most strongly related to the climate where they are produced, especially the length of the growing season, local soil types, and the level of agricultural development in each region. A surprisingly diverse set of production, harvest, and processing arrangements is possible. In temperate sugar beet production regions like

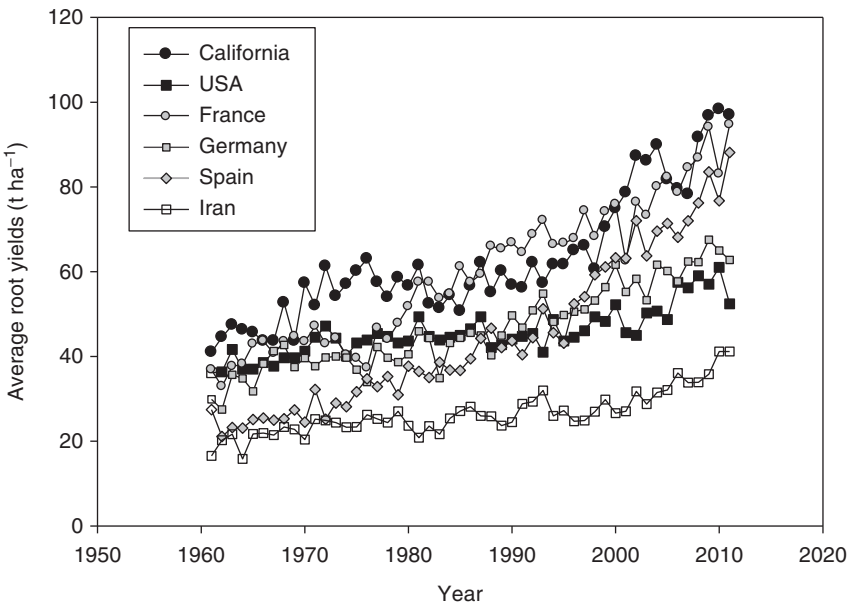


Figure 2 Root yield trends in selected sugar beet–producing countries (1961–2011). Reproduced from FAOSTAT, 2013. Food and Agriculture Organization of the United Nations. Available at: http://faostat.fao.org/default.aspx (accessed 18.02.14).

Northern Europe and most of North America, beets are planted as early as possible in spring after the danger of severe frost (usually March to April) and harvested in autumn (starting in September) for as long as soil conditions and the onset of continuously freezing weather allow. During a typical, concentrated autumn harvest campaign in Europe, factories process large amounts of raw beets to produce crystallized sugar and varying amounts of thick juice (sucrose syrup) that is stored and can be crystallized subsequently at a slower rate during the rest of the year. In the Red River Valley Region of Minnesota and North Dakota in North America, the early onset of extremely frigid temperatures shortens harvest of approximately 1 month but allows roots to be frozen in massive piles in autumn and processed until late spring, often for 200 days or more. In Mediterranean or semiarid to arid regions with milder winters, beets can grow for more than 6 months or even year round, and longer harvest campaigns are possible. In warm locations, roots must be processed shortly after harvest due to losses of sucrose from root respiration and to pathogens during storage.

Sugar Beet Growth and Management

A rapidly growing sugar beet crop is capable of high rates of sucrose accumulation. Dry matter (DM) accumulation and sugar yield are directly proportional to the amount of solar radiation absorbed by the crop (Jaggard and Qi, 2006). Other conditions being equal, the longer the growing season, the larger the yield potential. Under appropriate conditions, the plant develops quickly from seed with the seedling emerging from the soil within 5–10 days after planting under suitable soil temperature and moisture conditions. The taproot grows rapidly and may reach 30 cm or more by the time the first true leaf is developed. During the first 30 days, growth is confined primarily to its leaves and fibrous roots. After approximately 30 days both top and storage root growth proceeds rapidly, with tops reaching near maximum fresh weight in 60–90 days and canopy closure occurring at a leaf area index (LAI) of 3 (Milford, 2006). Subsequently, with favorable climate, top growth remains fairly constant but storage roots continue to grow rapidly for another 20–40 weeks (for a 10-month crop). As the crop develops, an increasing amount of DM accumulates in roots. While leaf number and area may remain relatively constant, in areas with longer growing seasons, roots consist of larger amounts of crown materials, so there is a tendency for impurities to accumulate as well. These impurities reduce sugar recovery from roots in factories (Harvey and Dutton, 1993).

As the storage root increases in size, there is a constant translocation of sucrose from the leaves to the root where it is stored primarily in concentric rings of vascular tissues derived from secondary cambium initiated early in the root's development and in root parenchyma cells that increase in number and enlarge during growth. Bell *et al.* (1996) and Milford (2006), summarizing a large number of studies, reported that DM partitioning in roots is regulated by the cells within the root and is independent of the photosynthate supply (**Figure 3**, Bell *et al.*, 1996; Milford, 2006). On a fresh weight basis, the sucrose content of the root remains relatively constant, unless suitable external factors cause the concentration to change. In temperate regions, these usually increase toward harvest but are also reported to decrease in warmer locations (**Figure 4**).

The largest average sugar beet yields come from California and France (**Figure 2**). California's Mediterranean to semiarid

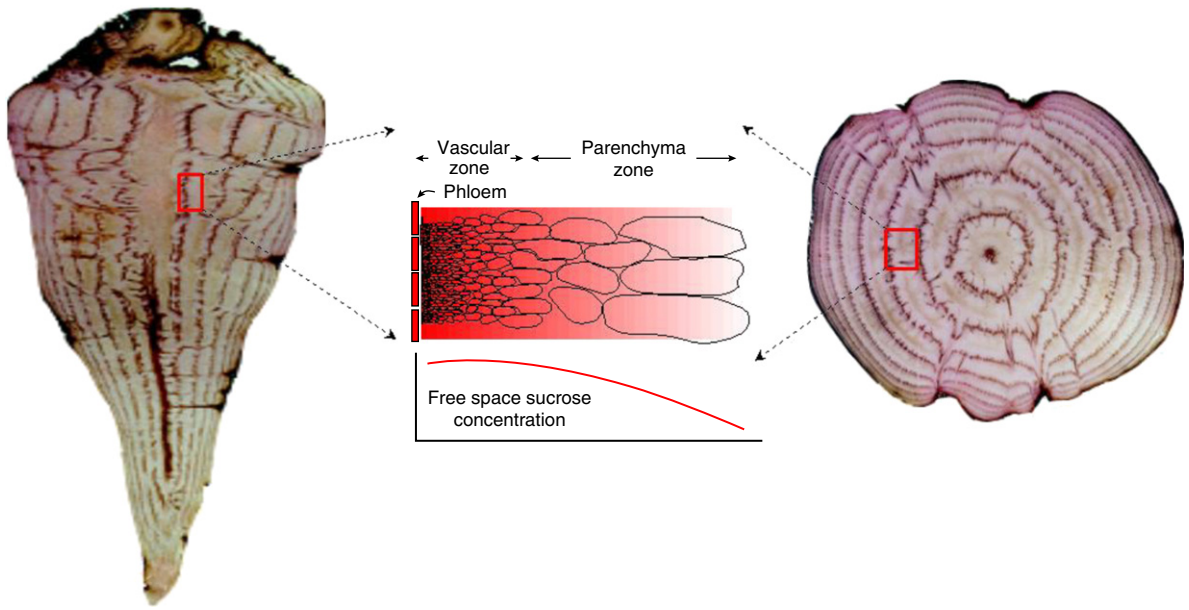


Figure 3 Longitudinal and transverse views of the secondary structure of sugar beet root. Sugar concentration is highest in cells in the vascular zones of the cambial rings visible in the root cross section on the right of the figure. Reproduced from Milford, G.F.J., 2006. Plant structure and physiology. In: Draycott, P. (Ed.), Sugar Beet. Oxford: Blackwell Publication Ltd, pp. 30–49 (Chapter 3), with permission from John Wiley and Sons.

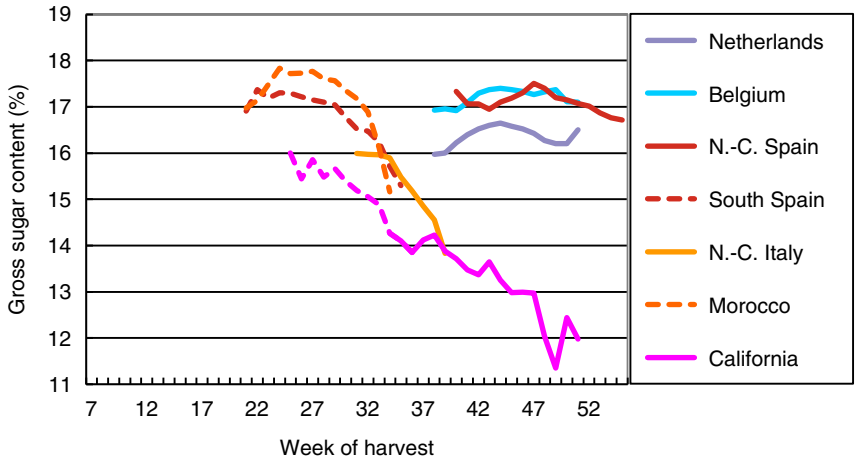


Figure 4 Root sucrose (gross sugar) concentration with time during harvest campaigns. In temperate countries or locations with cold autumn temperatures, sucrose concentrations are maintained during the harvest period, but in warmer Mediterranean locations, they tend to decline during the harvest period. Reproduced from Barbanti, L., Zavanella, M., Venturi, G., 2007. Losses in sugar content along the harvest campaign and means to contrast them. In: Proceedings International Institute for Beet Research Summer Congress, Marrakech, Morocco. pp. 165–175. Brussels, Belgium: International Institute for Beet Research.

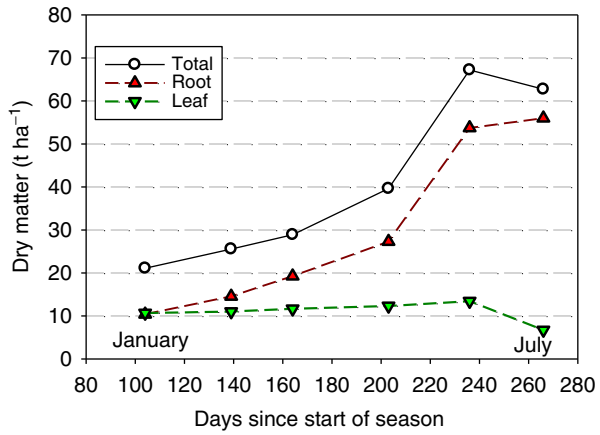


Figure 5 Dry matter accumulation (tons ha^{-1}) in a very high-yielding September-planted and July-harvested crop fertilized with 250 kg N per ha, from the Imperial Valley of California (Kaffka, 2007).

climate allows a long growing season, combined with high-quality soils and irrigation. The world's apparent commercial record yield has come from a field in the Imperial Valley in 2012 and equaled 28.0 Mg ha^{-1} of sucrose from a crop grown over a 300-day period from October to August (177 Mg ha^{-1} of roots at 15.89% sucrose; based on processor data). Average crops in this region reach 55% of the biomass and sugar yields of record crops. Over the total growing season, the record crop accumulated an estimated 147 kg total DM ha^{-1} day^{-1} (44.1 Mg total DM per 300 days) and 93.3 kg sucrose ha^{-1} day^{-1}. DM and sucrose accumulation is not uniform throughout the growing season. Initially it is relatively slow and then accelerates (Figure 5). Peak DM and sucrose accumulation rates can be double the average reported for the cropping season as a whole and most likely exceed rates of 200 kg sucrose ha^{-1} day^{-1}.

Sugar beet refining produces several products in addition to sucrose. These include molasses, dry root pulp, and monosodium glutamate, an amino acid salt used to enhance the flavor of foods. The sugar beet pulp left after sucrose extraction is used widely in the dairy and beef cattle industries as a feed supplement due to its highly digestible fiber and energy content. The tops of beets can be fed, grazed, or returned to soil as an organic matter and nutrient addition. Beet roots contain approximately 1% N, 0.1% P, and 1.1% K on a DM basis, although this varies (Cariolle and Duvall, 2006). An 80 Mg ha crop removes approximately 200 kg N, 20 kg P, and 200–250 kg K ha^{-1}, although actual amounts vary with yield and growing conditions. Because beets are efficient at accumulating photosynthate in a useful form, they are also efficient convertors of agricultural inputs, such as water and nitrogen. One of the reasons sugar beet requires relatively low use of fertilizer nitrogen is its efficiency in recovering residual soil nitrogen from previous crops or decomposed organic matter. Beets recover more of their N requirements from soils than other crops. The crop has been shown to require 25–50% less fertilizer nitrogen than maize (*Zea mays* L.) (Hills *et al.*, 1983).

Many interacting influences affect the balance between root growth and canopy growth. Sugar beets can redistribute N within the plant recovered from soils or take up additional N from soils. Redistribution buffers variations in soil N supply. As long as crops have the amount of N needed for optimum sugar yields, they are capable of sustaining fast rates of root growth and sugar production throughout the growing season without additional supply from the soil or fertilizer. A rapid increase in root sucrose content is correlated with cool night temperatures in the fall of the year coupled with a nitrogen deficiency. It has been repeatedly established that sugar beets require only modest levels of N to produce the highest sugar yields and that beets appear to recover more of their required N from soil reserves than other crops (Hills *et al.*, 1983). Ulrich and Hills (1990), working in California, established a method of plant testing to identify surplus or deficiency and suggested

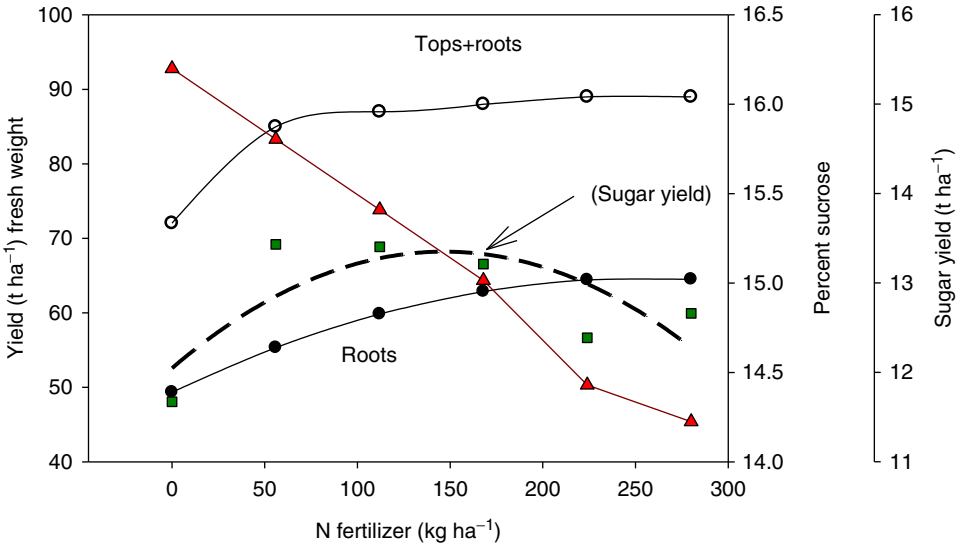


Figure 6 Root and sugar yields of a typical sugar beet crop. Reproduced from Hills, F.J., Sailsbery, R., Ulrich, A., 1982. 'Sugarbeet Fertilization,' Bulletin 1891. Oakland, CA: University of California, Division of Agriculture and Natural Resources.

that 1200 mg N per kg DM in mature leaf petioles was a reliable indicator for sufficiency of non-N limiting sugar beet growth. Generally, nitrogen fertilization is required for profitable sugar beet production. However, sugar yield is sensitive to the absolute amount and the timing of N availability, requiring sufficient amounts early for maximum vegetative growth, and also to a period of N deficiency before harvest for proper sugar accumulation in the storage roots. The highest sugar yields, a function of root yield and sucrose concentration, usually are achieved with a fertilizer rate lower than that which maximizes root yields (**Figure 6**; Hills *et al.*, 1982; Cariolle and Duvall, 2006). Excess N fertilizer results in larger total DM accumulation, but lower total gross and extractable sucrose yields, and could lead to losses of N to the environment. Milford *et al.* (1988), Armstrong and Milford (1983), and Hills *et al.* (1983) all reported that beets require lower levels of N than many other crops for maximum sugar yields and that sugar beet can serve as a nitrogen-scavenging crop to prevent possible nitrate pollution of groundwater. N fertilizer use has tended to decline with increasing yields. Milford (2006) and Milford *et al.* (1988) suggested that environmental or agronomic factors that affect the size and rate of development of the shoot influence sucrose accumulation in the root.

When N becomes deficient before harvest, leaf initiation and expansion is slowed relative to photosynthesis, and photosynthetically produced sucrose accumulates in roots as storage rather than as new vegetative growth. This is illustrated by results from California, where production occurred over a diverse set of climate conditions, allowing comparison of crops in different locations at the same time of year. Kaffka *et al.* (2001) found that very high sucrose concentrations occurred in sugar beet roots harvested in October from a high elevation growing region with a continental climate, where aridity results in very high levels of photosynthetically active radiation, but where higher elevations (1200 m) also correlated with night time temperatures at or near freezing in autumn. Naturally high organic matter soils provided large amounts of N mineralized from soil organic N. They suggested that leaf initiation and expansion (favored by excess N) was suppressed by cold temperatures at the end of the growing season to a greater degree than photosynthesis, favoring sucrose accumulation. Root storage tissues continue to develop in sugar beet as long as assimilate is available. Similarly, in California's milder central valley at the same time of year, sucrose concentrations in sugar beet roots typically declined in October under conditions with milder average temperatures, as deep-rooted crops recovered residual soil N supplies under conditions of declining water stress (**Figure 4**). Similar behavior with respect to beet sucrose concentration in autumn is widely reported from other temperate (Cariolle and Duvall, 2006) and Mediterranean regions with mild temperature conditions in late autumn that encourage additional crop growth (Barbanti *et al.*, 2007).

Improvements in plant breeding and seed technology have led to increasing levels of seed emergence and establishment, with the result that hand labor long associated with sugar beet production, especially around stand establishment, has been eliminated where modern agricultural technology is available. Over time, monogerm seed, improved weed control, improved planters, and seed treatments that reduce losses to pathogens and insect pests during the vulnerable period of crop emergence and establishment have reduced the need for large seed populations and hand thinning of seedlings. Planting to a stand and 70–80% emergence and establishment have become common in growing areas with advanced agricultural practices. Ideal plant populations are 75 000–80 000 plants per ha on 50–76 cm rows (Jaggard and Qi, 2006).

Most sugar beet production in temperate regions is based on rainfall and stored soil moisture. Variable weather at times results in water stress and yield limitations when rainfall is inadequate or poorly timed with crop demand. In arid and Mediterranean areas, careful and timely irrigation is essential for economic yields. Furrow or sprinkler irrigation is possible,

and some drip irrigation systems are being used. Irrigation water requirements in locations where irrigation supplements growing season rainfall are small (100–200 mm per year), but in climates where irrigation is necessary, they commonly range from 600 mm of water per ha per season in a cool climate where the soil is filled with plentiful winter rain to as much as 1200 mm per ha in an arid location with a long growing season like the Imperial Valley of California (Dunham, 1993; Hills *et al.*, 1990). DM accumulation and sugar yield are a linear function of transpiration, although both are more easily and commonly correlated with evapotranspiration (ET) (Dunham, 2003). Actual irrigation amounts depend on the depth of the rooted profile, soil water-holding capacity and available water at the start of irrigation, planting and harvest dates, the length of the growing season, and climate during the growing season. Diverse estimates of water-use efficiency have been measured reflecting this varying set of influences.

Water-use efficiency for both total DM yield and sugar yield tends to decrease in warmer climates with higher temperatures and light intensities, where season-long irrigation is required, compared with locations with supplemental irrigation. Empirically determined water-use efficiency values for total DM production (q_{et}) and for sugar production (s_{et}) are summarized by Dunham (2003) and modified with additional data by Langner (1996). For total DM these ranged from 0.0068 Mg cm^{-1} ha^{-1} in Great Britain for a spring-planted crop to 0.0023 Mg cm^{-1} ha^{-1} in California's arid summer for the same. For sugar yield, at the same locations, values ranged from 0.004 to 0.0013 Mg cm^{-1} ha^{-1}. Intermediate values were also reported from environments with growing conditions less mild or extreme (**Table 3**). Beets are deep rooted, with many reports of soil water depletion to 2 m and some to 3 m (Kaffka *et al.*, 1999; Hills *et al.*, 1990). When grown on soils that have been preirrigated or that have large amounts of available water in the soil profile, maximum yields can be achieved at levels less than 100% irrigation (**Figure 7**), (Morillo-Velarde and Ober, 2006; Langner, 1996). In irrigated regions, if beets can be produced during the winter period, very high levels of water-use efficiency can be achieved (**Table 3**).

Sugar beet is a halophytic species that requires Na (Draycott and Christiansen, 2003) and tolerates salinity. It is considered one of the most tolerant crops (Maas, 1990) and can be produced by using low-quality water resources, like saline tile drainage water, in part, and on salt-affected soils (Kaffka *et al.*, 2005, 1999; Moreno *et al.*, 2001). When using drainage or other wastewater, care must be taken to account for N present in the irrigation water, because that reduces sucrose yields, even if it does not affect total DM.

Controlling pests and diseases is important for profitable crop production. Sugar beet is slow to establish and is susceptible to weed competition in its early stages. Moderate weed infestation is controlled by crop rotation and a combination of chemical and mechanical methods. In the United States, herbicide-tolerant sugar beet is now being grown but is not widely used elsewhere due to regulatory restrictions. Sugar beet is susceptible to preemergence and postemergence seedling rots known collectively as damping-off diseases. Other important diseases that must be controlled in areas where they occur are as follows: curly top, a virus disease transmitted by the sugar beet leafhopper; sugar beet yellows, a virus complex consisting of one or more different aphid-transmitted viruses; powdery mildew (*Erysiphe polygoni* DC) and Cercospora leafspot (*Cercospora beticola* Sacc.), diseases caused by leaf fungi; rhizomania caused by a virus (beet necrotic yellow vein)

Table 3 Diverse estimates of water-use efficiency for total dry matter (DM) and sugar production for irrigated sugar beets.

Location	*Year(s)*	*Soil type*	*Estimated* ET_c *(or range applied) (mm)*	*Water-use efficiency (Mg* cm^{-1} ha^{-1}*)*		*Reference*
				DM (Q_{et})	*Sucrose* (S_{et})	
Spring-planted trials						
Suffolk, UK	1979–84	Sandy loam	450	0.0068	0.004	Dunham (1989)
Jena, Germany	1984	Deep Loess	500	0.0061	nr	Roth *et al.* (1988)
Utah, USA	1980	Silt loam		0.0055	0.0022	Davidoff and Hanks (1989)
Nebraska, USA	1966	Very fine sandy loam	800 Cloudy sunny	0.0058 0.0027	nr	Brown and Rosenberg (1971)
Washington, USA	1976	Silt loam	640–730	nr	0.002–0.0016	Miller and Aarstad (1976)
California, USA	1980	Clay loam	900	0.0023	0.0013	Ghariani (1981)
California, USA	1987	Clay loam	980–1140	0.002	0.0009–0.0007	Howell *et al.* (1987)
Fall-planted trials						
California, USA	1972–73	Silty clay	900–1200	nr	0.002–0.0016	Ehlig and Lemert (1979)
California, USA	1996	Clay loam	430–600 (May) 440–870 (June) 560–1000 (July)	0.0055 0.0037 0.0036	0.0022–0.0017 0.0025–0.0014 0.0022–0.0014	Langner (1996)

Abbreviation: nr, Not recorded.

Source: Reproduced from Dunham, R.J., 2003. Water use and irrigation. In: Cooke, D.A., Scott, R.K. (Eds.), The Sugar Beet Crop, Science into Practice. London: Chapman and Hall (Chapter 8), pp. 279–309.

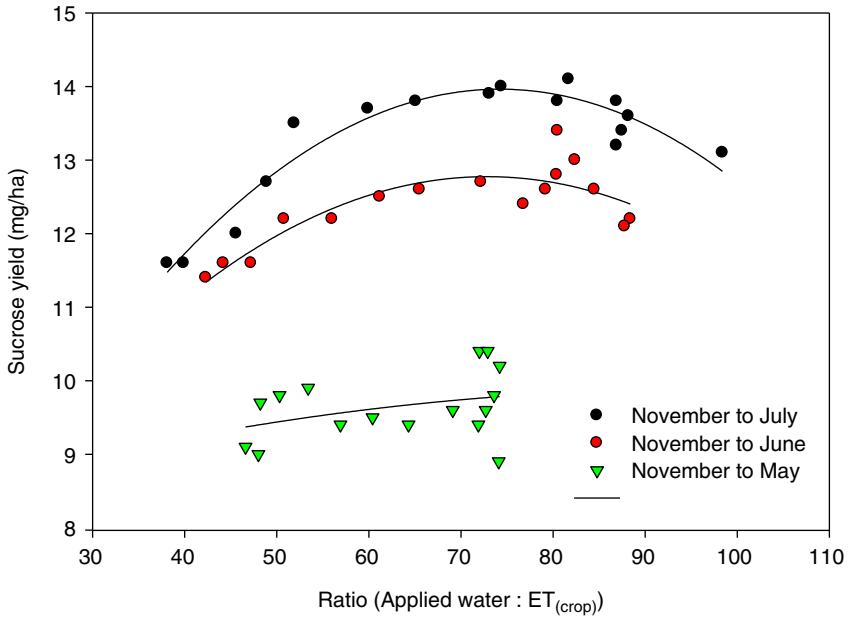


Figure 7 Sucrose yield in successive harvests from a fall-planted, summer-harvested trial in California's San Joaquin Valley, compared with the ratio of irrigation to measured crop evapotranspiration. There was little response to irrigation when the crop was harvested in May. In June and July, deficit irrigation resulted in the largest sucrose yields. Sugar beets were able to recover water from the soil profile in a way similar to their capacity to use residual soil N. Reproduced from Langner, P., 1996. Consumptive water use of fall planted sugarbeets in the San Joaquin Valley of California. MS Thesis, University of California, Davis.

transmitted by a soilborne fungus (*P. betae* Keskin); and sugar beet cyst nematode (*Heterodera schachtii* Schmidt) and root-knot nematodes (*Meloidogyne* sp.). Strategies for the control of these diseases involve development of resistant varieties, attention to time of planting, isolation of new plantings from old sugar beet fields that can serve as sources of virus inoculum in locations with year-round growing climates and practices, the selective use of fungicides, soil fumigation, and careful attention to crop rotation (Wisler and Duffus, 2000; Whitney and Duffus, 1986). Varietal resistance, including from transgenic sources, may become increasingly important (McGrath *et al.*, 2007). But currently there are limits. Foliar diseases, root rots, and insect predation are reasons why beets have not been widely grown in regions with humid, hot temperature conditions during the growing season.

Although diverse production conditions result in differing planting and harvesting practices, sugar extraction and processing is remarkably similar in most beet factories throughout the world. Because sugar factories are expensive industrial facilities, it is prudent to operate them for as many days as possible. In northern temperate growing regions, beets are harvested in early to late autumn as day length and particularly temperature decline. Severe frost damages roots and causes rotting, so freezing weather with temperatures sufficient to freeze soil marks the end of the harvest period. Consequently, factories are designed to maximize the amount of beets that can be washed, sliced into cossettes, and diffused each day. Still, many more tons of beets are needed to support a modern sugar factory than can be processed only during sometimes short harvest periods in autumn. The problem of extending beet supplies to factories is solved variably, depending on interacting local circumstances. In most of Northern Europe, some sugar beet roots are stored along field margins under cover and delivered in late autumn as factory capacity allows. In the northern tier of US states (Idaho, Montana, Wyoming, and Michigan) cold weather beginning in early autumn allows recently harvested roots to be stored outside in piles with ventilation to maintain cool but not frozen conditions. In the Red River Valley region of Minnesota and North Dakota (USA), exceptionally cold weather beginning early in autumn allows massive piles of recently harvested roots to be maintained throughout winter. Frozen beets are then processed during the winter months before temperatures warm sufficiently in the spring to thaw the piles. Processing campaigns can last 200 or more days.

In Mediterranean or warmer regions, beets cannot be stored without significant losses of sucrose to respiration, changes in sucrose to other hexose sugars that cannot be used to make commercial sugar, and losses to pathogens in storage piles. Consequently, daily harvesting and processing is normal. In many locations, this limits the length of time that a factory can operate. For example, in the Imperial Valley of California (mentioned previously), harvest begins in April following planting the previous September and October and lasts until late July or early August, when desert temperatures become too hot to maintain beets in fields without significant loss to root rots or other pests and diseases. In less extreme semiarid or Mediterranean locations, to allow factories to operate for longer periods, complementary planting and harvesting districts can be combined to allow daily harvest over a multimonth period. This occurred in California in the San Joaquin Valley, where both summer and winter temperatures allowed crops to grow year round. In that case, harvest began in April after winter rains using beets sown the previous May and continued until late October or early November, harvesting

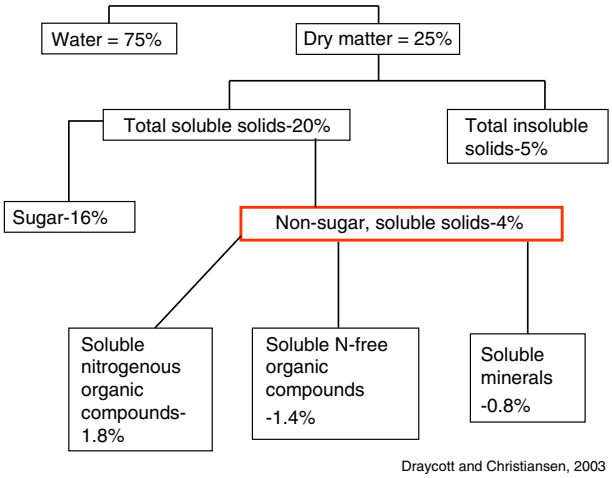


Figure 8 Composition of a typical sugar beet root at harvest. Total insoluble solids fraction is used as livestock feed (beet pulp). Adapted from Draycott, A.P., Christiansen, D.R., 2003. Nutrients for Sugar Beet Production. Cambridge: CABI Publishing, pp. 242.

beets from different regions with planting dates matched to expected harvest periods.

Creating a uniform, pure product (commercial sugar is 99.9% sucrose) from a variable feedstock is a challenging task on an industrial scale. Typical sugar beet composition is depicted in Figure 8, although all of these percentages can vary locally and seasonally. Sugar beets vary in quality as a function of many interacting factors, including agronomic practices, harvest conditions, location, and time of year. The goal of the sugar beet industry, both farmers and sugar manufacturers, is to maximize the recovery of sugar from beet roots. Sugar recovery is inhibited by the presence of large amounts of N compounds, like amino acids and by minerals like K and Na that are part of the ash content (Harvey and Dutton, 1993). Conversion of sucrose into its constituent sugars (fructose and glucose–referred to as inversion) during the diffusion process reduces commercial sugar yields and may lead to creation of other sugars that interfere with crystallization. The larger the molasses fraction, the less sucrose that can be recovered from the gross sugar stored in roots at harvest.

There is a long history in the sugar beet industry of trying to correlate crop production practices with decreased loss to molasses. Particular attention has been paid to the relationship between N fertility and fertilizer management with impurities in roots. There are a large number of regression-based formulas relating sugar recovery to amino N, Na, and K constituents in roots at harvest. These have been used to test beets at harvest and to encourage growers to produce higher quality beets through incentive payments. Formulas have varied over time and by region, with no particular formula proving to be universally applicable. The general consensus is that root quality remains elusively complex and a subject for ongoing research and empirical experimentation (Dutton and Hiuijbregts, 2006; Draycott and Christiansen, 2003).

On delivery to a factory, beets are first washed to make them free of soil and stones. Those processed immediately are then sliced into cossets and conveyed to large diffusers that dissolve sucrose and other soluble constituents from the plant. Dissolved sugar and other constituents are then passed through a series of steps that result in a purified sucrose syrup and byproducts, primarily molasses, monosodium glutamate, and proteins and amino acids (McGinnis, 1982). Residual fiber (called Marc or beet pulp) is a valuable livestock feed, not only for dairy cattle, but also for other livestock species, and even for human nutrition, and is dried for feeding purposes. Sugar beets have very little lignin, and the fiber is composed primarily of cellulose, hemicellulose, and pectin, in roughly equal amounts. Molasses may be added back to pulp if desired to further increase its energy and protein content.

The Sugarcane Crop

Sugarcane Breeding and Genetics

Sugarcane is a member of the *Saccharum* complex (Sreenivasan *et al.*, 1987). These tall, perennial, and tropical grasses include the originally domesticated sugarcane, *S. officinarum*; congeneric species, such as *Saccharum robustum*, *Saccharum sinensis*, *Saccharum barberi*, and *Saccharum spontaneum*; and various interspecific hybrids as well as related genera, such as *Erianthus*, *Ripidium*, and *Miscanthus*. *Saccharum officinarum* appears to have derived from selection and domestication of *S. robustum*. The early domesticated clones represented selection for multicolored stalks, high sap sucrose concentration, relatively low fiber, large diameter stalks, and limited tillering and flowering. The resulting 'noble canes' were those grown in household gardens in Papua New Guinea, were carried by Polynesians to the Hawaiian Islands, and formed the basis of early commercial production and crop improvement efforts.

Sugarcane improvement, as with sugar beet and other crops, is a constant requirement for the continued viability of the industry. Modern sugarcane improvement began with selection of high yielding *S. officinarum* clones in Java in the nineteenth century CE. These noble canes from the Javanese breeding collection initially dominated global commercial production. These were subsequently crossed with the wild species, *S. spontaneum*, to begin production of the modern hybrid, 'nobilized' cultivars in the early twentieth century. The noble canes were supplanted by the resulting interspecific hybrids, which exhibited improved disease resistance, broader environmental adaptation, and increased yield.

Wild *Saccharum* occurs across a surprisingly large range of rainfall and altitude (Irvine, 1983), frequently along nonsaline waterways where open vegetation allows high light penetration and where plant water deficit may be avoided. The broad adaptation is reflected in wide phenotypic diversity among *Saccharum* genotypes. For example, stalk diameter ranges from a few mm in some *S. spontaneum* genotypes to more than 10 cm in some *S. officinarum* chewing canes. Similar diversity is observed in genome structure (Hogarth, 1987; D'Hont *et al.*, 1996).

Saccharum spontaneum exhibits much greater diversity than *S. officinarum*, which does not exist outside of cultivation. *Saccharum spontaneum* is found in wild populations across Asia, North Africa, and the Middle East (Tew and Cobill, 2008). This diversity is reflected in observed variation in stress resistance (Moore, 1987) and genomic diversity (Zhang *et al.*,

2012). This diversity has contributed considerably to sugarcane improvement for the past century or more. *Saccharum spontaneum* exhibits lower stalk sucrose than the noble canes, higher fiber, thinner stalks, and sufficiently common flowering and tillering to make it a potentially invasive species. In commercial canes, sucrose accumulation and robust growth of thick stalks are derived mostly from *S. officinarum*, whereas genes for vigor, broad environmental tolerance, high fiber, and abundant tillering are derived mostly from *S. spontaneum*.

The sugarcane genome is a subject of considerable current investigation using modern genetic techniques. The *Saccharum* species are autopolyploids, with copy numbers (ploidy level) ranging from 5*x* to 16*x*. The genome of *S. officinarum* is relatively uniform among genotypes, being autooctaploid ($x=10$; $2n=8x=80$ chromosomes), with only a few possible exceptions (Zhang *et al.*, 2012). In contrast, *S. spontaneum* is more variable ($x=8$; $2n=36$–128), although approximately three-quarters of genotypes contain some multiple of 8*x* (Ming *et al.*, 2001). *Saccharum officinarum* and *S. spontaneum* appear to have diverged approximately 1.5–2.0 million years ago (Jannoo *et al.*, 2007).

The genome size differs between species, with ploidy level and with monoploid chromosome number. The monoploid genome size of *S. officinarum* is estimated to be approximately 985 Mb (million base pairs) and of *S. spontaneum* approximately 843 Mb, with much greater variation in *S. spontaneum* (Zhang *et al.*, 2012). The full polyploidy genome within the *Saccharum* complex ranges from 2–12 Gb/C (billion base pairs per diploid cell; Zhang *et al.*, 2012). Genome size is a useful surrogate for chromosome number (Zhang *et al.*, 2012).

Commercial sugarcane germplasm is largely derived from crosses of *S. officinarum* x *S. spontaneum*, with repeated backcrossing to *S. officinarum*. Current sugarcane clones contain approximately 90% *S. officinarum* and 10% *S. spontaneum* germplasm (Ming *et al.*, 2001; D'Hont *et al.*, 1996). In crosses of female *S. oficinarum* x male *S. spontaneum*, an unusual chromosomal transmission is often observed in which the diploid, somatic complement ($2n$) of the female is retained along with the haploid, gametic ($1n$) complement of the male. This so-called $2n+n$ transmission and the unpredictable pairing of the variable number of homologous chromosomes in such crosses (Ming *et al.*, 2013) result in considerable complexity in the genomes of commercial clones. Similar to other vegetatively propagated species, sugarcane is heterozygous at most loci, with no existing inbred lines that would be useful for crop improvement.

Autopolyploidy is observed in several important crop species, including sugarcane and sugar beet (Ming *et al.*, 2013; Zeven, 1979). Despite the common occurrence of this genomic replication, it presents challenges for modern genetic analysis and the search for useable markers for selection. Identification of quantitative trait loci (QTL; a genomic marker) for phenotypic traits of interest is complex, as several alleles may segregate in various combinations, and individual genes may contribute only marginally to phenotypic traits of interest.

A study of QTLs for two independent traits – sugar content and plant height – found that multiple copies of favorable alleles, in unlinked regions of the genome, had less than additive effects (Ming *et al.*, 2013). This suggests that one copy, among the multiple potential locations in the polyploid genome, may be sufficient to provide physiologically relevant protein synthesis. Additional copies may potentially be manipulated in pursuit of other desirable traits with minimal negative consequences. This may simplify development of transgenic lines, as insertion of one copy of a novel allele may be sufficient to drive improved phenotype, despite the presence of other loci with less favorable alleles. However, multiple copies of important genes may confer environmental stability (Ming *et al.*, 2013) as observed in other species. In highly selected commercial clones, favorable alleles (Lam *et al.*, 2009) have been fixed at several loci, so that identification of QTLs is more difficult than in less selected genotypes.

The recently sequenced genome of *Sorghum bicolor* (Paterson *et al.*, 2009) has proven useful as a template to understand the sugarcane genome (Ming *et al.*, 1998, 2013; Dufour *et al.*, 1997). The sugarcane monoploid size is similar to that of the haploid *Sorghum* genome (Zhang *et al.*, 2012). Sugarcane diverged from *Sorghum* less than 10 million years ago (Jannoo *et al.*, 2007; Lam *et al.*, 2009). QTLs in an *S. spontaneum* x *S. officinarum* segregating population, for both high and low sugar content (Ming *et al.*, 2013), all mapped to one of eight distinct regions of the *Sorghum* genome. Loci of interest in the larger sugarcane genome may reflect a small number of ancestral genes, simplifying manipulation during crop improvement.

Sugarcane Industry Organization

Sugarcane production took place in nearly one hundred countries (FAOSTAT, 2013) during 2001–12. Another 10 countries, mostly small producers, ceased commercial production during or before this period. Annual global sugar production from sugarcane over this period was approximately 1.7 billion tons (**Table 1**). More than 90% was produced in the top 20 producing countries (**Table 2**), concentrated in tropical and subtropical areas. Central and South America produced 53.1% of global output with an additional 36.9% from Asia and 5.3% from Africa. The remainder was distributed with 2% or less from the Caribbean region, Oceania (including Australia), North America, and Europe (0.0003%).

The largest single producer during this period was Brazil (**Table 2**), with more than 500 million tons of cane production, reflecting vigorous government investment in an integrated sugar and biofuel economy based on sugarcane. India and China produced approximately 300 million and 100 million tons, respectively. Total production is closely related to area harvested, although differences in yield per land area are observed.

Average yields were largest in Central and South America and Oceania (**Table 1**). Of the top 20 producers (**Table 2**), only three have yields at or above 100 tons ha^{-1} $year^{-1}$ – Peru (122 tons ha^{-1} $year^{-1}$), Egypt (119 tons ha^{-1} $year^{-1}$), and Colombia (100 tons ha^{-1} $year^{-1}$). Only 10 countries achieved long-term average yields of 99 tons ha^{-1} or above, mostly characterized by prolonged dry periods and long growing seasons (Waclawovsky *et al.*, 2010). Many major producers, such as Australia (82 tons ha^{-1} $year^{-1}$), the United States (78 tons ha^{-1} $year^{-1}$), and Brazil (75 tons ha^{-1} $year^{-1}$), exhibited lower average yields. Production areas, such as the

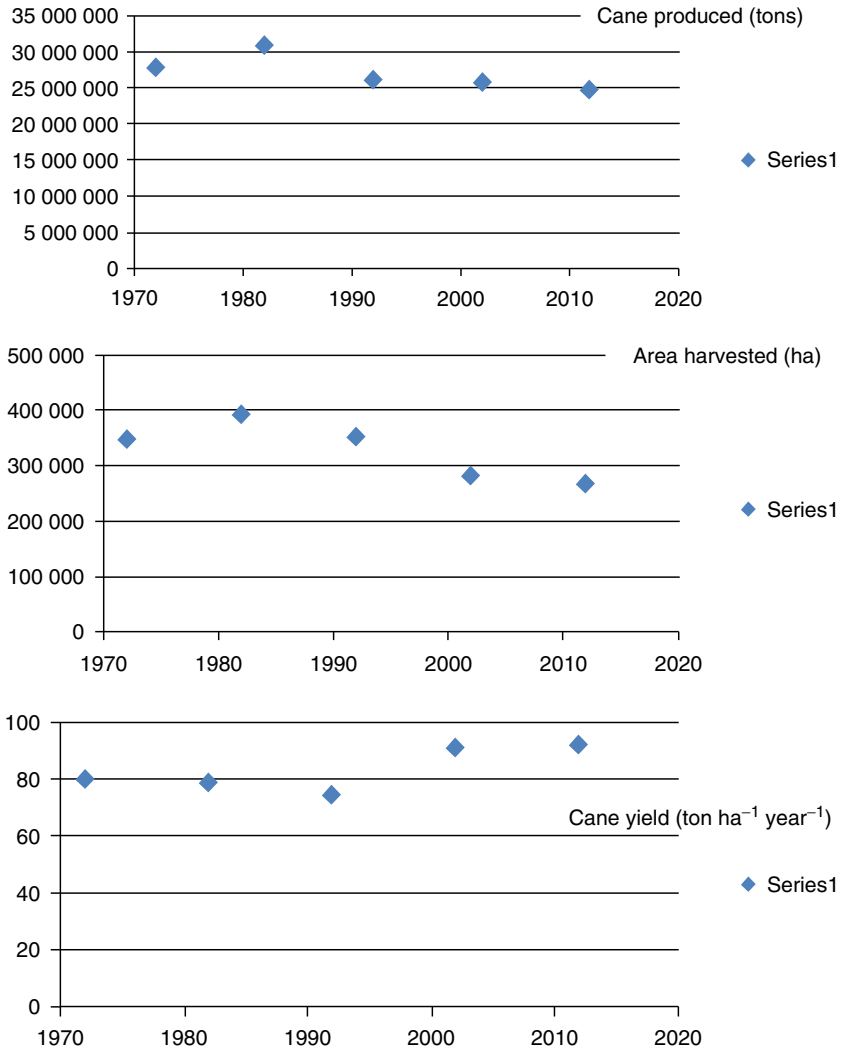


Figure 9 Fifty year trends in sugarcane production in the United States. Data obtained from the USDA National Agricultural Statistics Service (www.nass.usda.gov).

northern coastal deserts of Peru and the inland desert valleys of Southern California, arid and high irradiance environments, may provide substantial opportunities for very high yields and efficient use of limiting resources, such as land, water, and nitrogen.

Sugarcane production in the United States increased over the past 50 years (Figure 9) by 12%, although land area devoted to sugarcane increased by 28.7% (1972–2012). By 2011, the US industry had 45–47% of planted area in Florida and Louisiana, cool short season production environments, and 5.6% in southern Texas. Sugar production was 51% in Florida and only 38% in Louisiana and 5.6% in Texas. During this period the exceptionally productive Hawaiian industry declined by 87.3%. By 2011, Hawaii had 1.9% of US sugarcane plantings but 4.5% of US production. Hawaiian yields peaked at 220.0 tons ha^{-1} $year^{-1}$ shortly before the collapse of the industry on all but one of the sugar-producing islands. By 2013, only one sugar enterprise remained, on the island of Maui. These observations suggest that agronomic factors are not always decisive in determining the viability of a production system.

The sugarcane industry exists in a diverse matrix of countries, cultures, and economic systems. The organization of production reflects this diversity. In some areas, mills and production fields are owned by a single entity, commonly called a plantation system. This may represent large private enterprises or cooperative associations. A significant benefit of such organization is that improvements in both field operations (yield, production costs, sugar content) and mill operations (prevention of cane deterioration, recovery percentage, factory costs, and marketing) accrue to the benefit of both grower and refiner, and there are inherent incentives for improvement and investment in both operations. However, in much of the world, the industry is based on a large number of independent producers providing cane to mills that are operated by an unrelated entity. The result is an unavoidable conflict of interest in which incentives to increase cane quality and sugar recovery may not accrue to both parties, and

distortions of industry expansion and investment are common (Todd *et al.*, 2004).

These conflicts have been addressed through a variety of payment schemes (Todd *et al.*, 2004), each with advantages and disadvantages with respect to the economic viability of the national sugarcane industry. Payments for cane delivery may be based on the average quality of cane delivered to the mill, which removes individual grower's incentives to improve quality. They may be based on the quality of an individual grower's cane, which incentivizes the individual. This results in competition, either between the growers for a fixed share of revenues in fixed revenue-sharing systems, or between individual growers and with the mill operator for a share of total revenues in variable revenue-sharing systems. This latter option may spread risk and reward most equitably but is complex to administer and requires quality testing at multiple points in the production pathway.

An example of a management decision that may depend wholly on industry organization and payment scheme is length of the harvest and milling season. A longer season makes most efficient use of high cost-fixed equipment at the mill but inevitably reduces cane quality and sugar recovery by extending the harvest season to nonoptimal periods. Depending on grower incentives and ownership of fields and mills, this improves profitability for all participants, or only for the mill owners. In some production areas, a blended system provides individual incentives that are calculated on the basis the average quality of cane delivered during each phase of the harvest (Todd *et al.*, 2004), rather than over the entire harvest season.

Sugarcane Growth and Management

Sugarcane production methods depend on soil type, rainfall, drainage, and availability of labor and mechanized equipment. Adapted genotypes exhibit high productivity, whereas the perennial life cycle allows economically efficient production, with one or more ratoon (stubble) crops. Replanting from vegetative stalk segments is required only after several generations when yields decline due to soil compaction, disease or pest pressure, reduced plant population, or cumulative harvest damage.

Ratoon production varies with environment, cultivar, harvesting techniques, and management, ranging from no ratoon crop to four or more. From two to five appears to be a common range among current sugar production areas. Sugar yield eventually declines, necessitating a fallow period and replanting with vegetative stalk pieces. The length of the ratoon period is ultimately an economic decision, balancing replanting costs with foregone sugar yields but may be skewed by considerations of labor supply, availability of new and improved cultivars, and international sugar market conditions (Ellis and Merry, 2004).

Planting costs are substantial in sugarcane, due to its vegetative mode of reproduction. Before replanting, the seed bed is usually worked to remove the previous crop and any weeds and to optimize soil tilth. Sugarcane is planted from vegetative stalk segments. These may be long sections with only the tops removed, or they may be shorter sections, with one to three buds per section. Both types of planting material may be hand cut or delivered by mechanized harvesters from nearby fields that are dedicated to seed production. This set aside from production is a significant cost of sugarcane establishment.

Stalk segments are planted in furrows that may be subsequently filled to result in flat planting. This may provide more even water availability and is suitable for many mechanized operations. However, erosion due to water runoff and pressure from some soilborne pests may be exacerbated, and crop waterlogging in poorly drained fields may be increased. For these reasons, i.e., to channel runoff, to elevate cane above moisture and moisture-attracted pests, and to raise soil temperatures, cane is often planted in ridges separated by well-maintained furrows. Irrigation may then be provided through the furrows if available and as required. If moisture availability on the ridges is inadequate, the cane may be planted in the furrows and ridges later constructed along the plant line, although this disruptive activity may slow growth.

Row spacing reflects a balance between increased costs to produced seed cane (planting stalks) and the time required for the crop canopy to fully cover the ground for maximal interception of sunlight. Productivity is closely related to seasonal intercepted solar radiation. In practice, row separation is usually between 1 and 2 m, with narrower spacing under poorer growing conditions or where erosion is a threat (e.g., hillsides) and wider spacing where rapid growth and canopy closure is expected. In some cases, available equipment dictates row configuration.

In irrigated and highly favorable production environments, cane is harvested at approximately 12 months of age, although this may vary from 9 months in temperate climates with unsuitable winter temperatures to 24–36 months in cooler but nonchilling environments or dryland situations with water-limited growth. Sugarcane exhibits a sigmoidal growth curve, as observed in sugar beet and other crops (Figure 10). The sheer magnitude of the developing canopy has led to this exponential middle portion of the growth curve to be called the period of Grand Growth.

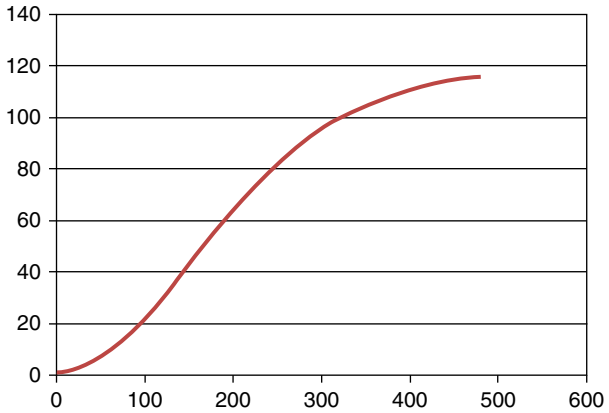


Figure 10 Biomass production in sugarcane during regrowth following harvest. This model from Simoes *et al.* (2005) describes the 4th and 5th rattoon of an early variety with vigorous regrowth in Brazil. Vertical axis is above-ground biomass (tons ha^{-1}); horizontal axis is days after cutting. The curve is generated from the equation given by Simoes *et al.* out to 480 days. $BM = 120 \times \exp(-(4.6981)) \times \exp(-(0.010098)) \times Days$.

In many production areas, sugarcane is harvested by hand, with cane knives or machetes and carried in bundles of 10–20 kg by individuals to collection points at the side of the field. Increasingly, harvest is mechanized, using machines that trim the tops and then sever the stalk near the base, leaving neatly aligned piles of intact stalks laid across the row. This type of whole-stalk or 'soldier' harvester imposes fewer cut surfaces and reduces risks of quality deterioration but requires burning in the piles and some additional logistical challenges. It is used to prepare seed cane for whole-stalk planting in some areas.

The alternative is a billet-cutting, or combine, harvester. This approach does not require burning of the trash, which is blown off during harvest by fans on the harvester. However, efficiency is improved by burning in the field. The cane is cut at the top to remove green portions, severed near the ground as above, and then chopped into convenient lengths before ejection into a receiving wagon pulled alongside. A highly mechanized system was in use throughout Hawaii until the recent decline of that industry. Fields were burned in place, then push-raked with large tracked vehicles into piles, which were loaded by infield cranes into trucks that were driven on private cane haul roads to the factory. Productivity and lodging in this system exceeded the capacity of available harvest equipment.

Burning of the cane requires that irrigation be terminated in a timely fashion and that rainfall does not occur during the critical period. The primary benefit of burning is to remove leafy field trash, both reducing the volume and weight of material to be hauled to the mill and increasing the efficiency of mill operations. Infield burning has the additional benefit of driving off or destroying pests and potentially dangerous wildlife, before entry of harvest crews. Disadvantages are the requirement for suitable weather and increasing concerns by neighboring populations regarding the hazards and nuisance of smoke inhalation.

Harvest method and the amount of soil and leafy trash carried to the mill have a large influence on sugar recovery. Growth conditions and management, particularly harvest date, may result in a wide range of juice content and soluble solids (Brix, %). High-quality sugarcane stalks typically have a Brix of approximately 18%, of which approximately 90% is sucrose. Additional factors within the mill associated with crushing and extraction, removal of impurities, and crystallization also have a large effect on sugar recovery. In general approximately 10% of fresh cane weight is recovered as sugar.

Sugarcane water requirements are substantial and highly dependent on environment and crop growth stage. Sugarcane is traditionally grown in the humid tropics, where ET is reduced by high relative humidity and where water is available for extended periods of the growing season. As cultivation has moved to higher radiation but drier environments, the risk of crop water deficit increased, and in many areas supplemental or full irrigation has been applied. Although sugarcane is considered a heavy user of water, the water requirements depend on the environment. It is most useful to consider water requirements relative to alternative crop choices. For example, in the hot, inland Imperial Valley of California, water requirements calculated from the crop coefficients provided by the UN FAO Irrigation and Drainage Paper No. 56 (Allen *et al.*, 1998) indicated that approximately 1.8 m of water was required, about the same as the existing dominant crop in the area, alfalfa (*Medicago*).

Sugarcane is sensitive to soil water depletion, with shoot extension growth declining as available soil moisture declines by less than 10%. Stomatal closure is slightly less sensitive, beginning to decline approximately 15% depletion (Nable *et al.*, 1999). In parallel experiments in large pots, the more drought tolerant, but closely related plant, *Sorghum* maintained both shoot growth and stomatal conductance until approximately 50% depletion.

Successful cultivation of sugarcane has been achieved with many types of irrigation systems, from furrow to sprinkler and drip. Under some conditions, flood irrigation of flat-planted cane may be appropriate. With the large inputs of water required by sugarcane, sufficient attention must be paid to drainage. This must provide for an unsaturated root zone to 60 cm or more (Ellis and Merry, 2004). Drainage must not lead to excessive losses of irrigation water, particularly as may occur with furrow systems in sandy fields, but must allow enough drainage through the profile to avoid buildup of salts. Available commercial sugarcane clones are not tolerant of saline conditions. Under conditions of poorly drained soils with flat gradients, it may be necessary to provide drainage aids. These may be closely spaced drainage ditches or even buried drain tile, which carry percolated soil solution to nearby ditches and away from the field.

In many production areas, runoff from sugarcane fields, with its burden of nitrates, phosphates, dissolved carbon, and pesticides, is an environmental threat to adjacent ecosystems and is highly regulated. These relatively recent pressures, as well as the long-standing imperative to control soil erosion losses, make control of water inputs and drainage an important component of management.

Fertilizer requirements depend on the environment, previous crop, and residual soil fertility. In heavier, nonpeat soils, substantial N fertilization is required for sustained yields. As in most cropping systems, nitrogen is the nutrient that is most likely to become limiting in sugarcane production (Irvine, 2004). In general, approximately 100 kg N ha^{-1} is required for the plant crop and approximately 150 kg ha^{-1} for each successive ratoon crop. Nitrogen applications must be accompanied by sufficient irrigation or rainfall to facilitate uptake. Because of the potential for losses due to deep drainage, runoff, and volatilization, application of nitrogen is typically delayed until rapid crop growth has begun and immediate uptake and utilization are most likely to occur. In production for sugar, nitrogen is applied early and the plant is allowed to deplete soil reserves. This along with dry, cool weather leads to ripening, or accumulation of sugar rather than fiber in the stalk. For bioenergy, later application of nitrogen will sustain the maximum period of biomass accumulation.

Sugarcane is understood to be less N efficient than many crop species, suggesting that alternative practices might be considered. There is recent evidence that *Saccharum* may differ from even closely related cereal crops, in preferentially utilizing ammonium rather than nitrate from the soil N pool (Robinson *et al.*, 2011). As nitrate fertilizers are labile in the environment, increased use of other, particularly more reduced, forms of N may reduce the environmental impact of sugarcane and energy cane cultivation and reduce the net greenhouse gas balance of associated biofuels.

Under some conditions, deficiencies of potassium, calcium, and phosphorous will have to be addressed, based on soil test. Other nutrients are essential but at much lower levels and are not commonly limiting, including magnesium, sulfur, iron, boron, manganese, zinc, copper, nickel, molybdenum, and chloride. Calcium is typically applied as lime before planting, usually with the intent to raise soil pH, as levels in most soils are sufficient. Addition of lime may increase the availability of phosphorous and reduce the availability of aluminum. Potassium is not often deficient, and oversupply of this element will carry over into the mill, passing through clarification to accumulate in the molasses where it impedes crystallization of sugar and reduces recovery (Irvine, 2004).

Pest management in sugarcane reflects the fact that sugarcane is typically grown in a monoculture. This accentuates the risk of epiphytotics, although sugarcane is not an extremely vulnerable crop. On a global basis, sugarcane is susceptible to a number of bacterial diseases, leading to stunted growth, occluded xylem, and foliar symptoms and a variety of fungal diseases from rusts, mildews, and smuts to rots that consume the sugar storage tissues in the stalk. Effective production requires vigilance, as unexpected diseases may appear suddenly. Although seed pieces (setts) may be treated with fungicide, the principal defense against known diseases is through genetic resistance acquired in sugarcane-breeding programs.

In some environments, insect pressure may be severe and may require treatment. Sugarcane is subject to attack by stalk-boring insects, and buried seed pieces are vulnerable to a wide variety of pests that may destroy the viable buds. Nematodes may be a problem in sandy soils. Leaf feeders are typically not a major challenge to sugarcane culture except that some, such as leafhoppers, may vector serious viral diseases. Where available, the use of biological control has often proven effective. As with pathogens, the most effective defense is genetic resistance derived in the breeding programs.

Weeds are a serious challenge in sugarcane culture because of the relatively slow canopy closure. This provides weeds a prolonged period of full sunlight and minimal competition from the developing crop. In particular, a wide variety of grasses are difficult to remove once the cane crop becomes established. If weeds can be suppressed in the early season, eventually the dense sugarcane canopy, with LAI up to seven, will provide effective suppression of most weeds. Tillage and preemergent herbicides are the most successful control strategies.

Sugarcane is grown in a large number of countries under a very wide range of conditions. Although the ancestral chewing canes were strictly tropical, with introgression of highly diverse wild relatives, sugarcane has now spread, often under irrigation, to environments characterized by cool winters and very hot summers. Sugarcane remains a dominant source of natural sweetener in global markets.

Future Prospects for Sugar Crops

Sugar Beet

With the use of sugar beets, the yield of sugar achieved in most of the principal beet-producing countries has increased substantially over the last several decades. Most of this yield progress is due to increasing root yields (**Figure 2**), although sugar content in beets has increased less or been largely stable (Jaggard *et al.*, 2012). Yield increases can be attributed to several interacting factors, including improvements in plant breeding techniques and information technology, improved seed quality and agronomic practices, and planting and harvesting machinery. Where adopted, all these practices have led to improved overall efficiency in the sugar beet industry, from crop production to factory operations (Parkin and De Bruijn, 2010). Increasing levels of atmospheric CO_2 have also contributed to increasing yields over time. Weigel and Manderschied (2012), Jaggard *et al.* (2007), Demmers-Derks *et al.* (1998), and others have correlated significant increases in root yield and total biomass under enriched CO_2 conditions when fertilization levels were sufficient to support increased crop growth. Part of the effect was attributed to warmer summer temperatures (Jaggard *et al.*, 2007). Crop nitrogen use efficiency was also improved in many industrialized production areas (**Figure 11**). Increasing levels of atmospheric CO_2 should support slowly increasing yield trends if other agronomic factors are adjusted appropriately for higher yield expectations. Donatelli *et al.* (2003) in a modeling study suggested that in regions where temperatures increase due to climate change, irrigation may be needed to sustain yield increases. Similarly, Jones *et al.* (2003) predicted significant yield increases but also increased yield variance due to more frequent occurrences of drought in parts of Europe.

Comparisons of yields and yield trends among developed and developing regions indicate that there is still substantial technical opportunity for improvement in beet crop yields in many areas of the world. For example, yields in California are two or more times greater than those in Egypt and Iran, with areas with similar climates. In recent years, there has been a significant investment made in molecular genetics and the use of transgenic traits for herbicide tolerance and pest and disease resistance has taken place. Currently, herbicide-tolerant sugar beets are grown in the United States and Canada but have not been accepted for use in other countries due to differing perceptions of risk and regulatory cultures. Nonetheless, the potential value of molecular breeding to improve crop productivity, reduce pesticide use, and increase overall efficiency is widely recognized within the industry and is expected to eventually become part of hybrid development programs (Lathouwers *et al.*, 2005).

Part of the value of molecular breeding techniques is their potential to improve environmental performance in sugar beet production systems, especially where intensive agricultural practices are carried out (McGrath *et al.*, 2007). Märländer *et al.* (2003) identified several additional new technologies for improving the environmental performance of beet production, including conservation tillage, and integrated production strategies to reduce inputs and use of pesticides and fertilizers per unit yield and off-farm emissions. Kaffka *et al.* (2005, 2001, 1999) had demonstrated the use of precision agricultural techniques and the capacity of sugar beets to use low-quality water for irrigation to improve salinity management in salt-affected areas and to recover nutrients where groundwater and surface water are affected by eutrophication. In general, there has been an improvement in the efficiency of sugar beet

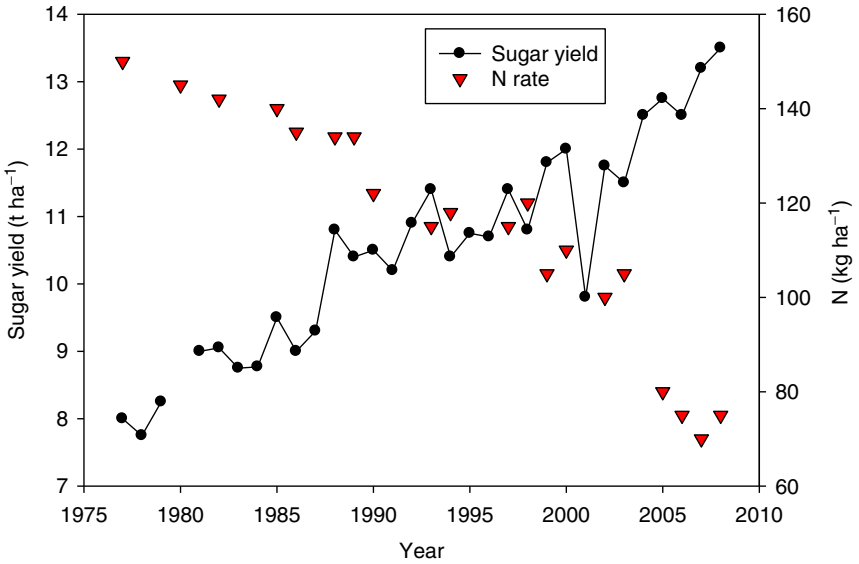


Figure 11 Yield and N fertilizer-use trends from France. Yields have increased, whereas N fertilizer use has declined. This phenomenon is common throughout the sugar beet industry in regions with developed, intensive agricultural systems. Reproduced from Cariolle, M., Duvall, R., 2006. Nutrition nitrogen. In: Draycott, P. (Ed.), Sugar Beet. Oxford: Blackwell Publication Ltd, pp. 169–184 (Chapter 8), with permission from John Wiley and Sons.

production over time. The labor invested in producing a hectare of sugar beets has declined, whereas yields have increased.

Both sugarcane and sugar beet provide a readily fermentable source of carbohydrates for conversion to ethanol, other higher alcohols, and biochemical feedstocks. The efficiency attributed to sugarcane as a biofuel source is due in part to the use of bagasse for the production of electricity needed to power the sugar or ethanol refinery. In contrast, sugar beet residues are commonly fed to livestock because they are a highly digestible feed for ruminant livestock. Because the fiber portion of beet roots is digestible and low in lignin, they can also be converted to C_6 and C_5 sugars using enzymes (Santek, *et al.*, 2010). This increases the overall sugar yield from beets available for fermentation to alcohols and makes beets a promising bioenergy feedstock (Panella and Kaffka, 2011), which compares favorably to both sugarcane and strictly cellulosic feedstocks (**Figure 12**). In Europe, some of the sugar produced at refineries in excess of sugar market requirements is converted to ethanol (Klenk and Kunz, 2008). Beet roots also digest readily when used in anaerobic digesters and are used for this purpose on a wide scale in Germany and elsewhere in Europe (Demirel and Scherer, 2008).

Sugarcane

Well-adapted sugarcane clones are considerably closer than most crop species, including those with the same photosynthetic pathway, to achieving theoretical maximal yields of approximately 6% of the energy available in sunlight (Zhu *et al.*, 2008). The maximum reported efficiency in the field is only approximately 4.3%. Maximum theoretical potential productivity of sugarcane is approximately 280 tons ha^{-1} $year^{-1}$, and with reduction for radiation striking bare ground during incomplete canopy closure, approximately 220 tons ha^{-1} $year^{-1}$ of above-ground biomass. With a harvest index of approximately 0.8 (leaving only roots, stubble, and some leafy trash in the field), potential above-ground dry biomass yield is 177 tons ha^{-1} $year^{-1}$, equivalent to 360–380 tons ha^{-1} $year^{-1}$ of fresh millable stalk material (Waclawovsky *et al.*, 2010). This is substantial relative to other potential crops.

Yields of sugarcane have increased steadily in many production areas, by approximately 1% $year^{-1}$, reaching approximately 150 tons ha^{-1} $year^{-1}$ of above-ground dry biomass under optimal experimental conditions in irrigated, high irradiance conditions in Brazil (Waclawovsky *et al.*, 2010). Record commercial yields were lower, approximately 120 tons ha^{-1} $year^{-1}$, and typical grower yields yet lower (**Table 1**), globally averaging approximately 35 tons ha^{-1} $year^{-1}$ dry biomass or 72 tons ha^{-1} $year^{-1}$ of millable cane over the first decade of the current millenium. In sugarcane, as in other crops, closing the gap between record and typical yields is an important goal for sugarcane production both for sugar and for bioenergy.

As producers around the world seek to expand production of sugarcane for sugar and bioethanol by expanding production into marginal areas, efforts will intensify to develop tolerance to drought, heat, and chilling. Efforts in Brazil to extend production to the south (higher latitudes), and in the United States to expand production northward and into the western inland valleys, have stimulated considerable efforts to enhance chilling tolerance in high-yielding clones. Genetic improvement of tolerance to heat and chilling appears feasible by selection among current germplasm, by further crossing with related wild species, particularly *S. spontaneum*, which exhibits considerable tolerance to abiotic stresses (Moore, 1987), and with the closely related genus, *Miscanthus*.

Sugarcane may represent a bridge crop for biofuel production from other sources. Current commercial clones provide sugar in high yields for direct fermentation. These clones

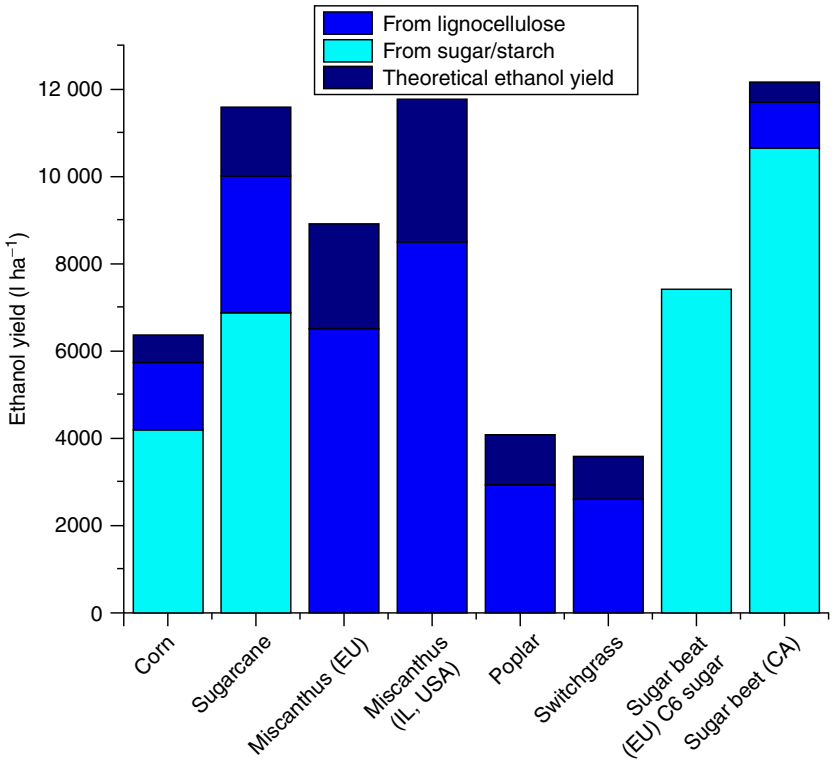


Figure 12 Potential ethanol yields from selected feedstocks. Crops like beets can be produced with high yields and efficiency using current or near-term technology. Light blue, current or simple technology, mid-blue (new or pilot-scale technology) and dark blue (no current technology available-the theoretical conversion limit). Reproduced from Kaffka, S.R., Zhang, T., Kendall, A.M., Yeo, B.-L., 2014. Advanced technology and modeling support biofuel production from beets in California. Proceedings of the 74th IIRB congress, Dresden. Available at: http://www.iirb.org/ (accessed 29.04.14).

also provide lignocellulose in bagasse and field trash (leaves) for current exploitation as a combustion fuel at the sugar mill and for future exploitation as a biofuel once required technologies mature. In many sugarcane systems, direct combustion of trash and bagasse provides much of the energy to evaporate sugarcane juice. In some areas, the material is used to cogenerate electricity, which may be produced in excess of mill requirements and sold into the local electricity grid. Current breeding programs are seeking to enhance stress tolerance and vigor, thereby reducing inputs and expanding production areas. This is done through selection and by increasing the percentage of other *Saccharum* species and related genera. Use of sugarcane to produce ethanol from sugar has the advantage of flexibility, as executed in Brazil. Here the sugar can be diverted between consumption and fermentation at short notice in response to market conditions.

Selection for high sugar has potentially created a genetic bottleneck that has narrowed the genetic resources from which high biomass and low- or high-lignin clones might be selected. This may have reduced maximum potential productivity in current commercial germplasm. This may be relieved as selection for total biomass in pursuit of efficient lignocellulosic bioenergy feedstocks is undertaken. Higher fiber clones that still contain relatively high sugar have been termed 'Type I Energy Canes' (Tew and Cobill, 2008). These were advocated some time ago by Alexander (1985). Selection within current breeding programs will most likely identify improved Type I cultivars, with somewhat higher fiber and lower sugar than conventional selections within these programs, but improved total biomass production Tew and Cobill, 2008). These may be a stop-gap solution toward maximum biofuel production.

In the long run, dedicated clones are more likely to outperform these compromise candidates in terms of biomass production, stress tolerance, and yields of lignocellulosic biofuel. These Type II clones are more likely to require separate crossing and selection programs. The emphasis will be on biomass production with stress tolerance. There appears to be considerable potential for enhanced productivity. Lignin and cellulose are coregulated at the level of gene expression (Ragauskas *et al.*, 2006) with studies in other species suggesting that repressing lignin may increase cellulose synthesis and digestibility. Further, stress tolerance has been linked to high fiber content (Ming *et al.*, 2001; Irvine, 1977), which will be more readily exploited for energy cane than it has been for sugarcane. As the lignocellulosic industry matures, selection for high- or low-lignin content may allow fine-tuning of cultivars for specific biofuel conversion processes. Improvement of tolerance to cold and heat will allow cultivation of the sugarcane feedstock in regions where the fuel markets are strongest, reducing transportation costs. In this case, market forces may reverse the decline in sugarcane and energy cane production observed in countries, such as the United States (**Figure 9**), as multiple product streams are developed.

Conclusions

A large amount of sugar from sugarcane production is diverted currently to ethanol. Brazil has demonstrated the feasibility of an integrated sugar/ethanol economy and many other countries are now developing this capacity. Ethanol from sugarcane sugar is at present one of the most efficient sources of biofuels that can be produced on a large scale. With future development of lignocellulosic processes, ethanol yields could increase by threefold, and the environmental benefits of sugarcane biofuel will be even greater (Oliverio *et al.*, 2010). However, once bagasse can be directly converted into other fuels, other cellulosic sources of biomass that produce little sugar but are inexpensive like crop residues and woody biomass will also become available. A distinct advantage of biofuel programs based on Type I or Type II energy cane clones is that the breeding, selection, management, and materials handling aspects of the production system are already well established for sugarcane. In a similar manner, this is also true for sugar beets that are used to a lesser extent as an ethanol source. These advantages of existing sugar crops will remain a factor in favoring their use compared with strictly cellulosic materials.

Some countries are more dependent on sugar production for their trade than others. Although sugar production is less important in nations that produce sugar beet, the crop has an important biological role in crop rotations and an important economic role in providing income to farmers and processing and refining jobs locally. Also, established industries representing significant capital investment have been developed to process beets into sugar. The cost of growing and processing sugar beet in the industrialized world is higher on an average than equivalent costs for sugarcane. This is due in part to differences in labor and other costs, the value of assets devoted to crop production in the industrialized and developing nations, and environmental regulations. It is unclear how trade issues affecting sugar beet production will be resolved in the future.

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www.nass.usda.gov
USDA National Agricultural Statistics Service.

Swine Diseases and Disorders

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Glossary

Autogenous vaccines Vaccine made from microorganisms isolated from the animal it will be used on; in the United States these are killed and, by permit, are extended for use in a farm, production system, or region.
Farrow Process of parturition; location where a pig is born and stays till weaning, usually 3–4 weeks of age.
Grow–finish Phase of production that follows the nursery period where pigs reach slaughter weight; used to describe pigs from 10 to 30 weeks of age.
Histopathology; -ic The science and microscopic examination of formalin-fixed and paraffin-embedded sections of diseased tissues.
Lesion Visible (microscopic or macroscopic) deviation from normal.
National Animal Health Monitoring Service A program administered by United States Department of Agriculture-Animal and Plant Health Inspection Service.
Nursery Phase of production that begins after weaning, used to transition pigs from the farrowing house to finishing; used to describe pigs from 3 to 10 weeks of age.
OIE World Organization for Animal Health created on 25 January 1924.
Pathognomonic Characteristic of a specific disease or disorder that, when present, is sufficient to make a diagnosis.
Veterinary diagnostic laboratory Location where samples are submitted and tests are run to determine the cause of disease.

In an approach to investigating any suspected disease or disorder in swine production, a history should be gathered first. Important history to understand from caretakers includes: age of pigs affected, duration of clinical signs, morbidity rate, mortality rate, treatments administered, response to treatments, and any other important information regarding previous diagnoses or disease in the affected group of animals. This is also the time to examine any production records that have been kept on the affected group of swine as well as previous groups for comparison. Records include but are not limited to: where the animals originated from; number in the herd; age; daily mortality; number treated; name of treatment, route of delivery and dose; feed and water usage; high–low temperatures; and vaccinations received or administered. After examining the production records and obtaining a history, proceed with a visual examination of the herd. Typically, it is a biosecurity custom to observe youngest groups first; however, in cases of suspected infectious diseases, it may be best to begin with the healthiest group advancing in order of increasing severity or prevalence.

Often, a definitive diagnosis is not achieved without an extensive clinical and pathological investigation. A postmortem examination, or necropsy, of affected pigs should occur last. Any pigs recently deceased of natural causes should be examined to establish trends, with the understanding that submission of tissues from these animals may not yield valuable diagnostic results. Tissues for diagnostic evaluation should be collected from clinically affected pigs that are euthanized immediately before necropsy. Sampling of five or more pigs may be required to obtain a valuable diagnosis. When investigating signs referable to the central nervous system (CNS), it is important to preserve brain and spinal cord tissue for microscopic evaluation in cases of neurological disease; therefore, blunt force trauma and brain penetration by captive bolt are not preferred methods of euthanasia. At minimum, fresh and formalin-fixed tissue samples should include: brain, tonsil, heart, lung, lymph nodes, spleen, kidney, liver, and intestine. Additional samples that may be beneficial for diagnosis include: premortem whole blood and ethylenediaminetetraacetic acid-chelated blood (for serum chemistry and complete blood count), spinal cord, intact stifle and hock joints (remove the leg at the hip), intact eyeball with optic nerve attachment, urine, feed, and water. Consult a diagnostic lab regarding any additional samples that may be required in determining an etiologic diagnosis. The etiologic diagnosis should be based on consistent history, signs, and pathology derived from a list of differential diagnoses that are most common or most likely to occur in that herd or production system.

A treatment, control, or prevention program should be formulated simultaneously. Before using any chemical, pharmaceutical, or biologic in swine intended for food, know the domestic use guidelines, importer requirements or producer-packer agreements regarding withdrawal times, residue and tolerance limits, prescribing guidelines, and prohibited substances.

Central Nervous System Diseases and Disorders

This section will focus on a practical approach to investigating signs of neurological disease in swine summarized in Table 1. It is important to determine if clinical signs are consistent with CNS or peripheral nervous system lesions (PNS). Common CNS signs in pigs include behavioral abnormalities (most commonly stupor), ataxia, loss of righting, seizures or

Table 1 Common central nervous diseases and disorders of pigs

	Preweaning	*Postweaning nursery*	*Postweaning grow–finish*	*Adult*
Streptococcus suis	++	+++	+++	
HPS	+	+++	+++	
Edema disease		+++	+	
PRV	+++	+		
Congenital tremor	++			
Hypoglycemia	+++			
Water deprivation		+	+++	

Note: The first column provides the diseases. The remaining columns represent the respective phases of production. The frequency of the occurrence is + (occasional), ++ (common), and +++ (routine).

seizure-like activity (paddling), nystagmus, and blindness. Musculoskeletal disorders may clinically confuse or complicate perceived PNS signs and must be differentiated from each other.

Streptococcus suis is a gram-positive cocci with 35 reported serotypes. Observational studies implicate sows as carriers and piglets are colonized as they pass through the birth canal (Amass *et al.*, 1996). Disease occurs most frequently during the suckling and postweaning period. Commingling pigs from different herds, concurrent infection with porcine reproductive and respiratory syndrome (PRRS), and other stress factors may increase the risk of developing *S. suis* meningitis (Villani, 2002; Thanawongnuwech *et al.*, 2000). Variable morbidity and mortality: mortality depends on early recognition and treatment. Clinical signs of *S. suis* meningitis include paddling, recumbency, nystagmus, and seizure. Isolation of *S. suis* from the lung, nasal secretions, or tonsil from normal pigs is clinically insignificant. In contrast, *S. suis* isolation from cerebrospinal fluid (CSF), meninges, joints, endocardium, or serosal surfaces with or without lesions is relevant (Pijoan, 1994). Few to no gross lesions may be observed during necropsy. Early recognition of clinical signs followed by injection with an antimicrobial that *S. suis* is susceptible is the most effective means of treatment. Administering an antimicrobial that *S. suis* is susceptible to in the drinking water has been proposed to control morbidity (Villani, 2002). Antimicrobial susceptibility patterns for *S. suis* isolates from regional diagnostic laboratories can be used to assist in selection of an appropriate antimicrobial while diagnostic tests are pending; ceftiofur is effective (Halbur *et al.*, 2000). Commercial and autogenous vaccines are available but due to *S. suis* serologic diversity may not be effective (Halbur *et al.*, 2000).

Haemophilus parasuis (HPS), also called Glässer's disease, causes bacterial meningitis, arthritis, and polyserositis similar to *S. suis*. Infections are not clinically or grossly distinguishable from *S. suis*. Definitive diagnosis is by bacterial isolation. However, HPS is a fastidious gram-negative rod and culture media must be supplemented with V factor for successful isolation. Owing to the difficulty in isolating HPS, Polymerase chain reaction (PCR) tests are a suitable alternative (Oliveira *et al.*, 2001). Like *S. suis*, isolation from the airways has little significance unless lesions are present (Hoefling, 1994). Antimicrobial susceptibility testing identifies ceftiofur or florfenicol that are typically effective first choice therapeutics (Oliveira, 2007b). Prevention may be achieved with medicated early weaning.

Edema disease results when a fimbrial (F18 or F4) and shiga-like toxin (StX-2e) positive strain of *Escherichia coli* successfully attaches to brush border receptors releasing toxin that damages blood vessels including those of the blood–brain barrier causing edema and encephalomalacia. Edema disease most commonly affects rapidly growing pigs, 2 weeks postweaning. Morbidity is moderate to high and mortality is high. Acute death of robust pigs, ataxia, eyelid swelling, and diarrhea are typical clinical signs (Rademacher, 2001). At necropsy, edema may be observed in the mesentery between the loops of the spiral colon and in the cardiac region of the gastric mucosa. Stomachs are usually full of feed. Bacteriologic isolation of a β-hemolytic strain of *E. coli* from affected pigs with meningoencephalitis is not sufficient for a diagnosis. Genotyping is necessary to confirm that the *E. coli* isolated was F18 or F4 and StX-2e positive and thus capable to induce such lesions. There is no effective treatment. Vaccination using an avirulent live culture of *E. coli* postweaning, thorough cleaning and disinfection between groups, and use of genetically resistance breeds that lack the fimbrial receptor are preventatives (Fairbrother and Gyles, 2006).

Pseudorabies (PRV), also known as Aujezsky's disease, is caused by a herpesvirus. PRV was eradicated from the US commercial swine herd in 2004 (USDA APHIS, 2008). Feral swine are potential reservoirs. Cattle, sheep, dogs, and cats can also be infected with PRV. High morbidity is due to large quantities of virus shed in saliva and nasal secretions for several weeks following infection. Mortality is inversely related to age approaching 100% in neonates. Clinical signs are also age dependent. Neonates may die without signs. Suckling and recently weaned pigs are those that commonly exhibit ataxia, tremors, excess salivation, and seizures. At necropsy, the brain appears congested and hemorrhagic. Necrotic foci occur in the spleen, liver, lung, lymph node, and specifically tonsils. Histopathologic lesions are characterized by nonsuppurative meningitis and intranuclear inclusion bodies. PCR, virus isolation (VI), immunohistochemistry (IHC), or fluorescent antibody can be used to confirm the diagnosis. No specific treatment is available. Vaccination and eradication are effective for control (USDA APHIS, 2008). In areas free of PRV, suspicion of the disease should be reported to state and federal agencies as required.

Congenital tremors result when hypomyelination or demyelination of the brain and spinal cord. Clinical signs are clonic muscle contractions that cause a general tremor of the entire body. Pigs are affected at birth but severity subsides with

age (Dewey, 2006). Mortality is variable and is the sequela of malnutrition because piglets are unable to nurse. There is no known treatment or prevention.

Hypoglycemia occurs when piglets fail to nurse the sow. This condition is observed within 24 h afterbirth. There is a low morbidity but high mortality. Pigs may appear disoriented, ataxic, recumbent, or dead. On necropsy, affected piglets will have empty stomachs. Assigning an employee to attend farrowing to ensure piglets nurse will reduce incidence.

Water deprivation, also referred to as salt poisoning, is an idiopathic disease resulting from a period of inadequate water intake (Carson, 2006). High morbidity with variable mortality occurs. The disease is suspected when there is a history of power outage or poor management (Thacker, 2000). Fighting over water access is the first clinical sign and occurs within hours. Dog-sitting, opisthotonous, convulsions, and fighting over water follow and develop after 24 h without water. Removal of the brain from an affected animal reveals edema and eosinophilic meningoencephalitis with perivascular cuffing and this is pathognomonic (Gudmundson and Meagher, 1961). Serum or CSF with a sodium level above160 mEq l^{-1} may also be used for supporting evidence (Osweiler and Hurd, 1974). Treatment of swine showing signs with an anti-inflammatory is variably effective. When water is restored, limit intake to short, 10–15 min intervals until all animals have had a chance to drink and fighting has ceased after which water can be provided *ad libitum*. Prevention is daily observation to ensure each animal can access water, adequate water delivery system, and equipping the facility with a generator or alternative method to deliver water during power outages.

Gastrointestinal System Diseases and Disorders

Gastrointestinal diseases and disorders can occur in all ages of swine as summarized in **Table 2**. Most digestive diseases are referable to the gastrointestinal tract and result in diarrhea and occasional vomiting. Diarrhea is the result of an intestinal dysfunction caused by malabsorption, excessive secretion, or effusion. Unfortunately, this is not an exclusive characterization of diarrhea and overlap occurs (Moeser and Blikslager, 2007). Rather, differentials for diarrhea should be referable to age at onset and site of infection.

Gastric ulcers are noninfectious and result when glandular mucosa specifically the pars esophagea is traumatized by gastric acid. Gastric ulcers have a wide variety of causes but are most commonly associated with small feed particle size (Ayles *et al.*, 1996) and interruption of feed intake whether caused by disease or poor management. It is common to see signs consistent with gastric ulceration increase following an acute PRRS or influenza outbreak. Morbidity and mortality vary with the scope of the underlying cause. Clinical signs include regurgitation, vomiting, pallor or jaundice, and acute death. An acutely dead pig with blood in its stomach is indicative of an active ulcer and is sufficient evidence for a diagnosis. In chronic cases, ulceration causes hyperplasia resulting in stricture of the pars esophagea and regurgitation. Feeding a coarse ground diet for 3 weeks significantly decreases severity (Ayles *et al.*, 1996) but is impractical in modern production facilities.

Rotavirus is a nonenveloped RNA virus with a double-layered capsid allowing it to remain stable and infective in the environment for months and intrinsically resistant to some disinfectants. Four serogroups infect swine: A, B, C, and E (the latter only reported from the United Kingdom). In addition, infections with particular serogroups vary by age: Type C mostly in suckling piglets and Type A predominately in nursery pigs (Stephenson *et al.*, 2013). Type A is the most prevalent serogroup. Severity of disease decreases with age and is self-limiting. The virus infects and destroys villous enterocytes resulting in villous atrophy. In response, crypt cells fill in the gaps but, because they are incapable of absorption, suckling piglets quickly loose body condition and have a gaunt or wasted appearance. Neither clinical signs nor gross lesions are pathognomonic although loops of small intestine appear thin-walled with moderate to large amounts of watery contents. A histopathologic report of blunted villi and crypt hyperplasia is suggestive of rotavirus infection. Infection with rotavirus can be confirmed by PCR or electron microscopy (EM). Enzyme-linked immunosorbent assay (ELISA) is also available but limited to detection of serogroup A. IHC and EM detect rotavirus and confirm its role in pathology, but both tests lack

Table 2 Common gastrointestinal diseases and disorders of pigs

	Preweaning	*Postweaning nursery*	*Postweaning grow–finish*	*Mature*
Gastric ulcer		+	+++	++
Clostridium difficile	+++			
Clostridium perfringens Type A (CpA)	+++			
Clostridium perfringens Type C (CpC)	+++			
Coccidiosis	++	++		
Salmonellosis		++	++	
Collibacillosis	++	++		
Swine Dysentery			+++	++
Porcine proliferative enteropathy (PPE) (Ileitis)			+++	+
Rotavirus	+++	++		
Transmissable gastroenteritis (TGE)	+++	++	++	++
Porcine epidemic diarrhea (PED)	+++	+	++	++
Whipworms			+++	+

Note: The first column provides the diseases. The remaining columns represent the respective phases of production. The frequency of the occurrence is + (occasional), ++ (common), and +++ (routine).

sensitivity. Treatment is supportive by administration of oral rehydration solutions. Acidifiers and antibiotics are sometimes administered to control secondary bacterial infections. Treatment success is variable and depends on the degree of malnourishment. Prevention among neonatal piglets is through ingestion of lactogenic virus neutralizing antibody from the sow, which is stimulated by administering feedback of Rotavirus positive piglet feces or intestines (Arruda *et al.*, 2011) or a modified-live commercial Type A vaccine no less than 3 weeks before farrowing. A modified-live commercial Type A vaccine is also available for pigs. It does not induce cross-protection for other serogroups and may be cost-prohibitive.

TGE is caused by TGEv, a coronavirus that is heat labile at temperatures above 21 °C, prone to dessication and photosensitization (Bay *et al.*, 1952). The epidemic form causes acute disease in all age groups within as little as 18 h of infection. Morbidity and mortality is high, approaching 100%, in an epizootic outbreak. The severity of disease is age dependent but all ages will develop diarrhea (Moeser and Blikslager, 2007). Postweaning infections result in high morbidity but low mortality; the most significant economic losses at this time are caused by reduced average daily gain, market weights, and overall system efficiency. Necropsy reveals that the small intestine and colon are fluid filled, the small intestinal wall is thin almost translucent, and lacteals are empty. Necrosis and atrophy are observed throughout the length of the villus. The colon and cecum are spared. The endemic form occurs when susceptible animals are introduced to the herd or after maternal antibody wanes. Prior exposure to porcine respiratory coronavirus (PRCV) may cause false-positive antibody test results. A TGEv/PRCV differential ELISA is available. In an outbreak, sows are fed tissue of diarrheic pigs to stimulate herd immunity and new introductions of animals are stopped. After the exposure and a subsequent cool-down period of 4–6 months or after clinical signs cease, sentinels can be introduced and monitored for seroconversion (Saif and Sestak, 2006). Absence of seroconversion indicates successful elimination of TGEv. Commercial vaccines are available but should be used with caution and only when elimination is not an option.

PED is caused by PEDv, a coronavirus that causes signs and histolopathologic lesions indistinguishable from TGEv. Unlike TGEv, PEDv is more environmentally resistant making elimination more difficult. The disease has been described in Europe, Asia, and, as of 2013, the United States. Prevalence of the enzootic form is approximately 50% (Chae *et al.*, 2000). Morbidity approaches 100% and mortality is 80% or more in a naïve sow herd resulting in 3–5 weeks of production losses. Clinical signs appear within 12 h; piglets develop a watery, fetid diarrhea leading to dehydration, metabolic acidosis, and death before caretakers are able to humanely euthanize them. Vomiting also occurs. The severity of disease is age dependent but all ages will develop diarrhea. Postweaning infections result in a high morbidity but low mortality; most significant economic losses at this time are caused by reduced average daily gain, market weights, and overall system efficiency. Viral shedding occurs up to 10 days postinfection. Reproductive failure and inefficiency is a sequela of an outbreak (Olanratmanee *et al.*, 2010). TGEv/PEDv differential PCR is available to confirm a presumptive diagnosis of PED. Serum can be submitted for ELISA or immunofluorescent antibody but collected no sooner than 3 weeks after diarrhea was o bserved. Immunoprophylaxis using egg antibody or hyperimmune serum and supportive care including electrolyte administration have been used for treatment. In an outbreak, sows are fed tissue and feces from diarrheic pigs to stimulate herd immunity (Olanratmanee *et al.*, 2010). Hygiene is the key to reducing environmental contamination. Preventing introduction of virus into a herd with biosecurity alone may not be sufficient because the virus has been found in aerosol up to 10 miles from a positive farm (Goede *et al.*, 2013).

Porcine coccidiosis is most often caused by *Isospora suis*. Farm hygiene, specifically farrowing rooms, and sow infestation influence the persistence of disease; however, age at infection rather than infectious dose has the greatest impact on severity (Worliczek *et al.*, 2009). The prepatent period is approximately 5 days. Morbidity is variable and mortality is low. Pasty diarrhea, unthrifty to potbellied appearance of 7–21 day old pigs, and below average wean weight is suspicious for coccidiosis. On necropsy, the small intestine often is thickened and the mucosal surface is necrotic and has an adherent pseudomembrane. Histopathologic examination of the affected portion of the intestine reveals larvae in the lamina propria. Sensitivity of fecal flotation is moderate. There is no effective treatment. Prevention is by oral administration of an anticoccidial (Maes *et al.*, 2007). Heat treatment (flaming) of flooring may reduce environmental contamination. Concrete, rubber coated and plastic flooring in the farrowing crates are difficult to clean and disinfect so removal may be the only option.

Swine dysentery (SD) is a spirochete of the genus *Brachyspira* that is an oxygen-tolerant anaerobe giving it the ability to survive for long periods of time in manure, pits, and lagoons (Schwartz *et al.*, 2012). Rodents, particularly mice, are known vectors and can serve as reservoirs. *Brachyspira hyodysenteriae* is the species known for causing SD. Other species of *Brachyspira* have been recently described in dysentery-like disease (Burrough, 2012). Incubation is 10–14 days but disease occurs in a 3–4 week cycle. Administration of tiamulin or lincomycin in the feed or water may alter the time to onset of signs after exposure. Morbidity is high and mortality is low to moderate characteristically causing disease in only the finisher and mature groups. Economic significance is mostly lost performance due to reduced daily gain and feed conversion. The specific mechanism of pathogenesis is not well understood but the spirochete does not invade the lamina propria. Clinical signs are the presence of mucohemorrhagic diarrhea containing flakes of frank blood or appearing as a generalized brick red to rust color. Lesions are mostly observed in the spiral colon where epithelial sloughing and mucosal invasion cause necrosis resulting in the formation of a pseudomembrane. The colonic walls may be thickened due to vascular congestion and mucosal hyperplasia. Bacterial culture produces strong β-hemolysis. PCR test for confirmation and speciation is recommended for any isolate with characteristic growth. Introduction of infected pigs and contaminated equipment or facilities are the source of infection. Pleuromutilins, like tiamulin, and the lincosamide, lincomycin, are effective for treatment. However, if the environment remains contaminated, clinical signs will recur. Depopulation has resulted in

successful eradication (Harms, 2011). Medicated elimination that combines thorough pulse medication with tiamulin, cleaning and disinfection, and employment of an aggressive rodent control program is also effective (Burrough and Sexton, 2013).

Escherichia coli is a gram-negative rod that infects all ages of swine but must express virulence factors to cause diarrhea. *Escherichia coli* colonize the small intestine by fimbria that binds receptors on the villous surface of enterocytes. Enterotoxigenic *E. coli* (ETEC) then produce toxin(s) that increase osmolality leading to diarrhea (Moeser and Blikslager, 2007). ETEC is subdivided by fimbria, toxin, and age of pig affected. Neonatal diarrhea (ND) is most common in pigs 0–7 days of age. The onset of postweaning diarrhea (PWD) caused by F18 is delayed, occurring 5–14 days postweaning, compared to that caused by F4 and its severity is indirectly related to wean age. Clinical signs are profuse diarrhea, rapid dehydration leading to emaciation, or death due to metabolic acidosis. Fluid filled and hyperemic sections of jejunum and ileum may be present at necropsy but few consistent gross lesions occur. Intestinal contents have a distinctly alkaline pH. Isolation of large numbers of *E. coli* and with dense layers of rod-shaped bacteria covering villi seen on histopathology in samples from pigs with diarrhea is sufficient for diagnosis of *E. coli* but not ETEC. Genotyping is necessary to determine fimbria and toxin types, which are essential to confirm diagnosis of ETEC. Treatment of affected pigs/litters/groups includes administration of antibiotics and oral rehydration solution or electrolytes to correct hyperkalemia (Kiers *et al.*, 2006). Control and prevention of ND is by passively derived lactogenic immunoglobins from vaccinated females (Kohler, 1974). Prevention of PWD include selection of genetically resistant breeds lacking K88 and F18 receptors, administration of an oral avirulent live culture to stimulate active immunity or competitively exclude field strains (Genovese *et al.*, 2000), feeding 2500 ppm zinc oxide postweaning and probiotics. Immunity and exclusion is unique to each fimbria; vaccines should include the prevalent genotype(s) causing the diarrhea.

Clostridium perfringens Type A (CpA) is a gram-positive bacillus and inefficient sporulator. Sows are regarded as the source of neonatal infection. Frequency of CpA diarrhea is on the rise in the USA. In uncomplicated cases, mortality is low whereas morbidity is high and below average weaning weights result. Cases of CpA diarrhea are associated with the expression of α and β_2 toxin. CpA is cultured from the stomach and upper third of small intestine but does not bind intestinal epithelium causing few to no histologic lesions. Because of its ubiquitous nature and prevalence among health pigs, CpA may be an opportunist and its role as a primary cause of neonatal enteritis is not definitive. Large numbers (3+ or 4+) of gram-positive bacilli cultured from feces or intestinal contents of diarrheic pigs is suggestive of CpA. Genotyping by PCR to confirm presence of *cpb2* gene in CpA isolates and rule out of other causes of ND are supportive to the diagnosis (Bueschel *et al.*, 2003). Treatment has variable success rates and is limited to administration of empirically selected antibiotics and oral rehydration solutions to affected piglets. Control of CpA enteritis is best accomplished by preventing other causes of ND. Following a thorough cleaning, sporicidal disinfectant should be applied to farrowing crates and equipment between litters and be allowed to dry before reloading. Feeding of bacitracin to sows has resulted in significant increases in weaning weights (Schultz, 2007). A commercial CpA toxoid vaccine is available (Hammer *et al.*, 2008). Autogenous whole cell vaccines are also in use. If vaccine is unavailable, feedback might be considered but should be pursued with caution (Robbins and Byers, 2013a).

CpC is a gram-positive bacillus and inefficient sporulator. Sows are regarded as the source of infection. Pathogenesis of type C is due to expression of β toxin leading to necrosis of intestinal epithelium resulting in hemorrhagic diarrhea or acute death of piglets less than 3 days of age. Gross necropsy reveals hemorrhagic and blood-filled loops of small intestine. A pseudomembrane may form on the luminal surface, and intestinal mucosa is edematous. Gross and histopathologic lesions in the presence of large numbers (3+ or 4+) of gram-positive bacilli cultured from feces or intestinal contents warrant a presumptive diagnosis. Genotyping by PCR to confirm presence of the *cpb* gene is confirmatory (Songer and Uzal, 2005). Treatment of affected piglets is unrewarding due to the rapid and debilitating course of this disease. Prevention is accomplished by vaccination of gestating females with a commercial toxoid and ensuring piglets consume sufficient colostral antibodies to result in protection.

Clostridium difficile is a gram-positive bacillus that easily sporulates making it environmentally resistant to many disinfectants. *Clostridium difficile* associated diarrhea leads to a 10–15% reduction in wean weights (Songer and Uzal, 2005). Although more than a third of piglet diarrhea involves *C. difficile*, it is the better known to cause healthcare-associated infections among humans. The pathogenesis of *C. difficile* infections is in response to the expression of toxins A and B. A watery diarrhea occurs in 1–7 day old piglets. Mesocolonic edema may be observed at necropsy. *Clostridium difficile* is difficult to culture and can be isolated from healthy piglets. Therefore, volcano lesions on histologic exam and confirmation of toxins in fecal contents by antigen ELISA are diagnostic. Treatment is ill-defined but is likely similar to that for CpA enteritis, because it is likely to be initiated based on clinical signs, which are similar. Autogenous vaccines are used to aid in prevention but efficacy is unclear.

PPE, commonly referred to as ileitis, is the general categorization of infections caused by *Lawsonia intracellularis*, an obligate intracellular bacterium. Because the bacteria cause lesions in the ileum, PPE is also referred to as ileitis. Seroprevalence in grow–finish herds can reach 100%. PPE can further be divided into four clinical forms (Kroll *et al.*, 2005). Porcine intestinal adenomatosis (PIA) is most common in 6–20 week pigs and causes little mortality. Porcine hemorrhagic enteritis (PHE) affecting pigs 28 weeks of age and older including breeding swine and can be associated with increased mortality and dark, bloody stools. Necrotic enteritis (NE) and subclinical ileitis, the most common form, occur among postweaning pigs. In all forms, transmission is by the fecal–oral route. Crypt enterocytes infected with *L. intracellularis* become hyperplastic. The altered ratio of villous and crypt enterocytes leads to malabsorption and subsequent increases in feed conversion and time to reach market weights. PIA results in variable degrees of thickened ileum that can be found at necropsy. The ileal lumen may contain a blood clot in PHE

or pseudomembrane in NE. When diarrhea ranging in color from normal (PIA, NE, and subclinical) to dark-red or black (PHE) is observed, PPE should be considered as a possible cause. Subclinical ileitis usually causes no clinical signs (Gebhart, 2007). Histopathologic lesions containing intracellular S-shaped organisms are suggestive of Lawsonia infection but IHC should be used to confirm diagnosis. PCR is helpful to detect infection and is highly specific but moderately sensitive. Cross-sectional or longitudinal serologic profiling using a widely available ELISA is the best tool for determining timing of exposure. Treatment is with effective antibiotics, such as tylosin, administered by injection or in the feed or water. Control is by administration of a commercially available modified-live oral vaccine before infection or feeding antibiotics when infection is known to occur. Vaccination should take place at least 8 weeks before seroconversion (Walter *et al.*, 2004).

Salmonellosis causing gastrointestinal disease in swine is most commonly associated with the species Typhimurium. *Salmonella* Typhimurium is commonly isolated from swine. Isolation of multidrug resistance strains of *S*. Typhimurium from swine at slaughter have garnered attention from public health and food safety professionals and it is this that make this infection significant to the pork industry (Foley *et al.*, 2008). Some European Union member states have implemented meat-juice serologic monitoring at slaughter to assess on-farm Salmonella control programs. Pathogenesis of *S*. Typhimurium is similar to *Salmonella cholerasuis* by invading enterocytes and subsequently macrophages leading to an infectious carrier state. Initial infection causes inflammation and cytokine release that result in watery, yellow diarrhea containing feed particles. Button ulcers may be visible on the mucosal surfaces of the colon and cecum on gross necropsy examination and, on histopathology, can be found to extend into the lamina propria. Bacterial isolation without using enrichment media and the presence of histopathologic lesions is consistent with a diagnosis of Salmonella enteritis. Treatment is with antibiotics administered symptomatically to diarrheic pigs. Antibiotic susceptibility of the isolate should be considered before initiating treatment. Rearing pigs on slatted floors, decreasing stocking density, and acidification of digesta are effective in reducing the prevalence of Salmonella infections in swine (Funk and Gebreyes, 2004; Boyen *et al.*, 2008). Cross-protection with *S. cholerasuis* vaccine has been reported and reduces carcass colonization (Husa *et al.*, 2009).

Whipworm infestations of swine are the result of *Trichuris suis* infection. Pigs kept on pasture, in outdoor lots, or facilities with a history of *T. suis* diagnosis are at greatest risk for disease (Pittman *et al.*, 2010a). The prepatent period is 6–7 weeks. The egg is not immediately infective, which requires 3–4 weeks in the environment. The infectious larva hatches from the egg and invades enterocytes in the small intestine and cecum. The entire life cycle of *T. suis* is completed in the intestine. Ulcerations in the mucosa and damage to capillary blood supply of intestinal epithelium lead to hemorrhage, anemia, and hypoalbuminemia. Clinical signs are depressed weight gain, increased feed conversion, bloody diarrhea, ill thrift, and death. Adult worms imbedded in the ileum, cecum, or proximal colon are sufficient for diagnosis of whipworms. Eggs are intermittently shed and thus not a reliable method of diagnosis (Pittman *et al.*, 2010a). Treatment and control are synonymous and require administration of an effective anthelmintic like fenbendazole. Prevention is by steam sanitation and drying; however, eggs are resistant to common disinfectants and remain infective for years.

Integument System Diseases and Disorders

The porcine integument or skin, like that of other domestic species, serves as a protective barrier between fragile internal tissues and harsh external hazards. Skin is comprised of layers (from external to internal): epidermis, dermis (superficial and deep), and subcutis. Blood vessels, hair follicles, sebaceous glands, and muscles are found in the dermis. Notably, the pig's skin does not contain sweat glands; therefore, modern swine facilities are outfitted with evaporative cooling systems for thermal regulation in hot climates. Skin diseases and disorders can be the result of viral or bacterial infections, parasite infestations, immunologic reactions, and idiopathic or iatrogenic causes that are summarized in **Table 3** by their various macroscopic and microscopic lesions.

Greasy pig is a skin disease of swine caused by a toxin produced by *Staphylococcus hyicus*. A break in the skin is the typical sequela. Gilt litters reportedly have a higher incidence of this disease, presumably due to deficient maternal immunity. All ages of pigs may be affected but suckling and nursery pigs are most likely to develop disease. Affected pigs develop focal crusts on the face, neck, and axillary region, and the crusts may coalesce as the disease progresses. Affected areas are greasy to touch and may appear black due to dirt adhering to it. If pigs are untreated or fail to respond to treatment, the trunk and extremities may become involved. Pyrexia and lethargy can be observed in severe cases and are followed by growth reduction. Gross appearance of affected skin is rarely confused with other skin conditions of swine. Submission of formalin-fixed skin sections that include the junction of affected and unaffected layers of epidermis and dermis for histopathologic examination is needed for a diagnosis. The pathognomonic histologic lesion is exudative epidermitis.

Table 3 Common integument diseases and disorders of pigs

	Crust	*Papule*	*Plaque*	*Pustule*	*Necrosis*	*Erythema*	*Scar*	*Scale*	*Vesicle*
Greasy pig	X			X				X	
Erysipelas	X				X				
Porcine dermatopathy and nephropathy syndrome (PDNS)	X	X				X			
Sarcoptic mange	X			X					

Note: The first column provides the diseases. The remaining columns represent the type of lesion that occurs.

The *S. hyicus* can be cultured from the surface of clinically normal skin sections. Treatment includes topical application of antimicrobials or disinfectants. Unaffected pigs with direct contact with affected pigs should also be treated to control spread. In cases where pigs exhibit systemic signs, administration of an injectable antimicrobial and anti-inflammatory is warranted. In the United States, no antimicrobials are labeled for the treatment, control or prevention of *S. hyicus* so all antimicrobial therapy is extra-label. Prevention should focus on facility hygiene and include a soap degreaser and disinfectant regimen to reduce contamination. In addition, scarification of the skin of breeding age females with the farm-specific *S. hyicus* strain can reduce disease incidence in suckling pigs (Murray and Rademacher, 2008).

Erysipelas or diamond skin disease is caused by a soil-borne gram-positive bacterium, *Erysipelothrix rhusiopathiae*. This zoonotic pathogen is transmitted by migratory fowl, turkeys, and pigs. Humans may become sickened when direct contact with blood from affected animals contaminates an open wound (Brooke and Riley, 1999). The finding of lesions at slaughter results in partial or complete carcass condemnation (Bender *et al.*, 2011). The disease is most common in growing, finishing, and breeding age swine. Bacterial emboli lodge in blood vessels causing vasculitis, thrombosis, and ischemia leading to lameness, abortions in gestating females, and raised, red to purple rhomboid skin lesions for which erysipelas is best known. Skin biopsies from the affected area should include epidermis and dermis, but histologic lesions are only supportive. Bacteriologic isolation or PCR identifying *E. rhusiopathiae* confirms the diagnosis. Treatment with β-lactam antibiotics including penicillin is effective. Commercial bacterins and avirulent live cultures are available for prevention (Wood, 1984) or in the face of outbreaks to prevent the chronic form.

PDNS has been associated with Porcine circovirus type 2 (PCV2) infection, but any disease process resulting in ischemia could cause result in PDNS. The condition is characterized by red to purple discoloration of skin that begins on the caudal surface of the hind limbs and the ventral surface of the abdomen resulting from ischemia. On necropsy, gross examination of the kidney cortex may be speckled with pinpoint, white foci caused by infarcted blood vessels. Pig of any age can be affected with PDNS, but it is more commonly observed during growing and finishing stages. Submission of fresh and formalin-fixed skin sections that include the junction of affected and unaffected layers of epidermis and dermis is required. There is no specific treatment or prevention; rather, diagnose the underlying cause to determine appropriate therapy (**Figure 1**).

Sarcoptic mange is the result of an allergic reaction to the saliva of ectoparasites, *Sarcoptes scabiei*. Mange may also be caused by *Demodex phylloides*. Mortality is low and morbidity is moderate. Economic losses are the result of reproductive inefficiency, growth reduction, and carcass condemnation. Infestation and subsequent clinical signs in the breeding herd, most notably an incessant scratching, develop following the purchase of infested genetic replacements. In addition, growing pigs placed in facilities that previously housed infected swine or facilities that reuse straw bedding or have solid wood partitions may also become infested. The mite is rare in modern, high-health swine operations. The burrowing mite causes red pustules and flaking skin. Individual pigs may develop signs in as few as 3 weeks but a herd may not show signs for several months. In the chronic stage, thick crusts develop at the corners of and inside the ears. Examination of a scraping from the crusts will reveal the mite (Averbeck and Stromberg, 1993). An ELISA test is used to determine prior exposure and determine success of eradication programs. Treatment can be applied topically using an antiparasitic, such as amitraz, to temporarily alleviate clinical signs. Control and eradication programs utilize feeding or injection of ivermectins (Mohr, 2001).



Figure 1 PDNS, skin, grow–finish pig. Hemorrhagic pustules, coalescing areas of erythema, crusts present on hind limbs and abdomen. Courtesy Dr. Glen Almond.

Musculoskeletal System Diseases and Disorders

The musculoskeletal system is comprised of tendons, ligaments, muscles, and bones. Disorders and disease of this system are typically characterized by lameness. Lameness is any deviation in normal locomotion including favoring a limb or failure to bear weight on the limb. Neurologic conditions, which also cause changes in locomotion, may be ruled out by postmortem examination of articular surfaces and diagnostic testing. Investigation of musculoskeletal diseases and disorders should always start with the claws that are easily traumatized causing pain resulting in lameness. Flooring and genetics also influence the incidence of lameness. Common musculoskeletal diseases and disorders of swine can be divided into osteopathies and myopathies and summarized in **Table 4**.

Mycoplasma hyosynoviae colonizes upper airways and tonsils resulting in a carrier state. Transmission is vertical from sow to pigs and lateral between pigs (Ross and Spear, 1973). *M. hyosynoviae* is most often diagnosed during the grow–finish phase. Morbidity is variable but mortality is low. Clinical signs are a stiff gait and difficulty in standing, most often the stifle or elbow and less frequently the hock, hip, and shoulder. Signs often occur 2–3 weeks after a stressful event; lesions begin to resolve 7 weeks postinfection. The affected joint contains yellow or blood-tinged effusion with moderate

Table 4 Common musculoskeletal diseases and disorders of pigs

	Preweaning	*Postweaning nursery*	*Postweaning grow–finish*	*Adult*
Mycoplasma hyosynoviae			+++	++
Mycoplasma hyorhinis		++	++	
Erysipelas			++	++
Osteochondrosis (OC)			++	++
Ricketts		++	++	
Mulberry heart disease (MHD)		++	+	
Splayleg	+++			

Note: The first column provides the diseases. The remaining columns represent the respective phases of production. The frequency of the occurrence is + (occasional), ++ (common), and +++ (routine).

villous proliferation but is not always observed despite lameness and does not necessarily correlate with presence of histopathologic lesions. Aseptic collection of synovial fluid by needle aspiration or sterile swab or submission of the affected joint intact is recommended for diagnosis. PCR is the most sensitive test; culture requires special media and lacks sensitivity (Gomes Neto *et al.*, 2012). Histopathologic examination of formalin-fixed synovium reveals nonsuppurative fibrinous polyarthritis and lymphoplasmacytic perivascular synovitis. ELISA is also available. Lincomycin has historically been an effective therapeutic choice (Burch and Godwin, 1984). Treatment should be initiated when lameness is first observed; however, spontaneous resolution is common. No commercial vaccines are available.

Mycoplasma hyorhinis is a ubiquitous bacterium that is an early colonizer of upper airways. Transmission is vertical from sow to pigs and then between pigs postweaning (Rovira, 2009). Infection can progress to polyarthritis, polyserositis, and otitis in the pre- or postweaning phases; arthritis develops postweaning. Clinical signs include lameness, arthritis, and fever that develop 3–10 days after septicemia occurs and persists for 10–14 days (Gomes Neto *et al.*, 2012). Disease may become chronic resulting in ill thrift, reduced growth, and death. Articular surfaces may be eroded. In cases of lameness, synovial fluid and formalin-fixed synovium can be submitted. Alternatively, the entire affected leg can be submitted; disarticulate above the infected joint keeping the affected joint intact. Submission of fibrin or fibrin covered tissue(s) should be included for PCR testing to differentiate *M. hyorhinis* from other bacteria that form fibrin on serosal surfaces like HPS and *S. suis* (Rovira, 2009). Histopathology reveals fibrinosuppurative inflammation in affected tissues. Treatment is empirical.

Erysipelas is the result of a chronic *E. rhusiopathiae* infection causing arthritis and endocarditis that follows the initial septicemia. Lameness and joint swelling is mostly noticeable in hock and carpal joints. Lameness may also occur in stifle and elbow but swelling cannot be appreciated. Synovial fluid appears serosanguinous and can be submitted for testing by bacterial culture or PCR. Alternatively, the entire affected leg can be removed to prevent contamination; disarticulate the leg above the infected joint. Histopathologic examination of formalin-fixed synovium reveals a proliferative synovitis. Other lesions that occur are nonsuppurative fibrinous polyarthritis and erosion of cartilage that can progress to pannus and ankylosis. Treatment with β-lactamase antibiotics including penicillin is effective. An anti-inflammatory is added to a treatment program for pain management. Commercial bacterins or avirulent live cultures are available for control and prevention.

OC is the result of a delay in ossification of articular cartilage, and represents the most common lesion among culled sows. Morbidity is most often reported in adult and breeding age pigs (Dewey *et al.*, 1993). Mortality is variable and is the result of humane euthanasia because the animal becomes nonambulatory. OC causes lameness, pain, and joint swelling. A noninfectious lameness most often affects the distal part of the humerus or femur. Lesions are typically bilateral and symmetrical. Diagnosis is made by ruling out other causes of lameness.

Ricketts occurs as a result of phosphorus deficiency, vitamin D deficiency, or secondary to iron toxicity but is not caused by dietary calcium deficiency. The condition should be suspected when there is an increase in nonambulatory pigs and broken bones during the finishing stage particularly at and immediately before marketing. Occasionally, joint swelling in the nursery stage is observed. Rachitic rosary (enlargement of costochondral junctions) and soft bones are observed on necropsy. If rickets are present, a bone ash analysis of the second rib will be below normal. Feed analysis can identify low levels of vitamin D or phosphorus. Low levels of vitamin D or phosphorous serum chemistry also will occur (Madson *et al.*, 2012). Supplementation of vitamin D is the only reported treatment and response that may be considered diagnostic. Prevention includes proper diet formulation for the stage of production.

MHD is a noninfectious disease of muscle caused by deficiency of vitamin E or selenium. It can occur if pigs are fed grain grown in selenium deficient soils (Dewey, 2006). Clinical signs are limited to acute death of large, robust pigs. On necropsy, the heart muscle has a mottled appearance. Feed analysis, response to vitamin E supplementation, and ruling out other causes support diagnosis of vitamin E/selenium deficiencies like MHD (Hooser, 1996). Supplementation with selenium is impractical in the United States because of environmental regulations, and overzealous supplementation may cause toxicosis.

Splayleg is a noninfectious, congenital condition resulting from delayed myofibril development with no known cause. Splayleg has low morbidity and mortality as long as it is identified and corrected before it leads to starvation or being crushed by the sow. Treatment includes the use of nonslip

flooring in farrowing crates and application of harness or tape that holds the rear legs under the pig until it is strong enough to walk on its own.

Reproductive System Diseases and Disorders

Reproductive failure occurs when insemination fails to result in pregnancy or pregnancy fails to produce viable pigs due to infectious and noninfectious causes summarized in **Table 5**. Reproductive failure should be considered when a low conception or farrowing rate, irregular returns to estrus, abortions, stillbirths, or mummies persist at an abnormal rate. Infertility occurs when fewer than four embryos are present at the time of maternal recognition of pregnancy resulting in a regular return to estrus and reduced conception rate for that breeding group. Irregular returns to estrus result from embryonic death or early term abortion after implantation but before calcification of the fetuses. Embryonic death of some or all of the embryos will result in low total born or irregular return to estrus, respectively. Early term abortion also will reduce farrowing rates. Mummies and stillborns can occur any time after calcification of the fetuses. The normal rates for mummies and stillborns are <0.5 and <1 pig per litter, respectively. Late-term abortions are classified as those occurring after 70 days of gestation. Total abortion rate should remain $<2\%$ of a breeding group. These are general guidelines; thus, familiarity with the herd's normal reproductive performance is the most sensitive means to identify a reproductive problem.

PRRS is, at this time, known only to occur among swine. The estimated cost of PRRS to the US pork industry is US$664 million annually (Holtkamp *et al.*, 2013). PRRS usually results when susceptible swine are infected with either the Leylystad or North American strains of PRRS virus (PRRSv), a member of the Arteriviridae family. Viremia lasts up to 42 days, but shedding of infectious virus can last much longer (Murtaugh and Genzow, 2011). PRRSv is most commonly transmitted by introduction of infected swine or contaminated fomites, use of contaminated semen, and aerosol. The pathogenesis of the reproductive form is believed to be arteritis of fetal umbilical cords during gestation (Lager and Halbur, 1996). Swine may show no signs when reinfected with a homologous strain. Conversely, infection with a heterologous strain will reproduce lesions and disease but is usually less severe than that of naïve swine (Murtaugh and Genzow, 2011). Clinical signs of PRRS in a breeding herd start with an epidemic of abortions followed by an increase in low viable piglets, stillbirths, and mummies. Abortions result due to fetal death or pyrexia of the gestating female. Sows and gilts may be anorexic, pyrexic, or lethargic. Periparturient females may become agalactic. In severe outbreaks of PRRS, sow mortality also increases. In utero infection of feti can result in persistently infected piglets (Rossow, 1998). Prewean mortality commonly increases and may remain above the herd average for weeks. Diagnosis can be made by submitting lung, spleen, and lymph node from fetuses or low viable piglets. Whole fetuses can also be submitted but should be refrigerated to prevent autolysis. Lesions are not pathognomonic so confirmatory testing such as PCR, IHC, or VI should be conducted. Tissues and thoracic fluid from stillbirths, aborted, or mummified feti can be submitted but may result in false negatives. Serum collected from aborted sows or low viable piglets and tested for PRRSv by PCR is another option for diagnosis. PRRSv ELISA indicates previous exposure but is not useful in a previously exposed herd. Treatment of PRRS is supportive. Anti-inflammatories to reduce fever and antibiotics for control and treatment of secondary bacterial pneumonia may be necessary. The most common methods for control include depopulation–repopulation and herd closure and rollover, also called load-close-homogenize, using commercial vaccine or herd-specific live virus exposure (Corzo *et al.*, 2010). Periods of closure vary based on facility capacity but a minimum of 180 days is recommended. Commercial modified-live and killed vaccines are available but do not prevent infection and should be used in accordance with label and domestic guidelines.

PPV is sometimes described by the acronym SMEDI (stillborns, mummies, embryonic death, and infertility). PPV is an enzootic infection of swine breeding herds in the United States. The virus is ubiquitous and is transmitted through ingestion of infected feces, afterbirth, or fetal tissue. The disease most commonly affects gilts and younger parity sows (Christianson, 1992). The pathogenesis is through damage to

Table 5 Common reproductive diseases and disorders of pigs

	Embryonic death	*Abortion*	*Mummies*	*Stillbirths*	*Infertility*	*Weak born pigs*	*Low total born*
PRRS	++	+++	+++	+++	++	+++	++
Porcine parvovirus (PPV)	++		+++	+++	++		++
Porcine circovirus type 2 (PCV2)	++	+	++	+++		++	++
Leptospirosis	++	++ (Pomona)		+++	++ (Bratislava)	+++	++
PRV	++	++	++	++			++
Brucellosis		+++				+	++
Carbon monoxide (CO) poisoning		+		+++			
Zearalenone	++				++		++
Swine Erysipelas		+++					
Autumn abortion syndrome (AAS) and seasonal infertility	++	+++			++		++

Note: The first column provides the diseases. The remaining columns represent the clinical signs. The frequency of the occurrence is + (occasional), ++ (common), and +++ (routine).

the placental epithelium resulting in fetal death. Clinical signs of PPV range from low total born, mummies of various sizes, irregular returns to estrus, and females diagnosed pregnant but fail to farrow. Diagnosis is based on vaccination history, clinical signs, and PCR testing of mummified fetuses. PPV ELISA may provide diagnostic value if acute and convalescent serum samples are used. There is no effective treatment for PPV; however, commercial killed vaccines are available and very effective. Exposure of unbred females to tissue or cull sows from a seropositive herd has been used for immunization when vaccine is unavailable.

Leptospirosis is caused by infection by spirochete bacteria. *Leptospira* species may be zoonotic (*Leptospira canicola*, *L. icterohemorrhagiae*), swine-adapted (*L. pomona* and *L. bratislava*), or incidentally infect swine (*L. grippotyphosa* and *L. hardjo*). Infection has been associated with exposure of swine to contaminated soil or untreated surface water, and exposure to urine from infected vectors, such as rodents. Infected swine can become carriers resulting in chronic disease. The pathogenesis is due to bacteremia resulting in transplacental infection followed by fetal death. Clinical signs include pyrexia, low conception rate, abortion, stillbirths, and low viability pigs resulting in increased prewean mortality. Diagnosis is made using dark field microscopy or IHC performed on tissues, particularly kidney, of aborted feti or stillbirths. Paired or matched serology for hemagglutination inhibition (HI) testing may be useful if suspected. Treatment with antibiotics, such as chlortetracycline, may be pursued (Henry *et al.*, 1993). Commercial killed bacterins are available to aid in prevention and should be given at least semiannually to breeding stock (Christianson, 1992) but may not be available in all countries. For example, federal regulations prohibit the use of these bacterins in France and The Netherlands (**Figure 2**).

PCV2 is a ubiquitous virus in swine facilities. Pigs become infected with PCV2 through ingestion (oral nasal contact). In addition, breeding females can become infected via insemination with contaminated semen (Madson *et al.*, 2009a). Gilts and low parity sows are affected most often, whereas boars show no clinical signs. PCV2-associated reproductive failure may occur in conjunction with PPV. Infection results in variable lengths of viremia. PCV2-reproductive failure is due to transplacental infection of fetuses. Clinical signs depend on the stage of gestation when the infection occurs. Embryonic death, early term abortions, stillbirths, mummies, low total born, or low viable pigs can result from infection. Mummies may vary in size, like PPV, and measuring crown to rump length is useful to determine the time when that fetus was infected. PCV2-reproductive failure is diagnosed by the presence of viral antigen confirmed by IHC or deoxyribonucleic acid confirmed by PCR along with the presence of lesions in fetal tissue notably myocardial mineralization. PCR testing of fetal thoracic fluid is sufficient to diagnose in utero infection of piglets (Madson and Opriessnig, 2011). Commerical killed baculovirus vectored vaccines are available and effective for prevention of disease but not infection or viremia (Madson *et al.*, 2009b).



Figure 2 Stillbirths, fetus, pig. Fully developed piglet born dead. On necropsy, lungs are deflated and fail to float in water. Presumably caused by Leptospirosis sp. Infection; breeding herd was unvaccinated. Courtesy Dr. Rebecca Robbins.

PRV or Aujezsky's disease virus was eradicated from the US commercial swine herd in 2004; a comprehensive review is available (USDA APHIS, 2008). PRV is a member of the Herpesviridae family and, like other herpesviruses, infection can result in a carrier state or latency within nervous tissue with the potential for recrudescence. The pathogenesis of PRV results from viremia, and then replication and necrosis of epithelial tissue including the placenta (Christianson, 1992). The period of viremia gives PRV time to cross the placenta and cause fetal death. Clinical signs following acute infection include embryonic death, abortion, mummies, and stillborns. Necrotic foci can be found in fetal spleen, liver, lung, and lymph node. Histopathology is not definitive; IHC is required to confirm presence of antigen. Diagnosis may also be made through serology; a commercial ELISA test is available and can differentiate between exposure to the gene-deleted vaccine and wild-type virus used extensively in the US eradication. Commercial PRV vaccines are available but only should be used in accordance with federal guidelines.

Brucellosis is a zoonotic infection caused by the bacteria, *Brucella suis* biovars 1 and 3. *Brucella suis* is transmitted through direct contact with susceptible swine, ingestion of infected tissue, or fluids including milk and contaminated semen. Pathogenesis of *B. suis* is initiated when the mucosal epithelium is penetrated, thereby resulting in bacteremia that commonly persists for 5 weeks and results in placentitis among other lesions. Clinical signs of infection in gilts and sows include abortion with or without vaginal discharge, whereas boars have reduced libido and fertility. Bacteriologic isolation of *B. suis* from vaginal discharge or tissue confirms diagnosis. Serology reflects prior exposure (or vaccination) to *B. suis* but not for diagnosis of acute disease. The US commercial swine herd is Brucellosis free.

Swine erysipelas (SE) is a zoonotic, gram-positive bacterium, which is ubiquitous among swine. *Erysipelothrix rhusiopathiae* is the sole causative species. Carrier swine shed the bacteria in saliva, nasal discharge, and feces. Infection may result from direct contact with carriers, exposure to infected facilities or soil (Wood, 1984). A bacteremia lasting several days precedes lesions. Reproductive failure is most often due to abortion but infertility and low total born following high fevers or endometritis at the time of breeding is also possible.

Clinical signs including rhomboid skin lesions, high fevers, lethargy, inappetence, withdrawal, and response to treatment with penicillin of affected sows and gilts are suggestive of acute and subacute SE. Serology is available; availability is by veterinary diagnostic laboratory (VDL) and value is limited when vaccine is in use. Bacterial culture and histopathologic examination of fetal tissue is unrewarding for diagnosis of SE but is helpful to rule out other causes of abortion. In chronic SE, culture of *E. rhusiopathiae* from vulvar discharges was successful (Gertenbach and Bilkei, 2002). Treatment involves injections of antibiotics and anti-inflammatories. Commercial vaccines are available and effective.

CO poisoning induces hypoxia resulting in an increased number of stillborns (Hooser, 1996). Concentrations of >250 ppm are toxic. Malfunctioning heating units or poorly ventilated farrowing rooms are the cause. Diagnosis is done by ruling out infectious causes of stillbirths. Fetal blood or thoracic fluid can also be measured for CO concentrations.

Zearalenone is a luteotropic mycotoxin produced by *Fusarium rosea*. It binds estrogen receptors resulting in irregular returns to estrus, signs of estrus in prepubertal gilts, and reduced litter size (Hooser, 1996). Diagnosis is by detection of elevated levels in feed samples. However, definitive diagnosis is rarely possible because the contaminated feed has long been consumed by the time reproductive failure occurs.

AAS and seasonal infertility is a noninfectious cause of reproductive failure. The declining photoperiod and temperature fluctuations during the fall months result in declining progesterone levels. High-ambient temperature experienced during lactation and the postweaning period are suspected but not confirmed as a cause. Diagnosis is done by ruling out infectious causes and careful assessment of management, facilities, and reproduction records (Rueff, 2000). Modern facilities that utilize gestation crates and evaporative cooling systems may improve but not prevent infertility during the fall months (Leman, 1992).

Respiratory System Diseases and Disorders

The respiratory system can be simply divided into upper and lower portions. The upper portion includes the nasal cavity and sinuses, throat, trachea, and bronchi for air conduction. The lower portion is the lung comprised of bronchioles and alveoli responsible for air exchange. The respiratory system is commonly involved in numerous infectious diseases of swine summarized in Table 6. The most notable infectious agents are the viral pathogens, PRRS and PCV2, which cause primary pathologic lesions to both the respiratory and the immune system. This damage to the immune system often leads to respiratory or systemic disease incited by secondary infectious agents. Such mixed respiratory infections can occur at any age, and, when they occur in growing and finishing pigs, are termed porcine respiratory disease complex (PRDC). Multifactorial respiratory disease can obscure histopathologic lesions complicating the diagnostic process.

APP is a host-adapted, fastidious, and gram-negative encapsulated rod that is transmitted vertically from sow to piglet. Morbidity and mortality are strain-specific; virulence varies with expression of ApxI and ApxII toxins. Inhalation of strains of APP expressing Apx toxins results in lung lesions within 24–36 h. The disease is economically significant because mortality occurs during the later part of the finishing phase, usually just before slaughter. Clinical signs of fever, lethargy, dyspnea, and acute death are common. Pigs found dead may have a frothy, blood-tinged discharge from the nose and mouth. Focal hemorrhage occurs in the diaphragmatic lung lobe, which is firm, and its appearance is likened to that of a bull's eye. Fibrinous, necrotizing bronchopneumonia containing streaming leukocytes is a key histopathologic feature. Bacterial culture is difficult and requires nicotinamide adenine dinucleotide (NAD)-supplemented media so diagnosis is traditionally made on finding characteristic postmortem and histopathologic lesions. A PCR test is also available. In an outbreak, the entire population should receive antimicrobial therapy parentally. Unlike many other gram-negative bacteria, APP is sensitive to a variety of antimicrobials; at Iowa State University VDL >90% of isolates were sensitive to ceftiofur, enrofloxacin, florfenicol, tiamulin, tilmicosin, and tulathromycin. Prevention is aimed at eliminating carrier swine through depopulation or by pulse medication (Marsteller and Fenwick, 1999).

Actinobacillus suis causes a hemorrhagic, necrotizing pneumonia during nursery and grow–finish phases. *Actinobacillus suis* infection has similar clinical signs and pathologic appearance to APP. Affected pigs are frequently observed in a dog-sitting position with elbows abducted. Unlike APP, lung lesions are random in their distribution and petechial

Table 6 Common respiratory diseases and disorders of pigs

	Preweaning	*Postweaning nursery*	*Postweaning grow–finish*	*Adult*
Actinobacillus pleuropneumoniae (APP)			+++	
Actinobacillus suis	+	+++	+++	
Atrophic rhinitis (AR)			+++	
Ascaris suum			+++	
HPS	+	+++	+++	
Mycoplasma hyopneumoniae (MH)		+	+++	+
Porcine circovirus associated disease (PCVAD)		+++ (PMWS)	+++	
PRRS (respiratory form)	+	+++	+++	++
Salmonella cholerasuis		+	+++	
Swine influenza (SIV)	+	++	+++	++

Note: The first column provides the diseases. The remaining columns represent the respective phases of production. The frequency of the occurrence is + (occasional), ++ (common), and +++ (routine).

hemorrhages may be seen in other organs due to the septicemia that follows *A. suis* infection (Yaeger, 1995). A PCR test is available to help differentiate disease from APP and HPS (Oliveira, 2007a). Like APP, outbreaks should be treated by parental delivery of an antimicrobial; however, treatment of only those individual pigs with clinical signs is usually sufficient. Autogenous vaccines can be used for control but response is variable because most pigs are already seropositive at the time of vaccination.

Ascaris suum, the swine roundworm, is the most common parasitic infection of swine. The reduced growth performance and liver condemnations are responsible for economic losses (Stewart and Hoyt, 2006). The prepatent period is 40–53 days. Adult roundworms are present in the manure but it is the migration of larvae through the lungs, occurring 8–10 days after ingestion of an infective egg that causes respiratory signs. A persistent cough and dyspnea result due to verminous pneumonia. The liver develops whitish spots, called 'milk spots' that are the cause of condemnations but resolve within 25 days (Stewart and Hoyt, 2006). The presence of eosinophils is suggestive of a parasite infestation. Treatment and control is accomplished using anthelmintics: dichlorvos, fenbendazole, levamisole eliminate adults and larvae; piperazine kills only adults. Proper cleaning and disinfection particularly removing fecal material between groups reduces potential for exposure but it is virtually impossible to get rid of *A. suum* once a premise is infested (Pittman *et al.*, 2010b). It is necessary to prevent access to contaminated soil.

AR is described in two forms: progressive (PAR) and nonprogressive (NPAR). PAR is caused by toxigenic strains of *Pasteurella multocida*, whereas NPAR is the result of toxigenic strains of *Bordetella bronchiseptica*. In both forms, the bacteria attach to cilia in the nasal passages and the cytotoxin production causes hypoplasia of nasal turbinates. Clinical signs include sneezing, deviated snouts, and, in cases of PAR, bloody nasal discharge occurring in a large number of grow–finish pigs. Mortality is low but the reduced growth that results due to AR makes it economically important. Beacause the cytotoxins are responsible for AR, isolation of either bacterium from nasal passages is not sufficient for diagnosis. In addition, *B. bronchiseptica* and *P. multocida* colonize the lung leading to bronchopneumonia causing cough and dyspnea in pigs postweaning, often part of PRDC (Hansen *et al.*, 2010). Therefore, examination of nasal turbinates at slaughter is the recommended method for diagnosis of AR (Gatlin *et al.*, 1996). Transmission is vertical; therefore, prefarrow vaccination of sows can protect piglets up to 16 weeks of age. If vaccination does not prevent AR, depopulation of the herd may be necessary.

HPS is also called Glässer's disease. There are 15 serovars identified and prefer to colonize the nose (MacInnes *et al.*, 2007). HPS may not actually result in pneumonia but does cause signs of respiratory disease including nasal discharge and dyspnea. In addition, fever, lethargy, and acute death are observed. On necropsy, one or all of the pleural, pericardial, epicardial, and peritoneal serosal surfaces become covered in fibrin. Effusion commonly occurs. Histopathologic lesions are described as fibrinopurulent. Definitive diagnosis is by bacterial isolation on culture media supplemented with V factor. Owing to the difficulty in isolating HPS, PCR testing is now available (Oliveira *et al.*, 2001). Isolation from the airways in the absence of lesions has little significance (Hoefling, 1994). Ceftiofur, enrofloxacin, or tulathromycin delivered parenterally to affected animals are effective therapeutic drugs. Use of water-soluble antimicrobials is for control. Maternal immunity, medicated early weaning, and controlling infections with PRRS, PCV2, and influenza postpone or prevent disease onset (Rapp-Gabrielson *et al.*, 2006). Commercial and autogenous vaccines are available but may experience limited efficacy due to serologic diversity; controlled exposure to low dose, live virulent culture is another option (Oliveira *et al.*, 2004) (**Figure 3**).

MH is known to infect pigs in production systems worldwide causing reduced growth performance and mortality. The disease is classified as enzootic pneumonia or a component of PRDC. Both manifestations of MH cause paralysis of the mucociliary escalator resulting in a severe cough and dyspnea known as thumping. Vertical and lateral transmission can occur; but, owing to its slow rate of transmission between pigs, the disease primarily occurs in grow–finish pigs (Meyns *et al.*, 2004). In addition, time of colonization with MH and disease severity are directly related (Fano *et al.*, 2007). On necropsy, well-demarcated (red to purple lobular consolidation occurs in the apical) diaphragmatic, and accessory lung lobes is visible. Histopathologic lesions characteristic of MH is bronchopneumonia with lymphocytic perivascular, peribronchial, and peribronchiolar cuffing. Because MH is difficult to isolate, PCR is the most sensitive method of detection. ELISA is available and is helpful in establishing herd status but must be interpreted in the context of vaccination as tests do not distinguish between antibodies produced subsequent to vaccination or field infection. Treatment of affected pigs with parental antimicrobials like enrofloxacin, tulathromycin, or lincomycin or administration of water-soluble lincomycin, tiamulin, or tetracyclines to affected groups is effective in outbreaks. Control can be achieved through pulse-medication in feed of chlortetracycline (Thacker *et al.*, 2006) beginning



Figure 3 Epicarditis, heart, nursery pig. Fibrin gives surface a granular appearance, caused by HPS infection. Note the enlarged (draining) mediastinal lymph nodes located cranial to the base of the heart and the excess thoracic fluid (reddish-brown) indicative of septicemia. Courtesy Dr. Glen Almond.

1 week before the historical onset of disease (Maes *et al.*, 2008). Commercial vaccines are whole cell bacterins marketed to reduce lesions but do not prevent disease or slow transmission rate. Simultaneous infection with PRRSv reduces efficacy of MH vaccination (Thacker *et al.*, 2000; Thacker, 2000). Eradication from the herd is preventative but practically difficult to accomplish.

PCVAD is any disease process where PCV2 infection results in lesions and includes PMWS (Ellis *et al.*, 1998) and PDNS. Infection with PCV2 is widespread. Morbidity and mortality is variable, often dependent on the occurrence of secondary infections and their virulence. Survivors of PCVAD remain stunted, owing to the economic significance of this collection of diseases. Clinical signs include wasting, dyspnea, depression, ill thrift, and diarrhea. Lungs are wet, heavy, and fail to collapse; pulmonary edema and lymphadenopathy also can be found at necropsy. Histopathology results include presence of interstitial pneumonia, lymphoid depletion, enteritis, nephritis, and dermatitis. For a diagnosis of PCVAD the following must occur: PCV2 antigen within characteristic lesions and lymph nodes are depleted (Sorden, 2008). IHC is used to confirm presence of PCV2 antigen within the histopathologic lesion. PCR has little value in diagnosing PCVAD unless the herd is considered free. Commercial vaccines are very effective and available with flex labels for administration to sows and pigs and as 1 or 2 doses (Chae, 2012). Nonvaccinated, subclinically infected pigs have poorer weight gain compared to their vaccinated counterparts (Kristensen *et al.*, 2011); therefore, it is part of most vaccination protocols by US pork producers (**Figure 4**).

PRRS is the result of infection with the Leylystad or North American strain of PRRSv. The estimated cost of PRRS to the US pork industry is US$664 million annually (Holtkamp *et al.*, 2013). PRRSv is the most commonly diagnosed viral respiratory pathogen at VDLs (Gauger, 2009). Infection is observed to increase susceptibility to other infections, particularly opportunistic bacteria. This apparent increased susceptibility to secondary and opportunistic infections is the result of the pathologic process in which PRRSv recruits and replicates in pulmonary alveolar macrophages, and then disseminates systemically (Rossow, 1998). Clinical signs are nonspecific including fever, lethargy, and dypsnea but not cough. Signs also depend on the type of secondary infection(s) present. Lungs fail to collapse and appear heavy, wet, and gray on postmortem examinations. Lymphadenopathy is caused by hyperplasia of germinal centers. Interstitial pneumonia, alveoli are lined with hyperplastic type II pneumocytes and contain necrotic debris, whereas the lining of bronchi and bronchioles is normal (Rossow, 1998). Vasculitis also occurs. PCR is the most sensitive method for confirming infection. Owing to the genetic diversity of PRRSv, sequencing of the ORF5 region is a common adjunct to PCR testing. Sequences are then used to create dendrograms for use by production systems pursuing PRRS control and epidemiologic investigations (Murtaugh, 2012). PRRSv ELISA is helpful for establishing herd status; National Animal Health Monitoring Service reports that a large percentage of US herds are seropositive. Treatment is limited to maintaining pig comfort, minimizing stress, and controlling secondary infections. Commercial modified-live vaccines (MLV) are available and administration during the nursery phase significantly reduces mortality and improves growth performance during the grow–finish phase of production (Robbins *et al.*, 2013b). MLV vaccines do replicate and should not be used in negative populations.



Figure 4 Pulmonary edema, lung, grow–finish pig. Interlobular edema associated with PCVAD, ventral portion of apical and diaphragmatic lung lobes is consolidated (purple) due to secondary bacterial infection. Courtesy Dr. Glen Almond.

Salmonella cholerasuis is the swine-adapted *Salmonella* from the C1 serogroup and, unlike *S.* Typhimurium, is not a foodborne pathogen. Ingestion or inhalation of the bacteria causes a septicemia resulting in low to moderate morbidity with high mortality within 1–2 days of infection that occurs postweaning, predominately during the grow–finish phase (Baskerville and Dow, 1973). Signs include high fevers ($>40\ ^{\circ}C$), lethargy, dyspnea, acute death, and cyanotic extremities and abdomen. The latter makes it impossible to differentiate clinically from classical swine fever virus (CSFv). Pleuropneumonia, interlobular edema, mediastinal, and tracheobronchial lymphoadenopathy, and occasionally white foci in the liver are apparent postmortem (Turk *et al.*, 1993). Acute histopathologic lesions that form in the lung are purulent bronchitis, lobular necrosis, and abscessation, whereas paratyphoid nodules are observed in the liver. Isolation is best achieved from the draining lymph nodes, lung, or liver using selective culture media. Serogrouping and typing is necessary for speciation and diagnostic confirmation. Owing to the rapid onset of disease, parental treatment is recommended. *Salmonella cholerasuis* isolates are commonly susceptible to ceftiofur. Increased hygiene particularly eliminating access to waste and vaccination is preventive (Husa *et al.*, 2009).

SIV is more accurately described as influenza, to encompass the infections occurring in swine, avian, and human species. Influenza virus is classified by its hemagglutinin and neuraminidase proteins; the three predominant strains in pigs are H1N1, H1N2, and H3N2. Rapid transmission and onset are characteristic; in the experimental inoculation of one nonvaccinated nursery age pig resulted in 10.66 more becoming infected (Romagosa *et al.*, 2011). Virus is shed for 3–5 days and uncomplicated lesions resolve 28 days postinfection (Gramer, 2007). Nasal discharge, fever, and lethargy occur but resolve quickly. Cough and dyspnea can last up to 2

weeks postinfection. PCR and VI detect virus for diagnosis of clinical cases. ELISA and HI detect antibodies; ELISA is helpful in establishing herd status, whereas HI is best for vaccination timing and measuring postvaccination titers (Allerson *et al.*, 2008). Necrotizing bronchitis, bronchiolitis, and alveolitis as lesion resolves affected areas appear vacuolated. Pigs recover quickly so treatment should focus on maintaining pig comfort, minimizing stress, and controlling secondary infections. All licensed vaccines are killed; commercial and autogenous products are in use in the United States. Vaccination reduces lung lesions and rate of transmission, but does not prevent infection and is complicated by antigenic shift and drift. In the United States, it is typical to vaccinate the sows rather than pigs to control disease and infection (Allerson *et al.*, 2013).

Diseases That Affect International Trade

Trade diseases are those listed by the OIE. When one of these diseases is suspected or confirmed, it results in closure of international market access, which would be economically devastating to import–export businesses. The primary method for managing diseases that affect trade is to prevent their introduction.

Foot-and-mouth disease (FMD) is caused by a picornavirus, FMDv, which causes mucosal lesions exclusively in cloven hoofed species. Clinical signs are excessive salivation, anorexia, and lameness causing high morbidity but low mortality. Gross lesions are vesicles at cutaneous junctions, on the snout, or in the oral cavity. Similar lesions can be caused by Seneca Valley virus, vesicular stomatitis, swine vesicular disease, and vesicular exanthema of swine; therefore, any blister in swine warrants diagnostic investigation. FMDv is highly transmissible within and between species.

African swine fever (ASF) is caused by ASFv, currently classified as an Iridovirus. Soft ticks can act as reservoirs or vectors. Current outbreaks are reported throughout Eastern Europe and Russia that have been associated with improper garbage feeding. The virus damages blood vessels resulting in clinical signs and gross lesions consistent with septicemia; including red to purple skin discoloration and enlarged spleen, liver, and lymph nodes. Excess blood and fluid in body cavities may occur.

Classical swine fever, historically referred to as hog cholera, is caused by CSFv, a pestivirus, eradicated from the United States in 1972. Transmission is associated with infected feeding, uncooked or undercooked garbage containing pork or pork by-products to swine. The virus remains infectious for months when refrigerated and years when frozen. Clinical signs are nonspecific and are easily confused with *S. cholerasuis*. The virus replicates rapidly in tonsils, which makes it the ideal tissue to collect for diagnosis of CSFv.

See also: Animal Health: Ectoparasites. Animal Health: Foot-and-Mouth Disease. Animal Health: Global Antibiotic Issues. Slum Livestock Agriculture. Vaccines and Vaccination Practices: Key to Sustainable Animal Production. Zoonotic Helminths of Livestock

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Terroir: The Application of an Old Concept in Modern Viticulture

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Glossary

Appellation A legally defined and protected geographical indication used to identify where the grapes for a wine were grown.
Chaptalization The process of adding sugar to unfermented grape must in order to increase the alcohol content after fermentation.
Chemometrics The science of extracting information from chemical systems by data-driven means.
Ecosystem A biological community of interacting organisms and their environment.
Geochemistry The science that uses the tools and principles of chemistry to explain the mechanisms behind major geological systems.
Jurisdiction The geographic area over which authority extends.
Plasticity The ability of an organism to change its phenotype in response to changes in the environment.
Topography The detailed description of the surface features of a region.
Transcriptome The set of all ribonucleic acid molecules produced in one or a population of cells (e.g., grape berries).
Véraison The onset of berry ripening (determined by the change in color or berry softening in red and white varieties, respectively).

Definition of the *Terroir* Concept

Terroir is considered a highly important concept in viticulture because it relates the sensory attributes of a wine to the environmental conditions in which the grapes are grown (Van Leeuwen and Seguin, 2006). *Terroir* can be defined as an interactive ecosystem, in a given place, including climate, soil, and the vine rootstock and cultivar (Van Leeuwen and Seguin, 2006), although human factors such as viticultural techniques and enological techniques may also be included (Seguin, 1986). The general assembly of the International Organization of Vine and Wine (OIV) recently adopted the broader definition for the descriptive use of the term *terroir* in viticulture and enology (Resolution OIV 333/2010; Anonymous, 2010). Vitivinicultural *terroir* is a concept that refers to an area in which collective knowledge of the interactions between the identifiable physical and biological environment and applied viticultural practices develops, providing distinctive characteristics for the products originating from this area. *Terroir* includes specific soil, topography, climate, landscape characteristics, and biodiversity features. The OIV resolution notes that the *terroir* concept is not to be confused with the legal definition of a Geographical indication (GI) used to describe viticultural production zones (Resolution OIV 333/2010), which are legally binding at the international level in both Old World and New World wine production regions (Anonymous, 2010).

History and Evolution of *Terroir*

Globalization of the international wine trade over the past 50 years has led to increasing production in New World countries with an emphasis on varietal and brand name wines and dominance of large companies (Rachman, 1999; Overton *et al.*, 2012). Concurrently, there has also been increasing interest, by both Old World producers in Europe and New World producers, in marketing wines from specific regions and localities to gain marketing advantages relating to source, heritage, control of winemaking, and perceptions that such wines are of higher quality (Gade, 2004). GIs are used to legally describe binding viticultural production zones (Resolution OIV 333/2010) with guidelines for zoning based on soil and climate characteristics established (OIV resolution 423/2012; Anonymous, 2012). In this context, the *terroir* concept establishes product individuality through an intimate connection between consumer expectation and the products offered (Gade, 2004), linking sensory attributes of wine to the environmental conditions in which the grapes are grown and processed (Van Leeuwen and Seguin, 2006). The first regions to be officially designated were the Chianti region in Italy in 1716, when four villages were recognized as the only producers of Chianti wines; the Tokaji (Tokay) region in Hungary in 1730 where vineyards were classified into three categories based on soil, sun exposure, and potential to develop noble rot, (*Botrytis cinerea*) (Wikipedia) and the Douro region in Portugal in 1756 (Cardosa, 2013).

The wine term, *terroir* appears to have first been applied in the fourteenth century in France to certain top-quality wine producing properties from the Cote d'Or in Burgundy (Whalen, 2009). Van Leeuwen and Seguin (2006) indicate that wine in the Bordeaux region of France was sold by the name of the Parish in the Middle Ages with the first estate wines sold in the seventeenth century. In the Bordeaux region, qualitative differences among wines produced led to a classification system being introduced in 1855 for wines from Medoc chateaux, which could be considered as *terroir* wines, as the grapes were exclusively from their own vineyards (Van Leeuwen and Seguin, 2006).

In the mid-1850s, winegrape production in Europe was almost annihilated due to the introduction of an aphid, Phylloxera, which attacks vine roots and the fungal diseases powdery mildew (oidium), downy mildew, and black rot from the Americas. This led to a complete restructuring of vineyards with the adoption of phylloxera-resistant rootstocks, derived from native American species, into solid management blocks, generally of the same variety, loss of varieties, and changes to management practices with the use of sulfur and copper-based sprays for fungal control (Gade, 2004; Whalen, 2009). Despite these significant changes in planting material and management practices the production of *terroir* wines from recognized vineyards in key regions has been maintained.

In France controlled appellation or place of origin labeling is the legal institution that mediates between the consumer and the producer and fixes the unique, place-based qualities of the product (Gade, 2004). The Appellation d'Origine Contrôlée (AOC) guarantees place of origin and lays out a set of production requirements for that bounded space identified with quality. Through appellation control, colloquial environmental space (*terroir*) becomes jurisdictional space (*territoire*), defined by its boundaries (Gade, 2004). In France, 'The Institut National des Appellations d'Origine', established in 1935, issues the decrees of local syndicates that meet certain requirements and implements quality standards with new AOCs added annually. It guarantees the consumer the authenticity of a region, the variety of grapes used, the vinification process, the maximum yield per hectare, and a defined level of alcohol (Lemaire and Kasserman, 2012) but does not specify climate, microclimate, and soil differences (Gade, 2004). Similar control of wine production, based on classification and regulation at the regional level exists in most European Union countries (Lemaire and Kasserman, 2012).

Over the past 50 years, with increasing globalization of the wine industry, traditional European winegrape producers have faced major issues of oversupply, increased production costs, increased awareness of environmental issues, and impacts of climate leading to well-documented changes in phenology and ripening (e.g., Jones, 2006) and shifts in consumer awareness and wine style. As a consequence, there has been significant changes in traditional European winegrape production to reduce production costs, with mechanization of harvest, pruning, canopy management, and new techniques for crop control (Intrieri, 2013); changes to soil management practices with the use of zero tillage, cover crops, and herbicides (Neethling *et al.*, 2013); adoption of integrated pest management and the use of new chemicals for the control of pest and diseases. There has also been significant adoption in many regions of modern winemaking techniques including the use of selected yeast strains rather than wild ferments, a subject beyond the scope of this treatise. Despite these major changes in the winegrape industry there continues to be strong support for the ongoing production and sale of *terroir* wines, an indication that the *terroir* concept is flexible and adaptable to change within a regulated framework (Gade, 2004).

New World wine producers, particularly in cooler, 'premium' regions have also shown a strong interest in establishing and marketing *terroir* wines from specific regions and localities to gain marketing advantages over large-scale commercial wines (Gade, 2004). Substantial research has been directed toward these aspirations. For example, in the Niagara Peninsular region of Ontario, Canada, sensory profiling of wines has been used to distinguish wines produced from the 'bench, plains, and lakes' viticultural areas for Riesling, Chardonnay, and the Bordeaux-style red varieties, Cabernet Sauvignon, Cabernet Franc, Merlot, and their blends (Douglas *et al.*, 2001; Kontkanen *et al.*, 2004), which have been linked to climate, topography, soil texture and water status, vine size, plant water status, and climate (Kontkanen *et al.*, 2004; Reynolds *et al.*, 2007; Reynolds *et al.*, 2013). In South Africa, natural *terroirs* have been identified in the Stellenbosch region based on homogeneous topography, climate, geological substrate and soil characteristics, vine growth characteristics, and fruit and wine composition of Cabernet Sauvignon and Sauvignon Blanc (Carey *et al.*, 2008; Carey *et al.*, 2009).

The strong international interest in the *terroir* concept is supported by the OIV definition provided in Resolution OIV 333/2010 embedded within the viticultural production zones (GIs, Resolution OIV 333/2010; Anonymous, 2010). Nonetheless, there is another school of thought, particularly in the popular press that the *terroir* concept is overrated and of little value to the modern wine industry. Rachman (1999) suggested that Europe should relax its wine laws, particularly with regard to the use of irrigation and alternative varieties, to take full advantage of modern technology, minimize seasonal fluctuations in quality to produce a consistent product, and adapt to consumer preferences. Gergaud and Ginsburgh (2008) concluded from a study undertaken in Bordeaux that *terroir* was of little importance and that technological choice including variety, vine age, and winemaking practices affect quality, based on international expert rating and price of wines, more than 'natural endowments' (land and soil). However, this study included very few parameters describing the 'natural endowment,' being limited to a crude soil description, soil nutrient content, altitude, and exposure (direction of the slope). In contrast, Vaudour (2002) indicated that scientific rigor can now be applied to update the *terroir* concept using integrated approaches that combine spatial modeling and geographical information systems (GIS) to describe the vineyard environment supported by modern technologies to measure grape and wine composition, enhanced approaches to sensory wine analysis and assessment of plant performance and physiology.

The Reality of *Terroir*

The *terroir* concept relates sensory attributes of wine to the environmental conditions in which the grapes are grown. It

embraces the key natural elements of climate, landscape characteristics, soil characteristics, and human factors (history, socioeconomics, selection of genotype, variety and rootstock selection, vineyard management practices, and winemaking technologies) leading to the production of unique, site-related, *terroir* wines (Van Leeuwen and Seguin, 2006). The relative importance of each element and their interaction will vary depending on the region and product style. In agreement with Vaudour (2002), Bodin and Morlat (2006) suggest that a rigorous scientific approach is required to validate the *terroir* concept. Integrated approaches involving the use of advanced climatic models, remote sensing, and new technologies to measure soil characteristics, aspects of vine physiology, fruit and wine composition and qualitative sensory analyses in combination with spatial modeling, GIS and multivariate data analysis are being used to validate the *terroir* concept and identify the relative importance of the various components. Furthermore, the understanding of *terroir* is also being enhanced through the use of molecular techniques. For example, measurements of the grapevine berry transcriptome of Corvina grown in the Verona region of Italy have reported seasonal effects of the environment on the expression and function of genes based on clustering of transcripts and groupings of vineyards sharing common viticulture practices and environmental conditions (Dal Santo *et al.*, 2013).

Climate and *Terroir*

Climate is considered to be the most important component of *terroir* as it largely determines the suitability of a region to different winegrape cultivars, their growth and production, the overall wine style, and vintage variability (Jones *et al.*, 2012). Differences in wine quality ratings across vintages can be attributed to seasonal differences in climate (Jones, 2005). The importance of climate to the expression of *terroir* was clearly shown in a study conducted in Bordeaux, where the impact on fruit quality parameters of soil, climate (vintage), and variety (Merlot, Cabernet Sauvignon, and Cabernet Franc) were studied simultaneously (Van Leeuwen *et al.*, 2004). Climate (vintage) was the dominant factor accounting for a high proportion of the variation in fruit composition (total acidity 70%, pH 73%, and anthocyanins 41%).

Jones *et al.* (2012) indicated that the influences of climate on *terroir* should be considered at the macroscale (synoptic climate), the mesoscale (regional climate), the toposcale (site climate), and at the microscale (vine row and canopy climate) taking into account the weather and climate structure for optimum quality and production; the climate suitability of different cultivars; the climate variability in a region; and the influence of climate change. Important components of the climate that influence vine growth, production, and fruit composition include solar radiation, which may be impacted by vineyard topography (slope and aspect), day length, cloud cover, reflective nature of the soil, the average temperature over the growing season, the day–night temperature difference, temperature extremes (i.e., winter freeze, frost, and summer heat stress), heat accumulation, wind, precipitation, and humidity (Jones *et al.*, 2012).

It has been suggested that wine regions have developed over time to best match their regional environmental conditions, allowing for generally consistent ripening of varieties that are best suited to the conditions (Jones, 2006). For wine production, the average temperature during the growing season ranges from 13 to 21 °C (Jones *et al.*, 2012). Maturity groupings have been developed to match the suitability of a variety to a regional climate based on average growing season temperature, i.e., cool (13–15 °C), intermediate (15–17 °C), warm (17–19 °C), and hot climate (19–21 °C) (Jones, 2006). Such groupings suggest that varieties could be grown in climatic regions where they are not currently grown in Europe and that current locations are historical and influenced by other human factors (e.g., trade, wine style preferences, etc.). Indeed, many of the varieties are not ideally suited to their region as chaptalization (addition of sugar) is required in many vintages to provide adequate levels of alcohol in the wine, although this requirement is decreasing as temperatures have increased over the past 50 years (Jones *et al.*, 2012).

Modern spatial analysis tools are providing methods to incorporate a wide range of climatic variables in the regional analyses of climate. Bioclimatic indexes describing the suitability of a particular region for winegrape production are a widely used zoning tool (Jones *et al.*, 2011). They used gridded data of temperature and precipitation to compute three of the indexes (i.e., the Winkler and Huglin degree day indices and a composite suitability index, Malheiro *et al.*, 2010) for Europe to study interannual variability (1950–2009). They conclude that strong regional contrasts were clearly apparent in the different index patterns, creating a wide range of local conditions that largely explain the quality and diversity of the winegrape growing regions across Europe. Furthermore, Bois *et al.* (2012) conducted a high resolution climate spatial analysis of European winegrowing regions across 260 regions in 18 countries at a 1 km resolution incorporating a wide range of climatic variables including the Huglin Index, the cool-night index, a dryness stress index, a heat stress index, winter freeze, and spring frosts risk. Clustering analyses of common characteristics were used to identify six climate types across Europe, not necessarily located in a particular region, to better depict the climatic components of *terroir*.

Geology, Soil, and *Terroir*

Winegrape production in Europe generally occurs on poor soils, not suited to other agricultural pursuits (Van Leeuwen and Seguin, 2006). The term *terroir* implies links between land and soil and wine quality. This ideology is pursued by Wilson (1998) who suggested that quality winegrapes are grown on a diverse range of soils and that each soil type contributes its own characteristics and mouthfeel to a given variety. For example, associations between the 'flint' character of Chablis wines and 'gunflint' character of Riesling and flint, shale, and slate bearing soils are reported (Huggett, 2006). However, there is very little scientific evidence to support such a connection. Indeed Maltman (2008, 2009) in reviewing the relationship between geology and wine concludes that any suggested link between geology (bedrock composition, soil mineralogy, and geochemistry) and wine flavor can be nothing more than a romantic myth. A view supported by detailed multivatiate *terroir* studies involving chemical and sensory wine analyses conducted by Cadot *et al.* (2012) in the Loire

valley of France with Cabernet Franc and Cabernet Sauvignon showed that bedrock type was not significant whereas the proportion of the varieties, harvest date, alcohol level, and winemaking practices were significant factors. Perceived saltiness in wines from specific regions, for example, the Manzanilla region of Spain which is close to the sea, may be an example where a direct linkage between the soil and a wine quality attribute can be made (Huggett, 2006), a view supported by studies where the salt content of wines has been shown to affect wine taste (Walker *et al.*, 2003).

Studies across a wide range of typical Bordeaux soil types (i.e., alkaline limestones, acidic gravels, neutral gravels, or heavy clay) indicate that soil type had no definite influence on the quality of harvests and wine quality of *terroirs* although certain *terroirs* consistently produced better wine in all seasons (Seguin, 1986; Van Leeuwen and Seguin, 2006). The soil effect on *terroir* can be better explained by the physical properties of the soil and their consequences for root development on regulation of water supply and nutrients to the vine. Seguin (1986) also noted that human factors such as soil cultivation, provision of drainage, and rootstock selection added further complexity to the issue. Van Leeuwen and Seguin (2006) indicate that the best expression of *terroir* is achieved, at least for red wine, when full ripeness is achieved at the end of the season from vines with moderate vigor. They describe the importance of root zone temperature associated with soil type (i.e., drier soils have higher soil temperature than wetter soils). In detailed studies across vintages, soil types and varieties in Bordeaux, Van Leeuwen *et al.* (2004) established strong links between soil and vine nutrition, plant water relations, vine growth, and berry composition. Soil type accounted for variances in predawn leaf water potential (40%), berry potassium content (32%), anthocyanins (30%), yield (32%), pruning weight (28%), vine nutrient status (petiole nitrogen, potassium, and magnesium, 24%, 42%, and 75%, respectively), must sugar (32%), and anthocyanins (32%). Huggett (2006) also noted the importance of drainage and water holding capacity and raised the issue of soil color for absorption of incoming radiation, leading to higher soil temperatures and night reradiation to reduce frost risk. Renouf *et al.* (2010) produced high resolution soil maps for prestigious vineyards in the Bordeaux area, which confirmed the importance of soil type, rootstock selection, and varietal selection on fruit quality, based on a quality index determined from fruit destinations over five vintages. Coipel *et al.* (2006) found that soil depth was more important than soil type in describing the *terroir* effect for Grenache vineyards in the Cotes du Rhone region of France. Grapes with the highest potential for making quality wine (i.e., those with lower yields, higher sugar, and anthocyanins) were obtained on soils with the lowest water holding capacity.

Bodin and Morlat (2006) developed a concept of basic terroir unit (BTU) to provide scientific rigor into zoning of *terroirs*, determined from soil depth and the degree of weathering of the underlying rock to account for soil effects on wine water supply, growth, and phenology. A BTU is defined by Goulet and Morlat (2011) as a ''territory with homogeneous vine behavior from a view point of ecophysiological conditions, as well as a sufficient area to make it agronomically and commercially worthwhile for viticulture.'' BTU maps that combine soil measurements and aerial photographs provide useful information on soil water, potential for early growth and vigor to assist growers in their choice of soil management, rootstock, and weed control. Validation studies for the use of BTU maps showed that soils with strongly weathered rock produced smaller berries with higher sugar, anthocyanins and phenolics and more aromatic wines associated with differences in plant water relations, timing of budburst, soil water, yield, canopy density, and pruning weight (Bodin and Morlat, 2006).

Measurement of soil electric resistivity provides a tool to rapidly assess available soil water holding content and potential root activity in studies of *terroir* (Goulet and Barbeau, 2006). Other soil parameters related to *terroir* include soil nitrogen status because of potential indirect effects on vine vigor and yeast assimilable nitrogen (Reynard *et al.*, 2011; Van Leeuwen *et al.*, 2011; Van Leeuwen and Seguin, 2006).

Plant Water Status and *Terroir*

Irrigation is prohibited in many European vine growing regions. Consequently, water holding capacity of soil is considered an important component of *terroir* and vintage effects of climate because of related effects on plant water status, vine vigor, phenology, and fruit composition (Van Leeuwen and Seguin, 2006). In Hungary, Zsofi *et al.* (2009) found strong relationships between plant water status, yield, and wine quality parameters and suggested that measurement of stomatal conductance and predawn leaf water potential provided reliable parameters for *terroir* classification across varying vintages. Moderate stress found on sloped vineyards compared with vineyards with higher water availability produced berries with higher sugar levels, anthocyanins, and phenolics associated with lower yields and better canopy and fruit exposure. In further studies Zsofi *et al.* (2011) showed that the enhanced sugar levels of berries from the moderately stressed vines was independent of berry size, despite lower levels of photosynthesis. Rezaei and Reynolds (2010) observed a strong link between vine water status and sensory characteristics of Cabernet Franc in Canada and also suggested that measurement of midday leaf water potential could be used for classifying the *terroir* effect across wet and dry seasons.

Van Leeuwen and Seguin (2006) recognized that measurements of plant water status can be important tools in *terroir* studies in regions such as Bordeaux noting that wines from moderately stressed vineyards are generally preferred, particularly for red wines, whereas severe stress may reduce aroma potential of white wines. For red wines, Tregoat *et al.* (2002) were able to describe differences across Merlot vineyards in Bordeaux based on measurements of plant water status (predawn water potential, stem water potential, and carbon isotope discrimination). They observed that vineyards with moderate water stress had early cessation of growth and produced smaller berries with improved composition (i.e., higher sugar levels, anthocyanins and phenolics and reduced malic acid levels). For Sauvignon Blanc vineyards in Bordeaux, vine vigor could be linked to vine water status and nitrogen status (Peyrot des Gachons *et al.*, 2005). Vines under severe water stress produced small berries with low sugar and limited aroma potential compared with mild water deficits. Their

results indicated potential to use targeted irrigation for Sauvignon Blanc in dry seasons. In Greece, Koundouras *et al.* (2006) were able to correlate predawn water with sensory assessments of the red variety Agiorgitiko across different sites. Differences in vine water status were highly correlated with cessation of shoot growth and earliness of véraison with stressed vines giving wines with higher levels of anthocyanins, phenolics, and aromatic characteristics, which were preferred in sensory assessments.

Van Leeuwen *et al.* (2001, 2011) suggested that carbon isotope discrimination in berries, which correlated with predawn water potential, can be a useful tool for use in *terroir* studies for assessing vintage and soil type effects, as it is an integrative indicator of vine water deficits during the ripening period. Similarly, in Switzerland, Reynard *et al.* (2011) found a strong correlation between carbon isotope discrimination measurements in berries and soil water holding capacity across three seasons and 23 sites. Mild deficits produced smaller berries with higher sugar levels and wines with higher color density. Similarly, for Sangiovese in Italy, strong relationships with carbon isotope discrimination measurements were found with soil water holding capacity, vine water status, and related effects on berry anthocyanins and must acidity (Costantini *et al.*, 2010).

Terroir Validation by Modern Sensory and Analytical Techniques

To be accredited as a *terroir* wine in the French AOC system it must show typicality (typicity; Cadot *et al.*, 2010). A range of modern sensory techniques using sensory profiles, sorting and ranking methods, and qualitative descriptions are now being used to give credence to *terroir* wine classification in protected regions (Cadot *et al.*, 2010; Etaio *et al.*, 2010; Maitre *et al.*, 2010). For example, Cadot *et al.*, 2010 used quantitative descriptive analysis by a sensory expert panel to discriminate between *terroir* wines of Cabernet Franc and Cabernet Sauvignon in the Loire Valley. Similarly, Segurel *et al.* (2009) were able to discriminate *terroirs* for Grenache and Shiraz in the Rhone valley by quantitative descriptive analysis.

Enhanced analytical techniques of fruit and wine, in combination with advanced chemometric techniques is providing underpinning evidence to support the *terroir* concept. For example gas chromatography mass spectrometry (GCMS) techniques for the analyses of volatiles associated with wine aroma and flavor compounds together with sensory evaluation have been used to discriminate between vineyard plots of Gewurtztraminer in Alsace (Diminger *et al.*, 1998), Grenache Noir in the Rhone Valley vineyard, a study that highlighted the importance of soil water holding capacity, early maturation, and must sugar content across the *terroirs* (Sabon *et al.*, 2002). Furthermore, in Australia sensory and chemical analysis, including GCMS analysis of volatiles, has been used to describe spatial variability at the within vineyard scale (Bramley *et al.*, 2011a), potentially adding further precision to the concept of *terroir*.

Other chemical methods used to validate the *terroir* concept include high-performance liquid chromatography anthocyanin analysis in Bordeaux, which showed impact of variety on *terroir* (De Gaulejac *et al.*, 2001), spectroscopy (ultraviolet/visible/near-infrared spectral analysis) in combination with chemometric tools, which was used to discriminate and authenticate subzones in the Rias Baixas region of Spain (Martelo-Vidal *et al.*, 2012), measurement of stilbenes (Tomasi *et al.*, 2013) and soil active lime (Gatti *et al.*, 2011) in Italy, NMR spectroscopy, which was used to distinguish varieties, vintages, and soil type in Bordeaux (Pereira *et al.*, 2006) and linked with soil characteristics (levels of carbonate, clay, and organic matter) across Italian Aglianico vineyards (Mazzei *et al.*, 2010). In Argentina, Di Paola-Naranjo *et al.* (2011) used analyses of inorganic and organic compounds and stable isotope analyses to match soil provenance using chemometrics and differentiate *terroirs* and varieties.

Classification of *Terrior* Using Geographic Information Systems with Multivariate Statistics

Modern multivariate statistical approaches in combination with GIS are now being used to improve zoning and *terroir* classification through the identification of homogenous terroir *units* (Gomez-Miguel *et al.*, 2013). Such studies may include combinations of high resolution climate data, geological and soil data and information on topography, altitude, variety and rootstock, vineyard management factors, fruit composition and product type (Gomez-Miguel *et al.*, 2013), a topography index (Herrera-Nunez *et al.*, 2011), the Huglin and Winkler bioclimatic indexes (Ince *et al.*, 2013; Jones and Alves, 2013), simulated plant water balance models and crop water stress indexes (Bonfante *et al.*, 2011), a categorized maturity index (Fraga *et al.*, 2013), and fruit composition (Gonzalez-Centeno *et al.*, 2012). Such approaches have been used to identify the key factors contributing to *terroir* effects and improve the *terroir* classification in the Douro region of Portugal (Gomez-Miguel *et al.*, 2013; Jones and Alves, 2013; Santos *et al.*, 2013), the Balearic islands of Spain (Gonzalez-Centeno *et al.*, 2012), the Loire valley of France (Cadot *et al.*, 2012), and in Italy, the Montepulciano d'Abruzzo region (Nunez *et al.*, 2011), Primitivo vineyards in the Apulia region (Ince *et al.*, 2013), and vineyards in the Campania region (Bonfante *et al.*, 2011). There is no doubt that such studies in the future will add further scientific rigor to both an understanding of the *terroir* concept and to enhance *terroir* classification.

Integration of *Terroir* with Modern Viticultural Practices

Low-Input Integrated Viticulture and *Terroir*

Integrated strategies of vineyard management, based on mechanization are widely adopted by winegrape producers in New World countries such as Australia (Clingeleffer, 2010; Clingeleffer, 2013) and increasingly in Europe (Intrieri, 2013). White *et al.* (2009) considered that the concept of *terroir*, although not easily reconciled with mechanization, must retain flexibility to keep the concept alive and meet challenges from New World producers and impacts of climate change. Clingeleffer (2010) provided an overview of approaches to integrated vine management available to enhance the consistency of supply and wine quality attributes over vintages, in

a low-input context. These integrated approaches include lighter pruning (mechanical hedging, minimal pruning, and mechanization of cane pruning based on high-cordon systems); application of crop control techniques other than winter pruning such as prebloom basal leaf and postset mechanical thinning; improved irrigation practices such as regulated deficit irrigation, prolonged deficits, and partial root zone drying; the use of low-moderate vigor rootstocks and high-density plantings. Adoption of all of these technologies may not be immediately applicable in traditional *terroir* vineyards as they may require changes to the regulatory framework (e.g., the use of irrigation in some regions). However, the widespread adoption of mechanical harvesting is an indication of the flexibility of *terroir* wine producers and the regulatory environment to accommodate change as management practices evolve to meet both the challenges of globalization and climate change. Future change and vineyard adaptation will be underpinned by the significant research effort in Europe, which aims to develop economically sustainable management practices and maintain or enhance wine quality attributes.

It is generally recognized that the traditional forms of management in Europe, based on systems involving vertical shoot positioning (VSP) not only have a high input requirement, particularly of labor, but also are suboptimal with regard to vine performance and wine quality (Carbonneau and Ojeda, 2011; Intrieri, 2013). From their studies in France with a diverse range of trellis/canopy management practices, Carbonneau and Ojeda (2011) concluded that the wide trellis lyre system (a form of U-trellis) and minimal pruning were optimum from a sustainability perspective based on canopy and berry exposure, use of the soil space, effects on water stress, soil management, energy, and carbon costs whereas the traditional, VSP systems rated poorly. Intrieri (2013) provided an overview of Italian research aimed at integration of mechanization with vineyard training and management to optimize yield and wine quality. Developments include permanent cordon trellis systems, including double-curtain wide U-trellises, which may be hand and machine pruned to replace the high input standard forms of cane pruning using guyot, sylvoz, and arched cane training. Refinements of these systems include the use of free cordon systems without shoot positioning, semiminimal pruning, improved crop regulation by early mechanical thinning of shoots, mechanical crop thinning prevéraison and basal leaf defoliation preflowering to reductions in yields, cluster compactness and botrytis rot, and the use of post-véraison antitranspirant sprays or canopy reduction by trimming to delay ripening.

In Europe, there is considerable interest in lighter pruning systems, which if integrated with mechanized yield regulation should be compatible with *terroir* wine production. Such approaches should also reduce the year to year variation in yield associated with climatic effects on fruitfulness and crop development (Clingeleffer, 2010). Beneficial attributes associated with lighter pruning systems adopted in Australia include development of vines with small, well-exposed bunches of small berries, spread over a large canopy surface, which lead to good disease control and improved berry composition, provided adequate sugar levels are reached (Clingeleffer, 2010). Compared with severe forms of pruning, minimally pruned vines generally produce juice with better organic acid composition, expressed as a superior tartrate to malate ratio, better wine color, and higher phenolics (Clingeleffer, 2010). Studies conducted in Europe generally support these results. For example, mechanical pruning has also been applied successfully to vertically shoot positioned Alfrocheiro vines, a red variety, in the premium Douro region of Portugal without effects on fruit composition and wine quality despite a doubling in yield (Cruz *et al.*, 2011). In long-term studies conducted in the Languedoc-Roussillon of France across a range of varieties, Rousseau *et al.* (2013a) observed that minimal pruning gave satisfactory results, except with late ripening varieties. Compared with standard management, minimal pruning at the same level of sugar had lower pH and more tartaric acid, and, although color and phenolics were lower, produced wines with sensory profiles preferred by consumers (i.e., less intense wines with more fruit driven and less herbaceous characters). Wine sensory profiles of both red and white varieties were also more stable across seasons. Similarly, for Riesling and other white varieties grown in a very cool climate in Germany, minimal pruned vines compared with those grown on a standard vertical shoot positioned system had higher yields (25–75%), looser clusters, and smaller berries with higher concentrations of aromatic precursors (Schultz and Weyand, 2005). This was reflected in enhanced sensory perceptions, despite having slightly lower levels of sugar.

To facilitate compatibility of modern management practices with the *terroir* concept there is considerable interest in Europe in mechanical and chemical techniques for yield regulation by removal of shoots, berries, inflorescences, and bunches. Gibberellic acid treatments have been successfully applied to reduce crop load and subsequent fruitfulness of minimal pruned Riesling in Germany while maintaining the quality benefits associated with minimal pruning, i.e., reduced bunch rot and enhanced flavor and aroma characteristics (Weyand and Schultz, 2006). Vertical rotational string thinners have also been used in Germany for early season shoot thinning of minimal-hedged vines (Schwab and Greber, 2013). One of the most promising techniques for crop regulation, which has been successfully tested across Europe, is the preflowering basal leaf removal which can be easily mechanized (Poni *et al.*, 2006, 2008; Intrieri *et al.*, 2008). This technique reduces fruit set and bunch compactness resulting in reduced incidence of bunch rots and improvements in fruit and wine composition. The technique has successfully been applied across a range of red and white wine varieties and regions in Italy, Portugal, and Spain (Diago *et al.*, 2013; Freire *et al.*, 2013; Moreno *et al.*, 2013; Queiroz *et al.*, 2011; Silva *et al.*, 2013; Taradaguila *et al.*, 2010, 2012). Postset mechanical thinning, which provides a final opportunity to adjust crop load after fruit set and before véraison has also been assessed in Italy and Spain (Diago *et al.*, 2013; Hanni *et al.*, 2013; Intrieri, 2013; Taradaguila *et al.*, 2008).

Precision Viticulture and *Terroir*

Over the past decade, techniques for rapid geospatial data acquisition, analysis, interpretation, and visual presentation have become available to characterize spatial variability within

a vineyard with regard to topography, soil characteristics, vine phenology, vigor and yield, and basic fruit quality attributes (Bramley, 2010; Johnson *et al.*, 2012; Green, 2012). Informed site-specific management decisions based on this knowledge is termed precision viticulture (Johnson *et al.*, 2012). Rapid site-specific data acquisition to facilitate adoption of precision viticulture includes remote sensing from satellite or aircraft to estimate vine vigor and health, ground-based mapping of soil characteristics, yield monitoring using harvester mounted devices and potentially, on-the-go sensing techniques of fruit quality attributes, (e.g., anthocyanins and phenolics, Bramley *et al.*, 2011b; Tisseyre, 2013). Furthermore, remotely sensed data have been linked to grape phenolics and color (Lamb *et al.*, 2004), berry sensory data (Rousseau *et al.*, 2013b), vine water status (Pons *et al.*, 2013), and incidence of ion chlorosis (Gonzalez-Flor *et al.*, 2013).

Bramley and Hamilton (2004) questioned the compatibility of the traditional *terroir* concept with precision viticulture where mandated management practices are applied at a regional level in designated GI zones in Europe whereas precision viticulture focuses on site-specific management. They concluded that the enhanced understanding provided by precision viticulture on the relationships between soil and land attributes on grape and wine production will provide a basis to impose management practices to gain greater control over fruit and wine quality and manage some of the elements of *terroir*.

High variability in vine vigor, yield, and fruit composition has been described in both New World vineyards (Bramley and Hamilton, 2004, 2007; Bramley, 2005) and in traditional European vineyards (Johnson *et al.*, 2012; Rousseau *et al.*, 2013a; Tisseyre *et al.*, 2007; Tisseyre, 2013). Bramley *et al.* (2011a) showed that variation in the chemical composition of grapes, wine, and sensory attributes could be linked to variation in vigor, yield, vine nutrient status, topography, and vineyard soil properties. Reynolds *et al.* (2007) demonstrated that the tools of prevision viticulture could be used to elucidate the basis for *terroir* based on vine size, fruit composition, soil texture, and wine sensory attributes.

Adoption of precision viticulture by traditional producers of *terroir* wines is likely to be highly varied depending on the region, wine style, and consumer expectations and may require changes in legislation in regulated GI regions. Nonetheless, there is strong interest in precision viticulture in Europe to manage production system complexity and provide information to more efficiently manage microscale variability for enhanced quality, yield, and revenue (Johnson *et al.*, 2012). Commercial services are emerging to provide decision support based on acquired geospatial data (De Filippis *et al.*, 2013; Rousseau *et al.*, 2013b). Adoption of precision viticulture by *terroir* wine producers is likely to fall into three main categories. These include the following:

Maintain the *Status Quo*

Maintenance of the *status quo* is an option based on the belief that the site-specific heterogeneity (i.e., in vigor, yield, ripeness, and fruit composition) is unique to the vineyard and thus a component of the *terroir*, which adds complexity to the wine.

Zonal Management

Precision viticulture techniques have been applied to identify zones within a vineyard for targeted vineyard and wine quality management (Proffitt *et al.*, 2006; Bramley, 2010). Targeted management techniques to improve vineyard homogeneity, largely addressing differences in vine vigor and fruit composition, include vineyard design and establishment based on soil characteristics, irrigation scheduling, soil and sward management including application of mulch (Newson and Nettelbeck, 2013; Newson *et al.*, 2013), choice of cover crop (Panten and Bramley, 2011), canopy management (Panten and Bramley, 2012; Newson and Nettelbeck, 2013), fertilizer management (Newson and Nettelbeck, 2013), and pest and disease management (Newson and Nettelbeck, 2013; Newson *et al.*, 2013). It is likely that a range of vine vigor control techniques such as lighter pruning in conjunction with various forms of crop regulation and where appropriate, use of rootstocks with varying levels of conferred scion vigor and adoption of enhanced deficit irrigation practices (Clingeleffer, 2010) will form part of integrated management strategies to improve homogeneity of vineyards producing *terroir* wines.

Benefits from the use of selective harvesting based on within vineyard zoning, either in real time or at different dates, have been shown to be a feasible and profitable strategy (Bramley *et al.*, 2005; Bramley *et al.*, 2011c). Such approaches provide options for improved harvest planning (Rousseau *et al.*, 2013a), batching, streaming and blending of fruit and wine, and production of different winestyles (Newson *et al.*, 2013; Bigot *et al.*, 2013a,b).

Variable Rate Technologies

There is significant interest, particularly in Europe, in the use of variable rate technologies (VRT) to refine precision viticulture to improve vineyard homogeneity compared with the coarse zonal management described above. Aspects of viticultural managements amenable to VRT include fertilizer application, soil cultivation (e.g., tillage depth), pest and disease management, weed management, mulching, irrigation supply, and canopy management (pruning, shoot thinning, leaf removal, and summer trimming; Johnson *et al.*, 2012; Vieri *et al.*, 2013).

Impact of Climate Change on *Terroir*

Climate projections for wine-producing regions are an increase in temperature of 0.5–1 °C by 2025 and approximately 2 °C by 2050, reduced rainfall, increased variability between seasons with increased occurrence and severity of extreme climatic events such as heat waves and drought (Jones *et al.*, 2012; Webb *et al.*, 2011). It is probable that current plantings will be influenced by future long-term climate changes as the economic life of a vineyard may exceed 40 years (Neethling *et al.*, 2013; Webb *et al.*, 2011). Predicted impacts of climate change on winegrape production include changes in phenology and ripening under warmer conditions, disruption of balanced composition in grapes and wine, alterations in

regional winestyles, and spatial changes in viable grape-growing regions (Holland and Smit, 2010; Jones, 2005; Ollat *et al.*, 2011; Jones *et al.*, 2012). Changes in climate will directly alter *terroir* and challenge the adaptive capacity of the industry, particularly in Europe where production practices are highly regulated and controlled by legislation. Such projections are likely to have serious consequences for regionality, in particular *terroir* because of the tight linkage between climate, soil, and adoption of varieties suited to premium wine production (Holland and Smit, 2010; Webb *et al.*, 2007a). Indeed, Hannah *et al.* (2013) predicted that the area suitable for viticulture in the major producing regions will decrease by 25–73% by 2050 without adaptation. As a consequence, shifts in the production base to higher elevations and higher latitudes are predicted (Hannah *et al.*, 2013; Neethling *et al.*, 2013; Duchene *et al.*, 2010; Malheiro *et al.*, 2010). Webb *et al.* (2007b) suggest that major shifts in the production base are unlikely because established regions have substantial investment in physical and social infrastructure, brand recognition, and in the case of many European vineyards, a history and recognition based on regionality and *terroir*. Consequently, grower adaptability to changing conditions will be critical for the maintenance of viticulture in existing regions and *terroirs* (Ollat *et al.*, 2011; Neethling *et al.*, 2013) and will require the cooperation of appellation boards and regulators (Pincus, 2003; Ollat and Touzard, 2013).

The dire predictions of Hannah *et al.* (2013) regarding the impacts of climate change on the suitability of the main producing regions appear to be overstated as the study did not account for the plasticity of varieties across temperature regimes and underestimate the adaptive capacity of viticulture management to warmer conditions (Van Leeuwen *et al.*, 2013). Furthermore, Hannah *et al.* (2013) did not include assessment of the significant body of research conducted in hot climates, which provides direction for adaptation by the industry in cooler regions. Schultz (2011) used Riesling and Cabernet Sauvignon as examples to demonstrate the climate adaptability of grapevine varieties (plasticity). He showed that these varieties are already grown internationally under very different climatic conditions in regions recognized for high-quality wine production, which exceed changes predicted by models of climate change. Furthermore, there is general agreement in the literature that the increase in temperature over the last 50 years over most winegrape regions, on average 1.3° (Jones *et al.*, 2005), has had a positive effect on wine quality associated with reduced year-to-year variation, longer and warmer growing seasons, less frost risk, and earlier and more consistent ripening conditions (Jones *et al.*, 2005; Jones *et al.*, 2012; Van Leeuwen *et al.*, 2013) except in hot production regions (Webb *et al.*, 2007b, 2008). However, it is predicted that with higher temperatures many varieties may be grown outside their optimum threshold temperature limits (Jones *et al.*, 2012; Holland and Smit, 2010).

Ollat *et al.* (2011) stressed the importance of developing adaptation strategies to assist the industry to cope with climate change particularly for the most at risk, warm and dry Mediterranean regions and by implication *terroir*, in Europe. Viticultural strategies suggested include use of noncompetitive interrow grass swards to minimize soil evaporation, targeted adoption of irrigation (i.e., when evaporative demand is high and water availability is low), canopy cooling by misting, shading, and canopy configuration. Neethling *et al.* (2013) reported that growers in the Loire valley in North West France have already made significant adaptive changes over the last 20 years, particularly in soil management. These adaptive changes include the use of less competitive cover crops, modifications to canopy management and rootstock choice to cope with warmer conditions and drier soils. They also indicate a willingness by growers to consider the introduction of new varieties and irrigation currently not allowed in the region. Ollat *et al.* (2011) indicated that breeding to develop new varieties and rootstocks with improved heat tolerance, drought tolerance, and water use efficiency must be a critical part of this strategy to maintain production in existing regions.

Research undertaken in hot regions provides further direction to develop and underpin adaptation strategies to increasing temperature and water stress. For example, vineyard management research conducted in a hot climate overviewed by Clingeleffer (2010) described opportunities to develop strategies to enhance the consistency of supply and wine quality through integration of lighter pruning, crop regulation, and irrigation practices together with adoption of low-moderate vigor rootstocks (see Section Low-Input Integrated Viticulture and Terroir). Further studies confirm that rootstocks are a powerful tool to manipulate growth characteristics, fruit composition and wine quality attributes, water use efficiency, and drought tolerance in hot climates (Clingeleffer *et al.*, 2011).

There is also considerable interest in Europe in the use of postvéraison leaf removal by trimming to delay ripening as an adaptive strategy to climate change (Filippetti *et al.*, 2011; Intrieri, 2013; Lanari *et al.*, 2013; Palliotti *et al.*, 2013; Pisciotta *et al.*, 2013; Rombola *et al.*, 2011; Stoll *et al.*, 2013). Furthermore, ripening has also been successfully delayed using antitranspirants (Filippetti *et al.*, 2011; Palliotti *et al.*, 2011). Technologies to reduce fruit and canopy temperatures may also offer significant benefit to facilitate ongoing production from high value regions and *terroirs*. They include particle film technology (Glenn *et al.*, 2010), artificial shade, and water misters (Ollat *et al.*, 2011).

Exploitation of genetic diversity is considered a critical component of adaptation to climate change. This will include sourcing of varieties successfully managed in warm and hot climates and breeding new varieties with more intense flavor, better color, lower pH, and improved acidity and organic acid composition with improved water use efficiency and drought tolerance (Ollat *et al.*, 2011; Ollat and Touzard, 2013; Webb *et al.*, 2011). Clingeleffer *et al.* (2013) described systematic studies that aimed to phenotype 500 varieties grown in a hot climate for traits considered important to climate change adaptability. These included optimal fruit composition with respect to total soluble solids, titratable acidity, pH, organic acid composition, total anthocyanins and phenolics, and flavor; varieties with high water use efficiency based on short seasonality and high fruit-to-leaf ratios; and varieties to extend the harvest period. The study showed significant potential to adopt a wider suite of varieties to facilitate adaptation by industry to meet future climate change scenarios. As mentioned above, the cooperation of appellation boards and regulators

will be required to permit *terroir* winegrape production from a wider spectrum of varieties (Pincus, 2003; Ollat and Touzard, 2013).

Conclusions

The *terroir* concept, which provides a link between the sensory attributes of a wine and consumer expectations and the environmental conditions in which the grapes are grown, evolved in European viticulture over many centuries. Evolution of the *terroir* concept has involved significant changes to vineyard management to accommodate challenges from pests and diseases, globalization of the winegrape industry with competition from New World producers and changes in consumer preferences, an indication that the *terroir* concept is flexible and adaptable to change within a regulated framework (Gade, 2004). There continues to be strong support for the ongoing production and sale of *terroir* wines with significant adoption of the concept in the New World by producers seeking marketing advantages over larger companies and blended products. The industry and regulators must embrace change and retain flexibility to meet future challenges associated with maintaining international competitiveness, environmental sustainability, climate change, and shifting consumer expectations. The challenge will be to keep the *terroir* concept alive, retain flexibility yet preserve the cultural connection between winemakers, the land and consumers (White *et al.*, 2009). This will be critical to the economies of historical *terroir*-based regions reliant on the significant investment in winegrape production and processing and established social infrastructure for survival (Ollat *et al.*, 2011).

New scientific tools are now available to integrate conceptually all the factors relating to *terroir* to enhance the understanding, accurately define zones, and provide guidance for vineyard management. These integrative tools include multivariate statistical analyses, geographic information systems (GIS) with high resolution climate and spatial modeling, rapid data acquisition of soil and plant characteristics to define the vineyard environment and modern technologies to measure grape and wine composition and wine sensory attributes. A suite of vineyard management practices and tools associated with precision viticulture, alternative varieties, and rootstocks are available to develop integrated approaches to facilitate adaptability by producers and ensure both the survival and future evolution of the *terroir* concept in modern viticulture. This will require flexibility by both producers and those involved in developing the future regulated legal framework for the production of *terroir* wines.

See also: Agricultural Mechanization. Climate Change: Agricultural Mitigation. Climate Change: Cropping System Changes and Adaptations. Climate Change: Horticulture. Climate Change, Society, and Agriculture: An Economic and Policy Perspective. Precision Agriculture: Irrigation. Sensory Science. Social Justice: Preservation of Cultures in Traditional Agriculture. Tree Fruits and Nuts. Weather Forecasting Applications in Agriculture

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Transgenic Methodologies – Plants

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Glossary

Agrobacterium-mediated transfer-deoxyribonucleic acid (T-DNA) delivery A technique that uses strains of *Agrobacterium tumefaciens* that have been modified to transfer transgenes into plant cells.

Cisgenics Transformation using a perfect copy of an allele within or between sexually compatible species or moving an allele to a new genomic position within or between sexually compatible species.

Direct DNA delivery A range of techniques for introducing either linear single- or double-stranded DNA fragments or plasmids into plant protoplasts, cells, or tissues using physical or chemical means, such as microprojectile bombardment, chemical methods, or electroporation.

Generational terminology F1: progeny of a cross between two different genotypes; R0 or T0: regenerated transgenic plant (hemizygous for the transgene); R1 or T1: selfed progeny of the R0 or T0, respectively, segregates for the transgene in Mendelian fashion. In floral dip transformation, the treated plant is the T0 generation and hemizygous T1 seed are recovered from selfing T0 plants.

Genetically modified, genetically engineered, and transgenic organism or plant Descriptions used to indicate a plant that has been stably transformed with transgenes from any gene donor, including synthetic genes in any combination that are stably integrated in the nuclear genome.

Intragenics Transformation using only sexually compatible species for the gene and element donor sources but not in the native configuration.

Selectable marker A gene that when expressed by the transgenic cell confers a positive selective advantage enabling the transgenic cell to survive and divide in the presence of a selective agent while multiplication of nontransgenic cells or plant populations is inhibited.

Totipotency The property of regenerating an entire organism from a cell or part of the organism. Regeneration of plants from a transgenic cell via tissue culture enables production of transgenic plants capable of transmitting the transgene to its sexual or asexual progeny.

Transformation Delivery of DNA into an organism for either transient expression of genes encoded by the delivered DNA or for stable integration into the nuclear, plastid, or mitochondrial genomes resulting in germline transmission to progeny or stable expression in asexual propagules.

Vector Assemblage of a transgene including the gene of interest and requisite expression elements along with other genes like the selectable marker and sequences required for DNA transfer and, when applicable, genomic integration.

Introduction

Transformation expands the gene pool for plant genetic manipulation to all organisms and all deoxyribonucleic acid (DNA) sequences. Used as a research tool to investigate gene function, to produce large quantities of valuable proteins and metabolites in plants and plant culture systems, and for crop improvement, plant transformation has become a widely used genetic manipulation tool since its first demonstration in 1983. Theoretically, all plants can be transformed. Practically speaking, transformation technologies have been developed for all major and most minor crop plants and model systems. The earliest successful demonstrations of plant transformation were achieved with tobacco (*Nicotiana tabacum*) and petunia (*Petunia hybrida*) models for plant transformation research at that time because of their well-developed tissue culture properties and high frequency of plant regeneration from those cultures, characterized response to specific selective agents, and susceptibility to *Agrobacterium* enabling DNA delivery (Fraley *et al.*, 1983a,b; Framond *et al.*, 1983; Schell *et al.*, 1983). From that first demonstration of plant transformation in 1983, transformation technologies were rapidly translated to crop plants. The first commercially available genetically engineered food product, the Flavr Savr tomato, was modified for improved shelf life and launched for commercial production in 1994 (Sheehy *et al.*, 1988; Krieger *et al.*, 2008). Although the Flavr Savr product was not a sustained commercial success, it was important from a historical perspective, because it was the first transgenic product to undergo commercial development and regulatory approval setting the stage for commercial launches of the transgenic crops to follow (Redenbaugh *et al.*, 1992). Roundup Ready soybean was then offered for commercial production in 1996 (Padgette *et al.*, 1995) and, along with later developments in other crops, initiated the widespread production of transgenic crops. Advancing from first demonstration in a model system to commercial production in a range of major crops in only 13 years is an astounding pace of technical achievement followed by commercial development. Because transgenic traits provide significant improvements in weed and insect pest control, the adoption rate of crops with transgenic traits by growers has also occurred at a remarkable pace most likely exceeding the rate of adoption of any other crop improvement advancement in the history of agriculture (Brookes and Barfoot, 2013; **Figure 1**). Furthermore, the significant impact of plant transformation on crop productivity is demonstrated by the fact that in 2011 72% of soy, 56% of cotton, 28% of corn, and 23% of canola acreages worldwide were sown to transgenic

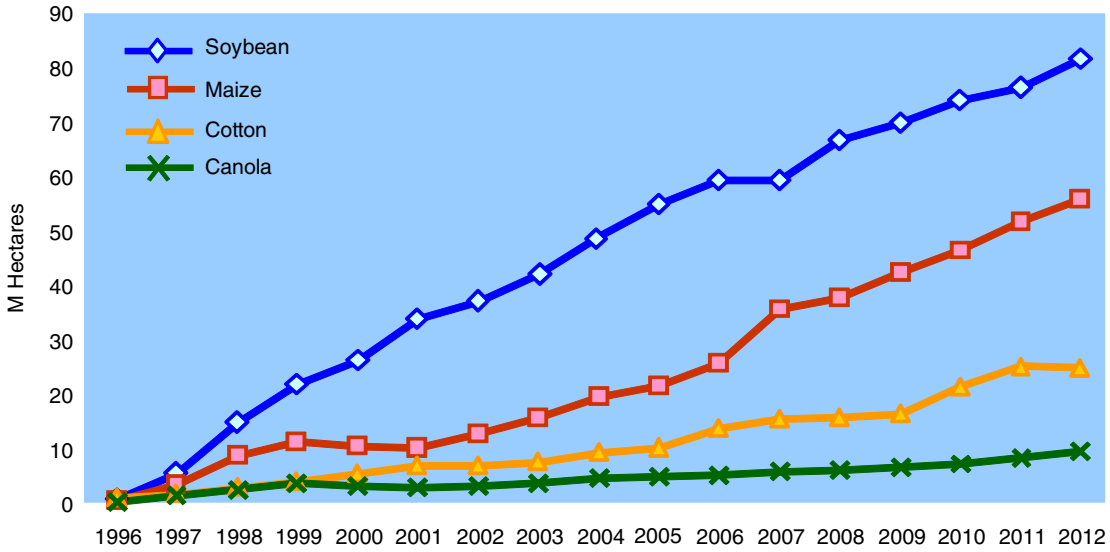


Figure 1 Global area of biotech crops, 1996–2012: By crop (million ha). Reproduced with permission from James, C. ISAAA.org, ISAAA Brief 46-2013.

crops only 30 years after the technology was first invented (Brookes and Barfoot, 2013). Accordingly, the seminal work demonstrating plant transformation in 1983 was recognized by the 2013 World Food Prize because of the major impact of transformation on crop improvement.

This article reviews the technical breakthroughs that resulted in the development of transgenic technologies. Genetic manipulation strategies enabled by transformation technologies as they are applied to both plant biology research and crop improvement are described to provide context to understanding the drive behind developing and utilizing these technologies. This article further focuses on methods for stable integration of transgenes into the nuclear genome because it is the main transformation method used for crop improvement applications to date. Finally, the requirements for and development of plant transformation methods and current challenges and likely future directions in improving transformation technologies are discussed. Many aspects of plant transformation technologies have been comprehensively reviewed. Citations in this article include both first and breakthrough reports along with these review articles. Transformation technologies developed for industrial-scale biopharming to produce valuable compounds are reviewed in the article in this volume by Ursin *et al.*

Genetic Manipulations Using Stable Transformation

Most eukaryotic somatic cell types randomly integrate any sequence of delivered exogenous DNA into the nuclear genome via double-strand break repair mechanism(s) at substantially greater frequencies than by homologous recombination or any other site-directed mechanism(s) (Windels *et al.*, 2003; Somers and Makeravitch, 2004; Tinland, 1996; Salomon and Puchta, 1998; Van Attikum *et al.*, 2001; Mayerhofer *et al.*, 1991; Puchta and Fauser, 2013). Following random integration of the transgene into the nuclear genome, the transformed cell will be hemizygous for the integrated transgene and, as long as it does not have a deleterious impact on cellular processes, the transgene will be transmitted through mitotic division to yield a transgenic cell line (**Figures 2** and **3**). Transformation via random integration is primarily used to add transgene(s) to the nuclear genome and the resultant transgenic plants exhibit dominantly inherited gain-of-function transgenic traits. The importance of this straightforward genetic manipulation approach in research and its significance to crop improvement cannot be overstated as demonstrated in **Figure 1**. Distinctions among the different transformation strategies defined in the glossary have a direct impact on the range of genetic manipulations they enable. From the perspective of the gene pool concept, transgenesis expands the gene pool for crop improvement applications to all DNA sequences. Intragenesis restricts the DNA donor source to relatives in the gene pool of a crop but enables new combinations of elements in the 'intragene,' whereas cisgenics primarily enable allele and cisgene stacking applications. See **Figure 4** for examples of transgene cassettes.

A transgenic strategy to suppress expression of an endogenous gene in the transgenic plant employing *trans*-acting suppression from randomly integrated transgenes was discovered early in the development of transformation technologies. Intentionally structuring the transgene cassette to express the antisense transcript of an endogenous gene in the recipient dominantly suppresses expression of the endogenous gene (**Figure 4(b)**). This 'antisense' strategy has been applied to a range of crop improvements and to impart virus resistance when the antisense sequence is taken from the viral genome. The first example of a commercialized antisense product was the Flavr Savr tomato (Sheehy *et al.*, 1988). The article by Krieger *et al.* (2008) addressed the mechanism underlying this example of antisense RNA technology.

For research applications, random transgene integration throughout the genome enables gene discovery opportunities similar to the uses of transposable element systems but

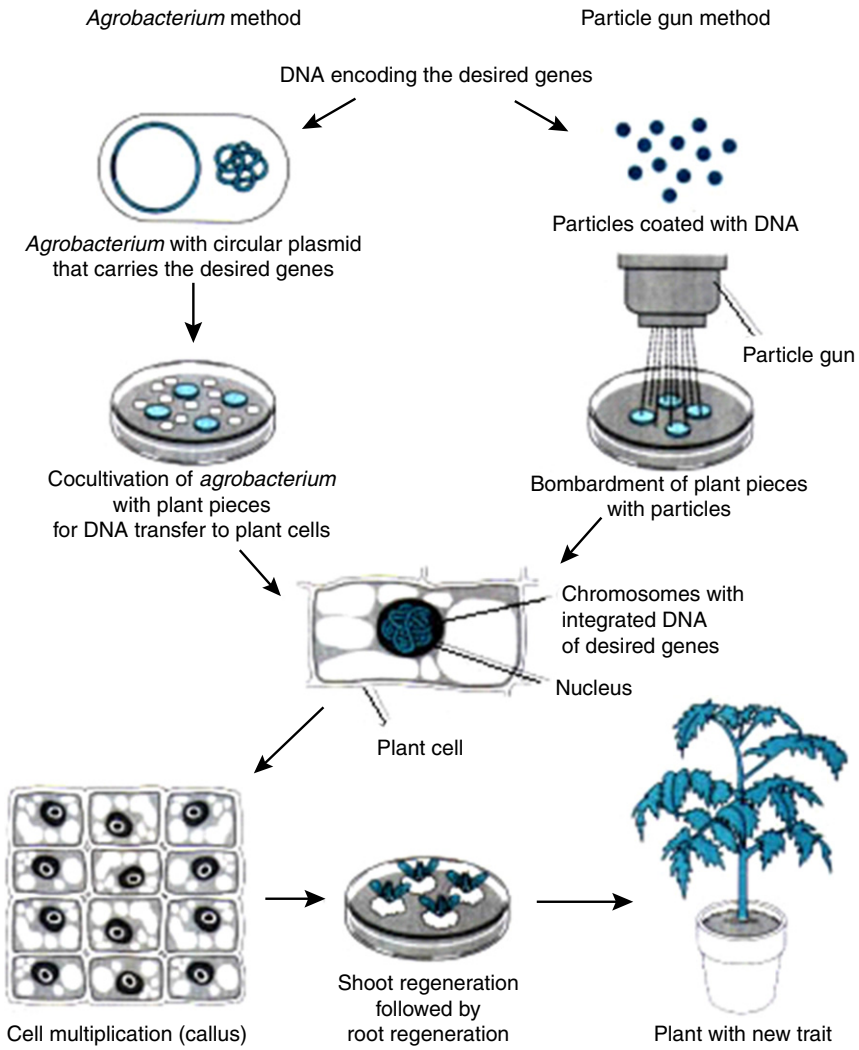


Figure 2 Plant transformation via *Agrobacterium* and particle gun-mediated DNA delivery.

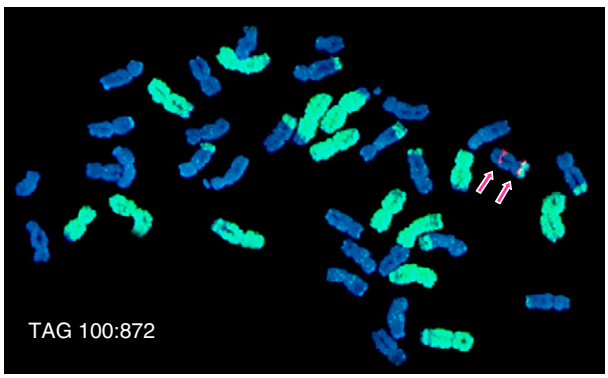


Figure 3 Chromosomes of an oat plant transformed using microprojectile bombardment that is hemizygous for two transgenic loci detected by fluorescent *in situ* hybridization (red and arrows). Oat is allohexaploid containing A, C (green probe for a C genome-specific repeat), and D genomes. Reproduced with permission from Svitashev, S., Ananiev, E., Pawlowski, W.P., Somers, D.A., 2000. Association of transgene integration sites with chromosome rearrangements in hexaploid oat. Theoretical and Applied Genetics 100, 872–880.

with the added advantage that, unlike an endogenous transposase, transgene insertion is not confined to a specific species. Using transgene integration either to knock out endogenous genes via insertion and deletion or to tag or trap endogenous expression elements by integration of cassettes designed to create transcriptional or translational fusions and trap a genetic element of interest has proven extremely useful in plant biology research. For example, transformation populations of *Arabidopsis* have been developed in which nearly every gene in the genome has been disrupted or tagged with a transfer DNA (T-DNA) (Alonso *et al.*, 2003; Kim *et al.*, 2003; Sawasaki *et al.*, 1999). In other examples, promoter tagging via insertional fusion has been used to identify useful expression elements. Detailed characterizations of large populations of T-DNA insertions indicate that a higher proportion of insertions occur in or near genic regions; whether this is because these regions are more accessible to integration because they are euchromatic, more active in double-strand break repair, or simply that selection of transgenic cells requires active transcription of the selectable marker gene is a subject that continues to be investigated. Fewer insertion events produced via direct DNA

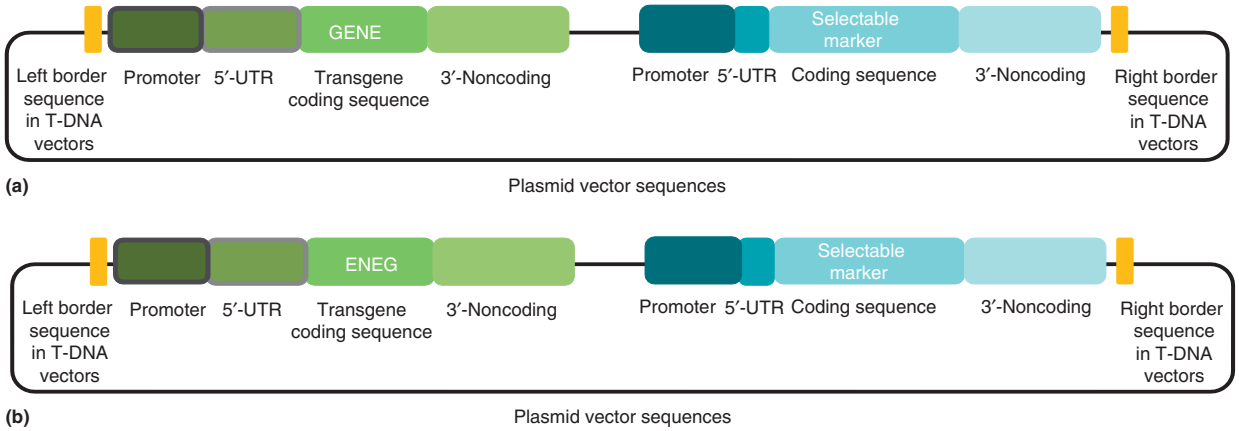


Figure 4 Examples of plant transformation cassettes showing coding and noncoding elements in untranslated regions (UTRs) necessary for expression of the transgene of interest. Selectable marker cassettes are often included on the same delivered DNA. In 2 T marker-free transformations the selectable marker cassette is introduced on a separate T-DNA. The primary difference with direct DNA delivery vectors is the T-DNA borders that are sequences that delineate the T-DNA for transfer from *Agrobacterium* into the plant cell. They have no role on T-DNA integration. (a) A standard format for a gain-of-function transgenic trait that enables positive selection for presence of the transgene. The vector shown is a T-DNA vector because of the presence of the T-DNA border sequences. For the direct DNA delivery, the T-DNA borders are usually not included. (b) The transgene is an antisense configuration of an endogenous gene for transacting suppression. Modified from Kjemtrup, S., Talarico, T.L., Ursin, V., 2014. Biotechnology: Pharming.

delivery have been characterized at this level, but the results suggest that transgene integration follows the same general rules as T-DNA insertion with the possible exceptions that there is less tendency for insertion into genic regions and a higher frequency of multiple transgene sequences (including small fragments) are integrated in multiple loci throughout the genome within a transgenic event (Windels *et al.*, 2001; Svitashev *et al.*, 2000; Makarevitch *et al.*, 2003).

Early in the development of plant transformation systems, it was observed that transgene expression levels are highly variable among transgenic plants transformed with the same transgene using conventional methods for random genomic integration (Horsch *et al.*, 1985). Most frequently this observation is attributed to the molecular structure of the transgene integration locus, the copy number of the transgenic inserts in the same or multiple transgene loci, and the effects of the position in the nuclear genome into which the transgene is integrated. In some transgenic plants, transgene expression can be lost over generations or lead to segregation distortion of the transgenic phenotype even though the transgene is inherited in Mendelian fashion. This phenomenon is referred to as transgene silencing and is triggered by structural duplications in the delivered DNA, rearrangements of the transgene integration locus, the genomic position and context of the transgene locus, by high levels of transgene expression, and likely factors that remain to be discovered. Eukaryotic gene silencing mechanisms were in part elucidated by observations of unexpected transgene expression patterns in plants resulting in an entirely new understanding of eukaryotic gene regulation. For more information on transgene silencing see reviews (Beclin *et al.*, 2002; Depicker *et al.*, 2007).

Plants containing only single copy, unrearranged transgene loci produced with the same transgene often exhibit substantial variation in transgene expression indicating that the position effect of transgene integration is an important variable in determining transgene expression potential. The current paradigm is to compensate for 'position effect variation' in transgene expression by producing multiple plants from a single transgene construct to identify those that exhibit the desired expression profile. Intuitively, site-directed integration is expected to reduce or eliminate position effect variation in transgene expression and preliminary reports support this expectation (Day *et al.*, 2002; Srivastava and Ow, 2001). However, establishing the extent to which this variation is reduced via site-directed integration will require the production and characterization of large numbers of transgenic events with transgenes targeted to individual specified genomic locations to determine whether variation in transgene expression is reduced among the genotypically identical events produced at the same locus and if all or some of the different genomic integration sites exhibit this behavior.

Targeting transgene integration to specific genomic locations or sequences to enable gene replacement and other sequence-specific manipulations has been the focus of intense research since the first demonstrations of transformation. First demonstrated in plants by Paszkowki *et al.* (1988), the frequency of transgenic plants resulting from site-directed integration was too low to be broadly applied to crop improvement (Terada *et al.*, 2002). Recent advances in site-directed genomic cutting strategies have shown that transgenes can be integrated via homologous recombination at improved frequencies bringing this transgenic approach into a useable range (Wood *et al.*, 2011; Li *et al.*, 2011; Zhang *et al.*, 2005; Frauser *et al.*, 2012). As site-directed integration and other genetic manipulations become routine enabling a shift in the transgene integration paradigm from random integration to sequence-specific integration, the range of genetic manipulations will be increased to include endogenous gene knockouts (recessive), directing transgene or allele stacking to specific genomic locations, and allelic or genomic editing (D'Halluin *et al.*, 2008; Ainley *et al.*, 2013; Curtin *et al.*, 2012). The demonstrations of site-directed integration reported to date

indicate that some frequency of R0 plants biallelic or homozygous for the transgene provide a further useful feature (D'Halluin *et al.*, 2013; Shukla *et al.*, 2009; Townsend *et al.*, 2009). Whether crops modified using endogenous gene knockouts or allelic editing will be considered transgenic remains to be determined.

Plastid transformation has been achieved in plants via homologous recombination of the introduced transgene DNA into the plastid genome enabling both gain of function manipulations and gene replacement. In plastid transformation, once the multiple genomes in a plastid and all plastids in the cells of a recipient are uniformly transgenic (called the homoplasmic state), transgene inheritance follows cytoplasmic inheritance (Maliga, 2004). Although very high levels of transgene expression have been observed as a result of plastid transformation, there are no examples of crop plants in production transformed via plastid transformation. To date there are no reported examples of mitochondrial transformation in plants.

Technical Framework for Transformation – Required Components

Conventional plant transformation requires only three components: (1) delivery of DNA into totipotent cells, (2) a means of selection or identification of the transgenic cell, cell culture, or regenerated plant, and (3) cells that are totipotent (**Figure 2**; Gasser and Fraley, 1992). This framework is based on the natural tendency for delivered DNA to be integrated into the nuclear genome via cellular processes resulting in a hemizygous transgenic cell. Plant regeneration from a totipotent transgenic hemizygous cell results in a uniformly transgenic organism enabling stable germline transmission of the transgene to the progeny in Mendelian fashion. From the beginning of plant transformation research, it was recognized that a far simpler route to producing a transgenic plant would be to deliver the transgene DNA into a gamete or gamete progenitor cell followed by pollination to produce a transgenic seed. To date, this method is only widely enabled in the model plant *Arabidopsis* (Bechtold *et al.*, 1993; Chang *et al.*, 1994; Clough and Bent, 1998; Bent, 2000) and to a lesser extent in its close relative canola (Wang *et al.*, 2003). Thus, the great majority of extant crop transformation systems follow the conventional framework, the development of which is examined in more detail from a historical perspective.

The sequence and structure of the DNA molecules themselves are critical for transformation success and for the desired transgene expression pattern for the trait of interest (Komori *et al.*, 2007, 2011). Direct DNA delivery transformation cassettes require only plant expression elements for appropriate tissue-specific and developmental expression of the transgene (**Figure 4(a)**). In addition to the transgene(s) of interest, plant transformation cassettes often contain a selectable marker gene. T-DNA-specific left and right border sequences shown in **Figure 4(a)** are utilized for mobilization of the T-DNA from *Agrobacterium* to the plant cell. No specific transgene cassette sequences are required to guide genomic integration for random integration via double-strand break repair. Site-directed integration requires homologous genomic sequences as substrates for recombination; however, prescriptions of homologous sequence length and nucleotide composition for optimizing site-directed integration frequency and fidelity remain to be determined.

Early transformation work was accelerated by the development of molecular detection methods and establishment of a simple set of basic criteria or proofs that together constituted convincing evidence that a transgenic plant was produced. To demonstrate stable transformation, this proof is simply the detection of the transgene integrated into the genome of the regenerated plant and its transmission following disomic Mendelian inheritance to sexual progeny or stable transmission in asexually propagated crops, i.e., demonstration of the transgenic genotype. Developed by consensus of the scientific community and later articulated in the scientific literature (Potrykus, 1990a,b) as new transformation technologies were developed and reported, these criteria set the bar for proof of transformation and the types of and ways that genetic and molecule assays should be conducted accelerating the development of new transformation technologies. From the current perspective of being able to simply order the synthesis of transgene cassettes from molecular services companies and detect transgenes via whole genome sequencing with the prospects of this approach becoming economically feasible (Kovalic *et al.*, 2012), it is difficult indeed to appreciate the challenges faced by early transformation scientists in demonstrating progress toward developing plant transformation methods. In the 1970s, molecular assay techniques that could be used to prove that a plant was transformed were under development, as were selectable marker and reporter genes that would ease the detection of transgenics. Since that time, plant transformers have rapidly adopted and, in some cases developed, the molecular toolkit for producing and characterizing transgenic plants.

Technical Framework for Transformation – Enabling Breakthroughs

Plant Cell Totipotency – The Regeneration of Whole Plants from Cells

Both animal and plant cells exhibit totipotency. However, in the decades leading up to the first breakthroughs in plant transformation, only plant cell totipotency had been demonstrated and at that time cell and tissue culture methods for regenerating whole plants were developed in only a limited number of species. Breakthroughs in defining tissue culture media and methods during the 1950–80s (Murashige and Skoog, 1962; Eriksson, 1965; Gamborg *et al.*, 1968; Nitsch and Nitsch, 1969; Schenk and Hildebrandt, 1972; Kao and Michayluk, 1975; Chu *et al.*, 1975; Lloyd and McCown, 1980) provided the scientific foundation for the developing field of plant cell and tissue culture (Gamborg and Phillips, 1995; Hall, 1999; Singh and Kumar, 2009). Driven by the demonstrated and potential usefulness of plant cell and tissue culture for diverse applications, including plant propagation, chromosome manipulations like doubled haploid production from microspore culture, mutant selection and as a source of totipotent target cells for transformation, methods for tissue culture establishment and plant regeneration were

rapidly translated to a wide range of plant species during the 1970–80s. By culturing on a defined media containing the requisite balance of phytohormones, a somatic cell in a plant tissue or a gametic cell is dedifferentiated to a state in which its development is rerouted to form a regenerable structure. For example, developmentally fated cells in the scutellum of immature embryos of corn and many other monocotyledonous plants can respond to tissue culture media to form regenerable structures (Green and Phillips, 1975). The fundamental key for the development of a transformation system is that at some stage in the tissue culture-induced processes of dedifferentiation and redifferentiation, a single cell that can be transformed gives rise to the regenerable structure. This generality is supported by the observation that the great majority of regenerated transgenic plants characterized to date are comprised of a single transgenic insertion and not a population of multiple transgenic events.

Plant cell and tissue culture processes commonly involve isolating a defined organ or cell type, often referred to as the 'explant,' and culturing it in media containing phytohormones to begin the dedifferention stage most often referred to as 'callus.' Explants can be as simple as leaf or stem sections of a plant or more specific structures, such as the immature embryo of corn or the cotyledonary node of soybean. In some plants, single cells can be isolated as protoplasts by using hydrolytic enzymes to digest away cell wall material leaving a plant cell bounded by only its cell membrane as first demonstrated by Cocking (1960). Protoplast cultures were initially recognized to be an attractive avenue for plant transformation because of the ease of DNA delivery due to the removal of the cell wall and the single cell nature of the culture simplifying the selection stage of the transformation process. In tobacco and related species, for example, protoplasts can be isolated directly from leaf tissue and cultured to form plant-regenerating (regenerable) callus (Nagata and Takebe, 1970; Frearson *et al.*, 1973; Nagy and Maliga, 1976). In most cases of plant cell and tissue cultures, as in bacteriological culture practices, plant explants can be cultured in liquid or solidified media and because sucrose or other sugars must be supplied in the media, the entire process including explant preparation must be kept axenic, usually involving both sterile technique and inclusion of antibiotics. Callus cells can also be cultured in liquid media to form suspension cultures of various levels of dedifferentiation. Some suspension cultures can be used for protoplast isolation; others are useful cellular targets for DNA delivery. Explant response to tissue culture to form a regenerable culture is dependent on the plant species and its genotype, the explant chosen and its developmental stage, culture media nutrient and phytohormone composition, and the culture environment including temperature, light regime, and humidity control.

Regeneration of whole plants from cells occurs via two different developmental pathways (Duncan, 2011; Vasil, 2008). In somatic embryogenesis, cell divisions result in the formation of an embryoid with a developed root and shoot meristem that can germinate and elongate following a very similar developmental path as a zygotic embryo. In organogenic regeneration, cell divisions result in the formation of an apical meristem-like structure that in a subsequent culture steps forms a root to give rise to the whole plant. Transformation has been achieved using both routes of plant regeneration indicating that as long as the regenerable structures originate from single cells into which DNA can be delivered, the developmental path is of lesser importance. However, in many plant species, regeneration is enabled only via a single developmental path, and in some cases the tissue culture response and plant regeneration capacity is modulated by genotype such that not all cultivars within a species respond to the same degree (Parrott *et al.*, 1989). For this section, it is important to recognize that the limitations imposed by the genotype effect stimulated extensive research in developing tissue culture and plant regeneration protocols that are more genotype flexible via targeting totipotent cells that undergo less dedifferentiation and for shorter periods before regeneration (Birch, 1997). Excellent examples of this approach include targeting cells in the meristem regions of legumes to directly regenerate a transformed shoot (Somers *et al.*, 2003; Ye *et al.*, 2008). The genotype dependence of plant regeneration and impact on transformation and eventual transgenic crop improvement are discussed in more detail in the Section Technical Limitations, Potential Solutions, and Future Transgenic Technology Directions.

A more attractive approach mentioned earlier is to bypass cell and tissue culture steps altogether by targeting gamete or gamete progenitor as in the widely used *Arabidopsis* floral dip method (Clough and Bent, 1998). In this method, plants at a specific developmental stage are inoculated with *Agrobacterium tumefaciens* carrying the gene of interest along with a selectable marker and allowed to self-pollinate and set seed to produce transgenic progeny. The mechanism(s) involved in this method have been characterized. As predicted from the above discussion on the single cell nature of cell and tissue culture-based transformation systems, in the *Arabidopsis* floral dip method a low percentage of the progeny of the treated plant are transgenic because only a few of the numerous gamete progenitor cells are transformed per plant during treatment (Clough and Bent, 1998). Some have postulated that the simplest transformation process would be to treat seed for DNA delivery followed by germination of a transgenic plant. Because mature seed of most plants are completely differentiated structures and have multiple cells that will give rise to the germline, the expected outcome would parallel the *Arabidopsis* floral dip observations in that only a few progeny resulting from the treated seed would be transgenic, most probably hemizygous T1 plants as opposed to the regeneration of a hemizygous T0 plant. Although numerous examples of this method have been reported over the years, only a few have demonstrated stable Mendelian transmission in the generations following the transformation treatment, thus meeting the criteria for demonstrating successful transformation described above. However, there is no doubt that continued research in this area will eventually lead to robust transformation systems that do not require cell and tissue culture.

Transgene DNA Delivery

Direct DNA Delivery

Discovering methods to deliver DNA into plant cells was a key enablement for transformation (Darbani *et al.*, 2008;

Nandakumar *et al.*, 2011). Many developments in plant DNA delivery technologies were built on progress in transformation of microbes and animal cell cultures. Because the plant cell wall is a significant barrier to the delivery of DNA and other biomolecules into the cell, strategies developed for mammalian cell transformation could not be directly applied to plant cells. Two general strategies evolved for delivering DNA into plant cells: direct DNA delivery and *Agrobacterium*-mediated T-DNA delivery. Two major technical breakthroughs in DNA delivery occurred in the late 1980s and early 1990s that enabled rapid expansion in the development of transformation methods to most crops. These were the development of cell wall penetrating DNA delivery methods and the demonstration that *Agrobacterium*-mediated T-DNA delivery occurred across plant taxa, including monocots opening up the range of crops that could be transformed by this method. A historical account of the development to these technologies is useful because it demonstrates how technology development progresses in a highly competitive area of science involving both stepwise incremental improvements and paradigm shifting breakthroughs and the interdependence of codeveloping the transformation framework. In this section, the interdependency is most strongly evident between the DNA delivery method and the cell culture potential of the target species. For historical context, the main conventional wisdom that drove DNA delivery technology option selection during the early 1980s was that *Agrobacterium*-mediated T-DNA delivery was unlikely to work well for transformation of monocot species. Thus, researchers interested in genetic manipulations of these species mostly focused on direct DNA delivery methods in the early years of plant transformation research.

Direct DNA delivery strategies were developed that either removed the cell wall to form protoplasts followed by delivering DNA across the plasma membrane or simply penetrated the cell wall to deliver DNA. Before cell wall penetrating methods were developed in the mid-1980s, translating methods from other systems was the most logical approach. Because protoplasts are structurally similar to mammalian cells, direct DNA delivery into protoplasts was intensely researched employing chemical methods, lipofection, microinjection, or electroporation for DNA uptake, resulting in high rates of transformation in some model systems (Paszkowski *et al.*, 1984; Shillito *et al.*, 1985). These demonstrations of protoplast transformation, in turn, spurred research to develop protoplast culture methods for crop species, especially the monocot crops, because at that time it appeared to be the only avenue for transforming these crops, i.e., methods for cell wall penetration had not been developed. Translation of some of these methods, such as microinjection and electroporation to whole cells, was successful, but these methods were not widely adopted. These early efforts with protoplast transformation were widely applied to plant species amenable to protoplast culture primarily in the Solanacea family. In retrospect, it is surprising that these methods did not produce the first transgenic plants. As indicated, regeneration of plants from tobacco protoplasts was first reported in 1971, providing substantial lead time for the development of DNA delivery methods and selection systems. The first plants produced via direct DNA delivery were reported by Paszkowski *et al.* (1984) and fueled an intense focus on protoplast culture research. As it turned out the extension of these methods to both dicot and monocot species, including corn, was only partially successful and these methods were not able to be widely applied because of the technical difficulty of establishing either direct protoplast cultures or suspension cultures that could produce protoplasts to regenerate fertile plants. The factors influencing plant cell and tissue culture success described in the Section Plant Cell Totipotency – The Regeneration of Whole Plants from Cells were not able to be overcome for these crops to enable development of protoplast-based transformation systems. As in the development of most technologies, the DNA delivery paradigm shifted rapidly with the invention of a cell wall-penetrating method of DNA delivery into plant cells causing most plant transformation researchers to prioritize this method over protoplast-based transformation methods.

As the axiom states "necessity is the mother of innovation" and based on the difficulties with developing regenerable protoplast cultures from the major crops along with the contemporaneous development of excellent cell and tissue culture regeneration for these crops and the still prevailing belief that *Agrobacterium*-mediated T-DNA delivery was not enabled in the monocots, the need to deliver DNA across the cell wall became increasingly clear, stimulating the conception of the simple strategy of 'shooting the DNA into the cell' by John Sanford and colleagues (Klein *et al.*, 1987). Referred to as the 'gene gun,' 'biolistics,' and 'microprojectile bombardment,' this retrospectively elegant innovation of accelerating dense gold or tungsten microparticles coated with DNA so that they penetrate the cell wall to deliver the DNA and the demonstration that the delivered DNA could be expressed by the recipient cells changed the focus of the transformation community from protoplasts as target cells for transformation to plant cells in culture and in intact explants dramatically expanding the options for developing transformation systems in a range of species. This first demonstration of DNA delivery via cell wall penetration initially using a gunpowder charge (Klein *et al.*, 1987) and later pressurized helium (Lowe *et al.*, 2009) along with an apparently simultaneous invention using electrical discharge (Lowe *et al.*, 2009) as the motive forces, followed by the development of the particle inflow technology (Finer *et al.*, 1992), stimulated researchers to apply this technology to transform plants. Within only a year of the publication describing DNA delivery into cells, the first demonstration of transformed model plants was published (Klein *et al.*, 1988a,b). Very soon thereafter were published the first reports of transformed corn and soybeans (Fromm *et al.*, 1990; Gordon-Kamm *et al.*, 1990; Walters *et al.*, 1992; McCabe *et al.*, 1988). To date, microprojectile bombardment remains the predominant direct DNA delivery method, even in light of somewhat simpler methods involving delivering DNA across the plant cell wall using nanoparticles and materials, such as silicon carbide fibers that penetrate the cell wall (Kaeppler *et al.*, 1990; Frame *et al.*, 1994). Surely, continued innovation in developing methods for direct DNA delivery will lead to new and even simpler procedures.

Direct DNA delivery transfers DNA into cells in any form, such as large chromosomal fragments, whole plasmids, or specific sequences either as a single- or double-stranded DNA molecules providing experimental flexibility in preparing the DNA to be introduced. However, because integration of the

delivered DNA into the genome occurs via double-strand break repair mechanisms and the process of DNA delivery can result in DNA breakage, resultant transgenes have been shown to occur randomly integrated throughout the genome, often in multiple copies, truncated, and rearranged, and to contain unwanted but introduced sequences. Evidence has been reported that introducing only the intended DNA sequences via direct DNA delivery will result in a higher percentage of transgene loci that do not exhibit these rearrangements (Fu *et al.*, 2000). Nevertheless, the difficulty and cost of producing sufficient amounts of an isolated DNA sequence for microprojectile bombardment or any other direct DNA delivery system along with the increased frequencies of rearrangements of the integrated transgene that drives up the numbers of transgenic plants required for recovering a plant with the molecular quality desired for commercialization has tended to sway the transformation community away from the widespread use of direct DNA delivery method, especially for production of commercial transgenic crop plants.

T-DNA Delivery

Agrobacterium-mediated T-DNA delivery was the method used to produce the first transgenic plants in 1983 (Fraley *et al.*, 1983a,b; Framond *et al.*, 1983; Schell *et al.*, 1983) and has been further developed to be the main plant transformation method in use today across crops. *Agrobacterium tumefaciens*, the causal organism in the crown gall disease, was recognized in the 1970s as potentially useful for plant transformation because it transfers genes encoded in the T-DNA from its tumor inducing (Ti) plasmid via a type IV secretion system into plant cells to cause the disease (Chilton *et al.*, 1977). The T-DNA carrying the causal genes of crown gall disease are delineated by left and right border sequences (lb and rb in **Figure 1**) that are recognized by the cellular machinery as cleavage sites for T-DNA mobilization (Gelvin, 2000, 2003; Tzfira and Citovsky, 2006; Wang, 2006). Characterization of this system resulted in the demonstration that deletion of the crown gall genes in the T-DNA followed by replacement with transgenes within right and left T-DNA borders enabled the transfer and genomic integration of the transgenes into plant cells. Further development of this system has enabled a series of the so-called binary plasmids that can be amplified in both *Escherichia coli* and *A. tumefaciens* enabling simplified vector construction in *E. coli* followed by transfection into *A. tumefaciens* (Komori *et al.*, 2007). In short, extensive research on *A. tumefaciens* and related bacteria over the past 40 years has resulted in the development of a simple, efficient DNA delivery system for plant transformation that has shown to be useful for research and crop improvement applications in both dicotyledonous and monocotyledonous plants. The previously mentioned prevailing conventional wisdom that monocots could not be efficiently transformed using *Agrobacterium* was corrected in the early 1990s, with the transformation of first rice and then corn achieved by identifying highly virulent strains for *Agrobacterium* and further enhancing them by modifying their Ti plasmids along with using acetosyringone to induce the T-DNA delivery (Hiei *et al.*, 1994; Ishida *et al.*, 1996). A major advantage of *Agrobacterium*-mediated transformation is that T-DNA integrations exhibit less rearrangement compared with transgene DNA introduced via direct DNA delivery (Somers and Makeravitch, 2004). This is presumably because the T-DNA vectors can be assembled to contain only transgene sequences of interest bounded by the left and right T-DNA border sequences and that most frequently only the T-DNA is delivered. Thus, the bacteria are essentially purifying the DNA sequence that is delivered to the plant genome, reducing the probability of undesirable transgene rearrangements that occur in direct DNA when more than the transgene cassette is introduced via direct DNA delivery, for example, entire plasmids containing the transgene. Although there are no direct comparisons of a large population of transgene loci produced via the two DNA delivery methods in the same species using the same selectable markers, the general simplicity of the current T-DNA-based transformation systems along with the increase in the frequency of nonrearranged transgene loci thereby increasing the efficiency of producing the desired transgenic genotype has resulted in its widespread adoption across crops.

A conventional plant transformation experiment with *Agrobacterium*-mediated T-DNA delivery involves inoculating explants with a culture of *Agrobacterium* carrying a binary vector to deliver the transgene cloned into the T-DNA (Gasser and Fraley, 1992). *Agrobacterium* growth and induction of virulence are important variables and are reviewed in Gelvin (2000). *Agrobacterium* adheres to explant cell walls, and chemical signals that are either produced by the plant due to wounding or added to the inoculation and coculture media induce the T-DNA transfer to the plant cell nucleus. Following inoculation, the explants are coculture for a specific duration to allow completion of the T-DNA transfer and initiation of transformed plant cell division. Following coculture, explants are transferred to media that contain antibiotics to inhibit the growth of the *Agrobacterium*. Selective agents are also added to the media to select cells that carry the selectable marker (**Figure 1**). Despite the added complexity of controlling *Agrobacterium* inoculation and growth during plant transformation, this simple method has been adopted across crops. Numerous aspects of *Agrobacterium*-mediated plant transformation are comprehensively covered in Wang (2006).

From Transient Expression to Transgene Integration – Vector Stacking and Selectable Marker Removal

In both direct DNA delivery and *Agrobacterium*-mediated T-DNA delivery, transient expression of transgenes can be detected shortly after DNA delivery. Transient expression assays are, therefore, routinely used with the appropriate marker and reporter genes to demonstrate and monitor transgene delivery when developing a new transformation system. Usually the transient transgene expression in a recipient explant is quite high, suggesting that DNA delivery has taken place into many cells. As the treated explants progress through culturing, transient transgene expression diminishes until stable transgenic tissue sectors develop. This general observation suggests that only a relatively small proportion of recipient cells that initially received the delivered transgene integrate it into the genome, stably express the integrated transgene, and resume cell division indicating importance of selection to isolate transgenic cell lines.

Transient transgene expression assays have been used to improve DNA delivery into cells and although the correlation between transient expression and stable transformation has not been well established, there are many reports indicating that this is a useful approach. In addition, transient expression per se has proven to be a powerful research tool to investigate gene expression and to characterize plant gene expression elements. In some specialized cases, such as in the production of pharmaceutical proteins in plants, *Agrobacterium*-mediated transient systems have been scaled for industrial production because of efficiency and cost savings compared with stable transformation, indicating that very high levels of DNA delivery and transient transgene expression can be achieved using this approach.

When two transgenes are delivered on the same DNA fragment or T-DNA, most frequently both are integrated into the same locus (Schocher *et al.*, 1986; Depicker *et al.*, 1985). This observation demonstrates the vector stacking strategy of introducing multiple transgenes into an integration locus. Conversely, when two transgenes are introduced either on independent DNA fragments by direct DNA delivery or on different T-DNAs, some portions of the transgene integration loci exhibit cointegration of both transgenes in linked form, whereas other loci integrate each transgene singly into different insertions sites that can be genetically either linked or unlinked (Depicker *et al.*, 1985; De Frammond *et al.*, 1986). Thus, there is the possibility of producing a near equivalent of a vector stack by this method as well. But more importantly and more useful are plants produced with transgene integration loci that contain only a single transgene and are unlinked. This transgene loci configuration enables the segregation of one transgene from another in the progeny of the transgenic plant and is especially useful for the elimination of the selectable marker. For commercial applications, as in the production of an improved crop with a transgenic trait, the production of a transgenic plant with only the transgene of interest and not the selectable marker is desired. This reduces the number of transgenes that must be approved for commercial development and reduces complications of transgene expression due to duplication of expression elements. Thus, a common *Agrobacterium*-mediated T-DNA delivery approach to producing marker-free plants is called two T-DNA transformation, where the transgene of interest is introduced on a separate T-DNA from the selectable marker (McCormac *et al.*, 2001). Transformed (T0) plants with unlinked T-DNAs are identified and marker-free, transgene only T1 progeny are recovered.

Alternative strategies for marker removal utilize the phage recombination systems Cre-lox and Flp-frt that have been modified to function in plants (Dale and Ow, 1991; Srivastava and Ow, 2004; Srivastava *et al.*, 2011). In both cases, the recombinases, for example, Cre and Flp recognize and recombine tandem receptor sequences lox and frt, respectively, flanking the transgene sequence to be removed, such as the selectable marker, essentially looping it out. These systems are generally used as two-component systems in which the recombinase is introduced via sexual hybridization with the transgenic plant carrying the transgene flanked by the recombination target sequences. In addition to selectable marker removal, these systems have been shown to be very useful in orchestrating a range of genetic manipulations of transgene sequences and for controlling gene expression.

Selection of Transgenic Cells, Tissue, or Plants

Building on substantial progress in plant tissue culture selection of mutant cell types and regenerated plants, the path to selection of transgenic cells in plant cell and tissue culture was clear. The founding concept for using positive cellular selection in plants to recover rare genetic events, such as mutations or transgene insertions, was derived from its demonstration by scientists conducting microbial and mammalian cell experiments. It was logical that selecting among millions of cells in culture would enable selection of extremely rare transformed cells followed by inducing totipotency to recover whole plants. Because transformation can add a new trait to the recipient cell, the vast majority of selection systems employ positive selection for cells that express a gain of function. During the 1970s and early 1980s, there was a proliferation of plant tissue culture and protoplast selection work that paved the way for the development of the first selectable markers that were used in plant transformation. In some cases, selection systems already defined in microbial or mammalian cell experiments were modified for plant expression (Fraley *et al.*, 1983a,b), in other genes for resistance to specific biochemical inhibitors were identified in other organisms, and in other plant genes were isolated that conferred a selective advantage for the transgenic cells. Selective agents to which their corresponding selectable markers provide resistance to the transgenic cell in general are inhibitors of metabolic or cellular processes, including antibiotics, herbicides, allosteric inhibitors, etc. and proteins encoded by the selectable marker genes are either not inhibited by or degrade or inactivate the selective agent. Selectable markers and their selective agents have been reviewed comprehensively by Joersbo (2011) and Sundar and Sakthivel (2008). The choice of selectable marker gene and selective agent application have been observed to have major impacts on transformation efficiency in terms of the number of T0 plants produced and the proportion of putative transgenic plants that are actually transgenic versus nontrangenic events that escaped selection (escape rate).

Resistance to the selective agent whether in tissue culture or regenerated plants by itself is indicative but not regarded as definitive evidence that transformation has taken place. Nontransgenic escapes often survive selection and regenerate plants. Several reasons have been suggested for this observation, ranging from cellular transport of nutrients from resistant cells to susceptible cells allowing survival to simple tissue-specific differences to the selective agent. Because of these phenomena, additional evidence, including molecular detection of the selectable marker gene or gene product, and/or the detection of the phenotype of an additional transgene are required. Accordingly, reporter, screenable, or visible markers that are extremely useful research tools to understand molecular mechanisms, including gene expression, have also been important in developing new transformation systems. Two widely used systems that require a substrate to produce a detectable product in transgenic cells and tissues are the enzymes *E. coli* B-glucuronidase (*gusA*) (Jefferson *et al.*, 1986)

and firefly luciferase (*luc*) (Ow *et al.*, 1986). Another marker green fluorescent protein (*gfp*) (Chalfie *et al.*, 1994) fluoresces when exposed to the appropriate wavelength. Of these, *gusA* and *gfp* have played major roles in transformation system development. These reporter genes are often used to track transgenic cell lineages in cell and tissue culture selection or to provide stronger evidence of transformation through the observation of reporter gene expression, in addition to resistance to the selective agent. Using a reporter gene to select transgenic plants has also been reported with some success (Kaeppler *et al.*, 2002) but has not been widely adopted most likely because of the extra labor associated with detecting relatively rare transformation events.

Transgenic plants have also been produced by simply conducting molecular screening of regenerated plants without any selection. Theoretically most useful when transformation frequencies are very high, this was first demonstrated by Shillito *et al.* (1985) when transgenic tissue cultures recovered from direct DNA delivery into protoplasts were detected by PCR analysis at a remarkably high frequency of 2% of cultures screened. Although demonstrated in other systems, the cost, time, and labor needed to sample and assay large numbers of plants have deterred wider adoption of this approach. For example, to identify transgenic plants, Shillito *et al.* (1985) required a 50-fold increase in molecular assays compared with employing a tight selection system to recover a 2% transformation frequency. However, future advances in molecular assays could reduce the cost of this differential, making this approach feasible.

Technical Limitations, Potential Solutions, and Future Transgenic Technology Directions

The ideal transformation system for crop improvement should be (1) rapid, simple, and inexpensive; (2) genotype flexible; and (3) efficient in that a high proportion of the transgenic plants produced are useable for commercial production, i.e., stably express the transgene(s) and have an intact single insertion of transgene cassette sequences. From the preceding discussion it is clear that some crop and model plant transformation systems are very efficient; however, none fully meet the criteria for an ideal system. Nevertheless, the impressive pace of transformation system development over the last 30 years combined with the large positive economic impact realized through the use of transgenic crops will continue to push crop transformation systems toward these ideals.

To become more rapid, simple, and inexpensive, a transformation system probably should be either automated to reduce labor or not be based on laborious tissue culture steps that must be conducted by specialists or require axenic culture conditions. As mentioned, only the model *Arabidopsis* is routinely transformed without a tissue culture step and that only a few progeny of the treated plant are transgenic and those selected are hemizygous for the transgene. Nevertheless, this is an extremely rapid process that requires only specialized *Agrobacterium* treatment capacity and controlled plant growth conditions that combined with the rapid growth characteristics of *Arabidopsis* with its short seed-to-seed life cycle and prolific seed production add up to an extremely efficient transformation system as seen in the production of libraries comprised of more than 100 000 T-DNA insertion events for gene function studies. However, nontissue culture-based transformation methods like floral dip or even seed transformation, if they became routine, may save labor and eliminate the need for specialized axenic propagation facilities but may not actually be as rapid as the extant systems when viewed from the genetic manipulation perspective. If, for example, soy could be transformed by the floral dip method like *Arabidopsis*, a transgenic homozygote would be recovered in the T2 progeny, whereas when soy is transformed using the cotyledonary node method, homozygotes are recovered in the T1 progeny produced by the T0 plant regenerated from tissue culture. Thus, the in planta method will most likely add another generation to produce transgenic homozygotes, even though the transformation treatment itself is apparently faster and simpler than the tissue culture methods. There is significant research activity in developing whole plant transformation systems, but all will more likely add another generation to the production of homozygous transgenic plants because of the intrinsic multicellular structure of the germline progenitor that has already been formed in the seed. Even if DNA delivery were so efficient that the majority of cells giving rise to the germline were stably transformed, they would be comprised of different transgenic insertions and the production of homozygous transgenic progeny would still occur in the T2 generation. Nevertheless, there is no doubt that advances in transformation technologies will result in faster and cheaper methods for transforming plants. Three areas emerge from the literature as likely directions. Specifically, tissue culture-based plant transformation systems will continue to be simplified, shortened, automated, increasing throughput and reducing costs. A good example of a simplified system has been developed for some legumes, including soy, in which cells in the apical meristems in germinated seed are targeted for DNA delivery followed by cell selection and plant regeneration. The transgenic cells under selection apparently form a transgenic apical meristem giving rise to a uniformly hemizygous transgenic T0 shoot that is later rooted. Explant isolation in this system has been automated dramatically increasing system throughput and reducing manual labor. In another approach, continued research into targeting seed and gametes or their progenitor cells may result in a breakthrough enabling its routine use in crop plants. Finally, dramatic improvements in site-directed transgene integration could enable integration into the same genomic DNA sequence in all transformed cells, including those in the multicellular germline such that male and female gametes had the same integrated locus producing a T1 homozygote. As mentioned, this site-directed DNA approach could be applied in a tissue culture system and result in the production of homozygous T0 plant, provided that the directed integration system was efficient enough to cause insertion into both homologs resulting in a homozygous transgenic cell rather than a hemizygote.

Genotype flexibility of crop transformation is desirable because it impacts the rate of development of and genotypic diversity of transgenic crop varieties. Conventional transgenic crop improvement begins with the identification of a transgenic plant that efficaciously expresses the transgenic trait and that has a simple, ideally intact, unrearranged transgene locus

inserted precisely into the genome in an acceptable region that does not impact adjacent endogenous genes. Following identification of a commercial quality insertion, the transgene locus is introgressed into breeding lines for variety development. The genetic relationship of the germplasm used to produce the transformed plant to the elite breeding lines is important for two reasons. First, the less related the two lines are, the more the cycles of backcrossing are required to transfer the transgene and recover the elite parent genotype. Second, the predictive value of transgenic trait efficacy in the transformation germplasm for its performance in the elite germplasm may be reduced. Thus, being able to transform any genotype of a crop or at least the most recent germplasm in a crop improvement program would be ideal because it could accelerate variety development from the transgenic line. In many crops, because of the time required to identify transformable genotypes and to optimize the efficiency of their transformation systems, the genotypes used for transformation have little relationship to the leading germplasm of the breeding program. Of course, the breadth of germplasm diversity within a crop around the globe makes this even more challenging. Thus, over the years there have been several efforts to develop transformation systems for crop plants that are more genotype flexible. Genotype effects on transformation potential are exerted on at least two different steps in the conventional framework, tissue culture regeneration, and DNA delivery. Tissue culture response can be further defined by responses to each stage of culture induction, for example, callus response and plant regeneration therefrom. The factors that effect tissue culture response have been discussed in the Section Plant Cell Totipotency – The Regeneration of Whole Plants from Cells. The effect of these factors varies with species, explant for culture initiation, culture type, and plant regeneration path, for example, somatic embryogenesis versus organogenesis. There has been some work to identify genes controlling the genotype responsiveness in maize and reports of intentionally breeding lines for culture response, but for the most part screening germplasm for its culture response is the main avenue to identifying transformable genotypes. An alternate approach is to develop tissue cultures from explants or with culture types that are less affected by genotype, as in the example using meristem explants for soy as described by Ye *et al.* (2008). It seems that advances along this path and a breakthrough in planta transformation are most likely to break the genotype barrier to transformation. The other genotype effect is in response to the DNA delivery treatment. This effect can be subdivided into at least two main categories – wounding responses and resistance to *Agrobacterium* infection. The response of cells and tissues treated for DNA delivery to wounding during DNA delivery or contact by *Agrobacterium* during inoculation and coculture can adversely affect culture response. Germplasm screening and genetic selection approaches can be applied to identifying responsive genotypes, but great progress has been reported on identifying factors to alleviate these effects, especially in *Agrobacterium*-mediated DNA delivery.

The third strategy to developing the ideal transformation system is to increase the proportion of transgenic plants produced from a single construct that could be advanced to commercial production. This can be achieved by improving the molecular quality of transgene integration loci and selecting transgene locus locations that increase the probability of recovering trait efficacy and stable expression over generations by dovetailing with the breeding strategy to combine transgenic and native traits for that crop. There are a few published examples that document the proportion of R0 events initially produced which meet all quality standards necessary for commercialization, but it usually is in the range of 1% or less. For example, in *Agrobacterium* transformation of soybean only ~20% of plants produced using standard procedures exhibit single copies of the transgene without any other sequences from *Agrobacterium* (Ye *et al.*, 2008). Of these, some portion would be expected to meet the transgene expression level for trait efficacy and stably express the transgene because of previously mentioned genomic position effects on the transgene locus. Then of these, some smaller portion would be in a desired genomic location and do not disrupt an endogenous gene. Ultimately, to produce plants meeting commercial requirements, the majority of transgenic plants initially produced are of no use. Examples in the literature show that molecular strategies can improve the frequency of single-copy transgene loci, but these methods only partly improve the frequency of useful plants, because they have no impact on the genomic location of transgene integration and thereby position effects on transgene expression. Instead, multiple transgenic plants are produced from the same transgene construct and must be evaluated to identify the plants with the desired molecular structure of the transgene locus and appropriate transgene efficacy and expression patterns that meets commercial product performance specifications and that will be introgressed into the breeding germplasm for eventual production as a commercial variety with a transgenic trait. Directing integration of transgenes into specific genomic sequence locations remains the most promising approach to produce quality transgene locus structures in a desired genomic location. As discussed previously in the Section Genetic Manipulations Using Stable Transformation, methods to accomplish this are currently undergoing rapid development and are approaching useful frequencies for applications of site-directed integration. By definition, directly integrating a specified transgene locus into a sequence-specified genomic insertion target, whether by homologous recombination or some manipulation of double-strand break repair, ensures that a single-copy transgene integration locus will be created at the targeted genomic sequence location, reducing the attrition of events due to the random transgene integration that takes place in all extant transformation systems. Theoretically, all plants recovered from directed integration of a transformation cassette will be identical at the level of the transgene locus structure and location eliminating position effects as a source of variation in transgene expression. In addition, some frequency of the T0 transgenic plants may be homozygous for the transgene providing a further advantage of time savings. Thus, fewer transformed plants may need to be produced per transformation cassette to validate transgene efficacy and all plants could meet the commercial quality criteria at the molecular level dramatically increasing the efficiency of transgenic crop improvement.

Future progress along these three paths toward the ideal transformation system is interesting to consider. First, it seems more likely that site-directed integration once developed as a

routine method will be enabled in all plant species, because site-directed integration either overrides or recruits cellular processes common to all higher eukaryotes. In addition, from a historical perspective, DNA delivery appears to be the most genotype-neutral component of extant transformation systems. This seems already to be the case based on recent literature on site-directed integration and it will be interesting to see if this speculation is borne out over the next few years. The effect of genotype on the totipotent explant and plant regeneration route appears to be the major constraint. However, as the understanding of the molecular and genomic basis of plant development continues to grow, it seems more likely that avenues for overriding the genotype effect on cell and tissue culture may become apparent. Furthermore, in keeping with the disruptive 30-year history of plant transformation research, a breakthrough will occur in whole plant- or seed-based transformation that will drive a paradigm shift away from cell and tissue culture-based transformation systems, obviating the challenges they present.

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Tree Fruits and Nuts

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Glossary

Coefficient of variation (CV) A normalized measure of variation in a dataset. Calculated as the ratio of the standard deviation to the mean.

Handler A business which receives nut crops after harvest, processes them for sale, and packages them for distribution in the retail food industry. Processing typically involves removing hulls, drying nuts, and fumigation to control pests.

Packing house A business which receives fruit after harvest, sorts fruit by size and quality, washes fruit, and packages fruit in crates or flats for distribution within the retail food industry.

Postharvest shelf life The period of time after harvest during which consumption is considered acceptable.

Standard deviation (SD) A measure of variation from the average value of a dataset. Calculated as the square root of the variance of a dataset.

Introduction

California is a center of agricultural production in the US. In 2012, the US produced approximately US$225 billion in agricultural crops, with almost 12% of total domestic production centered in California (all crops except for horticulture, NASS, 2012). Today California tree fruit and nut agriculture is a substantial component of the state's economy. In 2012, California tree fruit and nut production totaled almost US$17 billion (NASS, 2012). California is the primary producer of some of the largest specialty crops produced in the US. For example, almost all domestic almond, olive, pistachio, plum, prune, nectarine, processing peach, apricot, and English walnut are produced in California (NASS, 2012). Additionally, more than one-third of domestic sweet cherry and fresh market peach are grown in California (NASS, 2012).

California agriculture has not always been dominated by tree fruit and nut production. Over the past 30 years agriculture in California has shifted from field crops and livestock to a diverse array of specialty crops. Field crop and livestock production declined from 56% of agricultural sales in 1970 to 20% in 2000. In contrast, fruit and nut tree crops expanded dramatically during the same time period to 28% of agricultural production in 2000 (Johnston and McCalla, 2004).

In this article, the authors explore recent shifts in California industries that have had substantial impacts on farmers and production of tree fruit and nuts. Specifically, the authors highlight the importance of two factors: (1) long-term trends in crop prices and (2) changes in the handler, processor, and food retail industries in determining farm profit margins and competition among farmers. Changes in food industries are important determinants of the availability of research, marketing, opportunities for small farms, and changes in orchard management practices. The authors contend that shifts in California tree fruit and nut production differ between crops produced for fresh market consumption and crops produced for processing or commodity markets. As the largest producer of tree fruit and nut crops in the US, California constitutes a substantial portion of the worldwide market. The effects of fluctuations in crop prices, market demand, and changes in food retail industry on tree fruit and nut agriculture in California are likely to serve as a predictor of patterns that are emerging in other tree fruit and nut growing regions around the world, especially those that operate in free market economies or where there is consolidation of marketing channels. Finally, the authors review what is currently known about potential impacts of climate change on California tree fruit and nut agriculture.

Fresh and Commodity Market Tree Crops in California: Definitions and General Trends

The primary fruit and nut tree crops grown in California can be classified according to the market where they are sold. Tree fruit crops are produced for a wide range of applications including fresh market consumption and processed foods (canning, juice, frozen, and dried products). The stringency of fruit quality standards and postharvest storage life differ substantially between fresh and processing markets. Growers producing tree crops for fresh and processing markets use specialized farming and harvest operations tailored to the requirements of each market. Ninety-three percent of fruit and nut growers in California specialize either in fresh market or processing production because of different quality standards and orchard management practices (Lee and Blank, 2004).

Definition of Fresh Market and Commodity Market Crops

The authors define commodity crops as crops with a long (greater than 6 months) postharvest storage life and crops produced primarily for processing applications. The most common commodity tree crops grown in California are almond, pistachio, walnut, prune, olive, and cling peach. All nut crops, regardless of their end use, are classified as commodity crops because they have long storage lives and are almost all processed (hulled and shelled) before sale. Although a small percentage of prunes are sold for fresh consumption as 'sugar plums' (2–3%, Day and Buchner, 2012), the majority of prunes are dried immediately after harvest and have long storage lives (Thompson and Johnson, 2012). All olives produced in California are used in processed food applications. Forty-nine percent of olive production is used in canning and

46% is crushed for oil (NASS, 2012). All California clingstone peaches are produced for canning and processed food applications (NASS, 2012).

The authors define fresh market crops as crops with at least 70% of the annual production sold for fresh consumption with short (less than 6 months) storage life postharvest. The most common fresh market fruit tree crops grown in California are cherry, kiwifruit, nectarine, freestone peach, pear (except Bartlett), and plum. Although some fresh market fruit crops are used in processing, these industries are dominated by fresh market sales in California. Between 70% and 100% of production (tons) is sold for fresh consumption (Figure 1; NASS, 2012). For example, only 27% of freestone peaches produced in California are sold for drying, freezing, or other processed food applications (NASS, 2012).

Several fruit tree crops grown in California do not fit well into commodity or fresh market categories and merit separate discussion. Apple, apricot, and Bartlett pear grown in California are sold in both fresh market and processing applications, although many aspects of orchard management and production more closely resemble the other 'fresh market' crops. Only 46% of California apple production is sold to fresh market, with the rest sold to processing applications including juice, canning, and other processed foods (NASS, 2012). Similarly, 60% of apricot production is sold to fresh market and 40% is sold for drying, canning, or other processed food applications (NASS, 2012). Approximately 77% of California Bartlett pear production is sold for processed food applications, with only 33% of production sold to fresh market (NASS, 2012). These three crops will be discussed separately and used as a test case to compare and contrast the relative importance of different market pressures in driving tree fruit and nut production trends.

Long-Term Trends in Fresh Market and Commodity Crop Production and Markets

Commodity crop production currently dominates California tree fruit and nut agriculture (Figure 1). Seventy-three percent of the total tree fruits and nuts grown in California can be classified as 'commodity crops,' whereas only 27% are sold to fresh markets (Figure 1). Nut crops comprise 77% of the commodity crop production in California (NASS, 2012). The California fruit and nut tree crop industries have not always been as strongly skewed toward commodity crops. Over the past 30 years commercial nut production has increased dramatically, whereas fresh market fruit production has declined. Between 1982 and 2012 approximately 354 000 additional acres of almond were planted for a statewide total of 790 000 acres in 2012. In that same time period 64 000 new

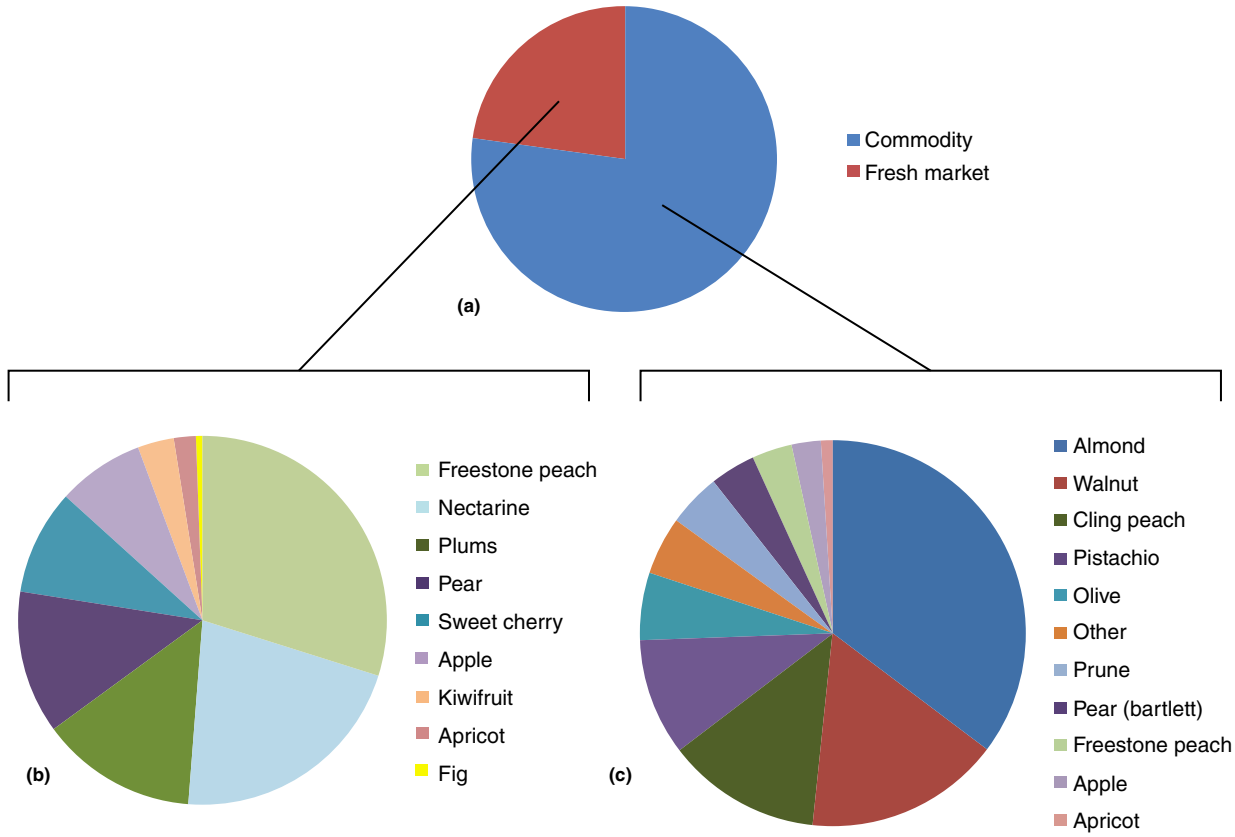


Figure 1 Total California fruit and nut tree crop production for fresh markets (838 060 tons) and commodity (2 842 500 tons) markets in 2012 (a). The distribution of fresh market (b) and commodity (c) production in tons for each major fruit and nut tree crop in 2012. Fresh market tree crop production was dominated by peach, nectarine, and plum in California. Almond, walnut, cling peach, and pistachio made up almost two-thirds of commodity crop production in 2012. Raw data on California fruit and nut production obtained from the National Agricultural Statistics Service (NASS), 2012. USDA National Agricultural Statistics Service Survey and Census Data Query Tool. Available at: http://quickstats.nass.usda.gov/ (accessed 16.04.13).

acres of walnut were planted for a statewide total of 264 000. Pistachio acreage also increased from 34 726 to 178 000 (NASS, 2012). In contrast, the number of acres devoted to peach production dropped by 36%, from 74 000 in 1982 to 47 000 in 2012. Approximately 65% of current California peach production is sold to food processing applications (NASS, 2012).

Long-term shifts in fresh market and commodity crop acreage align with long-term trends in crop value (price per pound). **Table 1** displays the 13-year average (1999–2012) price per pound and standard deviation in price per pound for nut crops (almond, walnut, and pistachio), fresh market crops (plum, freestone peach, and nectarine), and crops sold to both fresh and processing markets (apricot, Bartlett pear, and apple). These data reveal several trends in long-term mean prices for each crop and year-to-year variability in crop value. Fresh market fruit crops have a higher long-term average price per pound than fruit commodity crops. Additionally, fresh market crop prices have standard deviations that are two times greater than fruit crops produced for processing. Year-to-year variability in crop value has important economic consequences for small farms with fewer assets and financial resources available to withstand years when crop values are low (Perez and Ali, 2009). The reduced risk associated with stable crop values in fruit commodity crops may balance out the lower average crop values for small growers.

Increases in nut crop production over the past 30 years in California may be fueled by high average crop values. Nut crop prices have substantially higher long-term averages and standard deviations in crop value than fresh market and commodity fruit crops (**Table 1**). Higher average values result in greater profitability for individual growers, enabling small and medium-sized farms to withstand year-to-year variation in prices. Economic analyses demonstrate that a grower's decision to plant one crop over another in California is dominated by long-term average price per ton, not necessarily variation in value year-to-year or short-term drops or increases in price (McClarty *et al.*, 2007).

Table 1 Summary statistics for California fruit and nut production. The average price per pound and standard deviation were calculated from annual data available from 1997 to 2012. Apricot, Bartlett pear, and apple statistics are shown separately for sales to fresh market and processing markets. All cling peach and prune production was sold to processing markets

Crop	*Average ($ lb^{-1})*	*Standard deviation ($ lb^{-1})*
Fresh market crops		
Plum	0.24	0.06
Freestone peach	0.20	0.04
Nectarine	0.24	0.06
Apricot	0.38	0.16
Pear (exclusive Bartlett)	0.18	0.06
Apple	0.33	0.09
Average	0.26	0.08
Commodity crops		
Almond	1.64	0.54
Pistachio	1.59	0.44
Walnut	0.76	0.27
Average	1.33	0.42
Prune	0.25	0.10
Apricot	0.15	0.03
Bartlett pear	0.14	0.02
Apple	0.09	0.02
Cling peach	0.15	0.02
Average	0.16	0.04

Source: Raw data on California fruit and nut production obtained from the National Agricultural Statistics Service (NASS), 2012. USDA National Agricultural Statistics Service Survey and Census Data Query Tool. Available at: http://quickstats.nass.usda.gov/ (accessed 16.04.13).

Handling and Marketing of Fresh Market and Commodity Crops

After harvest almost all fruit and nut crops grown in California are sold to a packing house or handler who sorts the crop according to quality standards, markets the crop, and packages it to be sold (Lee and Blank, 2004). Packers and handlers typically sell directly to food retailers or to the food processing industry. Fruit crops that are sold fresh to retailers, and ultimately the consumer, are discussed here as fresh market crops. All nuts and fruit crops sold for processing are discussed here as commodity crops.

During the past 30 years tree crop production shifted from fresh market fruit to commodity crops. At the same time, the retail food industry consolidated into fewer large domestic and international companies (Johnston and McCalla, 2004; Richards and Patterson, 2003). The number and size of packing houses in California available to purchase and sort fresh market produce declined sharply from 278 in 1999 to 143 in 2009 (Linden, 2009). In contrast, the number of packers and processors available for nut crops in California increased. There are 178 unique almond and walnut handlers listed by the California Walnut Board and the Almond Board of California in 2013. The number of packing houses and handlers in each industry determines the number of entities available to purchase crops, the strength of competition among growers, and the importance of external marketing boards in domestic and international marketing.

Marketing and Sales Options for Fresh Market Fruit Crops

There are two primary avenues available to sell and market California fresh market fruit crops. Growers sell produce directly to consumers at local farmers' markets or fruit packing warehouses. Farmers' market sales typically result in a higher profit because produce is sold and marketed by the grower without additional overhead costs (Lee and Blank, 2004). However, the volume of produce sold at farmers' markets is limited and they are generally more appropriate for small farms or specialized crops. Approximately 32% of fresh market pome fruit (apple and pear) and 10% of fresh market stone fruit are sold directly to consumers in California (Lee and Blank, 2004). Outside local farmers' markets the majority of fresh fruit sales are brokered by large packing houses that work directly with domestic and international food retail chains. Forty-two percent of fresh market apple and pear production and 68% of fresh market stone fruit production are sold to independent shippers and brokers (Lee and Blank, 2004).

The majority of fresh market fruit sales in California are controlled by a shrinking number of large packing houses. The number and diversity of destinations to which fresh market crops are sold is also declining, resulting in increased competition among packers for limited access to domestic and international markets. Before the recent consolidation of packing houses, fresh market crop growers had a greater diversity of destinations for their crop and avenues of marketing to consumers and reduced direct competition among growers.

There is substantial competition among fresh market fruit growers and packers in the timing of fruit production due to the limited storage life of fresh market crops, the short season in which they are sold, and the need to harvest and sell fruit to packing houses at a time when they are not overwhelmed with fruit from other growers. For example, fresh market crop growers receive a significant price premium for early season fruit. In 2011, the average price of peaches at the beginning of the season was US$0.65 per pound (May). The price dropped sharply to approximately US$0.32 per pound throughout the rest of the season (ERS, 2011). However, yields of early season fruit cultivars are significantly lower and production costs are higher than later season cultivars. Differences in price do not necessarily reflect profit. It is very difficult to predict the long-term profitability of any cultivar a grower chooses to grow.

Marketing and Sales of Commodity Fruit and Nut Crops

The landscape of commodity crop marketing and sales differs in a few important ways from fresh market crops. The long shelf life of commodity crops facilitates international shipping and sales, resulting in lower competition among individual growers and reduced fluctuation in prices from year-to-year. The most common nut crops grown in California are regularly stored by processors and handlers for up to 1 year postharvest, substantially longer than fresh fruit crops. Fruit commodity crops used in processing have less strict grading and quality standards than fresh market fruit crops and can be stored longer than 6 months after processing. A long storage life ameliorates the need to time sales seasonally and stabilizes fluctuations in prices year-to-year. On average, processed fruit prices are substantially less variable across years than fresh market fruit prices in California. The long-term standard deviation in price per pound of fresh market crops is more than double the standard deviation in price per pound of fruit commodity crops (standard deviation in $/pound, **Table 1**).

Marketing boards are financed by grower or handler fee assessments and serve an important role in marketing specific crops to domestic and international consumers. The primary responsibility of marketing boards is to improve the visibility of a crop and increase consumer demand. In addition to grower and/or handler fee assessments, marketing boards receive funding from the US Department of Agriculture (USDA) Market Access Program to organize and finance promotional activities for US agricultural products. Increased worldwide demand and advertising campaigns funded by marketing boards and the USDA have reduced competition among individual commodity crop growers and handlers for sales to large domestic and/or international retail chains.

The destination of commodity crops grown in California varies among nuts, pome fruit, and stone fruit. The majority of nuts produced for processing applications are sold to marketing cooperatives (51%), with a smaller proportion sold to processors under contract without a predetermined price (33%, Lee and Blank, 2004). In contrast, commodity fruit crops are sold primarily to processors under contract (60% pome fruit and 58% stone fruit), with fewer sales to marketing cooperatives (13% pome fruit and 38% stone fruit, Lee and Blank, 2004).

Opportunities for Small Farms

Untied States agriculture is dominated by small farms. The most recent US agricultural census, in 2007, demonstrated that the majority of tree fruit and nut farms nationwide are small with less than 50 acres and US$40 000 in production value. In 2007, small tree crop farms also dominated the California fruit and nut tree industry. Seventy-four percent of the total fruit and nut tree operations spanned 0.1–50 acres. Of the remaining operations 24% spanned 50–500 acres, and only 2% spanned more than 500 acres (NASS, 2012).

Nationwide, larger farms have generated a greater proportion of total fruit and nut production than small farms. For example, between 2004 and 2006 only 5% of fruit and nut farms in the US were classified as large, but they produced 58% of sales. In that same time period small fruit and nut farms only contributed approximately 5% of total US sales (Perez and Ali, 2009). Although the majority of fruit and nut tree farms in California today are small, the number of small farms has declined steadily from 1998 to 2006. In contrast, the number of medium and large farms increased in the same time period, indicating that the fruit and nut tree industry is in the process of consolidation into larger entities (Perez and Ali, 2009). A close look at changes in the number of fruit and nut farms by size illustrates different trends between commodity and fresh market crop growers from 2002 to 2007. On average the number of small fresh market growers decreased, a pattern consistent with national trends, whereas the number of small commodity crop growers remained constant or increased (**Table 2**).

Trends in California Fruit and Nut Farm Size

Ninety percent of farms (across all crops) in the US are small, and the number of small farms is declining nationwide in favor of fewer large farms (Hoppe *et al.*, 2010; Perez and Ali, 2009). A closer look at the California tree fruit and nut industry distribution by farm size reveals distinct trends in fresh market crops, fruit commodity crops, and nut commodity crops (**Table 2**). Between 2002 and 2007 the number of individual fresh market fruit farms decreased in all categories but one. The only farm size category that increased over this time period was fresh market farms with over 500 acres. A decline in the number of fresh market fruit growers in all but the largest size category is consistent with observed long-term trends in crop value (**Table 1**) that reduce the profitability of fresh market farming in all but the largest, and most efficient, operations. In contrast, the number of very small farms growing fruit and nut commodity crops increased over the same time period, demonstrating the economic viability of

Table 2 Comparisons of the percent change in number of operators by farm size from 2002 to 2007

Crop	*> 500 acres (%)*	*100–500 acres (%)*	*50–100 acres (%)*	*5–50 acres (%)*	*0.1–5 acres (%)*
Fresh market crops					
Freestone peach	83.3	−15.1	−47.5	−35.1	5.8
Pears (exclusive Bartlett)	0.0	0.0	18.2	−41.5	−4.7
Plum	0.0	−34.1	−25.4	−30.7	−23.3
Sweet cherry	200.0	31.5	−4.9	−7.5	−2.4
Fresh market average	70.8	−4.4	−14.9	−28.7	−6.2
Commodity crops					
Bartlett pear	200.0	−40.0	−31.8	−40.6	−6.5
Cling peach	0.0	−47.9	−30.8	−36.3	81.0
Prune	−8.7	246.0	−38.4	−28.9	−32.9
Fruit commodity average	63.8	52.7	−33.7	−35.3	13.8
Almond	17.4	−1.4	−4.5	2.2	4.3
Pistachio	40.0	33.1	13.5	−6.1	17.8
Walnut	0	−6	−18	−11	−4
Nut commodity average	19.1	8.6	−2.9	−5.1	6.1

Source: Raw data on California fruit and nut production obtained from the National Agricultural Statistics Service (NASS), 2012. USDA National Agricultural Statistics Service Survey and Census Data Query Tool. Available at: http://quickstats.nass.usda.gov/ (accessed 16.04.13).

small commodity crop farms. This distinct trend in commodity crop grower numbers by farm size is consistent with the stable crop values in fruit commodity crops and substantially higher average value of nut crops.

Small Farm Profit Margins

There are several important differences in the economics of small and large fruit and nut tree farms that determine long-term competitiveness and sustainability. Average cash reserves, the difference between costs and income, differ substantially between small and large farms. The profitability of fruit and nut farms increases as the size of the operation increases. Large, specialized fruit and nut farms average US$72–74 in production costs per US$100 earned, whereas small farms run at a consistent deficit of US$113 spent on production costs per year for every US$100 in cash income (Perez and Ali, 2009). The differences in average profitability between small and large fruit and nut farms create significant hardships for small fresh market fruit growers over the long term. Small fresh market farmers are less likely to withstand sharp drops in crop value and increases in operational expenses (manual labor, fertilizers, and fuel) because they have fewer cash reserves available than large farms.

Sources of Risk and Opportunities for Small Farms

The number of packing houses available to purchase and market fresh fruit declined sharply from 1999 to 2009 (Linden, 2009), increasing competition between individual growers. Given the diminished average profits associated with small farms, small and medium fresh fruit farms are out-competed by larger, more efficient farms. McClarty *et al.* (2007) demonstrated that declines in acreage for fresh market stone fruit crops and increases in average farm size in California are associated with declines in long-term average crop value. This association helps explain the rapid transition from fresh market to commodity crops over the past 20 years.

Although the average price per pound for fresh market fruit is greater than fruit commodity crops, fresh market crop values fluctuate more from year-to-year (**Table 1**). Small and medium fresh market growers, with smaller cash reserves (Perez and Ali, 2009), are poorly suited to buffer against price crashes compared to larger growers with larger cash reserves (McClarty *et al.*, 2007).

Two factors can help ameliorate risk associated with small farms: income supplementation from off-farm sources and high average profit margins. In California smaller fruit and nut crop growers have a higher percentage of their total income derived 'off farm' than large farms (Lee and Blank, 2004), creating a financial buffer from price fluctuations and low profitability. The negative effect of exceptionally high variation in nut prices on small farms is ameliorated by a high average price per pound (**Table 1**). Approximately 63% of small fruit and nut tree farms in California specialize in high-value nut crops (NASS, 2012).

Availability of Research and Development Programs

Marketing boards are commonly used to organize an agricultural industry and consolidate funds for marketing, research, and development. Marketing boards are typically funded by an assessment from growers or handlers taken as a percentage of crop sales. Although growers and handlers forfeit a small portion of sales, they benefit from industry-wide consolidation of resources focused on improved marketing and research. Marketing boards use three primary methods to enhance the production and sales of a specific crop: (1) advocating for the interests of that industry to policy makers, (2) running crop-specific domestic and international marketing programs, and (3) funding independent research. California tree fruit and nut agriculture has a long history of marketing boards financed by growers and packers to promote specific fresh market and commodity crops. There are several important differences in the prevalence and longevity of fresh market and commodity crop boards that are linked to broader trends in each industry.

Commodity and fresh market crops have different histories of supporting marketing boards in California as a result of differences in the degree to which each is consolidated around large growers and handlers/packing houses. All of the major commodity crops in California (almond, cling peach, walnut, pistachio, olive, and prune) currently support marketing boards. Both pear and apple growers (crops that are split between processing and fresh markets) currently support marketing boards, although their influence is limited by insufficient funds available for research and marketing. Cherry is the only fresh market fruit crop grown in California that currently supports a marketing board with funding available for research programs. California peach, nectarine, and plum packers supported a marketing board, the California Tree Fruit Agreement (CTFA), for almost 100 years. However, in 2010 the CTFA was disbanded by members of the board. All attempts to organize an analogous apricot marketing board in the 1990s were unsuccessful. As a result, the California fresh market stone fruit industry is currently without consolidated domestic and international marketing programs and funding for research.

The lack of success in establishing and maintaining fresh market crop marketing boards is related to changes in these industries over the past 10 years. As the average farm size increases (McClarty *et al.*, 2007) and the number of small farms decreases (**Table 2**, McClarty *et al.*, 2007; Perez and Ali, 2009) there are fewer entities governing the fresh market tree fruit industry. This results in increased competition among large fresh market growers and packers with less incentive to fund widely available research and marketing programs that could give competitors an advantage in production, domestic, and international sales. Without consolidated marketing and research, fresh market crop growers must rely entirely on research conducted by increasingly large private companies and dwindling research programs in universities and the USDA.

Manual Labor Requirements, Harvest Technology, and Quality Standards

Tree fruit and nut crop production requires substantial manual labor throughout the year for pruning, pest management, fertilizer application, irrigation, and harvest (Martin and Calvin, 2011). On an average, specialized fruit and nut tree farms allocate 48% of variable cash expenses each year to pay for labor to maintain and harvest their crop. The second greatest expense for fruit and nut tree farmers is fertilizers and chemicals (15% of variable cash expenditures, Perez and Ali, 2009). As a result of increasing costs of manual labor and insurance, fruit and nut tree growers have modified many aspects of production to reduce labor requirements and increase mechanization. The extent to which fruit and nut tree growers have been able to reduce labor costs, and mechanize their operations, differs substantially between fresh market and commodity crops.

Manual Labor Requirements: Fresh Market Crops

The primary fresh market tree crops grown in California (freestone peach, nectarine, cherry, and plum) require substantial manual labor inputs throughout the year to maximize fruit quality and meet strict quality and grading standards set for fresh market produce. Fresh market fruit crop value is determined, in part, by fruit size, presence of blemishes or bruises, ripeness, and color. Each of these strict quality standards results in manual labor requirements for the typical fresh market fruit grower during fruit thinning, harvest, and pruning.

Fruit size

Fruit size is inversely related to the number of fruits on a tree. As a result, fresh market crop growers typically thin blossoms or young fruit to maximize individual fruit size. Hand flower and fruit thinning is very costly and a substantial amount of research has focused on finding a viable mechanical or chemical alternative. Research into mechanical and chemical thinning options has demonstrated the feasibility of some techniques and significant savings associated with reduced manual labor requirements (Baugher *et al.*, 2010; Glenn *et al.*, 1994; Schupp *et al.*, 2008).

Fruit blemishes, color, and ripeness

Fruit blemishes, color, and ripeness are primary determinants of fresh market crop value. Fresh market produce is fragile and requires careful handling to avoid bruising and blemishes. Additionally, the color and firmness of individual fruit must be inspected to determine whether it is at the appropriate stage of maturity for harvest. In general, the careful handling and individual fruit observation required to meet fresh market quality standards are only possible through the use of manual labor during harvest. Despite research to develop mechanical harvesting capabilities for fruit crops (Glenn *et al.*, 1995; Torregrosa *et al.*, 2006, 2008; Zhao *et al.*, 2013), there is currently no technology available that can efficiently assess the ripeness stage of individual fruit and handle fruit in a way that minimizes damage.

Pruning to enhance fruit color and canopy size control

Two important goals in fresh market fruit tree pruning are (1) maximizing light interception by fruit to enhance color (an important component of fruit quality) and (2) reducing canopy size. Fresh market fruit require some direct light exposure to achieve proper color. Manual pruning is typically conducted annually to open the canopy, improve fruit and leaf light interception, and encourage renewal of fruit-bearing wood. Manual pruning is also used to limit canopy height and minimize the need for ladders during harvest. Although mechanical pruning options are available, they do not allow fresh market growers to achieve the required level of precision in pruning for canopy shape. Canopy size can be limited by grafting varieties onto size-controlling rootstocks. University of California and USDA research programs have been successful in developing new size-controlling rootstocks for peach and nectarine that do not limit average fruit size (Tombesi *et al.*, 2010; Weibel *et al.*, 2003).

Manual Labor Requirements: Fruit Commodity Crops

Commodity fruit crop growers in California have been successful in reducing manual labor expenses as a result of several important differences between the fresh and commodity crop

markets. The quality and grading standards applied to fruit used in processing are less stringent than fresh market requirements. As a result, less attention to detail is required in fruit thinning to manipulate average fruit size. In the cling peach and prune industries this means that some growers rely on mechanical or chemical thinning. Glozer and Hasey (2006) estimated that 31% of cling peach production costs have been allocated to hand thinning. As a result, transition to mechanical and chemical thinning can result in significant savings to growers in these industries. Cling peach, apple, pear, and apricot fruit must still be picked by hand at a specific stage of maturity, and handled with care to avoid damage that would render it unusable for processing applications. Although cling peach growers have reduced their reliance on manual labor to conduct some orchard operations, they are more dependent on hand labor than nut and prune commodity crops (see Section Manual Labor Requirements: Olive, Prune, and Nut Commodity Crops). Until mechanical harvesting technology improves to the point where it can efficiently locate and pick individual fruit, the requirement for hand harvesting will impose a significant constraint on the fruit commodity crop industries in California.

Manual Labor Requirements: Olive, Prune, and Nut Commodity Crops

Olive, prune, and nut growers have been the most successful of all California tree fruit and nut growers in minimizing manual labor expenses. The ability of these industries to significantly reduce manual labor is a result of differences in basic biology and industry requirements between most tree fruit and olive, prune, and nut crops. The relationship between fruit number and size in nut and olive crops is not as strong as with other fruit crops. As a result there is no need to thin flowers or fruit, eliminating a significant expense incurred in fresh market and commodity fruit crop industries. Although prune is typically thinned to increase average fruit size, California prune growers can thin the crop mechanically using trunk-shaking machinery (Buchner *et al.*, 2012).

Prune and nut growers have also eliminated the need for manual harvesting by using mechanical trunk shakers. Mechanical shakers attach to the trunk, or a main scaffold, and use vibration to dislodge fruit. Walnuts and almonds fall to the orchard floor and are collected later by mechanical sweepers. Pistachio and prune are caught in large mechanical frames with belts to load the crop into bins for transportation. Mechanical harvesting equipment has also been developed recently for the California olive industry. Mechanical olive harvesters use a rotating 'comb' to knock fruit out of the canopy into harvesting bins (Ferguson *et al.*, 2004). However, mechanical harvesting has not been adopted by the entire olive industry and some orchards are still harvested by hand.

Mechanical harvesting by trunk shaking has two financial benefits for growers: it reduces costs associated with hand harvesting and minimizes the need to control the size of trees by pruning. Because nut and olive crops do not require direct sun exposure to achieve necessary quality standards they do not require the same level of detailed hand pruning as in stone fruit. University of California research has demonstrated that regular pruning does not significantly increase yield or quality in walnut (Lampinen *et al.*, 2009, 2012) and almond (Curtis, 2012). After initial orchard establishment and manual tree training, prune, pistachio, and olive can be pruned using machinery or by hand, allowing a grower to decide how much of their budget to allocate to manual labor in a given year (Beede and Ferguson, 2005; Kreuger *et al.*, 2012; Sibbett, 2004).

Relationship between Manual Labor Requirements and Geographic Distribution of Fresh Market and Commodity Crop Industries

The southern San Joaquin Valley is a traditional center of fruit, nut, and vegetable agriculture in California. As a result, seasonal manual labor availability is greatest in this area. The uneven distribution of manual labor pools throughout California has a substantial impact on fresh market fruit production, which relies heavily on manual labor throughout the year for fruit thinning, harvest, and pruning. Small fresh market fruit growers located outside the southern San Joaquin Valley cannot provide long-term employment for manual laborers, and are less likely to find sufficient help to maintain and harvest their orchards. Most commodity crops have reduced their reliance on manual labor and are less constrained geographically to specific regions where many seasonal manual laborers are available. Small commodity crop growers can expand throughout the state because they utilize mechanical pruning and harvesting technology. Data on the distribution of tree crop production by county in California illustrate a broad and even geographic distribution of commodity crops (**Figure 2**). In contrast, fresh market crops tend to be more concentrated in the San Joaquin Valley, the historic center of agriculture in California (**Figure 3**).

Noneconomic Impacts on Fruit and Nut Tree Industries: Climate Change

Perennial crops are long lived: each year they produce new vegetative tissues that support growth and yield in the current season and in future years. Leaf and flower tissues develop in lateral and apical buds, and then expand to produce leaves and flowers the following growing season. Because woody and vegetative tissue is carried over across years, the growth, development, and yield of an individual tree are influenced both by the environmental conditions encountered in the current year and those encountered in previous years when structural biomass and buds are produced. Most fruit and nut orchards in California are maintained for at least 20 years. Orchard management decisions (including irrigation, fertilization, and pruning) and weather patterns can have substantial impacts on current tree growth, and yield in subsequent years. Despite the potential impact of climate change on perennial tree crops in California, research focused on understanding potential sources of risk is relatively new.

Analyses of Historic Climate Data Reveal Significant Changes in Temperature and Precipitation

Analyses of historic climate data in California demonstrate a significant 1 °C increase in annual mean temperature over the

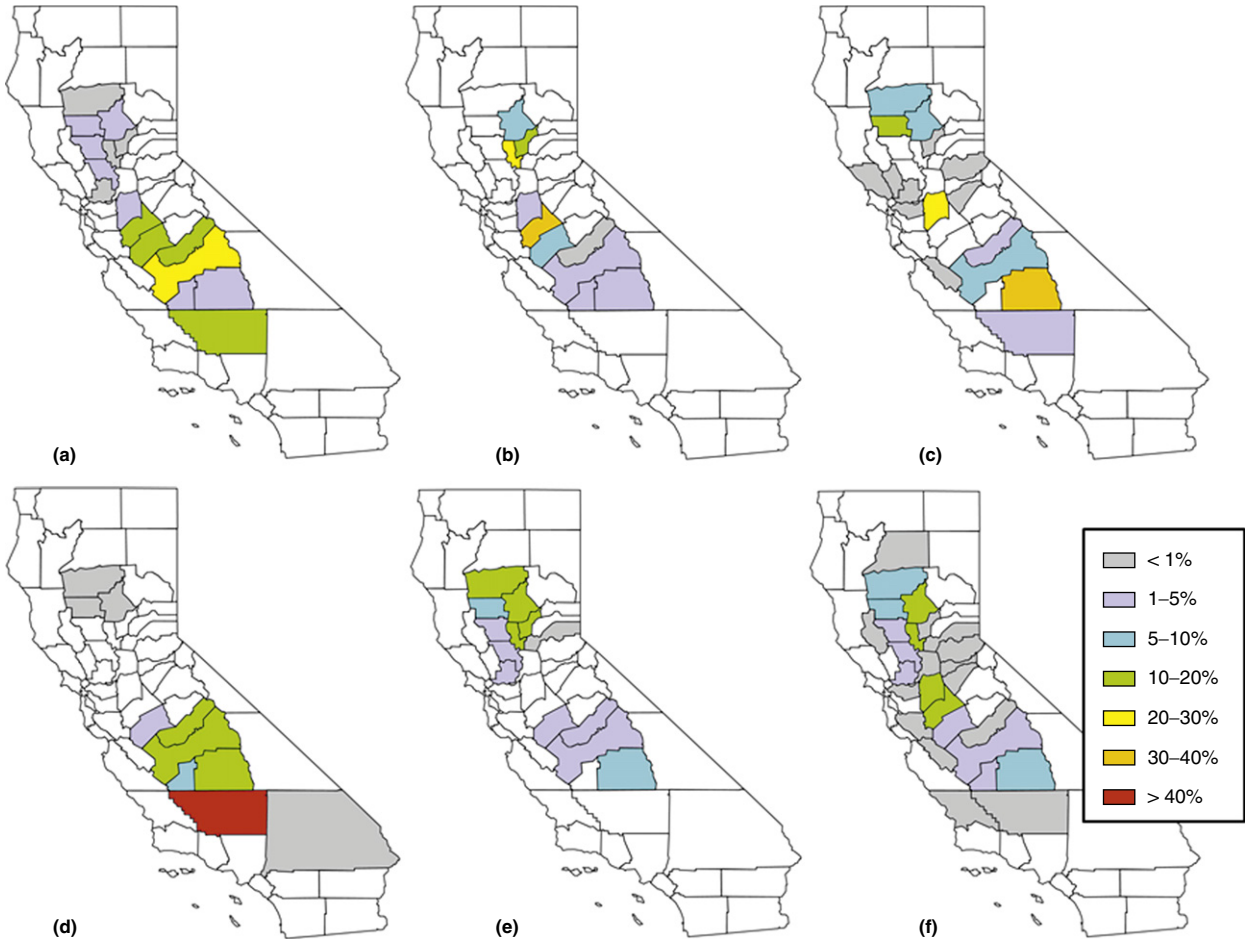


Figure 2 Geographic distribution of commodity crop production in California. Colors indicate the percentage of total statewide production reported in each county to local Agricultural Commissioners in 2011. Six major commodity tree crops are shown: almond (a), cling peach (b), olive (c), pistachio (d), prune (e), and walnut (f). Raw data were obtained from California County Agricultural Commissioners.

past 100 years. Observed long-term changes in temperature are a result of increased annual mean minimum temperatures and reduced variability in minimum temperatures (Anderson *et al.*, 2008). Between 1950 and 2000 mean and maximum daily temperatures increased in late winter and early spring. Additionally, minimum daily temperatures increased between September and January (Bonfils *et al.*, 2008). As a result of observed historic changes in temperature in California, several studies have used climate change models to anticipate future changes in temperature. Depending on the specific climate change scenario applied, average annual temperature is expected to increase between 1.5 and 4.5 °C over the next century (Cayan *et al.*, 2008).

In addition to changes in temperature the variability of precipitation (coefficient of variation) has increased significantly over the past 20 years, potentially resulting in earlier onset of snowmelt and diminished ability to store water reserves (Anderson *et al.*, 2008). Analyses of future climate change scenarios predict water availability deficits for both urban and agricultural users by 2065. Analyses using the most moderate climate change model predict severe agricultural water deficits in Southern California and the San Joaquin Basin (29% and 20% water deficits) with more moderate deficits in the Tulare Basin and Sacramento Valley (12% and 2%; Medellin-Azuara *et al.*, 2008). It is likely that California perennial crops, which use large amounts of water, will be vulnerable to prolonged water deficits predicted with climate change unless more efficient irrigation technology is developed (Jackson *et al.*, 2011).

Anticipated Effects of Climate Change on Tree Phenology and Yield in California

Changes in annual average temperature and winter minimum temperatures are likely to impact many different types of agricultural crops currently grown in California (Jackson *et al.*, 2011). Deciduous trees, including all of the major fruit and nut crops grown in California, require a period of cold over the winter to break dormancy and produce adequate yields the following year (Luedeling *et al.*, 2009). This cold requirement during dormancy is referred to as 'winter chill.' Winter chill is quantified using statistical models that count the number of hours below a threshold temperature in winter. Analyses of projected climate change scenarios using the four primary models (Utah, Dynamic, Chill Portions, and Positive Utah models) all predict decreases in winter chill over the next

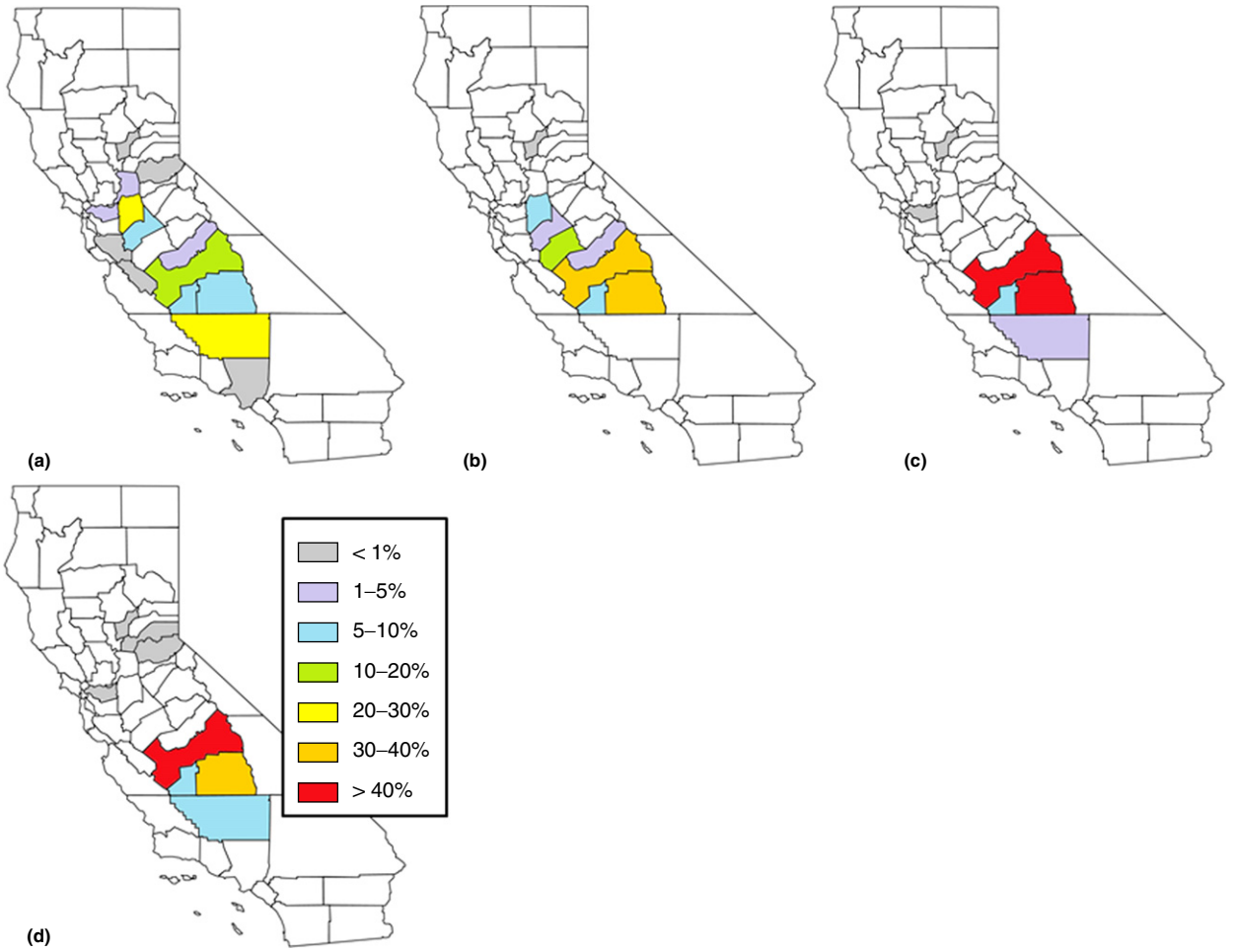


Figure 3 Geographic distribution of fresh market crop production in California. Colors indicate the percentage of total statewide production reported in each county to local Agricultural Commissioners in 2011. Four fresh market tree crops are shown: cherry (a), freestone peach (b), nectarine (c), and plum (d). Raw data were obtained from California County Agricultural Commissioners.

100 years in California, although predictions vary between models (Luedeling *et al.*, 2009). Analyses of long-term datasets demonstrate significant changes in the timing of leaf out and bloom in California walnut orchards as a result of increasing temperature (Pope *et al.*, 2013). Additional research is required to refine existing chill models to better understand specific future impacts on tree crop agriculture in California and resolve discrepancies among chill model predictions (Luedeling *et al.*, 2011). However, based on broad consensus across models, it is likely that breeding of new cultivars with low chill requirements, manipulation of orchard microclimate, and the use of rest-breaking agents will become important climate change adaptation tools for the tree crop industries in California over the next 100 years (Luedeling, 2012).

Potential Effects of Climate Change on Tree Crop Pests and Food Safety

In addition to the direct effects of climate change on tree crops (reduced winter chill and water deficits), long-term changes in precipitation and temperature could impact other organisms associated with fruit and nut tree agriculture including pests and pathogens. The distributions of agricultural pests, including annual weeds, have been shown to shift in response to changes in temperature and climate. These observations suggest that increased warming could result in shifts of southern pests into northern growing regions in California (Jackson *et al.*, 2011). Additionally, warmer winters and longer spring and summer conditions may result in reduced over-winter insect pest mortality and provide longer growing seasons for insects and more generations per year (Jackson *et al.*, 2011). The rate of illness associated with common foodborne pathogens, including *Campylobacter* and *Salmonella*, increases with average temperature worldwide (Tirado *et al.*, 2010). Because the relationship between pathogen-related illness and temperature varies among organisms and regions additional research in California is required to identify specific risks and solutions. Chemical prices have increased substantially over the past 10 years and constitute the second greatest annual expenditure for fruit and nut growers (Perez and Ali, 2009). An increase in pest damage and pathogen prevalence is likely to result in reduced yield and increased economic hardship for growers without proactive research to identify new control measures.

Parallel Trends in Tree Fruit and Nut Agricultural Regions Around the World

Many of the same factors driving shifts in tree fruit and nut agriculture in California are apparent in the other primary growing regions worldwide, including China, Chile, South Africa, Australia, and New Zealand. Production costs of both tree fruit and nut crops are rising worldwide. Increased production costs outside the US are primarily the result of rapid increases in wages for manual labor, as observed in China and Chile (Scott *et al.*, 2012, 2013). Because growers in China and Chile have not been able to mechanize operations for commodity crops to the extent that California growers have, this represents a serious threat to the industries in both regions. Production costs associated with pesticides, fertilizers, germplasm, and trellis systems can have an additional impact on growing trends. In China, a shift from peach to cherry production has been attributed to reduced pesticide and fertilizer use in cherry (Scott *et al.*, 2013). In South Africa, the average age of tree fruit acreage is increasing (25 years), with fewer new plantings, due to increased orchard establishment costs (Pickelsimer, 2013).

As in California, long-term price trends in China are an important driver of acreage and production of individual tree fruit and nut crops. For example, Chinese peach and nectarine acreage has been steadily declining as a result of decreased profit margins in favor of cherry acreage. Cherries receive a significant price premium by Chinese consumers, increasing the profitability of this industry to the extent that greenhouse cultivation is being used, despite the high overhead costs associated with establishing a greenhouse-grown orchard (Scott *et al.*, 2013). In South Africa, the price premium available for fresh market pear and apple growers has limited sales to processing industries to fruit that do not meet fresh market quality standards (Pickelsimer, 2013).

As tree fruit and nut growing regions worldwide expand their markets they are developing consolidated marketing groups to better communicate with increasingly consolidated food retail markets. In China, new government- and grower-run marketing cooperatives are being established to improve postharvest chain handling and increase competitiveness when compared to the US produce (Scott *et al.*, 2013). Growers in Australia, New Zealand, and South Africa also rely heavily on exports. Australian growers are in the process of transitioning from direct marketing between growers and retailers to a more consolidated system with strong marketing associations and grower groups (George, 1999).

One primary difference between California and other fruit and nut growing regions worldwide is the influence of local and national governments on production trends and costs. In China, the national and local governments have provided substantial subsidies to encourage walnut and almond planting in previously uncultivated or very steep terrain. It is estimated that a typical grower receives a government subsidy of $432 per acre to plant walnuts in China (Scott *et al.*, 2012). Government pressure and financial incentives to plant walnuts and almonds have dramatically increased acreage of both crops in China over the past decade. In contrast, Chilean tree fruit agriculture is currently faltering due to poor weather conditions and an almost 90% increase in labor costs over the past 10 years. This has generated a strong call for government support of this important industry, which employs almost 20% of Chilean labor.

Conclusions

The tree fruit and nut industry in California has shifted substantially over the past 30 years in response to long-term trends in crop value (**Table 1**) and consolidation in fruit packing and food retail industries (Johnston and McCalla, 2004; Linden, 2009). As a result of changes in these external factors the degree of competition among individual farmers, opportunities for small growers, research and development programs, and orchard management practices have shifted substantially. The specific impacts of long-term crop values and industry consolidation on individual growers differ between fresh market crops and commodity crops.

There are three factors unique to fresh market fruit crops that are imposing substantial constraints on the industry in California and in other parts of the world. First, fresh market fruit handlers and processors have undergone substantial consolidation over the past 15 years with fewer, larger packing houses available to purchase produce that conduct their own independent domestic and international marketing. As a result of consolidation in sales and marketing opportunities, competition among individual growers is high and there are fewer opportunities for small farms. Second, fresh market fruit industries are less willing to support crop-specific marketing boards to promote sales within the country and internationally as this responsibility shifts to large, consolidated marketing organizations. Without marketing boards or similar government-regulated entities there is less funding available for development of new cultivars and research to improve orchard management outside large private companies. Third, prices for manual labor and chemicals (pesticides and fertilizers) have increased substantially. Growers must rely on hand pruning and harvesting to ensure that fruit meet the high quality standards set for fresh market produce. Because manual labor is required for many farm operations year round, small farm profit margins are decreasing, making them more susceptible to year-to-year fluctuations in crop value and labor availability.

Commodity crop industries in California have expanded substantially over the past 30 years as a result of two favorable factors. First, all the primary tree fruit and nut commodity crops grown in California support marketing boards that conduct domestic and international marketing and promotion, as well as fund research and development. Marketing boards have been generally successful in increasing worldwide demand. Increased demand and independent marketing activities result in reduced direct competition among handlers and individual growers, and increased opportunities for small growers. Second, commodity crop growers have been successful in minimizing manual labor costs by transitioning to mechanical thinning and harvesting and using alternative pruning programs.

Tree fruit and nuts comprise a substantial proportion of agricultural production in the US. Both domestic and

international markets have played an important role in determining shifts in this industry over the past 30 years and will continue to do so. In addition to external market factors it is likely that tree fruit and nut agriculture will also be impacted by climate change in the next century as winter average temperatures rise, reducing chill hours available during dormancy, and water availability decreases and/or becomes more erratic.

See also: Agricultural Labor: Labor Market Operation. Agricultural Mechanization. Changing Structure and Organization of US Agriculture. Climate Change and Plant Disease. Climate Change: Horticulture. Climate Change, Society, and Agriculture: An Economic and Policy Perspective. Food Chain: Farm to Market. Industrialized Farming and Its Relationship to Community Well-Being. International and Regional Institutions and Instruments for Agricultural Policy, Research, and Development

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Vaccines and Vaccination Practices: Key to Sustainable Animal Production

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Glossary

Antigen A substance which the body recognizes as alien and induces an immune response.

Cluster of differentiation (CD) A nomenclature system to identify and characterize cell surface molecules.

Cytokines A group of small proteins that is important in cell signaling. Cytokines include interleukins which are important in the regulation of immune responses. Proinflammatory cytokines are important during the inflammatory process directly after infection.

Dendritic cells Cells of the immune system which process antigen and present it on the surface to other cells of the immune system.

Differentiating infected from vaccinated animals (DIVA) An approach in which animals are vaccinated with a vaccine that can be differentiated from infections with field virus by serological or other methods.

Major histocompatibility complex (MHC) A set of molecules displayed on cell surfaces that are responsible for lymphocyte recognition and 'antigen presentation'. The MHC molecules control the immune response through recognition of 'self' and 'nonself,' and consequently, serve as targets in transplantation rejection.

Pathogen-associated molecular patterns (PAMS) PAMS are molecules associated with groups of pathogens. PAMS include lipopolysaccharides, proteins, single stranded RNA fragments, and nonmethylated CpG DNA sequences. PAMS bind to pattern recognition receptors which is important for the initiation of immune responses by the host.

Pattern recognition receptors (PRR) Proteins expressed by cells of the innate immune response. PRR can be expressed on the cell surface and in the cytoplasm. Toll-like receptors are a specific group of PRR.

Quantitative trait loci (QTLs) Stretches of DNA containing or linked to the genes that underlie a quantitative trait.

Toll-like receptors (TLR) A specific group of PRR (see Pattern Recognition Receptors), TLR are evolutionary preserved and were first recognized in the fruit fly (see Pathogen-Associated Molecular Patterns).

Introduction

The projected increase in human population from 6.8 billion in 2010 to more than 9 billion in 2050, combined with the increase in disposable income in countries such as China and India, will have a major impact on the increased need for animal protein for human consumption. The current production of animal protein for human consumption is projected to continue increasing until 2050 (Table 1). To achieve these predicted increases it will be of crucial importance to improve feed conversion, production parameters, and genetic resistance to disease as well as control exposure to pathogens by improved biosecurity and vaccination.

The focus of this article is mostly on vaccines and vaccination technologies used in aquaculture, poultry, swine, and cattle. Unless specifically mentioned as a category, these four groups are referred to as production animals. Although small ruminant production is expected to increase until 2050 (Table 1), the amount of small ruminant products is dwarfed by the other four commodities, and vaccination of small ruminants is not covered here. Because vaccine-induced protection depends on the degree of genetic resistance to a given pathogen and on the degree of biosecurity, these topics are briefly addressed. In addition, the major groups of pathogens and immune responses relevant to vaccine-induced immunity are briefly reviewed.

There are several extensive publications on the production and quality control of vaccines, the use of vaccines, and related topics. For more detailed information see Gay *et al.* (2007), Jones *et al.* (2007), Lombard *et al.* (2007), Lubroth *et al.* (2007), McLeod and Rushton (2007), Scudamore (2007), O'Brien and Zanker (2007), Schat and Baranowski (2007), and Schudel (2007).

Pathogens

For the purpose of this article pathogens are defined as organisms infecting production animals, leading to disease or causing immunosuppression that leads to increased

Table 1 World production of meat, milk, eggs, and aquaculture from 1961 to estimates for 2050

Commodity	*Production in million tons*						*Increase from 2011 to 2050 (%)*
	1961/1963[a]	*2005/2007*[a]	*2011*[b]	*2012*[b]	*2013*[b]	*2050*[a]	
Bovine meat	30	64	62.7	66.5	70.2	106	69
Ovine meat	6	13	13.5	13.6	13.8	25	85
Pig meat	26	100	109	112.5	114.2	143	39
Poultry meat	9	82	102.1	104.6	106.4	181	77
Aquaculture	2.6[c]	49.9[d]	62.7	66.5	70.2	209.5[f]	234
Milk products	344	664	745.5	767.4	784.4	1077	44
Eggs	14	62	No data	65[e]	No data	102	65

[a]Data for 1962/1963, 2005/2007 and 2050 are derived from Alexandratos, N., Bruinsma, J., 2012. World agriculture towards 2030/2050: The 2012 revision. ESA Working Paper No. 12-03, pp. 1–147. Rome, Italy: FAO, unless superscript *c* and *d* are given for a specific value.
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[d]Data for 2007 from FAO, 2012. The State of the World Fisheries and Aquaculture. Rome, Italy: FAO, pp. 3–40.
[e]Data from Evans, T., 2013. Global poultry trends: World egg production sets a record despite slower growth. Available at: www.Thepoultrysite.com (accessed 16.04.14).
[f]From Wijkström, U.N., 2003. Short and long-term prospects for the consumption of fish. Veterinary Research Communications 27 (S1), 461–468 and Brugère, C., Ridler, N., 2004. Global Aquaculture Outlook in the Next Decades: An Analysis of National Aquaculture Production Forecasts to 2030. Rome, Italy: FAO, pp. 1–47, tonnes of aquaculture products required on the basis of stagnating capture fisheries.

susceptibility to infection and disease by other pathogens. Three broad categories of pathogens are relevant to this article: viruses, bacteria, and parasites. The latter category includes protozoa as well as helminths. Fungi constitute a fourth group of pathogens but are not discussed as there are no antifungal vaccines available for production animals. Research to develop vaccines for humans against *Candida albicans* and other fungal infections (Cassone, 2013; Spellberg, 2011) may lead to antifungal vaccines for use in production animals in the future.

Detailed descriptions of human and animal pathogens can be found in several textbooks, such as Medical Microbiology (Murray *et al.*, 2012), Veterinary Microbiology and Microbial Disease (Quinn *et al.*, 2011), and Georgis' Parasitology for Veterinarians (Bowman, 2014). A short description of viruses, bacteria, and parasites relevant for this article is provided for readers not familiar with the key characteristics of these pathogens.

Viruses

Viruses infecting production animals are small (15–300 nm) and cannot be seen by light microscopy with the exception of poxviruses. Viruses are inert outside of living cells and are strictly intracellular pathogens. Entrance into living cells is essential for their replication using cellular organelles for the production of viral proteins. Viruses have double-stranded (ds) or single-stranded (ss) deoxyribonucleic acid (DNA) or ribonucleic acid (RNA) genomes but never both. Some of the larger viruses have genomes coding for proteins that are needed for genome replication (e.g., poxviruses and herpesviruses), whereas other viruses depend on cellular enzymes to replicate their genomes. The genome is surrounded by a capsid that consists of proteins or sometimes by a lipid membrane derived from the host cell, which is referred to as the envelope. Viral proteins are inserted in the envelope during the development of virus particles. Enveloped viruses are in general susceptible to inactivation by disinfectants and external factors, such as sunlight, whereas viruses with only a protein capsid are more resistant to chemical and physical treatments, which have important consequences for biosecurity measures.

Bacteria

Bacteria are classified as prokaryotic cells lacking a nucleus and organelles in the cytoplasm. Individual bacteria range in size from 1 to 20 μm, but they can form clusters, chains, or biofilms. Bacterial genomes consist of a single ds DNA chromosome, which is often circular but can be linear. Bacteria reproduce by cell division. Small circular, autonomously replicating DNA sequences called plasmids may be present. These plasmids can contain virulence factors and sequences conferring antibiotic resistance. Plasmids can be exchanged between bacteria of the same or different species. Most bacteria have a rigid cell wall and may have flagella or fimbria. The composition of the cell wall is important for a broad classification into two groups: Gram-positive and Gram-negative bacteria. The only important pathogenic bacteria lacking a rigid cell wall are the Mycoplasmas, which have a plasma membrane. Some bacteria (e.g., *Bacillus antracis* causing antrax) produce endospores that are extremely resistant to chemical or physical treatments and can remain dormant for very long periods. The classification of bacteria was traditionally based on morphology, culturing on different media, motility, and metabolic activity, which all required the ability to grow the bacteria in inert media. With the advance of next generation sequencing, classification of bacteria can be achieved to the level of strain identification using the 53 genes coding for ribosomal protein subunits (ribosomal multilocus sequence typing (rMLST)) (Jolley *et al.*, 2012).

Parasites

This widely divergent group of organisms includes unicellular organisms, such as coccidia, Plasmodium, and *Theileria parva*,

as well as multicellular organisms that can vary tremendously in size, including 10-m long tapeworms. All organisms in this group are eukaryocytes with a defined nucleus including a nuclear membrane and with different organelles in the cytoplasm. The life cycle of parasites can be very complex, including sexual and asexual reproduction. Several economically important parasites affecting production animals have intermediate hosts (e.g., ticks for *T. parva*), whereas others do not use intermediate hosts (e.g., *Eimeria* species in chickens).

Relevant Immune Responses

To discuss vaccines and vaccination it is important to provide a brief overview of the major immune responses. A good introduction to the basics of veterinary immunology can be found in 'Veterinary Immunology: Principles and Practice' (Day and Schultz, 2011); more in-depth information is provided in 'The Immune System, third ed.' (Parham, 2009). Both books are focused on the immunology of mammalian species. Readers interested in the immunology of birds or teleost fish may consult 'Avian Immunology, second ed.' (Schat *et al.*, 2014) or 'Fish Defenses, vol. 1: Immunology' (Zaccone *et al.*, 2008), respectively. Most of the information on mammalian immunology is based on studies in mice or humans, whereas avian immunology is largely based on studies in chickens. Within these two classes of animals, major differences may exist among species of the same class. Similarly, major differences are expected to exist among the approximately 4000 teleost fish species. Key differences between the three classes of animals and, if appropriate, within classes are indicated.

Immune responses are often divided into innate and acquired (also called adaptive) immune responses, but this division is no longer seen as an absolute. Innate immune responses, although capable of directly killing microbes, are also absolutely required for the generation of adaptive immune responses. This is achieved by specific 'pattern recognition receptors (PRR)' that are located on the cellular membranes and in the cytoplasm of the cells. Toll-like receptors (TLR) are an example of PRR and were originally described in the fruit fly (*Drosophila melanogaster*). PRRs recognize specific 'pathogen-associated molecular patterns (PAMPs).' PAMPs are conserved among classes of microbes but should not be confused with virulence factors. Binding of PAMPS through TLRs or other PRR on the so-called professional antigen-presenting cells (APC), such as dendritic cells and macrophages or infected cells, results in the production of specific cytokines or interleukins (ILs) by APC. The ILs activate lymphocytes starting the activation of the adaptive immune system.

Innate Responses

Innate responses are activated rapidly within minutes to hours after an infection and have limited specificity and lack of memory. Pathogens first encounter physical and chemical barriers at the skin and epithelial surfaces in the respiratory and intestinal tracts. Mucus on the skin of fish as well as in the upper respiratory tracts acts as a chemical barrier, can trap pathogens, and prevent infection. If a pathogen successfully overcomes the physical barriers, it meets cells of the innate immune system that are equipped with secreted and cell-associated defense mechanisms. Soluble defenses induce inflammation and include interferons (IFN), defensins, and complements. Complement can promote phagocytosis by cells such as neutrophils (called heterophils in birds) and macrophages, which initiate cell-associated defenses, such as nitric oxide (NO) production. Natural killer (NK) cells exhibit both innate and adaptive-type responses. NK cells can kill tumor and virus-infected cells and are an important source of IFN-γ, which also enhances macrophage and neutrophil phagocytosis and microbial killing. Most of these innate responses are very similar in teleost fish, birds, and mammals, although minor differences among these three groups may exist.

Although innate immune responses are important for the initiation of vaccine-induced immunity, they are generally not considered important vaccine immune responses due to the lack of memory and specificity. However, in intensive production systems, such as the chicken broiler industry, vaccination especially with live attenuated vaccines may briefly boost innate responses, which can have a beneficial protective effect before the development of an adaptive, protective immune response. For example, in chickens, NK cells are activated after vaccination against Marek's disease (MD) herpesvirus (MDV) (Heller and Schat, 1987) and based on studies by Garcia-Camacho *et al.* (2003) may provide protection during the first few weeks when the birds are in the poultry houses. MD is discussed in more detail in the another article of this Encyclopedia.

Antibody Responses

The adaptive immune responses can be divided into antibody and cell-mediated responses. On exposure to an antigen (in this article typically a protein-based part of a pathogen) antibodies are generated by B lymphocytes, which may develop into plasma cells producing large quantities of antibodies. Immunoglobulins (Ig) consist of heavy chains and light chains. IgG (see below) consists of two heavy and two light chains, which represents the basic structure of an immunoglobulin. The heavy chains have a number of constant domains and one variable domain, whereas the light chain has one constant and one variable domain. The variable domains of the heavy and light chains form the antigen-binding site, whereas the constant domains of the heavy chain are important for additional functions, such as activation of complement or binding to cellular receptors. For further details on the general aspects of antibodies, the readers are advised to refer to the different textbooks mentioned earlier.

There are a number of different antibody classes and subclasses that vary among the teleost fish, birds, and mammals (**Table 2**). For the purpose of this article, the author has focused on the IgG, IgM, and IgA antibodies, or their equivalents. IgG (often referred to as IgY in birds) consists of two heavy and two light chains. It is the dominant antibody in serum and depending on the immunization schedule and vaccine used it is the key antibody produced in vaccine-induced, antibody-based protective immunity. After a primary infection or first vaccination, IgG antibodies are detected approximately 7 days postinfection (pi), which is named the primary response. One of the hallmark characteristics of an

Table 2 Antibody classes and subclasses in cattle, swine, chickens, and teleost fish

Species	*Antibody classes and subclasses*						*Key references*
	IgM[a]	*IgG*	*IgA*	*IgD*	*IgE*	*IgT*	
Fish	+	–	–	+	–	+	Fillatreau *et al.* (2013)
Chickens	+	Aka IgY	+	–	–	–	Härtle *et al.* (2014)
Cattle	+	3 subclasses	+	+	+	–	Zhao *et al.* (2006)
Swine	+	5 subclasses	+	+	+	–	Butler *et al.* (2006)

[a]Tetramer in fish and pentamer in birds and mammals.
Abbreviation: Aka, also known as.

acquired immune response is memory. Memory B cells are generated during the primary response, and on second exposure to the same antigen, they are responsible for a rapid increase of IgG antibody production. This is called the secondary response and is generally long lasting. These characteristics form the basis for vaccination.

Other classes of antibodies include IgM and IgA. IgM consists of five basic structures (pentamer) except in fish, which have tetrameric IgM-like antibodies. IgM antibodies are the first class that can be detected after exposure to a pathogen and are typically not detected in a secondary response. However, IgM is the major antibody response to pathogens in fish. IgA is important for mucosal immunity. IgA can exist as a monomer or a dimer joined by the so-called J chain. In addition, dimeric IgA is associated with a protein, the secretory component, which protects the antibody against degradation by proteolytic enzymes at mucosal surfaces. Fish lack IgA but produce IgT, which performs similar functions to IgA and is present in relatively large quantities in the skin mucosa.

Cell-mediated Immunity

Cell-mediated immune (CMI) responses are especially important for the control of intracellular pathogens and are primarily mediated by cytotoxic T lymphocytes (CTLs). CTLs have been described in all production animals from fish to cattle and swine and are characterized by the surface markers CD8α and CD8β. These cells recognize small antigen fragments of 8–12 amino acid peptides if these fragments are presented in the context of major histocompatibility complex (MHC) class I proteins, which are expressed on the surface of virtually all cells in the body. When CTLs recognize a small peptide expressed in the context of MHC class I, they kill the cells presenting the antigen through a rather complex system, eliminating pathogen-infected cells. Memory responses have been described for CTL; thus, once an animal has been immunized and a CTL response has been generated, antigen-specific CTL can rapidly expand after subsequent exposures, similar to memory antibody responses.

Antigen Processing

To understand the differences in immune responses generated by live versus inactivated (also referred to as killed) vaccines it is important to briefly discuss antigen processing. When a killed vaccine or an antigenic protein is injected into an animal it is typically processed by professional APC. The proteins are broken down in the phagolysosome of the APC to fragments of mostly 10–30 amino acids, which are then presented to B-lymphocytes in the context of MHC class II antigens on the cell surface of the APC. In mammalian species this process occurs in the lymph nodes. Chickens lack lymph nodes and antigen processing occurs mostly in the spleen.

Antigen processing for presentation to CTL differs fundamentally from the processing for presentation to B lymphocytes. For CTL presentation, *de novo* synthesis of proteins is needed, i.e., replication of virus, intracellular bacteria, or protozoa in an infected cell is needed for optimal presentation of antigen to CTL. The newly synthesized pathogen-derived proteins are broken down to small peptide fragments in the cytosol and are transported into the endoplasmic reticulum, where they bind to the MHC class I molecules. These MHC class I–antigen complexes are then transported via the Golgi apparatus to the cell surface for CTL recognition. The practical consequences for vaccinology are that inactivated vaccines induce antibody responses with little or no CMI responses, whereas live vaccines generate both antibody and CMI responses.

Maternal Immunity

The immune system of newborn animals is generally poorly developed and requires time to fully mature after birth. To protect the newborn against infections, antibodies are transferred in mammals from the dam to their offspring through the placenta or the colostrum. There is little or no transfer of IgG through the placenta in cows and sows; thus, it is of crucial importance that newborn calves and piglets receive colostrum during the first 24–48 h after birth (Butler, 2006). The neonatal intestinal tract of many mammals, including cattle and swine, allows efficient absorption of Ig only during the first 24–48 h after birth. In cows, the unique IgG subclass 1 is the major antibody in the colostrum. The intestinal tract allows the absorption of Ig in calves and piglets only during the first 48 h after birth. Sow colostrum consists of 60% IgG, 30% IgA, and 10% IgM. After 48 h the composition of immunoglobulins in sow milk changes to predominantly IgA. (Butler *et al.*, 2006). Maternal immunity in chickens is provided through transfer of IgY from the yolk to the embryo and newborn chicken. Although maternal immunity has been described for fish (Zhang *et al.*, 2013), the level of transfer of maternal antibodies to Atlantic salmon (*Salmo salar* L.) fry is apparently insufficient to provide protection against infection with *Yersinia ruckeri* (Lillehaug *et al.*, 1996). The importance of

maternal immunity for vaccination schedules is discussed in the Section 'Selected Examples of Vaccinations in the Four Groups of Production Animals.'

Immunosuppression and Immunoevasion

Many factors can influence the immune response to a given vaccine, especially in the more intensive production systems of swine, poultry, and fish units where large numbers of multiple age groups are kept in high density in confined spaces (e.g., the chicken layer industry). Stress levels can be high under these conditions and immunosuppressive viruses (e.g., chicken anemia virus and infectious bursal disease in chickens and porcine circovirus in piglets) often cause subclinical immunosuppression resulting in suboptimal protection after vaccination. In addition, a number of pathogens have developed strategies that interfere with immune responses. Poxviruses, herpesviruses, coronaviruses, and orthomyxoviruses have been especially successful in developing immune-evasive approaches, which have been well documented for chicken pathogens (reviewed in Schat and Skinner, 2014).

Importance of Biosecurity

Biosecurity is defined here as the complex of precautions taken to protect against the introduction and spread of harmful organisms and diseases into or within animal production systems. Some producers of production animals believe that vaccine manufacturers can always produce better vaccines and therefore biosecurity is not very important or is even irrelevant. However, the use of vaccines can never be an excuse for poor biosecurity. Most vaccines do not provide a sterilizing immunity, meaning that vaccination may prevent disease but not prevent replication of pathogens. As a consequence escape mutants may arise for which the vaccine no longer provides protection. Premises that are poorly cleaned after a previous flock or herd has been removed may allow naïve animals to be exposed by residual pathogens before the immune response matures or before solid vaccinal immunity has been established. An example of good and poor farm management for poultry is provided in Figures 1(a) and (b), respectively. In Figure 1(b) there is no clean area directly adjacent to the poultry house. The absence of a clean area facilitates the entrance of rodents and other fomites. It will be much more difficult to control diseases under these circumstances even when vaccination procedures are correctly executed.

Ideally, closed houses with proper ventilation and climate control, which are cleaned and disinfected after each cycle, are used for chickens and swine, but this is often impractical in warmer climates, especially in economically poor countries. Multiage farms, a reality in most poultry production systems for layers, are another problem for strict biosecurity, preventing thorough cleanup of the premises.

Biosecurity measures that can always be included are as follows: restriction of access to the farm to only essential personnel, a change of boots and coverall before entering a chicken or swine house, and the use of proper footbath with disinfectant that is changed daily. It is important to ensure that vaccination crews and other persons visiting several farms on one day do not enter the facility without change of clothes and ideally a shower before entering the premises. A specific problem is encountered in several countries where most of the chickens are sold through live markets. Traders come to the farms to get their quota of birds, often using trucks that have not been cleaned for a long time. In this situation it is recommended that the farmer brings the birds to the entrance of the farm so that the trader does not have to enter with his truck. As a consequence of the bird flu situation, biosecurity measures have been more strictly enforced in the poultry industry over the past 5–10 years, but in many instances a critical evaluation by a qualified poultry veterinarian will result in recommendations for further improvements. For more detailed information on biosecurity measures for poultry production, the readers may refer to 'Diseases of Poultry, thirteenth ed.' (Collett, 2013). Many of the recommendations made for biosecurity on poultry farms are also applicable to intensive production systems for other food animals.



(a) (b)

Figure 1 Layer parent farm (a) and commercial layer farm (b) in India. Both are multiage farms with natural ventilation and curtains. Note the clean environment and cement borders around the building in (a) in contrast with the commercial farm with plants growing up to the building and junk lying around in (b).

Genetic Resistance to Disease

Several factors favor the inclusion of genetic resistance in disease control programs for the four major production animal groups (reviewed in Gay *et al.*, 2007). The first factor is the concentration of genetic stock within a limited number of companies. In the poultry industry, for instance, there are only a few major breeders left in the world. These breeders are maintaining pure genetic lines under constant selection pressure for multiple traits. To produce a commercial product (layers or broilers), eight lines are used basically following the outline in **Figure 2**. Introduction of and subsequent selection for a new trait in one of the eight lines, indicated by the asterisk in **Figure 2**, will result in the presence of the new trait 4 years later in the production animals. Similar trends in concentration of genetic stocks are evolving in the salmonid industry and have started in the swine industry.

A second factor is the use of artificial insemination. In dairy cattle this had far-reaching implications as is illustrated by the impact of an elite sire and son duo on the distribution of candidate genes related to important production traits, including disease resistance. Each of these two bulls accounts for approximately 7% of the current genomes (Larkin *et al.*, 2012). However, the use of a highly desirable sire can also introduce unexpected new problems, as is illustrated by the case of leukocyte adhesion deficiency (LAD) disease. LAD has been linked to a point mutation in the gene coding for the leukocyte adhesion molecule CD18, and this defect was traced back to a specific sire Osborndale Ivanhoe, who was used extensively as a semen donor in the United States (Shuster *et al.*, 1992). Once the defect was identified at the molecular level, the disease was eradicated. Several other genetic diseases linked to the widespread use of semen from a single bull are mentioned by Shuster *et al.* (1992). The increased use of embryo transfer will have similar positive and potentially negative effects.

A third condition favoring the inclusion of genetic selection for disease resistance is the rapid progress in new DNA sequencing techniques, which has resulted in the (near) release of complete genome maps for chickens, swine, cattle, and salmonids. Genetic resistance to pathogen-induced disease can be at the level of receptors preventing infection. For example, chickens can be resistant or susceptible to infection with avian leukosis virus subgroup A (ALV-A) based on allelic differences in the receptor gene (Nair and Fadly, 2013). The poultry breeders have used this information in their genetic selection program to generate birds resistant to ALV (McKay, 2013, personal communication). In swine, a single-nucleotide mutation at position 307 (G/A) of the alpha-(1,2)-fucosyltransferase (FUT1) gene, the putative receptor for F18 fimbriae of *Escherichia coli*, is strongly correlated with increased resistance to enterotoxigenic and verotoxigenic *E. coli* (Wang *et al.*, 2012). Atlantic salmon are highly susceptible to infectious pancreatic necrosis (IPN) virus, a birnavirus, which can cause 30–80% mortality during the juvenile posthatch freshwater stage. A quantitative trait locus (QTL) has been identified that confers resistance to the infection (Houston *et al.*, 2012; Moen *et al.*, 2009). Including the resistance conferring QTL in the breeding program by AquaGen in Norway has led to a dramatic reduction in the incidence of IPN (Anonymous, 2013b).

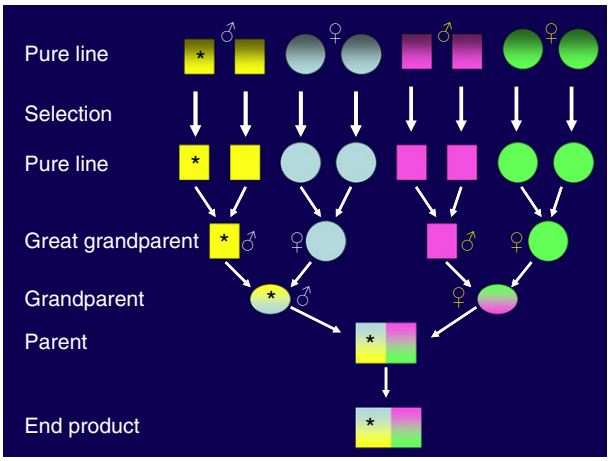


Figure 2 Breeding scheme used by primary poultry breeders to generate a commercial end product. The asterisk represents the introduction of a new trait and subsequent selection for the trait through the generations.

These examples suggest that transgenic approaches for disease control may be possible if regulatory and consumer resistance can be addressed. One example is the development of transgenic chickens that were unable to transmit avian influenza virus (AIV) to pen-mates, although the transgenic birds were not resistant to direct challenge. The resistance is based on the expression of a small RNA fragment that acts as a decoy to the viral polymerase complex (Lyall *et al.*, 2011). Transgenesis to increase resistance to specific diseases has been reported for several fish species (Dunham, 2009). Dunham suggests that the environmental risks of transgenic fish are minimal, but transgenic fish resistant to disease have not yet been used commercially. The Food and Drug Administration of the United States Department of Health and Human Services (FDA) has jurisdiction over the acceptance of transgenic fish for human consumption in the United States. In a preliminary document, the FDA concluded that transgenic Atlantic salmon containing the *opAFP-GHc2* recombinant DNA construct, produced by AquaBounty Technologies, are safe as a food source for human consumption.

Genetic resistance to certain diseases can also be based on the presence of specific MHC alleles or on the identification of QTL linked to resistance. For example, in chickens resistance and susceptibility to Marek's disease have been linked to the MHC complex (reviewed by Schat and Nair, 2013) and several QTL (Cheng and Lamont, 2013). In MD-resistant birds, viremia levels are lower than in susceptible birds during the first 14 days pi and vaccines provide better protection against virus replication in resistant than in susceptible chicken lines (Yunis *et al.*, 2004; Schat *et al.*, 1982). In a multigenerational challenge study using elite egg production pure lines, Fulton *et al.* (2013) reported an association between Marek's disease mortality and the MHC of the sire. This information combined with selection for production traits is actively used in the selection program to improve resistance to MD (Fulton *et al.*, 2013; McKay, personal communication). Because this type of selection experiment is not easily reproduced for other pathogens, selection for genetic control of immune responses is used rather than selection for resistance to specific pathogens

(Lamont *et al.*, 2014). In chickens, in addition to the QTL linked to MD resistance, QTL have been identified that are linked to resistance to Salmonellosis, *E. coli*, coccidiosis, and infectious bursal disease (Cheng and Lamont, 2013), but these QTL are currently not included in the breeding programs of at least one major breeder company (McKay, personal communication).

In conclusion, improvement in genetic resistance needs to be an important part of an integrated disease control program in conjunction with strong biosecurity measures and an optimal vaccine program.

Vaccines

To Vaccinate or Not to Vaccinate

It is generally accepted that the use of vaccines is an essential component of disease control, which also impacts the economic production and welfare of production animals. Although disease control is the main reason to use vaccines, there are several additional considerations when determining whether vaccines should be used (McLeod and Rushton, 2007). Of major importance are the restrictions on import and export of animals or animal products imposed by many countries. These exist as a consequence of the presence of specific diseases, such as avian influenza or foot-and-mouth disease (FMD). Vaccination results in the development of antibodies, which may not differ from antibodies present after infection, thus interfering with disease monitoring. As a consequence, countries may not want to import products that are antibody positive. Avian influenza not only causes major losses for the poultry industry but is also a zoonotic disease; however, FMD is an economically important disease that does not affect humans. In the case of avian influenza, some countries allow routine vaccination of poultry, whereas others rely exclusively on 'stamping-out' and inhibition of animal movement. In some countries, ring vaccination is allowed to prevent spread of AIV, whereas poultry flocks within the infected area are euthanized. This is especially attractive if a differentiating infected from vaccinated animals (DIVA) strategy can be used as is the case in avian influenza (Suarez, 2012; Capua *et al.*, 2003) (see Section Vaccines for Poultry). There is currently no DIVA strategy available for FMD (Clavijo *et al.*, 2004) and many countries rely, therefore, exclusively on stamping out; this has led to significant social problems as was the case during the 2001 outbreak in England (Scudamore, 2007). During this outbreak, the Netherlands used a ring vaccination to prevent the spread of FMD, euthanized all animals within the affected area, and subsequently destroyed the vaccinated (antibody positive) animals in order to be declared FMD free ('vaccinate to kill' policy) (Parida, 2009) (FMD vaccination is discussed in another article of this Encyclopedia).

McLeod and Rushton (2007) mentioned the possibility of eradication of a specific disease by international vaccination campaigns as a second reason to vaccinate. This approach has been successful in the case of rinderpest, a viral disease of cattle, which was officially declared eradicated in 2011 (Njeumi *et al.*, 2012). Other national or international campaigns are often initiated to reduce risks of transmission of zoonotic diseases to humans, for example, rabies and *Brucella abortus*, but these campaigns have not led to the global eradication of the diseases.

The third reason to vaccinate is to control economically important diseases. Decisions to vaccinate or not are often based on a cost/benefit analysis. For example, in the broiler industry, economic benefits were realized after the decision was made in 1983 to add the SB-1 vaccine strain to the herpesvirus of turkeys (HVT) vaccine against Marek's disease when HVT alone no longer fully protected birds against the disease. Within 3 months the industry had calculated that the addition of SB-1 was financially advantageous by reducing the condemnation rate of diseased birds (listed as leukosis in the USDA database on condemnations in poultry) enough to offset the increased vaccine costs. Another example is related to the overall costs of vaccines and medicines in relation to the overall production costs. The cost of all vaccines and medicines for an average broiler farm in the United States is US$ 0.05 per pound (=0.45 kg) live weight. In comparison, the chick cost is US$ 5.47 per pound live weight (Anonymous, 2013a), with profits ranging from approximately US$ 0.10 to a loss of US$ 0.01 per pound live weight. MD vaccines are the most expensive vaccines for broilers with the average prices in the United States ranging from US$ 2.65 per 1000 doses for HVT alone to US$12.00 per 1000 doses for HVT combined with the CVI988 vaccine strain (prices quoted for 2014). To reduce these costs, MD vaccines are often diluted, especially when the condemnation rates for 'leukosis' are very low (Schat and Baranowski, 2007; Schat and Nair, 2013). However, dilution of the vaccine reduces protection to virus replication and tumor development when birds are challenged with very virulent plus (vv+)MDV strains (Gimeno *et al.*, 2011) increasing the possibility of selection for more virulent strains (Atkins *et al.*, 2013).

Although vaccination of production animals against zoonotic and economically important diseases seems to be noncontroversial, there are some impediments, which are often regional. In Europe, consumers have expressed reservations about consuming meat from vaccinated animals, especially since the outbreaks of the highly pathogenic H5N1 avian influenza in poultry and the 2001 outbreak of FMD in the United Kingdom (Scudamore, 2007; O'Brien and Zanker, 2007). A second problem is related to the production and evaluation of vaccines that often involves animal testing for safety and efficacy, which has become problematic (O'Brien and Zanker, 2007). This is even more of a problem when new vaccines need to be developed for emerging or reemerging diseases. A third impediment is related to the control of transboundary diseases. Control of these diseases is frequently based on political decisions to vaccinate or to use 'stamping-out.' (Inter)national or regional vaccination campaigns may be needed if vaccination is allowed, which requires the willingness to commit economic resources and the cooperation of farmers. These conditions can be problematic, especially in politically unstable parts of the word (Lubroth *et al.*, 2007), but it can be done as has been shown with the eradication of rinderpest.

Characterization of Vaccines

Traditionally, vaccines have been developed by attenuating pathogens or using closely related agents that are not pathogenic in the target hosts. Since the advance in biotechnology,

vaccines have been developed using molecular approaches. In this section the author has first discussed the traditional vaccines and then the different approaches for biotechnology-based vaccines. Both categories can consist of live organisms or inactivated products. The latter group includes whole organisms, protein products, and DNA-based vaccines. A good overview of the different phases for the production of veterinary viral vaccines was recently published (van Gelder and Makoschey, 2012).

Determining vaccine efficacy

Independent of the type of vaccine, there is a need to establish methods for monitoring vaccine efficacy. When a new vaccine is submitted to the veterinary authorities, data are normally included showing protection against challenge. These tests are expensive and subject to animal use regulations, which vary among countries. To monitor vaccine 'takes' in field conditions, serology tests are most often used to determine whether adequate antibody titers have been achieved and are maintained over time. Most of these tests use different enzyme-linked immunosorbent assay (ELISA) approaches and commercial ELISA kits are available for most pathogens in cattle, swine, and poultry. Determining specific CMI responses is complicated and not used to measure vaccine responses. In chickens, a quantitative polymerase chain reaction (qPCR) assay can be used to determine whether the birds are adequately vaccinated by measuring CVI988, HVT, or SB-1 genome copies in the feather pulp between 7 and 14 days postvaccination (Baigent *et al.*, 2006; Renz *et al.*, 2013).

Traditional live vaccines

Most of the current vaccines for production animals are directed against viral and bacterial pathogens. Typically, a virus was isolated and passed a number of times in experimental animals, embryonated chicken eggs, or cell cultures, resulting in attenuation while remaining immunogenic. Probably the first example of attenuation of a virus was the use of rabbits by Pasteur to attenuate rabies virus (reviewed in Lombard *et al.*, 2007). Cell culture attenuation can be achieved by passaging the virus at its optimal temperature or at lower temperatures as has been done for the cold-adapted, live human influenza vaccine (Maassab and DeBorde, 1985). These approaches have been used successfully over the years, but the development of attenuated vaccines was empirical with often unpredictable results. Key requirements for the successful use of live virus vaccines are ease of (1) production, i.e., cell cultures using roller bottles or suspension cultures in bioreactors; (2) transport, i.e., liquid nitrogen (essential for Marek's disease vaccines), need of cold chain (either $-20\,^{\circ}C$ or $4\,^{\circ}C$, important for most vaccines), or ambient temperature (heat tolerant); (3) administration, and (4) good replication in the vaccinated animals without causing clinical or subclinical problems. The ease of administration is discussed in more detail in the Section 'Vaccination Procedures' and potential issues with subclinical problems discussed in the section on poultry vaccines. Production of live vaccines follows detailed protocols adhering to strict standards, which are determined by governments of individual countries (e.g., the Veterinary Services of APHIS-USDA), a group of countries (e.g., the European Union), or by the World Organization for Animal Health (OIE) (Jones *et al.*, 2007; Schudel, 2007).

Similar to viruses, bacteria have been attenuated by passage in animals or suboptimal culture conditions on artificial media. Pasteur and his coworkers have been credited with the production of an attenuated vaccine against swine erysipelas by passage of *Erysipelothrix rhusiopathiae* through rabbits and fowl cholera by using aged *Pasteurella multocida* cultures (reviewed in Lombard *et al.*, 2007). Bacterial vaccines are made in large bioreactors.

Different approaches have been used for some vaccines available for the control of unicellular and multicellular parasites (Lightowlers, 2014; Williams, 2002). Poultry coccidia vaccines have been developed by selecting precocious lines of coccidia, which replicate faster than wild-type strains and induce immunity without disease when given to young chicks. Control of lungworm, *Dictyocaulus viviparus*, in cattle is achieved by using irradiated attenuated L3 lungworm larva.

Since the advance in rapid sequence techniques, many of the attenuated vaccines have been properly characterized at the genomic level and shown to contain insertions or deletions. The finding of deletions has been helpful for the development of vaccines using recombinant technologies (see below).

Traditional inactivated vaccines

In general, the production of inactivated or killed vaccines follows similar guidelines, although somewhat more relaxed than for live vaccines. The more relaxed guidelines are best demonstrated for chicken embryo-produced killed virus vaccines. Although the production of live vaccines in embryos or chicken embryo-derived cell cultures requires the use of specific pathogen-free eggs, inactivated vaccines can be made in the so-called 'clean eggs,' which are not necessarily free of all pathogens. Inactivation can be achieved by several methods, such as treatment with alkylating agents (β-propiolactone and aminoethyl ethelene imines), different concentrations of formalin or glutaraldehyde, temperature, pH, and UV or gamma irradiation (Delrue *et al.*, 2012). Key concerns with the preparation of inactivated vaccines are immunogenicity and safety. Depending on the virus, some of the inactivation procedures damage the immunogenic epitopes, resulting in insufficient induction of protective immune responses. Viral safety can be compromised by incomplete inactivation of the vaccine virus or by the presence of extraneous pathogens in the cell culture media or embryos. Sera, trypsin, and embryonated chicken eggs can contain extraneous pathogens, some of which have only recently been described. The use of fetal bovine serum, for example, frequently results in contamination of vaccines with bovine viral diarrhea virus (BVDV). To avoid this problem, chemically defined cell culture media without animal components have been developed but may not be widely used for vaccines in, for example, the poultry industry. Another potential problem is incomplete inactivation of viruses belonging to the Circoviridae and the proposed new group of Anelloviridae. For example, chicken infectious anemia virus (CAV or CIAV) and porcine circovirus (PCV), belonging to the Gyrovirinae and Circovirinae subfamilies, respectively, of the Circoviridae are highly resistant to chemical inactivation (Schat and van Santen, 2013) and could remain present in inactivated vaccines. Application of PCR techniques has

become a major tool to determine the absence of known extraneous agents (Mackay and Kriz, 2010).

The choice of live versus inactivated vaccines

The choice between live and inactivated vaccines is not always simple and depends on many factors, such as the type of immune response that is required for protection. For example, a live vaccine will be preferred if cell-mediated immune (CMI) responses are essential for solid protection (see Section Antigen Processing), although inclusion of some adjuvants can stimulate CMI responses (see below). A live vaccine may also be preferred if mucosal antibody responses (IgA) are needed for protection. Production of IgA antibodies is stronger after natural exposure (see Section Vaccination Procedures) than after parenteral injection, which is typically used with inactivated vaccines. However, if IgG responses are critical for protection, inactivated vaccines will be highly effective, although adjuvants (see below) will be needed in most if not all inactivated vaccines.

In addition to the need to inject inactivated vaccines, which is a distinct disadvantage in the poultry and aquaculture industries, there is a second disadvantage: the need to produce high-titered products because there is no amplification of the vaccine in the vaccinated host. This is not always a problem; high titers can be obtained, especially when vaccines are made in embryonated chicken eggs. However, it makes the inactivated product more expensive than a live vaccine. Inactivated vaccines also have certain advantages over live vaccines. Because attenuation is not a linear process, live attenuated vaccines most likely contain populations that differ in the degree of attenuation, which may cause problems, especially if the animals are immunosuppressed by stress or subclinical immunosuppressive infections. Moreover, there is always the potential that the vaccine reverts back to become pathogenic or recombines with the wild-type viruses generating a recombinant. Live vaccines induce immune responses by replicating in the host, which can cause some degree of tissue damage. These vaccine reactions can be complicated by secondary infections leading to economic losses. Certain live vaccines are also contraindicated during pregnancies. None of these problems occur with properly inactivated vaccines except for some local tissue damage caused by adjuvants.

Inactivated vaccines are sometimes the only choice because virus cannot be attenuated as is the case for FMD. In other cases a new disease appears causing devastating losses, and a vaccine needs to be developed in a very short time span preventing the development of a live attenuated or recombinant vaccine. This was the case when Schmallenberg virus, a novel insect-transmitted Orthobunyavirus, appeared in 2011 in Europe, causing severe fetal malformation and still births in ruminants. The rapid development of inactivated vaccines has significantly reduced the impact of this pathogen (Wernike *et al.*, 2013). Autogenous vaccines are sometimes developed to solve local or regional problems by isolating the pathogen and producing a killed product. This type of vaccine is subject to authorization by the State Veterinarian in the United States.

If long-lasting immunity with high antibody titers is important, for example, for the transfer of IgY from the hen to her offspring through the yolk, a primer with a live vaccine followed by a killed vaccine is the best option. Boosting the immune response by second vaccination with a live vaccine is in general not recommended because the primary immune response will prevent replication of the booster vaccine.

Biotechnology-based vaccines

Since the advance in recombinant DNA technology several approaches have been used or proposed to produce new vaccines, but in actuality few have been authorized for use in the United States or elsewhere in the world. The following technologies have been used to develop commercial products: deletion mutants, vectored vaccines expressing antigens to different pathogens, subunit vaccines including virus-like particles (VLP), and DNA vaccines. The basic science on which these vaccines are based is briefly discussed in this section. More detailed information can be found in several review papers and the actual use in production animals is discussed in the four sections on vaccination in production animals. Many of the biotechnology-based vaccines can be used in DIVA strategies, and specific tests to differentiate between vaccine responses and pathogen infection are an integral part of the development of these vaccines. Tests include ELISAs as well as PCR-based assays. The former confirms the absence of antibodies against the deleted gene products after vaccination, although these antibodies are present after infection with the field strains of the pathogen. In the case of AIV, recombinant vaccines produce antibodies to the neuraminidase protein that is different from the field virus. PCR-based assays can also be used as in the case with the gE deletion mutant of bovine herpesvirus 1 (BoHV-1). In this test, a gE DNA fragment is amplified and analyzed by restriction enzymes (Schynts *et al.*, 1999). With the advance in new sequencing techniques, single-nucleotide polymorphism analysis could also be used in this example.

The possibility of deleting specific genes without significantly altering their immunogenicity was the basis for the first recombinant vaccine licensed in the United States. Deletion of two genes, Tk and glycoprotein III, in suid herpesvirus 1 (aka pseudorabies virus) led to the development of a marker vaccine that was successfully used to eradicate Aujeszky's disease in the commercial swine population in the United States in 2005 (USDA, 2008; Kit, 1990; CAST, 2008). Since then, several deletion and insertion techniques have been developed – mostly for herpesviruses and poxviruses but also for RNA viruses. The use of bacterial artificial chromosomes has increased the possibilities drastically by allowing the cloning of large DNA sequences, such as herpesvirus and poxvirus genomes and infectious cDNA (complementary DNA) clones of RNA viruses (Tischer and Kaufer, 2012). The use of *en passant* mutagenesis facilitates the deletion or mutagenesis of specific genes as well as the generation of vectored vaccines expressing foreign genes (Tischer *et al.*, 2010). Currently, several vaccines for chickens using fowlpox or HVT as a vector and expressing genes for AIV, infectious laryngotracheitis virus (ILTV), Newcastle disease virus (NDV), or infectious bursal disease virus (IBDV) have been licensed in the United States as well as in other parts of the world. There are currently no vectored vaccines for cattle and swine licensed in the United States (Anonymous, 2013c), but the gE deletion mutant of BoHV-1 has been licensed in the European Union for the control and

possible eradication of BoHV-1, which is the cause of infectious bovine rhinotracheitis.

In addition to poxvirus and HVT, NDV vaccine strains Lasota or B1 are also used as a vector for the expression of foreign genes, such as the HA gene of AIV (Park *et al.*, 2006). Recombinant NDV–HA vaccines are currently produced in Mexico. Adenoviruses have also been proposed as a vector for use in poultry and swine vaccines (Toro *et al.*, 2010) but are not yet available commercially.

Bacteria can also be used to generate apathogenic deletion mutants by removing pathogenicity genes. Curtiss and Hassan (Curtiss and Hassan, 1996) deleted genes for adenylate cyclase (*cya*) and cAMP receptor protein (*crp*) in *Salmonella enterica* serovar typhimurium (*Sa. typhimurium*) strain χ 3985. Vaccination of 1-day-old chicks generated significant antibody responses and booster vaccination at 16 or 18 weeks of age prevented egg transmission after challenge with highly invasive strains of *Sa. typhimurium* and *Sa. enterica* serovar enteritidis. The vaccine strain is currently licensed in the United States, Canada, New Zealand, and the Dominican Republic as AviPro Megan Vac 1 and AviPro Megan Egg (Lohmann Animal Health). This strain can also be used as a vector to immunize against other pathogens, especially when strong mucosal immunity is important; for example, to protect against *Eimeria acervulina* (Konjufca *et al.*, 2006). Since then several papers have been published showing protection against different pathogens after immunization with recombinant *Sa. typhimurium*, but it is not currently used commercially as a vector.

Subunit vaccines comprise the second group of biotechnology-derived vaccines and include proteins and VLP. Recombinant proteins and VLP can be produced by transfecting or infecting different cells, including *E. coli*, yeast, insect and mammalian cells. The choice of cells depends on a number of factors, such as posttranslational modifications, yield of protein, and purification methods. The platform of choice is currently the baculovirus system using insect cell lines or *Trichoplusia ni* (cabbage looper) larvae (Mena and Kamen, 2011; Crisci *et al.*, 2012). Recombinant protein vaccines that consist of the envelope glycoprotein E2 of classic swine fever (CSF) virus, a pestivirus, and produced in the baculovirus system have been licensed in Europe for the control of CSF. Vaccines that consist of recombinant proteins need to be injected and require adjuvants to induce strong immune responses. A problem with this type of vaccine is that the protein folding may not produce conformational (tridimensional) epitopes, which are often important for the production of relevant antibodies. This is not a problem if the antibodies are generated against linear epitopes.

VLP are self-forming virus-like structures lacking a virus genome that are generated when virus structural genes are expressed simultaneously (CAST, 2008). This can be achieved by infection of insect cell lines with recombinant baculoviruses expressing the structural genes. Crisci *et al.* (2012) listed several advantages for the use of VLPs: (1) the well-defined geometric structure with a highly repetitive expression of proteins on the surface presents PAMP motifs for triggering the immune response, (2) good cross-presentation to both MHC I and II by uptake by the APC resulting in CMI and antibody responses, (3) presents conformational epitopes, (4) is not infectious, and (5) can present foreign epitopes and can be used in DIVA strategies. One of the disadvantages of VLP vaccines prepared with the baculovirus system is that baculovirus particles that need to be removed can also be produced (Crisci *et al.*, 2012). Thus far only one VLP vaccine has been licensed for animals: Porcilis® PCV (Merck) for protection against PCV.

A slightly different approach has been used by Harrisvaccines (Ames, IA, USA) to generate RNA replicon vaccines for a H3N2 vaccine for swine. This vaccine has been licensed by the USDA (Anonymous, 2013c). The platform technology is based on alphavirus-derived nonstructural genes to which genes of interest can be fused. The construct is transfected into VERO cells, which then produce particles containing the recombinant RNA molecules. Although their website indicates that the method for particle production is proprietary, it is likely that these particles have the characteristics of VLP.

The finding that injection of mice with plasmid DNA encoding proteins resulted in expression of these proteins led to the concept that DNA could be used to immunize animals (reviewed by Dunham, 2002; Fowler and Barnett, 2012; CAST, 2008, and references therein). DNA vaccination is of interest because the DNA fragment codes only for part of the pathogen; thus, there is no risk that the pathogen escapes into the environment. The unmethylated CpG sequences in the DNA interacts with Toll-like receptors (TLR), thus enhancing innate responses. Interestingly, DNA vaccination sometimes induces strong CMI immune responses without the antibody responses, which complicates monitoring if appropriate levels of protection have been achieved. The proposed mechanism for the induction of both types of immune responses is that APC are directly stimulated by transfection of the plasmid into the APC or by proteins expressed in transfected somatic cells. Although DNA vaccines have attracted strong interest for their potential use in humans, the development of vaccines for production animals has been lacking with one exception. A DNA vaccine to protect salmonids against infectious hematopoietic necrosis virus has been licensed in Canada (Alonso and Leong, 2013) (see Section Vaccines for Fish). One of the problems is that injection of plasmids into the muscle or dermis does not always result in adequate responses without the addition of an immunogenic protein and or cytokines or unless multiple injections are given. The use of a gene gun administering gold particles coated with DNA has improved the results probably by delivering the vaccine into the epidermis, which is rich in professional APC (keratinocytes and Langerhans cells) (Fuller *et al.*, 2006).

Adjuvants

Killed vaccines, including recombinant protein vaccines, are frequently used with adjuvants to increase the immunogenicity. Most of the adjuvants used in vaccines for production animals and humans consist of aluminum- or oil-based emulsions (reviewed in Fox and Haensler, 2013; Schijns and Lavelle, 2011; Schijns *et al.*, 2014). Mineral oil or natural oils together with surfactants are used to prepare the oil-based emulsions. Squalene, a naturally occurring substance in plants and animals, including humans, has replaced mineral oil-based formulations in human vaccines (Fox and Haensler, 2013). Final compositions of adjuvants are frequently proprietary information and in animal vaccines are based in part

on price considerations, in addition to immunostimulatory properties.

Although the use of adjuvants has a long history, the actual mechanisms involved are still poorly understood (reviewed in Schijns and Lavelle, 2011; Schijns *et al.*, 2014; Mount *et al.*, 2013). The aluminum- and oil-based adjuvants remain present for some time after vaccination, providing a depot function for antigen release, which has been named signal 1 facilitators. However, the depot also causes tissue damage, thus facilitating an inflammatory response (signal 2 facilitators). The former results in gradual release of the antigen to macrophages and APC, whereas the latter activates the innate immune response pathway by providing ligands to PRR, such as TLR (see Section Relevant Immune Responses). The use of adjuvants in production animals can cause economic problems if the resulting tissue damage decreases the value of the product (see Section Selected Examples of Vaccines in the Four Groups of Production Animals).

Based on the current understanding of the initiation of innate immune responses, research to develop new and improved adjuvants stimulating CMI and antibody responses is being conducted (e.g., Mount *et al.*, 2013). Most of this research is directed toward the development of adjuvants for human vaccines. Incorporation of new adjuvants into vaccines for production animals will only be done if it provides economic value, for example, by less damage to meat products.

Vaccination Procedures

To obtain optimal protection, vaccines must be administered using the correct procedures as outlined by the manufacturers. Unfortunately, these recommendations are not always followed, especially if vaccines are provided by other methods than injection. In the case of cattle and swine, vaccines are mostly administered by subcutaneous (sc), intradermal, or intramuscular (im) injection. The location of injection may depend on the preference of the veterinarian and the owner of the animals. Some vaccines can be given intranasally, such as the recombinant vaccine against BoHV-1 (Schynts *et al.*, 1999) in cattle or deletion mutant vaccines for Aujeszky's disease in swine, but this may not always be practical. Oral vaccination can be used for some of the bacterial vaccines in swine by adding the vaccine to the drinking water. Aerosol vaccination to protect piglets against *Mycoplasma hyopneumoniae* is possible (Murphy *et al.*, 1993; Feng *et al.*, 2013), but it is not clear whether this is currently used.

Poultry vaccines can be given by *in ovo* injection or in chickens by spray, intraocular or eye drop, in the drinking water, wing-web stab, or by sc or im injection. In this article the author has briefly reviewed these different techniques: detailed information on the advantages and disadvantages has been discussed by Collett (2013). The concept of *in ovo* vaccination was developed by Sharma and Burmester (1982) for the HVT Marek's disease vaccine. The development of machines for *in ovo* vaccination was pioneered by Embrex (now Zoetis) and is widely used to vaccinate broiler embryos. Current machines can vaccinate up to 70 000 eggs h^{-1} and at the same time remove infertile eggs and eggs with embryos that died within the first 10 days of incubation (**Figure 3**). The mechanisms involved in early protection are not completely understood but probably involve early activation of innate immune responses and, if the machine is properly calibrated,



Figure 3 An automated *in ovo* vaccination device shown with an egg candling module and a capacity to inoculate up to 70 000 eggs h^{-1}. At approximately 18 days of incubation the flats with eggs are loaded on an egg remover module (right front) where infertile eggs and eggs with dead embryos are removed, thereby reducing chances of contamination. The flats are then moved to the next module for vaccine injection/delivery through a multiple-head, injector assembly that consists of a punch and needle system. After injection, the flats are moved to the transfer table module where eggs are automatically transferred to hatching baskets to be moved into the hatching incubator. Photo of the Embrex® systems (Inovoject® vaccination device with Vaccine Saver® feature and egg remover module) courtesy of Zoetis Inc.

approximately 100% of the embryos will receive the correct vaccine dose. This is in contrast with vaccination of newly hatched chicks at the hatchery by sc injection, where chicks are often not at all or improperly vaccinated. One-day-old chicks are vaccinated before leaving the hatchery by sc injection, spray, and ocular or nasal drop. Spray vaccination at the hatchery is done in a cabinet where the boxes with chicks receive the spray. At the farm, spray vaccination is often employed for respiratory vaccines using adaptations of insecticide spray equipment. Droplet size is crucial in both situations with 100–150 μm being optimal. Smaller droplets may cause undesirable vaccine reactions. The labor-intensive eye or nasal drop vaccination is probably not used in many countries due to labor costs, although it is used in countries like India at the farm level instead of spray vaccination. Vaccination by drinking water is effective but requires proper preparation of the equipment and birds. Flushing the system to remove all disinfectants is important and if the only water supply is chlorinated water it will not work at all. Before vaccinating, water must be withheld from the birds so that they drink as soon as water becomes available. Proper preparation of the vaccine solution is done by adding buffers to the drinking water (e.g., skim milk), which needs to be well mixed with the vaccine. Improper application of any of the vaccination techniques can cause disastrous results.

Vaccination of fish has become very important in aquaculture. Originally, it was thought that this could be done by immersion of fish in a tank with vaccine. However, this required large concentrations of vaccine, which made this method prohibitively expensive. Moreover, protective immunity was not uniformly achieved by this method. Currently, vaccination is done by intraperitoneal injection in almost all instances (Rødseth and Moen, personal communication). Fish are placed briefly in an anesthetic solution before being injected manually (**Figures 4(a)** and **(b)**). The Norwegian company Skala Maskon has developed a machine that can vaccinate 20 000 salmon h^{-1} and separate the fish into different weight classes while rejecting malformed fish (**Figure 5**). In some countries oral vaccination is used by encapsulating the vaccine in different components (reviewed by Gomez-Casado *et al.*, 2011).

Selected Examples of Vaccines in the Four Groups of Production Animals

In this section, the author has highlighted some of the specific aspects for each group of animals focusing on diseases of global interest. It is not possible to provide detailed vaccination schemes for production animals for several reasons. First of all, it is almost impossible to obtain reliable information on regional disease incidence and vaccine use. Two examples illustrate the geographic differences in vaccine use. The United States has been free of FMD virus (FMDV) since 1929 (McReynolds and Sanderson, 2014), whereas FMDV is still endemic in large parts of Asia. Similar examples can be given for the poultry industry in regard to H5N1 highly pathogenic (HP)AIV. Several countries in Asia and Egypt routinely vaccinate against the H5N1 AIV, whereas countries in Europe may use stamping out; however, the United States is free of HPAIV. Decisions on how to deal with these two diseases are determined by the national governments or the European Union.

The second reason is that veterinarians working for poultry producers often have to follow vaccination schemes that are implemented by the veterinary staff at the headquarters of large producers. These vaccination schedules can be based on regional differences in disease incidence, density of poultry farms in a given region, etc. This situation is very similar to that of the aquaculture industry. The list of bovine vaccines (**Table 3**, **Figure 6**) that are currently used in the United States is provided only to demonstrate the type of vaccines that are available, although these vaccines are not always used. Additional information on vaccines and their regional use can be obtained by accessing websites of the large vaccine manufacturers and government licensing agencies. Different articles in this Encyclopedia deal with descriptions of the common diseases in the four groups of food animals and the interested reader may refer to those articles for additional information.

Vaccines for Cattle

Cattle receive many vaccinations starting after 3 months of age when maternal immunity no longer interferes with vaccination by neutralizing the vaccine virus. **Table 3** provides an example



(a) (b)

Figure 4 (a) Manual vaccination of Atlantic salmon by intraperitonal injection. (b) Manual mass vaccination of Atlantic salmon performed by a professional team of vaccinators. Photos: MSD Animal Health.



Figure 5 A vaccination system for intraperitoneal injection of salmon. Fish enter in the Maskon anesthetizer and buffer tank (not shown) and are transported to the vaccination unit, which has injection sites. Location of the injection site and needle depth is adjusted for every fish based on the length of the fish. The unit is operated by one person and depending on the configuration, up to 20 000 fish can be vaccinated per hour.

Table 3 Vaccines for cattle available in the United States

Viruses	*Bacteria*	*Protozoa*
Infectious Bovine Rhinotracheitis (IBR)	Leptospira	*Neospora*
Bovine Viral Diarrhea (BVD)	Clostridia	Trichomoniasis
Bovine Respiratory Syncytial Virus (BRSV)	*Pasteurella* (Mannheimia)	
Parainfluenza (PI3)	Brucellosis	
Rotavirus	Vibriosis	
Coronavirus	Enteric *E. coli*	
Rabies	*Salmonella*	
Papilloma	Gram-negative core bacterins	
	Footrot	
	Hemophilus	
	Anthrax	
	Staphylococcus aureus	
	Johnes	
	Pink eye	
	Anaplasmosis	
	Foot warts	
	Mycoplasm	

Source: Warnick, L., Department of Population Medicine and Diagnostic Sciences, Cornell University.

of the types of vaccines available in the United States, whereas Figure 6 indicates the frequency of the use of the different vaccines (Data for 2007, provided by Professor L. Warnick, Department of Population Medicine and Diagnostic Sciences, Cornell University). It is noteworthy that the use of *Brucella* vaccines is different in the western part compared with the eastern part of the United States. This is most likely the consequence of the presence of *Brucella abortus* in free-living bison (*Bison bison*) and elk (*Cervus canadensis*) (Olsen, 2013) combined with the extensive ranching of cattle in the western half of the United States.

The following diseases are of global interest for which vaccines are available and are briefly discussed: mastitis, a major worldwide economic disease in dairy cattle; brucellosis is a major zoonotic disease, caused by *Brucella abortus* and a potential bioterrorism agent; and FMD.

Mastitis is an infection of the udder frequently caused by intramammary infection with *Staphylococcus aureus* (*St. aureus*) or different coliforms (e.g., *E. coli*, *Klebsiella* spp, and *Enterobacter* spp). The host response and pathogenesis of bacterial intramammary infections have recently been reviewed (Schukken *et al.*, 2011) and the interested reader may refer to this article for additional information. Production losses are caused by clinical mastitis, an obvious disease state, or subclinical mastitis when the somatic cell count (mostly leukocytes and some epithelial cells) is increased above 100 000 ml^{-1} of milk. Prevention of mastitis is primarily based on sound management practices and vaccination is considered an adjunct to the overall herd health management programs (Erskine, 2012). Vaccines against coliforms consist of Gram-negative 'core antigen' bacterins, referred to as GNCABs, using the Rc mutant strain O111:B4 of *E. coli*.

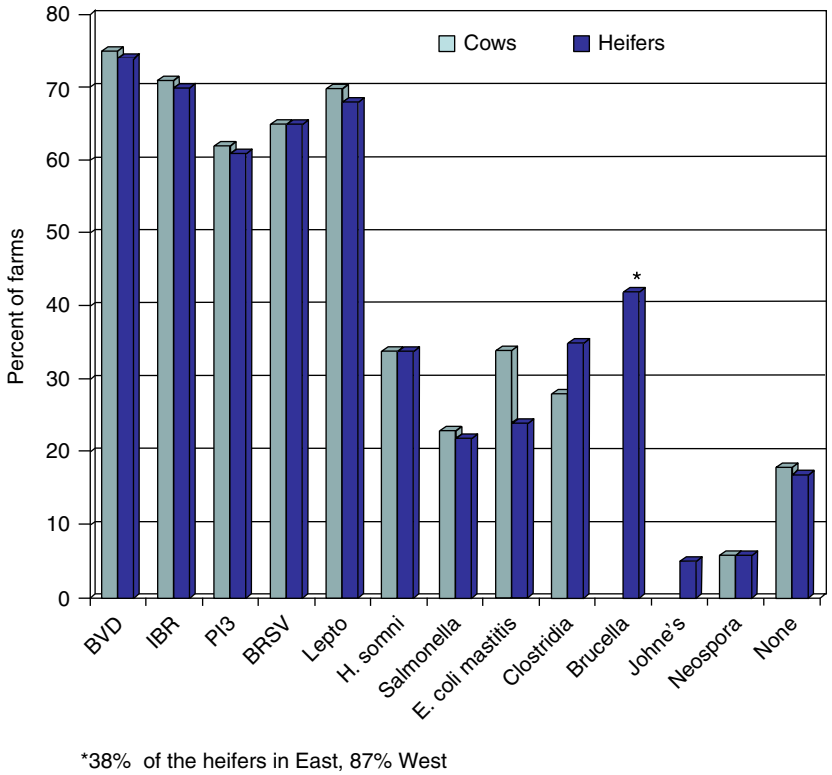


Figure 6 Graphical representation of the use of different vaccines for cattle in the United States. Note the difference in use of *Brucella abortus* vaccine between the eastern and the western half of the United States. Courtesy of Warnick, L.D., Department of Population Medicine and Diagnostic Sciences, Cornell University.

Vaccination with this vaccine, referred to as J5, provides moderate protection against coliforms. More problematic is the control of *St. aureus* mastitis by vaccination. Pereira et al. (2011) and Erskine (2012) reviewed the literature on *St. aureus* vaccines and found mixed results for the current commercial vaccines. New vaccine formulations using recombinant Target of RNAIII-Activating Protein (TRAP) (Leitner *et al.*, 2011) and ISCOMATRIX™ (Camussone *et al.*, 2013) show promising results for improved protection.

Brucella abortus, a Gram-negative intracellular bacterium, causes abortion and other reproductive diseases in cattle. Infection with *B. abortus* induces rather poor immunity because it can subvert innate and acquired responses. Vaccination using live attenuated strains (strain19 is most commonly used) together with elimination of positive animals is the preferred strategy. However, the currently available vaccine strains have some serious drawbacks. Vaccination can induce abortions in pregnant animals and does not prevent superinfection and seroconversion. Vaccinations need to be conducted with great care, because the vaccine strains can also cause infection in humans (Olsen, 2013).

Control of FMD by vaccination is complicated for several reasons (Parida, 2009). First of all, vaccine-induced protection lasts for the relatively short period of approximately 6 months; thus, yearly vaccinations are essential in endemic parts of the world. Second, there are at least seven distinct serotypes with considerable antigenic diversity within serotypes. As a consequence, vaccine formulations need to be carefully evaluated for efficacy, which is difficult to achieve. Challenge experiments for such evaluations require strict isolation facilities to prevent outbreaks. Third, current inactivated FMD vaccines require a cold chain, which is also a complicating factor, especially in tropical regions, impeding efficient immunizations.

In many parts of the world, tick-borne diseases are important in cattle with control often done by pushing the cattle into dip tanks that contain acaricides. The use of a recombinant vaccine based on gut glycoprotein BM86 of the *Rhipicephalus microplus* tick has been successfully used in Australia and Latin American countries (de la Fuente *et al.*, 2007). Unfortunately, the BM86 vaccine has limited activity against non-*Rhipicephalus* ticks, but it is likely that new candidate vaccine antigens will be discovered in the near future (de la Fuente and Merino, 2013).

Vaccines for Swine

The intensive swine industry uses several production systems, but all consist of farrowing, nursery, growing, and finishing units, with the latter two frequently combined into one unit. On some farms, all units are used in a continuous production system, preventing the use of an all-in/all-out system and thorough cleaning of the facilities. Other systems use fully separated facilities and the grower/finishing units may be completely different farms than the farrowing/nursery farms. Piglets are moved to nursery units after weaning at approximately 3 weeks of age, which is also the prime time for vaccinations by injection. In some instances a booster vaccination is given at 6 weeks of age. Sows can be vaccinated between

2 and 5 weeks before farrowing to increase antibodies in the colostrum. Although most vaccines are given by injection, attenuated live strains of bacteria (*Lawsonia intracellularis* causing ileitis and *Salmonella* and *E. coli* causing diarrhea) can be given in the drinking water. Over the past 20 years, two important new diseases have appeared worldwide in swine: PCV serotype 2 (PCV2) causing immunosuppression and wasting pigs, and porcine reproductive and respiratory syndrome (PRRS) caused by Arterivirus. Recombinant vaccines have been developed against PCV2 using VLP (Merck), a recombinant protein produced in a baculovirus system (Boehringer Ingelheim) or a recombinant hybrid inserting the VP2 gene of PCV2 into the genome of the nonpathogenic PCV serotype 1 virus (Zoetis). The latter is the only live vaccine against PCV2. Development of vaccines against PRRS is problematic for several reasons (Cruz *et al.*, 2010). Natural infection or attenuated vaccines induce weak innate immune responses and low levels of VN antibodies and virus-specific CTL. Moreover, PRRSV strains are highly diverse, especially for the immunodominant protein GP5. It is also suggested that CTL responses are more important for protective immunity than VN antibodies. Development of recombinant vaccines inducing strong CTL responses may solve the shortcomings of the current vaccines. Cruz *et al.* (2010) used a vectored vaccine with transmissible gastroenteritis virus as the backbone expressing two PRRSV antigens eliciting strong VN antibody and CTL responses as well as good mucosal immunity. Currently, this type of recombinant vaccine has not been licensed.

Vaccines for Poultry

Regional and national differences in prevalence of specific poultry diseases are well recognized. As a consequence, decisions on the selection of vaccines are frequently made by the veterinary staff of large integrated companies based on the regional needs and national policies. It is, therefore, not possible to provide detailed information on all poultry vaccines used in the world and hence only some general concepts are discussed.

Vaccination schedules depend on the type of bird; the needs for vaccination of grandparent and parent flocks are different than those for commercial layers and broilers. Because maternal antibodies are important for the protection of chicks, (grand) parent flocks are frequently vaccinated with a live vaccine to prime the immune response followed by a killed adjuvanted vaccine before lay to boost the antibody titers. Boosting with a live vaccine is not recommended because the neutralizing antibodies produced by the first vaccination interfere with vaccine virus replication from the booster vaccination.

The use of recombinant vectored vaccines has become a common practice in many parts of the world, mostly using HVT as the vector. Interestingly, HVT-vectored vaccines cannot be used together with conventional HVT, nor can different recombinant vaccines be used at the same time (e.g., HVT–IBD and HVT–NDV) unless the two inserts are present in the same vector. Possible explanations are that the insert negatively influences the replication rate of the vectored vaccine in the bird with the consequence that conventional HVT initiates immune responses before the recombinant HVT, thus curtailing the infection of the latter. The second explanation could be that the vectored vaccine has a higher passage level *in vitro* and therefore replicates slower in the bird with the same consequences. Similar circumstances may explain the recommendation against using two different recombinant HVT vaccines. The consequence of using recombinant HVT instead of the standard HVT is that protection against MD may be suboptimal and therefore protection to MD depends more on the inclusion of SB-1 and or CVI988 (aka as Rispens). The slower replication of, for example, recombinant HVT expressing VP2 of IBDV may still protect against IBD because maternal antibodies will provide sufficient protection against IBD during the first 14 days after hatching.

Vaccination against AIV provides a challenge, especially since the occurrence of highly pathogenic H5N1 AIV. Some countries do not allow vaccination, whereas others use killed adjuvanted vaccines. AIV, a member of the orthomyxoviridae, has a genome that consists of eight different RNA molecules, one of which codes for the hemagglutinin (H) protein and a second one for the neuraminidase (N) protein. Chickens make antibodies against both proteins, but the antibodies against H are the key for neutralizing the virus. By changing the N gene to a different neuraminidase gene (e.g., N2 in the case of a vaccine against H5N1), it is possible to monitor flocks for field exposure to H5N1. Recombinant vaccines expressing a different N protein than the field virus have successfully been used in Italy during outbreaks of avian influenza (Capua *et al.*, 2003).

Vaccines for Fish

Globally, approximately 600 fish species are farmed (Brudeseth *et al.*, 2013), but only a few species are produced at high densities, such as salmonids. Vaccine development has become an integral part of aquaculture management for these species and several review papers have summarized the availability of vaccines against viral and bacterial diseases (Gomez-Casado *et al.*, 2011; Salgado-Miranda *et al.*, 2013; Brudeseth *et al.*, 2013). One of the problems identified in these papers relates to the fact that almost all vaccines consist of water-in-oil emulsions that need to be injected. The adjuvants in the vaccine can cause adhesions in the peritoneal cavity, which negatively influences the quality of the fish meat. To reduce the impact of adjuvants on the meat quality, multivalent vaccines that contain antigens against different pathogens are frequently used. The type of combinations depends on the geographic locations (Brudeseth *et al.*, 2013). The other major problem is that a number of viral diseases can cause high mortality in swim-up fry. Unfortunately, the very young fish have an immature immune system, are too small to be injected, and maternal immunity is not very effective in fish (see Section Maternal Immunity). Live, attenuated vaccine strains cannot be used mainly because attenuation in one fish species does not translate to attenuation in other fish species. Vaccination by immersion is in general not cost effective, although it is used with some bacterins in channel catfish and salmonids (e.g., *Yersinia ruckeri* bacterin).

As mentioned in the Section 'Vaccination Procedures,' DNA vaccines for IHNV are licensed in Canada. IM inoculation of plasmid DNA that contain the IHNV glycoprotein G gene provides long-term protection against challenge without causing long-term lesions at the site of inoculation (Kurath *et al.*, 2006). Protective immunity is likely achieved by

a combination of VN antibodies, CTL, and NK cells based on studies in rainbow trout (*Oncorhunchus mykiss*) (Utke *et al.*, 2008). Interestingly, vaccination with plasmid DNA for IHNV glycoprotein G induced not only rapid protection against challenge with IHNV but also cross-protection against another rhabdovirus (viral hemorrhagic septicemia virus) infection for the first 2 months postvaccination (Lorenzen *et al.*, 2002). An experimental DNA vaccine expressing VP2 of IPNV encapsulated in alginate microspheres showed good protection against challenge 15 and 30 days after oral vaccination (de las Heras *et al.*, 2010). It is expected that DNA vaccines will become an important part of fish health management if oral vaccination works in general and if safety concerns can be overcome.

Conclusions

Vaccines remain an important part of health management programs in food animal production systems. It is expected that progress will be made over the next 5 years toward safe vaccines using different recombinant technologies. The use of vectored live vaccines in poultry and DNA vaccines in fish has shown that these applications are safe and provide strong protection. Research into the mechanisms of adjuvants will also lead to the development of science-based approaches stimulating innate and acquired immune responses.

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See also: Animal Health: Foot-and-Mouth Disease. Asian Aquaculture. Beef Cattle. Dairy Animals. Detection and Causes of Bovine Mastitis with Emphasis on *Staphylococcus aureus*. Genomics of Food Animals. Marek's Disease and Differential Diagnosis with Other Tumor Viral Diseases of Poultry. Poultry and Avian Diseases. Swine Diseases and Disorders

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Virtual Water and Water Footprint of Food Production and Processing

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Glossary

Blue water The ground- and surface water; it is the fraction of water which is available as drinking water, process water, water for irrigation in agriculture; it is used as a transport medium and many other purposes.

Evapotranspiration The sum of water evaporation and plant transpiration from the earth's land surface into the atmosphere.

Gray water The volume of freshwater that is required to assimilate the load of pollutants based on existing ambient water quality standards.

Green water The water which is bound in the soil and in green plants; it is under normal circumstances the basis for agricultural production.

Virtual water The amount of water needed for the production and handling of any type of product, for example, food; it is also referred to as hidden water.

The Origin of Water on Earth

Water (H_2O) is not only one of the most common molecules on the surface of the earth but it is also one of the most abundant molecules in the universe, where it originated within the clouds of interstellar media as a chemical compound of hydrogen and oxygen. It is not entirely clear where the Earth got its water from, but it can be assumed that water was part of the protoplanetary material from which the planets were formed. Some of this water was released during the formation of the Earth, and it is understood that there is still a major amount of water entrapped in the Earth's crust and mantle. Through volcanic activity, annually up to one-tenth cubic kilometer of juvenile water is expelled as overheated steam or as part of the magma, which may have a water content of 5% by weight, according to certain assumptions. A significant part of the water on earth may also have been contributed by icy comets which smashed into the young earth (Müller and Lesch, 2003; Shiklomanov, 1993).

Distribution of Water on Earth

Water on Earth is unevenly distributed in the Northern Hemisphere, where the world's oceans occupy 61% of the area and in the Southern Hemisphere 81%. On the so called water-sphere of the globe, approximately 89% of the surface is covered by water, and on the land-sphere 43% of the surface is covered by water; all together, 71% of the Earth's surface is covered by water, as depicted in **Figure 1**.

The total water resources on earth are approximately 1.4 billion km^3; the volume of freshwater resources is approximately 35 million km^3; this means that approximately 2.5% of the total volume is freshwater. Of the freshwater resources, approximately 24 million km^3 or 68.7% is permanently affixed in the form of ice and permanent snow cover in mountainous regions and the Antarctic and Arctic regions. Some 10.4 million km^3, i.e., 29.9% of the freshwater pool is stored underground as groundwater; soil moisture, permafrost areas, and swamps bind approximately 0.4 million km^3, or 1.14%; that leaves approximately 0.09 million km^3 of freshwater, or approximately 0.26% of the world's freshwater available for human use; that means only a minute fraction of the global water resources are accessible for economic needs. It should be noted at this point that there are slightly different reference data presented in the literature (**Table 1**; Pidwirny, 2006).

The Global Water Cycle

Energized by solar radiation, water evaporates and sublimates from open water, snow, and ice surfaces, as well as from all humid surfaces with a water vapor pressure and from plants transpiring into the atmosphere. It is estimated that the atmosphere contains a buffer of approximately 13 000 km^3 of water as vapor or in a condensed state. When the dew point of the water vapor in the atmosphere is passed, water precipitates as rain or snow. Globally all forms of precipitation are in equilibrium with all forms of evaporation and sublimation.

On a long-term average, rainfall on the land surface amounts to approximately 110 000 $km^3\ year^{-1}$; of this quantity, approximately 70 000 $km^3\ year^{-1}$ evaporates again into the atmosphere and approximately 40 000 $km^3\ year^{-1}$ runs off into the oceans to cover, together with a groundwater flow into the oceans, the oceans' net evaporation losses. These losses arise from the fact that the amount of evaporation from the ocean surface exceeds the amount of precipitation directly onto the oceans (Zehnder, 2002; **Figure 2**).

The residence times of the various water fractions differ considerably. The fastest turnover occurs in the atmosphere, where water is replaced every 8 days. Water in rivers is on average renewed every 16 days. Residence times in bodies of stagnant water and ice vary considerably, between several months to thousands or millions of years (**Table 2**).

The global water cycle is of primary importance for the hydrologic inventory. Through the evaporation of sea water and land surface water, a permanent supply of 'clean,' purified water is generated; this flux of water may contain different kind of aerosols when it precipitates. Because of the high specific heat and the high condensation/evaporation heat, evaporation and precipitation processes have also a pronounced impact on the global weather.

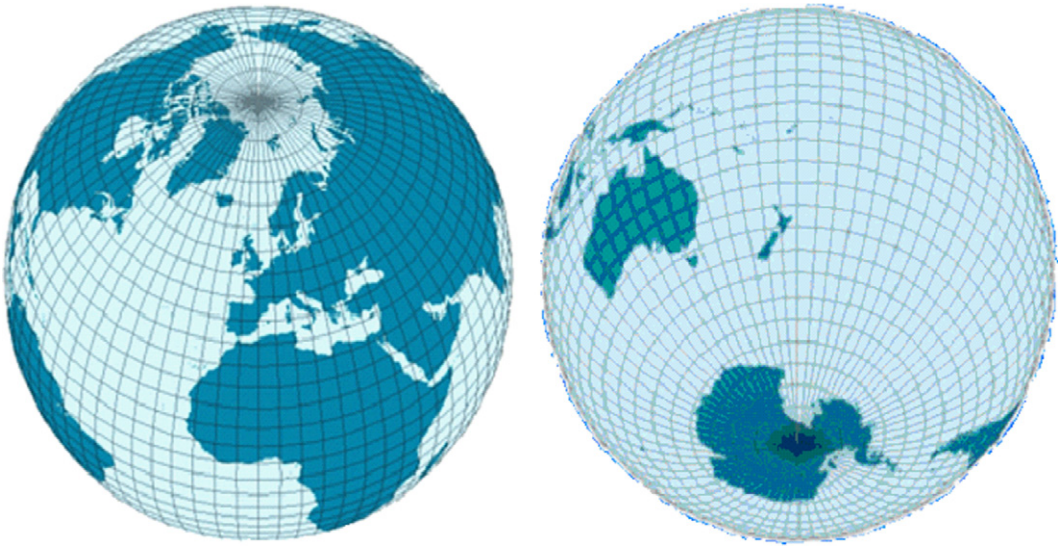


Figure 1 The land and the water sphere.

Table 1 Global water resources

Global water resources					
Approximately 1.4 billion km³ (1.386 billion km³)					
Sea (salt) water		*Freshwater*			
97.5%	*1.351 4 billion km³*	*2.5%*	*0.034 7 billion km³*		
Sea water composition		*Type of freshwater*	*Global water resources (%)*	*Freshwater resources (%)*	*Amount (in billion km³)*
Contributing to sea water salinity	Concentration in o/oo (parts per thousand) in average sea water	Glaciers and permanent snow	1.717 5	68.7	0.023 8
		Groundwater	0.747 5	29.9	0.010 4
		Soil moisture, swamps and permafrost	0.028 5	1.14	0.000 4
Chloride	19.345				
Sodium	10.752	Lakes and rivers (only water share)	0.006 5	0.26	0.000 09
Sulfate	2.701				
Magnesium	1.295	Utilization of renewable fresh water resources			
Calcium	0.416				
Potassium	0.390	Irrigation: 70%			
		Industry: 22%			
		Domestic use: 8% (12.500 km³)			
According to Castro and Huber, 2012					
		Total	2.5	100	0.034 7

Source: Reproduced from United Nations Environment Programme. Available at: http://webworld.unesco.org/water/ihp/publications/waterway/webpc/definition.html

The precipitation as rain or snow is not evenly distributed on the earth's surface; nor is it evenly distributed over the year. Areas with high precipitations are located between the equator and the 30th degree of southern latitude. Examples of seasons with high precipitations are the West African and Asian-Australian monsoons. Besides zones of high precipitation, zones with almost no precipitation stretch mainly from the equator to 30° N; zones of moderate precipitation are mainly above 30° N (**Figures 3** and **4**).

It is anticipated that with rising environmental temperatures in future years, more areas around the globe will experience droughts, especially in the Americas, Southern Africa, the Middle East, and Australia.

High precipitation rates such as monsoons, however, as well as cases of sudden snowmelt, frequently cause major floods; the runoff of floodwater into the ocean may consist of 75% (30 000 $km^3\ year^{-1}$) of the water flux into the oceans. Heavy rainfalls and floodwater runoff are of significant

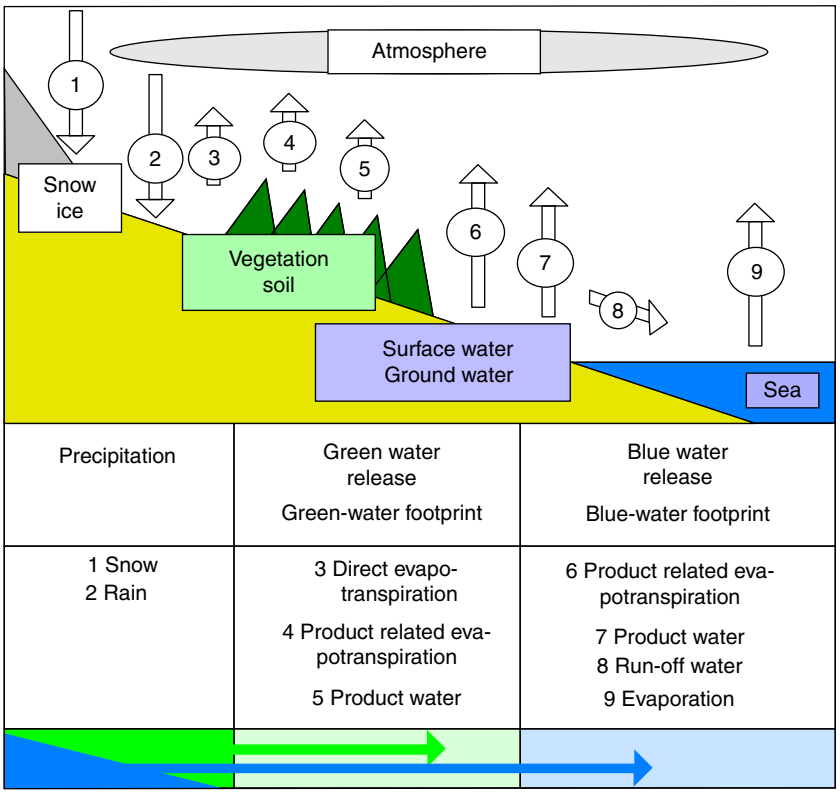


Figure 2 The water cycle.

Table 2 Typical residence times of water found in various reservoirs

Reservoir	*Residence time*
Oceans	3000–3230 years
Glaciers	20–100 years
(Antarctic glaciers)	Millions of years (Ingólfsson, 2004)
Seasonal snow cover	2–6 months
Soil moisture	1–2 months
Groundwater: shallow	100–200 years
Groundwater: deep	10 000 years
Lakes	50–100 years
Rivers	2–6 months
Atmosphere	9 days

Source: Reproduced from Pidwirny, M., 2006. The Hydrologic Cycle. Fundamentals of Physical Geography, second ed. Available at: http://www.physicalgeography.net/fundamentals/8b.html (accessed 07.11.13).

importance for the desalination of the soil and cleaning of contaminated water systems.

Physical Properties of Water Related to Food Processing

Water is the only substance that occurs in large amounts in all three physical states on earth and in the atmosphere. It is present as vapor, ice (particles), as a liquid (rain drops) in the atmosphere, in liquid form as surface water, and in various forms as underground water, as well as snow and ice in the polar and alpine regions of the globe. It is frequently overlooked that water also can be found in the supercritical phase in volcanic vents.

A water molecule consists of one oxygen and two hydrogen atoms connected by covalent bonds. Because of the nonlinear structure and the fact that the oxygen atom has a higher electronegativity than the hydrogen atoms, and the hydrogen atoms are slightly positive, water is a polar molecule with an electrical dipole moment. Because of the electrical properties of its molecule, water usually forms large molecule clusters and exhibits special physical properties including high surface tension and capillary forces. A schematic orbital model is given in Figure 5.

Through its unique physical-chemical properties, water is one of the substances on which life on earth depends; without water life on earth would not exist in its present form. In nature, water acts as a solvent, as a carrier of nutrients and metabolites, as a catalyst of reactions, as a stabilizer of biopolymers, as a plasticizer, and many other reactions. Because of its properties as a solvent, water can hardly be found as a pure substance. Water is the major component of almost all living species, including food materials, with an average water content of approximately 80%±10% of the total weight. Water determines the properties of the food materials, their structure, appearance, taste, and stability, and, in the end, the ways in which a product can be processed. The rather low viscosity and high surface tension of water allow for fast flows and for storage of major amounts in porous systems like soil (for details on these physical properties see Tables 3 and 4 and Figure 6).

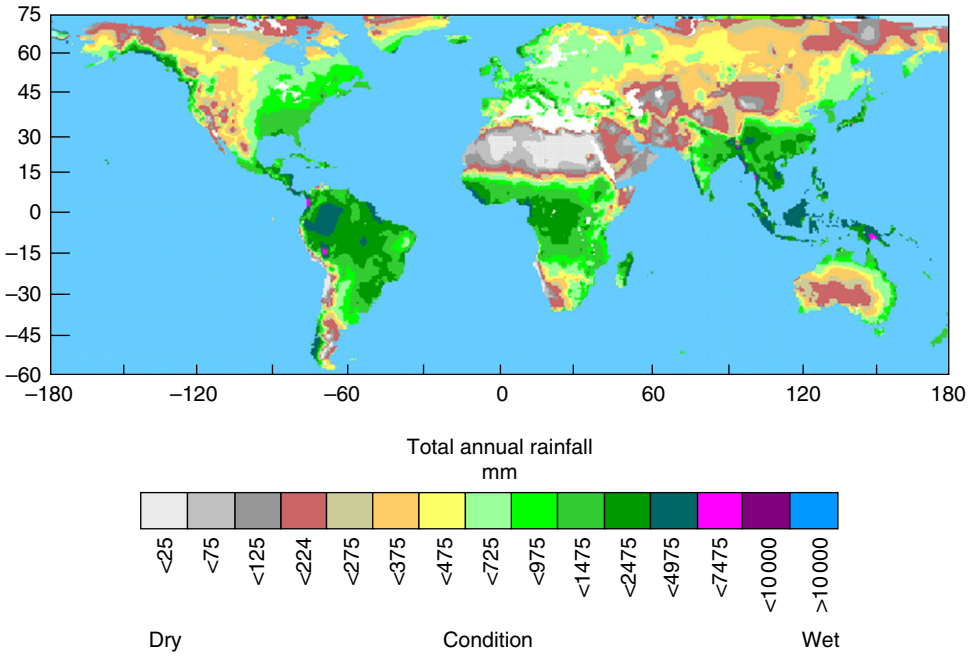


Figure 3 Present time global distribution of rainfall. Reproduced from Dai, A., 2010. Drought Under Global Warming: A Review. Available at: http://www2.ucar.edu/atmosnews/news/2904/climate-change-drought-may-threaten-much-globe-within-decades#mediaterms (accessed 29.01.14).

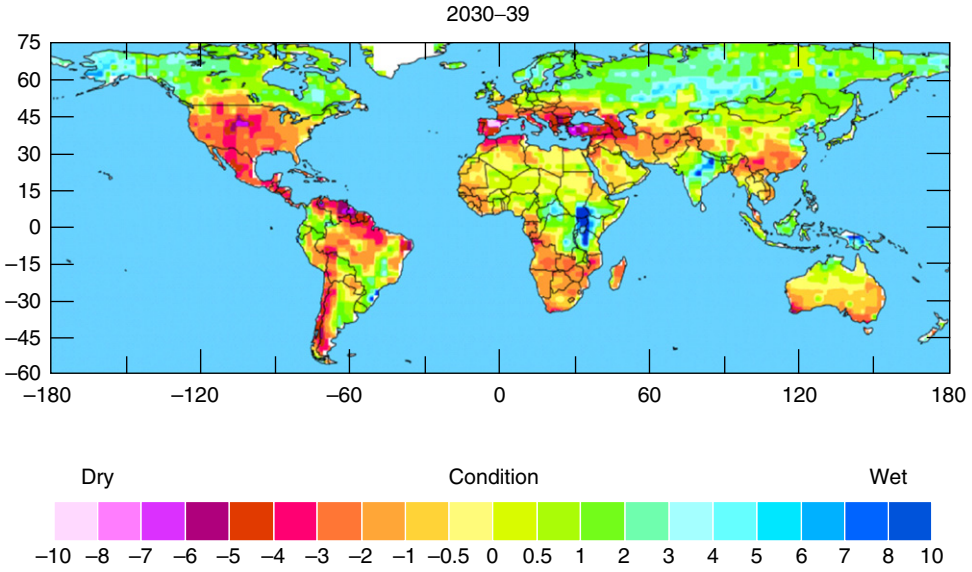


Figure 4 Predicted global distribution of rainfall in the decade 2030–39. Reproduced from Dai, A., 2010. Drought Under Global Warming: A Review. Available at: http://www2.ucar.edu/atmosnews/news/2904/climate-change-drought-may-threaten-much-globe-within-decades#mediaterms (accessed 29.01.14).

The Virtual Water and the Water Footprint Concept with Regard to Food Production, Processing, and Distribution

Global Water Availability and Water Consumption

Precipitation of water is not evenly distributed over the globe, as mentioned above (see Figure 4); major amounts of precipitation are released over areas where they cannot be utilized for food production and other human needs. To satisfy the needs of populations with water shortages, or more precisely with an insufficient water supply for the production of an adequate food supply, export and import of goods relying on the presence of water for their production is the consequence.

To make things more complicated, the distribution of water resources does not correspond to the distribution of the world's population (Table 5).

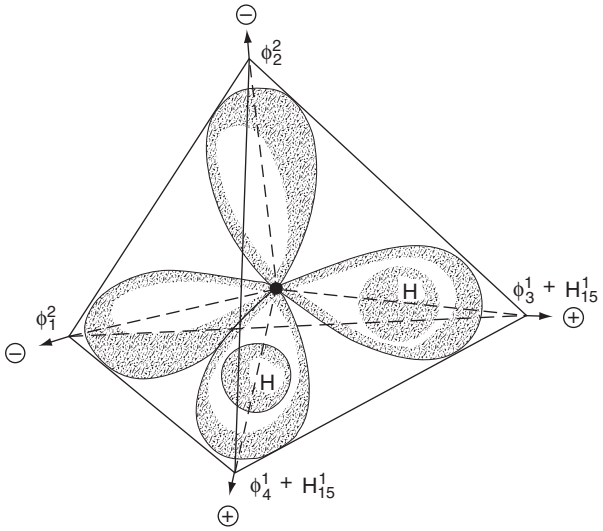


Figure 5 Schematic orbital model of a water molecule. Reproduced from Spiess, W.E.L., 2002/2003. Chilling and Freezing: An Introduction Chilling and Freezing to Food, Lectures on Freezing of Food Materials. Seoul National University.

Table 3 Physical properties of water

Physical properties of water	
General properties	
Molecular formula	H_2O
Molar mass	18.015 28(33) g mol^{-1}
Density	1000 kg m^{-3}, liquid (4 °C) 917 kg m^{-3}, solid
Melting point	0 °C
Boiling point	99.98 °C
Acidity (pK_a)	15.74 ~35–36
Basicity (pK_b)	15.74
Refractive index (n_D)	1.333 0
Viscosity	0.001 Pa s at 20 °C
pH	7 at 25 °C
Surface tension	72.8 mN m^{-1}
Dielectric constant ε	(0 °C) 87.9; (50 °C) 69.88; and (100 °C) 55.58
Heat capacity C_p	(0 °C) 4.2; (20 °C) 4.18; and (100 °C) 4.22 J $(g\ K)^{-1}$ at 100 kPa
Heats of vaporization H_v	(100 °C) 2256 kJ kg^{-1}
Heats of fusion H_f	(0 °C) 333.55 kJ kg^{-1}
Dissociation constant K_w	(25 °C) 10^{-14}
Thermal conductivity λ	Liquid water (0 °C) 0.56 W $(m\ K)^{-1}$; Ice (0 °C) 2.18 W $(m\ K)^{-1}$;
Dielectric constant ($e_r = e/e_0$)	81.1 (18 °C)
Vapor pressure	
Temperature (°C)	Pressure/Pa
0	611
12	1403
25	3168

Source: Reproduced from Spiess, W.E.L., 2002/2003. Chilling and Freezing; An Introduction Chilling and Freezing to Food, Lectures on Freezing of Food Materials. Seoul National University.

Table 4 Physical properties of ice

*Triple points of water (see also **Figure 6**)*		
Phases in stable equilibrium	*Pressure*	*Temperature (°C)*
Liquid water, ice I_h, and water vapor	611.73 Pa	0.01
Liquid water, ice I_h, and ice III	209.9 MPa	−22
Liquid water, ice III, and ice V	350.1 MPa	−17.0
Liquid water, ice V, and ice VI	632.4 MPa	0.16
Structure		
Crystal structure	Hexagonal	
Molecular shape	Bent	
Dipole moment	1.85 D	

Source: Reproduced from Spiess, W.E.L., 2002/2003. Chilling and Freezing; An Introduction Chilling and Freezing to Food, Lectures on Freezing of Food Materials. Seoul National University.

Currently, approximately 4000 km^3 of freshwater are withdrawn annually from the various resources. The main sectors of water consumption are agriculture, industry, and private households; also in addition, recreation and the environment take a share. On a global average, approximately 70% of the amount withdrawn from water resources is used for agriculture, 20% for industrial purposes, and 10% for the domestic sector, mainly private households. It is estimated that the agricultural sector benefits in addition from a direct water supply through rain on agricultural production sites, on the order of 6400 $km^3\ annum^{-1}$. The share of the industrial sector may vary considerably from country to country; for example, according to Food and Agriculture Organization (FAO) data, North America and Europe use up to 50% of the water withdrawn from the available resources.

Main industrial consumers are thermoelectric power plants, ore and oil refineries, the chemical industry, and other industrial branches. In the highly developed industrial countries, water used as an intermediate process aid is usually released in high quality (drinking water quality) and can be easily reused.

The hotspots of the various types of consumption are also not equally distributed over the globe; most of the water for agriculture production is used at latitudes south of 30 °N, whereas water for various industrial purposes is mainly used above this line. Water for domestic use is almost evenly spread around the globe (Figures 7 and 8).

Under extreme threat of water shortage is Asia, with close to two-thirds of the world population and less than one-third of the worlds water resources; according to FAO data, the most populous countries on the globe withdraw together almost one-third of the entire amount withdrawn, despite the fact that the per capita consumption in these countries is rather low. Further, the top consumers are the US, Pakistan, Iran, Japan, Thailand, Indonesia, and Bangladesh. Especially difficult is the situation in Africa, because of an extremely underdeveloped infrastructure for distributing scarce water resources.

Globally, per capita water withdrawal varies between major consumers, for example, the cotton producing countries in Central Asia, and countries with an extremely small consumption in Central Africa; highly industrialized countries and countries with a medium-sized agricultural sector occupy the middle ground (Table 6).

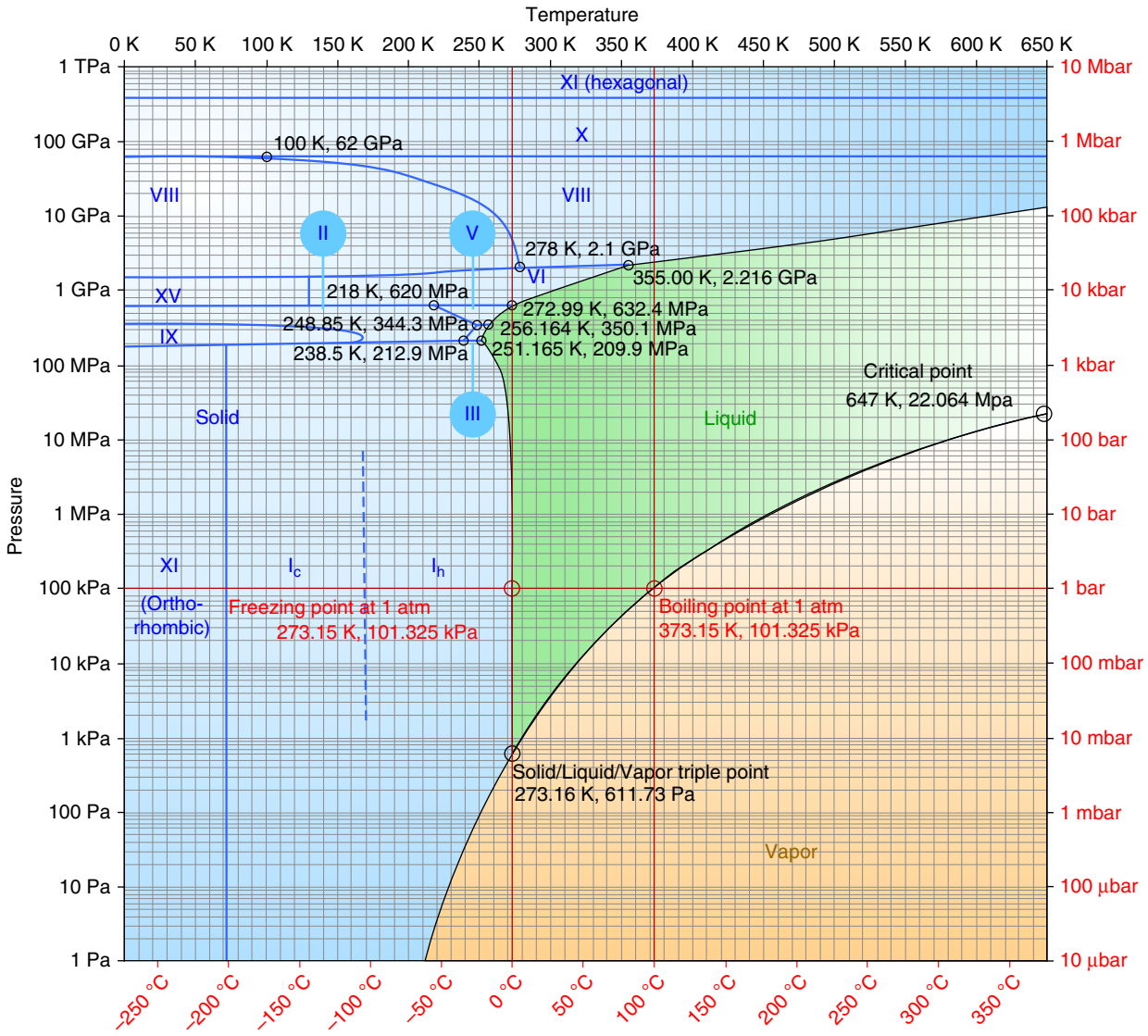


Figure 6 State diagram of water.

Table 5 Allocation of water resources with regard to the distribution of the world population

Continent	*Water availability (%)*	*The world population (%)*
Asia	36	60
South America	26	9
North and Central America	15	5
Africa	11	14
Europe	8	11
Australia and Oceania	5	<1

Source: Data derived from Figure 5.5 in Saladié, Ò., Oliveras, J., 2010. Sustainable Development. Available at: http://www.desenvolupamentsostenible.org/index.php?option=com_content&id=109&Itemid=174&lang=en (accessed 10.11.13).

Serious problems arise when water supply does not correspond to water consumption, as in India, Northern and Central Asia, and countries around the Mediterranean Sea, the majority of sub-Saharan Africa, the central US, Mexico, and Argentina.

According to various sources, difficulties around the worldwide water supply will increase in the years to come. Estimates predict that in approximately 30–40 years, 3–4 billion people will be affected by severe water shortages. On the demand side, an increase in the world population and an increasing demand by industry have to be accounted for, and in addition there will be an increase in private consumption arising from a strong tendency to urbanization and changes in lifestyle; on the supply side, unlocking the scarce resources will become increasingly difficult because of extreme climate conditions. It is anticipated that the demand for water will increase by 50–64 billion $m^3\,year^{-1}$ in the years to come. One way to cope with the upcoming problems is to minimize the use of water in all water-consuming technologies and production lines, especially in agriculture; as part of this effort, however, the reduction and treatment of wastewater should be considered. According to the presently available technologies,

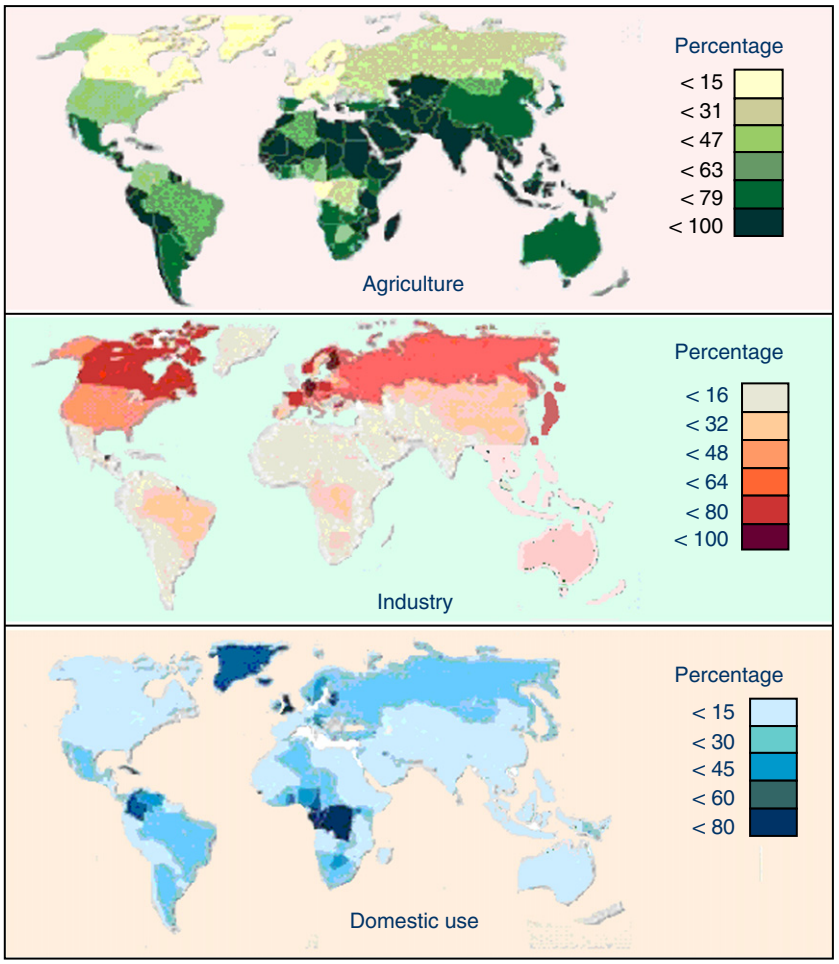


Figure 7 Freshwater withdrawal by sector. Reproduced from Rekacewicz, P., 2000. World Resources 2000–2001. People and Ecosystems: The Fraying Web of Life. World Resources Institute. Available at: http://www.grida.no/graphicslib/detail/freshwater-withdrawal-in-agriculture-industry-and-domestic-use_2fc0# (accessed 10.11.13).

1 volume unit of wastewater pollutes 8 volume units of freshwater.

The Virtual Water Concept

Because of the global imbalances in the availability of water which together with other climate factors cause an imbalance in food production, a global trade in food materials of various kinds is required to satisfy the nutritional needs of major parts of the world's population; inherent in this trade is the trade in the water that was needed to produce the agricultural commodities. This water content is called the virtual water content; in other words, the amount of virtual water of a product is the amount of water embedded in that particular product in an imaginary way. Basically, all goods and services that rely in one way or the other on the presence of water 'contain' a virtual amount of water. The term, however, truly makes sense in the case of water that was directly used for the production of a product. Together with complementary information as described below, the indication of the virtual water content of a product or commodity can provide a simple undifferentiated basis for decisions on the production of goods on a local, national, or international level. In a sophisticated model of considering the virtual water content, one has to distinguish between the amount of virtual water which was required to produce a product at its production site and the amount of virtual water which would have been required to produce the product at the site of consumption. This concept can be extended in such a way that not the amount of water to produce a real product is considered, but the amount of water required for a product with a specific nutritional value. This approach would allow defining the virtual water content of sea food, which actually does not require any sweet water for its 'production.' Although there is a large body of data on the virtual water content of agricultural produce in the literature, no reliable data on the virtual water consumption for processing are available.

To allocate and determine the virtual water content of a product is rather difficult, as the virtual water content is influenced by many factors. Hoekstra and his group, who have pioneered the research on virtual water and the WFP

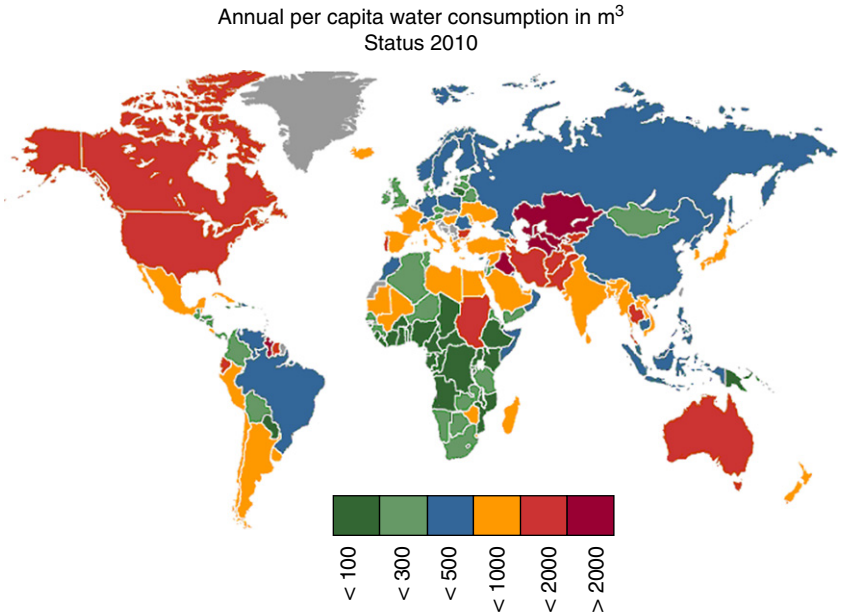


Figure 8 Annual per capita water consumption. AQUASTAT. Available at: http://chartsbin.com/view/1455 (accessed 08.05.14).

Table 6 Per capita consumption of water. Countries with high and small consumption figures

Major consumer		*Moderate and small consumers*	
Country	*Annual consumption m^3 cap^{-1} $year^{-1}$*	*Country*	*Annual consumption m^3 cap^{-1} $year^{-1}$*
Turkmenistan	5375	Brazil	305
Uzbekistan	2345	UK	212
Kazakhstan	2214	Ethiopia	80
USA	1550	Niger	78
Canada	1468	Angola	42
Azerbaijan	1415	Mozambique	36
Australia	1149	Rwanda	18
Mexico	735	Uganda	13
Germany	390	Republic Congo	12
Global average: ~600 m^3 cap^{-1} $year^{-1}$			

Source: Reproduced from FAO AQUASTAT database. Available at: www.waterfootprint.org/Reports/Report12.pdf (accessed 08.05.14).

(Hoekstra, 2003), recommend that the following factors should at least be considered and preferably provided together with the estimates:

- The place and period (e.g., which year and season) of production. Individual water requirements for plant materials can be calculated for specific countries with the CROPWAT model provided by FAO in conjunction with the CLIMWAT database for climate data and the FAOSTAT database for produce yields. Those data consider also the release of water into the atmosphere through evaporation from the land surface and the transpiration of plants; the sum of the two types of water release is called evapotranspiration (ET). If plants are under water stress, the ET has to be considered through the ET coefficient (Crop evapotranspiration).
- The point of measurement. In the case of irrigated crop production, the question is, for instance, whether one measures water use at the point of water withdrawal or at the field level.
- The production method and associated efficiency of water use. A relevant question is whether water wasted is included in the estimate.
- The method of attributing water inputs into intermediate products to the virtual water content of the final product.
- Denotations of the amount of virtual water should always be presented with a reference base, for example, quantity of water per mass of product (l kg^{-1} or m^3 ton^{-1}) or quantity of water per crop area (m^3 ha^{-1}) or quantity of water consumed per year (m^3 $year^{-1}$) or per person (m^3 cap^{-1}) or even per year and person (m^3 (year × cap)$^{-1}$) etc. If a produce is being processed into various products like wheat

into flour, dunst, cream of wheat, bran, germ oil, etc., the virtual water content of the individual fractions has to be assigned proportionally.

Especially important for optimizing any production of any produce on a global scale is the information on the place of production, its environmental conditions, and the production method. If the water requirements at a specific location, for example, through high ET, are significantly higher than at other locations or than the average, it would appear ecologically and economically worthwhile to consider ceasing this production. Such considerations are especially relevant because the amount of evapotranspired water determines in the first instance the virtual water content of a product, or, as will be demonstrated in this article, the WFP of a product is almost entirely determined through the WFP of the raw material to be processed.

Trading of food commodities means trading the virtual water which is embedded in the produce. According to various studies, the international food-related trade is dominated by the trade in vegetal products, followed by animal products, products of marine origin, and meat. The various published data are not directly congruent but point in the same direction (see also Table 7).

If the international virtual water trade is considered alongside the exchange of food commodities, it becomes obvious that the Americas and Oceania are distinct exporters of virtual water; Asia and Africa, two continents with a huge agricultural production and thus burdened with a high consumption of virtual water, are importers of virtual water; in the case of Europe, which has also a significant agricultural production, exports and imports are almost balanced (see Table 8 and Figure 9).

A further aspect is added to the picture when the production and export/import figures are related to the population of the six continents. The per capita import figures, especially for Africa but also for Asia, indicate that these populations rely heavily on imports; their daily consumption is around 1.1 and 1.4 $m^3\ cap^{-1}\ day^{-1}$, respectively, extremely low compared with the consumption of the average person in the Americas and Europe, at 2.6–3 $m^3\ cap^{-1}\ day^{-1}$. According to Zimmer and Renault (2003), approximately 75% more virtual water would be required if the present world population adopted the diet of the developed countries. The presently low global consumption figures are mainly due to the low virtual water consumption in Asia for details (see Table 9). The tendency in Asian metropolises to move away from a more vegetarian-oriented diet to a more animal product-based diet is therefore an alarming development.

Table 7 Assessment of global virtual water trade between nations (in 2000)

Global virtual water trade (from the perspective of importing countries)	*Volume ($gm^3\ year^{-1}$)*	*Percentage*
Associated with trade of vegetal products	795	60
Associated with trade of animal products	180	13
Associated with trade of meat	173	13
Associated with trade of fish and sea food	192	14
Total	1340	100

Source: Reproduced from Hoekstra, A.Y. (ed.), 2003. Virtual water trade: Proceedings of the International Expert Meeting on Virtual Water Trade, Delft, The Netherlands, 12–13 December 2002, Value of Water Research Report Series No.12. Delft, The Netherlands: UNESCO-IHE. Available at: www.waterfootprint.org/Reports/Report12.pdf (accessed 29.01.14).

The Water Footprint Concept

The idea of considering the use of water along the production, processing, and distribution chain is analogous to the ecological footprint concept of Wackernagel and Rees (1996). For example, the concept of the CO_2 footprint as WFP was developed and widely published by Hoekstra (2003). This concept is based on the virtual water concept of Allan (1994).

Definitions

With regard to its physical localization, two types of 'nonsaline water' are defined for the purpose of the WFP

Table 8 Total water consumed for crop production and virtual water traded from continents in $km^3\ year^{-1}$

Water consumed for crop production and virtual water traded from continents for year 1999, assuming an annual increase of 1% in water productivity

All values in $km^3\ year^{-1}$ except for (%)

Continent	*Water for crop production*	*Virtual water imported*	*Virtual water exported*	*Net virtual water balance*	*Virtual balance water for food[a] (%)*
North and Central America	684	164	317	−153	−22
European Union	386	384	377	7	2
South America	445	52	175	−123	−28
Asia	1673	426	182	244	15
Oceania	71	8	117	−109	[b]
Africa	241	97	19	78	32

[a]This value excludes grass and other noncropped fodder products.
[b]Value meaningless without considering grass and noncropped fodder products.
Source: Reproduced from Zimmer, D., Renault, D., 2003. Virtual Water in Food Production and Global Trade; review of Methodological Issues and Preliminary Results; Proceedings of the expert meeting held 12–13 December 2002, Delft, The Netherlands: UNESCO-IHE.

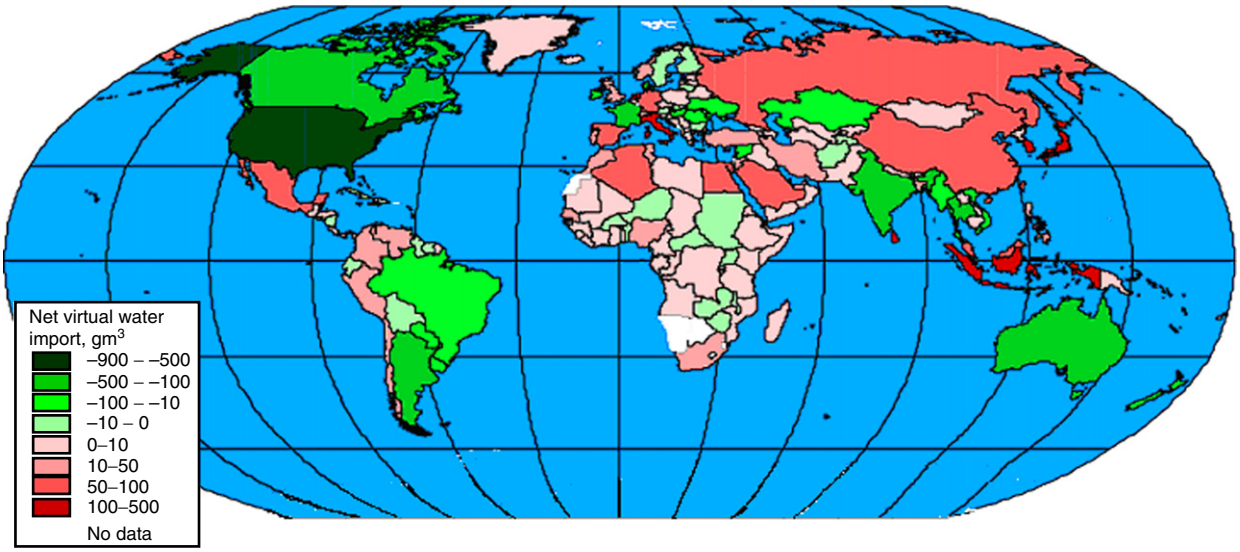


Figure 9 National virtual water trade balances over the period 1995–99. Red represents net import, black/green net export. Reproduced from Hoekstra, A.Y., Hung, P.Q., 2002. Virtual Water Trade – A Quantification of Virtual Water Flows between Nations in Relation to International Crop Trade Value of Water Research Report Series no. 11. The Netherlands: IHE Delft.

Table 9 Specific water consumption for crop production and virtual water traded from continents m^3 (cap × year)$^{-1}$

Water consumed for crop production and virtual water traded from continents for year 1999, assuming an annual increase of 1% in water productivity

All values in m^3 (cap × year)$^{-1}$ except for (e)

Continent	*Water for crop production (a)*	*Virtual Water imported (b)*	*Virtual water exported (c)*	*Net virtual Water balance (d)=(b)–(c)*	*Consumption per day[a] (e)=(a+d)/360*
North and Central America	1421	342	659	–317	3.0
European Union	1026	1020	1002	18	2.9
South America	1305	153	514	–361	2.6
Asia	436	118	50	68	1.6
Oceania	2345	281	3898	–3617	[b]
Africa	311	125	25	100	1.1

[a]This value excludes grass and other noncropped fodder products.

[b]Value meaningless without considering grass and noncropped fodder products.

Source: Reproduced from Zimmer, D., Renault, D., 2003. Virtual Water in Food Production and Global Trade; review of Methodological Issues and Preliminary Results; Proceedings of the expert meeting held 12–13 December 2002. Delft, The Netherlands: UNESCO-IHE.

concept: 'blue water' and 'green water.' Under blue water, groundwater and surface water are understood; this is the fraction of water which is available as drinking water, processing water, and water for irrigation in agriculture; it is used as a transport medium and for many other purposes. Green water is water which is bound in the soil and in green plants; it is, under normal circumstances, the basis for agricultural production. According to Zehnder (2002), approximately 35% of global water resources are available as blue water, whereas the majority of the water resources, i.e., 65%, are available as green water. To account for the amount of water which is being polluted, for example, during processing, a third, notional type of water, 'gray water,' has been introduced (Chapagain and Hoekstra, 2010). Specifically, it is defined as the volume of freshwater that is required to assimilate the load of pollutants based on existing ambient water quality standards (Hoekstra *et al.*, 2009).

Green water provides the basis of agricultural production (see also Section The Virtual Water Concept); the amount used for a specific product is released into the atmosphere through ET. If blue water is being used for plant production, for example, for irrigation it will be also released through ET and it has to be accounted for in a similar way as green water. The scientific methods of determining the share of gray water in a process are still disputed among the experts; it is estimated to be approximately 7% of the total WFP. Gray water is therefore no longer considered in detail in this chapter. Modern agricultural and industrial processes are designed in a way that the amount of gray water is truly minimized.

The WFP of any product can be denoted in various ways, analogous to the denotation of virtual water as water consumed related to the product mass (l kg^{-1} or m^3 ton^{-1}), or related to the crop area (m^3 ha^{-1}), or to the year of production

($m^3\,year^{-1}$), or per person ($m^3\,cap^{-1}$), or even per year and person ($m^3\,(year \times cap)^{-1}$). In normal cases, the presented data refer to the place of origin (cultivation or manufacture).

The WFP is more sophisticated information than the virtual water content. The WFP is an analytical tool to account in a differentiated way for the various issues of direct and indirect utilization and consumption of water for human activities; examples include the production of any type of goods, hygienic measures, services, etc. in and for a country, a municipality, a family, or an individual. In addition, the WFP allows one to indicate whether a certain amount of water has been taken from domestic resources, from a particular catchment area, or from outside a country or continent. In other words, the WFP can be expressed for a nation, a community, a family, an individual, a factory, a processing operation, a service rendered, or anything similar.

Especially in the case of the production of goods, the detailed WFP allows us to evaluate where and when water was withdrawn from its sources and consumed along the supply, production, and processing/distribution chain. The detailed WFP for a product indicates the amount of water which was directly used for individual production and processing steps and, very importantly, for adjunctive measures, as demonstrated by the example of a sugar-containing carbonated beverage 0.5 l polyethylene terephthalate (PET) bottle (Table 17). The WFP cannot be used as an indicator for the impact of water consumption on local environments or as a measure of pollution. If only the green and blue WFP is considered, the WFP allows us to develop water balances for particular activities, areas, individual social groups, communities, or even lifestyles; it therefore allows among other things the comparison and evaluation of specific processing and consumption activities.

The significance of the water footprint

In a global society with an extensive export and import of all types of goods, the WFP allows us, in analogy to the virtual water content, though in a more sophisticated way, to estimate the export and import of two types of water. This is especially of relevance for goods of agricultural origin such as food, cotton textiles, paper, and others, because almost 90% of the world's consumption of water is related to agricultural production.

If the WFPs of larger entities are considered, for example, all food consumed in a specific area or country, one can evaluate which amount and type of water was consumed, where and when the water was withdrawn, and whether the withdrawal was beneficial for the source or not. A comparison of WFPs for various products allows us to determine the ratio of the water consumption for products imported and domestically produced (Hoekstra).

The detailed WFP also allows us in the end to evaluate to what extent the consumption of specific goods or an activity in question is sustainable and socially acceptable or not, if considered with other relevant information such as water availability or sustainability of water utilization. WFP data alone do not offer any clue whether a water source is being overexploited or not; such statements can only be derived from comprehensive water-material balances. This is, for example, of relevance with regard to the question of whether the export/import of commodities with a high WFP such as tropical fruits or any other product from developing countries into developed countries is ethical or not. This question can only be correctly answered when considering all factors around the water resources of the donating country. If the water balance of the producing area is not negatively influenced, no concern should arise (Table 10).

From the data presented in Table 10, it becomes evident that the highly developed countries have a high WFP per capita and year; the US is on top with 2483 $m^3\,cap^{-1}\,year^{-1}$, whereas emerging nations like China, India, and South Africa are much below the global average. India imports only approximately 2% of its WFP compared to Germany, which imports more than 50% of its WFP.

At this point it should be mentioned that the literature provides a treasury of data on all aspects of the WFP as well as on the virtual water content of a great variety of products; not all of these data are congruent, though the tendencies match each other. A rich source of data is provided by Hoekstra and his group, as is evident from the list of references.

Assessing the water footprint

In this article, the WFP for producing and processing of food is being considered; it should, however, be mentioned at this point that the major part of the WFP of any food material derives from the agricultural production; the share of processing is in many cases almost negligible.

In Table 11, data on the total WFP of some products of daily life are presented as a first look at the WFP; of interest are the large differences between, for example, a beef hamburger and a slice of 30 g bread with 10 g of cheese, or a cup of coffee and a cup of tea. The WFP for a large number of produce and products is given in the following tables and in Annex Tables 19 and 20.

The water footprint of processing food

As indicated for almost all activities which consume water, the WFP can be analyzed, estimated, or calculated. As in any analysis, the scope and goal of the analysis and the boundary conditions have to be clear. Reasons for a WFP analysis can be of international, national, or even local interest, or of a private nature. National governments or supranational organizations may have an interest in understanding the flow of virtual water in order to identify stress points, for example, areas of over- or underexploitation, and they might be interested in identifying problem zones and hotspots of water use. Communities of any type may have an interest in understanding whether their particular water resources are managed in a sustainable way; producers/processors of commodities may want to understand whether their use of water is economic, sustainable, and appropriate. Finally, consumers may be interested in learning whether their choice of a product is in compliance with their social attitudes and ethical principles (Hoekstra *et al.*, 2011).

If the WFP of a food product is considered in a detailed analysis, besides production the processing, storage and distribution, retailing, and home preparation and consumption have to be taken into account.

The WFP_p of an individual product, also called its invisible-inherent or virtual weight-related water content, is basically the sum of all WFPs derived from the amount of M (m^3)

Table 10 Composition of the water footprint (WFP) for some selected countries. Period: 1997–2001. Includes both blue and green water use in agriculture

Country	Water footprint		Water footprint by consumption category				
			Domestic internal WFP	Agricultural goods		Industrial goods	
	Total (gm^3 $year^{-1}$)	Per capita WFP (m^3 cap^{-1} $year^{-1}$)	(m^3 cap^{-1} $year^{-1}$)	Internal WFP (m^3 cap^{-1} $year^{-1}$)	External WFP (m^3 cap^{-1} $year^{-1}$)	Internal WFP (m^3 cap^{-1} $year^{-1}$)	External WFP (m^3 cap^{-1} $year^{-1}$)
Australia	26.56	1393	341	736	41	64	211
Canada	62.80	2049	279	986	252	366	166
China	883.39	702	26	565	40	65	6
Germany	126.95	1545	66	434	604	228	213
India	987.38	980	38	907	14	19	2
Japan	146.09	1153	136	165	614	108	129
South Africa	39.47	931	57	644	169	26	33
UK	73.07	1245	38	218	592	114	284
USA	696.01	2483	217	1192	267	609	197
Global total/average	7452	1243	57	907	160	79	40

Source: Reproduced from Hoekstra, A.Y., Chapagain, A.K., 2007. The water footprints of nations: Water use by people as a function of their consumption pattern. Water Resources Management 21, 35–48. doi:10.1007/s11269-006-9039-x.

Table 11 The water footprint of different food products of daily life

Food item	*Unit (kg) (if not otherwise specified)*	*Global average water footprint (l)*
Apple or pear	1	700
Beef 'hamburger'	150 g	2400
Beer (from barley)	1 Glass of 250 ml	75
Bread (from wheat)	1	1300
Bread	1 Slice of 30 g with 10 g of cheese	90
Chocolate	1	24 000
Coffee (roasted)[a]	1 mug of 250 ml	(1450–8375) 5175
Sugar (from sugar cane)	1	1500
Tea	1 mug of 250 ml	30–35
Wine	1glass of 125 ml	120
Cotton T-shirt 8000	200 g	2000
Microchip	2 g	32

[a]Processing is seen to cause the high WFP for roasted coffee beans. For the coffee fruit (coffee cherry) after harvesting the WFP≈2800 l kg^{-1} (global average). As only the seeds (beans) of the coffee cherry can be used while the pulp will be discarded, the utilized mass of product is being reduced. In turn the WFP of this mass will increase accordingly. Drying during the roasting process will further increase the content of virtual water. In contrast, the contribution of the water required during processing to the WFP of the roasted coffee beans remains negligibly small – even in the case of wet processing (approximately 10 l kg^{-1} coffee cherry). Thus, it is not true that processing coffee requires large amounts of water, as is sometimes claimed.

Source: Reproduced from Hoekstra, A.Y., Chapagain, A.K., 2007. The water footprints of nations: Water use by people as a function of their consumption pattern. Water Resources Management 21, 35–48. doi:10.1007/s11269-006-9039 and Hoekstra, A.Y., 2008. The Water Footprint of Food. The Netherlands: Twente Water Centre, University of Twente. Available at: http://doc.utwente.nl/77216/1/Hoekstra08waterfootprintFood.pdf (accessed 11.11.13).

blue water *b*, green water *g*, and gray water *gr* used to process the mass *P* (kg) of a material in *n* process steps *s* which may be operated in parallel or successively:

$$M(b,g,gr)/p = \{\mathrm{WFP}_p = \mathrm{WFP}_{pb1} + \mathrm{WFP}_{pb2} + \mathrm{WFP}_{pb3} \ldots + \mathrm{WFP}_{pbn} + \mathrm{WFP}_{pg1} + \mathrm{WFP}_{pg2} + \mathrm{WFP}_{pg3} + \ldots \mathrm{WFP}_{pgn} + \mathrm{WFP}_{pgr1} + \mathrm{WFP}_{pgr2} + \mathrm{WFP}_{pgr3} \ldots + \mathrm{WFP}_{pgrn}\}[\mathrm{m}^3\ \mathrm{kg}^{-1}] \quad [1a]$$

In other terms:

$$\mathrm{WFP}_p = \sum_{s=1}^{k} (\mathrm{WFP}_{pb} + \mathrm{WFP}_{pg} + \mathrm{WFP}_{pgr})[\mathrm{m}^3\ \mathrm{kg}^{-1}] \quad [1b]$$

where

- WFP_p is the total water footprint for product A expressed in volume water per material mass,
- $\mathrm{WFP}_{pb1}+\mathrm{WFP}_{pb2}+\mathrm{WFP}_{pb3}\ldots+\mathrm{WFP}_{pbn}$ is the sum of blue water footprints,
- $\mathrm{WFP}_{pg1}+\mathrm{WFP}_{pg2}+\mathrm{WFP}_{pg3}+\ldots.\mathrm{WFP}_{pgn}$ is the sum of green water footprints,
- $\mathrm{WFP}_{pgr1}+\mathrm{WFP}_{pgr2}+\mathrm{WFP}_{pgr3}\ldots+\mathrm{WFP}_{pgrn}$ is the sum of gray water footprints,

in *s* process steps and also expressed in volume water per material mass.

In the case of the production of vegetal products the amount of blue and green water is lost through ET.

In process operations during which the mass of the product is submitted to changes (losses and gains), an adequate factor ($PF = P_{inc}/P_{outg}$) has to be introduced into the calculation.

Factors affecting the water footprint of production and processing

Independent of the material to be processed, the first step in evaluating the WFP of a processed product is to establish the flow sheet of the process. For a detailed evaluation, the flow sheet should reflect all relevant steps from raw material production to consumption. Those steps comprise preharvest measures, postharvest processing directly on the field, transport to the processing site or sites, on-site storage or transport to a storage facility, distribution, retailing, and finally home preparation. The flow sheet should also contain an indication of product losses, amounts of water entering and leaving the process, as well as types and amounts of energy used in the process, as well as details on indirect operational features.

In many cases the agricultural produce is preprocessed directly after harvesting; postharvest processing may consist of threshing, dehusking, mechanical dry or wet cleaning, or similar operations.

Final processing, mostly in central processing units, may comprise various types and combinations of classical unit operations, i.e., thermal (blanching, drying, canning, freezing, roasting, etc.) or mechanical processing (sorting, grinding, staining, homogenizing, etc.) operations, packaging, and on-site storage.

The WFP of transportation, storage, and distribution and retailing operations, even when material or commercial goods are transported over long distances or stored over longer periods of time by biofuel energized transportation/storage systems, can be neglected in most cases because it is relatively small compared to the WFP of, for example, agricultural production.

In detail, the WFP has to be calculated on the basis of the water used directly for production (direct operational water) and water which is used to support the production process (indirect operational water) (see also Figure 10).

Water which is used for the agricultural production includes that

- Directly used as green and blue water.
- Indirectly used for fertilizer and other supporting measures, etc.
- Water which is directly used for processing.
- Constitutive water, for example, as part of a beverage.
- Process water, for example, steam generation, washing, cooling, etc., water which is usually discarded after its use and not directly reused; basically it is not to be considered as gray water because it does not necessarily carry any pollutants.
- In addition, there might be a fraction of water which is contaminated by organic materials from various sources (leaching/extraction processes, etc.) and which has to be treated in sewage treatment plants. This fraction of water has to be considered as gray water. In many cases, water received from food processing plants is most welcome by the sewage treatment plants because of its load, which is most favorable for the biological degradation processes in the sewage plants.
- The water which has been used for the adjunctive supply must also be considered in calculating the WFP for direct processing, for example, water used for producing major and even small food additives (spices and condiments), packaging and transport materials, etc.

As water which is indirectly used for processing, all water fractions have to be considered that are used to enable the production as such and for maintaining the processing operations, including the processing environment, administration,

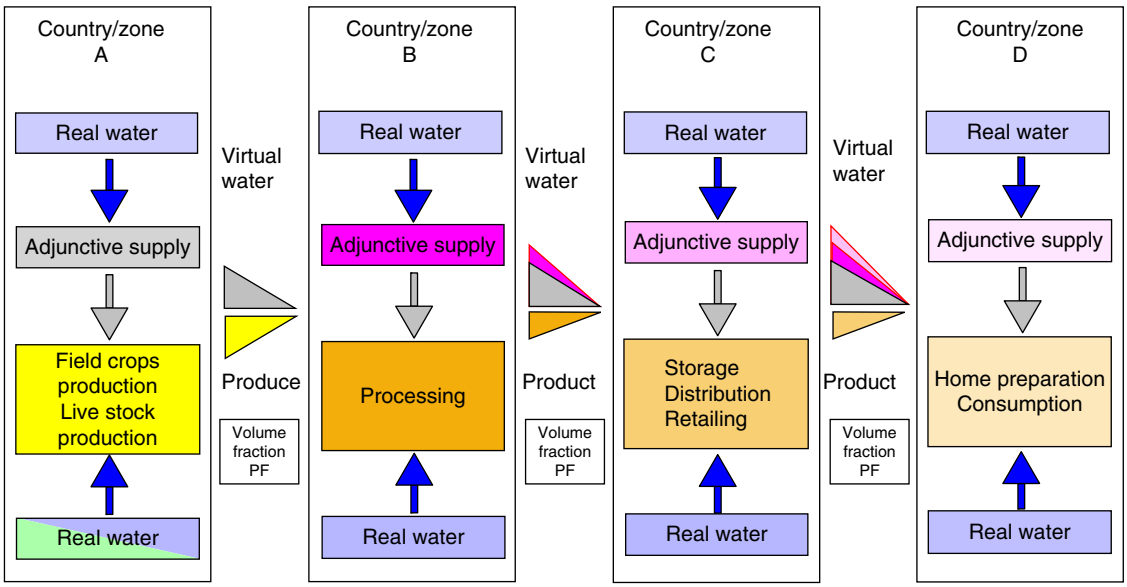


Figure 10 Simplified flow sheet of virtual water. Blue and green stand for blue and green water respectively. Yellow, light brown to very light brown stand for the changes which the raw material undergoes on its way from farm to home preparation/consumption. Grey, dark purple to light purple stand for various adjunctive supplies. PF- Ratio of the volume of the resulting product to the volume of the original product; unit m^3 per m^3.

administrative tools, and different kind of services, etc., for example

- Water used to set up the factory (buildings and machinery).
- Energy in all forms if water is utilized for its production, for example, production of biofuel.
- Water for maintenance and cleaning of processing units, storage facilities, vehicles and vehicle halls, leisure rooms for staff, administrative units inclusive building, etc.
- Water for operating toilets, showers, etc.
- Water for indirect cleaning operations (washing of working garments and personal hygiene of staff).

Water which is used for feeding the staff is usually not included in detailed WFP analysis for a product because those fractions of water are in the general part of different supply chains.

The production of agricultural raw (staple food) materials

The water footprint of meat and animal products

The method of calculating the WFP of an (agricultural) animal product is briefly illustrated by the example of beef (Hoekstra and Chapagain, 2007).

To obtain the WFP of beef, eqn [1] has to be modified in such a way that the various types of actual and virtual water required for raising cattle are reflected in the calculation. Specifically, water is needed for drinking and cleaning purposes (stables, farmyard, animal, etc.), etc., as well as for producing the *feed*.

$$\mathrm{WFP}_{beef} = \mathrm{WFP}_{drink} + \mathrm{WFP}_{feed} + \mathrm{WFP}_{clean}$$

Method of processing: industrial agricultural environment
Output: 200 kg beef
Input:

- 24 m^3 of water for drinking and 7 m^3 of water for cleaning.
- 3060 m^3 of water for producing
  - 1300 kg of grains (wheat, oats, barley, corn, dry peas, soybean meal, and other small grains)
  - 7200 kg of roughages (pasture, dry hay, silage, and other roughage)

Input related in output:

- 155 l water kg^{-1} beef for drinking and cleaning
- 15 300 l water kg^{-1} beef for
  - 36 kg roughage kg^{-1} beef
  - 6.5 kg grain kg^{-1} beef

Total water requirement for producing 1 kg of beef amounts to ~15 500 l, equivalent to 15 500 (m^3 ton^{-1}).

The data presented by Hoekstra and Chapagain have been compiled according to standardized procedures mainly developed by the authors starting around the year 2000; earlier data presented in various sources must therefore be used with precaution, as demonstrated in **Table 12**. The wide span of these data demonstrates the need for standardized data acquisition (Hoekstra *et al.*, 2011).

A detailed compilation of WFP data on major animal products (**Table 13**) indicates that beef has indeed the highest WFP independent of the place of production; the data for beef and pig meat are quite close to each other, with the exception of the data from the Netherlands. Chicken meat is obviously related, with the lowest WFP. The low WFP data for the Netherlands indicate that economic and controlled production methods allow for a low water consumption.

From the data, it becomes evident that the WFP of a specific product may differ considerably across various geographical locations, with, for example, different climates, where an animal/product is raised/grown and where different breeding/cultivation techniques are applied.

Table 12 Water required to produce 1 kg of boneless, conventionally raised beef

Water footprint (m^3 ton^{-1})	*References (individual or organization)*
3 668	Oltjen *et al.*, 1993
6 988	Durning, 1991
20 499	Kreith, 1991
43 378	Schulbach *et al.*, 1978
99 901	Pimentel, 2001

Source: Reproduced from Olson-Sawyer, K., 2011. Beef: The 'King' of the Big Water Footprints. Available at: http://www.gracelinks.org/blog/1143/beef-the-king-of-the-big-water-footprints (accessed 11.11.13).

The water footprint of vegetal produce

If starch-containing vegetal products are considered, tubers of all kinds have a much lower WFP than cereals; it must, however, be taken into account that cereals have a higher starch content (wheat: ~60% starch) than tubers (potato/cassava: ~16–20%/~35–40% starch). In addition, cereals contain protein (wheat gluten) and oil (maize and wheat). Valuable sources of protein are legumes, which certainly could be used to replace meat (**Table 14**).

All together, the data in **Tables 13** and **14** demonstrate very clearly that "the water footprint of any animal product is larger than the water footprint of crop products with equivalent nutritional value. According to FAOSTAT and other data 29% of the total WFP of the agricultural sector in the world is related to the production of animal products; one-third of the global water footprint of animal production is according to this data related to beef cattle" (Mekonnen and Hoekstra, 2012).

The water footprint of processed products

In most industrialized countries and to some extent also in emerging countries, modern processing technologies are designed in such a way that the use of water is strictly minimized. This is true in cases where water is used for cleaning and washing, steaming, blanching, cooling, and other water-consuming operations. Soiled or otherwise polluted water is mostly cleaned on factory premises and reused; only minor amounts are usually discarded into sewage plants, where they are processed into water of process-water quality.

Including material losses which are process related (e.g., peeling, hulling, boning, and similar operations) into the WFP calculation may increase the WFP for the core product considerably. In the case of major amounts of water used for indirect operations, care has to be taken that these fractions are correctly distributed (taking in account lifespan of utilization and rate of capacity utilization, etc.) to the individual

Table 13 The green (G), blue (B), and gray (Gr) water footprint (m^3 ton^{-1}) of selected animal products for farming system in selected countries and weighted average

Animal products		*China*	*India*	*Netherlands*	*USA*	*Weighted average*	*Total*
Beef	G	12 795	15 537	5684	12 933	14 414	15 415
	B	495	722	484	525	550	
	Gr	398	288	345	733	451	
Pig meat	G	5 050	5 415	3723	4 102	4 907	5 988
	B	405	1 191	268	645	459	
	Gr	648	554	438	761	622	
Chicken meat	G	2 836	6 726	1545	1 728	3 545	4 325
	B	281	873	77	187	313	
	Gr	854	768	165	303	467	
Egg	G	2 211	4 888	1175	1 206	2 592	3 265
	B	217	635	55	130	244	
	Gr	666	542	111	230	429	
Milk	G	927	885	462	647	863	1 020
	B	145	130	41	60	86	
	Gr	210	63	25	89	72	
Butter	G	5 044	4 819	2513	3 519	4 695	5 553
	B	789	706	224	324	465	
	Gr	1 141	341	134	483	393	
Milk powder	G	4 309	4 117	2147	3 007	4 011	4 745
	B	674	603	191	277	398	
	Gr	975	291	114	413	336	

Source: Reproduced from Mekonnen, M.M., Hoekstra, A.Y., 2012. A global assessment of the water footprint of farm animal product. Ecosystems 15, 401–415. doi:10.1007/s10021-011-9517-8.

Table 14 Water footprint of starch-containing produce (for further data see **Table 19**)

Product description	*Global average water footprint (m^3 ton^{-1})*			
	Green	*Blue*	*Gray*	*Total*
Cereals				
Maize (corn)	947	81	194	1222
Rice (paddy)	1146	341	187	1673
Wheat	1277	342	207	1827
Tubers				
Manioc (cassava)	550	0	13	564
Potatoes	191	33	63	287
Sweet potatoes	324	5	53	383
Legume				
Beans, green	320	54	188	561
Groundnuts shelled	3526	214	234	3974
Peas, green	382	63	150	595
Soya beans	2037	70	37	2145

Source: Reproduced from Mekonnen, M.M., Hoekstra, A.Y., 2011. The green, blue and grey water footprint of crops and derived crop products. Hydrology and Earth System Sciences 15, 1577–1600.

targeted entities leaving the processing unit or the supply chain if transport, intermediate storage, distribution, and retailing are incorporated in the WFP balance. If several products are manufactured in a processing unit, care has to be taken that individual products are charged with the correct proportion of utilized water. Also, material losses or gains which may occur during processing have to be considered when the WFP for a finished product is being evaluated (**Table 15**).

Considering the example of coffee and tea, it becomes evident that that the WFP increases mainly because of material losses through pulping, hulling, drying and roasting, withering, rolling, and oxidizing/firing, respectively; the technical processes as such do not really contribute to the WFP. The same is true for Coca-Cola and Nestlé's Bitesize Shredded Wheat product. The contribution to the WFP from the process itself is extremely small in the case of Coca-Cola, but packaging adds a significant contribution.

The same picture arises when more complex products like a sugar-containing carbonated beverage and/or Italian pasta and pizza (**Table 16**) are considered; the main contributions to the WFP of such products are caused by the basic raw materials and ingredients. The latter may contribute substantially if they are concentrates or extracts, for example, caffeine and vanilla extract. Processing and indirect operations, for example, construction materials and other materials (indirect operations) such as concrete, steel, paper, natural gas, electricity, vehicles, and fuel, are insignificant with regard to the WFP of the final product.

The WFP of selected materials used directly and indirectly for processing of a 0.5 l PET bottle are detailed in **Table 17**; it becomes obvious that the WFP for PET is rather small, especially when the mass of a 0.5 l bottle is considered. Important in this context is that if several products are manufactured in a factory, the WFP of indirect operations has to be allotted to the

Table 15 Water footprint (WFP) for processing coffee, tea, and two processed food products

Operation	*Product*			
	Coffee	*Tea*	*Coca-Cola (0.5 l regular Coke, Europe) (All values in litre)*	*Nestlé's 'Bitesize shredded wheat'*
Comments	Wet product. In Brazil	Produced in India (conservative method)	Produced in Europe	Produced in UK
Agricultural production	3028 cbm ton^{-1}	1290 cbm ton^{-1}	All natural ingredients WFP_b: 7.8 (litre blue water) WFP_g: 14.5 (litre green water) WFP_{gr}: 5.6 (litre grey water) WFP_{total}	+ WFP_b: 0^{++} WFP_g: 239^{++} WFP_{gr}: 49^{++} WFP_{total}: 288.00^{+}
Postharvest operation	Pulping: * 7.5 cbm ton^{-1} PF**: 0.44 Res.***WFP 6899 cbm ton^{-1}			Storage: WFP_b: 0.005^{++} WFP_g: 239^{++} WFP_{gr}: 49.005^{++} WFP_{total}: 288.01^{++}
Processing	Soaking and washing: WR 5 cbm ton^{-1} PF: 0.9 Res.***WFP 7671 cbm ton^{-1}	Withering and rolling WR: /. PF: 0.36 Res.***WFP 3584 cbm ton^{-1}	All operations WFP_b: 0.4	
	Drying: WR./. PF: 0.5 Res.***WFP 15 159 cbm ton^{-1}			Processing (causes weight loss) PF: 0.791 WFP_b: $0.929\ 8^{++}$ WFP_g: 302^{+}
	Hulling: WR./. PF: 0.89 Res.***WFP 16 844 cbm ton^{-1}			
	Polishing/grading: WR./. PF: 0.9 Res.***WFP 18 925 cbm ton^{-1}	Oxidizing/firing WR: /. PF: 0.72 Res.***WFP 4978 cbm ton^{-1}	Packaging WFP_b: 0.5 (litre blue water) WFP_g: 1 (litre green water) WFP_{gr}: 5.8 (litre grey water) WFP_{total}	WFP_{gr}: 62^{++} WFP_{total}: 365^{++}
	Roasting: WR./. PF: 0.84 Res.***WFP 22 530 cbm ton^{-1}		Total WFP_{total}: 35 (total litres)	Total WFP_{total}: 365^{+} In case the product is eaten according to Nestle's instructions the WFP for milk has to be added: WFP_g (milk): 722^{++}
Explanations	*WR Water requirement for process step**PF ratio of the weight of the ***resulting product (Res.) to the weight of the original product; unit ton ton^{-1}			$^{++}$ Unit of WFP: cbm ton^{-1}
References	Chapagain and Hoekstra (2003a)	Chapagain and Hoekstra (2003b)	Coca-Cola Services N.V. (2011)	Chapagain and Orr (2010)

Source: Reproduced from Chapagain, A.K., Hoekstra, A.Y., 2003a. The water needed to have the Dutch drink coffee. Value of Water Research Report Series No. 14. Delft, The Netherlands: UNESCO-IHE; Chapagain, A.K., Hoekstra, A.Y., 2003b. The water needed to have the Dutch drink tea. Value of Water Research Report Series No. 15. Delft, The Netherlands: UNESCO-IHE; Chapagain, A.K., Orr, S., 2010. WWF (for WFN) water footprint of Nestlé's 'Bitesize Shredded Wheat.' A pilot study to account and analyse the water footprints of Bitesize Shredded Wheat in the context of water availability along its supply chain. Available at: http://www.waterfootprint.org/Reports/Nestle-2010-Water-Footprint-Bitesize-Shredded-Wheat.pdf (accessed 08.11.13); and Coca-Cola Services N.V., 2011. Towards Sustainable Sugar Sourcing in Europe: Water footprint sustainability assessment (WFSA). Available at: http://www.waterfootprint.org/Reports/CocaCola-2011-WaterFootprintSustainabilityAssessment.pdf (accessed 08.11.13).

Table 16 Water footprint (WFP) of sugar-containing carbonated beverage and Italian pasta and pizza

Operation	*Product*	
Unprocessed ingredients	Supply chain: *Major ingredients: Beet sugar* Highest (Iran) WFP_{total}: 98.5, Approximate global average (Italy) WFP_{total}: 46.5 Low (The Netherlands) WFP_{total}: 26.0 *Cane sugar* Highest (Cuba) WFP_{total}: 167.0 (USA): WFP_{total}: 56.8 Lowest (Peru) WFP_{total}: 43.9 HFMS 55 ~Global average (China) WFP_{total}: 63.2	*Durum wheat* WFP_b: 525^{++} WFP_g: 748^{++} WFP_{gr}: 301^{++} WFP_{total}: 1574^{++} *Bread/common wheat* WFP_b: 495^{++} WFP_e: 125^{++} WFP_{gr}: 166^{++} WFP_{total}: 786^{++} *Tomato, industrial quality* WFP_b: 35^{++} WFP_e: 60^{++} WFP_{gr}: 19^{++} WFP_{total}: 114^{++}
	Minor ingredients: CO_2: $WFP_{b/total}$: 0.33 • Phosphoric/citric acid: WFP_{total}: ./. • Caffeine: $WFP_{b/total}$: 52.8 • Vanilla extract: $WFP_{b/total}$: 79.8 • Lemon oil: $WFP_{b/total}$: 0.01 • Orange oil: $WFP_{b/total}$: 0.9 *Casing and packaging:* • Bottle/PET: $WFP_{gr/total}$: 4.582 5 • Closure/HDPE: $WFP_{gr/total}$: 0.7 • Label/PP: $WFP_{gr/total}$ 0.07 • Tray cartoon/paperboard: $WFP_b/WFP_{gr/total}$: 1.5 • Tray shrink film/PE: $WFP_{gr/total}$: 0.38 • Pallet stretch wrap/PE: $WFP_{gr/total}$: 0.057 • Pallet label /coated paper: $WFP_b/WFP_{gr/total}$: 0.001 5 • Pallet – painted wood $WFP_b/WFP_{gr/total}$: 0.04 Construction materials and other materials (indirect operations): Concrete; Steel; Paper; Natural gas; Electricity; Vehicles; Fuel: WFP_{total}: 0.725 Supply chain total without sugar: 141.57	*Milk* WFP_{total}: 1308 l kg^{-1}
Processed ingredients	Water WFP_{total}: 0.5	*Durum wheat flour (semolina)*[#] WFP_b: 914^{++} WFP_{gr}: 642^{++} WFP_{gr}: 368^{++} WFP_{total}: 1924^{++} *Bread wheat flour*[#] WFP_b: 605^{++} WFP_{gr}: 154^{++} WFP_{gr}: 202^{++} WFP_{total}: 961^{++} *Tomato puree*[#] WFP_b: 117^{++} WFP_{gr}: 200^{++} WFP_{gr}: 63^{++} WFP_{total}: 380^{++} *Mozzarella*[#] WFP_{total}: 7117^{++}
Final products	*Beet sugar basis* Highest WFP_{total}: 240.6 Low WFP_{total}: 168.1 *Cane sugar basis* Highest WFP_{total}: 309.1	Pasta (Durum wheat 100%) WFP_{total}: 1924^{++} *Pizza Margherita* Mozzarella: ~73%; Bread wheat flour: ~24%; Tomato puree: ~3%

(*Continued*)

Table 16 Continued

Operation	*Product*	
	Lowest WFP_{total}: 168.0 *HFMS 55 basis* Global average WFP_{total}: 205.3	WFP_{total}: 1677^{++}.
Explanations		$^{++}$Unit of WFP: cbm ton^{-1} $^{\#}$The WFP of the processed product increases because of processing losses. In case of wheat bran and germ are removed during milling resulting in a final yield of ~80% for the flour. In case of tomato paste the final yield is ~30%.
References	Ercin *et al.* (2011)	Aldaya and Hoekstra (2010)

Abbreviations: HDPE, high-density polyethylene; PE, polyethylen; PP, polypropylen.

Source: Reproduced from Ercin, A.E., Martinez Aldaya, M., Hoekstra, A.Y., 2011. Corporate water footprint accounting and impact assessment: The case of the water footprint of a sugar containing carbonated beverage. Water Resources Management 25, 721–741 and Aldaya, M.M., Hoekstra, A.Y., 2010. The water needed for Italians to eat pasta and pizza. Agricultural Systems 103, 351–360.

Table 17 Water footprint (WFP) of selected materials used directly and indirectly for processing a 0.5 l PET bottle sugar-containing carbonated beverage

WFP of selected materials used directly and indirectly for processing a 0.5 l PET bottle

Item	*Raw material*	*Selected location for the calculation of the water footprint*	*Water footprint of raw material (m^3 ton^{-1})*			*Process water requirement (m^3 ton^{-1})*		
			Green	*Blue*	*Gray*	*Green*	*Blue*	*Gray*
Materials used indirectly for processing operations								
Concrete	Cement	Belgium(process)	0	0	0	0	0	1.9
Steel	Steel	Sweden (process) USA (raw material)	0	4.2	0	0	0	61
Paper	Wood	Finland (process)	369.4	0	0	0	0	125
Natural gas	Gas	World average	0	0	0	0	0	0.11
Electricity	Several	World average	0	0	0	0	0	0.47
Vehicles	Steel	Sweden (process) USA (raw material)	0	4.2	0	0	0	61
Fuel	Diesel	World average	0	0	0	0	0	1.06
Materials used directly for processing operations								
Bottle-PET	Oil	Sweden(raw)–Germany (process)	0	10	0	0	0	225
Closure-HDPE	Oil	Sweden (raw)–Germany (process)	0	10	0	0	0	225
Label-PP	Oil	Sweden (raw)–Germany (process)	0	10	0	0	0	225
Label glue	Glue	Germany	0	0	0	0	0	0
Tray glue	Glue	Netherlands	0	0	0	0	0	
Tray cartoon-paperboard	Wood	Belgium	369	0	0	0	0	180
Tray shrink film – PE	Oil	Sweden (raw)–Germany(process)	0	10	0	0	0	225
Pallet stretch wrap – PE	Oil	Sweden (raw)–Germany (process)	0	10	0	0	0	225
Pallet label (2 ×)-coated paper	Wood	Finland (process)	369.4b	0	0	0	0	125
Pallet – painted wood	Wood	Sweden	369.4b	0	0	0	0	75

Abbreviations: HDPE, high-density polyethylene; PE, polyethylen; PP, polypropylen.

Source: Reproduced from Ercin, A.E., Martinez Aldaya, M., Hoekstra, A.Y., 2011. Corporate water footprint accounting and impact assessment: The case of the water footprint of a sugar-containing carbonated beverage. Water Resources Management 25, 721–741. doi:10.1007/s11269-010-9723-8.

individual products according to their fractions of the total output.

Where the water is used

The conclusion which can be derived from the data presented in Tables 16 and 17 and other data presented reflects the general observation that can be derived from the data presented in Table 20, "Global average WFP of crop products derived from primary crops." The products derived from various primary crops have on average a significantly higher WFP than the original product, almost exclusively because of concentration/extraction processes and not because of the water used in processing operations. It can therefore be stated that the WFP of producing agricultural raw materials

Table 18 The water footprint (WFP) of 150 g of soy burger

150 g of soy burger	*WFP (m^3 ton^{-1})*				
	Green	*Blue*	*Gray*	*Total*	*% in total*
Operation					
Water incorporated into the soy milk	0	0.1	0	0.1	0.06
Water consumed during process	0	0	0	0	0
Wastewater discharge	0	0	0	0	0
Operational WFP	0	0.1	0	0.1	0.06
Ingredients					
Soybean (basemilk)	69.1	4.8	29.5	103.4	65.5
Maize	2.6	0.8	1.1	4.5	2.8
Soy milk powder	10.9	0.6	0.1	11.7	7.4
Soya paste	1.7	0.1	0.0	1.8	1.1
Onions	0.3	0	0.1	0.4	0.3
Paprika green	0.2	0	0.2	0.4	0.3
Carrots	0.1	0	0	0.2	0.1
Ingredients total	84.9	6.3	31	122.4	77.5
Other components					
Sleeve (cardboard)	9.2	0	2.7	11.9	7.5
Plastic cup	0. 0	0	3.5	3.5	2.2
Cardboard box (contains six burger packs)	15.4	0	4.5	19.9	12.6
Stretch film (LDPE)	0	0	0.1	0.1	0.06
Other components total	24.6	0	10.8	35.4	22.36
Supply-chain WFP	109.5	6.4	41.8	157.8	99.9
Total	109.5	6.5	41.8	157.9	

Abbreviation: LDPE, low-density polyethylene.

Source: Reproduced from Ercin, A.E., Aldaya, M.M., Hoekstr, A.Y., 2012. The water footprint of soy milk and soy burger and equivalent animal products. Ecological Indicators 18, 392–402.

far exceeds the WFP of processing and of all the operations along the food chain, from processing to consumption. Apparent increases in the WFP of a finished product are very often due to the fact that the product was subjected to drying/concentration processes, for example, production of roasted coffee beans or tea leaves. The WFP for various direct and indirect processing operations is in many cases almost negligible compared to the WFP of the raw agricultural product.

The Water Footprint and Water Management

From the data presented it becomes obvious that the WFP of materials, especially food materials, is a powerful tool to control the inherent/virtual utilization of water and the water flow and trade within narrow and broad systems, households, communities, nations, and continents. The various analyses reveal that the major part of water which is used for the global food production and for maintaining the global food supply chain is being used in the agriculture sector. The data also reveal that the WFP of processing steps is minimal compared with the amount of water spend for producing agricultural produce.

One of the merits of the concept is certainly that production methods within countries and between countries with regard to the amount of water used for producing specific goods can be compared. The same is true for the comparison of various production systems and even products; one prominent example in this context is the question whether the proliferation of Western meat consumption habits into Asia, where water and land resources are becoming scarce, should be supported or possibly restricted.

In Table 18 the WFP of a 150 g soy burger is detailed; the total WFP amounts to 157.9 l, the operational WFP amounts to 0.1 l, the WFP of the ingredients to 122.4 l, and the WFP of the other components to 35.4 l; a 150 g beef burger produced in the same country (the Netherlands) has a water consumption of 1000 l. The difference in water consumption between the soy product and the beef product is evident. If the protein contents of the soy product and beef product are considered, it has to be stated, however, that the nutritional-physiological values do not compare one to one. If the protein concentrations in the two products are considered, approximately 290 g of soy protein (tofu) would be required to match 100 g of beef meat (Watzl *et al.*, personal communication). This example demonstrates also that the operational WFP is negligible.

A Major Deficit of the Water Footprint

A major shortcoming of the virtual water and the WFP concepts is that they do not provide any information regarding the sustainability of the water withdrawal from a resource. It is evident that the utilization of 'green' water in agriculture is sustainable; however, if 'blue' water resources are overexploited, i.e., the amount withdrawn is larger than the supply,

Table 19 Global average water footprint of primary crops (period: 1996–2005)

Product description	*Global average water footprint (m^3 ton^{-1})*			
	Green	*Blue*	*Gray*	*Total*
Cereals				
Barley	1 213	79	131	1 423
Maize (corn)	947	81	194	1 222
Millet	4 306	57	115	4 478
Oats	1 479	181	128	1 788
Rice (paddy)	1 146	341	187	1 673
Rye	1 419	25	99	1 544
Sorghum	2 857	103	87	3 048
Wheat	1 277	342	207	1 827
Tubers				
Manioc (cassava)	550	0	13	564
Potatoes	191	33	63	287
Sweet potatoes	324	5	53	383
Taro (*Colocasia esculenta* – yam)	587	3	15	606
Sugar-containing plants				
Sugar beet	82	26	25	132
Sugar cane	139	57	13	210
Legume				
Beans, green	320	54	188	561
Beans, dry	3 945	125	983	5 053
Broad beans and horse beans, dry	1 317	205	496	2 018
Chick peas, dry	2 972	224	981	4 177
Groundnuts shelled	3 526	214	234	3 974
Peas, dry	1 453	33	493	1 979
Peas, green	382	63	150	595
Lentils, dry	4 324	489	1060	5 874
Soya beans	2 037	70	37	2 145
Nuts				
Almonds, with shell	4 632	1 908	1507	8 047
Cashew nuts	12 853	921	444	14 218
Coconuts	2 669	2	16	2 687
Oil palm	1 057	0	40	1 098
Olives	2 470	499	45	3 015
Rapeseed	1 703	231	336	2 271
Sesame seed	8 460	509	403	9 371
Seed cotton	2 282	1 306	440	4 029
Sunflower seeds	3 017	148	201	3 366
Walnuts, with shell	2 805	1 299	814	4 918
Vegetable				
Artichokes	478	242	98	818
Cabbages and other brassicas	181	26	73	280
Carrots and turnips	106	28	61	195
Cauliflowers and broccoli	189	21	75	285
Chilies and peppers, green	240	42	97	379
Cucumbers and gherkins	206	42	105	353
Eggplants (aubergines)	234	33	95	362
Lettuce	133	28	77	237
Maize, green	455	157	88	700
Okra	474	36	65	576
Onions (including shallots), green	176	44	51	272
Pumpkins, squash, and gourds	228	24	84	336
Spinach	118	14	160	292
Tomatoes	108	63	43	214
Fruits				
Apples, fresh	561	133	127	822
Apricots	694	502	92	1 287
Bananas	660	97	33	790
Blueberries	341	334	170	845
Cranberries	91	108	77	276
Currants	457	19	23	499
Dates	930	1 250	98	2 277
Grapes	425	97	87	608
Mangoes, mangosteens, and guavas	1 314	362	124	1 800
Oranges	401	110	49	560
Papayas	399	40	21	460
Peaches and nectarines	583	188	139	910
Pineapples	215	9	31	255
Plantains	1 570	27	6	1 602
Plums and sloes	1 570	188	422	2 180
Strawberries	201	109	37	347
Natural stimulants and spices				
Coffee, green	15 249	116	532	15 897
Cocoa beans	19 745	4	179	19 928
Green and black tea	7 232	898	726	8 856
Hop cones	2 382	269	1414	4 065
Pepper of the genus piper	6 540	467	604	7 611
Chilies and peppers, dry	5 869	1 125	371	7 365
Cinnamon (canella)	14 853	41	632	15 526
Cloves	59 834	30	1341	61 205
Ginger	1 525	40	92	1 657
Vanilla beans	86 392	39 048	1065	126 505
Tobacco, unmanufactured	2 021	205	700	2 925

Source: Reproduced from Mekonnen, M.M., Hoekstra, A.Y., 2011. The green, blue and grey water footprint of crops and derived crop products. Hydrology and Earth System Sciences 15, 1577–1600. Available at: www.hydrol-earth-syst-sci.net/15/1577/2011/; doi:10.5194/hess-15-1577-2011.

Table 20 Global average water footprint of crop products derived from primary crops (period: 1996–2005)

Product description	*Global average water footprint (m^3 ton^{-1})*			
	Green	*Blue*	*Gray*	*Total*
(*Wheat*	1 277	342	207	1 827)
Wheat flour	1 292	347	210	1 849
Wheat bread	1 124	301	183	1 608
Dry wheat pasta	1 292	347	210	1 849
Wheat pellets	1 423	382	231	2 036
Wheat, starch	1 004	269	163	1 436
Wheat gluten	2 928	785	476	4 189
(*Rice, paddy*	1 146	341	187	1 673)
Rice, husked (brown)	1 488	443	242	2 172
Rice, broken	1 710	509	278	2 497
Rice flour	1 800	535	293	2 628
Rice groats and meal	1 527	454	249	2 230

(*Continued*)

Table 20 Continued

Product description	*Global average water footprint (m^3 ton^{-1})*			
	Green	*Blue*	*Gray*	*Total*
(*Barley*	1 213	79	131	1 423)
Barley, rolled or flaked grains	1 685	110	182	1 977
Malt, not roasted	1 662	108	180	1 950
Malt, roasted	2 078	135	225	2 437
Beer made from malt	254	16	27	298
(*Maize* (*corn*)	947	81	194	1 222)
Maize (corn) flour	971	83	199	1 253
Maize (corn) groats and meal	837	72	171	1 081
Maize (corn), hulled, pearled, sliced, or kibbled	1 018	87	209	1 314
Maize (corn) starch	1 295	111	265	1 671
Maize (corn) oil	1 996	171	409	2 575
(*Oats*	1 479	181	128	1 788)
Oat groats and meal	2 098	257	182	2 536
Oats, rolled or flaked grains	1 998	245	173	2 416
(*Potatoes*	191	33	63	287)
Tapioca of potatoes	955	165	317	1 436
Potato flour and meal	955	165	317	1 436
Potato flakes	694	120	230	1 044
Potato starch	1 005	173	333	1 512
(*Manioc* (*cassava*)	550	0	13	564)
Tapioca of Manioc (cassava)	2 750	1	66	2 818
Flour of manioc (cassava)	1 833	1	44	1 878
Dried manioc (cassava)	1 571	1	38	1 610
Manioc (cassava) starch	2 200	1	53	2 254
(*Sugar cane*	139	57	13	210)
Raw sugar, cane	1 107	455	104	1 666
Refined sugar	1 184	487	111	1 782
Fructose, chemically pure	1 184	487	111	1 782
Cane molasses	350	144	33	527
(*Sugar beet*	82	26	25	132)
Raw sugar, beet	535	167	162	865
(*Soya beans*	2 037	70	37	2 145)
Soya sauce	582	20	11	613
Soya paste	543	19	10	572
Soya curd	2 397	83	44	2 523
Soy milk	3 574	123	65	3 763
Soya bean flour and meals	2 397	83	44	2 523
Soybean oil, refined	3 980	137	73	4 190
Soybean oilcake	1 690	58	31	1 779
(*Groundnuts in shell*	2 469	150	163	2 782)
Groundnuts shelled	3 526	214	234	3 974
Groundnut oil, refined	6 681	405	442	7 529
Groundnut oilcake	1 317	80	87	1 484
Palm, oil	1 057	0	40	1 098
Palm nuts and kernels	2 762	1	105	2 868
Palm oil, refined	4 787	1	182	4 971
Palm kernel/babassu oil, refined	5 202	1	198	5 401
Palm nut/kernel oilcake	802	0	31	833
Olives	2 470	499	45	3 015
Olive oil, virgin	11 826	2388	217	14 431
Olive oil, refined	12 067	2437	221	14 726

(*Continued*)

Table 20 Continued

Product description	*Global average water footprint (m^3 ton^{-1})*			
	Green	*Blue*	*Gray*	*Total*
Sunflower seeds	3 017	148	201	3 366
Sunflower seed oil, refined	6 088	299	405	6 792
Sunflower seed oilcake	1 215	60	81	1 356
Rapeseed	1 703	231	336	2 271
Rape oil, refined	3 226	438	636	4 301
Rape seed oilcake	837	114	165	1 115
Cotton seed	2 282	1306	440	4 029
Cotton lint	5 163	2955	996	9 113
Cotton linters	1 474	844	284	2 602
Cotton-seed oil, refined	2 242	1283	432	3 957
Cotton seed oilcake	487	279	94	860
Cotton, not carded or combed	5 163	2955	996	9 113
Cotton yarn waste (including thread waste)	950	544	183	1 677
Cotton, garneted stock	1 426	816	275	2 517
Cotton, carded or combed	5 359	3067	1034	9 460
Cotton fabric, finished textile	5 384	3253	1344	9 982
Tomatoes	108	63	43	214
Tomato juice unfermented and not spirited	135	79	53	267
Tomato juice, concentrated	539	316	213	1 069
Tomato paste	431	253	171	855
Tomato ketchup	270	158	107	534
Tomato puree	360	211	142	713
Tomatoes, peeled	135	79	53	267
Tomato, dried	2 157	1265	853	4 276
Apples, fresh	561	133	127	822
Apples, dried	4 678	1111	1058	6 847
Apple juice unfermented and not spirited	780	185	176	1 141
Grapes	425	97	87	608
Grapes, dried	1 700	386	347	2 433
Grapefruit juice	490	114	71	675
Grape wines, sparkling	607	138	124	869
Pineapples	215	9	31	255
Pineapple juice	1 075	45	153	1 273
Coffee, green	15 249	116	532	15 897
Coffee, roasted	18 153	139	633	18 925
Cocoa beans	19 745	4	179	19 928
Cocoa paste	24 015	5	218	24 238
Cocoa butter, fat and oil	33 626	7	305	33 938
Cocoa powder	15 492	3	141	15 636
Chocolate	16 805	198	193	17 196
Hop cones	2 382	269	1414	4 065
Hop extract	9 528	1077	5654	16 259

Source: Reproduced from Mekonnen, M.M., Hoekstra, A.Y., 2011. The green, blue and grey water footprint of crops and derived crop products. Hydrology and Earth System Sciences 15, 1577–1600. Available at: www.hydrol-earth-syst-sci.net/15/1577/2011/; doi:10.5194/hess-15-1577-2011.

an unsustainable situation will arise. To deal with this deficit, Schubert (2011) suggests splitting the amount of blue water into an unsustainable and a sustainable fraction. The problem around this interesting suggestion is that complex and detailed

water balances have to be executed for well-defined control areas.

With regard to food processing and other operations along the food chain, the WFP plays only a minor role. Food science and technology play an important role in reducing the WFP of raw materials through the reduction of food losses starting right after harvest. Reducing post-harvest losses means optimizing the use of available water resources.

Acknowledgment

Major information presented in this compilation has been derived from the large number of detailed publications by Professor dr.ir. A.Y. Hoekstra, A.K. Chapagain, M.M. Mekonnen, A.E. Ercin and M. Martinez Aldaya at the Faculty of Engineering Technology, Department of Water Engineering & Management, University of Twente, P.O. Box 217, 7500 AE Enschede. Arjen Y. Hoekstra and his coworkers have developed the concept of the WFP in an admirable and concise way; they have published a large number of case studies on this subject. Most of the data referenced in this chapter are drawn from the Hoekstra group; those data are easily accessible for further in-depth studies and they have been elaborated under standardized condititions suited for direct comparisons.

See also: Beef Cattle. Dairy Animals. Energy and Greenhouse Gases Footprint of Food Processing. Food Engineering. Food Security: Development Strategies. Food Security: Food Defense and Biosecurity. Food Security: Postharvest Losses. Food Security: Yield Gap. Global Food Supply Chains. Land Use: Catchment Management. Root and Tuber Crops. Slum Livestock Agriculture. Soil Fertility and Plant Nutrition. Sugar Crops. Tree Fruits and Nuts. Water: Advanced Irrigation Technologies. Water Use: Recycling and Desalination for Agriculture. Water: Water Quality and Challenges from Agriculture. World Water Supply and Use: Challenges for the Future

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Vitamins and Food-Derived Biofactors

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Glossary

Adenosine diphosphate (ADP) ribosylation ADP ribosylation is the addition of one or more ADP-ribose moieties to a protein. ADP ribosylation reactions are involved in cell signaling and the control of many cell processes, such as the deoxyribonucleic acid (DNA) repair.

Apoptosis The process of programed cell death, in which the cell uses specialized cellular machinery to catabolize itself in order to control cell number and eliminate cells that threaten survival.

Calvin cycle A series of biochemical light-dependent redox reactions located in the stroma of chloroplasts in photosynthetic organisms.

Cell signaling The process of relaying of molecular signals (chemical or physical, such as light) from a cell's exterior to its intracellular response elements and signaling molecules. The signals may be hormonal (produced in specific cells, glands, or tissues and transported to other parts of the body to provoke a given physiological response), paracrine (cell–cell communication in which a cell produces a signal to induce changes in nearby cells), autocrine (agents arising from the same cells that are signaled), or external in nature (e.g., caused by a given dietary biofactor).

Mitochondriogenesis (mitochondrial biogenesis) The production of new mitochondria; a process that can occur independently of normal cell division.

Myelin An electrically insulating material that forms a protective layer around the axon of a neuron. Loss of myelin leads to a decrease in the rate at which nerve impulses are propagated.

Osteocalcin Proteins secreted by osteoblastic bone cells implicated in bone mineralization and calcium ion homeostasis.

Pentose phosphate pathway Also called the hexose monophosphate shunt pathway; an important source of nicotinamide adenosyl phosphodinucleotide (NADPH) and pentose sugars (5-carbon sugars).

Transcriptional activators and coactivators Transcriptional activators are DNA-binding proteins and function by binding at a DNA site located in or near a promoter of a gene; thus aiding in the enhancement or inhibition of gene expression. Other essential proteins that facilitate the process are called coactivators. They aid in forming complexes that may include the transcription factor and other accessory factors important in the overall regulation of transcription.

Xenobiotic metabolism Metabolic pathways, usually found in the ER, designed to modify the chemical structure of xenobiotics, compounds that are foreign to an organism's normal metabolism, as well endogenously derived products.

Vitamins

The compounds generally classified as vitamins are among those dietary factors for which critical amounts are required for normal physiological processes and functions. As typically defined, vitamins are viewed as essential as they are either not synthesized in endogenous metabolic pathways or in amounts that are adequate for optimal health. Accordingly, dietary sources are required. The dietary amounts needed (usually expressed for humans as an amount per day) in certain cases remain a subject of debate due to differences in opinion regarding the health parameter(s) that are chosen for the establishment of the requirement (Dietary Reference Intakes, 2004).

An appreciation that certain food components can be linked to growth and health has been appreciated for millennia (Carpenter, 1986; Grivetti, 2000; Goldblith and Joslyn, 1964). The Egyptian medical text, the 'Papyrus Ebers' (written approximately CE 1550–70) contains references that described consumption of liver as a potential treatment to improve vision including night blindness. During the Tang Dynasty, the Chinese physician, Sun Simiao, wrote medical texts that contained nutrition guides that are still used in traditional Chinese medicine. By the sixteenth century, fresh fruits and vegetables were documented as effective in the treatment of scurvy and by the late 1800s, an association between the consumption of certain foods and prevention from other disease conditions could be inferred; as examples, the association between maize and pellagra (Section Niacin) and between polished rice and polyneuritis (Section Thiamine) can be considered.

At this point, seminal concepts were also emerging that accelerated progress in identifying specific compounds in foods as nutritionally essential. Analytical approaches were developed that focused on defining the composition of foods. The utility of using experimental animals as models for nutrition and toxicological studies was appreciated, along with food-derived energy concepts, that is, the association between caloric intake and work (e.g., by the early twentieth century, the physiological

 doi:10.1016/B978-0-444-52512-3.00071-1

fuel values for fat, carbohydrate, and protein were established). There was also a good understanding that indices, such as the respiratory quotient, could change depending on the composition or the amount of a food that was consumed. However, at this time, the concept of disease was largely based on the 'germ theory of disease' proposed by Pasteur and others, that is, diseases were caused by infectious agents (Toledo-Pereyra, 2009). It was also commonly held that only the gross constituents of the diet, that is, carbohydrates, protein, fat, and minerals, were needed for complete nourishment.

As an example, an early explanation related to the ability of a factor isolated from rice husks to reverse the signs of beriberi (a disease associated with thiamine deficiency) was that beriberi was caused by an infectious agent or toxin in rice polishing and the husks of rice contained some type of antidote. Nevertheless, the more nutritional explanation eventually prevailed, that is, that rice contains an essential factor in the outer layers of the grain that on its removal (e.g., by polishing) potentiated a type of nutritional 'deficiency disease.' When coupled with the observations of E.V. McCollum and M. Davis and those of T. Osborne and L. Mendel, that a factor in butter and egg yolk was necessary for growth and vision in rats, a true step forward was achieved. The fat-soluble component in butter and egg yolk was designated factor A. The factor in rice hulls was designated factor B (later B_1, on discovery of other essential factors). As the concept of essential factors was further solidified, the term *vitamine* was coined and used as early as 1912 (by the Polish biochemist, Kazimierz Funk). The term was a combination of 'vital' and 'amine,' meaning amine of life. As the list of factors grew and better chemical characterizations became possible, it became evident that not all vitamins could be classified as amines. Thus, *vitamine* was shortened to vitamin (Goldblith and Joslyn, 1964).

As of 2013, there are 13 compounds and related vitamers (i.e., physiologically active isomers and precursors) that are widely accepted by the scientific community as meeting the criteria for being classified as vitamins for humans. Specific subcategories and further classifications are arbitrary and based on general biological activity, chemical properties, and historical precedents (**Table 1**). For example, the letter designations for vitamins (e.g., vitamins A, B_1, B_2, or C, etc.) evolved in part from their sequential discovery. Not included in this discussion are a number of compounds that are often described as conditional/vitamin-like compounds. Many of these compounds are derived from amino acids. Included in this group of compounds are carnitine, various carotenoids, choline, glutathione, inositol, lipoic acid, and taurine. Selected phytochemicals (historically designated as vitamin P) and polyquinones, such as pyrroloquinoline quinone, are also sometimes included.

Health Effects: General Properties and Primary Functions of Vitamins

The need for vitamins stems in part from our evolution from prokaryotes and eukaryotes wherein energy utilization involved the need for oxidation of inorganic compounds, nitrogen fixation, and phototrophic processes (e.g., the presence of a Calvin cycle). Although animals no longer have the ability to capture solar energy or fix nitrogen, remnants of such processes have been retained as essential features of energy-related metabolism (e.g., the ability to effect energy and proton gradients, maintain energy charge, or catalyze the formation of high-energy intermediates). Further, whether aerobic or anaerobic, the need to deal with reactive oxygen species (e.g., superoxide and hydrogen peroxide) has resulted in the need for compounds, such as the tocopherols (e.g., compounds with antioxidant potential, such as vitamin E). To transfer heat and engage in work efficiently, living systems maintain their state of complexity by increases in entropy. In this regard, to circumvent prohibitive energy barriers and increase the ability to incrementally regulate energy processes, ranges of catalysis with differing attributes are needed. Vitamin-derived cofactors, along with given mineral elements, provide such range and diversity. Specific vitamins have largely evolved to extend the catalytic capacity of enzymes (e.g., beyond that is provided by amino acids) and provide novel catalytic or cell regulatory and signaling functions. Examples include functioning as agents for electron transfer, carbonium and carbanion stabilization, nucleophilic and electrophilic transfers, carbonyl-amine reactions, and oxidative and nonoxidative bond cleavage. With such cofactors, the metabolism of a cell is more easily achieved, particularly the coupling of the spontaneous processes of catabolism to the nonspontaneous processes of anabolism (McCormick, 2007).

Most vitamins act as a coenzyme, cosubstrate, or as a prosthetic group. A coenzyme is defined as an organic molecule that binds specifically within an apoenzyme to create a catalytically competent holoenzyme. If tightly bound and nondissociable, a coenzyme may be referred to as a prosthetic group, and if readily dissociable, they may be called cosubstrates.

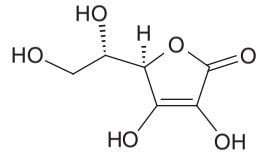
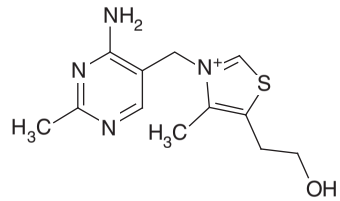
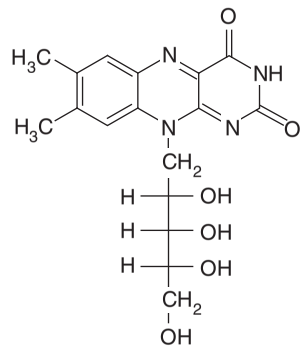
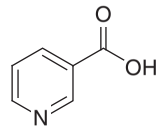
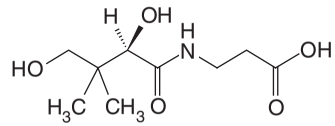
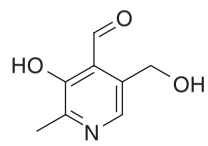
Important Systemic Functions of Vitamins

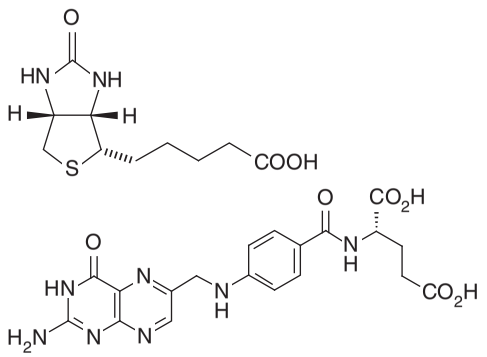
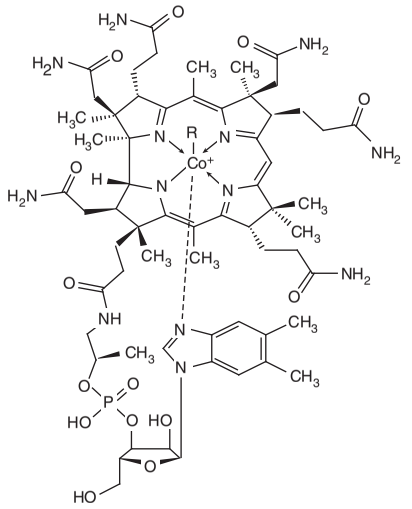
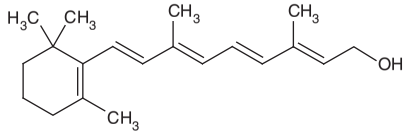
Vitamins involved in oxidation–reduction reactions

- Ascorbic acid

  Ascorbic acid (vitamin C; 2,3-enedial-gluconic acid) is a powerful reducing agent. Both hydrogens of the enediol group in ascorbic acid are capable of dissociation. Reductions initiated by ascorbic acid usually occur in a stepwise fashion with monodehydroascorbic acid, as a semiquinone intermediate. This intermediate then disproportionates to dehydroascorbic acid. Ascorbic acid serves as a cofactor for mixed-function oxidations catalyzed by microsomal mono-and dioxygenases, which are commonly referred as hydroxylases and oxidases. These enzymes catalyze the hydroxylation of prolyl and lysyl residues in collagen and proteins with collagen-like domains as well as elastin, conotoxins, argonaute 2, and C1q-complement (Rucker *et al.*, 2008). The hydroxylation of carnitine, neurotransmitters, the synthesis and catabolism of tyrosine, and the metabolism of numerous xenobiotics and secondary metabolites by microsomal oxidases are also dependent on ascorbic acid.

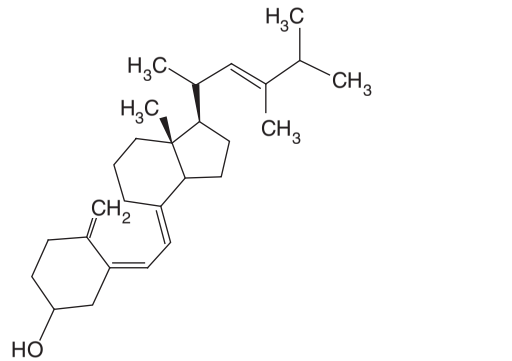
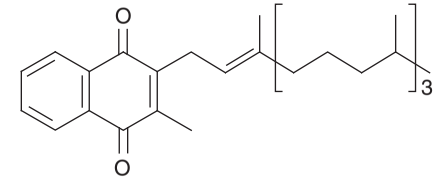
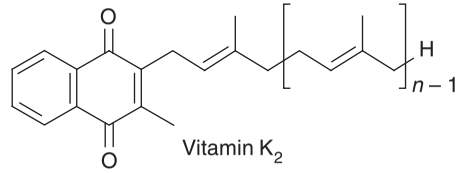
Table 1 Vitamin sources and requirements

Vitamin	*Human adult requirements females–males amount per day*	*Common sources*	*Chemical structure*
Water-soluble vitamins			
Ascorbic acid (vitamin C)	45 mg (RDA)[a] 60 (DRI)[c]	Red and green peppers, various citrus fruits, and broccoli	
Thiamine (vitamin B_1)	1.0–1.5 mg (RDA)[a]	Whole grains, lentils and beans, and fish (e.g., tuna)	
Riboflavin (vitamin B_2)	1.1–1.8 mg (RDA)[a]	Eggs, milk, and legumes	
Niacin and nicotinic acid (vitamin B_3)	14–20 mg (RDA)[a]	Meat, fish, poultry, whole grains, and high-quality protein sources containing ample tryptophan	
Pantothenic acid (vitamin B_5)	~5 mg (AI)[b]	Chicken, beef, potatoes, oats, cereals, and tomatoes	
Pyridoxine (vitamin B_6)	1.5–2.0 mg (RDA)[a]	Grains, cereals, soy products, and organ meats	
Biotin (vitamin H or B_7)	~30 μg (AI)[b]	Liver, fruits, and meats	

Folic acid, folacin (vitamin M or B_9)	400 μg (RDA)[a] 200 μg (DRI)[c]	Dark, leafy vegetables; whole grains; and fortified breads and cereals	
Cobalamin (vitamin B_{12})	3.0 (RDA)[a] 2.0 (DRI)[c]	Fish, poultry, meat, and fortified cereals	
Fat-soluble vitamins			
Vitamin A (retinol)	800–100 μg (RDA)[a]	Sweet potatoes and related tubers, carrots, and Brassica family leafy vegetables (e.g., spinach and kale)	
Vitamin D (calciferol)	400 μg (RDA)[a]	Fish liver oils, fortified milk products and cereals, and also sunlight exposure	

(*Continued*)

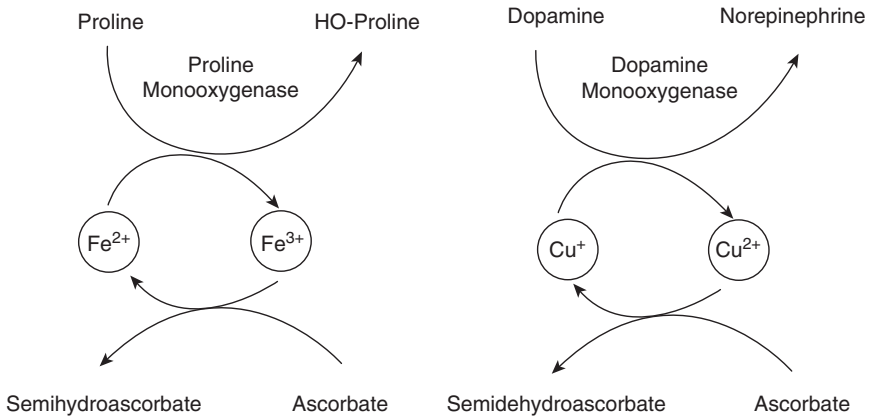
Table 1 Continued

Vitamin	*Human adult requirements females–males amount per day*	*Common sources*	*Chemical structure*
Vitamin E (tocopherol)	12–15 mg (RDA)[a]	Plant and plant germ seed oils, plant seeds, and nuts	
Vitamin K_1 and K_2	55–80 μg (RDA)[a]	Green vegetables	 Vitamin K_1  Vitamin K_2

[a]The range of values reflects those for young females and males. Values are recommended dietary allowances (RDAs), defined as the quantities of nutrients in the diet that are required to maintain good health in people. RDAs were established by the Food and Nutrition Board of the National Academy of Sciences, and are periodically revised.

[b]When there are insufficient data to estimate a RDA or dietary reference intake (DRI), an adequate intake (AI) estimate is used, which is a based on intake levels derived from food compositional data, rather than nutritional balance data that requires knowledge of relative absorption and whole body retention.

[c]The DRI was introduced in 1997 in order to broaden the existing guidelines known as RDAs. The DRI values, however, are not currently used in nutrition labeling.



The hydroxylases and oxidases that require ascorbic acid often have iron and copper at their catalytic sites. In this regard, ascorbate acts as a reducing agent, donating electrons and preventing oxidation, which maintains iron and copper atoms in a reduced state (Mandl *et al.*, 2009). This is needed for the coordination of oxygen leading to favorable transfer to various substrates. Peptidylglycine α-amidating monooxygenase also requires ascorbic acid. The protein contains two enzymes that act sequentially to catalyze the α-amidation of neuroendocrine peptides important to their activation.

$$\text{Peptidylglycine} + \text{ascorbate} + O_2 \rightarrow$$
$$\text{peptidyl-(2-hydroxyglycine)} + \text{dehydroascorbate} + H_2O$$

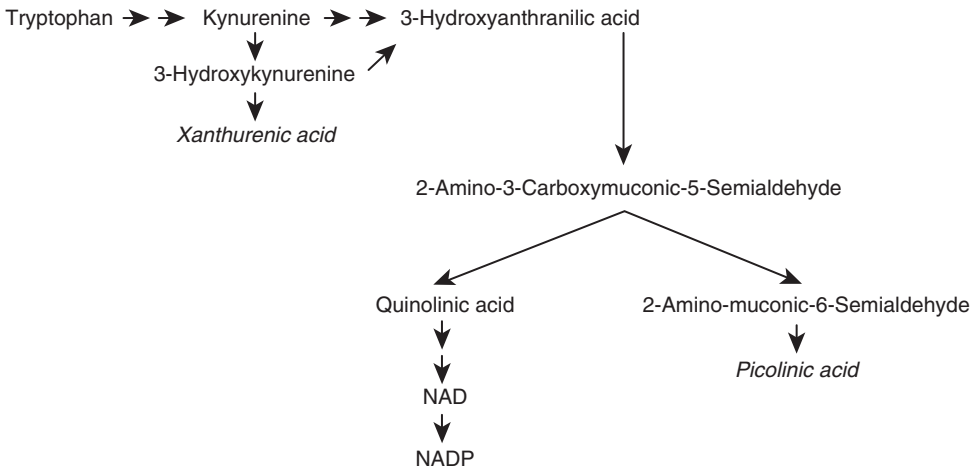
The first step of the reaction is catalyzed by peptidylglycine α-hydroxylating monooxygenase; peptidyl-α-hydroxyglycine-α-amidating lyase catalyzes the second step of the reaction.

When the activity of ascorbic acid-dependent hydroxylases or oxidases is limited, the result can be a decreased production of proteins, such as collagen (the major structural protein in the body) or select components of the immune system (e.g., such as the C1q complex, important for immunoglobulin binding and interactions). Further, important metabolites, such as carnitine (important for fatty acid transport into the mitochondria) can be affected. Accordingly, the result of ascorbic acid deficiency or 'scurvy' can be capillary fragility, delayed wound healing, impaired immune responsiveness, and impaired bone formation. Described in the classic treatise by Lind, scurvy was one of the most common diseases associated with maritime travel, often killing large numbers of the passengers and crew on long-distance voyages or migrations of people without ready access to fruit and vegetable sources of ascorbic acid.

- Niacin

  Niacin is an unsubstituted pyridine-3-carboxamide. With respect to redox functions, nicotinamide adenosyl dinucleotide (NAD) and nicotinamide adenosyl phosphodinucleotide (NADP) are the coenzymes derived from niacin that are designed to facilitate the abstraction of a hydride ion (H:) from substrates. These cofactors are produced in reactions that link potential niacin precursors to adenosyl phosphates (McCormick, 2007).

  In many animals, NAD and NADP can be formed from metabolites arising from tryptophan catabolism as outlined in the following schema. NAD (containing niacin) is eventually formed following amidation; a subsequent phosphorylation leads to NADP. Xanthurenic and picolinic acid are principal excretory products. Factors that stimulate their production compromise NAD production. Virtually all cells are capable of converting niacin into NAD or NADP.



NAD and NADP function in numerous oxidoreductase systems (e.g., dehydrogenase or reductase systems) important to the conversion of alcohols (sugars and polyols) into aldehydes or ketones, hemiacetals into lactones, aldehydes into acids, and certain amino acids into keto acids. From a redox perspective, NAD is often utilized in catabolic pathways and NADP in synthetic pathways. In addition, NAD serves as a substrate in mono- and poly-adenosine diphosphate (ADP)-ribosylation reactions. ADP ribosylation occurs with the addition of one or more ADP-ribose moieties to a protein. ADP ribosylations are important in cell signaling and the control of many cell processes, including deoxyribonucleic acid (DNA) repair and apoptosis. In many cells, more than 50% of the cell's NAD may be directed or involved in some type of ribosylation reaction (Kirkland, 2013).

A severe deficiency of niacin can result in pellagra (characterized by diarrhea, dermatitis, forms of dementia, and eventually death). Pellagra may be first present with sensitivity to sunlight; followed by dermatitis, alopecia (hair loss), edema (swelling); glossitis (tongue inflammation); mental confusion; and ataxia (lack of coordination). Other mental disturbances can include restlessness, tense and quarrelsome behavior, and paranoid emotional disturbances.

Pellagra was once endemic in the southern parts of the United States, the disease being particularly common in individuals housed in jails, as well as children in orphanages. With the recognition of the dietary causes of pellagra in the early 1900s, the disease was largely eliminated in the United States by the 1940s (Goldblith and Joslyn, 1964); however, pellagra remains endemic in parts of Africa, where corn is a major dietary staple. A deficiency of niacin can result from either a dietary insufficiency of niacin per se or the predominant consumption of protein sources, such as maize. The nutritional availability of niacin from maize is poor and the concentration of the amino acid, tryptophan is also low. For example, sufficient quantities of niacin may be obtained from high-quality proteins, rich in tryptophan (Kirkland, 2013).

- Riboflavin

  Riboflavin (7,8-dimethyl-10-[(*2S,3S,4R*)-2,3,4,5 tetrahydroxypentyl]benzo[*g*]pteridine-2,4-dione) is present in tissue and cells as flavin adenine dinucleotide (FAD) and flavin adenine mononucleotide (FMN). FAD and FMN are cofactors in aerobic processes, usually for oxidases, although FAD can also function in anaerobic environments as a dehydrogenase cofactor.

  In some enzymes, riboflavin is covalently linked (e.g., succinic dehydrogenase in which riboflavin is linked to a specific histidinyl residue). In general, FMN and FAD, even when not covalently bound, are not easily dissociated; thus, they may often be viewed as prosthetic groups. Flavins catalyze one-electron and one-proton transfer reactions. Oxygen is utilized as a cosubstrate. Flavins also act as oxidizing agents, because of their ability to accept a pair of hydrogen atoms. Substrates for flavin-requiring enzymes are usually compounds that contain carbon–carbon double bonds and disulfide-containing compounds (e.g., oxidized lipoic acid). Reduced NADP commonly serves as a reductant in processes to regenerate $FADH_2$ or $FMNH_2$ (McCormick, 2007).

Signs of riboflavin deficiency include lesions of the oral cavity, the lips, and the angle of the mouth (cheilosis), inflammation of the tongue (glossitis), and a seborrheic dermatitis that presents as scaly, flaking, and inflamed skin. The sebaceous-gland-rich areas of the skin (e.g., the nasolabial fold) and scalp are most affected. The filiform papillae of the tongue may also be lost with changes in color from pink to magenta. Anemia and increased vascularization of the eye are present in some animals with riboflavin deficiency (Rucker *et al.*, 2008).

Vitamins important to the generation of leaving group potential

- Thiamine

  Thiamine (2-[3-[(4-amino-2-methyl-pyrimidin-5-yl) methyl]-4-methyl-thiazol-5-yl] ethanol) is central to the metabolism of carbohydrates as energy sources. The five-member (thiazole) ring of thiamine is an arrangement of atoms (–N═CH–S–) called an ylide. The central carbon has carbanion character that acts as an electron-rich center for reactions at which a carbonium ion is the potential point of attack, such as the α carbon of ketoacids, common intermediates in the oxidation of carbohydrates. In addition, the ylide configuration provides a transitory matrix that has a good leaving group and transfer potential.

  Thiamine pyrophosphate (TPP) is the major coenzyme derived from thiamine, for which there are two general types of reactions. The first is the decarboxylation of α-keto acids (the condensation of the thiazole moiety of TPP with the α-carbonyl carbon on the acid leads to loss of CO_2 and production of a resonance-stabilized carbanion). An example is the first step in the tricarboxylic acid cycle (TCA) cycle involving oxidation of pyruvate (**Figure 1**). The second type is the transketolase reaction that reacts with a carbonyl group, cleaves the adjacent carbon–carbon bond, and then transfers the cleaved moiety to another aldose substrate subunit. The pentose phosphate pathway is especially active in the adipose tissue, mammary glands, and the adrenal cortex, but it is more limited in the skeletal muscle and liver.

  The two stages of the reaction are reversible. This pathway can bring about the interconversion of pentoses, hexoses, and other lengths of sugars as needed. The pentose phosphate pathway also generates the reduced form of NADP, which in turn is required for a wide range of biosynthetic reactions, including the synthesis of fatty acids. The fundamental reaction is a two-carbon (glycolaldehyde group) transfer from one sugar phosphate to another.

  Xylulose-5-phosphate (C5) + Ribose-5-phosphate (C5)

  ⇆Glyceraldehyde-3-phosphate (C3)

  +Sedoheptulose-7-phosphate (C7)

  Xylulose-5-phosphate (C5) + Erythrose-4-phosphate (C4)

  ⇆Glyceraldehyde-3-phosphate (C3)

  +Fructose-6-phosphate (C6)

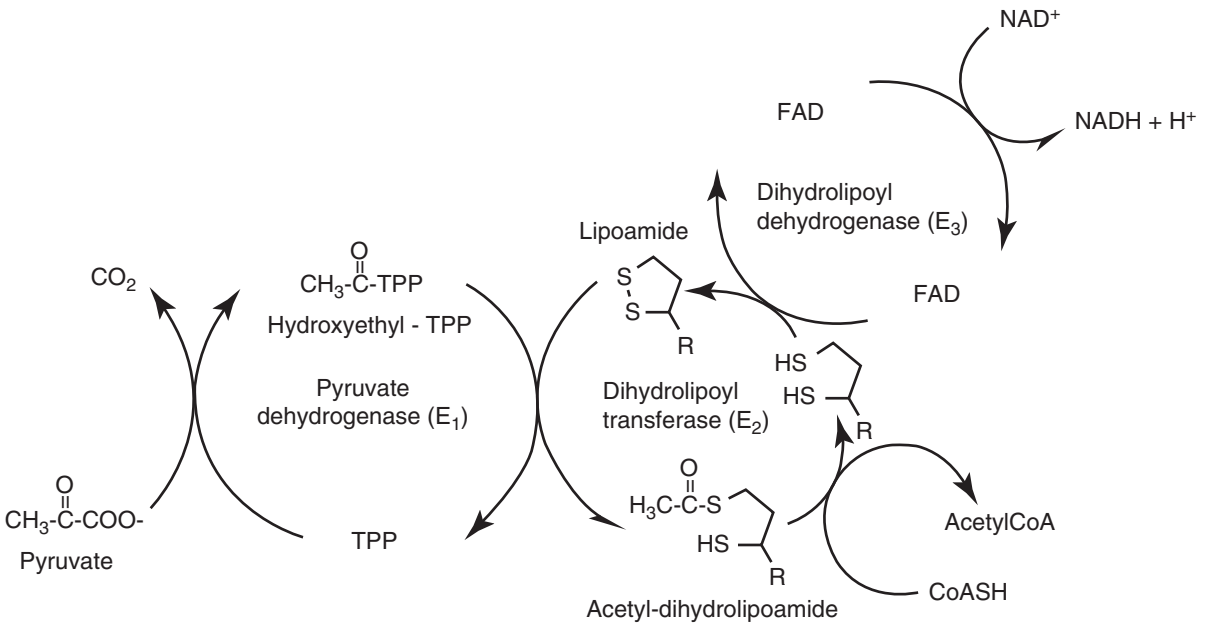


Figure 1 Thiamine. Thiamine in the form of thiamine diphosphate (TDP) is an essential cofactor for the pyruvate dehydrogenase (PDH) complex, which is composed of three enzymes that catalyze the conversion of pyruvate into acetyl-CoA. Acetyl-CoA may then be used in the citric acid cycle to carry out cellular respiration. This complex is also related structurally and functionally to the oxoglutarate dehydrogenase complex (found within the citric acid cycle), as well as the oxoacid dehydrogenase multienzyme complexes important to the metabolism of branched-chained amino acids. Given its central role in carbohydrate and energy metabolism, PDH is regulated in part by changes that affect ATP production or the production of cellular oxidants or reductants important to energy utilization (e.g., NAD and NADP derivatives).

Transketolase acts in conjunction with the enzyme transaldolase (nonthiamine-requiring), which catalyzes

Sedoheptulose-7-phosphate (C7)
+ Glyceraldehyde-3-phosphate (C3)
⇆Erythrose-4-phosphate (C4)
+Fructose-6-phosphate (C6)

Other forms of thiamine include adenosine thiamine triphosphate (TPPP) or thiaminylated adenosine, which accumulates in bacteria as a result of carbon starvation. It is also present in low amounts in yeast, roots of higher plants, and animal tissue. In neural tissue, TPPP is a neuroactive form of thiamine thought to be involved in sodium and potassium gating (transport) in neural cells. TPPP also exists in bacteria, fungi, and plants. Like thiaminylated adenosine, it seems to play a role in response to carbon or amino acid starvation.

In the TCA cycle, the principal enzymes affected by thiamine deficiency are PDH and α-ketoglutarate dehydrogenase. Accordingly, thiamine deficiency adversely affects any organ system dependent on oxidative metabolism. Thiamine deficiency commonly presents subacutely, but can eventually lead to metabolic coma and death. A lack of thiamine can be caused by malnutrition, diets high in thiaminase-rich foods (raw freshwater fish, raw shellfish, and ferns), foods high in antithiamine factors (e.g., tannins and caffeic acid found in tea and coffee), and gastrointestinal diseases induced by alcohol or systemic inflammation.

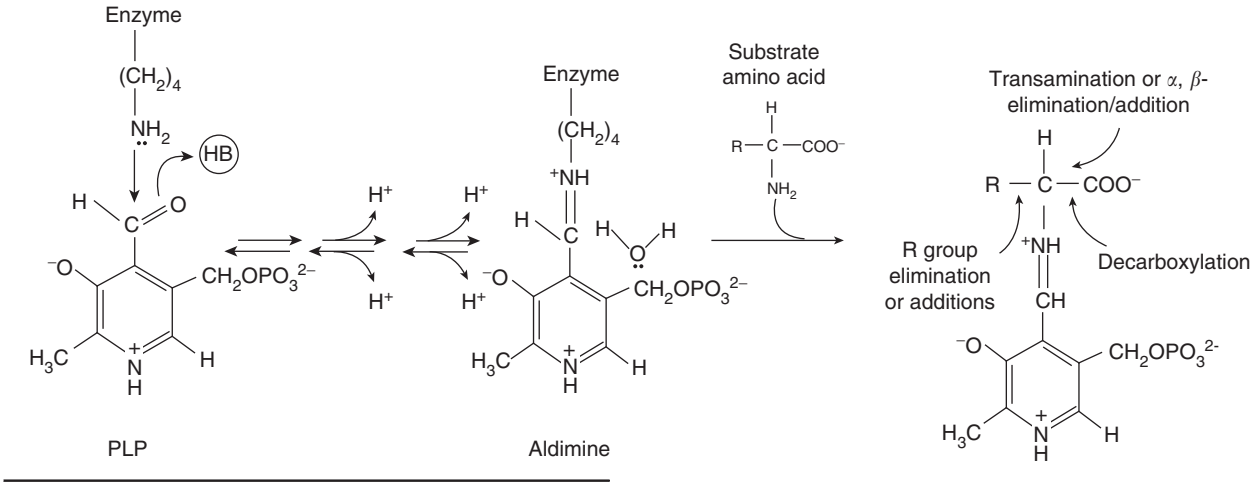
Syndromes caused by thiamine deficiency include beriberi, which causes cardiomyopathy and weakness due to impaired pyruvate and eventual Adenosine triphosphate (ATP) production and Wernicke–Korsakoff syndrome which expresses as a triad of symptoms: ocular disturbances, changes in mental state, unsteady stance, and gait. Although the mechanisms underlying the neurologic responses to thiamine deficiency have been firmly established, low levels of TPPP are thought to play a role. TPPP is the major form of thiamine in neural tissue. There is evidence that suggests that TPPP may be important in maintaining normal voltage-gated ion channels in nerve tissues. Voltage-gated ion channels are a class of transmembrane ion channels that are activated by changes in electrical voltage potential and are especially critical in neurons (Oliveira *et al.*, 2007).

- Pyridoxine

  Pyridoxine or vitamin B_6 is a collective term for pyridoxine, pyridoxal, and pyridoxyl amine. Pyridoxine is most abundant in plants; pyridoxal and pyridoxyl amine are most abundant in animal tissues. Although vitamin B_6 deficiency is rarely seen as most diets provide adequate amounts of the vitamin, drug-induced vitamin B_6 deficiency can occur following administration of certain drugs, such as isoniazid or penicillamine or naturally occurring antagonists. Isoniazid (used to treat tuberculosis) is a hydrazide that can form hydrazone derivatives with pyridoxal moieties, which in turn act as inhibitors of B_6-requiring enzymes. Penicillamine (β-dimethylcysteine) used in the treatment of Wilson's disease also can interfere

with normal B_6 metabolism due to the formation of thiazole derivatives. A naturally occurring antagonist to vitamin B_6, linatine (1-amino-D-proline), which is present in flaxseed can also be a stable product with pyridoxal phosphate.

Accordingly, a consequence of a severe B_6 deficiency can be a microcytic anemia due to impaired heme production.



The complications from B_6 deficiency are to a large degree a consequence of insufficient activity of pyridoxal-5′-phosphate (PLP)-dependent enzymes. The major form of vitamin B_6 in cells is PLP; vitamin B_6 is essential for amino acid synthesis and catabolism. The ability of PLP to condense its 4-formyl substituent with an amine, usually the α-amino group of an amino acid, to form an azomethine (Schiff base) linkage, produces a conjugated double-bond system extending from a carbon of the amine (amino acid) to the pyridinium nitrogen in PLP. This results in reduced electron density around the α-carbon, which in turn weakens each of the bonds to facilitate the transfer reactions. There are three major types of pyridoxine-dependent reactions: decarboxylation reactions, transaminations, and elimination/addition reactions. Decarboxylations include the conversions of tyrosine to tyramine, 5-hydroxytryptophan to serotonin, histidine to histamine, and glutamate to γ-aminobutyric acid (GABA). Signs of convulsions associated with severe vitamin B_6 deficiency are often associated with impaired GABA metabolism. Transaminations are reversible oxidation–reduction reactions in which an amino group is transferred typically from an α-amino acid to the carbonyl carbon atom of an α-keto acid. The inability to effectively utilize protein as an energy source or use the given amino acids as gluconeogenic precursors result from compromised transaminase activity. Elimination and addition reactions include electron withdrawal from the β-, γ-carbons of amino acids. This sets the stage for hydride condensations or aldol reactions (McCormick, 2007). Examples of aldol and hydride reactions are the conversion of serine to glycine and the formation of α-aminolevulinic acid, the first step in heme biosynthesis.

Another novel reaction, not directly linked to amino acid metabolism, is the role of vitamin B_6 as a cofactor for glycogen phosphorylase. The phosphate group on PLP donates a proton to an inorganic phosphate molecule, allowing the inorganic phosphate to, in turn, be deprotonated by the oxygen forming the α-1,4 glycosidic linkage (Fischer, 2013). The overall reaction is

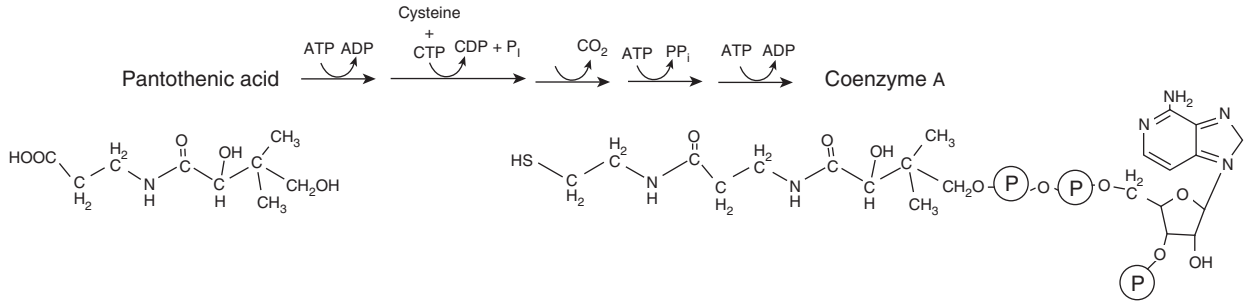
$$(\alpha\text{-1,4 glycogen chain})_n + \text{Pi} \leftrightarrows (\alpha\text{-1,4 glycogen chain})_{n-1} + D\text{-glucose-1-phosphate}$$

Although the reaction is reversible in solution, within the cell the enzyme only works in the forward direction as shown above because the concentration of inorganic phosphate is much higher than that of glucose-1-phosphate.

Acyl activation and transfer

- Pantothenic Acid

  Pantothenic acid is a precursor of coenzyme A and the prosthetic group of the so-called acyl carrier protein domain in certain enzymes (e.g., fatty acid synthase). The active form of the cofactor is produced by the formation of a peptide bond to cysteine followed by decarboxylation of the cysteine residue, and then by conjugation to the remainder of the coenzyme. The thiol ester at the terminus of coenzyme A enhances the activation of acyl compounds for ultimate attack of their carbonyl functions by nucleophiles. The carbonyl carbon of a thiol ester (CoA–S–C═O–R) is more positively polarized and less stabilized by resonance than a corresponding oxy ester (CoA–O–C═O–R). Thus, the acyl moiety is relatively activated for transfer and is often described as a high-energy bond.



Modifications of acyl side- or tail-chains may also be enhanced. Thioesters more easily undergo enolization by permitting the removal of hydrogen as a proton than oxyesters. The enolate that is formed is stabilized by delocalization of its negative charge between a carbon and the acyl oxygen, which makes it thermodynamically more accessible as an intermediate. As the developing charge is also stabilized in the transition state that precedes the enolate, it is also kinetically accessible. Thiolesters are more like a ketone than an oxyester. The resonance electron delocalization is due to an overlap of sulfur *p*-orbitals with the acyl *p*-bond.

CoASH is the principal moiety for the vectorial transport of acyl and acetyl groups in synthetic and catabolic reactions. A pantothenic acid deficiency is characterized by impaired acetyl and acyl metabolism. For example, the ability to utilize fatty acids as fuels is clearly compromised in experimental pantothenic acid deficiency. There is also an increased production of short-chain fatty acids and ketone bodies, which can lead to metabolic acidosis. Dermal lesions may also occur because of impaired fatty acid metabolism (Combs, 2012).

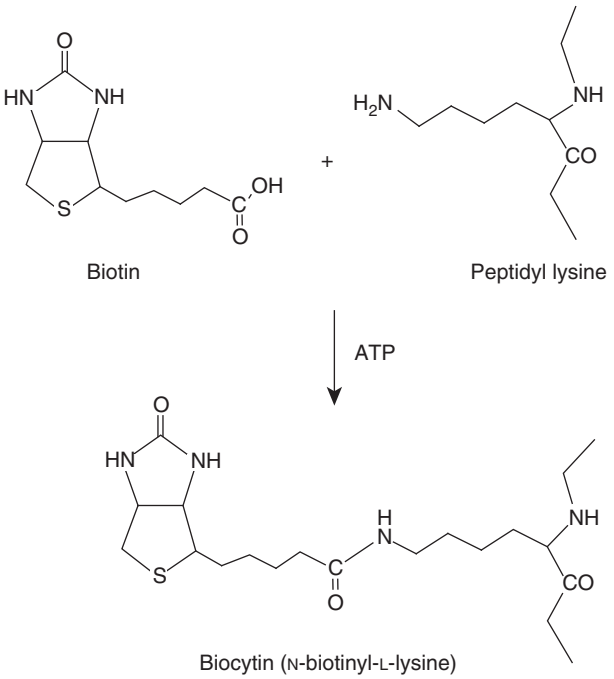
Carboxylations

- Biotin

  Biotin is necessary for cell growth, the metabolism of fats and amino acids, as well as gluconeogenesis. There are nine known biotin-dependent enzymes: six carboxylases, two decarboxylases, and a transcarboxylase. Of these, four carboxylases have been found in tissues of humans and other mammals. Examples include (1) acetyl-CoA carboxylase (a cytosolic enzyme that catalyzes the formation of malonyl-CoA for fatty acid biosynthesis), (2) pyruvate carboxylase that forms oxalacetate for citrate formation, (3) propionyl-CoA carboxylase, and (4) β-methylcrotonyl-CoA carboxylase important in the catabolic pathway for L-leucine.

  The coenzymatic form of biotin is linked to the ε-amino group of specific lysyl residues in the family of biotin-dependent carboxylase and transcarboxylase. The flexible side arm of biotin allows for flexible movement so that an activated CO_2 moiety can be transferred to an accepting substrate. In addition to the stereochemical features, biotin's chemical role is to enhance nucleophilicity (McCormick, 2007). The reactions occur in two separate steps. ATP is required for activation in the first step. Phosphorylation of bicarbonate by ATP to form carbonyl phosphate provides an electrophilic mixed-acid anhydride, which then reacts to generate reactive N(10)-carboxylbiotinyl enzyme. This in turn sets the stage for the transfer of the activated carboxylate function to an accepting substrate, typically at a carbon with carbanion character. Further, biotin binds very tightly to the protein avidin with a dissociation constant K_d on the order of 10^{-15} M, which is one of the strongest known protein–ligand interactions.

  Biotin was discovered following a long search for factors important to the condition that causes egg white poisoning, which is associated with poor growth, alopecia, and dermatitis in animals fed raw eggs or egg whites as a primary source of dietary protein. It was eventually found that biotin-binding factors in eggs (e.g., avidin) could reduce biotin nutritional availability. Dietary biotin exists in free and protein-bound forms. The latter, biocytin (N-biotinyl-L-lysine) is released as a product of proteolysis by intestinal proteases. Cellular biocytinases next catalyze biocytin cleavage to release free biotin for reutilization.



Human biotin deficiency is rare because intestinal bacteria can produce biotin in excess of the body's daily requirements. However, several conditions can cause a deficiency, such as exposure to the binding protein, avidin, and metabolic disorders, such as a deficiency in the carboxylase synthetase enzyme that covalently links biotin onto biotin-dependent

carboxylases or biocytinase that facilitates biotin reutilization. Biotin deficiency has been postulated to be a risk factor for pregnancy complications in humans, although the extent to which this occurs is a subject of considerable debate (Dietary Reference Intakes, 2004).

- Vitamin K

  Vitamin K is a group of structurally similar, fat-soluble vitamins. The active forms of vitamin K are essential for posttranslational modifications of proteins for blood coagulation cascades (e.g., thrombin and related coagulation factors), and in metabolic pathways important to the regulation of calcification of bone. The vitamers of vitamin K are all derivatives of 2-methyl-1, 4-naphthoquinone. Plants synthesize vitamin K_1, also known as phylloquinone, phytomenadione, or phytonadione. Vitamin K_2 is the principal derivative found in animals. Bacteria in the colon convert K_1 into vitamin K_2. Vitamin K_3 (2-methyl-1,4-naphthoquinone, menadione) can also act as a vitamin K precursor if an isoprene side chain is attached. The isoprene side chain can be synthesized by bacteria or derived from the cholesterol synthesis pathway. In addition, colonic bacteria can lengthen the isoprenoid side chain of vitamin K_2 to produce vitamin K_2 derivatives that range in isopreneoid side chain length from 7 to 11 side chain residues (Suttie, 2013).

  The major function of vitamin K in animals is acting as a cofactor for enzymes that are involved in protein posttranslational chemical modifications (Suttie, 2013); specifically, the carboxylation of glutamyl residues to γ-carboxyglutamyl (Gla) residues in certain proteins important in blood coagulation and bone formation (Figure 2). The presence of two -COOH functions on the same carbon in a γ-carboxyglutamyl residue facilitates the binding of calcium ion, which in turn activates Gla-containing proteins and enzymes.

  The following human Gla-containing proteins have been characterized: (1) the blood coagulation factors II (prothrombin), VII, IX, and X, (2) the anticoagulant proteins C and S, (3) bone Gla-containing protein osteocalcin, (4) calcification-inhibiting matrix Gla protein, and (5) cell growth-regulating growth arrest-specific gene 6 protein (Gas6), which is thought to be involved in the stimulation of cell proliferation. In addition, four transmembrane Gla proteins exist for which function currently remains unknown. Gla-containing proteins are known to occur in a wide variety of vertebrates: mammals, birds, reptiles, and fish. In contrast, in plants and bacteria, vitamin K functions either as an electron acceptor in photosystem I and as a consequence is essential for photosynthesis (plants), or is important to anaerobic respiration during oxygen-independent metabolic energy production processes (bacterial anaerobic respiration).

  With respect to perturbations in vitamin K metabolism in animals, a deficiency may result from dietary insufficiency or intoxication with antagonists that act as anticoagulants, such as warfarin or coumadin. Although a dietary deficiency of

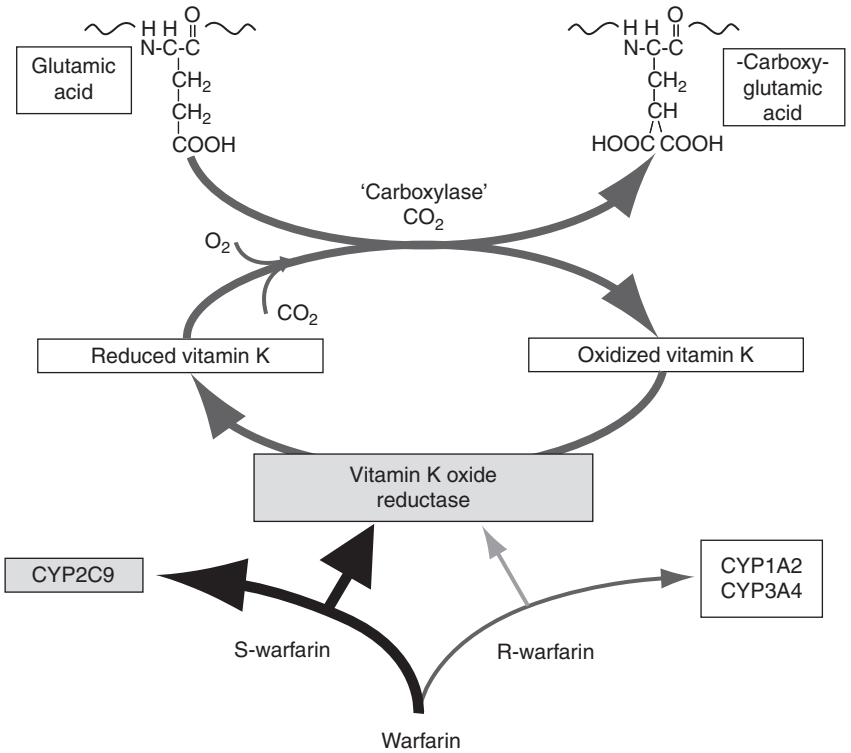


Figure 2 Vitamin K-dependent carboxylases. The vitamin K-dependent carboxylases use the oxidized form of vitamin K to convert glutamyl residues into glutamyl residues. These residues facilitate calcium binding and activation of vitamin K-dependent carboxylases to initiate hemostasis, apoptosis, bone development, arterial calcification, signal transduction, and growth control. Warfarin and coumadin derivatives inhibits the vitamin K oxidoreductase that generates the reduced vitamin K cofactor required for continuous carboxylation The cytochrome P450 (CYP) microsomal enzymes that play major roles in the oxidation of xenobiotic and endogenous compounds, such as coumadin and warfarin.

vitamin K is rare, liver disease, cystic fibrosis, or inflammatory bowel disease can increase the need for vitamin K. With respect to drug interactions, in addition to anticoagulants, other drugs associated with vitamin K deficiency include salicylates, barbiturates, and cefamandole. The reduction and subsequent reoxidation of vitamin K coupled with carboxylation of Glu is called the vitamin K cycle. Warfarin and coumadin derivatives function by inhibiting the reduction steps of the cycle. This can cause a decreased concentration of vitamin K hydroquinone in the tissues. When the carboxylation reaction is inefficient, the result is the production of clotting factors and calcium-binding proteins with inadequate Gla. Accordingly, symptoms of K_1 deficiency include anemia, bruising, and bleeding, as well as changes in bone turnover and architecture. Primary and secondary vitamin K deficiencies are also recognized to be teratogenic in humans Schaefer, 2006).

One-carbon transfer reactions and rearrangements on vicinal carbons

- Folic acid

  Deficiencies of folic acid are associated with macrocytic anemias and degenerative neurologic and developmental disorders (e.g., neural tube defects). In human populations the frequency of folic acid deficiency, either due to low dietary intakes of the vitamin or genetic polymorphisms that negatively influence its metabolism, in non-supplemented populations can be surprisingly high. Illustrative of this is that neural tube defects (presumably due in part to embryonic folate deficiencies) in Canada were reported to be reduced by close to 50% over a 10-year period following food folate fortification. The folate family of compounds is a group of heterocyclic compounds that contain 4-(pteridin-6-ylmethyl)-aminobenzoic acid conjugated with one or more L-glutamate units. The reactions that involve folic acid include the generation and utilization of formaldehyde, formimino, and methyl groups. For these conversions to occur, folic acid must be reduced in the form of tetrahydrofolic acid (THFA). The formyl, methyl, and methylene forms of THFA are utilized for purine synthesis and thymidylate synthesis (**Figure 3**), which are essential for rapid DNA synthesis and normal cell division and proliferation (e.g., cells arrest in the S-phase of the cell cycle).

  In addition, folate vitamers participate in reactions involved in the interconversion and catabolism of amino

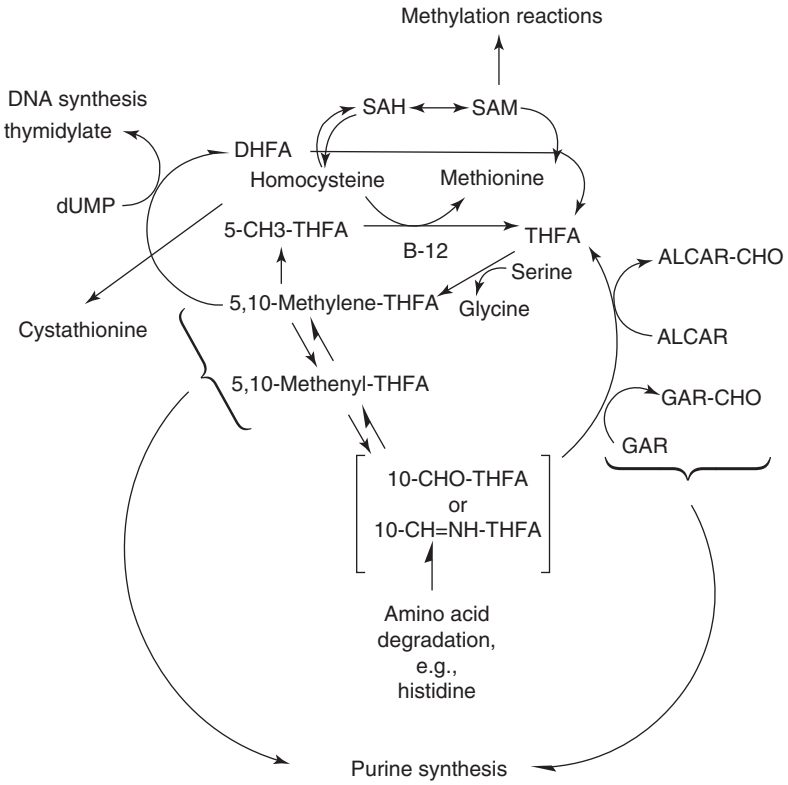


Figure 3 Folic acid, B_{12}, and single-carbon transfer reactions. Folic acid in its reduced form (THFA) and its interaction with vitamin B_{12} are essential to (1) methylation reactions (via the vitamin B_{12}-dependent methionine synthetase step), (2) DNA synthesis (the conversion of deoxyuridylate into deoxythymidylate via a single-carbon transfer from N_5, N^{10}-methylene-THFA), and (3) purine synthesis (via transfer of a single carbon from N^{10}-formyl-THFA into the purine pathway). The formyl, methanyl, and methylene forms of THFA are utilized as substrates for given reactions. Not shown in detail are reduction steps that result in the regeneration of THFA from oxidized folic acid. 5-Aminoimidazole-4-carboxamide ribonucleotide (ALCAR) and glycinamide ribonucleotide (GAR) are intermediates in the generation of purine derivatives. *S*-adenosyl methionine (SAM) is a common cosubstrate involved in methyl group transfers. It is derived from ATP and methionine. It is hydrolyzed to homocysteine and adenosine by *S*-adenosylhomocysteine hydrolase. The homocysteine is then recycled back to methionine through transfer of a methyl group from 5-methyltetrahydrofolate.

acids. The key elements of some of these reactions involve the removal of the methyl group from methyl-THFA and an irreversible transfer to methionine by the vitamin B_{12} requiring enzyme, methionine synthetase. The movement of single-carbon units from folate through methionine synthetase in the formation of methionine is also important for *S*-adenosylmethionine (SAM) formation. SAM is essential to methylation of phospholipids, and production of methylated forms of various amino acids and carbohydrates. SAM also serves as the methyl source in DNA methylation. Prolonged folic acid and vitamin B_{12} deficiencies can also result in serious neurological disorders due to the degeneration of the myelin sheath (Halsted *et al.*, 2009).

- B_{12} (Cobalamin)

  Vitamin B_{12} consists of a porphyrin-like structure of tetrapyrrole rings with a monovalent cobalt ion at its center. There are two major cofactor forms. Methylated vitamin B_{12} serves as a cofactor for methionine synthetase. Vitamin B_{12} in the form of the adenosyl derivative catalyzes the conversion of methylmalonyl-CoA into succinyl-CoA.

  Deficiency of vitamin B_{12} leads to intracellular accumulation of homocysteine (**Figure 3**) and methylmalonic acid. The conversion of methylmalonic acid into succinate is essential to herbivores and ruminants because it facilitates the utilization of odd-chain fatty acids as potential gluconeogenic precursors. A high level of homocysteine is often associated with endothelial injury and vascular inflammation. These events are in turn associated with atherogenesis. As noted, deficiencies of both vitamin B_{12} and folic acid can produce clinical signs of macrocytic anemia and desynchronies in the growth and development owing to the importance of folic acid to purine and DNA synthesis. However, a form of vitamin B_{12} deficiency, pernicious anemia (also known as Biermer's, Addison's, or Addison–Biermer anemia) is specific to a lack of vitamin B_{12}.

  For effective absorption, vitamin B_{12} must first bind to an intrinsic factor, made in gastric parietal cells (Section Sources, Availability, and Absorption). When autoimmune destruction of gastric parietal cells occurs, it can lead to loss of parietal cells and a decreased production of intrinsic factor. Replacement of oral vitamin B_{12} does not correct the autoimmune form of B_{12} deficiency; effective treatment involves injections of B_{12}. B_{12} supplementation will reverse the signs of anemia and protect from future peripheral permanent nerve damage (a predominate feature of prolonged and severe B_{12} deficiency). When and if pernicious anemia affects the nervous system, symptoms include cognitive impairment, loss of peripheral sensations, and difficulty in navigation (ataxia). These complications are due to the degeneration of spinal cord and myelin sheet (Halsted *et al.*, 2009). Methylmalonic acid, which is elevated in vitamin B_{12} deficiency, remains in the myelin sheath and is thought to contribute to fragility. Reduced production of methionine may also be a factor, given the importance of methionine to the production of various neurotransmitters.

Cell signaling

Vitamin signaling can fall into each of the traditional endocrine categories related to cell signaling (hormonal, paracrine stimulation by cytokines, and autocrine stimulation). Dietary biofactors, such as plant secondary metabolites and vitamins, may initiate an action through transmembrane proteins (receptors) on the surface of given cells, trigger changes in the metabolism or gene expression within the cell, or cause an immediate change in an electrical charge across the plasma membrane.

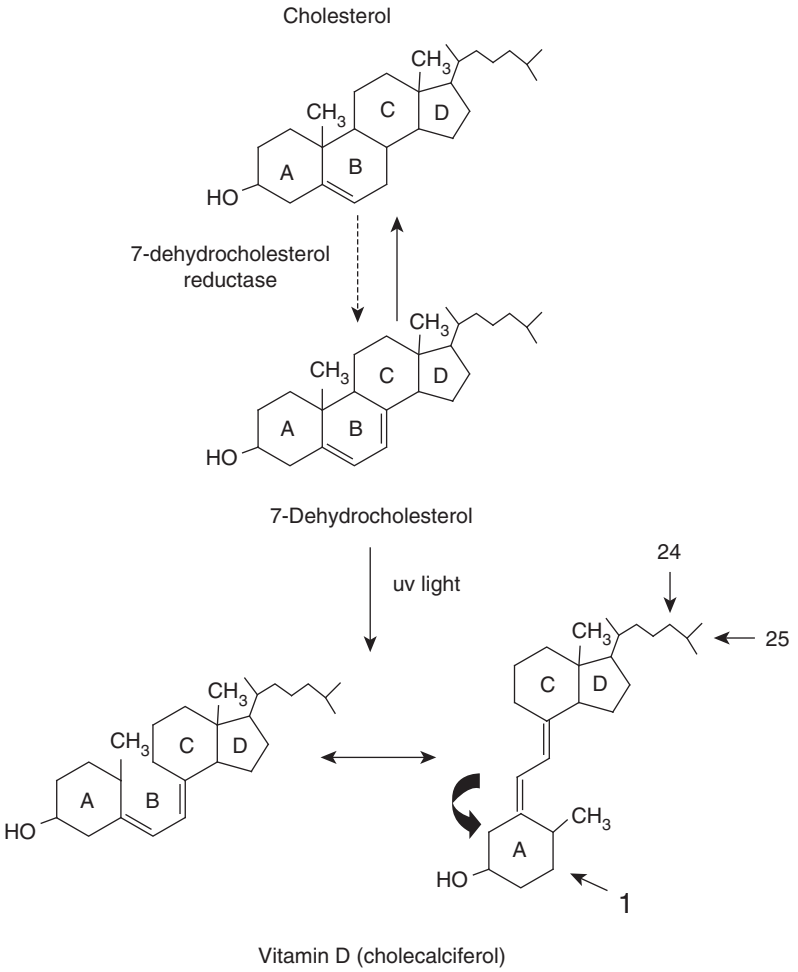
- Vitamin A

  Vitamin A is directly involved in signaling events related to vision and cell differentiation, particularly epithelial cell differentiation. Vitamin A can be derived from the hydrolysis of retinyl esters to retinol and fatty acids, or cleavage of β-carotene, one of the many carotenoid pigments in plants, into retinal (Combs, 2012; Ross, 2012; Gershwin *et al.*, 2000).

  In the visual system, retinal is found in retinal rod and cone cells bound to the protein opsin as retinene. The retinene–opsin complex is called rhodopsin. When retinene interacts with light, retinene undergoes a cis–trans isomerization, which in turn changes the conformation of rhodopsin. This event initiates as series of cellular responses that alter bipolar cells from releasing neurotransmitters to the ganglion cells, which in turn alters nerve impulses in the ocular system of the central nervous system. In the presence of light, the retinal molecule changes configuration and as a result a nerve impulse is generated. The lack of vitamin A can promote a type of nyctalopia, also called night blindness, a condition that makes it difficult or impossible to see in relatively low light intensities.

  Vitamin A in the form of retinoic acid can also interact with a family of the so-called retinoic acid or retinoid signaling receptors, which are types of nuclear receptor that can act as cellular transcription factors. Retinoid binding induces conformational changes that promote recruitment of coactivators, histone acetyltransferases, and other components of the basic transcription machinery. Vitamin A deficiency influences virtually all aspects of growth and development. As noted, epithelial cells are affected in addition to the ability of immune cells to ward off infections (Ross, 2012; Gershwin *et al.*, 2000).
- Vitamin D

  Vitamin D can be synthesized endogenously from the cholesterol precursor, 7-dehydrocholesterol (Rucker, 2007). The reaction is novel because it requires exposure of skin to ultraviolet light or sunlight (270–300 nm). Peak synthesis of vitamin D occurs between 295–297 nm. Although vitamin D is commonly called a vitamin, it is not an essential dietary vitamin, because it can be synthesized in adequate amounts by most mammals exposed to sunlight. From an evolutionary perspective, photosynthesis of vitamin D by phytoplankton has existed for more than 500 million years and it is estimated that land animals have been making their own vitamin D for more than 350 million years.



Vitamin D (cholecalciferol)

Vitamin D is a group of fat-soluble secosteroids responsible for cell signaling. One of the most active vitamin D-related secosterols is 1,25-dihydroxycholecalciferol (calcitriol). The calcitriol receptor, also known as the vitamin D receptor (VDR), is a nuclear receptor, which acts as a transcription factor. A deficiency of an active secosteroid form of vitamin D, whether due to a gene defect or a dietary deficiency (or lack of sunlight) can cause defects that range from decreased intestinal absorption of calcium and phosphate (e.g., rickets) to altering insulin and glucagon sensitivity or steps important to optimal immune function.

The production of calcitriol is normally closely regulated through feedback control and the influence of parathyroid hormone (PTH) on the activities of the 1α- and 24-OH-hydroxylases. A fall in plasma calcium triggers the release of PTH from the parathyroid gland, which stimulates 1α-hydroxylase production and leads to an increased output of calcitriol from the kidney. A separate hydroxylase that catalyzes 24,25-$(OH)_2$-D_3 production is activated under eucalcemic and hypercalcemic states.

The two major sites of action of calcitriol in relation to calcium homeostasis are bone and the intestine. Calbindin, an intestinal calcium-binding protein, is a major product synthesized in intestinal cells in response to calcitriol. Calbindin influences the movement of calcium across the intestinal cell. Binding of calcium to this protein allows the intracellular concentration of calcium to be elevated. In addition to intestinal cells, the osteoblasts of bone are another target of vitamin D metabolites and play a major role in short-term calcium homeostasis. In bones, 1,25-$(OH)_2$-D_3 is required for mineralization during skeletal growth and remodeling. VDR in bones are located in osteoblasts and progenitor cells of the bone and control the synthesis and secretion of a number of bone-specific proteins by osteoblasts, such as osteocalcin – a Gla-containing protein (Section Vitamin K), – osteopontin, collagen, and alkaline phosphatase. The actions of vitamin D metabolites are both direct (e.g., transcriptional regulation via VDR interactions) and indirect (modulation of secondary signaling pathways, e.g., protein kinase C-regulated pathways). For the most part, vitamin D metabolites attenuate the action of polypeptide hormones, such as PTH or calcitonin, which stimulates bone resorption and accretion, respectively.

VDR have also been found in a large number of cell types, ranging from skeletal muscles to cells important to immune and phagocytic functions, for example, macrophages. In pancreatic β-cells, 1, 25-$(OH)_2$-D_3 appears to be important to normal insulin secretion. Vitamin D increases insulin release from isolated perfused pancreatic cells. Moreover, vitamin D metabolites can suppress immunoglobulin production by activated B-lymphocytes. Further, T-cells are affected by vitamin D

metabolites. 1,25-$(OH)_2$-D_3 exhibits permissive or enhancing effects on T-cell suppressor activity (Gershwin *et al.*, 2000).

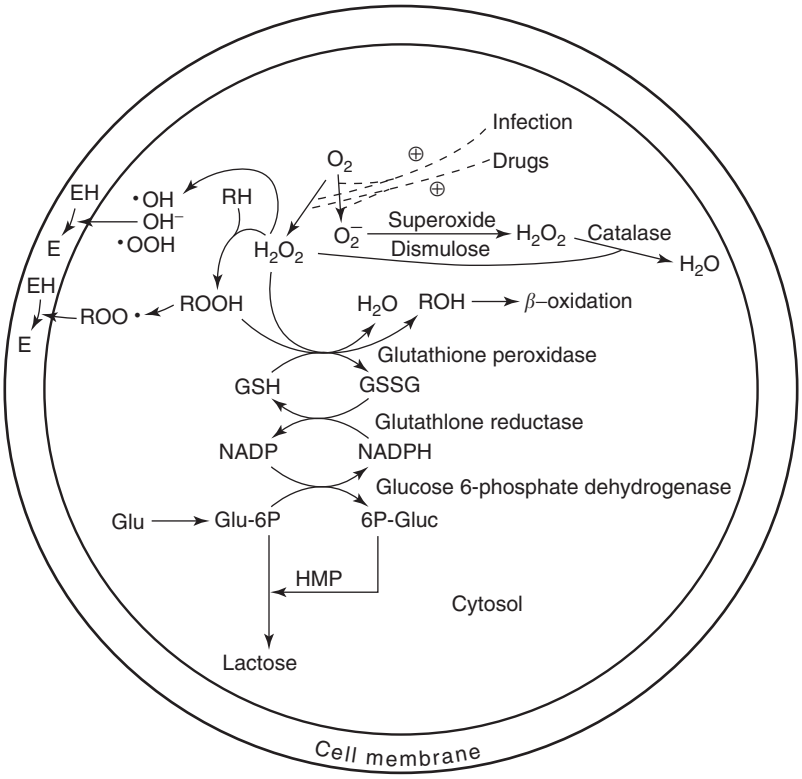
In children, vitamin D deficiency can result in rickets, which presents as bowing of the legs due to inefficient deposition of bone mineral. In adults, vitamin D deficiency results in osteomalacia, which presents as a poorly mineralized skeletal matrix. At the beginning of the twentieth century, it is estimated that approximately 90% of the children living at latitudes above 40 N (e.g., New York, Boston in the United States) or the Netherlands in Europe were afflicted with rickets, a bone-deforming disease. The connection to sunlight was made in the late 1980s with the discovery that 'sunbathing' was important for preventing rickets. During the past decade there has been an increasing interest in the idea that vitamin D might play a role in vascular health and this is currently an area of considerable research.

Antioxidative defense

- Vitamin E

  An antioxidant is a molecule that inhibits the oxidation of other molecules, that is, slows or inhibits the transfer of electrons or hydrogen to an oxidizing agent. This is important, because oxidation reactions can produce free radicals that, in turn, can start damaging oxidative chain reactions. Polyunsaturated lipids and proteins are often targets. Within lipid membranes, vitamin E can act as an antioxidant at a chemical (i.e., nonenzymatic) level. The intercalation of various forms of vitamin E into lipid-enriched membranes provides protection. In this regard, vitamin E vitamers in plants and animals represent one part of a complex system of antioxidants that includes glutathione, vitamin C, and enzymes, such as catalase, superoxide dismutase, and various peroxidases (**Figure 4**).

  Vitamin E is present in plants in eight different forms with largely similar antioxidant potential; nevertheless, in higher organisms α-tocopherol is preferentially retained suggesting a specific mechanism for its uptake. It also has the apparent ability to inhibit protein kinase C, 5-lipoxygenase, and phospholipase A2 and activate protein phosphatase 2A, diacylglycerol kinase, or modify the activity of certain receptors that respond to oxidants. However, more information is necessary to ascertain the exact mechanisms. As an example, oxygen-free radicals can be generated by advanced glycation end products (AGE), which are nonenzymatically glycated and oxidized proteins. Cellular interactions with AGE also influence cell signaling and the expression of specific genes (e.g., increased expression of mitogen-activated protein kinase organizer 1, which is linked to the control of several extracellular signal-regulated kinases). Given that vitamin E vitamers can influence the formation of AGE,



Integrated view of the oxidant defense system

Figure 4 Vitamin E. Vitamin E defends against abnormal lipid peroxidation at a chemical level in lipid membranes. Enzymes, such as superoxide dismutase, catalyzes superoxide radicals to hydrogen peroxide, catalase, glutathione peroxidase (catalyzes lipid and hydrogen peroxides to water or hydroxy fatty acids), and related systems for oxidant defense (generation of NADPH and reduced glutathione (GSH)) also play seminal roles.

the role of vitamin E vitamers may be indirect, in contrast to an interaction directly with specific receptors important to gene expression (Combs, 2012).

Requirements, Sources, and Assimilation

Requirements and Factors Related to Deficiency

The vitamin requirements for adult humans, as currently set by the United States and Canadian dietary reference intakes, are presented in **Table 1**. In this regard, there are two external sources of water-soluble vitamins; a dietary source that is often complemented or augmented by vitamins generated by the intestinal microbiota. Acute deficiencies can be induced under experimental conditions for most of the vitamins. Fortunately, deficiency diseases are not typically observed unless specific food sources are severely limited due to poor food distribution, exposure to antagonists, or severe economic constraints that limit access to food. Nevertheless, subclinical deficiencies can be observed when individuals consume a monotonous diet in which food variety is limited. Select genetic polymorphisms can also result in an increased need for certain vitamins. Polymorphisms can cause protein structural alterations that in turn can result in abnormal vitamin-derived cofactor binding to a given enzyme or abnormal cellular transport. In addition, disturbances of absorption (e.g., pancreatic insufficiency, biliary obstructions, alcohol, and enteropathies), antagonists (e.g., antibiotics, tannins, caffeic acid, and alcohol), or metabolic conditions (e.g., pregnancy and diabetes) can contribute to an increased need for select vitamins.

The nutritional essentiality for some of the vitamins results from an inability to synthesize the corresponding aromatic compounds that act as precursors. A good example is the lack of a shikimatic acid pathway, which is utilized in the bacteria, fungi, algae, parasites, and plants for the biosynthesis of aromatic amino acids, such as phenylalanine, tyrosine, and tryptophan. Another example is the absence or a defect in a specific component of a metabolic pathway. In some animals, the enzyme gulonolactone oxidase is absent in the pathway for glucose or galactose oxidation. If gulonolactone oxidase is missing, ascorbic acid (vitamin C) synthesis is compromised. Most animals with the exception of primates, guinea pigs, fruit-eating bats, some invertebrates, and salmonoid fish can synthesize ascorbic acid. These animals have either no gulonolactone oxidase activity or insufficient amounts for effective synthesis of ascorbic acid.

The need for niacin, vitamin A, and vitamin D in some carnivores is also worthy of comment. In animals that must be sustained on carnivorous diets, there is less capability than omnivores and herbivores to adapt to wide variations in dietary composition. In cats, the obligatory dietary requirements for niacin (NAD) and vitamin D result from the high activities of enzymes that catabolize and divert precursors of these vitamins to other compounds. As examples, many carnivores metabolize tryptophan to picolinic acid instead of quinolinic acid, which results in a decrease in NAD production (See Schema Niacin). Ineffective vitamin D synthesis in cats is due to the high activity of the 7-dehydrcholesterol (7-DHC) reductase, which converts 7-DHC into cholesterol, instead of vitamin D (See Schema Vitamin D). In contrast, the absence of enzymes required for cleavage and oxidation of carotenoids (e.g., β-carotene) can result in inefficient conversion into vitamin A (Rucker *et al.*, 2008).

Sources, Availability, and Assimilation

Vitamins in foods are usually present as highly modified derivatives. Pancreatic and intestinal cell-derived enzymes are required to initiate normal uptake in absorption. Intestinal nucleosidases, phosphatases, and peptidases are key factors in processing cofactors to vitamins (Combs, 2012; Rucker, 2007; Said, 2011). Transport of given vitamins can be receptor mediated, occur via pericellular-related processes, passive transport (usually at high luminal concentrations), active transport (requires energy), or facilitated processes (requiring a transporter or chaperone). Some examples are given in **Figure 5**.

It is now well established that intestinal absorption of the water-soluble vitamins occurs by means of specific carrier-mediated processes. Regulation involves transcriptional and posttranscriptional mechanisms. It is also now appreciated that the large intestine also possesses specific and efficient uptake systems to absorb, in particular, a number of water-soluble vitamins that are synthesized by the gut microflora (Said, 2011). Some selected characteristic of water-soluble vitamin transporters are described in **Table 2**.

The fat-soluble vitamins, in general, are absorbed similar to lipids. As lipids, they are partitioned into liposomes and intestinal micelles in preparation for absorption. Once inside enterocytes, fat-soluble vitamins and their derivatives can be partitioned into either chylomicron or very low-density lipoprotein (VLDL) particles and transported into the lymphatic system to targeted tissues, or they can be complexed to given transporters for deliver via blood. Analogous to the water-soluble vitamins, each fat-soluble vitamin has specific and highly regulated processes that are associated with their delivery to targeted cells. For some fat-soluble vitamins, transporters that are compatible with transport in blood are also expressed, usually in the liver. As examples, after delivery of vitamins A, E, and K to the liver via chylomicron or VLDL particles, vitamin A is transported from the liver to targeted tissues by the retinol binding protein; vitamin E by α-tocopherol transfer protein or high-density lipoprotein particles and remnants; whereas vitamin K (particularly the forms made or modified in the liver) is predominately transported by VLDL-derived particles.

Although beyond the scope of this article, it is important to appreciate that at cell surfaces there are multiple transport systems for the cellular influx and efflux of compounds, such as vitamins and biofactors. Many of the transporters are within the large family of ATP-binding and dependent cassette transporters (the so-called ATP-binding cassette (ABC) transporters). Further, within the cell, vitamins undergo specific and metabolically controlled modifications before they are activated or converted into functional forms (e.g., modifications that lead to enzymatic cofactor formation or lead to compounds that interact with cell or cellular organelle receptors to initiate specific cell signals).

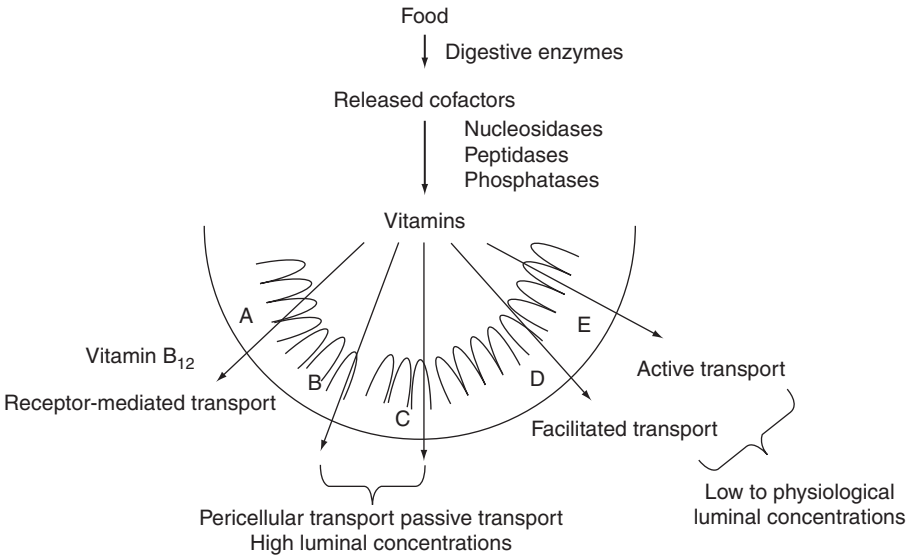


Figure 5 Vitamin absorption. Vitamins in foods are often present as cofactors or in chemically complex forms. Accordingly, pancreatic, some liver-derived (via biliary secretions) and intestinal cell-derived or microbiota-derived enzymes are required to initiate normal uptake in absorption. Nucleosidases, phosphatases, and peptidases are key factors in processing cofactors to vitamins. Transport of given vitamins can be receptor mediated, occur via pericellular-related processes, passive transport (usually at high luminal concentrations), active transport (requires energy), or facilitated processes (requiring a transporter or chaperone).

Physiologically Important Metabolites and Biofactors in Foods

One of the most promising new areas of food- and nutrition-related research focuses on edible plant and intestinal microbiota-derived compounds that have been reported to elicit positive health effects that are in some cases 'vitamin-like.' The designations used to define such compounds include biofactors, primary metabolites, and secondary metabolites, although these designations are somewhat arbitrary. For example, primary plant and microbial metabolites are compounds that function directly in photosynthesis, respiration, and growth. In contrast, secondary metabolites are organic compounds that are not directly involved in the normal growth, development, or reproduction of a species, but their absence may result in select long-term impairments and shortened survivability.

For example, there is growing evidence that many biofactors when present at certain concentrations reduce the risk for age-related chronic diseases, such as cardiovascular disease or macular degeneration. In plants, compounds that serve as secondary metabolites have evolved to provide protective camouflage, repel predators, or facilitate electron transport and in the transformation of specific wavelengths of light into chemical energy. Much of what is known about biofactors extends from studies that were originally designed to define aspects of drug, pharmaceutical, and xenobiotic metabolism. A xenobiotic is an external chemical that a given organism does not normally produce and is either eliminated or put to a novel use. Our diets contain thousands of such compounds. With respect to health effects, epidemiological studies have shown correlations between the numerous dietary intake bioactive factors and the risk of chronic diseases (Schaefer, 2006; Shenoy *et al.*, 2011).

Table 3 lists some of the major secondary metabolites that have been studied to date, along with their putative functions (Demain and Fang, 2000). Not included are the 'nonsmall molecules,' such as derivatives of DNA, ribonucleic acid, ribosome, or polysaccharide. With regard to the discussions that follow, they are also limited, focusing primarily on secondary metabolites that influence ATP production and nutrient partitioning. These compounds are typically classified as flavonoids, flavanols, or polyphenolics. Included in the discussion are descriptions for resveratrol, quercetin, various procyanidins, hydroxytyrosol, and pyrroloquinoline quinone (Schroeter *et al.*, 2010; Shenoy *et al.*, 2011; **Figure 6**).

The authors have had constant environmental exposure to primary and secondary metabolites; thus, it is reasonable to propose that we have evolved to recognize patterns of these metabolites. One possible function of such recognition may be to set the stage, via complex cell signaling, for assimilating complex food mixtures and energy sources.

Resveratrol

Resveratrol is a stilbenoid (3,5,4′-trihydroxy-trans-stilbene; a type of natural polyphenolic compound) and a phytoalexin, a class of compounds produced by some plants when under attack by pathogens, such as bacteria or fungi. It is found predominately in purple grapes, red wine, peanuts, and some pigmented berries. In animals, at high amounts resveratrol has been reported to have biological properties that range from cardioprotection to enhanced neuronal activity. Although resveratrol was initially thought to be one of the primary protective substances associated with the so-called French Paradox, and to possess antiaging properties, recent research has failed to demonstrate an extension of lifespan in lean, genetically normal mice. Nevertheless, when administered at

Table 2 Characteristics of water-soluble vitamin intestinal transporter

Vitamin	*Transporter and receptor system(s)*	*Description*
Ascorbic acid (AA)	Transport is facilitated by both Na-dependent and Na-independent vitamin C transporter systems	Studies on the mechanism of intestinal absorption of AA indicate the involvement of an Na-dependent, carrier-mediated mechanism. In contrast, the transport of dehydro-AA occurs via Na-independent carrier-mediated mechanisms that can be competitively inhibited by hexoses. The dietary level of AA adaptively regulates AA absorption
Biotin	Transport is facilitated by an Na-dependent multivitamin transporter	In the intestine, protein-bound biotin (as biocytin) is digested by gastrointestinal proteases and peptidases to release biocytin (biotinyl-L-lysine) and biotin – short peptide conjugates. Free biotin is produced by the action of the enzyme biotinidase. An Na-dependent carrier-mediated transporter facilitates absorption. Uptake is adaptively regulated by the luminal content of biotin. The Na-dependent transporter is described as a multivitamin because of its role in the transport of pantothenate and lipoate in addition to biotin
Cobalamin (vitamin B_{12})	Receptor for the intrinsic factor(IF)/B_{12} complex; receptor for transcobalamin II	Protein-bound vitamin B_{12} is released from dietary proteins by low pH and the action of pepsin from gastric secretions. The R-proteins (haptocorrins and cobalaphilin) next bind the released B_{12}. The B_{12} is then exchanged to IF, a protein that is synthesized by gastric parietal cells. The exchange from R-proteins to IF occurs in the duodenum. A B_{12}/IF complex must be formed in order to interact with receptors on enterocytes found in the terminal ileum. Accordingly, absorption of B_{12} from food requires the normal function and presence of the stomach, exocrine pancreatic factors, IF, and the small bowel. Following absorption, vitamin B_{12} is transferred to transcobalamin II, the primary plasma transporter, which carries B_{12} to targeted cells
Folic acid	Reduced folate carriers; Proton-coupled folic acid transporter (a pH-dependent, Na -independent carrier-mediated receptor)	Dietary folate exists as mono- and polyglutamates. Folate polyglutamates are first hydrolyzed to folate monoglutamates before absorption. This digestion process occurs mainly in the proximal part of the small intestine catalyzed by folylpoly-γ-glutamate carboxypeptidase. The reduced forms of folate (e.g., tetrahydrofolic acid (THFA)) interact with a pH-dependent, Na-independent carrier-mediated receptor. THFA is eventually transferred to plasma transport proteins that have high affinity for THFA
Niacin	Proposed transporters include an acidic pH-dependent and Na-independent transporter and monocarboxylate transporters 1 (low affinity) and 2 (high affinity)	Intestinal absorption of niacin appears to involve several distinct transporters. The pH-dependent intestinal uptake of nicotinic acid is proton-coupled and involves an active carrier-mediated transport mechanism, rather than a simple diffusion, as one was believed
Pantothenic acid	A sodium-dependent multivitamin transporter	The same sodium-dependent multivitamin transporter responsible for biotin and lipoic acid transport also is responsible for pantothenic acid transport
Pyridoxine	Evidence for a pH-dependent, non-Na-dependent carrier-mediated mechanism	Regulation is sensitive to changes in vitamin B_6 intake, and appears transcriptionally mediated and linked to a protein kinase A/cAMP-dependent process
Riboflavin	Riboflavin transporter 1 (found on the luminal surface) and riboflavin transporter 3 (found on the serosal surface)	Absorption is sensitive to changes in dietary riboflavin intake
Thiamine	Thiamine-specific transporters located on the lumen and serosal surfaces of enterocytes. The transport process is pH dependent, but not Na dependent	Dietary thiamine levels adaptively regulate (at the level of transcription) intestinal thiamine uptake

pharmacologic doses (several hundred of milligrams per kilogram of diet) many investigators have reported increased telomerase activity enhancement, antiinflammatory effects, and improvements in glucose regulation in numerous rodent models. Mice treated with resveratrol have been reported to respond better than nontreated mice to oxidative stresses induced by exposure to various chemical agents. For perspective, in humans, a daily dose in the range of 300–3000 mg is often required to achieve a significant clinical response, such as bringing abnormally high levels of blood glucose back into

Table 3 Important secondary metabolites

General classifications	*Definition*	*Examples*	*Characteristics and potential health-related functions*
Alkaloids	Alkaloids are difficult to characterize because of their structural diversity. Most contain basic N atoms and are derivatives of any of the following compounds: acridine, benzylamines, colchicine, diterpenes, indoles, indolizidines, imidazole, isoquinoline, isoxazoles, oxazoles, phenyl-ethylamines, piperidine, polyamines, pyrrolizidines, pyridines, purines, quinolines, quinolizidine, quinazolines, muscarines, steroids, thiazoles, and tropanes	Adrenaline, bufoteni, caffeine, catecholamines, cathinone, cocaine, colchicine, dopamine, dimethyltryptamine, ephedrine, ergot, morphine, mescaline, nicotine, noradrenaline, pseudoephedrine, psilocybin, quinine, serotonin, and tyramine	Most alkaloids taste bitter and many are poisonous. In plants, alkaloids can act as protectants. Some animals have evolved the ability to detoxify alkaloids. Their uses range from medical applications to recreational drugs
Glycosides	A glycoside is a molecule in which a sugar is bound via a glycosidic bond. There are numerous subcategories including those described under the heading of general categories in this table	Cardiac glycosides: ouabain and digoxin; rhamnosides, such as the flavonol glycosides (azalein, eupalin, eupatolin, kaempferitrin, myricitrin, quercitrin, and rhodionin)	Many secondary metabolites are sequestered or stored in organisms as glycosides. They act through xenobiotic-sensing nuclear receptors (important to the expression of detoxification and clearance pathways) or cell-signaling systems in ways that often initiate changes in metabolism
Phenols and natural ketones including: flavonoids, flavanols, and polyphenolics	Phenolic compounds and those with flavanoid character can be formed either via the shikimate pathway, the acetate/malonate (polyketide) pathway, or the acetate/mevalonate pathway. Some may also be produced by chemical or enzymatic annulation (e.g., the condensation of tyrosine and glutamic acid to produce pyrroloquinoline quinone)	Catechin, epicatechin, hydroxytyrosol, procyanidins, pyrroloquinoline quinone, quercetin, and resveratrol	In plants, the actions and functions of phenolics and flavonoids range from colorants, ultraviolet, and ionizing radiation protectants to growth factors to antimicrobials/phytoalexins and antioxidants. In animals and humans, exposure to flavonoids, flavanols, and polyphenolics contribute to reduced mortality rates and have a number of health attributes related to improving blood pressure control, vision, inhibition of nitric oxide production, decreased platelet aggregation, and neuroprotective, among others
Phenazines	Produced mostly in bacteria, such as *Pseudomonas* spp., *Streptomyces* spp., and *Pantoea agglomerans*. The biosynthesis of phenazines branch from the shikimic acid pathway at a point subsequent to choristic acid. Chorismate-derived intermediates are brought together to form the basic phenazine scaffold. Sequential modifications result in phenazines with differing biological activities	Pyocyanin, phenazine-1-carboxylic acid, and related derivatives	Phenazines increase of bacteria survival in soil environments improves the ability to colonize; however, these compounds may have the same effects in aerobic environments, such as the lung; thereby promoting inflammation and gram-negative bacterial proliferation

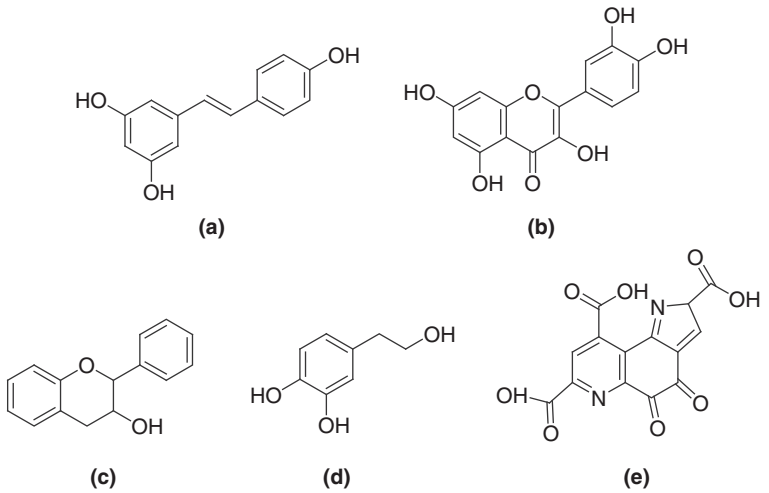


Figure 6 Biofactors important to mitochondrial metabolism and regulation. (a) Resveratrol is a stilbenoid and a phytoalexin. (b) Quercetin is a flavonoid with the basic structural characteristics of a flavanol. (c) Flavanols (the basic backbone structure is shown) include derivatives of catechin, epicatechin, and procyanidins (various condensed tannins including dimers, trimmers, and longer polymeric forms). (d) Hydroxytyrosol is a phenylethanoid, a type of phenolic phytochemical with antioxidant properties. (e) Pyrroloquinoline quinone serves as a redox cofactor in certain bacteria and also found in plant and animal tissues.

normal range. When administered orally, resveratrol appears readily absorbed; however, this is followed by extensive hepatic gluconuridation and sulfation to form resveratrol-3-O-glucuronide and resveratrol-3-sulfate. The conversion is very efficient. Less than 5 ng of nonderivatized resveratrol per milligram of blood are detected in the blood after a 25 mg oral dose in humans, even though resveratrol and its derivatives are efficiently absorbed. To achieve a clinical response in humans, microgram amounts per milliliter are required, which usually corresponds to oral intakes of 1 g or more per day.

Studies designed to elucidate resveratrol's actions have nevertheless been useful as research templates for the now hundreds of studies dealing with the role and function of biofactors in general (Shenoy *et al.*, 2011). An example is studies on resveratrol's ability to modulate cell signaling important to mitochondriogenesis. Resveratrol is capable of competitively inhibiting various phosphodiesterases, which results in an increase in cytosolic concentration of cyclic adenosine monophosphate (cAMP). cAMP in turn acts as a second messenger for the activation of major energy pathways, which result in increases in the oxidation of fatty acids, mitochondrial biogenesis, mitochondrial respiration, and gluconeogenesis. In addition, several mitochondrial enzymes are induced whose function is to aid in controlling damaging reactive oxygen species levels (e.g., catalase and mitochondrial Mn-superoxide dismutase).

Quercetin

Quercetin derivatives, derivatives of 2-(3,4-dihydroxyphenyl)-3,5,7-trihydroxy-4H-chromen-4-one, are flavonols (a subclass of the flavonoid family) found in fruits and vegetables, particularly onions and apples. Quercetin as an aglycone is not a common dietary component. Normal diets contain quercetin glycosides, which are converted into quercetin in the gastrointestinal tract (Mendoza and Burd, 2011). Mice fed quercetin have increased levels of cellular mitochondria, based on the mitochondrial DNA content and increased cytochrome c oxidase activity (a measure of mitochondriogenesis). These observations are supported by evidence of increased exercise tolerance in mice exposed to quercetin. Several studies have shown that quercetin may have antiinflammatory properties, act as an antihistamine, as well as influence induction of insulin secretion by the activation of L-type calcium channels in pancreatic β-cells (Mendoza and Burd, 2011).

The estimated intake of quercetin for humans ranges from 10 to 25 mg per day. Like resveratrol, however, substantial amounts (e.g., >100 mg quercetin per day in humans) are needed to elicit clinical changes in humans (e.g., improvements in assays designed to assess antiinflammatory or antioxidant potential). In typical studies, a dose of 500–1000 mg per day is administered.

However, many of the health claims ascribed to quercetin have been difficult to replicate, particularly those focusing on athletic performance. In this regard, a comment that applies to all exercise studies involving biofactors is that the level of prior training is often a factor, given that exercise and controlled food intake influence the mitochondrial function and measurements important to the assessment of athletic endurance (Mendoza and Burd, 2011).

Flavanols

Flavanols are another subclass of flavonoids that exist in a variety of chemical forms and derivatives. Specifically, flavan-3-ols are derivatives of flavanols that have 2-phenyl-3,4-dihydro-2H-chromen-3-ol as the functional moiety or backbone. Flavan-3-ols include the catechin, epicatechin gallate, epigallocatechin, epigallocatechin gallate, and their oligomers,

proanthocyanidins or procyanidins, theaflavins, and thearubigins. Flavanols are the predominant pigments in wine, tea, and cocoa (Schroeter *et al.*, 2010). The daily estimated intake of flavanols (both monomeric and polymeric forms) is higher than that for flavonols (i.e., compounds similar to quercetin) and intakes in the range of 100–300 mg per day are commonly reported. The consumption of flavanol-rich cocoa, chocolate, and tea has been associated with the decreased risk of some vascular diseases, including cardiac events and strokes and improvements in blood pressure. True of most biofactors, the smaller or less polymerized forms of flavanols (monomers and dimers) are more bioavailable than their larger oligomeric counterparts, such as procyanidins or highly condensed polymers, often designated as tannins.

Flavanols are thought to be able to influence the mitochondrial function both by activation and control of processes important to programed cell death, that is, apoptosis. For example, epigallocatechin-3-gallate functions as an inhibitor of certain nuclear proteins important to the control (rate) of mitochondriogenesis and apoptosis. Although a good balance is maintained between mitochondrial efficiency and orderly apoptosis in normal cells, exposure to epigallocatechin-3-gallate in cell culture appears to tip the balance toward apoptosis in certain cancer cell lines. In addition, epigallocatechin-3-gallate may have the potential to improve oxidative metabolism.

Low concentrations of epigallocatechin-3-gallate (micromoles) inhibit glucose production and also reduce the expression of genes critical to glucose production. Such events can increase lipid oxidation and improve insulin sensitivity. Analogous to the other biofactors described herein, activation of 5′-AMP-activated protein kinase (important in oxidative metabolism signaling) appears to be involved. However, it is important to note that a caveat to much of the work in this area of flavanols has been done using cell culture models, and parent compounds, rather than the metabolites that exist *in vivo*. As is true for much of the work in the area of biofactors, there is a need for studies that are conducted *in vivo* using amounts of biofactors that are within the range of dietary intakes. With respect to mechanistic studies, when possible they should be conducted with the metabolites that occur *in vivo* at physiologically relevant concentrations (Schroeter *et al.*, 2010).

Hydroxytyrosol

Olive oil contains hydroxytyrosol, a biofactor often associated with the healthful effects of consuming a Mediterranean diet, a diet characterized by a proportionally high consumption of olive oil, legumes, unrefined cereals, fruits, vegetables, and fish, but low to moderate consumption of meat and dairy products. The Mediterranean diet has been associated with a lowered incidence of cardiovascular disease and certain cancers, particularly compared with cultures wherein the consumption of meat and saturated fat predominate. Extra-virgin olive oil (produced with no chemical processing) has been identified as an important contributor to the reduced mortality associated with consuming a Mediterranean diet (Shenoy *et al.*, 2011).

In Mediterranean countries, such as Italy and Greece, dietary intake of olive oil polyphenols are estimated at approximately 10–20 mg per day with daily intakes of 25–50 ml of olive oil. Hydroxytyrosol is absorbed in a dose-dependent manner according to the phenolic content of the olive oil administered. However, similar to other sources of biofactors, typical daily doses of olive oil often do not promote changes of putative health-related markers *in vivo* (e.g., serum or plasma antioxidant activity). However, the relationship between diet and achieving an effective dose of hydroxytyrosol is complex. Although extra-virgin olive oil is the principal source of hydroxytyrosol, wine contains modest amounts of hydroxytyrosol. In addition, an interesting phenomenon is that endogenous hydroxytyrosol synthesis is promoted by alcohol consumption. Exposure to alcohol redirects pathways that normally produce dopamine to hydroxytyrosol production (Shenoy *et al.*, 2011).

Analogous to quercetin and resveratrol, hydroxytyrosol's putative biological effects include antioxidant activity and modulation of energy-related pathways. Regarding modulation of energy-related phenomenon, hydroxytyrosol has been reported to enhance endurance capacity. It also has been reported to reduce fatigue and muscle damage caused by excessive or exhaustive exercise based on data from both *in vivo* and *in vitro* studies. Hydroxytyrosol has been observed to stimulate mitochondrial fission, and increase peroxisome proliferator-activated receptor gamma coactivator 1-α (PGC-1α) expression. PGC-1α is an essential coactivator in processes important to mitochondrial fusion, enhanced complex I and II activities, and mitochondriogenesis (Shenoy *et al.*, 2011).

Pyrroloquinoline Quinone

In addition to being a plant growth factor and bacterial cofactor, pyrroloquinoline quinone (PQQ) protects the mitochondria from oxidative stress and promotes mitochondriogenesis. Recent evidence suggests that compounds like PQQ are components of interstellar dust and considered a precursor of organic materials in early life on Earth. The ubiquitous presence of PQQ suggests that there has been constant exposure to this compound throughout evolution.

Similar to resveratrol and hydroxytyrosol, PQQ can influence energy-related metabolism, albeit at relatively lower doses. The mechanism of action involves interactions with cell-signaling pathways and mitochondrial function (Rucker *et al.*, 2009). PQQ administered at a dose of 0.2–0.3 mg PQQ per kilogram in humans effects changes in antioxidant potential and indices of inflammation (e.g., plasma C-reactive protein, interleukin (IL)-6 levels). PQQ supplementation also results in significant changes in urinary metabolites consistent with enhanced mitochondria-related functions. In addition, nutritional deprivation results in a wide range of systemic responses, including growth impairment, compromised immune responsiveness, and abnormal reproductive performance in experimental animal models.

Dietary sources of PQQ include many fermented products, wine, tea, cocoa, and legumes. In animals, deficiency signs are observed at levels at or below 300 micrograms PQQ per kilogram of highly purified diets. Repletion with PQQ to

mice-fed diets devoid of the compound results in improvements in growth, mitochondrial function, and immune responsiveness. In humans, amounts of 5 or more mg PQQ per day are needed to effect changes in clinical indices, (such as antioxidant activities or C-reactive protein levels). Human dietary consumption of PQQ is estimated to be 200–400 μg PQQ per day.

Concluding Comments

Vitamins and most probably many biofactors have evolved to serve unique and complex roles: as cofactors, as signaling agents in cells, as regulators of gene expression, and as redox and free-radical quenching agents. With the possible exception of vitamin D, all recognized essential vitamins are derived solely or in part from organic food substances found only in living things. As is the case for any substance that is essential to a given function, all vitamins and perhaps some biofactors at some point in development can be viewed as limiting nutrients, the absence of which results in specific deficiency signs and symptoms. What is emerging is that biofactors and their combinations have regulatory potential and may be linked to important biological processes, which are controlled and linked in turn to cellular transporter systems, such as the solute carrier (SLC) and the ABC multispecific 'drug' transporters. Highly regulated transporter networks are by necessity linked to cell sensing and signaling networks to maintain precise homeostasis. In this regard, it should be appreciated that some of the mechanisms underlying a given process are not necessarily intuitive. For example, SLC and ABC transporters are important to both the influx and efflux of substances from cells. If a given biofactor attenuates increased transport out of cells, it may also decrease the likelihood that various toxic xenobiotics or substances accumulate within given cells or tissues. Coordinated communication allows both the systems to contribute to the overall metabolism, detoxification, antioxidant capacity, and redox capacity.

We are routinely exposed to more than 5000 known phytochemicals, particularly when a mixture of fruits and vegetables are a major part of the diet. Although current research tends to focus on single compounds and concerns may be expressed, as done by the authors, regarding the seemingly high concentrations needed for demonstrating effects of the single compounds, little is known about synergisms and complementary interactions between complex mixtures of biofactors. Future research will undoubtedly begin to address such interactions and in a broad sense better define the potential requirements or suggested intakes for functional classes of biofactors. As a final point, given that many of these compounds have characteristics that promote survival, an argument may be made that their selection over eons has reduced or resulted in less exposure to those foods with definable toxins.

See also: Determining Functional Properties and Sources of Recently Identified Bioactive Food Components: Oligosaccharides, Glycolipids, Glycoproteins, and Peptides. Food Safety: Food Analysis Technologies/Techniques. Food Toxicology. From Foraging to Agriculture. Human Nutrition: Malnutrition and Diet

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Water: Advanced Irrigation Technologies

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Glossary

Chemigation The injection of water-soluble chemicals, such as herbicides and pesticides, through an irrigation system for application to the land using the irrigation system.

Feedback control A control system that monitors the effect on the system that it controls and modifies output accordingly; for example, a system that controls irrigation application rate based on real-time soil moisture monitoring.

Fertigation The injection of water-soluble fertilizer products through an irrigation system for application to the land using the irrigation system.

Microirrigation Microirrigation, also known as drip or trickle irrigation, is an irrigation method that drips water slowly onto plant roots, either via the soil surface or directly onto the root zone, through a system of pipes, valves, tubing, and emitters.

Partial root zone drying A potential water-saving irrigation strategy which irrigates only one side of a root system, potentially saving 50% water with no impact on yield. This is because plant water potential equilibrates with the wettest part of the soil. There is some evidence to show that this effect is not long term.

Introduction

Limited opportunities to expand the volume of global freshwaters allocated to irrigation means that advanced irrigation technologies, aiming to improve efficiency of existing systems are needed, timely, and are of paramount importance.

There is little scope for greater use of allocated global freshwaters for irrigation, due to unprecedented expansion since the 1950s, plus other multiple demands on that resource to meet higher living standards: projected as +400% (manufacturing), +140% (thermal electricity generation), and +130% (domestic use) by 2050 (OECD, 2012).

Providing for a further 2 billion people by 2050 will challenge our ability to manage and restore natural assets, including freshwaters, on which life depends (OECD, 2012). Irrigation will need to support a projected 50% increase in global food supply to feed the additional 2 billion people (Jury and Vaux, 2007).

Irrigated Areas and Volumes Abstracted

Globally, agriculture is the largest user of freshwater, with irrigation withdrawals representing approximately three-quarters (70%) of the total freshwater use (Fischer *et al.*, 2007). Of this, only-one half is estimated to reach the crop – the remainder is lost during storage, conveyance, or as subsurface drainage after application (Jury and Vaux, 2007). In many developing countries, the proportion used in agriculture is upwards of 80% of withdrawals (Turral *et al.*, 2010) highlighting the dependence on water for food crop production in rural-based economies (Knox *et al.*, 2012).

Recent food shortages and commodity price spikes have raised questions regarding food security at both global and national scales (IAASTD, 2009). In this context, securing adequate water of sufficient quantity and quality for agriculture will be essential in meeting future food demands for a growing population with increasingly diverse dietary requirements. Augmentation methods, such as rainwater harvesting, are necessary to boost freshwater supplies (see e.g., **Figure 1**), but improving the efficiency of use is of paramount importance to assist sustainable use of this resource. Agriculture sits at the interface between the environment and society, so any increase in water use will need to take into account the consequent impacts on freshwater ecosystems and the multifunctional nature and diversity of benefits that irrigated agriculture provides, not just to food production (Knox *et al.*, 2010).

The value of using freshwaters for irrigation should include not only direct benefits to the party who stands to gain from the product but also the wider ecological consequences of these decisions, and the social goals being served by the decision (Costanza *et al.*, 1997). Owing to this, there will be greater government and regulatory demands for

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(a) (b)

Figure 1 Rainwater harvesting schemes supplement freshwater allocations for irrigation (Left: Opuha Dam, New Zealand, photo: Opuha Water Ltd.; Right: Arvari River, India). Photo: C. Glendenning

environmental protection of freshwaters, adding further competition for agricultural demands.

Irrigated croplands globally have increased from approximately 100 Mha in 1950 to 275 Mha in 2000 (Lal, 2009), being twice as productive as nonirrigated croplands. However, meeting future food demand will be significantly more challenging than in the 1960s when the first Green Revolution occurred, and agricultural efficiency was generally low everywhere (Jury and Vaux, 2007). Once surface waters become fully allocated, communities turn to groundwaters with less tangible accompanying ecosystem services. The unprecedented demands on global groundwaters for food production has led to overdrafting (rate of extraction > rate of recharge), which is calculated to be as much as 163 km^3 per year, with approximately 80% of this occurring in India and China (Postel, 1999). The implications of this are that close to 500 million people are being fed by a water supply that could disappear in the near future.

Seckler *et al.* (1999) estimated that up to 25% of India's grain harvest could be in jeopardy due to declining freshwater resources. China increasingly faces water shortage and food security challenges, with the area of land irrigated in 2003 having increased 3.5 times since 1949, and 75% of its grain crop being dependent on irrigation.

Improving Irrigation Efficiency

Increases in the productivity (defined as the amount of yield per unit of land, ton ha^{-1}) of irrigated land through changes in management and improvements in efficiency offer the greatest potential for global water savings (e.g., Sadler *et al.*, 2005), because irrigated agriculture is the dominant consumptive user of water.

Seckler *et al.* (1999) estimated the average irrigation efficiency (water required for 100% yield divided by irrigation withdrawals) for 118 countries around the world in 1990 as 43%, and showed that increasing irrigation effectiveness to 70% would produce a total water saving of 944 km^3 per year and reduce the need for development of further water supplies for all sectors in 2025 by approximately 50%. In reality, when

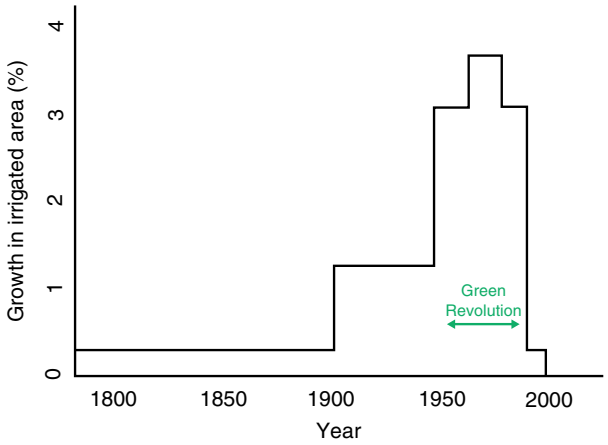


Figure 2 Reported rate of growth (% per annum) in the global irrigated area over the past 200 years. Modified from Jury, W.A., Vaux, H.J., 2007. The emerging global water crisis: Managing scarcity and conflict between water users. Advances in Agronomy 95, 1–76.

freshwater resources are limited, it is possible that saved water will be directed elsewhere to increase overall productivity. The efficiency gains enable increased food production, but do not address the need to allocate freshwaters for irrigation at a sustainable rate. Efficiency gains therefore need to be accompanied by catchment regulation to maintain a sustainable total allocation of freshwaters for irrigation (Perry, 2007).

Irrigation efficiency will become increasingly important as constraints deepen on further expansion of irrigation. There is also growing evidence that the expansion of irrigated lands, which has been steadily rising since the 1950s, has slowed as we enter the twenty-first century (**Figure 2**; Jury and Vaux, 2007).

To create efficiency gains, innovative irrigation technologies will therefore be required:

- more uniform application of water (Burt *et al.*, 1997);
- reduction of evaporation or runoff losses (Burt *et al.*, 1997);
- improvement of sprinklers by lowering the spray to reduce air losses and kinetic energy of impact (Jury and Vaux, 2007);

- improvement of irrigation scheduling and water delivery timing to reduce water losses, as well as addressing crop sensitivity at certain developmental stages (Jury and Vaux, 2007);
- use of soil monitoring and PET estimates to ensure that correct amounts of water are applied at the correct time (Jury and Vaux, 2007);
- correct tillage and field preparation to enhance infiltration and reduce evaporative losses (Wallace and Batchelor, 1997); and
- development of canal linings and other repair measures to improve the efficiency of water supply from source to field, which is estimated to average approximately 70% globally (Bos, 1985).

Summary

There is much evidence in the scientific literature which confirms that global agriculture will face a major challenge over the next few decades – supplying more food to meet increasing demands while simultaneously reducing its environmental impact (Beddington, 2010; OECD, 2012). Dwindling water supplies, an increasing frequency of droughts, and longer term uncertainties associated with a changing climate, all mean irrigated agriculture needs to do more with less. This implies both increasing water productivity (ton ha^{-1}) and raising the economic benefits attributed to irrigated production (US$ per m^3) (Monaghan *et al.*, 2013).

Farmers and agribusinesses are under pressure to reduce production inputs and costs. There are, not surprisingly, a number of emerging risks – climate change, demands for greater environmental protection, and increasing competition for water resources.

Future advances in irrigation management are likely to provide still more precision, greater automation, and increasingly ingenious and efficient irrigation options to farmers. The challenge will be to meet farmer demands for smart irrigation management in an increasingly water-constrained world.

This article therefore discusses the latest technologies designed to improve the application of water by irrigation systems both at the farm-scale and at larger regional schemes. It presents the latest advances, such as precision tools, remote sensing and web enablement. Finally, it presents an insight into future needs and trends for advanced irrigation technologies.

Technological Advances in Irrigation Application Methods

Section Overview

The traditional irrigation application methods (surface and pressurized) are now dated technologies and are at the limit of their irrigation performance under current management practices. Future gains in performance can be achieved both through improved design and through the use of advanced technologies and management, in particular the use of adaptive control. The goal is for these adaptive control systems to automatically and continuously readjust the irrigation application system to a desired performance, and account for any variability (temporal or spatial) in crop water requirements or water intake across the field.



Figure 3 Surface irrigation of sugarcane in Swaziland. Gravity fed furrow irrigation schemes are widespread in Africa although some are being converted into either pressurized sprinkler or drip irrigation to improve efficiency and manage limited water resources. Photo: J. Knox.

This section describes research directed at modernizing the application methods, and focuses on both the factors that limit performance and the simulation tools and control systems that aim to deliver the needed improvements in this performance.

Surface Irrigation

Introduction

In various types of surface irrigation (e.g., **Figure 3**), the furrows, bays (border dykes), or basins serve both as a means to convey water across the field and as a surface through which infiltration occurs. The soil infiltration characteristic more than any other factor serves to determine the level of performance or efficiency achievable from surface irrigation. The soil infiltration characteristic can vary both across the field and also from one irrigation event to the next (Walker, 1989; McClymont and Smith, 1996; Emilio *et al.*, 1997; Gillies, 2008). Khatri and Smith (2006) and Gillies (2008) identified this variability as a major physical constraint in achieving higher irrigation performance in furrow-irrigated fields.

In surface irrigation, infiltration variability causes non-uniformity in water absorption rates and furrow stream advance rates (Trout, 1990). Furrow irrigation efficiency is further compounded by the furrow-to-furrow inflow variability in both gated pipe and siphon tube operated systems (Trout and Mackey, 1988). For example, in a typical field under furrow irrigation, it is very difficult to identify one furrow that is representative of the entire field. Therefore, any field evaluation of infiltration characteristics based on measurements from only a single furrow is unlikely to give an accurate estimation of irrigation performance (Schwankl *et al.*, 2000; Langat *et al.*, 2008; Gillies, 2008).

Well-designed and managed precision surface irrigation systems thus have the potential to address both spatial and temporal variations in soil infiltration through the appropriate use of simulation, optimization, and adaptation, that is, through real-time control.

Simulation

Software packages for simulating surface irrigation hydraulics have been developed to accurately simulate the depth of water applied over the field. The two most commonly used models to date are SIRMOD (Walker, 1989) and WinSRFR (Bautista *et al.*, 2009) largely because of their ready availability. Other similar models that have been reported include BORDEV and FURDEV (Zerihun and Feyen, 1996) and that of Mailhol and Gonzalez (1993).

The software is typically based on a numerical solution of the full hydrodynamic (St. Venant) equations (see Walker and Skogerboe, 1989), or, in the case of WinSRFR, of a reduced form of these equations (the zero-inertia approximation). In all cases their accuracy is limited only by the accuracy of the input parameters, in particular the soil infiltration parameters and the resistance provided by the surface roughness of the furrow or bay (represented by the Manning's n parameter (Limerinos, 1970)).

Depths of infiltration can be calculated at a fine spacing along the length of a furrow or bay. Across the field the scale is determined by the width of the irrigation unit (furrow or bay). In either case, the prediction scale is finer than the scale at which applications can be controlled or managed. Therefore, typically an average infiltration characteristic for the entire furrow or bay is used, and this may lead to infiltration being under- and overestimated in many parts of the field (Emilio *et al.*, 1997) due to small-scale variations in the infiltration characteristics. The parameters are usually estimated from measurements (inflow, advance, flow depth, and runoff) taken during an irrigation event. Methods of estimation range from direct solution as in the two-point method of Elliott and Walker (1982) to more data intensive but robust methods involving error minimization techniques as in the volume balance-based Infiltration PARameter Model (IPARM) (Gillies and Smith, 2005; Gillies *et al.*, 2007) or the multilevel method of Walker (2005).

The analytical irrigation model of Austin and Prendergast (1997) differs from the other simulation models in that it employs an analytic solution of the kinematic equations and a simple linear infiltration function. However, its use is limited to bay irrigation of cracking clay soils, and its accuracy is inevitably limited in some field situations.

An example of simulation in the improvement of surface irrigation performance is the use of the IRRIMATE™ suite of tools (Raine and Walker, 1998; Smith *et al.*, 2005), which is now an accepted practice in the Australian cotton industry. IRRIMATE is a process of field measurement, evaluation, simulation, and optimization that uses data from a measured irrigation to evaluate the performance of that irrigation and to provide advice on the best management of future irrigation events (which in any case could be occurring under different soil conditions). The IRRIMATE system currently employs IPARM (Gillies and Smith, 2005; Gillies *et al.*, 2007) to determine the infiltration parameters from measurements of the irrigation advance and runoff. These parameters are then used in the simulation model SIRMOD in which the optimization (selection of the best or preferred irrigation flow rate and/or time to cut off) is a manual trial and error process. These are two significant limitations of the system.

The recently developed Surface Irrigation Simulation Calibration and Optimization (SISCO) model, which was applied in an evaluation of bay irrigation in the Goulburn Murray Irrigation District of Southern Australia by Smith *et al.* (2009) and Gillies *et al.* (2010), removes these limitations. As with earlier models, it employs a solution of the full hydrodynamic equations to simulate the irrigation advance and recession and provides an estimate of the irrigation performance. However, it is also self-calibrating in that it performs the inverse solution for the infiltration parameters from any of a wide selection of measured data including the irrigation advance, runoff, recession, and depth data; and optimizes the irrigation against user-defined objectives that involve some combination of the usual performance measures.

Understanding and accommodating spatial and temporal variability of infiltration in furrow irrigation is another unique feature of the SISCO model. Given some knowledge of the variation in the infiltration characteristics across a group of furrows or across a number of irrigation events (e.g., Gillies *et al.*, 2008, 2011), the model allows selection of the flow rate and time to cut off that give the best overall irrigation performance for the entire group of furrows.

Automation and control of surface irrigation

Automation and adaptive real-time control has been proposed for the management of temporal variability of infiltration characteristics (e.g., Emilio *et al.*, 1997; Mailhol and Gonzalez, 1993; Khatri and Smith, 2006). It can provide an even higher level of irrigation performance than the traditional evaluation (as demonstrated by Raine *et al.*, 1997; Smith *et al.*, 2005; Khatri and Smith, 2007) along with substantial labor savings.

Control systems used in surface irrigation can be implemented at diverse levels of sophistication and can be manual or automatic. Automation is not essential to the achievement of efficient surface irrigation; however, it does provide convenience, reduced labor requirements, and greater certainty over the control of irrigation durations.

The use of irrigation evaluations to modify future irrigations (e.g., the IRRIMATE process) is essentially an example of temporally separate feedback control where data from one event are used to control the next or future events. Real-time control as applied to surface irrigation implies that measurements taken during an irrigation event are processed and used for the modification and optimization of the same irrigation event. The real-time control system monitors the advance of water along the furrow or bay, and through a simulation process modifies the management variables (flow rate and time to cut off) accordingly before the end of that particular irrigation event. If the management variables are continually and automatically varied it is a form adaptive control.

Adaptive or real-time control of furrow irrigation potentially leads to higher irrigation efficiencies and hence substantial water savings by better matching the irrigation to the prevailing soil conditions.

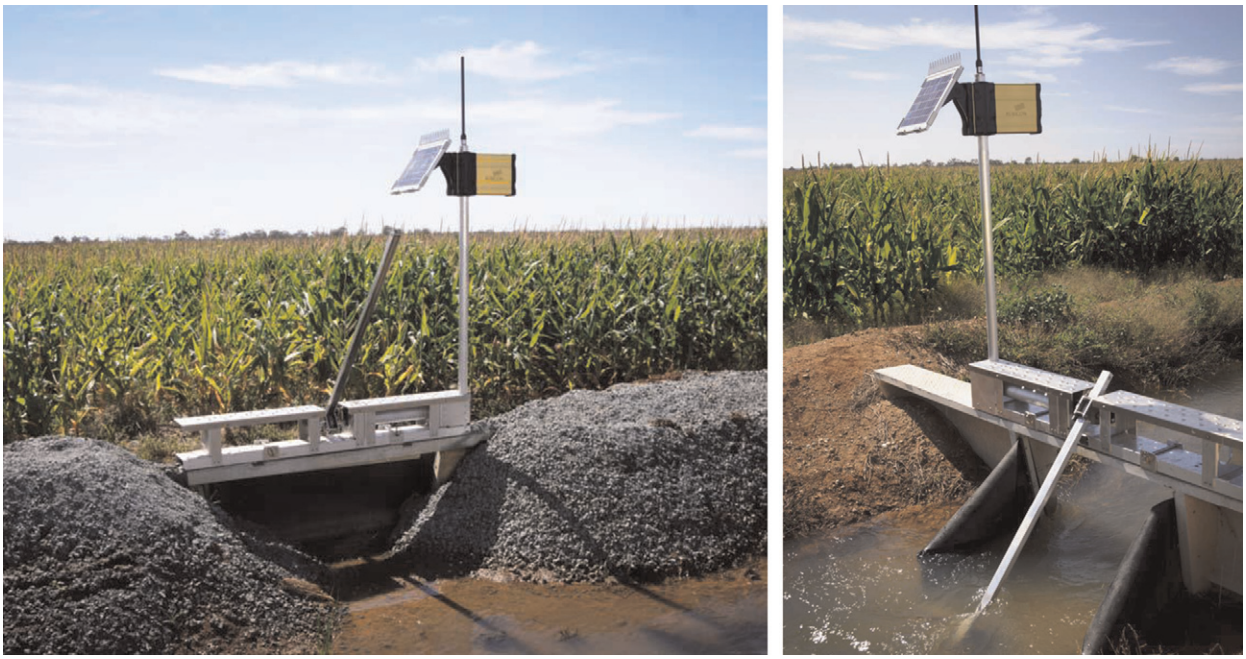


Figure 4 Rubicon farm channel actuator (left) and bay inlet actuator (right). Photos: Rubicon Water.

Automated feedback control systems have been attempted for various configurations of surface irrigation (e.g., Clemmens, 1992; Hibbs *et al.*, 1992; Humpherys, 1995a–c; Niblack and Sanchez, 2008; Uniwater, 2008). In these cases the response being sensed was the water advance down the field, where the sensing was by contact (Humpherys and Fisher, 1995) or noncontact (Lam *et al.*, 2007) means. In most cases, the control systems were able to deliver better irrigation performance (typically measured by higher application efficiencies) than the conventionally managed systems. Furrow irrigation has seen little automatic control compared with other surface irrigation techniques. Humpherys (1969) observed that border and basin irrigation systems are generally better suited to automation and control than furrow because the inflow into the bay is more easily controlled. Some previous attempts at furrow irrigation automation and control include surge flow irrigation systems (Walker, 1989; Mostafazadeh-Fard *et al.*, 2006), and conventional continuous flow (Hibbs *et al.*, 1992; Lam *et al.*, 2007).

A significant challenge in controlling surface irrigation is to obtain the data needed by the control system in sufficient time to control the irrigation. An example of this is provided by Hibbs *et al.* (1992), who developed an adaptive control system based on measurements of the outflow at the downstream end of the furrow. However, the system is impractical because in most surface irrigation systems the control decisions need to be made long before the occurrence of any outflow.

All these cases can be considered a form of adaptive control where the response being sensed is the water advance down the field and the output is the depth of water applied and the usual performance measures of efficiency and uniformity (rather than a crop response). Systems such as these account for the temporal variation in soil moisture deficits and soil hydraulic properties. Varying the management to accommodate spatial variations in the soil infiltration characteristic is usually not considered. Despite the published research, few if any of these systems have been commercialized.

Recently, Khatri and Smith (2006, 2007) established the basis for the practical real-time control of furrow irrigation, involving the following:

- continuous measurement of that inflow through inference from measurements of pressure in the supply system;
- measurement of the advance down the furrows at a single point about midway through each irrigation;
- real-time estimation of the soil moisture deficit and the current infiltration parameters from that observation of the irrigation advance; and
- real-time simulation and optimization of the irrigation for selection of the time to cut off that will give maximum performance for that irrigation.

Preliminary trials of this system, Koech (2012) show that the irrigation cutoff times predicted were shorter than those used by the farmer in irrigating the remainder of the field. This translated to reduced runoff, deep percolation, and higher application efficiencies as a direct result of real-time optimization. The system proposed has been kept simple, by using a fixed inflow and varying only cutoff time, to encourage implementation of the system. Although the real-time optimization can be operated as a manual system the greatest benefits occur when it is integrated with automation. The current phase of development of this system is the integration with the Rubicon Water FarmConnect® system (**Figure 4**). The FarmConnect® system combines short-range radio telemetry, solar power, mobile telecommunications, and cloud software on the internet to automate and remotely control surface irrigation.

In all these systems, the focus is on the control of the individual irrigation event. Although this is an important aspect to improve precision of surface irrigation delivery it is not



Figure 5 Uniform center pivot irrigation on a sugarcane crop (left) (Photo: J. Knox), and variable rate center pivot irrigation for dairy pasture (right). Photo: C.B. Hedley.

sufficient. These systems require comprehensive decision support to provide the seasonal water management that will deliver maximum water use efficiency.

Sprinkler Systems

Sprinkler or 'overhead' irrigation systems deliver water to the plant from above, and may be solid set, motorized with a boom with sprinklers attached, or hand moved, for example, rain guns. In comparison to surface irrigation systems, these systems commonly require a power source to move, and provide greater control of the applied water depths and position (see Figures 5 and 6).

Sprinkler pattern simulation

Prediction of how adjacent sprinklers overlap to give the pattern of application is essential to the design of effective sprinkler irrigation systems. In its simplest form it involves the overlapping of known patterns such as in the package SpacePro (Cape, 1998) to select the nozzle size and spacing for a given application. Here the objective is to maximize the uniformity of applied depths. It relies on knowledge of the sprinkler patterns for the given nozzle, pressure, and height above ground. Wind effects are typically ignored and the answer is relatively insensitive to uncertainties in the individual sprinkler pattern used in the analysis (Christiansen, 1941).

Simulation of sprinkler distribution patterns can not only provide input data for use in models such as SpacePro but also the basis for decision-support models for sprinkler systems in the development and application of optimum irrigation management strategies. Central to an accurate simulation of sprinkler distribution patterns is the prediction of the impact of wind (speed and direction) on the overlapped pattern. In general, higher wind speeds lengthen the sprinkler distribution pattern downwind, shorten the distribution pattern upwind, and narrow the distribution pattern normal to the wind direction (Figure 7; Shull and Dylla, 1976). Greater overlap of adjacent sprinkler patterns is thus required to obtain acceptable uniformity.



Figure 6 Overhead irrigation on onions using a mobile hosereel fitted with a boom. These methods are used on high value crops on light soils where small, frequent applications help to avoid soil and crop damage. Photo: J. Knox.

Simulation of sprinkler irrigation distribution patterns in windy conditions has evolved significantly over the past two decades. Two major approaches have been used: a deterministic approach, which applies traditional ballistic theory to calculate the flight trajectories of individual water droplets; and empirical methods, which involve extrapolation from measured sprinkler distribution patterns for various wind speeds and directions for the same nozzle, pressure, and trajectory angle.

An example of the empirical approach is the work of Richards and Weatherhead (1993) and Al-Naeem (1993), both of whom used measured wind-affected patterns to determine six empirical factors that are then used to adjust any no-wind pattern for that sprinkler to deal with the effects of wind. This same approach was extended in the TRAVGUN model of Smith *et al.* (2008), which used field-measured transects of applied depths from passes of a traveling irrigator first to calculate the no-wind sprinkler pattern and second to determine the six factors (Figure 8). Output from the model is

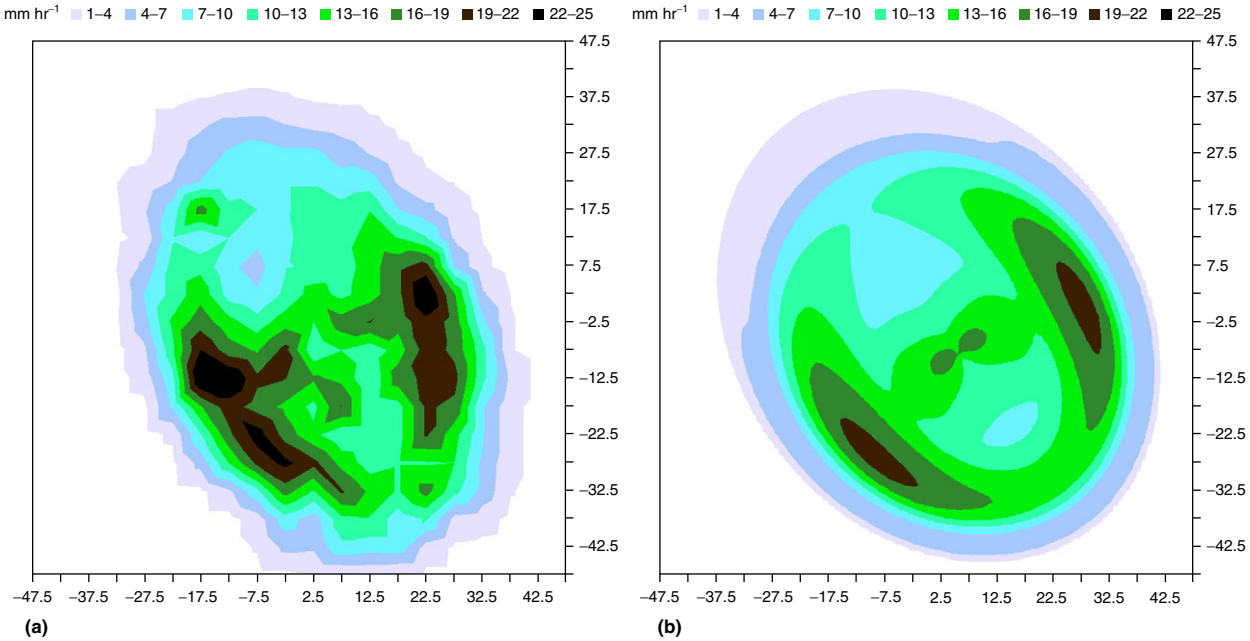


Figure 7 (a) Measured spray pattern for a rain gun sprinkler with a wind speed of 3.58 m s^{-1} (left) and (b) predicted spray pattern for a rain gun sprinkler with a wind speed of 3.58 m s^{-1}. Reproduced from Smith, R.J., Gillies, M.H., Newell, G., Foley, J.P., 2008. A decision support model for travelling gun irrigation machines. Biosystems Engineering 100 (1), 126–136.

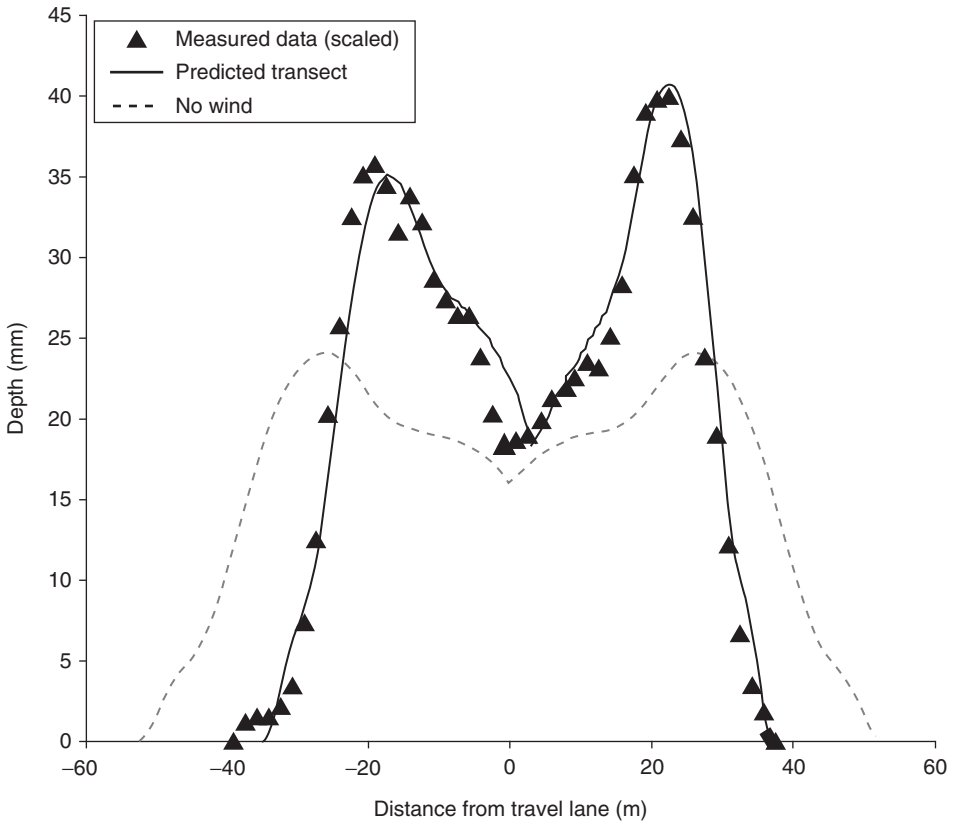


Figure 8 Fit of the TRAVGUN model to a wind affected transect, following calibration. Reproduced from Smith, R.J., Gillies, M.H., Newell, G., Foley, J.P., 2008. A decision support model for travelling gun irrigation machines. Biosystems Engineering 100 (1), 126–136.

an estimate of the uniformity of applications for any selected wetted sector angle, lane spacing, travel direction, and wind speed and direction. The user can change the various operating parameters such as the lane spacing and sector angle to identify the optimum values for those parameters.

An advance on this notion was reported by Ghinassi (2010), where the performance of a traveling gun sprinkler is maximized by real-time variation of pressure, travel speed, wetting angle, and speed of rotation.

The SIRIAS model (Carrion *et al.*, 2001; Montero *et al.*, 2001) reflects the latest thinking in simulation using sprinkler droplet ballistics. To simulate the wind-affected pattern for a single sprinkler, SIRIAS requires a radial leg pattern measured in still air (for the given sprinkler, nozzle height, and pressure). The model uses an inverse solution to determine the droplet size distribution that would give that sprinkler pattern and then uses that distribution in the prediction of the wind-affected pattern. It has been validated for a wide range of nozzles and configurations (e.g., Montero *et al.*, 2001). The patterns predicted by SIRIAS can then be used in packages such as SpacePro to determine the overlap patterns for whole systems.

For the large mobile center pivot and lateral move systems, models that predict sprinkler patterns to estimate the uniformity of applications along the machine provide an alternative simpler method to field trials using large numbers of catch cans. However, field trials add value as they also assess machine maintenance issues, such as blocked sprinklers and hoses. Examples of this type of model are those of Smith (1989) and Thompson *et al.* (2000). Both used a similar statistical description of the droplet size distribution and combined the ballistic model with the overlap along the machine and aggregation of the pattern in the travel direction. An alternative approach was used in the mBOSS model of Foley (2011), who applied the overlap and aggregation to wind-affected patterns imported from SIRIAS.

Ballistic models typically assume that the jet from the nozzle breaks up into the assumed drop size distribution instantaneously or at some defined distance from the nozzle. In either case drag coefficients are modified in a calibration process designed to make the measured and predicted sprinkler patterns match. In an attempt to overcome this deficiency, Grose *et al.* (1998) used a three-dimensional two-phase plume, which consisted of modeling the interaction of the jet with the surrounding air, simulating the separation of the jet into individual droplets. However, this approach has not gained any acceptance.

Unless the break-up of the stream can be predicted from the fundamental fluid mechanics as attempted by Grose *et al.* (1998), any ballistic model requires a droplet size distribution for the particular nozzle type and size, and pressure to be used in the simulation. Obtaining these data is still relatively difficult, time consuming, and expensive.

In all the above models, the usual purpose is estimation of the uniformity of applications and the selection of appropriate nozzles and nozzle spacing. Although their accuracy is limited primarily by the accuracy of the ballistic models (including the use of time and vertically averaged wind speeds and directions), they are sufficiently accurate for research and design purposes. However, none are sufficiently accurate to predict applications at particular points in an irrigated field with confidence; hence they are not suitable for use in a farming decision support system for precision irrigation.

To counter the adverse effect of wind on sprinkler patterns, Ozaki (1999) developed a prototype robotic self-traveling sprinkler system that controls the nozzle sector and trajectory angles and the water supply instantaneously in response to windy conditions to minimize the distortion of the sprinkler pattern by wind and the amount of wasted water.

Spatially varied applications – Center Pivot and Lateral Move Machines

The development of mobile sprinkler systems has provided a level of convenience and efficiency as well as the greatest potential for uniform applications, although they need to be well designed and maintained to achieve this potential. For example, in a study of 39 machines, Foley (2011) showed that less than one-third were operating to specification. In addition these machines are readily adaptable to deliver spatially varied applications.

The ultimate performance from these types of machine occurs through the adoption of low-energy precision application (LEPA) technology (Lyle and Bordovsky, 1981, 1983). The LEPA system involves the use of very low pressure sprays or bubblers located just above the soil surface on the end of long drop tubes. Efficiency is improved through the reduction of spray drift and canopy interception and evaporation. Spatial uniformity is also higher than for machines fitted with conventional sprinklers.

Research into precision irrigation sprinkler systems was initiated in the USA in the early 1990s. Initially this work focused on the modification of center pivot and lateral move irrigation machines to apply spatially varied applications of water and nitrogen (Evans *et al.*, 1996; Duke *et al.*, 1997; Heermann *et al.*, 1997; Sadler *et al.*, 1997, 2000; Camp and Sadler, 1998; Camp *et al.*, 1998; King and Wall, 1998), with the system control often based on stored databases of spatially referenced data. Readers are referred to Camp *et al.* (2006) and Evans and King (2012) for comprehensive reviews of research undertaken in this field. More recently, the emphasis has shifted to the purpose and performance of spatially varied irrigations. Examples of this work include King *et al.* (2005), Sadler *et al.* (2005), Camp *et al.* (2006), Chavez *et al.* (2006), and Dukes and Perry (2006). Perry *et al.* (2003) showed substantial amounts of water conservation for center pivots, and later Han *et al.* (2009) developed and tested equipment and software for variable rate irrigation (VRI) application of water using a lateral move irrigation system.

An interesting use of a system designed for spatially varied applications was provided by Chavez *et al.* (2010). In this case, the spatially variable capacity was used to compensate for nonuniformity inherent in the irrigation applications from the machine by providing greater uniformity.

Various technologies have been used to deliver VRI applications, including

- multiple discrete fixed-rate application devices operated in combination to provide a range of application depths (see McCann *et al.*, 1997; Camp and Sadler, 1994);

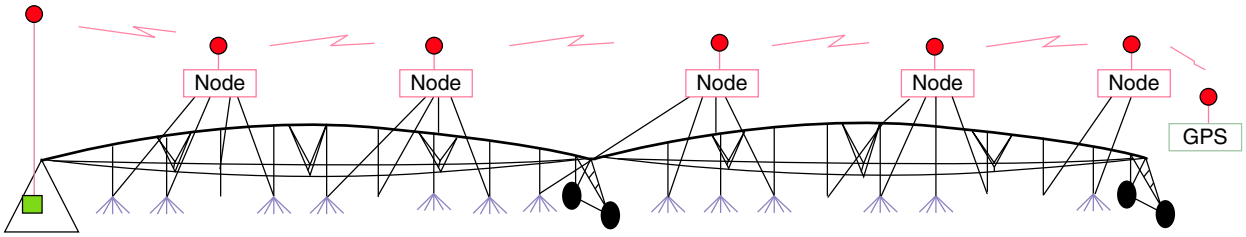


Figure 9 Schematic diagram of individual sprinkler control on a center pivot using GPS and wireless node technology (Available at: www.precisionirrigation.co.nz).



(a) (b)

Figure 10 (a) Drip irrigation used for pasture establishment in South Australia. (b) Taps control water supply to the drip tape installed at 0.2 m depth, with pressure compensating emitters at 0.4 m spacing releasing water at 1 l h^{-1}. Photos: L. Finger.

- flow interruption to fixed-rate devices to provide a range of application depths that depend on pulse frequency (see Evans and Harting, 1999); or
- variable-aperture sprinklers with time-proportional control (see King and Kincaid, 2004; King *et al.*, 1997).

Research to date has resulted in the development of prototype systems for variable rate application, with increasing commercial uptake of these products in the past few years. Appropriate decision-support systems, particularly those that incorporate the outputs from real-time monitoring technologies have not reached an equivalent stage of development. Evans *et al.* (1996) acknowledged that the greatest difficulty faced in the implementation of spatially varied irrigation is associated with determining appropriate prescriptions for the application of water and nutrients. This issue is discussed further in Section Technological Advances In Irrigation Management.

Examples of commercial systems for control of variable applications from center pivot machines are the Farmscan 7000 VRI system developed in Australia and a similar system developed in New Zealand by Precision Irrigation (Precision Irrigation, 2014). The New Zealand system was released into the market in 2008, and incorporates individual sprinkler control using wireless nodes and GPS technology (**Figure 9**).

Microirrigation Systems

Microirrigation systems are typically designed to wet only the soil zone occupied by plant roots and to maintain this at or near an optimum moisture level, using emitters spaced along drip lines. The obvious advantages of microirrigation include a smaller wetted surface area, reduced evaporation from the soil surface, reduced weed growth, and potentially improved water application uniformity within the crop root zone by better control over the location and volume of application (see e.g., **Figure 10**).

A particular benefit of microirrigation (also known as drip or trickle) is the ability to apply small amounts of water at short intervals. This provides scope to maintain the soil at a specified moisture content for part or all of the season and hence the opportunity for increased effectiveness of rainfall during the irrigation season. However, the low soil moisture

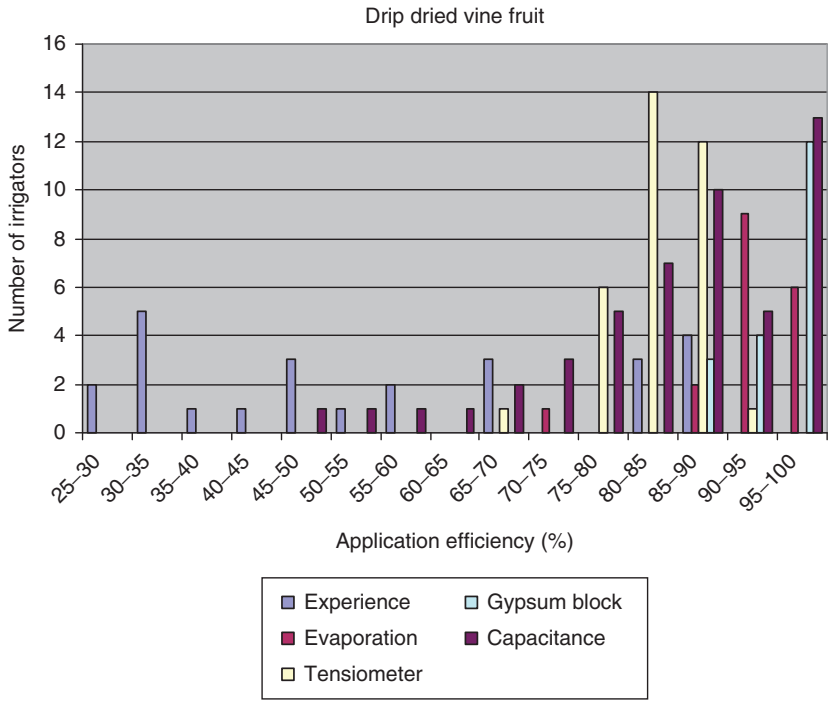


Figure 11 Application efficiencies varying with the method of scheduling irrigations for drip-irrigated vines in the Sunraysia region of Victoria, Australia. Reproduced from Schache, M., 2011. Identifying best management practice through irrigation benchmarking: Would you like probes with your drippers? In: Irrigation Australia, 2011 Irrigation & Drainage Conference, Launceston, Tasmania. Mascot, NSW, Sydney: Irrigation Australia Limited.

deficits maintained under such systems also limit opportunities for any excess rainfall to be stored in the soil. This can reduce the amount of effective rainfall and exacerbate runoff and nutrient leaching.

The potential efficiency of microirrigation systems is often quoted as being greater than 90%. Losses of water in microirrigation systems occur principally through evaporation from the soil surface, surface runoff, and deep drainage. Evaporation losses are generally small due to the limited wetted surface area and the absence of ponded surface water due to the low discharge rates. The application of water usually occurs beneath the crop canopy, either directly onto or beneath the soil surface, further reducing the potential for evaporative loss. Runoff losses are also usually small due to the low application rates. However, as with all irrigation systems, the ability to achieve high levels of efficiency is more a function of the management of the system rather than some inherent property of the system. For example, Shannon *et al.* (1996) found that drip irrigation application efficiencies under commercial conditions in the Bundaberg area ranged from 30% to 90%. Given the nature of the system, these losses were most likely from overirrigation and deep percolation. Similarly, Schache (2011) found application efficiencies of drip-irrigated vineyards in the Sunraysia region of Southern Australia to range from 25% to 100% (**Figure 11**). In this case, the identified causal factor was the method used for irrigation scheduling, with grower experience (subjective approaches) faring worst when compared with more scientific (objective) methods. Similar experiences were also observed in drip-irrigated crops under supplemental irrigation conditions (Knox and Weatherhead, 2005).

Placement of the drip lines is an important consideration in achieving high efficiencies. For example, Henderson *et al.* (2008) demonstrated a 25% gain in efficiency when drip lines were placed adjacent to each row of broccoli rather than between every second row.

Dominant causes of nonuniform applications under microirrigation systems are pressure variations along the lateral pipelines, variability in the emitters occurring during manufacture, and blockage of the emitters. Extensive evaluations of the uniformities of applications from microirrigation systems have been conducted in the USA (e.g., Hanson *et al.*, 1995) using mobile field laboratories. These have shown that emission uniformities are less than desirable with commercial systems commonly operating with an emission uniformity (E_u) of less than 80%. This is supported by Australian data from McClymont *et al.* (2009) and Hornbuckle *et al.* (2009), who reported distribution uniformities as low as 32% from a sample of drip-irrigated vineyards in Southern Australia. These observations highlight the need for improved design and in-field evaluation, diagnosis, and correction of microirrigation systems if their potential for precision irrigation is to be realized.

Systems for recording and reporting the results of performance evaluations of microirrigation systems are available, for example, Hornbuckle *et al.* (2009). However, these do not provide diagnostic capability and cannot be readily integrated with the software used for system management.

Microirrigation systems also have greater potential for accurate irrigation delivery than other systems. They are easily controlled and are commonly automated on a time, soil moisture, or time–temperature basis (e.g., Phene and Howell,

1984; Meron *et al.*, 1996; Dukes and Scholberg, 2004; Wanjura *et al.*, 2004; Evett *et al.*, 2006). They also lend themselves to adaptive control and have the potential to apply spatially variable applications at a range of scales from individual laterals to individual emitters. Variable rate-controllers that respond to real-time sensing and decision making are particularly applicable to microirrigation systems. They have not been used to apply water variably down an individual lateral or drip line, and would require additional modification for this to occur.

Research into precision irrigation for microirrigation systems has been undertaken primarily in horticultural crops including viticulture (Ooi *et al.*, 2008; Capraro *et al.*, 2008a,b) and fruit tree orchards (Coates *et al.*, 2004; Uniwater, 2008; Adhikari *et al.*, 2008).

Capraro *et al.* (2008a,b) utilized closed-loop irrigation control systems with moisture measurements in the root zones to maintain the soil moisture level around a set value. Regulated deficit irrigation (RDI) strategies were incorporated within the irrigation control system to achieve particular quality targets, that is, the enological quality of the grapes.

Coates *et al.* (2004, 2005, 2006) focused their efforts on the development of a spatially variable microsprinkler system that would allow for management of individual trees in an orchard. More specifically, the objective was to supply water and dissolved chemical fertilizers differentially to one or more individual trees fed by a single microsprinkler drip line.

Preliminary results show that spatially variable management at this scale is possible. Another example of sensor-based control of spatially varied applications from a microsprinkler system is provided by Torre-Neto *et al.* (2000).

More recently, Ooi *et al.* (2008) developed and tested an automated irrigation system for microirrigation. Two irrigation controllers – a soil-moisture-based controller and an ET-based controller – were integrated into a wirelessly networked irrigation control system in an apple orchard and a commercial vineyard. Results have shown that automated irrigation using closed-loop control systems improved water productivity by 73% compared with manual irrigation (Uniwater, 2008). These results demonstrate the potential of closed-loop irrigation control for irrigators at the lower end of the spectrum to 'leapfrog' rapidly to the upper end of the efficiency spectrum. For those irrigators already at the upper end of the spectrum, adoption of the technology would lead to substantial labor and time savings.

Technological Advances in Irrigation Management

Section Overview

This section covers the following aspects:

- advances in irrigation scheduling,
- soil moisture mapping,
- wireless sensor networks (WSNs), and
- precision irrigation management.

The technological advances in irrigation systems described in Section Technological Advances in Irrigation Application Methods must be accompanied by state-of-the-art decision support tools to determine when to turn on the irrigator and how much irrigation to apply; aiming to maximize any benefits gained from the investment in new technology. Decision-support tools either evolve alongside equipment development because the new equipment provides new and enabling methods for optimizing irrigation timing, placement, and amounts, or they may develop independently and be appropriate for use with a range of different types of irrigation systems.

Advanced irrigation scheduling (Section Section Overview) therefore aims for accurate placement of optimized amounts of irrigation at critical times. This, in turn, is primarily determined by crop water demand and soil moisture supply; and new sensor technologies are being used to define crop demand and soil moisture supply at high spatial and temporal resolution (Greenwood *et al.*, 2010). Knowledge of daily crop water demand is useful, but monitoring soil moisture supply to crop provides a predictive tool for scheduling. Section Advances in Irrigation Scheduling discusses these latest developments in soil moisture mapping; Section Soil Moisture Mapping describes methods to update static maps at regular time intervals.

Recent WSN technological advances and their commercial availability provide the means for site-specific monitoring to inform irrigation management decisions. These technological advances include smart integration of sensors, wireless nodes (for communication), internet- and cellular-enabled transfer, and processing and reporting protocols. A specific example, the sensor web enablement (SWE), an initiative of the Open Geospatial Consortium (OGC) will be discussed in Section Wireless Sensor Networks.

The term 'precision irrigation' reflects the precision agriculture concept, applying GPS with sensors to prescribe inputs in the right place, at the right time, and in the right amount. Precision agriculture addresses in-field variability, largely ignored until the 1980s, and new GPS-enabled technologies are enabling precise irrigation management tools, which will be discussed in Section Wireless Sensor Networks.

Advances in Irrigation Scheduling

Designers typically plan for the peak flow rate of a new irrigation system to meet the seasonal crop water requirements for the area to be irrigated plus any freshwater allocation requirements. Once in place, appropriate scheduling tools are then used to assess seasonal changes to daily evapotranspiration (ET) demands from specific crops, and irrigation is then scheduled accordingly.

Advanced technologies for assessing regional ET losses include remote sensing by satellite or airborne scanners (e.g., Gonzalez-Dugo *et al.*, 2006). Multispectral satellites, such as advanced very high resolution radiometer, moderate resolution imaging spectroradiometer (MODIS), and Landsat TM (Thematic Mapper), have been used since the 1970s to estimate ET. These systems are generally limited by their spatial (30 m–1 km pixel) and spectral (5–36 band) resolutions. However, maturation of imaging spectrometry technology combined with greater availability of airborne imaging spectrometer data present new opportunities for improved accuracy of ET estimates by airborne remote

sensing. These researchers tested the 'gold standard' of airborne imaging spectroscopy, NASA's airborne visible/infrared imaging spectrometer, which has 224 spectral bands at 10-nm intervals, and concluded that imaging spectrometers are suitable for determining ET and understanding associated physiological processes, although they are limited by spatial extent, and at present are most appropriate for regional estimates rather than site (field)-based estimates.

Site-specific irrigation scheduling is frequently based on soil water balance models that determine a daily soil moisture deficit using soil, crop, climate, and latitude inputs (Allen *et al.*, 1998), with a modeled daily ET value. A critical soil moisture deficit is used for timing irrigation events. Such traditional modeling tools are very useful but do not easily address commonly encountered within-field variability, and cannot easily account for factors such as ponding due to soil compaction, high water tables, variable crop growth due to shading, etc. Advanced scheduling tools need to address within-site variability due to these factors, that is, topographic relief, short-range changes in soil depth, texture and moisture storage capability and management effects including tillage, fertility, pests, and various irrigation system characteristics (Sadler *et al.*, 2005; Green *et al.*, 2006; De Jonge *et al.*, 2007; Evans *et al.*, 2012) and technologies are emerging to address the challenge (e.g., Peters and Evett, 2007, 2008).

Site-specific crop stress measurements (Green *et al.*, 2006; Peters and Evett, 2007, 2008) have been trialed for improved irrigation scheduling. Peters and Evett (2008) used a 'temperature-time-threshold method.' Crop leaf temperature is used as an indicator of crop stress, which is measured on a fully automated center-pivot irrigation system, where infrared thermocouple thermometers are attached to the trusses of the pivot. A field datalogger is accessed once a day to assess whether canopy temperature is above threshold level. Another novel method determines time for irrigation from crop stress assessed indirectly through soil moisture measurements. Onset of crop stress is indicated by a reduced apparent daily crop water uptake (Thompson *et al.*, 2007).

Soil moisture monitoring tools for triggering irrigation are perhaps the most widely used and most important tools for irrigation scheduling (Fang *et al.*, 2007) and a range of new improved sensors for monitoring soil water are now available (Cardenas-Lailhacar *et al.*, 2010). Improved accuracy of soil moisture sensors is obtained by site-specific calibration and ensuring good soil contact on installation (Greenwood *et al.*, 2010). Recent advances have been made to link soil moisture monitoring sites automatically to software decision tools linked to irrigation systems. Blonquist *et al.* (2006) installed a soil moisture sensor (time domain transmission) to log volumetric soil water content compared with an irrigation threshold, and connected this to a solenoid valve on the irrigation line supplying water to the irrigation system. This system applied 53% less water than under the conventional method. Kim *et al.* (2009) also linked soil moisture monitoring equipment to software control of a site-specific precision linear-move sprinkler irrigation system.

Other technologies have been developed for other methods of irrigation application. In surface irrigation schemes, where farmers receive a fixed amount of water during a fixed period, site-specific scheduling is limited. Here regional scheduling tools become important; and GIS-integrated tools have been developed for equitable irrigation supply to account for variability in soil and crop conditions, unreliable intake of water into the main canal, absence of storage reservoirs, and uneven distributions of water into tertiary canals (Rowshon *et al.*, 2009). The GIS tool links field irrigation demand predictions and then simulates and recommends optimal irrigation supply strategies in the Tanjung Karang Irrigation Scheme for rice growers in Malaysia.

Australian researchers have developed an integrated model for simulating border-check irrigation of dairy pastures that combines a biophysical model of the soil–plant–climate interaction with a hydraulic irrigation model, which models infiltration and movement of water through the soil matrix (Douglas *et al.*, 2010). This model was used to assess how pasture production varied with irrigation management, such as irrigation duration, to improve overall scheduling of irrigation within the scheme.

An Australian review of software tools for on-farm water management (Inman-Bamber and Attard, 2005) lists a number of irrigation scheduling software packages that are increasingly being integrated into irrigation control via web and cellular control systems. Hornbuckle *et al.* (2009) describes a remote sensing method for assessing within-field crop health variations (using NDVI) and links this to reference ET values from nearby weather stations to provide field-specific scheduling information. This crop coefficient derivation process uses a short message service (SMS) to provide information through a simple mobile phone text message service to irrigators on a daily basis. Such technologies enable real-time adaptive control systems for irrigation application (Smith *et al.*, 2010). Adaptive control means that scheduling parameters are based on feedback from the process (Fig. Smith *et al.*, 2010, p. 62) aiming for continued system improvements.

These scheduling methods assess crop and soil status, as well as other management effects – regional and some site specific – to improve scheduling tools. Site-specific measurements are obviously preferable and the next section explains how mapping tools can be combined with site-specific measurements to (1) optimize positioning of the sensors and (2) provide a map of soil or crop condition to add further refinement to decision support tools and technologies for irrigation scheduling.

Soil Moisture Mapping

Recent technological advances in GPS-enabled proximal (ground-based) sensing methods are providing rapid affordable mapping methods of land, soil, and crops to inform irrigation management decisions. For example, electromagnetic induction (EM) surveys typically use very accurate positioning equipment (e.g., real-time kinematic differential GPS, RTK-DGPS), quantifying soil spatial variability at resolutions of <10 m, and simultaneously providing a digital elevation map (DEM) with an accuracy of <0.1 m.

The EM sensor measures soil apparent electrical conductivity (EC) which is influenced by soil texture and moisture in nonsaline soils (e.g., Sudduth *et al.*, 2005; Brevik *et al.*, 2006). Soil EM maps provide the basis for targeted soil sampling

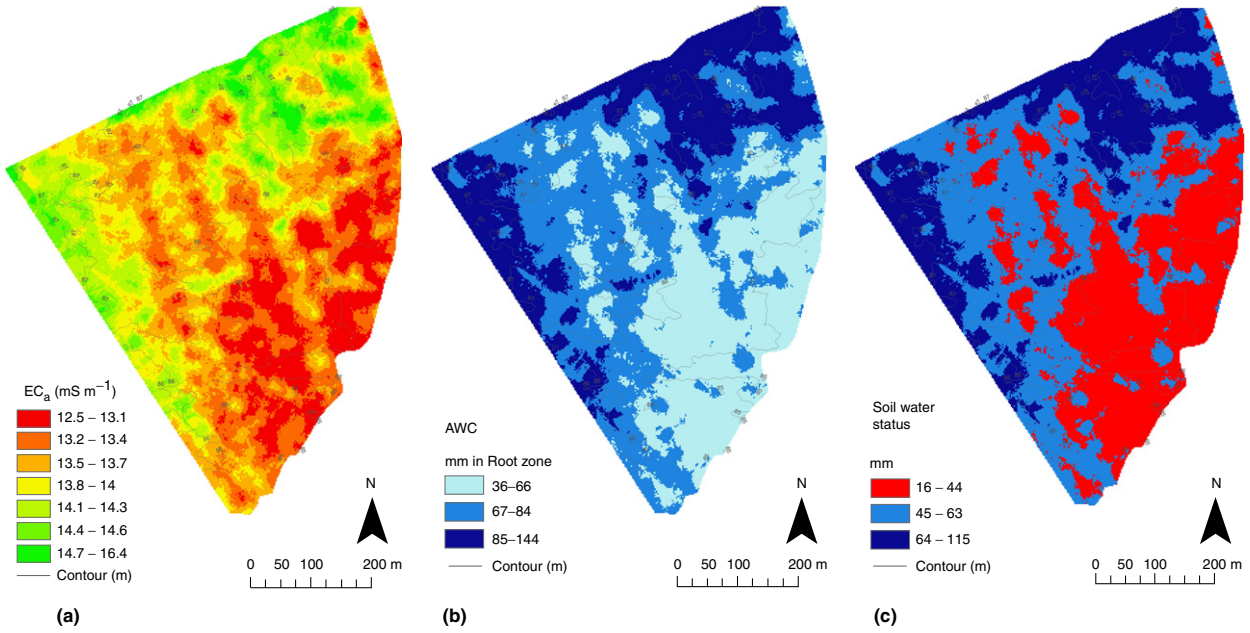


Figure 12 (a) Soil EC map, (b) available water-holding capacity map, and (c) derived soil water status map. Reproduced from Hedley, C.B., Yule, I.J., 2011. Soil water status maps for variable rate irrigation. In: Clay, D., Shanahan, J., Pierce, F. (Eds.), GIS Applications in Agriculture – Nutrient Management for Improved Energy Efficiency. Third Book in CRC GIS in Agriculture Series. Boca Raton, FL: CRC Press, pp. 173–190.

strategies to sample the full range of likely soils encountered in the area of interest. An area of 50 ha can easily be mapped in one day, by pulling the sensor behind an all-terrain vehicle, with on-board GPS, datalogger, and field computer.

Topographic features that are likely to influence irrigation efficiency (e.g., slope, aspect, and slope angle) can be derived from the DEM, and used in conjunction with EC to derive optimal sampling and monitoring positions (Minasny and McBratney, 2006).

The EM map is not only used to select soil moisture monitoring sites, but can also be used to calibrate soil EC values against soil available water-holding properties (Waine *et al.*, 2000; Godwin and Miller, 2003; Hedley and Yule, 2008; Hedley and Yule, 2009) so that a soil available water-holding capacity map can be produced, for spatial irrigation scheduling (**Figure 12**). Hezarjaribi and Sourell (2007) also used EM mapping to define zones for targeted soil sampling to assess soil AWC.

Triantafilis *et al.* (2009) describe how EM surveys employing root-zone sensing Geonics EM38 and vadose-zone sensing Geonics EM31 sensors are related to subsurface soil properties such as texture, moisture, and depth to water table; and are used to define management classes for precision management. Sherlock and McDonnell (2003) found that EM38 data could explain >70% of gravimetrically determined soil moisture variance.

Primary terrain attributes derived from the DEM, collected as part of the EM survey, or by other means, include surface derivatives such as slope, aspect, and curvature (Bishop and Minansy, 2006). Secondary terrain attributes are calculated from a combination of two or more primary terrain attributes to model spatial variation of processes across a landscape, the most commonly used being the 'topographic wetness index,' which is defined by Moore *et al.* (1991) as the natural logarithm of specific catchment area divided by the tangent of the slope, and another being the SAGA wetness index (Olaya and Conrad, 2009).

Other methods that show promise for mapping soil moisture over large areas include airborne and spaceborne remote sensing by passive microwave radiometry or active radar instruments. However, both methods are highly sensitive to surface roughness and their effectiveness is limited to flat and bare ground studies (Jonard *et al.*, 2011; Kseneman *et al.*, 2012), despite the advantage that they are not influenced by cloud cover.

Ground-based versions of these sensors (ground penetrating radar and L-band radiometer) are required for site-specific irrigation management, and these sensors are available, and have been tested on a vehicle for mapping soil moisture in a field. Differences observed between the two methods were related to different sensitivities to surface roughness, and different exploration depths; these technologies require further development before becoming commercially viable. The sensor data were calibrated against TDR-derived soil moisture measurements at each position, and 20% of the reference TDR data was required to produce a good roughness calibration model for the entire field, to correct the sensor data.

Other methods for mapping spatial heterogeneity of soil moisture include electrical resistivity tomography (Kelly *et al.*, 2011). While a strength of this method is its excellent vertical resolution, a weakness is that electrode arrays are inserted into the ground for imaging and the method cannot be mobilized. However, Kelly *et al.* (2011) used it to delineate zones of excessive water loss due to deep drainage, and this technology is therefore an advanced irrigation management technology. Kelly *et al.* (2011) used the information to position monitoring sensors to assist irrigation scheduling.

Soil moisture mapping aids advanced irrigation scheduling because this scheduling directly measures the amount of

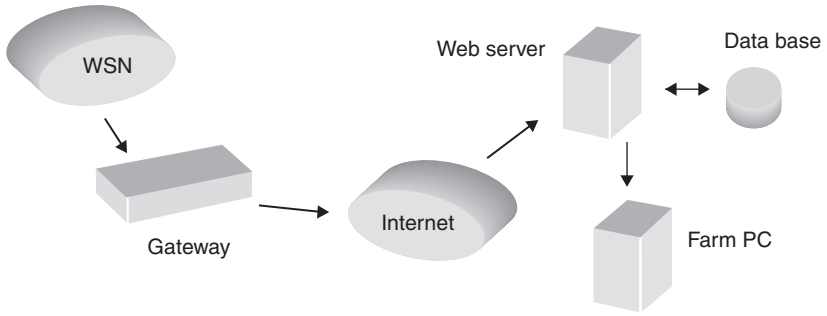


Figure 13 Schematic diagram for a wireless sensor network (WSN) suitable for irrigation control. Adapted from Ruiz-Garcia, L., Lunadei, L., Barreiro, P., Robla, J.I., 2009. A review of wireless sensor technologies and applications in agriculture and food industry: State of the art and current trends. Sensors 9, 4728–4750.

available water left in a soil profile at any one time, and the rate at which it is being used by the crop. It therefore directly monitors crop water use (Thompson *et al.*, 2007) and soil water storage under any irrigation system, and provides information in a digital form and can be used for open-loop or closed-loop decision support tools.

Recent technological advances in WSNs provide the tool for real-time high-resolution soil moisture monitoring within each management zone defined by the EM survey so that soil moisture maps can be updated on a daily basis and used either for direct control of irrigation systems or for informing land managers.

Wireless Sensor Networks

The high spatial resolution provided by GPS-enabled sensing methods (Section Advances in Irrigation Scheduling) can be further refined by smart WSN technologies, and these technologies are rapidly developing from off-line sensors using field loggers with manual downloading to wireless on-line sensor networks, within interoperable and autonomous sensor webs (see **Figure 13**). The sensor web concept is based on the SWE framework of the OGC. Within this framework, standard protocols, interfaces and web services to discover, task, exchange, and process data from different sensors and sensor networks have been defined (Thessler *et al.*, 2011). Irrigation benefits from the resulting high temporal measuring resolution with real-time data transfer from spatially optimized management zones, and spatiotemporal models can be produced to update static maps, on a daily basis, for improved irrigation scheduling (Hedley *et al.*, 2013).

These recent innovations in low-voltage sensor and wireless technologies combined with advances in internet and cellular communication technologies offer opportunities for development and application of real-time management systems for agriculture (Evans *et al.*, 2012; Pierce and Elliott, 2008; O'Shaughnessy and Evett, 2010; Coates and Delwiche, 2009).

Ruiz-Garcia *et al.* (2009) reported that wireless sensor technologies are entering a new phase as a consequence of decreasing costs, increasingly smaller sensing devices, and achievements in frequency technology and digital circuits. Nodes, each with sensors attached, wirelessly form the most efficient communication network to send data to a base station where they are stored and can be accessed remotely. Alternatively, the data are transmitted via internet or cellular means to a secure database for storage, manipulation, and informing irrigation schedules. Owing to a large number of sensors and differing accompanying protocols, a coherent infrastructure is required to treat sensors in an interoperable, platform-independent and uniform way. Standardized access to sensor observations and sensor metadata provided by the OGC compliant Sensor Observation Service (Broring *et al.*, 2011) acts as a mediator between a client and a sensor data archive or a real-time sensor system.

WSN technologies have significant potential to monitor inherent soil variability present in fields with more accuracy than existing systems. Thus, the benefit for the producers is a better decision support system that allows maximized productivity while saving water. Installation of WSNs is easier than the existing wired systems and sensors can be more densely deployed to provide local, detailed data; rather than irrigating an entire field in response to broad sensor data, each section could be activated based on local sensors.

Vellidis *et al.* (2008) developed a prototype of smart sensor array for scheduling irrigation in cotton. The system integrates moisture sensors, thermocouples, and radio frequency identification (RFID) tags. Qian *et al.* (2007) designed a new groundwater-monitoring instrument based on WSN that monitors groundwater table and temperature through a sensor. An embedded single chip processes the monitoring data and a GSM data module transfers the data wirelessly. Bogena *et al.* (2007) evaluated a low-cost soil water content sensor in a wireless network application, and Kim *et al.* (2009) developed an in-field WSN for implementing site-specific irrigation control in a linear move irrigation system. Communication signals from the sensor network and irrigation controller to the base station were successfully interfaced using low-cost bluetooth wireless radio communication. Hedley *et al.* (2013) used a wireless soil moisture sensor network optimally positioned into EM-defined management zones to inform a precision irrigation scheduling tool (**Figure 14**). The WSN monitored soil moisture and depth to water table, the latter providing a means of calculating the contribution of a high water table for subirrigating the crop.

Underground systems for monitoring soil conditions, such as water and mineral content, to provide data for appropriate irrigation and fertilization are emerging (Akyildiz and Stuntebeck, 2006) and these systems can also be used for monitoring the

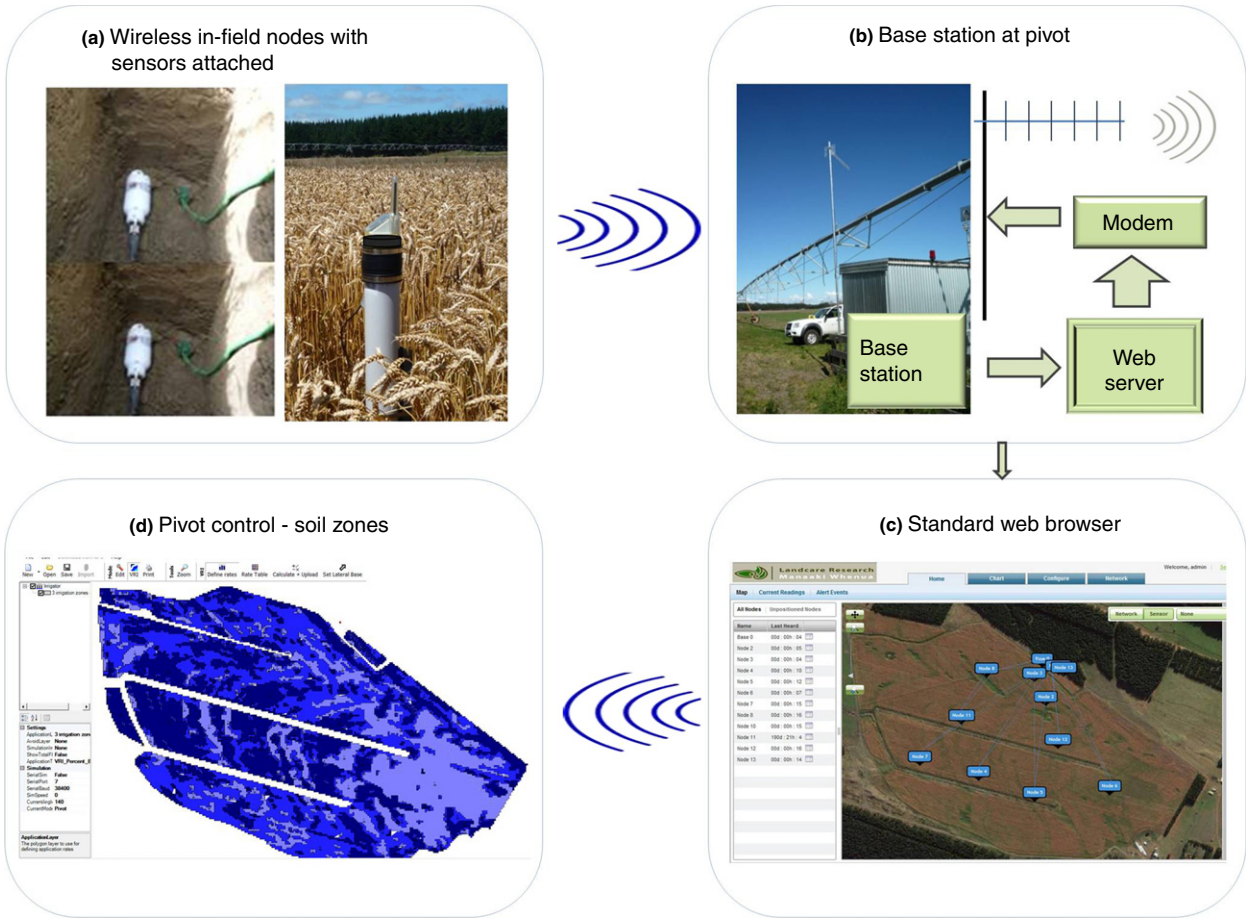


Figure 14 Flowchart to show WSN for precision irrigation scheduling. Reproduced from Hedley, C.B., Roudier, P., Yule, I.J., Ekanayake, J., Bradbury, S., 2013. Soil water status and water table modelling using electromagnetic surveys for precision irrigation scheduling. Geoderma 199, 22–29.

presence and concentration of various toxic substances in soils near rivers and aquifers, where chemical runoff could contaminate drinking water supplies. Another application can be landslide prediction by monitoring soil movement.

Further recent WSN technological advances for irrigation scheduling include

- energy-efficiency gains using adaptive decentralized reclustering protocols for node communications (Bajaber and Awan, 2011; Nesa Sudha *et al.*, 2011);
- algorithm development for handling orphaned nodes for optimal restoration into the network (Maheswararajah *et al.*, 2011);
- inclusion of wireless lysimeters for real-time online soil drainage monitoring (Kim *et al.*, 2011); and
- incorporation of bluetooth and RFID technologies for automated data capture and identification applications (Kim *et al.*, 2009; Ruiz-Garcia *et al.*, 2009).

Precision Irrigation Management

Available water supplies for irrigation are becoming increasingly limited globally and this will force major changes to the design and management of water delivery for on-farm irrigation management, as discussed elsewhere in the article (Section Simulation). Section Simulation discusses a technology that will potentially play an important role in future irrigation management of limited water supplies: site-specific variable-rate sprinkler irrigation or 'precision irrigation' modification of self-propelled center-pivot and linear-move systems (Hedley and Yule, 2009; Evans and King, 2012) (see **Figure 15**). These systems are particularly suited to site-specific management approaches because of their current level of automation and large area coverage with a single lateral pipe. Where sprinklers are modified for site-specific control, new opportunities arise to conserve water, reduce plant stress at localized positions, and reduce nutrient leaching and drainage.

Trials in New Zealand have shown that water savings are typically between 10% and 25% where variable soils occur under one system, and further savings are made by excluding irrigation from tracks, waterways, yards, sheds, and other unproductive areas (Hedley and Yule, 2011).

Management systems being developed alongside these precision irrigation systems include EM mapping to derive management zones with real-time soil moisture monitoring within each zone. The Valley VRI system uses CropMetrics, a system that derives EM and landscape change layer to identify

water-holding capacity variability across the field. These data layers are delivered through a 'Virtual Agronomist,' where the degree of field variability is used to decide on irrigation management strategies. The amount of variability relates to the amount of opportunity present, that is, the higher the variability the greater the opportunity for variable rate to benefit. Varying application rates increase input efficiency and improve yield production.

Findings from a modeling study by Hedley and Yule (2009) at five case-study sites in New Zealand found that where soil available water-holding capacity varied by 50 mm under one irrigation system then the potential water savings were approximately 10%, and variation by >100 mm gave a potential water saving of $\geq 15\%$. Savings are potentially greater in humid temperate regions (where some rainfall occurs during the irrigation season) in comparison with arid regions, where the main benefit of VRI for variable soils is a staggered start to irrigation at the beginning of the irrigation season, plus different watering strategies for soils of contrasting textural and drainage properties. Research has also been conducted to introduce wireless soil moisture sensor networks into EM and landscape-derived management zones for provision of real-time digital soil moisture information to the VRI controller. VRI control is established on-site or remotely through a software package with internet or cellular connection.



Figure 15 Variable rate irrigator, with sprinklers switched off as the irrigator crosses a farm track, saves water and reduces lameness risk in dairy cows. Photo: C.B. Hedley.

Smart phone applications are being derived for irrigation control and management, which is often more suited to operational farmer use, than a computer sitting back in the farm office. The WaterBee system has been developed in Europe independently from a VRI system, and is the result of a project undertaken by a team of 10 partners from eight European countries targeting a sustainable solution to contribute to reducing freshwater use by the agricultural sector. WSNs send readings to a soil-moisture model that automatically adapts irrigation requirements to different irrigation installations, and it is suggested that this WaterBee system will achieve real water savings while enhancing crop quality.

The importance of scale in precision irrigation

One of the most important areas that may be ignored or oversimplified in precision irrigation is in choosing an appropriate scale at which variable rate (or other) technologies should be implemented. It is quite feasible to map spatial soil variabilities and crop canopy differences at high resolution, and to engineer an application system to apply water variably. However, it is much more difficult to explain scientifically the reasons for underlying heterogeneity in crop growth and link this with confidence to decisions on variable water application. Deciding on the appropriate scale for applying water needs to be informed by a thorough understanding of the consequences of soil and crop variability on yield. Advances in precision agriculture thus need to be integrated with equivalent knowledge in precision irrigation to identify the appropriate scale(s) for system implementation. Although it may be technically and practically possible to apply water variably, it may not be economically beneficial or agronomically sensible (see Table 1).

Other Advanced Irrigation Developments

Section Overview

This section provides an introduction to a selection of other advanced irrigation technologies including the modernization

Table 1 Spatial scales of common irrigation systems

System	*Spatial unit*	*Order of magnitude of spatial scale (m^2)*
Surface – furrow	Single furrow	1000
Surface – furrow	Set of furrows	50 000
Surface – bay	Bay	10 000–50 000
Sprinkler – solid set	Wetted area of single sprinkler	100
Center pivot, lateral move	Wetted area of single sprinkler	100
LEPA[a] – bubbler	Furrow dyke	1
Traveling irrigator	Wetted area of single sprinkler	5000
Drip	Wetted area of an emitter	1–10
Microspray	Wetted area of a single spray	20

[a]Abbreviation: LEPA, low-energy precision application.

Source: Smith, R.J., Raine, S.R., McCarthy, A.C., Hancock, N.H., 2009. Managing spatial and temporal variability in irrigated agriculture through adaptive control, Australian Journal of Multi-Disciplinary Engineering 7 (1), 79–90.

of irrigation district networks and the use of smart meters to improve the monitoring of water usage at the farm and field levels. Selected on-farm irrigation technologies to improve crop water productivity using partial root zone drying (PRD) and deficit irrigation strategies, vision sensing of crop responses for irrigation management, and the application of fertigation and chemigation are also discussed.

This section covers the following aspects:

- modernization of irrigation district networks,
- smart water metering,
- PRD and RDI,
- applied machine vision of plants for irrigation management, and
- fertigation and chemigation.

Modernization of Irrigation District Networks

The modernization of irrigation districts often involves converting the water distribution network from intermittent to 'on-demand' water supply for farmers. On-demand irrigation schemes supply water to the farm via either gravity-fed channels or pressurized pipe networks. The conveyance efficiency of pressurized pipe networks are normally significantly greater (of order 30%) than for channel systems. Pressurized water at the farm gate also provides farmers with an incentive to convert existing on-farm surface irrigation systems to potentially more efficient sprinkler or microirrigation systems.

The change from intermittent to on-demand water supply has implications not only for water use efficiency but also for irrigated crop productivity and energy usage. For example, although modernization of irrigation districts in Southern Spain has reduced the amount of water diverted to farms for irrigation, consumptive water use has increased, mainly due to a change in crop rotation (Rodriguez-Diaz *et al.*, 2011). However, in this area, the costs for system operation and maintenance have increased dramatically ($\sim$400%), primarily due to increasing energy consumption for pumping (Rodriguez-Diaz *et al.*, 2011).

In Southern Australia, Jackson *et al.* (2010) found that conversion to pressurized irrigation methods reduced energy consumption in regions where groundwater is used, the result of an increase in efficiency of water use. They also suggested that conversion of on-demand gravity-fed systems into pressurized networks is generally not appropriate where surface water supply is available. In these cases, regional investments should focus on improving the volumetric efficiency of the channel network and avoid increased energy requirements (Jackson *et al.*, 2010). However, in the Harvey Irrigation district in Western Australia (Harvey Water, 2012), the availability of elevated surface water dams close to lower elevation farms has provided the opportunity to convert a channel distribution system into a pressurized piped network that does not require pumping. Here, increased volumetric distribution efficiencies have provided water for alternative uses, whereas the delivery of low-cost pressurized water on farm has enabled the conversion of irrigation application systems and the establishment of higher value horticultural crops.

The service performance of water supply schemes is a function of the scheme and component capacities as well as the irrigation demand. Perez-Urrestarazu *et al.* (2009) observed that on-demand systems should be designed to deliver water with flow rates and pressures required by on-farm irrigation systems, taking into account the time, duration, and frequency as defined by the farmers. However, due to the probabilistic nature of users irrigating simultaneously (Anwar *et al.*, 2006) these systems are often designed with excessive distribution capacity, making them more expensive than intermittent systems (Planells-Alandi *et al.*, 2001). Similarly, pump-pressurized, on-demand systems are commonly designed and operated to supply the target pressure in each component of the pipe network irrespective of the water supplied. Sectoring, where farmers are organized to use water in turns, has been shown (Carrillo Cobo *et al.*, 2011) to be one of the most effective methods of reducing energy consumption in pressurized, on-demand irrigation networks. Computational tools involving integrated geographic information systems, real-time monitoring, and modeling of hydraulic data with decision support systems are also being used (e.g., Perez-Urrestarazu *et al.*, 2012) to improve the operational performance of pressured irrigation networks.

An alternative approach has been taken in the modernization of the open-channel delivery systems in Southern Australia. Here the decision was made to retain the open earthen channels and to seek the efficiency gains through automation along with rationalization of the network involving retirement of some smaller channels and some limited gravity pipelining and channel lining to reduce seepage losses. The classical ideas from system identification and control are used to automate the channels to provide a near on-demand system (Mareels *et al.*, 2003, 2005; Cantoni *et al.*, 2007). This system has been implemented under the name of Total Channel Control® and has resulted in distribution efficiencies in excess of 90% compared with the efficiencies of 70–75% typically achieved under manual control (see **Figure 16**).

Smart Water Metering

Knowing the amount of water being used and where it is used are important elements associated with practicing efficient irrigation. Typical pressurized irrigation farms are characterized by complex hydraulics due to numerous pipe fixtures and modifications that occur over time, and variable irrigation block flow delivery due to poor design and setup. Where flow monitoring occurs, it is often conducted by manual readings of a water meter at irregular intervals.

Smart irrigation metering involves the assessment of unique hydraulic characteristics at the source of a delivery system with multiple outlets (Pezzaniti, 2009). This requires an ability to record and automate analysis of high-frequency flow and pressure sensor data and allows not only for the continuous monitoring of water consumption but also for the identification of individual irrigation valve operation. Smart water meters have the following attributes (Giurco *et al.*, 2008): real-time monitoring, high-resolution interval metering ($\geq$10 s), automated data transfer (e.g., drive by, GPRS, and 3G), and access to data via the internet or SMS. Most modern mechanical and electronic water meters and pressure sensors have features (e.g., pulse output) that allow flow to be monitored or logged. Hence, the implementation of smart water meters for monitoring on-farm irrigation typically



(a) (b)

Figure 16 Modernization of open-channel delivery in Australia provides a near on-demand system. Photos: Michael Kai courtesy Rubicon Water.

involves the addition of a datalogger and communications to a traditional water meter and pressure sensor.

Coupling the identification of valve operation with the measured meter flows makes it possible to disaggregate the water flow so that any component within an irrigation system can be identified. This enables the flow and total volume applied to each irrigation block within the system to be recorded, providing comparative data for both the assessment of irrigation efficiency and the identification of maintenance and operating issues (e.g., pump wear, filter blockages, pipeline leaks, and emitter variations). The water use information obtained may be used to improve irrigation design and practice. Similarly, the subsequent analysis of smart water meter data can be automated and integrated with controllers to optimize water, energy, and maintenance requirements.

Partial Root Zone Drying and Regulated Deficit Irrigation

PRD and RDI strategies involve manipulating the placement of irrigation water and moisture deficit within the root zone to increase crop water use efficiency. The major differences between PRD and RDI are associated with the nature of the localized soil moisture and plant water status conditions (Ruiz-Sanchez *et al.*, 2010). Both hydraulic and biochemical signals are involved in regulating stomatal and plant growth rates in response to changes in the abiotic environment (Chalmers *et al.*, 1981; Davies and Zhang, 1991). PRD involves creating alternate drying and wetting of subsections of the plant root zone (**Figure 17**) to elevate biochemical signaling while maintaining plant water status (Loveys *et al.*, 2000; Stoll *et al.*, 2000; Dodd *et al.*, 2006). Hence, PRD strategies maintain plant water status and create a favorable physiological response through elevated biochemical signaling. RDI involves reducing the moisture availability throughout the entire plant root zone resulting in a reduced plant water status (Kriedemann and Goodwin, 2003). RDI improves crop WUE by maintaining plant water status within the prescribed limits of deficit with respect to maximum water potential (Kriedemann and Goodwin, 2003).

PRD strategies attempt to maintain water availability and plant water status simultaneously while elevating the biochemical signaling (increasing ABA levels and alkalization of sap pH) within the plant. The elevated ABA has been found (Loveys *et al.*, 2000; Stoll *et al.*, 2000) to coincide with a partial reduction in stomatal conductance and a differential effect on vegetative and reproductive production (Davies *et al.*, 2000), both of which lead to an improvement in crop water use efficiency for fruiting crops.

Practical limitations in the successful application of PRD and RDI are related to the soil hydraulic properties, volume, and frequency of irrigation water applications, and the occurrence of in-season rainfall. PRD and RDI strategies are difficult to apply in furrow irrigation systems and PRD is also difficult to implement under sprinkler irrigation systems. However, both PRD and RDI may be implemented using drip irrigation and precision applicators on large mobile irrigation machines. White and Raine (2009) suggested that the creation of a soil moisture gradient across the plant root zone large enough to trigger a PRD response is most likely to be achieved

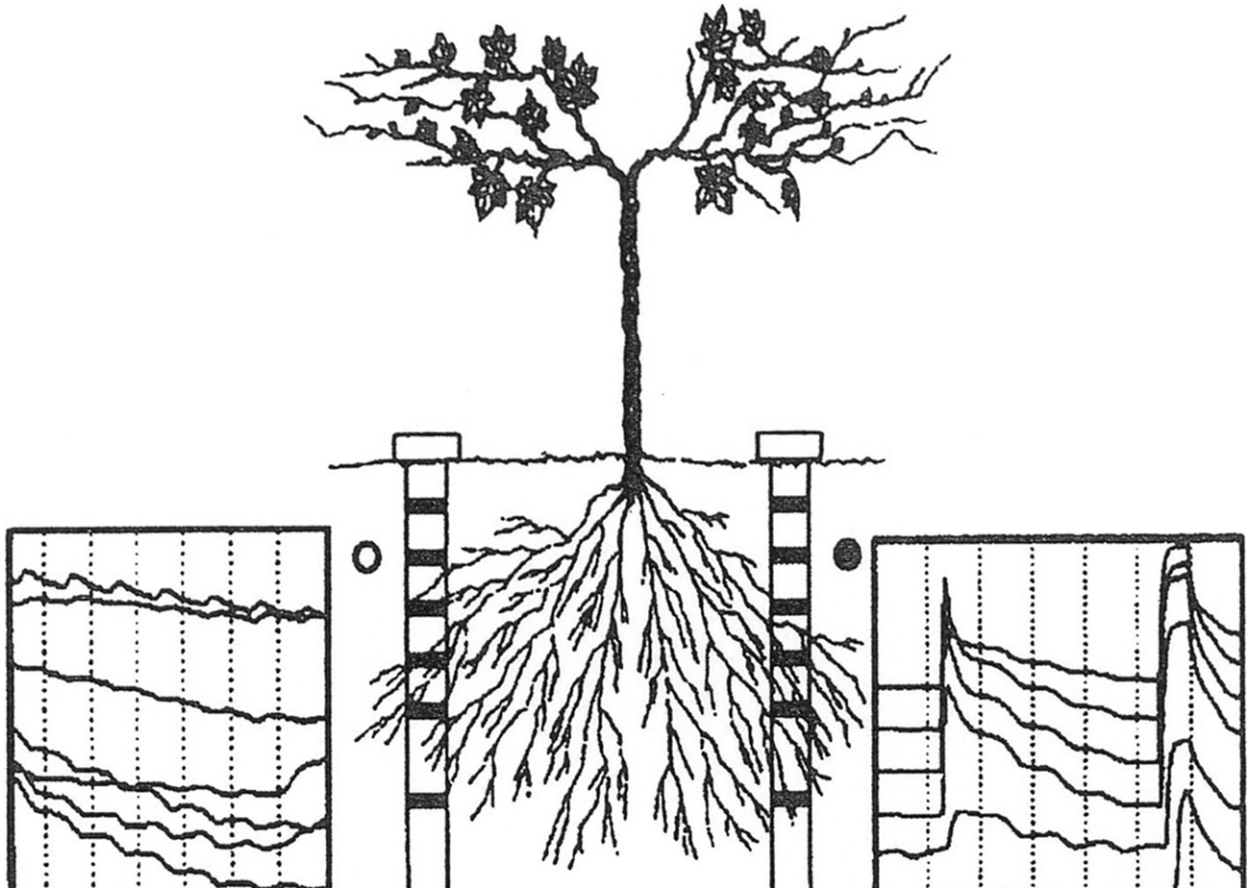


Figure 17 PRD in grapevines. Subsurface drip lines supply water to one side or the other of the vine. In this diagram water is supplied through two irrigation cycles to the right hand line. The water content of the soil at various depths is shown as output from Enviroscan sensors. Although the soil around the right hand sensor wets and dries in response to the irrigation, the soil on the left hand side of the vine continues to dry. Reproduced from Loveys, B.R., Grant, W.J.R., Dry, P.R., McCarthy, M.G., 1997. Progress in the development of partial root-zone drying. Australian Grapegrower and Winemaker 403, 18–20.

on light-textured soils located in semiarid regions that experience minimal in-season rainfall events.

RDI is particularly useful in controlling vegetative growth and increasing fruiting in indeterminate crops (e.g., cotton). For example, White (2006) found RDI (79% of predicted ET) of cotton under field conditions produced a 31.5% improvement in crop water use productivity over commercial practice (i.e., applying 100% of predicted ET). However, the largest benefits derived from deficit irrigation were associated with the management of crop agronomy (i.e., vegetative growth, fruit retention rate, and crop earliness) and the increased utilization of in-season rainfall.

Applied Machine Vision of Plants for Irrigation Management

The automated visual assessment of plant condition, specifically foliage wilting, reflectance, and growth parameters, using machine vision has potential use as input for real-time VRI and fertigation systems in precision agriculture. Crop-sensing tasks that have been successfully demonstrated using machine vision in outdoor conditions include automated identification of weed species (Slaughter *et al.*, 2008), nitrogen status (Noh *et al.*, 2005), plant size (Shrestha and Steward, 2005), and multispectral properties using narrow band imaging (e.g., Carter and Miller, 1994). McCarthy *et al.* (2010) have reviewed the use of applied machine vision for plant sensing in irrigation applications.

Farm managers typically include visual assessment of crop condition to inform management decisions (e.g., irrigation timing) and treat the whole field uniformly based on their manual observations. For example, internode length measurement (i.e., the distance between branch junctions, **Figure 18**) is part of a plant-based water stress monitoring regime for cotton suggested for growers (Milroy *et al.*, 2002). A machine vision system with access to a large proportion of the field potentially enables automatic condition assessment for different plants at high spatial frequency in the field. Such sensing capability, in conjunction with the implementation of appropriate variable-rate application hardware, enables agricultural fields to be treated as a conglomerate of control units for operations such as irrigation and fertigation (e.g., Smith *et al.*, 2009).

The design of a vision system for the measurement of plant attributes is affected by many factors, including the scale of the plant measurement (i.e., leaf- or canopy-level) and the measurement environment (e.g., a laboratory or in the field).

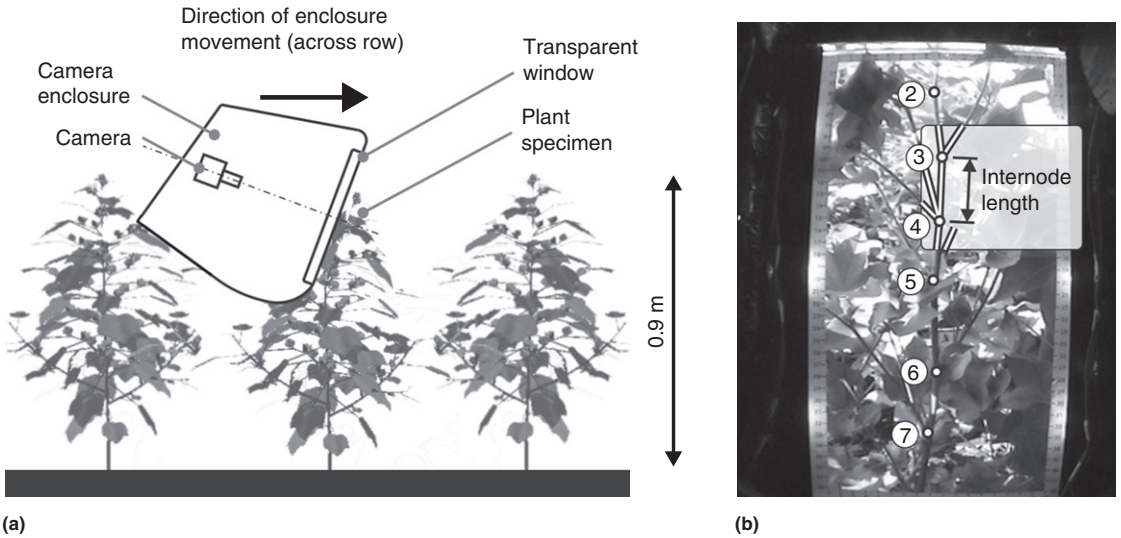


Figure 18 (a) Moving image capture apparatus; and (b) stylized sample image from apparatus, with main stem nodes numbered. Reproduced from McCarthy, C.L., Hancock, N.H., Raine, S.R., 2009. Automated internode length measurement of cotton plants under field conditions. Transactions of the ASABE 52 (6), 2093–2103; Cotton plant graphic adapted from University of Hamburg, 1998. Virtual Plants. Available at: http://www.biologie.uni-hamburg.de/b-online/virtualplants/ipivp.html (accessed 19.10.12).

Automated machine vision sensing of individual plants in the field is presently limited to early stage crops (where neighboring plants are too small to touch or overlap), or, for more mature canopies, to whole-plant characteristics such as plant biomass. The use of near-infrared (NIR) imaging, background boards, and shade structures with artificial illumination reduces the complexity of the segmentation process but adds extra components and potentially physical bulk to the overall measurement system. In the indoor environment, a monocular vision system can identify small canopy changes for irrigation scheduling purposes.

Identification of plant structure using stereo vision enjoys greater success for smaller plants. Applications in the outdoor environment typically provide overall canopy geometry, which is useful for monitoring crop growth in areas of a field or identifying plant height changes, for example, between different species (i.e., weed and crop). Determination of leaf and branching structure of individual plants is currently limited, even in indoor environments, and relies on the image having a plain background. Knowledge of plant growth patterns (e.g., phyllotaxis) potentially assists measurement by image analysis.

The sensing and image analysis task may be simplified by imaging only in that part of the electromagnetic spectrum that accentuates features of interest more effectively than the broad visible bands provided by standard RGB cameras. Sensing of different regions of the electromagnetic spectrum potentially enables discrimination of plant materials based on color (visible), cellular structure (NIR), thermal (mid-infrared), or hardness (X-ray) properties.

Machine vision systems for field use must be designed to be robust to sunlight variations (Slaughter *et al.*, 2008). Active sensing systems are less susceptible to ambient sunlight than passive sensing systems. However, low-cost (passive sensor) cameras with simple imposed illumination may also have reduced dependency on sunlight (e.g., Edan *et al.*, 2000).

Attaching a machine vision system to the gantry of a center pivot or lateral move irrigation machine potentially enables crop condition to be measured in real-time as the irrigation machine moves across the field (e.g., Colaizzi *et al.*, 2003; McCarthy *et al.*, 2009). Alternatively, tractor-mounting of the system may be desirable, so assessments can be made as the tractor moves alongside the field. On-the-go in-field sensing of geometric crop plant parameters is currently limited to leaf shape identification and biomass estimation in the foliage of small plants, or plant height and biomass estimation in fully developed canopies. To measure plant leaf-level attributes (e.g., internode length and leaf shape) in maturing field plants requires the design of a robust outdoor machine vision system that achieves a detailed structure sensing. These systems have so far only been reported for automated laboratory or greenhouse systems on a limited number of crops under controlled lighting and environmental conditions.

Fertigation and chemigation

Efficient nutrient and chemical use in agriculture involves accurate spatial and temporal placement of the applied fertilizer or chemical. Fertigation involves supplying dissolved fertilizer to crops through an irrigation system (Bar-Yosef, 1999). Although fertigation has the advantage of being able to accurately apply fertilizer, liquid application of ammoniacal fertilizers can lead to deleterious drops in soil pH (Stork *et al.*, 2003), because roots release hydrogen ions to take up ammonium ions, and this should be considered when fertigating with these compounds. Fertigation is commonly applied using both surface and pressurized irrigation application systems. When combined with an efficient irrigation system, both nutrients and water can be manipulated and managed to maximize marketable yield and nutrient efficiency (New South Wales Dept of Primary Industries (NSW DPI), 2000). Soluble

inorganic nutrients are normally used for fertigation but the application of humic substances via fertigation systems has also been found (Selim and Mosa, 2012) to increase root zone moisture holding capacity in sandy soils and increase crop productivity.

Chemigation in broad-acre crops is most commonly applied by large mobile irrigation machines (i.e., center pivots or linear moves). Herbicides, insecticides, and fungicides may be injected into the main irrigation water pipe for distribution through the irrigation emitters (e.g., Quad-Spray, Senninger Irrigation Inc., Clermont, FL, USA) with the water. Alternatively, chemigation may be conducted using a separate system of distribution pipework with spray heads suspended underneath the irrigation machine truss rods to enable the application of chemical either with or without irrigation water (Foley and Raine, 2001).

The efficiency of fertigation and chemigation strategies is highly dependent on the performance (i.e., uniformity) and management of the irrigation system. Fertigation uniformity in microirrigation systems is primarily a function of emitter discharge uniformity where the fertilizer is injected during the middle third or half of the total irrigation time (Hanson *et al.*, 2006). Fertilizers injected into water applied to furrow irrigation systems are similarly affected by the nonuniformity of the applied water, with efficiencies often low due to percolation losses at the head end of the field and tailwater runoff losses. Simulation models combining the overland water flow (Saint-Venant equations), solute transport (advection–dispersion), and infiltration have been developed (Perea *et al.*, 2010; Burguete *et al.*, 2009) to evaluate and optimize the application of fertilizers in furrow irrigation systems. Modifying the water inflow hydrograph to improve the uniformity of water application and reducing tailwater runoff has been found to improve both nutrient uniformity and efficiency (Moravejalahkami *et al.*, 2012). Similarly, using alternative furrow irrigation strategies has also been found (Ebrahimian *et al.*, 2012) to increase lateral water movement, reducing water and nitrate losses via runoff and deep percolation.

Decision support systems are increasingly being used (e.g., Incocci *et al.*, 2012) to identify optimal fertigation requirements based on crop growth and environmental conditions. Site-specific fertigation of zones within conventional pressurized irrigation systems may be achieved by the installation and control of separate injection facilities for each zone. However, implementation of separate systems to date has been limited because of the expense and control complexity (Coates *et al.*, 2012). Where a centralized injection facility is used, the selection of the optimum injection strategy will be a function of the crop needs, scheduling limitations, and system design parameters including emitter type, fluid distribution system travel time, and field slope (Coates *et al.*, 2012).

Future Directions – Emerging Risks, Technical Challenges, and Future Developments

Section Overview

Despite concerns regarding international food security, and the drive to support sustainable intensification, agriculture still faces a number of challenges that are likely to hamper any widespread uptake of advanced technologies, including precision irrigation. This section identifies the emerging risks and 'drivers for change,' highlights the environmental and technical challenges constraining innovation in precision irrigation, and briefly considers selected novel technologies on the horizon that will support the future sustainability of irrigated agriculture and horticulture.

Emerging Risks

In most countries, agriculture provides significant societal benefits, by making important contributions to national economies and underpinning rural employment. Although the most obvious contribution is probably in the production of 'food' and 'nonfood' crops, agricultural ecosystems also provide other services, including regulation of air quality, climate, and water purification. Agricultural land delivers nonmaterial cultural benefits such as land for recreation and valued characteristic landscapes, supporting habitats, wildlife, biodiversity, and ecosystem services. The importance of agricultural land, including irrigated croplands, therefore goes far beyond food production – the future actions of farmers can thus have positive or negative effects on these services, all of which are likely to be affected by climate change.

Climate impacts on irrigated production

Internationally, agriculture is regarded as one of the sectors at most risk from a changing climate, due to the impact of increased temperatures, reduced rainfall, and increased frequency of extreme events, not only in the tropics but also in humid and temperate environments (Falloon and Betts, 2010; Knox *et al.*, 2012). Outdoor rainfed and irrigated crops are particularly sensitive, both directly from changes in rainfall and temperature and also indirectly, as any change in climate will also impact on the agricultural potential of soils by modifying soil water balances and changing land suitability for production (Daccache *et al.*, 2012). These changes will in turn affect the availability of water to plants and impact on other land management practices (e.g., trafficability for seedbed preparation, spraying, and harvesting) including the demand for irrigation (Daccache *et al.*, 2011). In regions where rainfed agriculture is dominant, changes in the timing, distribution, and reliability of rainfall may force a gradual switch to irrigated production, to maintain crop yields. Here precision irrigation could become important, particularly for supplemental irrigation. By combining better weather forecasting techniques to make better use of effective rainfall with, for example, VRI, the negative impacts of agroclimate uncertainty on crop yield and quality could be reduced.

Farmers also face a range of 'nonclimate' risks that potentially represent a more immediate threat to sustainable food production than climate change. Most notable is the increasing burden of environmental protection and its consequent impacts on water resources (both supply and allocation) for irrigated agriculture (Knox *et al.*, 2010). However, investment in advanced precision irrigation technologies still requires consistent and reliable supplies of water.

Demands for greater environmental protection

Governments and society are seeking greater levels of environmental protection. In irrigated agriculture, probably the greatest short-term risks relate to the impacts of new water regulation. For example, in Europe, a number of new directives have recently been enforced, including the Water Framework Directive (WFD 2000/60/E). Despite its title, the WFD is as much about land management as it is about water management. It is the most substantial legislation produced by the European Commission and provides the major driver for sustainable management of water across Europe. By 2015, it requires that all inland and coastal waters within defined river basins reach at least 'good status' and defines how this should be achieved through the establishment of environmental objectives and ecological targets for surface waters. The WFD applies to all waters to tackle diffuse source pollution, ranging from fertilizer and pesticide applications on rainfed and irrigated land to urban runoff. In agriculture, the dependence on fertilizers and pesticides means that many farms may be subjected to much greater levels of surveillance to ensure that diffuse pollution from cropped areas is not contributing to water quality degradation. Irrigated agriculture is widely viewed as a key target for improvement. Similar pressures on irrigated farming are known to exist in other continents including the US and Australasia.

However, the rising costs for fertilizer (and energy for water pumping) are themselves acting as an industry brake, with many irrigated farms actively seeking new measures to reduce fertilizer inputs and water use. Collectively, these may provide a positive indirect response to water regulation and drive the uptake of precision irrigation technologies. These could help reduce nitrate leaching risks, nonbeneficial losses of water off-farm, and levels of energy consumption (and hence carbon footprint) for irrigated production.

Although most environmental regulations are implemented at the river basin or catchment scale, their impact will be felt at the farm level, particularly when irrigated farms are located in water-stressed catchments or in proximity to internationally protected habitats or environmentally designated sites. Under these conditions, precision agriculture practices, including irrigation, could again help reduce some of the impacts of agricultural water abstraction on local habitats and the risks associated with nitrate leaching to the environment.

Finally, farms in the future may be subjected to increasing levels of monitoring and scrutiny (traceability) to demonstrate compliance with national and international regulation. Precision irrigation technologies will undoubtedly have an increasing role in demonstrating 'best practice' in irrigation management. In this context, technologies that target water applications both spatially and temporally, taking into account heterogeneities in soil moisture, crop development, and climate, are likely to be viewed positively by environmental regulators. In parallel, changes in water regulation are exposing irrigated farms to new water supply risks.

Competition for water resources

Internationally, irrigated agriculture faces rising competition for access to reliable, low-cost, and high-quality water. In Northern Europe, for example, farmers are under increasing regulatory pressure to improve irrigation efficiency; indeed, demonstrating 'efficient' water use is a prerequisite for renewing an abstraction license (permit) (Knox *et al.*, 2012). In Mediterranean Europe, where irrigated agriculture accounts for approximately 60% of all abstractions (OECD, 2012), production is at risk due to increasing water scarcity and competition for scarce resources (Wriedt *et al.*, 2009). In some countries, abstraction regimes are in place, but in others new frameworks for regulation, including those for irrigation control are being implemented. Within these frameworks, higher levels of water efficiency will inevitably be required. Precision irrigation, often only considered in the form of drip (or trickle) irrigation, is often seen by water regulators as being 'good' for the environment. Other forms of precision and VRI will no doubt be encouraged.



Figure 19 Overhead irrigation on iceberg lettuces using a modified mobile hosereel fitted with a boom. Before harvest, the sprinklers are replaced with drop tubes to avoid soil splash impacting on crop quality. Photo: J. Knox.

In many catchments where irrigated agriculture is concentrated, rising demand for water between different sectors (notably, agriculture, public/domestic supply, and industry) coupled with reduced allocations to meet environmental flows means that allocations for irrigation are becoming less reliable and more expensive. The situation is exacerbated by examples where irrigated agriculture is cited as being the primary cause of environmental damage and overabstraction, mainly during the summer months when river and groundwater levels are at their lowest and irrigation demands peak.

In future, farmers will need to demonstrate more efficient and sustainable use of water to secure rights (licenses/permits) for irrigation abstraction. Technical measures such as switching from sprinkler to micro (drip)-irrigation are often promoted by industry and the regulator to reduce the environmental impact of abstractions and increase water efficiency. Replacement of overhead irrigation sprinklers with drop tubes is an example of system modification to efficiently deliver irrigation to the root zone of a salad crop, also minimizing soil splash onto the plant, to reduce the amount of washing required during the processing stage (Figure 19). However, any environmental gain may be limited if more efficient techniques such a precision irrigation do not result in a reduction in net water use, but simply support an increase in irrigation command. Any water 'saved' via precision irrigation could be reallocated to other crops; the

environmental impact could thus be negative not positive, due to reduced return flows from previously 'inefficient' irrigation (Hedley and Yule, 2008; Perry *et al.*, 2009).

Drivers for Change

Development of innovative approaches to combine better spatial and temporal knowledge of soil, crop, and equipment management practices to reduce variability in crop yield and quality through advanced irrigation technologies is a major 'driver for change,' whether driven by consumer (market), regulatory, and public demands for greater environmental sustainability.

To maintain output, agriculture has intensified and become much more specialized, and for many farmers, investment in irrigation has provided the basis to maintain or increase profitability. For example, in high-value cropping, irrigation is not a marginal activity used to boost yield, but an essential component of production to deliver premium quality, continuous supplies of produce to processors and retailers. It has also become a prerequisite for meeting the increasing market demands for quality and continuity of supply. Despite this external driver, irrigation of field crops in many parts of Europe and elsewhere has changed relatively little over the last few decades. However, with rapidly rising labor and energy costs, farm businesses are now assessing the impacts of irrigation variability (nonuniformity) on crop yield and quality much more proactively (see e.g., **Figures 5**, **6**, **15** and **19**). This is because the quality assurance benefits of irrigation can be substantial and relate to the whole crop, not just to the extra marginal yield due to irrigation. Quality criteria are increasingly specified as a condition of contract and sale, and failure to meet quality requirements can lead to large price discounting, and possibly rejection and loss of contract.

Over the past decade, grower or crop assurance schemes have also played an important part in driving water efficiency in irrigation and supporting uptake of advanced irrigation technologies. These schemes require growers to audit their irrigation systems and provide traceability and accountability in support of public health and environmental protection regulation. These schemes have also provided the basis for growers to comply with industry protocols for food safety and crop assurance (Monaghan and Hutchison, 2012).

In the future, water cost is likely to become a major driver for change – not necessarily the unit cost for securing access to a water supply, but more likely the energy costs associated with conveyance and pressurized delivery of in-field irrigation. With increased attention to water conservation during drought spells, competition from environmental, recreational, public/domestic use, and regulatory constraints, the current economics of VRI, which are proving a deterrent to investment, may well change (Sadler *et al.*, 2005; Hedley and Yule, 2009).

Future Developments

Combining wireless technologies with variable rate application

On most farms, making maximum use of soil moisture and rainfall, knowing precisely where and when irrigation has to be applied, and then applying it accurately and uniformly are the fundamental steps in the pathway to water efficiency (Knox *et al.*, 2012). Although irrigation is an essential component of production to maximize yield in arid and semiarid regions, there is growing evidence that optimized irrigation regimes under temperate and humid conditions can also lead to improved postharvest quality resulting in reduced crop waste through the food supply chain. However, at present most farmers are restricted in their ability to match the timing and frequency of irrigation applications to inherent spatial and temporal variations in soil moisture and crop growth. They generally have only limited information on plant water status, rely on limited *in-situ* point measurements of soil as a proxy for field-scale soil moisture availability, and use conventional irrigation systems that lack sufficient flexibility and technology (control) for variable water application.

However, developments in crop and soil moisture sensing, coupled with wireless telecommunications for in-field soil moisture monitoring and thermal imaging, now provide opportunities to develop smarter, closed-loop systems capable of applying water variably both across and along fields. Most research to date has focused on developing such technologies for use under sprinkler (center pivot and linear move) irrigation systems. The potential for VRI using individually controlled solenoid valved sprinklers, similar to those used in the sports turf (golf) industry, is also now being evaluated in high value horticulture, where sprinkler irrigation is still the preferred method of application.

Digital advances in cloud computing and remote sensing

Alongside innovations in irrigation systems and soil moisture monitoring, digital advances using the latest cloud computing technologies are also moving swiftly into precision agriculture. Put simply, cloud computing involves using networks of remote servers hosted on the internet to store, manage, and process data, rather than hosting information and data on local servers. They generally rely on wireless data transfer and mobile web applications, in combination with other tools and spatial technologies including GPS and GIS. Cloud technology is well established within data-intensive industries, but only recently emerging in agriculture where various applications are being marketed. For example, in the USA, cloud services provide on-farm support from agribusinesses and consultants, for agrochemical application management. Other precision-related tools are now emerging.

New uses relating to precision irrigation could include applications for mobile devices operating in the cloud to spatially monitor soil moisture, crop growth, and irrigation in real-time via in-field sensor arrays. Other cloud uses include providing data to refine planting and harvest operations, by integrating GPS and GIS data or managing equipment performance (pressures, flow rates, abstractions) at district or catchment scales. RFID tags, which automatically download data, are also becoming more widespread in agriculture. For example, tagging systems have been developed to collect data on the moisture content of straw bales, weight, and in-field position (GPS); in the future, similar cheap, possibly biodegradable, microtags could be deployed across fields to measure seasonal changes in soil moisture, organic content, crop canopy development, and canopy stress, or for

monitoring and optimizing energy needs across pressurized irrigation distribution networks (Carrillo Cobo *et al.*, 2011). However, data security issues relating to confidentiality, integrity, availability, and accountability still need to be resolved before cloud technology can be fully integrated into precision irrigation.

There is also increasing potential for new applications linking the use of high-resolution and -frequency remote sensing data (e.g., MODIS) to inform on-farm irrigation management, including mapping croplands, and monitoring spatial changes in crop cover in support of farm monitoring of irrigation water use and evapotranspiration (ET) (Thenkabail *et al.*, 2012). Recent remote sensing developments provide scope for mapping croplands in a routine, rapid, and consistent way, with sufficient accuracy (Congalton and Green, 2009). There is also potential to use remote sensing to identify irrigated regions, where improvements in water productivity should be targeted to reduce 'yield gaps' (Fereres *et al.*, 2011). By integrating advanced technologies such as cloud computing with developments in precision irrigation and remote sensing, there is also broader scope to improve one's understanding of the links between food production and water scarcity, and the impacts of climate change on food supplies.

Summary

In the future, committed efforts will be needed to implement advanced irrigation technologies that are appropriate for different types of farming systems to improve both water and energy efficiency while maintaining or improving crop yield and quality. Considering the demands on natural resources, precision irrigation is likely to play an increasingly important role, but a number of factors remain important. These include the changing economics of irrigation, the rising cost of energy, the increasing importance of crop assurance, and the role of retailers (supermarkets) in influencing consumer attitudes and behavior toward quality assurance and fresh produce.

The uptake of precision irrigation is likely to be slow and dependent on appropriate support systems and knowledge transfer to engage farmer support and trust. Insufficient recognition of field variability, the lack of a whole-farm approach, limited knowledge of the links between crop quality and precision irrigation, and the alignment of crop assurance schemes with environmental auditing will all need to be resolved.

The way forward for precision irrigation seems to mirror observations from precision agriculture. Here the key has been to keep the farmer's perspective central to the objective. Farmer needs, of course, vary depending on the agricultural system (e.g., intensive horticulture vs. extensive broad-acre cropping), the scale of business (e.g., family farm vs. agribusiness), underlying agroclimatic conditions (e.g., arid vs. humid), and many other socioeconomic factors (e.g., attitudes to risk, etc.). The tacit knowledge of farmers is thus critical.

New farm-scale precision equipment assists farmers to fine-tune the existing management procedures, but requires the accompanying decision support tools to monitor and adapt this new level of control.

Such technologies can be carefully positioned to fill specific (and crucial) gaps in the existing irrigation toolkits using the tacit knowledge of farmers (McBratney *et al.*, 2005) to assist improved farm-scale irrigation practice.

The limited opportunity to increase global freshwater allocations for irrigation (OECD, 2012) will require collective initiatives beyond the farm gate to optimize regional-level tradeoffs. These include tradeoffs between improved water use efficiency of modern pressurized systems versus their greater energy consumption; as well as tradeoffs between the best use of irrigation to meet global food demands and the pressing need to maintain the multiple ecosystem services that global freshwater resources provide.

See also: Climate Change: Agricultural Mitigation. Climate Change and Plant Disease. Climate Change: Cropping System Changes and Adaptations. Climate Change, Society, and Agriculture: An Economic and Policy Perspective. Food Security: Food Defense and Biosecurity. Food Security, Market Processes, and the Role of Government Policy. Food Security: Postharvest Losses. Food Security: Yield Gap. Precision Agriculture: Irrigation. Virtual Water and Water Footprint of Food Production and Processing. Water Use: Recycling and Desalination for Agriculture. Water: Water Quality and Challenges from Agriculture. World Water Supply and Use: Challenges for the Future

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Water Use: Recycling and Desalination for Agriculture

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Glossary

Biochemical oxygen demand The amount of dissolved oxygen needed by aerobic biological organisms in a body of water to break down organic material present during 5 days of incubation at 20 °C (BOD_5).

Desalination Technological process that allows the removal of salt and other minerals from saline water to produce freshwater suitable for human consumption and agricultural or industrial use.

Drainage water The water naturally or artificially removed at surface or subsurface from an agricultural area and that contains chemicals, mainly salts leached from the soil.

Refractory organic chemicals Organic compounds, either natural or synthetic, that are resistant to being broken down through conventional treatment processes.

Sodium adsorption ratio (SAR) A measure of the sodicity of soil, hence of the suitability for use in irrigation and is determined from the ratio of the concentrations of the Na^+ ion relative to those of the Ca^{2+} and Mg^{2+} ions.

Water reclamation Treatment or processing of wastewater to make it reusable.

Water recycling The wastewater after appropriate treatment is redirected back to its original use.

Water reuse The use of treated wastewater for beneficial purposes such as agricultural use.

Water scarcity A situation when water availability in a country or in a region is below 1000 m^3 per person per year. Water scarcity refers to various regimes affecting water availability: Natural aridity and drought, and man-made water scarcity and desertification.

Introduction

Global socio demographic and environmental change poses unprecedented challenges to mankind. Drivers of global change such as climate change, population growth, urbanization, industrialization, and rising income, living standard, and energy demand will all characterize the future demand for water. Population growth and water scarcity also drive the need to the use/recycling of nonconventional water resources, mainly saline and drainage waters, treated wastewater and desalinated water for irrigation and other uses in many countries (Pereira *et al.*, 2009; Wichelns and Drechsel, 2011; Hanjra *et al.*, 2012).

The use of waters with different degrees of salinity, either drainage water or groundwater from low-quality aquifers, is a common and old practice in water-scarce regions. Differently, the reuse of wastewater or desalinated water is a relatively recent practice. All have in common the need to control the impacts on the environment, to manage crops in agreement with characteristics of the used water and, in case of wastewater, the need to avoid health consequences for workers and consumers of the produces.

Appropriately treated wastewater is a drought-proof and renewable supply of water. Wastewater irrigation can supply plant food nutrients inexpensively, mitigate water scarcity, save disposal costs, reduce pumping energy cost, and thus minimize carbon emissions. However, the negative health and environmental risks of wastewater irrigation need to be addressed, such as pathogens, excess nutrients, salts, toxic elements, and heavy metals (WHO, 2006a,b; Pereira *et al.*, 2009; Hanjra *et al.*, 2012). These negative impacts often result in negative consumer attitudes toward the use of wastewater for irrigation. Nevertheless, awareness of health risks is not high among farmers. These facts call attention to the need for developing educational and awareness programs that may make easy the adoption of best management practices and acceptability by the consumers.

A better understanding of the positive and negative environmental health impacts of wastewater use in agriculture can improve management of wastewater use and offer positive-sum solutions for human welfare and the environment. The wastewater demand for irrigation will continue to increase, especially by the millions of small farmers who depend on wastewater irrigation (Qadir *et al.*, 2010). Hence, in aiming at health safety of consumers and field workers, the challenge is to satisfy that demand with wastewater treated to the appropriate level, which justifies that particular attention is given to wastewater treatment as well as to health-related issues.

Concern about the sustainability of water use for feeding the future human population is the strong motivation to understand the potential of the use/recycling of nonconventional water resources and nutrient energy recycling in irrigated agriculture. These uses call for the development of innovative governance strategies to meet the future water demand, to enhance participation of water users in healthy and environmentally sound management of water at system and farm levels. The socioeconomic benefits from treated wastewater use in agriculture (Winpenny *et al.*, 2010) have so far not been adequately quantified and innovative approaches are required.

Seawater desalination will play an important role in addressing the challenge of global water scarcity. Nevertheless, desalinized water is very expensive and high in energy consumption, yet it is available as demineralized. This calls for mineralizing it when used for irrigation, so that fertilizers, microelements, and other elements as calcium are added to enhance the balance of nutrients for crops. Differently, using saline waters and wastewater requires careful attention to the salt components to avoid soil degradation by salinity and

plant toxicity by salts or phytotoxic elements and compounds. Attention is therefore given to the impacts on soils and the environment.

The sustainable use of nonconventional water resources needs that water uses are mostly beneficial, the water productivity is high, and the economic results are positive in terms of farming returns. To achieve that sustainable use of water, it is required that the respective pathways be known to clearly identify benefits and problems (Figure 1).

When using freshwater or low salinity water, the focus is on water conservation and saving, thus applying only the water that is required for achieving the crop yield, minimizing water wastages and losses and maximizing the water productivity and the economic return. Differently, when using wastewater the priority must be assigned to safe use of water in terms of public health (Figure 1). Maximizing the beneficial uses keeps a high priority for wastewater or saline water uses but an at least equal priority must be assigned to minimize environmental impacts due to pathogens, phytotoxic effect and excess of salts that may degrade the soil, the flora, and the fauna. This includes the preservation of water bodies that function for the disposal of the excess water and related riparian fauna and flora. Maximizing the water productivity must then be a priority constrained by the control of health and environmental impacts and by the economic farm return.

Agricultural Use of Saline Water and Recycling of Drainage Water

Characteristics and Impacts of Saline Waters

Saline water includes water commonly called brackish, saline, or hypersaline from different sources, including aquifers that are naturally saline or became saline due to human activities, and drainage effluents from agricultural land. Agricultural drainage waters are a resource for irrigation and other uses. However, drainage water may be the source for various pathogens and appropriate care is required. When treated this water may be reused for several processes (Tanji and Kielen, 2002; van der Molen *et al.*, 2007). Freshwater is considered to have a total dissolved solids (TDS) concentration of less than 500 mg l^{-1}, that is, electrical conductivity (EC) below 0.7 dS m^{-1}. Saline and brackish water will have TDS of 500–30 000 mg l^{-1}(0.7–42 dS m^{-1}), whereas seawater has TDS averaging 35 000 mg l^{-1}(49 dS m^{-1}).

Drainage water is used for irrigation in many parts of the world, mainly in CA, USA; India; Egypt; Israel; China; North Africa; and Middle East. There are abundant reports on its use (e.g., Minhas *et al.*, 2006; Rhoades *et al.*, 1992; Shahid *et al.*, 2013; Sharma and Minhas, 2005; Singh, 2009). The use of highly saline waters may be feasible for halophytes, which

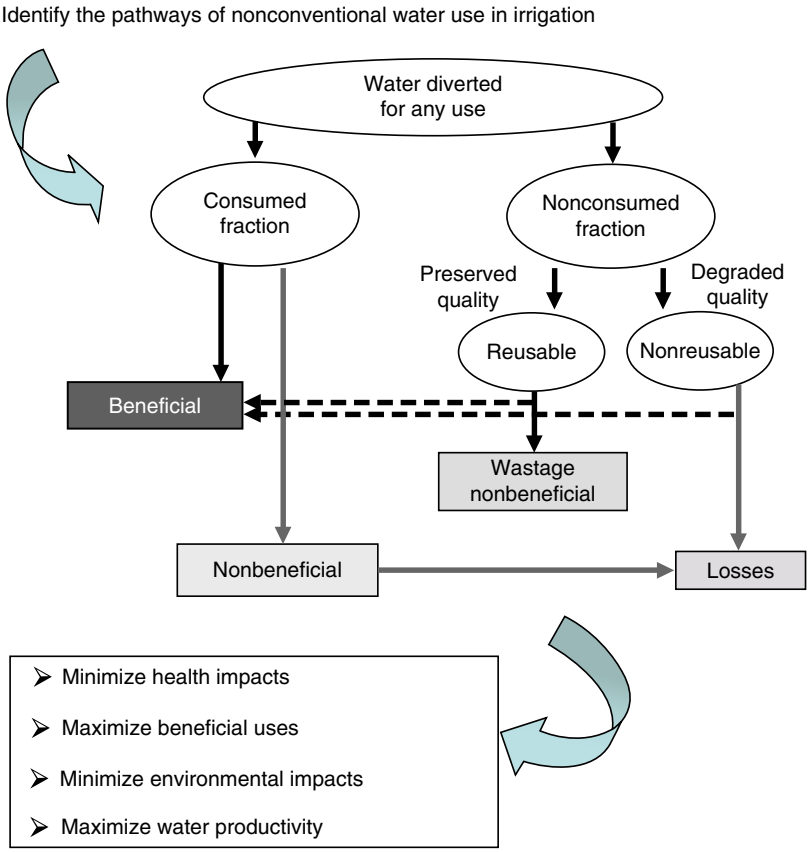


Figure 1 Efficient nonconventional water use and identification of related pathways. Adapted from Pereira, L.S., Cordery, I., Iacovides, I., 2009. Coping with Water Scarcity. Addressing the Challenges. Dordrecht: Springer, p. 382 and Pereira, L.S., Cordery, I., Iacovides, I., 2012. Improved indicators of water use performance and productivity for sustainable water conservation and saving. Agricultural Water Management 108, 39–51.

could be explored for human and animal consumption or for landscape uses (e.g., Cassaniti *et al.*, 2012; Díaz *et al.*, 2013).

The quality of drainage water for use in irrigation may be summarized as follows (van der Molen *et al.*, 2007):

- very good, <1 dS m^{-1}, appropriate for all crops;
- good, 1–2 dS m^{-1}, appropriate for most crops;
- moderate, 2–3 dS m^{-1}, appropriate for tolerant crops;
- poor, 3–6 dS m^{-1}, appropriate for tolerant crops, with appropriate leaching;
- very poor, >6 dS m^{-1}, appropriate but not recommended for irrigation. Usable to irrigate halophytes, maintain water levels in fish ponds, secure water levels in brackish coastal lakes, leaching salt-affected soils during the initial stage.

Waterlogging, salinity, and related problems have arisen in many irrigation areas where freshwater is used for irrigation. Such problems could arise even more quickly and more severely when saline water is used. The major potential hazards associated with the use of saline water in agriculture may be summarized as follows:

1. Yields decrease, which relate to:
   - reduced soil water availability to the crop due to increased soil water osmotic potential and reduced soil infiltration rates;
   - soil crusting, affecting infiltration, erosion, and crop emergence;
   - toxicity to the crop when the concentration of certain ions exceeds that of crop tolerance; and
   - imbalance of nutrients available to crops.
2. Soil degradation due to:
   - salinization when salts accumulate in the root zone if leaching and drainage are insufficient or inappropriate;
   - sodification when there is high sodium content in relation to other cations and the soil complex accumulates this excess sodium. Sodification causes soils to lose their structure, tilth, become dispersive, and these soils have reduced infiltration and permeability; and
   - loss of soil productivity in relation to salinization, sodification, imbalance of nutrients, and reduced water availability.
3. Environmental hazards from:
   - soil degradation;
   - groundwater and surface water salinization;
   - damages to the soil environment affecting plant and animal communities, and soil biodiversity;
   - desertification due to degradation of the soil, water, and environmental conditions;
   - development of aquatic weeds, algal blooms, and eutrophication in water bodies receiving nutrients and drainage effluents, particularly nitrates, thus affecting waterways and canals as well as the wildlife that inhabits ponds, lakes, and reservoirs; and
   - presence of particular ions to levels exceeding specific health and safety thresholds, which affect either plants sensitive to those ion concentrations, or animals that drink those waters, such as the selenium in drainage waters in California.
4. Public health hazards due to:
   - toxic ions such as heavy metals that, despite infrequent ingestion, are cancerous when accumulated in humans and
   - vectors of disease, such as mosquitoes and snails, which develop better in saline waters, mainly when rich in nutrients, which may affect populations living in areas using saline water or reusing drainage waters.

The use of saline water for irrigation requires:

- integrated management of water of different qualities at the levels of the farm, the irrigation system, and the basin (e.g., Rhoades *et al.*, 1992; Wallender and Tanji, 2012);
- adopting irrigation methods with high performance as discussed below;
- adopting appropriate irrigation scheduling providing for the satisfaction of crop water and using minimal leaching fractions to minimize deep percolation and runoff (Allen *et al.*, 1998, 2007);
- monitoring of soil and water quality, providing feedback that helps implement the optimal operation and control of the irrigation systems (Shahid *et al.*, 2013; Wallender and Tanji, 2012);
- promotion of tools, particularly models (Oster *et al.*, 2012), to predict long- and short-term effects of irrigation water quality on crop yields, soil properties, and quality of the environment;
- training of irrigation farmers and agricultural officers; and
- pilot areas to test and assess irrigation and soil and crop management practices for using saline water, including shallow water tables associated with deficit irrigation.

Criteria and Standards for Assessing the Suitability of Water for Irrigation

Consolidated standards have been made available in FAO publications (Ayers and Westcot, 1985; Rhoades *et al.*, 1992) and further developed in various other publications such as Tyagi and Minhas (1998) and Wallender and Tanji (2012). This has made it possible to define the main water quality parameters and management that need to be known to allow saline waters to be used safely in irrigation. Standards include:

1. Water quality characteristics to be considered for irrigation to assess the suitability of saline water concerning
   - salinity hazards (TDS and EC);
   - soil crusting and permeability hazards (sodium adsorption ratio (SAR) or adjusted SAR, EC, and pH);
   - specific ion toxicity hazard (e.g., Na^+, Cl^-, B, and Se, among others); and
   - nutrient imbalance hazard (excess NO_3^-, limited Ca^{2+}, PO_4^{3-}).
2. Parameters required to evaluate the quality of saline water on a routine basis including TDS, EC, concentration of ions (mainly Ca^{2+}, Mg^{2+}, Na^+, CO_3^{2-}, HCO_3^-, Cl^-, and SO_4^{2-}), SAR, or the adjusted SAR under certain conditions, trace elements (such as Se, As, B, Mo, Cd, Cr, and Cu), as well as other potentially toxic substances of agricultural origin.

Table 1 Water quality for irrigation and required restrictions in use

Problems	*Water quality characteristic*	*No restrictions*	*Slight to moderate restrictions*	*Severe restrictions*
Salinity effects on water availability	Electrical conductivity (dS m^{-1})	<0.7	0.7–3.0	>3.0
	Total dissolved solids (TDS) (mg l^{-1})	<450	450–2000	>2000
Salinity effects on soil infiltration	Sodium adsorption ratio (SAR) <3	EC > 0.7 dS m^{-1}	EC: 0.7–0.2 dS m^{-1}	EC < 0.2 dS m^{-1}
	3–6	>1.2	1.2–0.3	<0.3
	6–12	>1.9	1.9–0.5	<0.5
	12–20	>2.9	2.9–1.3	<1.3
	20–40	>5.0	5.0–2.9	<2.9
Toxicity	Sodium			
	Surface irrigation: SAR	<3	3–9	>9
	Sprinkle/spray (meq l^{-1})	<3	>3	
	Chloride			
	Surface irrigation (meq l^{-1})	<4	4–10	>10
	Sprinkle/spray (meq l^{-1})	<3	>3	
	Boron (mg l^{-1})	<0.7	0.7–3.0	>3.0
	Trace elements	Variable		
	Bicarbonate (meq l^{-1}) (sprinkle/spray)	<1.5	1.5–8.5	>8.5
Plant nutrition	pH	6.5–8.5		

Source: Adapted from Ayers, R.S., Westcot, D.W., 1985. Water quality for agriculture. FAO Irrigation and Drainage Paper 29 Rev. 1. Rome: FAO.

3. Water quality standards already available should be adjusted for the specific conditions of saline water use, including soils, climate, crops and crop sequences, and irrigation methods.
4. Attention must be paid to possible hazardous effects of trace elements on people or livestock that consume crops produced using water having such elements (e.g., As and Se).

The main water quality characteristics for saline waters are summarized in **Table 1**, with indications of the restrictions on their use, which mainly concern crop tolerance to salts, the need for leaching, specific requirements for the irrigation methods and systems, plus soil management practices and fertilizer practices.

Crop Irrigation Management using Saline Water

Crop responses to salinity vary with species and, to a lesser degree, with the crop variety. The tolerance of crops to salinity is generally classified into four to six groups from sensitive (or nontolerant), where most horticultural and fruit crops are included, to the tolerant, which includes barley, cotton, jojoba, sugarbeet, several grass crops, asparagus, and date palm. Full lists of crop tolerance classes are given by Hoffman and Shalhevet (2007). In addition, halophytes may be commercially explored using highly saline water (e.g., Cassaniti *et al.*, 2012).

The behavior of various crops under irrigation with water of different degrees of salinity varies with species, varieties, and the crop growth stages. As irrigation water salinity increases, germination is delayed. Germination is adversely affected for most field crops when the EC of the irrigation water, or the soil saturation extract, reaches a threshold of 2.4 dS m^{-1}. Adverse effects occur at lower values (<1 dS m^{-1}) for nontolerant crops, and at higher values for tolerant crops (generally not more than 4 dS m^{-1}). However, responses of a tolerant crop become affected when the crop is irrigated with saline water in successive years.

The germination and seedling stages are the most sensitive. Any adverse effects at such stages will lead to a reduction in crop yields proportional to the degree of plant loss during germination and establishment. At this stage, water of good quality should be used, especially if plants are sensitive. Besides germination and crop establishment, most crops are more sensitive to salinity during the reproductive phase. Other critical stages vary from crop to crop. Case studies are reported in the literature (Tyagi and Minhas, 1998; Sharma and Minhas, 2005; Wallender and Tanji, 2012).

The effects of the salinity on yields may be estimated as follows (Ayers and Westcot, 1985; Rhoades *et al.*, 1992; Allen *et al.*, 1998):

$$\frac{Y_a}{Y_m} = 1 - (EC_e - EC_{e\ threshold})\frac{b}{100} \quad [1]$$

where Y_a and Y_m are the actual and potential crops yields (kg ha^{-1}), when the crop techniques are appropriate to the local environmental conditions and no water stress affects the crop; b is a crop-specific parameter, which describes the rate of yield decrease per unit of excess salts (% per dS m^{-1}), and EC_e and $EC_{e\ threshold}$ are, respectively, the actual EC of the soil saturation extract and the crop-specific $EC_{e\ threshold}$ above which the crop is affected by salinity. The $EC_{e\ threshold}$ ranges from 1.0 dS m^{-1} for very sensitive crops, such as carrots and beans, up to more than 7.5 dS m^{-1} for barley, cotton, and tolerant grasses. The b rate of decrease in yield per unit increase in EC varies from more than 15 (% per dS m^{-1}) for the sensitive crops, down to 5 or less (% per dS m^{-1}) for tolerant crops. The parameters b and $EC_{e\ threshold}$ are tabled in Allen *et al.* (1998) and Hoffman and Shalhevet (2007) for the main crops.

The suitability of water for irrigation based on salinity, leaching and drainage requirements, and crop tolerance to salinity must be related to irrigation management. Water and crop management must be selected to minimize accumulation

of salts in the active root zone and to eliminate salt stress, especially during the critical growing stages of the plants. These include (Pereira *et al.*, 2002, 2009; Allen *et al.*, 1998):

- appropriate selection of irrigation methods;
- efficient leaching management, including volumes and frequency, and respective drainage of the salty water away from the cropped land (Section Leaching Requirements and Strategies for Controlling Impacts on Soil Salinity);
- proper irrigation scheduling, in agreement with the available irrigation system; and
- crop rotations adapted to the prevailing conditions; considerations must include irrigation water quality, soil salinity levels, chemical and physical properties of the soils, and climatic conditions.

A major factor when using saline irrigation is scheduling and frequency. Saline water requires more frequent irrigation than freshwater because salts in the water and the soil increase the osmotic potential of the soil water, which makes water uptake by the crop roots more difficult. For irrigation scheduling purposes, it is possible to consider the total available soil water smaller than that for nonsaline soils through correcting the soil water content at the wilting point (θ_{WP}, $cm^3\ cm^{-3}$):

$$\theta_{WP\ \ salt} = \theta_{WP} + b\left(\frac{EC_e - EC_{e\ \ threshold}}{10}\right)(\theta_{FC} - \theta_{WP}) \quad [2]$$

where θ_{FC} is the soil water content at field capacity ($cm^3\ cm^{-3}$), $\theta_{WP\ salt}$ is the soil water content at wilting point ($cm^3\ cm^{-3}$) for saline conditions and b, EC_e, and $EC_{e\ threshold}$ are as defined in eqn [1]. The $\theta_{WP\ salt}$ varies from a crop to another with b and $EC_{e\ threshold}$, and varies for the soil with EC_e. Equation [2] implies the reduction of the depth of water applied at each irrigation and, simultaneously, increasing the irrigation frequency. However, those depths depend on the irrigation method and the off-farm system delivering water to the fields.

The use of straw mulch to control soil evaporation also helps controlling the upward transport of salts to the root zone, particularly when irrigation and leaching are appropriate (Bezborodov *et al.*, 2010; Pang *et al.*, 2010).

The selection of the irrigation method must consider the quality of the water and the potential for both the water and the irrigation method to produce negative impacts. A summary of the more relevant considerations is presented in **Table 2**. These refer to the capabilities for controlling:

- soil salinity hazards due to salt accumulation in the root zone;
- toxicity hazards caused by direct contact of the salty water with the plant leaves and fruits;
- soil infiltration and permeability hazards caused by the modification of the soil physical properties, mainly due to the Na ion; and
- yield hazards when the irrigation system does not allow adoption of appropriate irrigation management, that is, frequency and volumes of irrigation.

Irrigation methods are described in various irrigation manuals and their adaptability for using saline and wastewater is discussed in numerous papers. Surface irrigation methods, particularly flat basins and borders, are appropriate to apply saline waters and for salt leaching. However, they are not adequate to apply small irrigation depths. When water is delivered to the farms through surface canal systems, the delivery schedules are generally of the rotation type, and are often rigid, delivering large irrigation volumes at long intervals. These systems are well adapted for leaching, but are less appropriate for irrigation of less tolerant crops that would require small and frequent applications, for example, vegetable crops. Differently, drip irrigation is appropriate for these crops because small and frequent irrigation depths are used. Drip systems require that irrigation be monitored to avoid salts returning into the wetted bulb. Cracks forming at the soil surface must be avoided. Moreover, emitters must be carefully selected, that is, not having too small orifices, and filtration must be carefully practised with filter sizes in agreement with sizes of orifice emitters, and the system must be carefully maintained and cleaned to avoid accumulation of salts within the piping, which could induce emitter clogging.

Leaching Requirements and Strategies for Controlling Impacts on Soil Salinity

The leaching requirement is usually computed from (Ayers and Westcot, 1985)

$$LR = \frac{EC_{iw}}{5EC_e - EC_{iw}} \quad [3]$$

where EC_{iw} is the electrical conductivity of the irrigation water and EC_e is the electrical conductivity of the saturated extract of the soil. The EC_e should be the average soil salinity tolerated by the crop, not that for achieving maximum yield but to provide for attaining 70–90% of the potential yield. When a leaching fraction is applied with the irrigation water, the salinity built up of the soil is reduced nonlinearly with the size of that fraction. This may be expressed as

$$EC_e = \frac{1 + LF}{LF} \times \frac{EC_{iw}}{5} \quad [4]$$

where LF, the actual leaching fraction, is used in place of the leaching requirement, LR. This equation shows that the soil salinity EC_e increases proportionally to the salinity of the irrigation water, EC_{iw}.

The salinity built up cannot be prevented by drastically increasing the leaching fraction because this would dramatically increase the percolation of water, causing the water table to rise, plus waterlogging and degradation of the ground water quality. This further contributes to water scarcity. Therefore, depending on the crop, and the salinity of the water and soil, the minimum LF is recommended. Moreover, the application of an LF is only effective when there is high uniformity of irrigation water distribution. When uniformity is low, water percolates abundantly in some areas of the field whereas other areas are insufficiently wetted. Then farmers tend to apply more water but this produces only more percolation (e.g., Pereira *et al.*, 2007). Under conditions of water scarcity, this would be a very poor use of the available water. As reported by Hanson *et al.* (2007), leaching with drip irrigation is more effective when application depths are large

Table 2 Evaluation of the irrigation methods for use with saline water

Irrigation method	*Flat basin irrigation*	*Corrugated basin irrigation*	*Border irrigation*	*Furrow irrigation*	*Sprinkler irrigation*	*Drip and subsurface drip irrigation*	*Microsprinkling and microspray*
Salt accumulation in the root zone	Not likely to occur except for the underirrigated parts of the field when uniformity of water application is very poor. Leaching fraction difficult to control in traditional systems	Salts tend to accumulate on the tops of the ridges. Leaching before seeding/planting is required for germination and crop establishment	As for basin irrigation but infiltration control is more difficult, as is the control of the leaching fraction	Salts tend to accumulate on the tops of the ridges. Leaching is required before seeding/planting	Not likely to occur when set systems are used except for the under irrigated parts of the field due to low uniformity. Instead, problems occur with equipment designed for light and frequent irrigation	Not likely to occur except for the under irrigated parts of the field due to low uniformity, including that resulting from nozzle clogging when water filtration is poor	Not likely to occur except for the underirrigated parts of the field due to low uniformity and clogging; leaching could then be more difficult
Foliar contact, avoiding toxicity	It is possible only for bottom leaves in low crops and fodder crops, and during the first stage of growth of annual crops	Unlikely because crops are grown on ridges	As for flat basins	Unlikely because crops are grown on ridges	Severe leaf damage can occur affecting yields. Damage greater with more frequent irrigation	Not likely to occur	Leaf damage can occur, affecting yields of annual crops. Less damage for tree crops
Ability to infiltrate water and refill the root zone	Adequate because large volumes of water are generally applied at each irrigation and water remains in the basin until infiltration is complete	As for flat basins, above	As water infiltrates while flowing on the soil surface, runoff losses increase when infiltration decreases	Salinity-induced infiltration problems cause very high runoff losses	Salinity-induced infiltration problems including soil crusting may cause very high runoff losses	Problems generally do not occur except when there are not enough emitters and underirrigation is practised	Problems are similar to those for set sprinklers, so runoff losses may be important
Control of crop stress and yield reduction	Adequate because toxicity is mostly avoided, salts are moved down through the root zone, infiltration is completed, and irrigation can be scheduled to avoid crop stress	As for flat basins but depending on avoiding salt stress at plant emergence and crop establishment	Crop stress is likely to occur due to reduced infiltration, so inducing relatively high yield losses	Crop stress is very likely to occur due to reduced infiltration, so inducing yield losses	Crop stress is very likely to occur due to toxicity by contact of water with the leaves and fruits, and due to reduced infiltration, thus crop stress and yield losses may occur	These systems are able to provide for crop stress and toxicity control, so yield losses are minimized	Toxicity due to direct contact with the leaves. Nonuniform irrigation may produce crop stress and runoff. Yield losses likely

Source: Adapted from Pereira, L.S., Cordery, I., Iacovides, I., 2009. Coping with Water Scarcity. Addressing the Challenges. Dordrecht: Springer, p. 382.

enough to appropriately control the water and salts within the wetted bulbs.

Equation [4] predicts that $EC_e = 1.5\ EC_{iw}$, when the salinity of the soil and the irrigation water are in equilibrium. Lower EC_e can occur if good quality water, including rainwater, is employed for leaching. Therefore, the conjunctive use for irrigation of saline water and good quality water is advocated, and similarly for the case of using wastewater for irrigation. An updated discussion on LF practices is given by Hoffman and Shalhevet (2007) and by Letey *et al.* (2011). The latter suggest that using a smaller LF than usually recommended may be a better option.

Several strategies are usually adopted to facilitate irrigation with saline water (e.g., Rhoades *et al.*, 1992; Shahid *et al.*, 2013). The main strategies are listed below:

1. The *dual rotation*, in which sensitive crops (e.g., lettuce and alfalfa) in the rotation are irrigated with low-salinity river water, and salt-tolerant crops (e.g., cotton, sugarbeet, wheat, and barley) are irrigated with saline drainage water. For the tolerant crops, the switch to drainage water is usually made after establishment, that is, irrigations at preplanting and at the initial crop stages are made with low salinity water. Benefits from this strategy include: (1) harmful levels of soil salinity in the root zone do not occur because saline water is used only for a fraction of the time; (2) substantial alleviation of salt buildup in the soil occurs during the time when salt-sensitive crops are irrigated with freshwater; and (3) proper preplanting irrigation and careful irrigation management during germination and seedling establishment leach salts out of the seed layer and from shallow soil depths. Difficulties include the complexity of water management for farmers and system managers and the possible lack of freshwater when it is required.
2. *Blending*, where water supplies of different salinity levels are mixed in variable proportions. Irrigation water having a quality superior to that of the saline water is obtained. Blending may be more practical on large farms because the farmer may take into consideration the crops grown and the respective growth stages. Differently, with large irrigation systems supplying many small farms it would be difficult to properly satisfy the requirements of all the crops, unless a cropping pattern is imposed for all farms.
3. *Cyclic application* of saline water and freshwater. Salinity must not be above the acceptable thresholds for the crops grown. Cycles of application of freshwater should coincide with the more sensitive growth stages, particularly for planting and seedling development, and for the leaching of the upper soil layers. This strategy has more potential and flexibility than the blending strategy.

Monitoring and Evaluation

Using brackish and saline irrigation water can be successful on numerous crops but uncertainty exists concerning the long-term effects of these irrigation practices on the physical and chemical quality of the soil. These effects largely depend on the chemical and physical characteristics of the soil, on the climate, and on the possibility of leaching with natural rain or using high-quality water for leaching. A great concern refers to the reduction of water infiltration capacity. This is especially important where reuse is practised on poorly structured soils and the drainage water has $SAR > 15\ (mmol\ l^{-1})^{1/2}$. However, the capability to predict changes in soil infiltration and permeability is still insufficient.

Long term effects on soil salinization are often considered with simulation models (Minhas *et al.*, 2006; Oster *et al.*, 2012). However, the existing knowledge is still limited. Soil variability in space and irrigation variability both in time and space produce large uncertainty in predictions. Soil salinity under a cyclic strategy of application will fluctuate more, both spatially and temporally, than if using a blending strategy. Predicting or anticipating plant response and effects on the soil would be more difficult when cyclic application is used. However, management strategies must be selected that keep the average root-zone salinity levels within acceptable limits.

Another cause of uncertainty refers to elements such as the boron and chloride contained in drainage water that may produce more long-term detrimental effects than salinity. Furthermore, the reuse of drainage water poses a long-term problem relative to the potential for accumulation of heavy metals in plants and soils. These metals can be toxic to human and animal consumers of the crops. Nevertheless, there is only limited potential for using prediction models to estimate long-term impacts.

Monitoring soil salinity, leaching, and drainage adequacy is therefore paramount to evaluate the long-term impacts from using saline waters, either groundwater or drainage water (Shahid *et al.*, 2013). Monitoring and evaluation should pay attention to:

- The dynamics of salts throughout the soil profile for detecting temporal changes in salinity levels, particularly to identify when salt buildup is steadily increasing.
- The functioning and performance of the drainage system, including observations of drainage outflows and salts transported with the drainage water.
- The irrigation performance, mainly relative to the uniformity of water distribution and the leaching fractions actually applied.
- The irrigation schedule with respect to the satisfaction of irrigation and leaching requirements, and the related constraints due to delivery, or other restrictions that may hamper appropriate irrigation management.
- Sampling EC_e and EC_{iw} throughout the irrigated area to identify the occurrence of problem areas requiring specific water management.
- Sampling for specific ions that may be present in the irrigation water that could have toxicity effects or create health risks, as for heavy metals.
- Follow-up impacts from using saline water such as changes in groundwater quality, plant ecosystems, wetlands, or in riverbed fauna and flora.

New approaches for laboratory and field techniques are required (e.g., Rhoades *et al.*, 1999; Wallender and Tanji, 2012). Environmental impact assessment methodologies for irrigation and drainage projects may also be adapted for surveying and monitoring areas where water of inferior quality, such as saline and wastewater, is used for irrigation.

Wastewater Reclamation and Recycling

Wastewater/Effluent Characteristics

General wastewater characteristics

Municipal wastewater mainly comprises water with relatively small concentrations of suspended and dissolved organic and inorganic solids. Organic substances include carbohydrates, lignin, fats, soaps, synthetic detergents, proteins, and their decomposition products, as well as various natural and synthetic organic chemicals from the process industries. Typical domestic wastewater can be classified as strong, medium, or weak, depending on the concentration of the major constituents. Chemical oxygen demand is 1000, 500, and 250 mg l^{-1}, respectively, for strong, medium, and weak wastewater (Sincero and Sincero, 2003). In arid and semiarid countries, domestic water use is often fairly low, so sewage tends to be very strong.

Municipal wastewater also contains a variety of inorganic substances, including heavy metals, which can have phytotoxic effects and health impacts, thus limiting reuse in agriculture.

Microbiological characteristics – Pathogens

From the point of view of human health, the contaminants of greatest concern are the pathogenic micro- and macroorganisms. Pathogenic viruses, bacteria, protozoa, and helminths may be present in municipal wastewater and will survive in the environment for long periods. At one time, coliforms were thought to be exclusively of intestinal origin, but it is now known that some are free living in the environment and are associated with soil and freshwater. Current practice uses *Escherichia coli* and other fecal indicator organisms, including intestinal *Enterococcus*, to ascertain levels of fecal pollution in water, with their numbers usually being given in the form of fecal coliforms (FC) per 100 ml of wastewater. Although these organisms may not be pathogenic, there is however well-documented correlation with deleterious health effects whenever exposed to measureable levels of fecal indicator organisms.

Pathogenic organisms give rise to the greatest health concern in the use of wastewaters. In areas of the world where helminthic diseases caused by *Ascaris* and *Trichuris* spp. are endemic in the population, and where untreated sewage is used to irrigate salad crops or vegetables eaten uncooked, transmission of these infections is likely to occur through the consumption of such crops. Further evidence was provided to show that cholera could be transmitted through the same pathway. Indian studies have shown that farmworkers exposed to sewage wastewater in areas where *Ancylostoma* (hookworm) and *Ascaris* (nematode) infections are endemic have significantly higher levels of infection than other agricultural workers. More detailed information on health risks and vector-borne diseases are given by WHO (2006a–c, 2011) and Mara and Sleigh (2010a,b). They can be summarized as follows:

- high risk (high incidence of excess infection) due to helminths (*Ancylostoma*, *Ascaris*, *Trichuris*, and *Taenia*);
- medium risk (low incidence of excess infection) due to enteric bacteria (*Vibrio cholera*, *Salmonella typhosa*, and *Shigella*); and
- low risk (low incidence of excess infection) related to enteric viruses (viral diarrheas and hepatitis A).

The main microbiological parameters that are particularly important from the health point of view when characterizing wastewaters (Pereira *et al.*, 2009) are summarized in **Table 3**.

Table 3 clearly shows that there is a wide variety of pathogens present in wastewater, depending upon the region concerned. These pathogens are the cause for a variety of diseases; some of them are of high risk for human health care workers and consumers of produces. Moreover, their survival time in water may be very large. These conditions imply appropriate care when treating and using wastewater.

Xenobiotics

Xenobiotics are either naturally occurring or synthetic compounds that interfere with the functioning of endocrine systems causing unnatural responses. For that reason they are receiving growing attention. Xenobiotics include

Table 3 Main pathogenic parameters relative to wastewaters

Pathogens	*Survival time*	*Presence in wastewater*
Coliforms and fecal coliforms (*Citrobacter*, *Enterobacter*, *Klebsiella*, *Escherichia coli*)	Up to 60 days in water and 70 days in the soil	*E. coli* count is a main indicator
Fecal *Streptococci* (*Streptococci bovis*, *Streptococci equines*, *Streptococci faecalis*)	–	Occur both in man and in other animals
Clostridium perfringens	Survival characteristics similar to viruses or even helminth eggs	Useful in wastewater quality reuse studies
Salmonella spp. (*S. typhi* agent for typhoid)	If removal of Salmonellae is achieved Shigellae and *Vibrio cholera* are probably also removed	Typical in a tropical urban sewage
Enteroviruses: Poliomyelitis and Meningitis, and respiratory infections	May attain 120 days in water	Especially under tropical conditions
Rotaviruses: Gastrointestinal problems	More persistent than enteroviruses	Removal in parallel with that of SS, virus are solids-associated
Intestinal Nematodes: Ascaris lumbricoides	Several months	Infections can be spread by effluent reuse practices

Source: Reproduced from Mara, D., Cairncross, S., 1989. Guidelines for the Safe Use of Wastewater and Excreta in Agriculture and Aquaculture. WHO and UNEP, Geneva and Pescod, M.B., 1992. Wastewater treatment and use in agriculture. FAO Irrigation and Drainage Paper 47. Rome: FAO.

pharmaceuticals (e.g., antibiotics as trimethoprim and erytromycine; analgesics and antiinflammatory drugs as codein, ibuprofen, and diclofenac), plus personal care products (e.g., fragrances, sunscreen agents), pesticides, and disinfectants. Some of these compounds, for example, pentabromobiphenylether, 4-nonylphenol, C_{10}–C_{13} chloroalkanes, and the di(2-ethylhexyl)phthalate (DEHP), have been listed as priority hazardous substances in the field of water policy by the European Directive on Environmental Quality Standards (Directive 2008/105/EC). WHO (2011) also identified some of the above-mentioned xenobiotics through the hazard identification process.

In wastewater treatment plants (WTP), hydrophobic compounds are adsorbed into the sludge, whereas persistent hydrophilic compounds remain in the treated effluents. Whenever these compounds, their metabolites, or transformation products are not removed during wastewater treatment process, they may enter the aquatic environment. As a result, increased attention is being given to the use of reclaimed water to avoid the introduction of xenobiotic compounds into the environment, which is highly relevant in areas where reclaimed water is used for irrigation.

Graywater

Graywater (GW) is defined as the urban wastewater that includes water from baths, showers, hand wash basins, washing machines, dishwashers, and kitchen sinks, but excludes streams from toilets (Santos *et al.*, 2012). GW is an important alternative source of water as it makes up the largest volume of the waste flow from households, and it has a nutrient content that can be beneficially used by crops, and also has a low pathogen content (WHO, 2006c). Owing to the low levels of pathogens and nitrogen, reuse and recycling of GW is receiving more and more attention (Li *et al.*, 2008) as it can be used for any purpose provided it is treated to the desired quality standard. The treatment system varies based on the site conditions and GW characteristics.

The design of a graywater reuse system primarily depends on the quantity to be treated and reuse applications (WHO, 2006c). The reclaimed graywater should fulfill the four criteria (hygienic safety, esthetics, environmental tolerance, and economical feasibility) for reuse. One should also keep in mind that different reuse applications require different water quality specifications and thus demand different treatments varying from simple processes to more advanced ones.

Various studies show the usefulness and limitations of GW for irrigation. Rodda *et al.* (2011) showed that irrigation with GW increased plant growth and yield relative to crops irrigated with tap water. However, the soil irrigated with GW showed increased EC and increased concentrations of metals over time, coupled with an increase in sodium and metal concentrations in crops. Accumulation of surfactants and sodium in soil may also occur due to GW reuse, then affecting adversely agricultural productivity and environmental sustainability. Travis *et al.* (2010) verified that GW could change soil properties impacting the movement of water within the soil and the transport of contaminants in the vadose zone. As for the drainage reuse referred before, appropriate monitoring is required to support further expansion of GW reuse in irrigation and a better definition of treatment requirements.

Wastewater Treatment

General aspects

An appropriate degree of treatment needs to be provided to raw municipal wastewater before it can be used for agricultural and landscape irrigation, or other uses. The required quality of effluent will depend on the proposed water uses, crops to be irrigated, soil conditions, and the irrigation system.

The best available wastewater treatment for agricultural uses is that which allows meeting the recommended microbiological and chemical quality guidelines at low cost, minimizes operational and maintenance requirements, and keeps nutrients in the reclaimed water. Simplicity and robustness of the treatment process is even more important in developing countries. Pathogen removal is a primary concern (Asano *et al.*, 2006; WHO, 2006c).

Irrigation with effluent directly from the treatment plant is generally not feasible and some form of storage of the treated effluent is necessary. Additional benefits can result from storage in reservoirs but their management is particularly demanding because of the need to manage both water quantity and quality (Kfir *et al.*, 2012).

Conventional Wastewater Treatment

Conventional wastewater treatment consists of a combination of physical, chemical, and biological processes and operations to remove solids, organic matter, and, sometimes, nutrients from wastewater (**Figure 2**).

Different degrees of treatment can be considered:

1. Preliminary treatment: The objective is the removal of coarse solids and other large materials from the raw wastewater. Treatment includes coarse screening, grit removal, and trituration.
2. Primary treatment: The objective is the removal of settable organic and inorganic solids. Large fractions of the total suspended solids, oils, and grease are removed but only a fraction of the biochemical oxygen demand (BOD_5, when the test is carried out during 5 days) is removed. If coagulants are used, particulate and colloidal matter are removed together with heavy metals, polychlorinated biphenyls (PCBs), and polycyclic aromatic hydrocarbons (PAHs). This may be considered a sufficient treatment if the wastewater is to be used to irrigate crops that are not consumed by humans or to irrigate orchards, vineyards, and some processed food crops as discussed in the Section Management Strategies for Minimizing Health Hazards in Wastewater Use in Irrigation.
3. Secondary treatment: The objective here is to remove the residual organics (soluble BOD_5) and suspended solids. It often involves the removal of biodegradable dissolved and colloidal organic matter using aerobic biological treatment processes. When coupled with a disinfection step such as chlorination, these processes can provide substantial removal of bacteria and viruses. The use of membrane bioreactors (MBR), coupling of a membrane to a bioreactor,

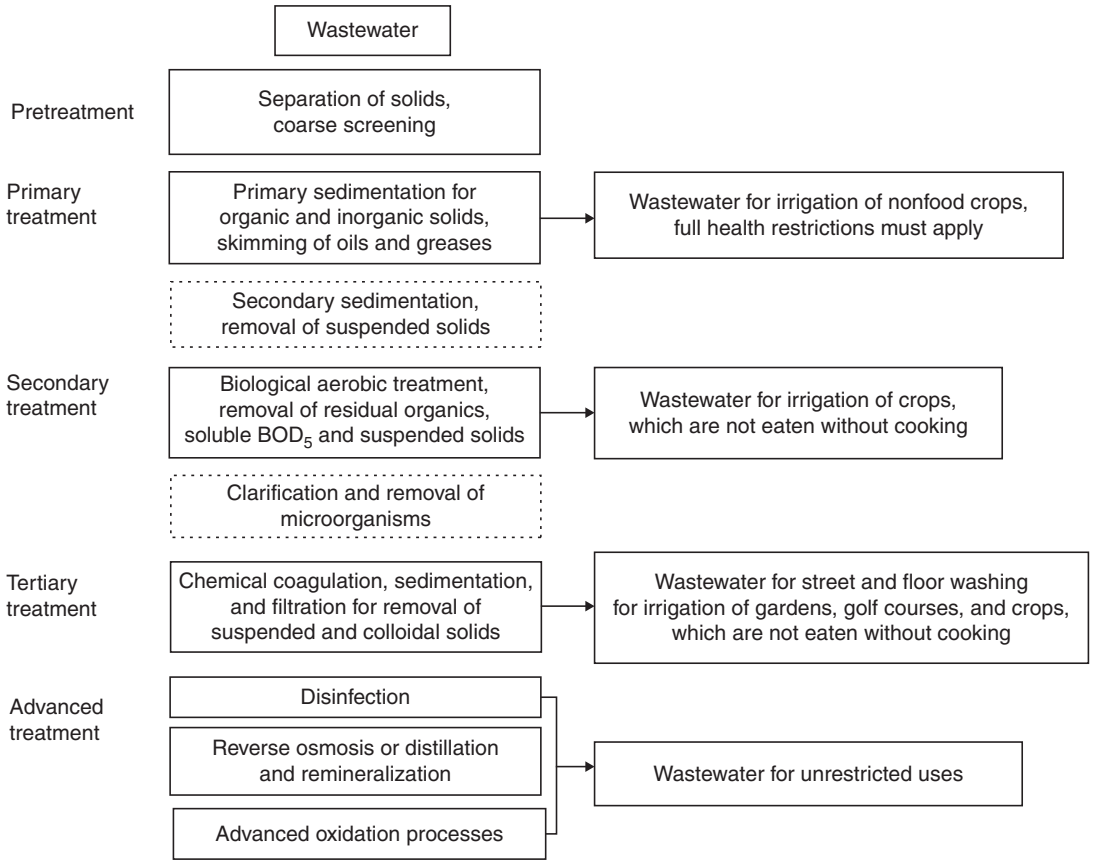


Figure 2 Conventional wastewater treatment and related conditions for water reuse. Modified from Pereira, L.S., Cordery, I., Iacovides, I., 2009. Coping with Water Scarcity. Addressing the Challenges. Dordrecht: Springer, p. 382. Boxes with stippled borders refer to supplemental treatments.

allows achieving an effluent that can be reused without restrictions in irrigation (Fatone *et al.*, 2011).

4. Tertiary treatment is employed when specific undesirable wastewater constituents cannot be removed by secondary treatment, for example, additional suspended solids and refractory organic chemicals (resistant to be broken down through conventional treatment processes).
5. Advanced treatment aims at unrestricted water use, namely in irrigation. It is required because secondary effluents commonly still contain low levels of pathogens, nutrients, and dissolved solids. It includes membrane technology, ultra-/nanofiltration, or reverse osmosis (RO) as well as water remineralization RO membrane filtration. This has been accepted as a proven technology to achieve the quality required for unlimited irrigation reuse (Oron *et al.*, 2008). However, its application is limited due to the requirement for extensive pretreatment along with the associated high operational and maintenance costs. Meanwhile, low-pressure RO is emerging as an alternative to the conventional method. Advanced oxidation processes are considered a highly competitive treatment for removal of refractory organic chemicals. These processes include photochemical degradation, photocatalysis, and chemical oxidation processes. Disinfection normally uses a chlorine solution but ozone and ultraviolet irradiation can also be used.

Natural/biological treatment systems and present advances

Natural/biological treatment systems consist of the following:

1. Stabilization ponds, which according to the metabolic regime present, can be classified as anaerobic, facultative, aerobic or maturation, and aerated ponds. Dissolved or suspended organic matter is metabolized by heterotrophic bacteria with uptake of oxygen, whereas dissolved oxygen is replaced through photosynthetic oxygen produced by microalgae.
2. Overland treatment of wastewater, where the effluent is distributed over gently sloping grassland on fairly impermeable soils, and it moves evenly down the slope to collecting ditches. Suspended and colloidal organic materials are then removed by sedimentation and filtration through the surface grass and organic layers. Pathogens are also removed at levels comparable with conventional secondary treatment systems, without chlorination. The impact on groundwater should be considered in the case of highly permeable soils.

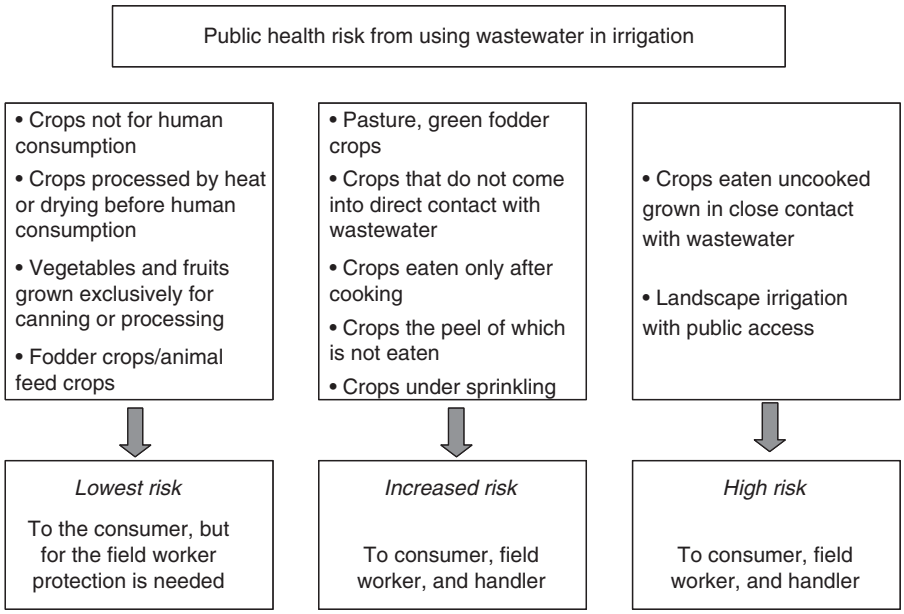


Figure 3 Levels of health risk for consumers and workers due to wastewater use in irrigation. Adapted from Westcot, D.W., 1997. Quality control of wastewater for irrigated agriculture. FAO Water Report 10. Rome: FAO and Pereira, L.S., Cordery, I., Iacovides, I., 2009. Coping with Water Scarcity. Addressing the Challenges. Dordrecht: Springer, p. 382.

3. Wetland treatment systems, where treatment occurs in maturation ponds that incorporate floating, submerged, or emergent aquatic species (macrophytes). Floating macrophytes, desirably having large root systems and very efficient nutrient extraction, include the *Eichornia crassipes* and the *Ceratophyllum demersum*. In wetlands having emergent macrophytes, for example, *Phragmites communis* and *Scirpus lacustris*, aerobic treatment takes place in the rhizosphere as oxygen passes to it from the atmosphere through leaves, stems, and roots, whereas anoxic and anaerobic treatment takes place in the surrounding soil. Nutrients and heavy metals can be removed by plant uptake.
4. Constructed wetlands (CW) have the appearance of a natural wetland habitat and employ many of the biological processes found in natural wetland ecosystems. CW can produce a biologically treated effluent with sufficiently low pathogen content to be safely used for irrigation. As these systems can be constructed from local materials and are simple to operate and maintain, they have the potential to be applied in a variety of countries (Tanaka *et al.*, 2011). Removal processes depend on CW type/configuration and inflow loading (Vymazal and Kröpfelová, 2008). Operation and maintenance activities are essential to guarantee an appropriate performance of CW, including water-level control, weeds control, and plant inspection (Galvão *et al.*, 2009).

Management Strategies for Minimizing Health Hazards in Wastewater Use in Irrigation

Pathogens brought with the wastewater can survive for many days in the soil or on the crops. Thus, a potential for disease transmission exists when wastewater is used for irrigation. Factors influencing transmission of disease include the degree of wastewater treatment, the crops grown, the irrigation method used to apply the wastewater, and the crop and harvesting practices adopted (Westcot, 1997). These factors define the degree of public health risk as depicted in **Figure 3**. Examples of crops representing low risk include olive trees, date palms, and energy crops.

The risk of infection of field workers relates to their direct contact with the crop or soil in the area where wastewater is used. This risk directly relates to the level of protection needed for field workers. Workers safety requires adoption of preventive measures against infection. The following risk situations for field workers are identified (Westcot, 1997):

1. Low risk of infection:
   - mechanized cropping practices;
   - mechanized harvesting practices;
   - irrigation ceasing long before harvesting; and
   - long dry periods between irrigations.
2. High risk of infection:
   - high wind and dust areas;
   - hand cultivation and hand harvesting;
   - moving of sprinkler or other irrigation equipment; and
   - direct contact with irrigation water.

Preventive measures to minimize health hazards for field workers include wearing protective clothing, for example, impermeable boots that prevent any direct skin contact with the wastewater, maintenance of high levels of hygiene, and immunization against infections that are likely to occur.

International guidelines or standards for the microbiological quality of wastewater for irrigation when used for a particular crop do not exist. The standards and guidelines for the quality of wastewater used for irrigation are focused on effluent standards at the wastewater treatment plant, rather than at the point of use. These standards are often used for

Table 4 Health-based targets for wastewater use in agriculture

Exposure scenario	*Health-based target (DALY[a] per person per year)[b]*	*Log_{10} pathogen reduction needed[b]*	*Number of Helminth eggs per litre[c,d]*	Escherichia coli *(number per 100 ml)*
Unrestricted irrigation	$\leq 10^{-6}$			$<10^3$
Lettuce		6	≤ 1	Relaxed to $<10^4$ for high-growing leaf crops or drip irrigation
Onion		7	≤ 1	
Restricted irrigation	$\leq 10^{-6}$			$<10^5$
Highly mechanized		3	≤ 1	Relaxed to $<10^6$
Labor intensive		4	≤ 1	When exposure is limited or regrowth is likely
Localized (drip) irrigation	$\leq 10^{-6}$			
High-growing crops		2	No recommendation[e]	
Low-growing crops		4	≤ 1[d]	

[a]Disability adjusted life years.
[b]The health-based target can be achieved, for unrestricted and localized irrigation, by a 6–7 log unit pathogen reduction (obtained by a combination of wastewater treatment and other health protection measures). For restricted irrigation, it is achieved by a 2–3 log unit pathogen reduction.
[c]When children under 15 years are exposed, additional health protection measures should be used (e.g., treatment to ≤ 0.1 egg l^{-1}).
[d]The mean value of ≤ 1 egg l^{-1} should be obtained for at least 90% of samples.
[e]When no crops to be picked up from the soil.
Source: Adapted from WHO, 2006b. WHO Guidelines for the Safe Use of Wastewater, Excreta and Greywater, vol. II. Wastewater Use in Agriculture. Geneva: World Health Organization and WHO, 2006c. WHO Guidelines for the Safe Use of Wastewater, Excreta and Greywater, vol. IV. Excreta and Greywater Use in Agriculture. Geneva: World Health Organization.

process control at wastewater treatment plants. On the basis of an epidemiological review, WHO adopted water quality guidelines for wastewater use in agriculture as shown in Table 4. These guidelines are for the microbiological quality of treated effluent from a wastewater plant when that water is intended for irrigation.

It is advisable to utilize the WHO (2006a–c) guidelines for controlling the quality of water used in irrigation (Table 4). Using them as irrigation standards would help to:

- identify the areas currently being contaminated;
- reduce the disease infection risk until suitable wastewater treatment is adopted;
- improve the basic health level in rural areas; and
- provide indication and data of unsatisfactory areas to assist in planning for wastewater management.

Using the helminth standard throughout all cropping systems aims at increasing the level of protection for agricultural workers, who are at high risk of intestinal nematode infection (WHO, 2006b). It is assumed that if the recommended helminth egg limit could be reached, then equally high removals of all protozoa would be achieved. No bacterial guidelines were considered by WHO for protection of agricultural workers because there was little evidence of such a risk to workers, and some degree of reduction in bacterial concentration would be achieved with efforts to meet the helminth levels. Guidelines shown in Table 4 should be adapted according to local requirements and specifications.

As urban populations grow enormously, the degree of river and irrigation water supply contamination in developing countries will likely increase. Pressure will also increase to use partially treated wastewater for irrigation until adequate treatment facilities can be constructed. In addition, predicting long-term effects of wastewater use is yet not supported by sufficient research (Xu *et al.*, 2010). Thus, there is an immediate need to control wastewater use in high-risk cropping systems such as vegetable crop production. The guidelines proposed by WHO (2006a–c) could be applied in areas where wastewater is utilized directly for irrigation or where use is indirect, for example, where contaminated river water, including when a treatment plant exists, is diverted for irrigation.

Indicative expected removal levels of pathogens are shown in Table 5 for various treatment processes. Results depend not only upon the treatment, but also on the time of detention (Westcot, 1997; Pereira *et al.*, 2009). Further disinfection may be required for products that are eaten fresh (Bichai *et al.*, 2012).

Crop Restrictions and Irrigation Practices

To minimize the health risk from using wastewater in irrigation, the prime approach is to treat the wastewater to the level recommended above. However, untreated or insufficiently treated wastewaters are still used for irrigation when uncontrolled flows are used. Then, the application of crop restrictions is a required measure to protect the consumer and to protect public health. Crop restrictions focus on salad or vegetable crops that are normally eaten raw as indicated before. Unfortunately, in countries where institutional arrangements and enforcement of standards are usually not strong enough, crop restrictions are not effectively enforced and do not ensure that unsafe food products are not presented to the consuming public.

Table 5 Indicative log unit reductions or inactivation of pathogens achieved by selected wastewater treatment processes

Treatment process	*Log unit pathogens removals*[a]			
	Viruses	*Bacteria*	*Cysts*	*Helminth eggs*
Low-rate biological processes				
Waste stabilization ponds	1–4	1–6	1–4	1–3
Wastewater storages and treatment reservoirs	1–4	1–6	1–4	1–3
Constructed wetlands	1–2	0.5–3	0.5–2	1–3
High-rate processes				
Primary treatment				
Primary sedimentation	0–1	0–1	0–1	0 to <1
Chemically enhanced primary treatment	1–2	1–2	1–2	1–3
Secondary treatment				
Activated sludge + secondary sedimentation	0–2	1–2	0–1	1 to <2
Trickling filters + secondary sedimentation	0–2	1–2	0–1	1–2
Aerated lagoon + settling pond	1–2	1–2	0–1	1–3
Tertiary treatment				
Coagulation/flocculation	1–3	0–1	1–3	2
High-rate granular or slow-rate sand filtration	1–3	0–3	0–3	1–3
Dual-media filtration	1–3	0–1	1–3	2–3
Membranes	2.5 to >6	3.5 to >6	>6	>3
Disinfection				
Chlorination	1–3	2–6	0–1.5	0 to <1
Ozonation	3–6	2–6	1–2	0–2
Ultraviolet radiation	1 to >3	2 to >4	>3	0

[a]The log unit reductions are $\log_{10}$ unit reductions. A 1 log unit reduction = 90% reduction; a 2 log unit reduction = 99% reduction; a 3 log unit reduction = 99.9% reduction; and so on.

Source: Adapted from WHO, 2006b. WHO Guidelines for the Safe Use of Wastewater, Excreta and Greywater, vol. II. Wastewater Use in Agriculture. Geneva: World Health Organization.

Crop restrictions need a strong institutional framework and the capacity to monitor and control compliance with the regulations (Pereira *et al.*, 2009). Regulations and governance on the use of wastewater, namely for irrigation, are required (Hanjra *et al.*, 2012). Planning, management, and operation of reservoirs for wastewater reuse are essential in terms of wastewater quality and related reuse performance (Kfir *et al.*, 2012).

The following factors favor the adoption of crop restrictions:

- A law-abiding society or strong law enforcement.
- Allocation of wastewater is controlled by a public body that has legal authority to enforce crop restrictions.
- The irrigation water conveyance and distribution system is controlled by strong central management.
- There is high demand and price advantage for the unrestricted crops.
- There is little market pressure in favor of the excluded crops.
- Wastewater is used by a small number of large farms.

Very large, dispersed irrigation schemes and those having poor or weak management make it difficult to enforce crop restrictions. Difficulties also occur when producers are mainly small farmers and the market prices do not favor adopting lower risk crops. In many developing countries, when wastewater, including untreated effluent, is discharged directly to surface waters and these are diverted downstream for irrigation purposes there is a widespread distribution of the wastewater and crop restriction becomes extremely difficult.

Irrigation practices should be designed according to the quality of used wastewater. Salinity hazards associated with wastewater are considered in the Section Crop Irrigation Management Using Saline Water (**Table 2**). Aspects referring to the control of health hazards were discussed in the precedent sections. However, the selection of methods of irrigation with wastewater to comply with guidelines for controlling health risks requires particular attention. Irrigation methods differ on several aspects as summarized in **Table 6** They mainly concern:

- The probability of direct contact of workers with the irrigation water, thus referring to the need for adopting more stringent preventive measures.
- The direct contact of the water with the harvestable yield, thus implying the need for a careful implementation of consumer protection measures, including crop restrictions.
- The foliar contact with the water that may cause phytotoxic problems.
- The capability for avoiding salt concentration in the crop root zone, which would require measures to avoid soil degradation (Muyen *et al.*, 2011; Xu *et al.*, 2010) as referred above in relation to the use of saline water.

Drip irrigation is often preferred. Then filtering is essential for appropriate functioning of the system. Media filters may be recommended due to their ability to remove turbidity and the ability to recover dissolved oxygen (Elbana *et al.*, 2012).

Aspects relative to health risk reduction have been discussed in the sections above and may be found in several references, such as WHO (2006a), Pescod (1992), and Westcot (1997). Toxicity hazards to the crops (Ayers and Westcot,

Table 6 Evaluation of the irrigation methods for irrigation with wastewater

Irrigation methods	*Basin irrigation and border irrigation*	*Corrugated basin irrigation*	*Furrow irrigation*	*Sprinkler irrigation*	*Micro irrigation: drip and subsurface irrigation*	*Microirrigation: microsprinkling and microspray*
Human contact (health hazard)	Likely to occur, mainly when water is controlled manually. Preventive measures including clothing requirements	Likely to occur when water is controlled manually, less with automation. Preventive measures including clothing are required	Likely to occur, when water is controlled manually, less when automation is adopted	Workers may have contact with wetted equipment. Small droplets will inevitably be spread by wind, so workers will always be at risk	Not likely to occur except contact with wetted irrigation equipment	Generally workers are not in the field when irrigating but they may have contact with wetted equipments. Small drops will inevitably be spread by wind, so workers will always be at risk
Contact with fruits and harvestable yield (contamination hazard)	Not occurring for tree crops and vines, most horticultural and field crops. May occur for low vegetable crops such as lettuce and melon	Not likely to occur because crops are grown on ridges	Not likely to occur because crops are grown on ridges	Fruits and harvestable yield are contaminated	Not likely to occur	Fruits and harvestable yield of vegetable crops may be contaminated. Less likely for under-tree irrigation with no wind
Salt accumulation in the root zone (salinity hazard)	Not likely to occur except for the underirrigated parts of the field when uniformity of water application is very poor	Salts tend to accumulate on the top of the ridge. Leaching before seeding or planting is required for assuring germination and plant establishment	Salts tend to accumulate on the top of the ridge. Leaching is required before seeding/planting	Not likely to occur except for the underirrigated parts of the field resulting from low uniformity of water application	Not likely to occur except for the underirrigated parts of the field resulting from low uniformity of water application	Not likely to occur except for the underirrigated parts of the field resulting from low uniformity of water application
Foliar contact (toxicity hazard)	Possible for bottom leaves in low crops (e.g., lettuce and melon) and fodder crops during first stage of annual crops	Exceptionally because crops are grown on ridges and water flows in furrows between them	Exceptionally because crops are grown on ridges	Severe leaf damage can occur affecting yields. Edible leaves would be contaminated	Not likely to occur	Severe leaf damage can occur definitely affecting yields of annual crops, but not for irrigation of trees and vines if drops are large enough and jets are oriented to the soil. Hazardous for edible leaves

Source: Reproduced from Pereira, L.S., Cordery, I., Iacovides, I., 2009. Coping with Water Scarcity. Addressing the Challenges. Dordrecht: Springer, p. 382.

1985) mainly require avoiding direct contact between the water charged with toxic ions and the crop leaves and other sensitive parts of the crop. Dilution of ion concentrations by mixing charged waters with freshwater is generally more costly than to select an irrigation method where such foliar contact is minimized.

Salts in wastewater used for irrigation are a source of soil pollution (Kalavrouziotis and Koukoulakis, 2012). The salt accumulation in the root zone is generally controlled by leaching of the salts from the root zone naturally when rainfall is abundant, or by applying a leaching fraction with the irrigation water. Leaching is discussed in the Section Leaching Requirements and Strategies for Controlling Impacts on Soil Salinity. Appropriate application of a leaching fraction depends on the irrigation method and the performance of the irrigation system. Practising overirrigation to be sure that salts are leached down from the root zone is common but leads to excessive percolation to the groundwater and may cause waterlogging. The groundwater quality can be degraded. Drainage has to be considered. However, problems may be controlled easily if the irrigation system is designed carefully allowing for control of volumes applied and for a uniform distribution of water over the field.

In summary, the safe use of wastewater in irrigation requires not only compliance with guidelines for the control of health risks, but also well-designed and efficiently managed irrigation systems. Several case study examples are provided in the literature (e.g., Oron *et al.*, 1999).

Monitoring and Control for Safe Wastewater use in Irrigation

Developing a program to promote safe crop production areas should occur alongside and as an alternative to crop restrictions. This can be achieved with a phased process as listed below:

1. Development and implementation of a sound program for water quality monitoring to evaluate the existing levels of contamination in the water and its use, including
   - appropriate recognition of observation areas and sites;
   - selection of water quality and contamination indicators;
   - selection of analytical methods and participating laboratories;
   - identification of sampling techniques; and
   - selection of field sites, considering
     - the water sources,
     - crop patterns, and
     - cropping and irrigation practices.
2. Conducting the field water quality monitoring program, evaluating the water quality data, and developing procedures to assess the levels of contamination. In addition, it is advisable to follow-up soil salinity aiming at protecting the soil resource.
3. Developing a database aimed at defining safe production areas and to control or regulate contaminated water use in vegetable or other high risk production areas.
4. Through the combination of field monitoring and exploring the database, to install certification programs that assure consumers on the quality and safety of production methods applied in a given area. The last phase is developing mechanisms to regulate the use of potentially contaminated water on high-risks crops, thus also supporting certification programs.

A follow-up of farmers' attitudes and behavior relative to the use of wastewater, particularly when it does not comply with the required guidelines, is also important because changes in water use aimed at health safety of consumers and workers can only be effective with the involvement of farmers and their institutions (e.g., Qadir *et al.*, 2010).

Desalination as an Alternative Source of Water for Agriculture

General Aspects and Treatment Processes

The main desalination processes (Fritzmann *et al.*, 2007; Li *et al.*, 2008) are listed below:

1. Thermal distillation (TD): When a saline solution is boiled, the vapor that comes off is pure water and when this is cooled (condensed), the resulting water contains no salt. Three types of thermal distillation units are used commercially, namely, multistage flash, multiple effect distillation, and vapor compression.
2. Electrodialysis (ED): If a current is passed through a saline solution, the different ions (cations and anions) in the solution will carry the current from one electrode to the other by drifting in opposite directions. If an ion-selective membrane is placed in this flow, say an anion-permeable membrane, only the anions will manage to pass through. ED is only an economical process when used on brackish water, and tends to be most economical at TDS levels of up to 4000–5000 mg l^{-1}.
3. RO: This is a membrane separation process in which the pressure of the water is raised above the osmotic pressure of the membrane. No heating or phase change is necessary for this separation, and the major energy requirement is for pressurizing the feed water. Seawater reverse osmosis (SWRO) has emerged as the leading technology for future seawater desalination facilities because of its relatively low energy consumption and produced water cost compared with thermal desalination technologies (Greenlee *et al.*, 2009). However, the perceived costs and energy requirements of seawater desalination continue to be a barrier to its implementation, especially seawater desalination for agricultural use. The stringent boron and chloride standards make the process more energy intensive than desalination for potable use. The total energy consumption by a state-of-the art SWRO facility producing agricultural irrigation water is in the range of 3–7 kWh m^{-3} of produced water (WRA, 2011). A combined seawater desalination process using emerging forward (FO) technology coupled with RO could potentially reduce the energy consumption of the seawater desalination process, and thus lower barriers to its implementation. The FO process is strictly direct osmosis across an RO-type membrane.
4. Desalination can use photovoltaic technology to provide electrical energy to operate standard desalting processes like RO or electrodialysis. Solar desalination has been receiving

considerable interest as it allows producing potable water in a sustainable way, which is particularly important in arid areas.

Use in Agriculture, Impacts, and Constraints

In the past, the high cost of desalinating and the energy required have been the major constraints on large-scale production of fresh water from brackish waters and seawater. However, desalinated water is becoming more competitive because desalinating costs are declining and the costs of surface water and groundwater are increasing. Nevertheless, the costs of desalinating water do not allow its full use in irrigated agriculture, with the exception of intensive horticulture for high-value cash crops, such as vegetables and flowers, mainly grown in greenhouses (Martínez-Beltrán and Koo-Oshima, 2006).

However, besides cost, there are other important drawbacks that prevent the wide use of desalinated water in agriculture, because when essential nutrients, including Ca, Mg, and S, removed during RO, are not reintroduced as observed by Ben-Gal *et al.* (2009) serious deficiencies in crops occur. The deficiency of calcium may harm the development of terminal buds and of root apical tips (Yermiyahu *et al.*, 2007), whereas magnesium is vital to the photosynthesis and protein synthesis operations of plants. Irrigation with low-magnesium-content water (10 mg l^{-1}) resulted in a decrease in leaf magnesium and chlorophyll contents, and the fruit produced was lacking in the basic nutrients like magnesium, calcium, and sulfate. This implies the need for additional fertilization (Birnhack and Lahav, 2007). Moreover, the very low buffering capacity of desalinated water can cause sudden changes in pH during fertilizer addition and can have a great impact on nutrient availability and ultimately on agricultural productivity (Yermiyahu *et al.*, 2007). In addition, the high levels of boron (B) have been found to cause boron toxicity in a number of B-sensitive crops (Yermiyahu *et al.*, 2007).

To overcome these negative impacts there are two possible strategies, either previously mineralizing the desalinated water, or blending desalinated and natural water in order to achieve the required quality. Ben-Gal *et al.* (2009) evaluated both the strategies for supplying these nutrients: Blending 30% saline water with 70% desalinated water brought Ca, Mg, and S minerals to satisfactory levels, whereas producing water with salinity of EC = 1.35 dS m^{-1} which led to satisfactory yields. These researchers noted that the environmental cost of the increase in irrigation water salinity through blending was substantial. Summarizing, fertilizer management must be carefully defined to avoid problems because of the absence of Ca, Mg, and other elements as well as to avoid problems of inhibition of use of nutrients due to unbalanced composition of the soil water and soil extract.

The main environmental impacts of water desalination relate to the production of a flow of brine containing the salts removed from the raw water. This needs to be disposed. Environmentally safe disposal depends mainly on the site of the treatment plant. If situated near the sea or close to brackish environments, such as estuaries, brine disposal is comparatively easier than that from inland desalinating facilities. In addition, it is worth mentioning that the energy consumption associated with the desalination process has an indirect environmental impact on greenhouse gas emissions.

Concluding Remarks

The use of low quality waters in agriculture, either drainage water or groundwater from low-quality aquifers, as well as the reuse of wastewater or desalinated water, need appropriate practices for controlling the impacts on the environment, on the crops, and particularly on human health. Crops, soil, and irrigation must be managed in agreement with characteristics of the used water in relation to the sensitivity of the crops, the fragility of the soils and environment, and, in case of wastewater, to avoid health consequences for workers and consumers. When appropriate technologies and management are applied, large benefits result from recycling and desalination for agricultural use helping to cope with water scarcity and drought. As described in this article, it is possible to develop strategies based on appropriate resource management and the adoption of the best available technologies, which support human health control, minimizing environmental impacts, and achieving positive farm returns, thus leading to sustainable development. Nevertheless, it is definitely required to develop educational and awareness programs that may make easy the adoption of best management practices and acceptability by the consumers.

See also: Climate Change: Agricultural Mitigation. Climate Change, Society, and Agriculture: An Economic and Policy Perspective. Computer Modeling: Applications to Environment and Food Security. Computer Modeling: Policy Analysis and Simulation. Critical Tracking Events Approach to Food Traceability. Economics of Natural Resources and Environment in Agriculture. Edaphic Soil Science, Introduction to. Farm Management. Food Safety: Emerging Pathogens. Global Food Supply Chains. Land Use: Catchment Management. Land Use, Land Cover, and Food-Energy-Environment Trade-Off: Key Issues and Insights for Millennium Development Goals. Land Use: Restoration and Rehabilitation. Plant Abiotic Stress: Salt. Plant Abiotic Stress: Water. Precision Agriculture: Irrigation. Root and Tuber Crops. Slum Livestock Agriculture. Soil: Conservation Practices. Soil Fertility and Plant Nutrition. Soil: Nutrient Cycling. Tree Fruits and Nuts. Water: Advanced Irrigation Technologies. Water: Water Quality and Challenges from Agriculture. World Water Supply and Use: Challenges for the Future

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Water: Water Quality and Challenges from Agriculture

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Glossary

Confined animal feeding operations (CAFOs) Raising animals in confined areas. All feed is brought to the animal.
Critical source areas Areas of a field, farm, or catchment that account for the majority of nutrient and sediment loss.
Ecosystem services Benefits people obtain from ecosystems. These include provisioning services such as food and water; regulating services such as flood and disease control; cultural services such as spiritual, recreational, and cultural benefits; and supporting services such as nutrient cycling.
Farm dairy effluent Liquid waste material derived from washing down cattle excreta from farm dairies and yards. It is usually land applied to capture its nutrient value.
Manure Dung collected from animal housing and applied to land for its nutrient value.
Slurry Semi liquid waste from animal confinement facilities that contains a high concentration of sediment. It is stored in tanks or ponds before land application for its nutrient value.

Introduction

The requirement to feed an expanding human population and make a profit has driven the expansion and intensification of agricultural production systems. The two main production systems, cropping and livestock, present different challenges to water quality due to contrasting geographic and climatic factors and management decisions. For example, unless animal manure is spread onto cropped fields, issues associated with fecal contamination of waterways is generally restricted to livestock or integrated crop–livestock systems. However, common among both production systems are losses of nitrogen (N), phosphorus (P), and sediment. Their effects vary from direct toxicity (e.g., nitrate-N; NO_3^--N) to indicators of, for example, poor esthetic and recreational values (N and P stimulation of periphyton (algae)) or inhibition of fish spawning (suspended solids). This article examines and highlights many of the processes, transport systems, and management decisions that exacerbate N, P, and sediment losses at a local scale and reviews some of the systems, strategies, and policy that influence these losses at a regional or national scale.

Water Quality Effects of N, P, and Sediment

The quality of stream water is strongly influenced by factors such as catchment bedrock, climate, soil type, and land use. Effects can be seen locally or downstream in larger rivers and lakes due to the cumulative effects of upstream inputs. Development of land ultimately results in a greater load of nutrients (N and P) and sediment entering streams, rivers, and lakes that stimulates plant growth. Research on the North American Great Lakes in the 1960s established that phytoplankton growth was driven by P inputs, rather than N or other elements. The same appears to be true for many lakes in Europe and for periphyton growth in streams and rivers worldwide (Hecky and Kilham, 1988; Vollenweider, 1968; McDowell *et al.*, 2009). Nutrient limitation occurs when the ratio of N:P differs from 7:1 (Redfield *et al.*, 1963), whereby, if on a weight basis, more than 7 units of N are present relative to P, biomass is limited by P. However, the Redfield ratio (7N:1P) should always be confirmed by measuring N:P in periphyton biomass.

Once cleared of adjacent trees, streams that were cool and weed free with ample shading become warmer and often choked with periphyton and aquatic weeds (macrophytes). In addition to being esthetically poor, some algae can be toxic and produce offensive odors and tastes in water that requires substantial treatment to be potable or suitable for contact recreation. Increased plant growth and photosynthetic production also causes large diurnal variation in dissolved oxygen and pH (Wilcock *et al.*, 2007). The respiration associated with decaying vegetation may cause dissolved oxygen concentrations to decrease below that necessary for aquatic life, whereas pH may increase in the afternoon, potentially inducing ammonia (NH_3) toxicity. Ammonium-N (NH_4^+) is nontoxic, but as pH increases, the ratio of toxic NH_3:NH_4^+ increases until both are approximately equal at a temperature of 20 °C and a pH of 9.4. A general rule of thumb is that when NH_4^+ concentrations reach 1–2 mg l^{-1}, unionized NH_3 concentrations can become toxic to stream life, especially invertebrates (Hickey and Vickers, 1994). Nitrate, usually the dominant form of N in freshwater (surface and ground), has also been shown to be toxic to invertebrates (Carmargo *et al.*, 2005) and some fish species (e.g., trout; Hickey and Martin, 2009). Consumption of nitrate (e.g., in groundwater used for drinking) has also been linked to methemoglobinemia in infants, whereas nitrite (and nitrosamines) has been linked to an increased prevalence of some cancers (WHO, 1996). This has been the basis of widespread policy aimed at restricting nitrate-N in potable water (e.g., 11.3 mg NO_3^--N, EU, 1991).

The effects of sediment loss are varied. Generally, water becomes more turbid due to light scattering by suspended particles (Davies-Colley and Smith, 2001), which inhibits the ability of fish to detect prey and may damage the respiratory structures of aquatic animals (Ryan, 1991). The deposition of fine sediments in gravel-bed streams can also smother the bed,

decreasing available habitat for invertebrates and fish and decreasing spawning success in native and introduced fish.

Sources of Nutrient and Sediment Loss: System and Regional Effects

Cropland versus Grassland

Agricultural systems can be categorized into cropping or grassland systems with or without animals that either graze forage outdoors or are confined to a barn and supplied feed. Most N and P loss originates as diffuse sources from agricultural production systems due, in part, to the success in identifying and mitigating point sources (Withers *et al.*, 2011). Losses of N, P, and sediment occur via runoff, termed here as the sum of surface runoff and subsurface flow (viz., subsurface runoff or leaching). Surface runoff from forests, grasslands, and other noncultivated soils carries little sediment, so the loss of P, which binds readily to soil and sediment, tends to be dominated by dissolved P, an immediately algal-available form (Sharpley, 1993). In contrast, nitrate, the main form of N loss, is soluble and hence largely lost in subsurface flow, although substantial losses of N can also occur in surface runoff via the erosion and loss of N in particulates.

Under cropping, the generation of N, P, and sediment is a function of inputs (for nutrients), soil and crop type, and their response to cultivation. The quantity, type, and timing of N and P inputs affect the rate at which both nutrients are taken up or lost to runoff. Poor application timing, when the crop is not growing, results in much of the applied N or P being available for loss. Application in forms that are not immediately plant available, or saturation of the soil solution with N or P, can also exacerbate losses. For example, the use of low water-soluble P fertilizers can decrease P losses in surface runoff compared with highly water-soluble superphosphate (McDowell *et al.*, 2010).

The differing yield, root morphology, and growth rates of various crops can be optimized (and crops rotated) so that both N uptake at depth is maximized and the area of soil exposed to surface runoff (and thus erosion of P and sediment) is minimized. The cultivation of crop land greatly increases erosion, and with it the loss of particulate-bound P (60–90% of total P; Sharpley *et al.*, 1995). Some of the particulate-bound P is not readily available but can be a long-term source of P for aquatic biota (Sharpley, 1993). Cultivation also stimulates the mineralization of organic matter, and with it organic N is transformed into nitrate that is potentially available for loss should drainage occur. The quantity of sediment lost from a field can be predicted by models, such as the revised universal soil loss equation (Renard *et al.*, 1997), which includes factors such as slope length, rainfall, soil type, and management. Under the same rainfall intensity and slope, water erosion tends to be greater in soils with a high proportion of silt and very fine sand and low organic matter. Increasing the time a field spends in fallow and the coincidence of either spring snowmelt or strong winds can also result in substantial topsoil loss (Wade and Kirkbride, 1998).

Under grassland, the loss of N, P, and sediment can vary just as much as under cropland. Under a cut and carry system (pasture is cut and removed from site), losses are expected to be very low. However, with the introduction of grazing animals, factors such as animal treading and excretal returns influence losses. Animal behavior and stocking rate can interact with catchment characteristics (e.g., slope or soil type) and exacerbate losses. For N, the main factors driving losses from grazed grassland are animal type and stocking rate as related to urine deposited on the ground. The N content of a urine patch greatly exceeds that required by grasslands, especially for dairy cattle but also red deer and sheep (Hoogendoorn *et al.*, 2011), which results in the surplus being lost should drainage occur (Ledgard *et al.*, 1999). For P, losses relate to soil P concentrations, animal treading, and inputs via fertilizer (see above), manure (covered in the next section), and excretal returns (McDowell *et al.*, 2007). The relative contribution depends on how well or poorly each is managed. For instance, soil P can contribute 80% of annual losses, especially if the soil contains little aluminum and iron oxides or if P concentrations are highly enriched (McDowell and Condron, 2012).

Although most low-producing permanent grasslands tend to lose little nutrients or sediment, high-producing grasslands, such as those often used for dairy farming, are cultivated and resown every 6–10 years. Storage of N as organic N in grassland (despite grazing) is well known. For instance, Whitehead *et al.* (1990) estimated some 600 kg N ha^{-1} had accumulated during grazing of a sward for 15 years. Once cultivated, much of this N could be mineralized and lost. In some cases, grassland is interspersed with a crop intended to be grazed *in situ* over winter or summer should feed be in short supply. However, the urine and dung deposited on a mature forage crop, together with the soil damage caused by treading and removal of the crop canopy, can result in large losses of nutrients and sediment (McDowell *et al.*, 2005).

Confinement versus Grazed Systems

An added complexity found in livestock production systems is the opportunity to intensively utilize housing, for example, confined animal feeding operations (CAFOs). Owing to economics, CAFOs tend to be larger but with less land than grazed operations (McDowell and Kleinman, 2011). The development of intensive and often specialized farming systems as CAFOs has led to regional surpluses of N and P due to imports in fertilizer and animal feed exceeding exports in farm produce (Kellogg *et al.*, 2000). For example, the application of manures and slurry is often guided by advice or regulation based on N content and the N requirement of crops. However, during storage, manure and slurry lose N in gaseous form (NH_3, N_2, and N_2O), lowering the N:P ratio and potentially resulting in oversupply and enrichment of soils with P. The enrichment of manures can be exacerbated by overfeeding of P. For example, Dou *et al.* (2003) surveyed 612 dairy farms in the Northeast USA and observed that dietary P concentrations for lactating cows ranged from 3.6 to 7.0 g kg^{-1} of feed dry matter. The mean concentration (4.4 g kg^{-1}) was about a third greater than that recommended by the National Research Council (2001) but seen as insurance to ensure good reproductive efficiency (Tallam *et al.*, 2005).

One of the first steps in decreasing P losses from CAFOs is, therefore, to balance P inputs with outputs at the farm, catchment, or regional scales. However, a near-zero P balance may maintain only the present rate of P loss if, for example, soil P concentrations are enriched and are above plant requirements (Woolsey *et al.*, 2007). This requires the use of mitigation technologies (see mitigation section), in addition to a negative P balance, to obtain a level of P loss that is environmentally and agronomically acceptable.

Dealing with manure is central to the successful environmental operation of a CAFO. The method, rate, and timing of application all influence losses of N and P. Surface application of manure concentrates P on the soil surface where it is prone to loss by surface runoff. In contrast, a direct ground injection system injects slurries containing $<12\%$ solids below the soil surface, minimizing surface runoff losses but also decreasing NH_3 emissions by up to 60% compared with surface application (Morken and Sakshaug, 1998). Elsewhere on the farm, NH_3 emissions, and hence N left that is available for loss to water, are dominated by manure storage systems, with the highest losses associated with anaerobic lagoons and the lowest losses with pits or bedded packs (Powell *et al.*, 2004).

The loss of N and P from surface-applied manures decreases within time, because application as rainfall washes manure nutrients into the soil. Crusting and invertebrate action also protect N and P from interacting with runoff (Webb, 2001; Kleinman and Sharpley, 2003; Vadas *et al.*, 2007). Hence, if applied at a time when runoff is frequent, losses of N and P can be large. Preedy *et al.* (2001) reported that 1.8 kg ha^{-1} of P was lost in runoff within 7 days of applying dairy slurry to grassland, whereas Mueller *et al.* (1984) reported that dissolved P concentrations in surface runoff decreased by 76% two months after manure was applied.

Moving from confinement to grazing can significantly alter the N loss profile away from manure and toward the high concentrations of NO_3^- that have been shown to leach from urine patches (Di and Cameron, 2000). The low proportion of a field covered, and patchiness in which urine is deposited, means that N-use efficiency is low, as supplemental N fertilizer is needed to ensure uniform sward production. Although the management of N losses from a farm can be addressed via a mass balance approach, factors such as stocking rate hold more relevance in grazed systems due to the dominance of N loss via urine patches. Globally, the literature on grazed farm N balances is varied, with some not accounting for biologically fixed N. However, when N fixation is factored into the mass balance, differences between outputs in grazing and CAFOs are not obvious and obscured by management factors (**Table 1**). Whether or not surplus N will translate into N losses in either system will depend on where and when animals are grazed and fertilizer or manure is applied (**Figure 1**).

For P and sediment, grazing offers some flexibility to maintain low soil test P concentrations and therefore minimize the application of manure (largely dairy shed effluent in grazed systems) and fertilizers. However, grazing operations are also limited by their ability to adjust to poor weather conditions, which can mean that they lose just as much P as a CAFO (**Table 1**). For example, if animals are grazing a field adjacent to a stream, there is a very high potential for runoff to reach the stream. Owing to a high concentration of animals that are rotated around fields on grazed dairy farms, the runoff (especially surface runoff) from a recently grazed field is most likely to be enriched in sediment (from treading damage to wet soils) and P. Furthermore, during spring, inclement weather means that effluent may have to be applied to wet fields potentially resulting in large losses of effluent P (e.g., 2–4 kg P ha^{-1} yr^{-1}; Houlbrooke *et al.*, 2004).

With more animals grazing grassland, erosion rates increase. For instance, Matthaei *et al.* (2006) found that stream beds surrounded by ungrazed tussock grassland had significantly less fine sediment than those with pasture grazed by dairy cattle or red deer. Much of the sediment was derived from the treading of grazing animals on stream banks, which destabilizes soils, causing slumping and loss of soil into stream channels (McDowell *et al.*, 2008). In contrast, stream channels in forested catchments tend to be wider than in grassland catchments, because sediment is temporarily stored by pasture grasses, resulting in narrow and incized channels that release sediment during flood events (Davies-Colley, 1997).

In general, sediment inputs to streams in agricultural catchments without extensive drainage networks may be dominated by sheet and rill erosion from cropland systems (Wischmeier and Smith, 1978) and by bank erosion in grazed pastures. For example, a Danish study found that streambank erosion contributed more than half the annual catchment export, much greater than forested or cropland areas (Laubel *et al.*, 1999). However, the response can also be seasonal with streambank erosion of greater importance than surface runoff or bed erosion in winter when animals were not intensively grazing grassland (due to a lack of grass cover or they were being housed) but less important in spring and autumn when grazing is occurring (McDowell and Wilcock, 2007). In cropland or grassland catchments that are artificially drained, Walling *et al.* (2002) found that 30–60% of sediment came from subsurface drains compared with 6–10% from channel bank erosion. A similar result was found for sediment-associated P entering a stream in an intensively farmed dairying catchment in Southland, New Zealand (McDowell and Wilcock, 2004).

Animal behavior can also contribute to sediment and P losses in grazed systems. Sheep tend to avoid streams, whereas red deer and cattle both like to stand in stream beds and tend to defecate more than when grazing or resting on a field (Collins *et al.*, 2007). Red deer also seek out ephemeral channels and dig them out until a wallowing area is created. This can add substantial P (3–4 kg P ha^{-1} yr^{-1}) and sediment ($>$ 1000 kg ha^{-1} yr^{-1}) to field-scale losses (McDowell, 2009).

A solution, at least for dairy systems where profit is better than grazed drystock farms, is to utilize components of both confinement and grazing farming systems – termed a hybrid farm. McDowell and Kleinman (2011) presented an argument that hybrid-grazing operations have a high degree of flexibility to adjust to catchment and climatic conditions. For example, they can choose to graze or not if grassland fields are too wet and surface runoff losses of P and sediment are likely. Measured data also suggest that less time spent grazing fields minimizes N losses, provided manure- and effluent-handling practices for the off-field part of the operation are well managed (**Table 1**).

Additional evidence shows that even within catchments dominated by grazed grassland, loads of N, P, and sediment vary

Table 1 Examples of nitrogen (N) and phosphorus (P) inputs, surplus, and losses to water (all kg ha^{-1} yr^{-1}) in confined, hybrid, and grazed dairy systems

System	Location	N added	N surplus	N lost	P added	P surplus	P lost	References
Confined (*dairy manure*[a])								
Mixed rotations	Sweden	270	164	9 (80)	24	2	0.20	Granstedt (2000)
Corn – winter	NY	415	–[b]	98.8[c]	108	–	18.4	Klausner *et al.* (1976)
Corn	WI	–	–	–	100	–	6.20	Mueller *et al.* (1984)
Corn – spring[c]	MN	248	–	6 (1)[c]	29	–	0.60	Young and Mutchlerm (1976)
Corn – autumn[c]	MN	387	–	6 (1)[c]	55	–	1.60	Young and Mutchlerm (1976)
Fescue – dry	AL	415	–	14 (2)	104	–	8.21	Reese *et al.* (1982)
Fescue – slurry	AL	403	–	16 (4)	112	–	13.55	Reese *et al.* (1982)
Fescue	SC	151	–	34 (3)	142		1.30	McLeod and Hegg (1984)
Hybrid								
60% grazing[d]	PA	193	143	45 (71)	15	6	1.00	Rotz *et al.* (2002)
100% grazing[d]	PA	175	125	35 (76)	11	3	1.00	Rotz *et al.* (2002)
50% grazing	Netherlands	496	253	52				Aarts *et al.* (2000)
30% grazing, 1.1 cows per ha	NY	136	27	25	10	3	1.90	Ghebremichael *et al.* (2007)
30% grazing, 1.8 cows per ha	NY	183	27	32	14	4	2.20	Ghebremichael *et al.* (2007)
Grazed								
0N, 3.3 cows per ha	NZ	178	−20	40	–	–	–	Ledgard *et al.* (1999)
200N, 3.3 cows per ha	NZ	338	18	79	–	–	–	Ledgard *et al.* (1999)
400N, 3.3 cows per ha	NZ	452	13	150	–	–	–	Ledgard *et al.* (1999)
Noneffluent block	NZ	–	–	31	38	–	0.65	Houlbrooke *et al.* (2008)
Effluent block	NZ	–	–	37	31	–	2.55	Houlbrooke *et al.* (2008)
Tile drained, 100N	NZ	–	–	34	50	–	0.16	Monaghan *et al.* (2005)
Tile drained, 400N	NZ	–	–	56	50	–	0.26	Monaghan *et al.* (2005)
2.9 cows per ha	NZ	215	–	32	61	–	1.41	Monaghan *et al.* (2008)
3.5 steers per ha[e]	Chile	67	–	41	40	–	0.01	Alfaro *et al.* (2008)
5.0 steers per ha[e]	Chile	67	–	26	40	–	0.01	Alfaro *et al.* (2008)

[a]Dairy manure applied to land and P lost in surface runoff.
[b]Not determined.
[c]Only surface runoff losses.
[d]Percentage of total farm area grazed by cattle from May to October.
[e]Steers grazing on dairy farm over winter.
Note: Numbers in parentheses refer to N lost as NH_3 gas.

considerably among different land use as denoted by stock class (Figure 2). This means that there is considerable scope for improvement, even for land used for dairying, which is perceived to lose more water quality contaminants than other land uses (Davies-Colley and Nagels, 2002). However, mitigation practices that decrease the impact of intensive agriculture on water quality vary in effectiveness and cost depending on a number of site-specific factors. Strategies need to be fully assessed (including cost) and matched to the farming system and catchment so that their efficacy is maximized and cost minimized.

Scope for Improvement

Technologies to Mitigate N, P, and Sediment Losses

Mitigation measures include those that instigate better management of existing resources/inputs, apply amendments to decrease losses, and mitigate losses after they have left the field. Mitigation strategies and expected decreases in sediment and nutrient loss are summarized in Table 2.

Agricultural nutrient management plans (NMPs) quantify nutrient imports and exports within agricultural systems. They provide a means to balance fertilizer inputs with crop nutrient requirements (i.e., outputs), thereby helping to prevent excess application (Genskow, 2012). Routine soil testing can provide a guide for applying nutrients and assist in identifying and mitigating against potential nutrient loss. In the United States, farmer's adoption of NMPs has generally been coupled with a decrease in overall farm nutrient inputs (Shepard, 2005), resulting in some decreases in nutrient loss but often financial benefits (Genskow, 2012).

The presence of good grassland or crop covers, and crop residues, help to minimize nutrient and sediment losses by decreasing soil erosion, surface runoff, and nitrate leaching (Gabriel and Quemada, 2011). Constantin *et al.* (2010), for instance, showed that cover crops can decrease NO_3^--N leaching by approximately 36–62%. Variation, however, results from changes in soil type (Fullen *et al.*, 2006) and tillage management (Deasy *et al.*, 2010). Soils under arable crops are most susceptible to structural damage due to the frequency with which they are tilled (Regan *et al.*, 2012). Furthermore, arable soils can have higher P concentrations than grassland soils due to the more intensive use (e.g., planting, fertilization, and removal) of crops. Minimizing tillage, usually through shallow cultivation (i.e., <10 cm), helps to conserve soil

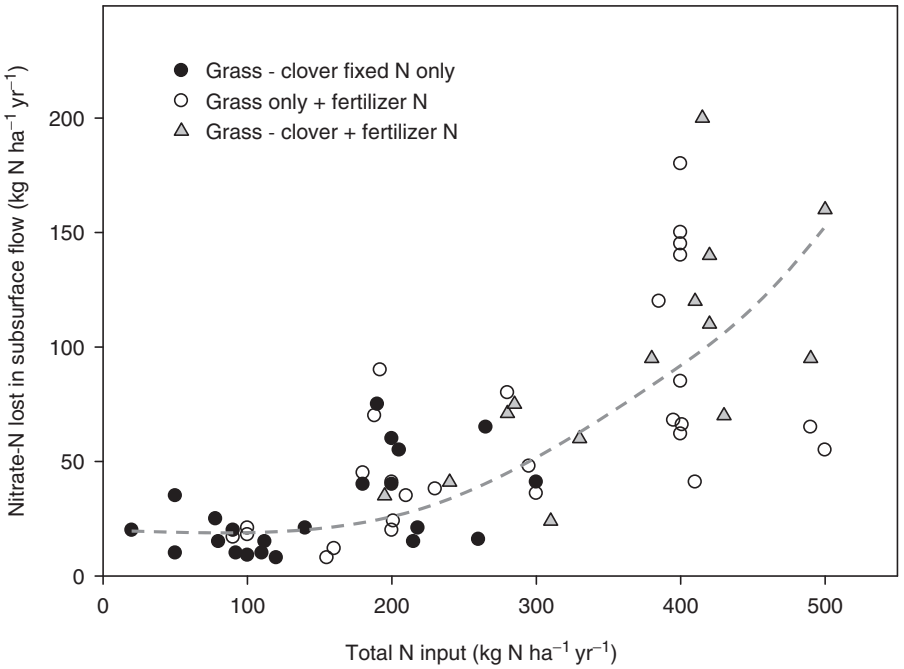


Figure 1 Nitrate-N lost in subsurface flow (leachate) from grazed grass – clover systems with and without N fertilizer and grazed grass systems with N fertilizer. Redrawn from Ledgard, S.F., 2001. Nitrogen cycling in low input legume-based agriculture, with emphasis on legume/grass pastures. Plant and Soil 228, 43–59.

carbon and promote aggregation, thereby reducing erosion and maintaining soil infiltration (Quinton *et al.*, 2010). Such techniques have been shown to decrease NO_3^--N and dissolved P losses by 49% and 17%, respectively (Kay *et al.*, 2009), and sediment loss by 78% (DeLaune and Sij, 2012). However, judiciously timed mechanical tillage and aeration can also decrease nutrient loss, particularly P, by facilitating greater redistribution of nutrients throughout the soil profile and increasing soil infiltration.

Fencing streams reduce streambank erosion and the direct deposition of excreta to streams by grazing animals (McDowell and Nash, 2012). In the Cannonsville Reservoir catchment, New York, fencing of streams decreased P loss by 32% (James *et al.*, 2007), whereas in New Zealand, a 90% reduction in total P concentrations was achieved once a headwater stream had been fenced off from red deer (McDowell *et al.*, 2008). Where fencing is impractical, provision of water troughs may help to reduce the time livestock spend near streams (Byers *et al.*, 2005).

At the field scale, surface runoff pathways may transport significant amounts of sediment and nutrient. Practices that intercept and slow flows, such as riparian zones, buffer strips, wetlands, and small reservoirs, encourage soil infiltration and sedimentation, thus decreasing sediment and nutrient loss. Wetlands have been shown to decrease NO_3^--N and P concentrations in surface runoff by 80% and 84%, respectively (Fisher and Acreman, 2004). However, large variation in removal efficiency is generally apparent (45–95% and 0–99% for N and P, respectively; Mitsch and Gosselink, 2007) in response to contaminant loading rate, hydraulic residency time, inflow concentrations, and substrate age (Fisher and Acreman, 2004). Riparian buffer strips, especially where trees are included, help to reduce light penetration, thereby limiting algal growth in streams (Hutchins, 2012). Vegetated buffer strips may decrease sediment and P loading by 9–97% (Bailey *et al.*, 2013) but can be easily circumvented and therefore ineffective if preferential or convergent flow paths operate (Verstraeten *et al.*, 2006).

Amendments added to soil and manures have also been used to decrease nutrient and sediment losses. Decreasing the solubility of P that would otherwise be available to surface and subsurface flow may be achieved through the application of aluminum sulfate to soils (McDowell and Houlbrooke, 2008; Smith *et al.*, 2001). Nitrification inhibitors (e.g., dicyandiamide (DCD)) are increasingly being used in grazing and cropping systems as a means to decrease NO_3-N leaching (Carneiro *et al.*, 2012; Di and Cameron, 2005; Monaghan *et al.*, 2009). DCD applied to grazed grassland in New Zealand was effective in decreasing N losses by 21–56% (Monaghan *et al.*, 2009). A similar decrease was reported (38–42%) following the application of cow urine to soil lysimeters (Dennis *et al.*, 2012). Nitrification inhibitors have also been applied in conjunction with the application of effluents. For instance, Corre and Zwart (1995) measured a 10% decrease in NO_3-N losses following DCD incorporation with a cattle slurry product. However, the effectiveness of DCD varies between soil types in response to drainage characteristics (Shepherd *et al.*, 2012) and soil temperature (Kelliher *et al.*, 2008). Recent detection of low-level residues of DCD found in New Zealand milk powder in 2012 has raised international consumer concern and is most likely to instigate international regulatory developments. Anionic

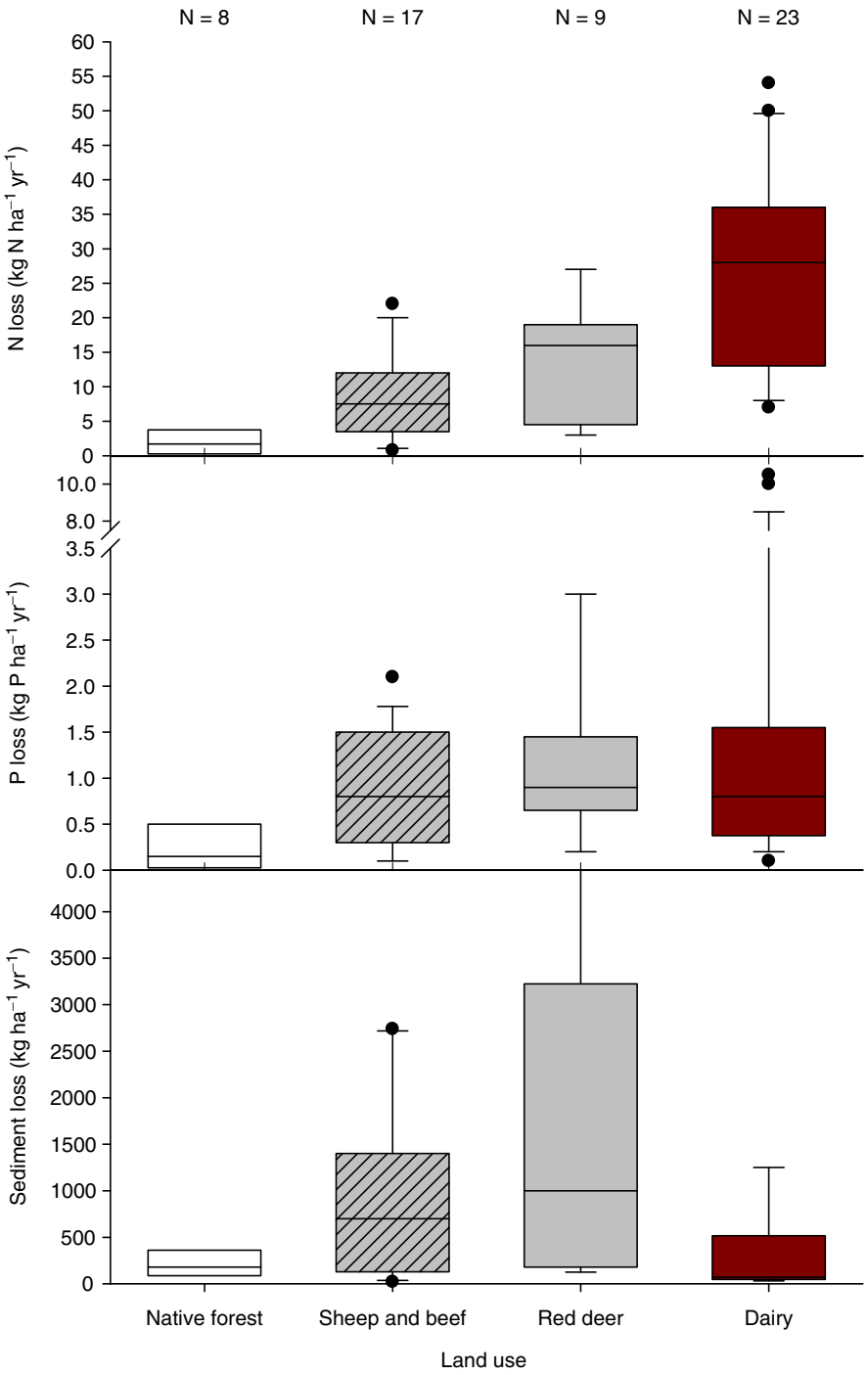


Figure 2 Nitrogen (N), phosphorus (P), and sediment annual loads for all catchment-scale studies conducted in New Zealand from 1975 to 2011 for different grazed grassland-based land uses compared with native forest with no agricultural development. Loads are shown as box plots showing the median and 25th and 75th percentiles (bottom and top parts of the box, respectively). The 10th and 90th percentiles are shown as whiskers and outliers. *N*=the number of studies in each stock class. Modified and updated from McDowell, R.W., Wilcock, R.J., 2008. Water quality and the effects of different pastoral animals. New Zealand Veterinary Journal 56, 289–296.

polyacrylamide has been applied to agricultural soils to control soil erosion by improving infiltration and aiding aggregate stabilization. Application has been reported to decrease sediment loss by 80–99% and improve infiltration by 15–50% (Sojka *et al.*, 2007).

As noted in the previous section, confinement of animals increases the emphasis placed on managing manures. Because the availability of manure N and P to loss in runoff declines exponentially with time since application, applying manure should be restricted to times of year when runoff is

Table 2 Mitigation strategies to control the impact of agriculture on water quality and examples of expected decreases in field-scale losses of nitrogen (N), phosphorus (P) and sediment when implemented

Mitigation strategy	*P (%)*	*N (%)*	*Sediment (%)*	*References*
Management				
Nutrient management planning[a]	5–25	15–25		McDowell and Nash (2012); Smeltz *et al.* (2005); Aarts *et al.* (2000); Oenema *et al.* (2012); Groot *et al.* (2006)
Stock exclusion from waterways	25–90	21–78	25–44	McDowell and Nash (2012); James *et al.* (2007); Owens *et al.* (1996); Miller *et al.* (2010); Line *et al.* (2000)
Restricted grazing	30–50	36–40	72	McDowell and Nash (2012); Curran-Cournane *et al.* (2011); Christensen *et al.* (2012); de Klein *et al.* (2006)
Effluent management	10–30	0–50		McDowell and Nash (2012); Monaghan *et al.* (2010)
Minimum tillage	17–90	49	78	Kay *et al.* (2009); DeLaune and Sij (2012); Sharpley *et al.* (1995)
Cover crops		32–62		Constantin *et al.* (2010)
Amendments				
Alum	5–30			McDowell and Nash (2012)
Polyacrylamide			80–99	Sojka *et al.* (2007)
DCD		21–56		Monaghan *et al.* (2009); Dennis *et al.* (2012)
Edge of Field				
Grass buffer strips	30–95	10–100	9–100	McDowell and Nash (2012); Bailey *et al.* (2013); Collins *et al.* (2009)
Dams and wetlands	0–99	45–95	77	McDowell and Nash (2012); Fisher and Acreman (2004); Mitsch and Gosselink (2007); Knox *et al.* (2008)

[a]Includes optimized fertilizer applications.
Abbreviation: DCD, dicyandiamide.

unlikely (including snowmelt). Manure on grazed dairies can often be in the form of dilute slurry called farm dairy effluent (<1% solids). Poor land application strategies (i.e., when soils are wet) can often result in significant N and P losses that can be avoided by increasing storage capacity and applying effluent at a low rate (e.g., <4 mm h^{-1}) to dry soil. This enhances the interaction and uptake of nutrients by the soil, thereby decreasing their loss (Monaghan *et al.*, 2010).

Many of the mitigation strategies employed on cropping farms, and farms using animal confinement, are applicable to grazing operations as well. However, additional or modified strategies that encompass grazing management are required. For instance, reduced soil infiltration due to animal treading can lead to increased nutrient loss in surface runoff (Curran-Cournane *et al.*, 2011). Strategies such as restricting the grazing time of animals to 3–4 h (for maintenance feeding) when soils are wet have been demonstrated to limit soil damage and maintain infiltration, particularly during spring (Christensen *et al.*, 2012; Houlbrooke *et al.*, 2009; Piwowarczyk *et al.*, 2011). Drewry (2003), for instance, showed that the practice of grazing cows on wet soils resulted in significantly lower soil macroporosity (12.8% v v^{-1}) relative to a short 3-h grazing period (16.3% v v^{-1}) and full stock exclusion (21.6% v v^{-1}). Avoiding traffic on wet soils also applies to cropping systems whereby the use of farm machinery can be restricted or modified to maintain soil porosity and decrease nutrient and sediment loss via reduced axle loading, larger tyres, and minimizing tillage to increase soil-bearing strength (Chamen *et al.*, 2003; Prikner and Grečenko, 2007; Silgram *et al.*, 2010; Tullberg, 2010). Positioning obvious infiltration-excess areas, like farm tracks, lanes, and gateways, so that flow from these areas does not reach waterways also decreases contaminant losses to streams (Monaghan and Smith, 2012).

Single strategies that mitigate a component of nutrient and sediment loss can often be easily implemented. However, greatest mitigation efficiency is usually achieved when measures are implemented collectively and in the right place and at the right time. The concept of critical source areas (CSAs) that describes areas where contaminant sources coincide with transport mechanisms to isolate small areas of a field, farm, or catchment that account for the majority of nutrient and sediment loss is now widely recognized (Pionke *et al.*, 1997). Mitigation strategies that target CSAs tend to be more cost effective than measures that use blanket mitigation strategies across an entire area (McDowell and Srinivasan, 2009).

Legislation/Subsidies and Socioeconomic Instruments

Financial and technical support provided to farmers by taxpayers and consumers has declined in recent years. For instance, globally, financial contributions from government and industry comprised 37% of farm gate profits in 1986–88, whereas in 2008–10 the contribution was 20% (OECD, 2012). Despite this, the need for strategies to decrease pollution of water, particularly those aimed at curtailing diffuse nutrient inputs to waterways, has become paramount. A diverse range of strategies has been established to decrease the impact of agriculture on water quality and is implemented on local, catchment, national and international levels. However, it is increasingly recognized that these strategies are both affordable and cost effective so that policy and water quality objectives can be met without undue financial hardship or

land-use change (Shortle *et al.*, 2012). This is aided by a mix of economic incentives, environmental regulations, and information transfer to farmers.

Most Organisation for Economic Co-operation and Development (OECD) countries have overarching National Water Policies that are usually implemented at the state/regional level. National Water Policies, for example, Clean Water Act (US), Water Framework Directive (EU), and Resource Management Act (NZ), generally minimize point source pollution, even those from intensive livestock operations, via a permitting system that aims to meet quality guidelines (Wisen and Porter, 2006). Control of nonpoint pollution is generally regulated to a lesser degree and encouraged through provision of financial and technical assistance (Feather and Cooper, 1995). In the United States, a voluntary approach has delivered mixed results (Shortle *et al.*, 2012; Williams, 2002), whereas in the European Union production-based subsidies (e.g., Common Agricultural Policy) have often failed in controlling nonpoint source pollution (OECD, 2012). In New Zealand, a lack of government subsidies (i.e., an open market) causes a greater reliance on making 'the polluter pay' as opposed to 'pay the polluter.' However, a combination of technical assistance and compliance has shown promise in curtailing pollution from nonpoint sources (Caruso, 2000). For example, an agreement called the 'Dairying and Clean Streams Accord' was signed in 2003 by local and national government and the major dairy company Fonterra. The Accord is both a statement of intent and a framework for actions to promote sustainable dairy farming in New Zealand. One major performance target was the exclusion of dairy cattle from 90% of waterways by 2012 (Ministry of Agriculture and Forestry, 2009). This has, by and large, been achieved primarily due to voluntary leadership shown by industry. However, meeting effluent management objectives has continued to be a greater challenge with only 73% of farms meeting compliance standards. Although command and control policies internalize more costs within industry, high rates of noncompliance remain a challenge. Regarding voluntary efforts, barriers such as the economic cost to the farmer relative to the perceived gain, the lack of knowledge within the industry, or personal unwillingness and on-farm labor shortages mean collectively these voluntary approaches may fail. Financial incentives offered to farmers may better facilitate changes in farm practices to protect water quality. In most OECD countries, support (where given) is increasingly being tied to conditions to which the producer is obligated to fulfill (e.g., water quality targets). For instance, between 2008 and 2010, 30% of OECD subsidies were conditional on some type of contribution from the receiver, as opposed to 4% in 1986–88 (OECD, 2012).

Payments for ecosystem services schemes also incentivize environmental actions that protect water quality rather than control activities through legal obligation. By placing a value on the provision of environmental services that have a definable social benefit, a user (or beneficiary) pays approach can be established (Mayrand and Paquin, 2004). In the United States, for instance, the Conservation Reserve Program, operating since 1985, incentivizes farmers to retire environmentally sensitive farmland from production or avoid agricultural practices that impact on water and air quality and wildlife diversity. In return, government- or community-raised funds are paid to participating farmers. Such schemes implemented around the world have, by and large, been successful, although some issues over farmer financial flexibility have been raised (Landell-Mills and Porras, 2002; Mishra and Khanal, 2013). Common to all schemes enacting water quality targets is the need for informed scientific objectives as well as an overarching view of biophysical and socioeconomic drivers that cause nutrient and sediment loss.

Lag Times and Legacy Issues

One of the major challenges for those trying to improve water quality in agricultural catchments is the fact that despite remedial or mitigation actions, losses of N, P, and sediment may not decrease to desired levels that result in satisfactory water quality outcomes. Lag times often account for this phenomenon. Reasons for a long lag time include the following: (1) targeting the wrong contaminant causing water quality impairment, (2) changing hydrology (e.g., more frequent storm events), (3) incomplete or insufficient uptake and implementation of mitigation practices, (4) slow or tortuous transport pathways (e.g., nitrate via deep groundwater), (5) transformation and storage (e.g., deposition of particles and uptake of dissolved P), and (6) poor measurement or monitoring regimes. Many of these factors may also be defined as legacy issues, i.e., a hangover of past action of management.

An example of a legacy effect is the transport of nitrate via groundwater to the catchment outlet. The scientific and technical advisory committee of the Chesapeake Research Consortium (STAC, 2005) concluded that due to the varying age of groundwater within the catchment (1–50 years), and that much of the water flowing into the Bay was from groundwater, a scenario to manage N in the catchment would cause a 50% decrease in baseflow nitrate concentrations but would require 35 years lead-in time. Until then, nitrate in the streams and rivers of the Bay will reflect the legacy of past N losses from agriculture and may increase in line with more recent intensification before decreasing.

Legacy issues have also been noted when large storms deliver significant quantities of sediment into river networks. As a result, it can take a long time before storage and remobilization processes interact with stream beds, banks, and floodplains to clear this sediment out. Land-use change, such as deforestation, is a major cause of the sediment input into many rivers. For instance, conversion into agriculture in the late 1800s of the Coon Creek catchment in Wisconsin, part of the upper Mississippi, caused large losses of sediment to occur. In response, soil conservation measures were initiated, but it is only in the last few decades that these have begun to decrease sediment loads (Meade and Moody, 2010).

Although processes like sediment size sorting, dispersion, and flocculation can complicate the modeling and estimation of sediment time lags and legacy effects, the picture is more complicated for P, which, in addition to particulate forms, contains dissolved inorganic and organic fractions. Once enriched, soil test P can take a long time to decrease to a concentration that has little potential for P loss to runoff. By not applying P fertilizer, McCollum (1991) found that it took >17 years for Mehlich-1 extractable P concentrations within a fine

sandy loam in an arable system in the United States to decline from 99 g P m^{-3} to the agronomic optimum value of 20–25 g P m^{-3}. Similarly, Dodd *et al.* (2012a) estimated that it would take 23–44 years for 4 grazed grassland sites in New Zealand to reach a proposed environmental limit for water extractable P in surface runoff following cessation of fertilizer P inputs. Other strategies, such as the application of N fertilizer, may increase the rate at which P declines (Dodd *et al.*, 2012b). However, in the interim, sufficient P may have escaped to cause permanent damage in receiving water bodies (Bennett *et al.*, 2001).

Phosphorus in sediments can persist and dissolve into the water column long after P inputs have declined. This is a common problem associated with wastewater treatment plants that discharge into stream and rivers, enriching and saturating sediment with P and negating the capacity of the stream to buffer any additional P inputs (Ekka *et al.*, 2006). In deep stratified lakes the supply of P from bed sediment, termed internal loading, can persist for decades. In shallow lakes, P may be flushed within a decade (Hamilton, 2012). Perhaps of more concern is the fact that P enrichment has also been found in groundwater (Holman *et al.*, 2008), leading to the possibility that P concentrations may eventually be enriched in baseflow, viz., nitrate.

The influence of legacy issues and time lags must be taken into account if mitigation strategies are to prove effective. If not, they will confound efforts to meet water quality targets. However, Meals *et al.* (2010) outlined a number of steps that would aid in setting an achievable target despite a lag time. These include the follwing: good characterization of the catchment and contaminant transport processes (i.e., establishing a lag time), careful placement of monitoring stations to maximize the chance of seeing a mitigation effect, and design of an appropriate sampling regime (incorporating spatial replication) to ensure statistical significance of the target contaminant. Together with good communication, these should ensure that stakeholders and regulators reach a consensus on a target.

Conclusions

The challenge of decreasing the impact of agriculture on water quality is large and only projected to increase as either more land is brought into production or higher outputs are achieved from existing land. Many of the challenges are a function of geography whereby farming systems have arisen to feed local populations without consideration of climate or catchment conditions. These have led to local specialization that has resulted in regional water quality problems that have been exacerbated by poor management decisions. Much of the focus to improve water quality has been on the manipulation of current management systems or the incorporation of on-farm or catchment-scale mitigation technologies. Globally, there are many initiatives that aim to buffer the economic impact of changing management and strategies whose aim is to quickly decrease nutrient or sediment loss without regard for cost. Alternatively, there has also been greater focus on strategies to mitigate nutrient and sediment losses while improving profitability. Whichever approach is used, consideration of the time lags involved will be an important factor that communities must recognize if desired water quality outcomes are to be achieved.

See also: Agricultural Policy: A Global View. Climate Change: Agricultural Mitigation. Farm Management. Government Agricultural Policy, United States. Land Use: Restoration and Rehabilitation. Soil: Conservation Practices. Soil Fertility and Plant Nutrition. Soil: Nutrient Cycling. World Water Supply and Use: Challenges for the Future

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The International Union for Conservation of Nature.

Weather Forecasting Applications in Agriculture

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Glossary

Agricultural meteorology The study of meteorological and micrometeorological conditions in agriculture.

Agrometeorological bulletin A report usually issued by the National Weather Services, describing current weather conditions and the evolution expected for the following week from the perspective of the agricultural management. An example is the Weekly Crop Bulletin published weekly by the US Department of Agriculture.

Climate outlook Often considered as a synonym of seasonal forecast.

Ensemble forecast A set of different forecasts all valid at the same forecast time usually obtained from running a forecast model many times starting from different initial conditions. This technique is used to quantify and convey uncertainties.

Probabilistic forecast Not to be confused with a probability forecast, it refers to the presentation of the outcome of ensemble predictions in probabilistic terms, usually a set of summary statistics.

Seasonal forecast A forecast with a lead time of 3–6 months.

Strategic decision problem An agronomic or agricultural problem referring to planning of agronomic relevant actions on time scales of a season, a year, or a few years.

Tactical decision problem An agronomic or agricultural problem that involves taking decisions on short time scales, usually of the order of days.

Introduction

Agricultural production and, more in general, the agricultural sector are highly sensitive to weather. Temperature, radiation, humidity, and wind conditions, along with water and nutrient availability, define the conditions for crop growth and yield formation. Weather further controls the emergence and spread of weeds, pests, and diseases and has a strong impact on animal health and performance (LeRoy Hahn, 1994). But weather is also important for the food chain as a whole. The storage of food and fodder can badly suffer from adverse weather conditions. Likewise the distribution of food and forage at local, regional, and global scale can be obstructed by the action of weather elements. As a result, prices of agricultural commodities are in many instances susceptible to variations in weather conditions (Shafer and Mjelde, 1994).

The establishment of agricultural practices reflects an evolving process in which optimal management strategies are identified with respect to what is perceived as normal climatic conditions. The occurrence of anomalous situations tend to move production systems away from the optimum, have negative effects on productivity, and prompt the implementation of protection plans. Knowledge of the forthcoming weather, even if imperfect, can markedly improve the preparedness and the capacity of farmers to cope with adverse conditions. Hence, possibilities to anticipate weather conditions have always been pursued by farmers and agricultural communities.

In earlier times, forecasting relied on the observation of natural phenomena, from which empirical rules could be inferred. A well-documented example is the practice of indigenous Andean communities to predict summer rainfall from changes in the apparent brightness of stars in the Pleiades during the spring (Orlove *et al.*, 2000). In this particular case, predictive capabilities are rooted in the fact that star visibility decreases in the presence of high-level clouds, which is often the case during El Niño years. Along the western slopes of the Peruvian Andes, the establishment of El Niño is indicative of reduced rainfall during the following growing season, a situation that eventually delivers the rationale for forecasting.

The availability of forecasts has dramatically improved in modern times, especially during the twentieth century with the establishment of the science of numerical weather prediction. The possibility to access weather forecasts at a wide range of spatial and temporal scales reflects the enormous advances that have taken place in the field since the first successful numerical integration experiments and the completion of the first operational numerical weather forecasts in the 1950s (Harper *et al.*, 2007; Lynch, 2008). Various aspects have contributed to these advances.

On the one hand, there have been impressive improvements in the quality of prediction systems, owing to a more realistic representation of the atmospheric and oceanic dynamics, the adoption of more refined numerical algorithms and parameterization schemes, advances in data acquisition and data assimilation, and the creation of multimodel ensemble forecasting systems (e.g., Palmer *et al.*, 2004). Such developments would not have been possible without an equally extraordinary increase in computational resources.

On the other hand, observational, technical, and scientific programs initiated by United Nations agencies, especially the World Meteorological Organization (WMO) along with the Intergovernmental Oceanographic Commission and the United Nations Environment Programme, were vital for establishing the global monitoring needed for a better understanding of climate variability at the seasonal scale. Ultimately, it is thanks to the Tropical Ocean Global Atmosphere program, a major component of the World Climate Research Program operated by the WMO, that the first successful predictions of El Niño by a prototype coupled ocean–atmosphere model system was delivered in the 1980s (Zebiak and Cane, 1987).

But weather forecasting has profited from decisions at the institutional level as well. An example is the establishment of

the European Centre for Medium-Range Weather Forecasts (ECMWF). With far-reaching implications is also the recent decision by the WMO to promote seasonal forecasting through the so-called WMO Global Producing Centres (GPCs) for Long-Range Forecasts. Currently, twelve weather forecasting services from all over the world are officially designated as WMO GPCs, including:

- The Bureau of Meteorology (BOM) (Australia)
- China Meteorological Administration (CMA)/Bejing Climate Center (BCC) (China)
- Climate Prediction Center (CPC), National Oceanic and Atmospheric Administration (NOAA) (United States of America)
- ECMWF (United Kingdom)
- Japan Meteorological Agency (JMA)/Tokyo Climate Centre (TCC) (Japan)
- Korea Meteorological Administration (KMA) (Korea)
- Meteo-France (France)
- Met Office (United Kingdom)
- Meteorological Service of Canada (MSC) (Canada)
- South African Weather Services (SAWS) (South Africa)
- Hydrometeorological Centre of Russia (Russia)
- Center for Weather Forecasts and Climate Studies/National Institute for Space Research (CPTEC/INPE) (Brazil)

Other major centers providing global seasonal forecasts are:

- The International Research Institute (IRI) for Climate and Society (United States of America)
- Asia-Pacific Economic Cooperation (APEC) Climate Center (APCC) (Republic of Korea)

Also worth mentioning in this context is the creation of consortia for promoting high-resolution limited area modeling, such as the Consortium for Small-Scale Modeling (COSMO) and High Resolution Limited Area Model (HIRLAM) consortium. There is little doubt that the possibility to run forecast models at spatial resolution of the order of 2–10 km opens new perspectives regarding the application of forecasts in agriculture.

Traditionally, the dissemination of weather forecasts has taken place at a national or regional level. Forecasts issued by the national weather services are distributed through various channels, including newspapers, radio and television, and, more recently, the Internet and mobile telephones. Nonetheless, in many areas of the word access to forecasts remains limited. This is especially the case concerning the access to seasonal forecasts and climate predictions in developing countries. Adoption of seasonal forecasts has suffered not only from inadequate distribution but also from the lack of interaction between providers and users. The creation of the so-called Regional Climate Outlook Forums (RCOFs) starting in the 1990s has considerably improved on this situation.

Types of Forecasts, Forecast Characteristics, and Formats

There are two basic kinds of forecasts that are potentially of use for agriculture: public forecasts, on the one hand, and more specialized forecasts, advisories, and other products, on the other hand (Flynn, 1994; Das *et al.*, 2012). Traditionally, both types of forecasts have been issued by national weather and agrometeorological services. However, in recent years an increasing number of private companies have appeared on stage, offering a portfolio of products that is of great interest for farmers and consultants.

General-purpose forecasts can be classified according to the time span embraced by the prediction. In broad terms the following categories can be identified:

- Nowcasts: Forecasts with a lead time of between 1 and 6 h issued for a limited geographic area at high spatial resolution through consideration of persistence and evolution of patterns identified on satellite or radar imageries and the analysis of local observations. Owing to their very short lead time, nowcasts are most valuable for early warning.
- Very short-range forecasts: Predictions of the local weather for up to 12 h that are concerned with the evolution of smaller scale, short-lived, often intense weather phenomena, such as tornadoes, hail storms, and flash floods. Very short-range forecasts are issued at high spatial resolution using a variety of techniques, including extrapolation of trajectories and the interpretation of model-based, limited area forecasts.
- Short-range forecasts: Predictions of the evolution and movement of large- and medium-sized weather systems with lead times of 12–72 h.
- Medium-range weather forecasts: Deterministic or probabilistic (ensemble) predictions referring to the evolution of synoptic weather patterns out to 7–10 days, obtained from the integration of numerical models of the atmospheric circulation.
- Monthly or extended forecasts: Monthly or extended forecasts usually refer to predictions with a lead time longer than the 10 days achievable with medium-range forecasts but not exceeding the monthly scale. These forecasts are issued at the global scale and with moderate spatial resolution.
- Long-range or seasonal forecasts: Probabilistic forecasts at the global scale extending out to 3–6 months. As with monthly forecasts, seasonal forecasts are produced by an integrated forecasting systems built around a coupled ocean–atmosphere model. Because variability at these time scales can be considered as a fundamental aspect of climate, the expression 'climate outlook' is often used as a synonym of 'seasonal forecast.'

Depending on lead time, forecasts are either deterministic or probabilistic. Deterministic forecasts are obtained from a single integration of the differential equations that describe the dynamics of the atmosphere and are appropriate for predicting weather a few days ahead. Beyond approximately 1 week, the evolution of the state of the atmosphere becomes unpredictable in a deterministic sense. Reasons for this are the chaotic nature of the atmosphere and the sensitive dependence of its dynamics to initial conditions (Lorenz, 1993). Therefore, rather than considering a single evolutionary path, forecasts with lead times exceeding the week are issued by running atmosphere (or coupled ocean–atmosphere) models several times with slightly varying initial conditions.

Increasing lead time is usually associated with decreasing quality of the forecasts (Das *et al.*, 2012). In the case of monthly and seasonal forecasts, forecast quality is higher for temperature than for precipitation and higher in regions where the local effects of the El Niño-Southern Oscillation (ENSO) are strongest. According to Murphy (1997), quality should be defined with reference to the totality of the statistical characteristics of the forecasts, the verifying observations, and their joint distribution. Specific aspects of quality can then be recovered from the conditional and marginal distributions associated with the factorization of the joint distribution. Accuracy and skill are often considered in verification studies. The former refers to the average degree of correspondence between individual forecasts and observations and is typically quantified in terms of the mean square error or the mean absolute error. The latter is a relative measure of accuracy that compares the accuracy of the actual forecast with the accuracy of a naïve forecasting system based, for example, on climatology or persistence.

Monthly and seasonal ensemble forecasts of temperature and precipitation are usually presented in a probabilistic format. Very common is the adoption of three equiprobable categories to represent below-normal, normal, and above-normal conditions. Graphically, forecasts are often provided as probabilities for each category or, as in the case of the climate outlooks prepared and disseminated by the IRI for Climate and Society, as probabilities of the most likely category.

As opposed to public forecasts, specialized forecasts and agrometeorological advisories are issued for crop growers and livestock producers. Besides predictions for relevant weather elements (maximum and minimum temperature, precipitation probability and expected rainfall amounts, sunshine duration, cloud cover or radiation, air humidity, dew, and wind), they usually deliver farm management information and early warnings (Flynn, 1994). Farming aspects include the handling of crop production (planting, harvesting, postharvest processing, measures to abate the risk of frost or heat stress, irrigation, and fertilization); the control of weeds, pests, and diseases (spraying operations); and the management of animal production (environmental requirements, nutritional needs, and health).

Agrometeorological advisories are issued for the local or regional scale. The common practice is to provide forecasts for the following 5 days, which represents a minimum time lapse for implementing preventive measures and capitalizing the benefits of favorable periods. The preparation of advisories is usually carried out by trained agricultural meteorologists at national weather services in consultation with a panel of experts in agricultural and animal sciences, viz., agronomists, soil scientists, entomologists, horticulturists, plant breeders, cattle farmers, and plant and animal pathologists (Das *et al.*, 2012).

In addition to public forecasts and agrometeorological advisories, other types of products can provide useful information to growers, consultants, and authorities. In view of the enormous implications that drought has on agricultural production and food security, drought bulletins play a key role for agricultural risk management (Sivakumar *et al.*, 2005; Sivakumar and Motha, 2007). Drought bulletins are available from the National Weather Services, specialized Drought Monitoring Centers, and other public institutions. Examples are:

- The Australian BOM, which releases the Rainfall Deficiencies and Drought Information).
- The US CPC maintained by the National Center for Environmental Predictions as part of the NOAA, which publishes a Drought Monitoring that relies on the Palmer Drought Severity Index (PDSI) and Crop Moisture Index (CMI).
- The US Drought Mitigation Center associated to the University of Nebraska, which issues the US Drought Monitor;
- The Drought Early Warnings available from the Climate Services Centre run by the Southern African Development Community (SADC).
- The Intergovernmental Authority on Development (IGAD) Climate Prediction and Applications Centre (ICPAC) with seat in Nairobi, which is responsible for the dissemination of the Africa Drought Monitor.
- The International Water Management Institute (IWMI), which issues the Southwest Asia Drought Monitor.

Agricultural Decision Problems and Forecasting Applications

There are a variety of agricultural decisions that benefit from weather forecasts (e.g., Wilks, 1997; Meza *et al.*, 2008; and Das *et al.*, 2012) and it has become customary to distinguish between tactical and strategic applications (Stepanski *et al.*, 2012).

Tactical applications refer to short-term decisions that are concerned with field operations on time scales ranging from a few hours to up to a few days. Examples of tactical decision problems are the following:

- Field preparation – This is a preseason activity that aims at providing optimal conditions for sowing, seed germination, and the early stages of growth. Field preparation thus addresses soil water and nutrient availability. Elimination of weeds is also part of the preseason program. In dryland farming, the goal is often to achieve an optimum soil water profile. Consideration of soil moisture is also a key element in relation to trafficability. Therefore, precipitation forecasts play a major role at this stage, but forecasts for temperature and radiation are important in connection to workability. To be effective, preseason forecasts should have a validity period of not less than a week (Das *et al.*, 2012).
- Sowing/planting – Soil temperature, soil moisture, and radiation are all important elements in relation to seed germination and the establishment of the crop. Specific requirements vary across crops and varieties and depend on soil characteristics. Frost occurrence around sowing can adversely affect seedling development and low temperatures can increase the bolting risk. However, alternating temperatures assist the germination of many species of seeds and frost during presowing can improve soil quality. For rainfed agriculture in the seasonally arid tropics, the decision of sowing is connected to the onset of the rains. Rules to determine the optimum time for sowing are

generally formulated with respect to amount and duration of the first rains and the risk of a potentially false start in the absence of significant rain after sowing (Stern *et al.*, 1982; Sivakumar, 1988). Thus, short-range forecasts of temperature are usually appropriate at the sowing time, whereas in rainfed agriculture the decision of sowing benefits most from medium-range precipitation forecasts.

- Irrigation – When the natural availability of water and nutrients limits crop development, irrigation and the application of mineral or organic fertilizers are essential to sustain growth and obtain adequate yields at harvest. The economic problem is often one of minimizing at the same time crop damages and costs. In practice, irrigation is scheduled taking into account the crop water requirements. Standard procedures for assessing crop water requirements have been developed by the Food and Agriculture Organization of the United Nations starting in the 1970s, with a major update in the 1990s related to the adoption of the Penman–Monteith equation as a basis for computing the reference evapotranspiration (Allen *et al.*, 1998). Data for daily minimum and maximum temperature, solar radiation, air humidity, and wind are required on input to the latter; accordingly, forecasts for the same variables are needed to support this specific decision problem. In addition, day-to-day precipitation forecasts can be used to avoid unnecessary irrigation and limit the environmental problems associated with fertilizer and pesticide leaching (Wilks, 1997).
- Fertilization – As nutrient access through the roots is controlled by the dilution process at the surface and the movement of the solutes through the soil, scheduling of fertilization primarily relies on short-term precipitation forecasts.
- Harvesting – In cereal and forage production, the basis for scheduling harvest operations is a consideration of grain or hay quality at harvest and drying requirements for post-harvest processing. Because of the risk of mold formation, too high a moisture content makes crop products unsuitable for storage. But too low a moisture content is also undesirable because it reduces the profits. Premature harvests have thus negative impacts on grain quality, as have delayed harvests in persisting cool wet weather conditions (Hayward, 1987). Early harvest may often be the preferred option, even though there is a risk of incurring in extra costs for artificial drying. Clearly, both short-term and medium-range forecasts are needed for a successful planning of harvest operations.
- Frost protection – In orchards, frost protection is necessary when air temperatures fall below the freezing point in nights characterized by clear-sky conditions and radiative cooling. This is often the case in hilly or mountainous regions, where cold air tends to pile up in the valleys, and in the humid subtropics. When and where active or passive measures of frost protection can be put in place, this is usually done on the basis of forecasts for minimum temperature. Traditional approaches to forecasting minimum night temperatures rely on extrapolating weather data for the past day by empirical methods (Georg, 1978). More accurate predictions can be obtained from simulations with physically based models (e.g., Lhomme and Guilioni, 2004) or more advanced statistical techniques (e.g., Ghielmi and Eccel, 2006). In many areas of the world, the availability of short-range, limited area forecasts at very high spatial resolution provides further support for frost protection activities.
- Management of pests – Insects are an important class of pests and affect crop production and orchards alike. At the global level, climate is the dominant factor determining the abundance and distribution of harmful insects. Insects are cold blooded; development rates and number of generations per season are determined by temperature (Logan *et al.*, 2006). Excessive temperatures, however, reduce insect longevity and increase mortality. Wind conditions are important in relation to insect migration, suggesting that some aspects of insect control may profit not only from short-range temperature forecasts but also from a broader palette of forecasts products.
- Foliar application of agricultural chemicals – The treatment of crops and trees with chemicals, such as herbicides, insecticides and fungicides, growth regulators, and hormones, can be necessary to prevent damages from pests and diseases and support the development of crops. Forecasts are needed not only to schedule and guide the application of such products but also to avoid unwanted environmental pollution. An accurate evaluation of time schedule and applied amounts is often of economic relevance, because the costs of chemicals can easily become very high. Timely forecasts of air temperature and humidity can be translated into forecasts of leaf temperature and wetness, which are the critical elements for guiding the application of chemicals. Depending on the application technology, knowledge of the expected wind conditions is also of great importance, with emphasis on possible changes in speed and direction during the time of the application. As precipitation can dilute and wash off the chemicals, the decision of whether and how to apply chemicals can further profit from short-term precipitation forecasts.
- Transport of agricultural products and animals – In market-oriented agriculture, products are usually transported over long distances. Conditions during transport must be such as to prevent deterioration of the products. Temperature has a strong impact on product quality, and therefore temperature forecasts are decisive for planning transport, especially when substantial temperature variations are expected along the transport routes. In relation to the carriage of living animals, weather is even more decisive, because it has a direct impact on animal health. Finally, severe weather conditions can disrupt transportation itineraries. Hence, forecasts of storms, floods, and the like are vital in regions frequently exposed to weather hazards.
- Forage production – Although hay making can be considered by the same tokens as crop production, in grazing systems the objective is to maintain equilibrium between herbage demand and supply. Hence, the decision problem is primarily the one of a judicious choice of feeding patterns. This requires monitoring sward conditions and adjusting stocking densities. Weather forecasts should, therefore, be aligned with both aspects. Considerations of forage quality are equally important, because they can have profound implications for animal health (Hugh-Jones, 1994).

- Forage preservation – The traditional approach to forage preservation is by drying the harvested biomass in the field during one or more days. Rain occurring during this time can damage the forage and extend the drying period. In the latter situation, the forage may become exposed to further damage from later rains. In areas where the skill of rain forecasts out to 5 days is sufficiently high, hay-making reliability can markedly profit from short-range forecasts (Dyer and Baier, 1981).
- Livestock management – As with crops production, animal production is exposed directly and indirectly to variations in weather conditions. Aspects of animal farming that require the attention of farmers are nutrition, performance and production, reproduction, and health. Direct effects of weather are those that influence in first place the thermal regime of animals. Accordingly, weather elements that need to be monitored and forecasted are dry-bulb temperature, air humidity, solar radiation, and wind. Indirect effects of the atmospheric environment on animals are those relative to forage production and the outbreak of diseases.
- Diseases in animal production – A variety of viral, bacterial, and parasitic diseases can harm animal health and cause severe setbacks in animal production. Economic losses can be particularly severe in the tail of epidemic outbreaks. In tropical regions, there is a considerable interest in vectorborne diseases that are mediated by hot-weather insects, such as mosquitoes, midges, mites, flies, and others. As mentioned by Hugh-Jones (1994) various forms of livestock parasitism and diseases can be forecasted using weather data. An example is congenital hypocuprosis of sheep, which can be forecasted from the number of days with snow cover. From an epidemiological perspective, forecast applications should primarily address prevention and intervention programs. Successful applications have been documented, for example, in relation to the outbreak of foot-and-mouth disease in northern countries (Hugh-Jones, 1994), an airborne disease whose progress in mid-latitudes and high latitudes is mostly related to weather.

As opposed to tactical applications, strategic applications are concerned with decision problems on time scales ranging from the intraseasonal to the multiannual and with spatial scales exceeding the regional. There are a number of atmospheric circulation phenomena that are responsible for seasonal to interannual fluctuations in temperature and rainfall, including the Madden–Julian Oscillation (Madden and Julian, 1972), the ENSO (Philander, 1990), and the North Atlantic Oscillation (Hurrell *et al.*, 2003). The first is largely responsible for intraseasonal variability in the tropical atmosphere. The second is a phenomenon of coherent variations in sea surface temperatures, atmospheric pressure, and atmospheric convection with a characteristic time scale of a few years that has its roots in the equatorial Pacific Ocean but whose implications for precipitation are felt at the global scale. The third is a swing in the atmospheric sea-level pressure difference between the Arctic and the subtropical Atlantic associated with changes in seasonal mean heat and moisture transport across the Atlantic that has significant impacts on terrestrial, agricultural, and marine ecosystems.

Strategic decision problems are encountered in a wide spectrum of agricultural activities (Meinke and Stones, 2005):

- Intraseasonal decisions – These include decisions concerned with logistics (for instance, scheduling of planting and harvest operations) and crop management (for instance, fertilizer application and the use of pesticides). Time scales involved extend from 2 to 6 months.
- Seasonal decisions – Choice of crop type and herd management. Time scales involved are of between 6 months and 1 year.
- Seasonal to interannual decisions – Choice of crop sequences and stocking rates. Time scales involved are of between 6 months and 1 year.
- Annual to interannual decisions – For instance, decisions in relation to crop rotations. Time scales involved are of between 1 and 2 years.

In market-oriented agriculture, insurance solutions to hedge weather risks and associated economic losses represent one of the many options available for risk management. Complementing traditional insurance instruments, such as hail insurances, weather derivatives, and index-based weather contracts, have gained in attractiveness in recent years (Jewson and Brix, 2005). In many situations, hedging weather with derivatives or indexed-based products represents a perfect complement to weather forecasts. On the one hand, weather derivatives can, namely, support forecast-based decisions by covering the costs of taking action and by hedging the possibility that a forecast is wrong. On the other hand, weather forecasts play an important role for the valuation of weather derivatives, because the availability of forecasts reduces the range of outcomes that needs to be covered by the insurance. Regarding cropping systems, contracts usually extend over the growing season. In this case, combination of medium-range forecasts and seasonal predictions is often the preferred option, in spite of the challenge to merge the two types of forecasts.

Operational Aspects

Successful application of weather forecasts and climate outlooks to agricultural decision problems are conditional on matching the specific requirements of each application. Relative to crop production and animal farming, information is usually needed at the local and daily scale. Knowledge of temperature and precipitation is at times sufficient to resolve management questions, but in many cases predictions for a more specific set of variables are needed.

These requirements are basically satisfied by short-term forecasts obtained from nesting limited area models into regional and global models. This strategy, also denoted as dynamical downscaling, requires substantial computing resources and has gained relevance in the operational context only during the recent decades. Examples of operational high-resolution systems are COSMO, a European enterprise with partners from Germany, Switzerland, Italy, Greece, Poland, and Romania , and HIRLAM, a European initiative as well, with partners from Denmark, Estonia, Finland, Iceland, Ireland, the Netherlands, Norway, Spain, and Sweden.

The handling of operational seasonal forecasts, however, is less straightforward for at least four reasons:

- first, their coarse spatial resolution, which is typically of the order of a few degrees longitude and latitude;
- second, the need to correct for systematic errors in the predicted fields, which arise from increasing model drifts as the integration is carried forward (Stockdale, 1997);
- third, the need to recover daily values from the average statistics used for the dissemination of the forecasts;
- and fourth, the need to retrieve information not directly available from the forecasts.

Enhancing spatial resolution and bias correction are often tackled with the help of the so-called statistical or empirical spatial downscaling (Wilby and Wigley, 1997; Wilks, 2011). To be precise, statistical downscaling refers to a full array of techniques that comprises among others analog techniques, multiple linear regression, singular value decomposition analysis, canonical correlation analysis, the application of empirical orthogonal functions, and nonlinear statistical methods, such as artificial neural networks. Irrespective of the specific procedure adopted in practice, at the core of statistical downscaling is the development of transfer functions for mapping large-scale predictors (a set of explanatory variables) onto different realization of the local weather.

The simplest option for bias correction is to calibrate the forecast using additive or multiplicative shifts. The former are suitable for temperature, the latter for precipitation. For temperature, this solution provides in general satisfactory results because temperature biases are for the most part caused by an improper representation of the earth's orography in weather forecast models. For precipitation, applying multiplicative shifts to forecasted daily precipitation often provides only limited benefits because atmospheric models are known to systematically overestimate the frequency of rainfall events, especially in the extratropics (e.g., Frei *et al.*, 2003). Systematic errors in predicting the succession of wet and dry spells can have serious consequences for assessing crop water requirement or for scheduling fertilizer or chemical applications. This calls for correction strategies that are able to recover both the persistence of wet and dry spells and the transition probabilities between wet and dry spells, which is not the case for standard bias correction algorithms (Ines and Hansen, 2006; Schmidli *et al.*, 2006).

A more sensible alternative is to generate synthetic daily weather conditioned on the forecasts (Hansen *et al.*, 2006). Weather generators of either the Richardson type (Richardson, 1981) or the serial type (Racsko *et al.*, 1991) have been around since the 1980s. Nowadays they are often integrated into crop models and decision support systems and are increasingly used in forecast applications, not seldom in combination with statistical downscaling (Feddersen and Andersen, 2005). Stochastic weather generators are computationally inexpensive, making it possible to simulate weather sequences of basically unlimited length, out of which subsamples with the desired statistical properties can be taken (Calanca *et al.*, 2011).

Once the postprocessing of the forecasts is completed, the content of the forecasts can be passed to specialized models that translate the information into operational terms. Well known are crop simulation models (Alexandrov, 2002), but process-based or empirical models exist for a full range of agricultural activities, including models for the management of water resources, for forecasting frost occurrence, for the control of pests and diseases, for predicting grain quality of cereals, for predicting the moisture content in hay, for the control of storage facilities, and the like.

Many of these models came into life as specialized tools for a narrow field of applications. However, recognizing the need for integrated approaches, efforts have been undertaken to assimilate sectorial models into comprehensive decision support systems (Weiss, 1994). Examples of sophisticated modeling environments that can address multiple tasks are:

- The Agricultural Production Systems sIMulator (APSIM) (Keating *et al.*, 2003), a highly advanced simulator of agricultural systems that can address a range of plant, animal, soil, climate, and management interactions. APSIM has been used for the assessment of the value of seasonal climate forecasting and in a broad range of other applications (support for on-farm decision making, farming systems design for production or resource management, analysis of supply chain issues in agribusiness, development of waste management guidelines, risk assessment for policy making, and as a guide for research and educational activities).
- CropSyst (Stöckle *et al.*, 2003), a multiyear multicrop simulation model developed as an analytic tool to study the effects of management on the productivity of cropping system and their environmental implications, including soil erosion. Apart from the crop simulation component, the CropSyst suite provides access to the following: ClimGen, a climate generator based on WGen; Arc/Info – CropSyst Cooperator, a utility for running simulation models over Arc/INFO GIS map coverages; CANMS, the Comprehensive Animal Nutrient Management System for the simulation of on-farm production of animal fodder; and the Rural watershed model, a component for erosion and a runoff simulation at the regional scale.
- The Decision Support System for Agrotechnology Transfer (DSSAT) (Jones *et al.*, 2003; Hoogenboom *et al.*, 2012). DSSAT is a software application program that comprises crop simulation models for more than 28 crops and is supported by database management programs for soil, weather and crop management as well as experimental data. DSSAT has been used for many applications ranging from on-farm and precision management to regional assessments of the impact of climate variability. The target user group is wide, embracing researchers, educators, consultants, extension agents, growers, and policy and decision makers.
- A model for Epidemics Prediction and Prevention (EPIPRE) (Zadoks, 1981, 1984). It is one of the whole family of models that can be used for guiding the application of chemicals in response to the appearance of pests, diseases, and weeds in cropping system and orchards. EPIPRE is a well-documented example of a decision support system that has effectively been operated by the producers (Weiss, 1994).
- The Gossypium Simulator/Cotton Management Expert system (GOSSYM/COMAX). Initially developed in the

wake of the economic competition for synthetic fibers in the 1980s (Lemmon, 1986). Its crop component, GOSSYM (Baker *et al.*, 1983), is one of many models available for simulating the growth of cotton (genus *Gossypium*). GOSSYM is a comprehensive software that has widely been used in commercial agriculture to aid in making crop management decisions (McCauley, 1999), especially in the Southeastern United States, where a network of automated weather stations has been run by producers to collect the necessary input data. Recently, GOSSYM has been coupled to the Climate extension of the Weather Research and Forecasting model (CWRF) (Liang *et al.*, 2012). This integration makes it possible to run GOSSYM in a spatially distributed setup.

Economic Value of Weather Forecasts

Many investigations conducted in the past have shown that real economic benefits can be obtained from the adoption of weather forecasts. Surveys of case studies can be found in Omar (1980), Mjelde *et al.* (1989), Johnson and Holt (1997), Wilks (1997), Hill and Mjelde (2002), Meza *et al.* (2008), and on Richard Katz's web page. In *ex ante* assessments, the potential benefits are valuated before the forecasts are actually adopted by the end users. In contrast, *ex post* assessments seek for outcomes following adoption. In both cases, the focus is on the benefits for individual actors, but examples are also available that address the economic benefits at the market level.

Another distinction often considered in assessments of the economic value of weather information is the one between descriptive studies (e.g., Stewart, 1997), in which the decision process is analyzed in the light of actual user responses, and prescriptive studies (e.g., Wilks, 1997), in which the decision process is analyzed within the framework of a normative theory. In practice, prescriptive studies seek to identify optimal solutions by looking at how forecasts should be used in theory, often assuming that the decision makers act to maximize monetary returns. Although assumptions are, as a rule, idealized, the results can sometimes be used to formulate explicit recommendations. This can help improving decisions made by users who face the uncertainties regarding future weather conditions.

The rationale for the economic valuation of weather forecasts has often been explained with the help of so-called static cost/loss models (Richardson, 2012). These are prototype models in which the decision maker can only choose between two possible actions ('protect' against 'do not protect') and future events are limited to the occurrence, or not, of adverse weather conditions. Taking protective action always generates costs, whereas losses have to be assumed if protective action is not taken in spite of adverse weather. Given a probability of adverse weather conditions from climatological data, the optimal decision is to protect if this probability exceeds the ratio between costs and losses (whence the name), and not to protect otherwise.

As pointed out by Katz and Murphy (1997a), the possibilities to apply static cost/loss models to real situations are limited because:

- Forecasts are usually far from perfect, which requires introducing a measure of the forecast quality (Murphy, 1997). It can be shown that in this case there exists a quality threshold below which the additional information provided by the forecast has no value, no matter its content.
- Decision-making problems are dynamic, rather than static. This means that current decisions influence future actions. An orchardist, for instance, must decide in spring whether to protect or not, because this is the season when the buds are potentially exposed to damage from freezing temperatures. But because buds that are damaged or killed cannot recover and decisions taken in spring affect the rest of the season, the problem has clearly a dynamic component.
- Price levels cannot be assumed as constant, and in practice discount rates need to be taken into account.
- Successive realization of the weather are only ideally independent from one other, because most weather variables do show a tendency for persistence on time scales that may differ from variable to variable.

Access to Long-Range Forecasts in Developing Countries

Developing countries are most vulnerable to climate variability at the seasonal scale. In tropical countries, where food production still relies on rainfed cropping systems, changes in seasonal rainfall patterns can threaten the livelihood and the survival of entire communities and societies. The occurrence of a record-breaking El Niño event at the end of 1997, with its impacts on the global scale, helped raising the awareness of the public opinion concerning the societal implications of climate variability at the seasonal scale. Because operational El Niño forecasts were already available at that time, it also fostered the belief that long-range forecasts can significantly contribute to cope with negative impacts of weather vagaries.

The adoption of forecasts by farmers and rural communities, stakeholders, advisory and agricultural extension services, as well as authorities, is facilitated if the forecasts are tailored to meet the information requirements by the various end-user groups. It was at a Workshop on Reducing Climate-Related Vulnerability in Southern Africa (Victoria Falls, Zimbabwe, October 1996) that the idea of creating consensus forecasts for the benefits of society through the interaction of different actors was first discussed. That workshop marks the birth of the RCOFs (Ogallo *et al.*, 2008). Socioeconomic sectors addressed by RCOFs are numerous, including public health, energy production, and disaster risk prevention. Still, agriculture, food security, and the management of water resources have received special attention.

The RCOF process is strongly supported by the WMO and has profited much from efforts undertaken by the WMO to establish the GPCs for Long-Range Forecasts. RCOFs are primarily participatory initiatives at the regional scale that seek to deliver relevant information through the involvement of National Weather Services, regional climate institutions, and other local partners. The development of targeted seasonal forecasts in the context of RCOFs involves several steps (Ogallo *et al.*, 2008):

- determining the critical seasons for the various socioeconomic sectors and establishing a timetable for the delivery of forecasts;

- convening the expert team, including meteorologist and stakeholder representatives;
- reviewing current climate conditions and forecasts for the season ahead;
- reviewing the possible impacts of current and future conditions on human activities within the region of interest and formulating response strategies;
- producing consensus forecasts that will be applied and fine-tuned by the national weather services;
- developing strategies for a timely delivery of the consensus forecasts;
- accompanying the process of the adoption of the consensus forecasts, evaluating their practical outcomes.

Aside from issuing consensus forecasts, RCOFs have also taken a leading role in capacity building, offering training sessions for regional meteorologists. In addition, RCOFs have offered a platform for reviewing impediments to the use of information, discussing reasons for lack of reliability in the delivered information, and evaluating strategies for new developments.

The level of acceptance of the consensus forecasts, and the RCOFs as a process, has not always been high. In a review of first experiences in Southern Africa, Patt *et al.* (2007) identified several critical issues. For instance, restrictions on credits by the banks and an overly cautionary attitude by the farmers were observed in Zimbabwe in response to likely dry conditions that were forecasted in relation to the 1997 El Niño episode. This led to frustration when people realized later in the season that rain amounts would actually come close to normal. Similarly, the decision to delay the humanitarian programs for several million people facing a food crisis in Ethiopia and neighboring countries during 2000 can be explained by the skepticism in the forecast issued in 1999 for drier-than-normal conditions during the spring of 2000 in the Greater Horn of Africa.

Nonetheless, in many cases the adoption of forecasts from RCOFs has been seen in a positive light (Patt *et al.*, 2007). For instance, in Mali and Zimbabwe farmers benefitted from receiving timely forecasts along with support from local extension services. Successful stories have also been reported from other continents. This is the case for Western South America (Martínez Güingla and Mascarenhas, 2009), where considerable efforts have been undertaken to develop community information systems with the support of mobile telephone companies and to translate climate bulletins in native languages. As a result, by 2009 long-range forecasts distributed via the Internet, e-mails, radio, and mobile telephones were available to more than 60% of the potential users, and this number has been steadily increasing ever since.

To sum up, the success or failure of RCOFs has been a matter of fulfilling, or not, three basic conditions:

- Availability of personalized forecasts. Although communicating forecast uncertainties by adopting a probabilistic framework is important (Ogallo *et al.*, 2008), experiences gained from the African RCOFs have clearly indicated that there is scope to provide guidance to the interpretation of probabilistic seasonal forecasts (cf. also Wilks, 2000).
- Commitment at the institutional level. The development of consensus forecasts that do effectively meet the end-user needs has been possible whenever user groups and organizations have taken an active role in the RCOFs. But when participation in planning the agendas and in forecasting activities has been little, forecasts have remained at a very general level.
- Implementation of capacity building and training programs.

Although the RCOFs were pioneered in Africa, their expansion to other areas of the world has been rapid. Currently, the following RCOFs are in operation:

- The Greater Horn of Africa COF (GHACOF), which covers the countries Burundi, Djibouti, Eritrea, Ethiopia, Kenya, Rwanda, the Sudan, Somalia, Tanzania, and Uganda and is being coordinated by the Intergovernmental Authority on Development (IGAD) Climate Prediction and Application Center (ICPAC), Nairobi, Kenya.
- The Southern Africa COF (SARCOF) coordinated by the SADC Drought Monitoring Centre (SADC-DMC), Gaborone, Botswana and covering the fourteen countries comprising the SADC Member States, namely, Angola, Botswana, the Democratic Republic of Congo, Lesotho, Malawi, Mauritius, Mozambique, Namibia, Seychelles, South Africa, Swaziland, Tanzania, Zambia, and Zimbabwe.
- Prévision Saisonnière en Afrique de l'Ouest (PRESAO), the West Africa COF coordinated by the African Centre of Meteorological Application for Development (ACMAD), Niamey, Niger.
- The Southeast of South America COF (SSACOF) with participation from Argentina, Brazil, Paraguay, and Uruguay. As opposed to other RCOFs, SSACOF is coordinated by each of the participant countries by rotation, and the latest seasonal outlook and related products may be obtained from the web sites of the respective National Weather Services.
- The Western Coast of South America COF (WCSACOF) coordinated by Centro Internacional para la Investigación del Fenómeno de El Niño (CIIFEN, International Research Centre on El Niño), Guayaquil, Ecuador, with participation of Bolivia, Chile, Colombia, Ecuador, Perú, and Venezuela.
- Foro Regional del Clima de América Central (FCCA) the COF for Central America, which sees the participation of Belize, Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica, and Panamá.
- CARICOF, the COF for the Caribbean area established in 2012 after closure of the CCOF (Caribbean FOC). Participating countries are Antigua, Bahamas, Barbados, Belize, Cayman Islands, Cuba, Dominica, Dominican Republic, Grenada, Guyana, Haiti, Jamaica, Montserrat, Panama, St. Vincent & Grenadines, St. Lucia, St. Kitts, Suriname, and Trinidad and Tobago.
- The Pacific Islands COF (PICOF) coordinated by the Australian Bureau of Meteorology and covering Cook Islands, Fiji, Kiribati, Niue, Papua New Guinea, Samoa, Solomon Islands, Tonga, Tuvalu, and Vanuatu. Participants use a statistical-based model to run the seasonal climate outlooks for the upcoming 3-month period.
- The Forum On regional Climate monitoring, assessment and prediction for Regional Association II (Asia) (FOCRAII), which covers all the countries in Asia and is coordinated by the BCC of CMA.

- The South Asian Climate Outlook Forum (SASCOF) established in 2009 and covering Afghanistan, Bangladesh, Bhutan, India, Maldives, Myanmar, Nepal, Pakistan, and Sri Lanka.
- The Southeastern Europe COF (SEECOF) launched in 2008 with participation of Hungary, Slovenia, Croatia, Serbia, Bosnia, Montenegro, Albania, the Former Yugoslav Republic of Macedonia, Greece, Turkey, Bulgaria, Romania, Moldova, Israel, Cyprus, Armenia, Georgia, and Azerbaijan.
- The North Eurasia COF (NEACOF) supported by the North Eurasia Climate Center (NEACC), which was launched in 2011 for the benefits of the Commonwealth Independent States (CIS) of Armenia, Azerbaijan, Belarus, Kazakhstan, Kyrgyzstan, Moldova, Russian Federation, Tajikistan, Turkmenistan, Ukraine, and Uzbekistan.

Outlook

In spite of continuous improvements of agronomic practices and field technologies and advances achieved through breeding programs, agriculture remains and will continue to remain sensitive to weather and climate variability. Positive impacts of climate change are expected in a few places but in many areas agriculture is most likely to become more exposed to climatic risks in the future. Access to targeted and reliable weather forecasts will, therefore, play a main role in risk management and remain an important component of decision making, with respect to both tactical and strategic issues.

The skill of deterministic forecasts out to 10 days has significantly improved over the past decade. Moreover, owing to a tremendous increase in computer resources it is now possible to produce limited area forecasts out to 2–3 days at a spatial resolution suitable for applications at even the farm scale. Still, much remains to be done to improve the predictability at the seasonal time scale. This requires a better understanding of ocean–atmosphere interactions and of the large-scale modes of variability in both components of the climate system.

During the last decades, much attention has been paid to understanding and predicting the onset and development of the various phases of the ENSO, but unfortunately advances in the prediction of other large-scale phenomena have been slow or inexistent. This is the case for the North Atlantic Oscillation (NAO) (Bojariu and Gimeno, 2003), a large-scale mode of climate variability that has significant impacts on terrestrial ecosystems (Hurrell *et al.*, 2003). Well documented with respect to agriculture is the link between the NAO wheat yield quality in the United Kingdom (Kettlewell *et al.*, 1999; Atkinson *et al.*, 2005), an example demonstrating how much the agricultural sector in Europe could benefit from reliable NAO forecasts.

For various reasons, translating seasonal forecasts into agricultural terms remains a challenge. As noted by Garbrecht *et al.* (2005), in many areas of the world farmers, consultants and policy makers do not have access to appropriate information, mainly because specific impact indicators and relevant decision variables cannot be directly inferred from the public forecasts usually available. Improving on this situation will require scientific advances, for instance, in relation to downscaling.

The integration of different models into end-to-end information systems will also play an important role for the supply of specific information (Weiss, 1994; Doblas-Reyes *et al.*, 2006). The participation of the end users will be essential in relation to the design of expert systems (Fraisse *et al.*, 2006). Needs for information technologies in developing countries may differ from those in developed countries and have to be addressed by the climate community to close the gap in accessing information in different areas of the world. One of the recommendations formulated by the workshop of the WMO Expert Team on 'Climate Change/Variability and Medium- to Long-Range Predictions for Agriculture' organized by the Commission for Agricultural Meteorology (CAgM) of the WMO and the Queensland (Australia) Department of Primary Industries and Fisheries (DPI&F) in 2004 was that information transfer to low-tech end users in developing countries should be considered with priority in the future (Garbrecht *et al.*, 2005).

Participatory approaches at all stages of forecast dissemination will remain crucial for ensuring a better understanding and interpretation of the forecasts (McCrea *et al.*, 2005). As underlined by the experiences gained in the context of the RCOFs, lack of trust in the forecasts has been a major impediment toward their adoption in the past (Patt *et al.*, 2007). Clearly, capacity-building activities are required to make sure that end users are sufficiently confident in the forecasts (Garbrecht *et al.*, 2005). Farmers, stakeholders, consultants, and other actors have to learn not only to take better decisions given a forecast that will eventually be verified but also to handle situations that arise from taking decisions on a wrong forecast or not taking decision at all. In this respect, communicating forecast uncertainties is of paramount importance. This will require among other things extending ensemble forecasting techniques to agricultural decision support systems (Challinor *et al.*, 2013).

A more systematic examination of the value of weather information is also needed, especially concerning agricultural applications of seasonal weather forecasts in developing countries. *Ex ante* assessments (e.g., Sultan *et al.*, 2010) have disclosed potential benefits. But possibilities to investigate actual applications have been limited by the fact that in many areas open access to operational seasonal forecasts have only recently become reality. Shifting the focus from *ex ante* to *ex post* impact studies will provide a more realistic basis for assessing the value of seasonal forecasts (Meza *et al.*, 2008).

Further Readings

Given the breadth of the topic, it is not possible to cover all aspects related to the application of weather forecasts in agriculture, nor it is possible to cover selected aspect in depth within the space provided by a single article in this Encyclopedia. Turning to other sources of information is, therefore, necessary to gain a more thorough understanding of specific issues.

Yet, providing a comprehensive review of the relevant literature is also an almost impossible task. Too many are the books, peer-reviewed articles, and reports that have been and are continuously published on subjects that, in a way or the

other, are of relevance in the context of weather forecasting for agriculture. The following list of references is, therefore, intended only as a starting point.

Books

- *Agricultural Meteorology*: Griffiths (1994) and WMO (2012) are two complementary handbooks on agricultural meteorology that perfectly serve the purpose of getting acquainted with the many facets of the application of weather forecasting to agriculture. They were both written by recognized experts and contain a wealth of further readings. Topics covered are among others the basics of agricultural meteorology, crop and animal production, pest and disease management, forestry, aquaculture and fisheries, desertification and other environmental risk, and decision making and economics.
- *Application of seasonal forecasts and climate predictions to agriculture*: Hammer *et al.* (2000) summarize the Australian experience in the application of seasonal forecasts to agricultural decision problems. It provides a nice introduction to seasonal forecasting, addresses agricultural applications at the farm scale as well as large-scale issues related, for example, to agribusiness and government policy. Sivakumar and Hansen (2007) report the outcomes of the 'International Workshop on Climate Prediction and Agriculture – Advances and Challenges' and a 'Synthesis Workshop of the Advanced Institute on Climatic Variability and Food Security,' reviewing the advances made up to 2007 in seasonal predictions and their applications for the management of agricultural enterprises. Harrison *et al.* (2007) provide a summary of the experiences collected by the 'Working Group on the Use of Seasonal Forecasts and Climate Predictions in Operational Agriculture,' an expert panel established in 1999 by the Commission for Agricultural Meteorology of the WMO. The book discusses case studies from different areas of the world, including South America, Africa, Australia and the Pacific, and South Asia.
- *Climate and weather risks*: Sivakumar *et al.* (2005) and Sivakumar and Motha (2007) are excellent complements to Sivakumar and Hansen (2007) with a focus on natural disasters and the management of climate risks in agriculture. All three books adopt a similar layout and include the discussion of numerous case studies from all over the world.
- *Weather forecasting*: Kalnay (2003) and Warner (2011) both introduce the science of numerical weather prediction and many of the aspects associated with the operational implementation of weather forecasting.
- *Forecast verification*: Jolliffe and Stephenson (2012) is the first book that deals specifically and comprehensively with the assessment of forecast quality and forecast value.
- *Value of weather forecasts*: Katz and Murphy (1997b) provide a nice overview of issues that need to be considered in assessing the economic value of weather and climate forecasts. It contains a short introduction to the science of weather prediction, a systematic treatment of forecast quality, the basics for assessing the value of weather information, and a review of descriptive and prescriptive decision studies. The latter includes a useful selection of case studies from the agricultural sector.
- *Weather derivatives*: Jewson and Brix (2005) review the meteorological, mathematical, statistical, and financial issues that arise in the pricing and managing of weather derivatives. Although this topic has only been mentioned in margin in the present article, it is included here because many are the applications of weather derivatives to agriculture, other components of the food chain, and the trading of agricultural commodities.
- *Statistics in the atmospheric sciences*: Wilks (2011) authored a textbook on statistical methods needed to describe and analyze atmospheric data and forecast products. Although rigorous, it is accessible for a wider audience than more mathematical-oriented books, such as by von Storch and Zwiers (1999).

Reports

- Several technical notes of interest are published on a regular schedule by the WMO and more specifically by its Commission for Agricultural Meteorology.
- Articles of relevance for the subject can also be found in the WMO Bulletin, the official journal of the WMO. The latest issue of the WMO Bulletin and archives are available online.

Special Issues (In Reversed Chronological Order)

- *Agricultural and Forest Meteorology*, Vol. 170, 2013. A special issue on 'Agricultural prediction using climate model ensembles' (http://www.sciencedirect.com/science/journal/01681923/170, accessed 02.12.13).
- *Climate Research*, Vol. 33, No. 1, 2006, Special issue 16 on 'Advances in applying climate prediction to agriculture,' which reports on the results of the international Climate Prediction and Agriculture (CLIMAG) program initiated in 1999 by the WMO. It is a complement to the book edited by Sivakumar *et al.* (2007) (http://www.int-res.com/abstracts/cr/v33/n1/, accessed 02.12.13).
- *Climatic Change*, Vol. 70, Issue 1–2, 2005, A special issue devoted to 'Increasing climate variability and change; reducing the vulnerability of agriculture and forestry' (http://link.springer.com/journal/10584/70/1/page/1, accessed 02.12.13).
- *Philosophical Transactions of the Royal Society B*, Vol. 360, No. 11, 2005, Discussion meeting issue 'Food crops in a changing climate' (http://rstb.royalsocietypublishing.org/content/360/1463.toc, accessed 02.12.13).
- *Tellus, Series A*, Vol. 57 A, Issue 3, 2005, A special issue devoted to Research Conducted in the Framework of the Project DEMETER (Development of a Multimodel Ensemble System for Seasonal to Interannual Climate Prediction) (http://onlinelibrary.wiley.com/doi/10.1111/tea.2005.57.issue-3/issuetoc, accessed 02.12.13).
- *Agricultural Systems*, Vol. 74, No. 3, 2002, A special issued dedicated to 'Applying seasonal climate prediction to agricultural production' (http://www.sciencedirect.com/science/journal/0308521X/74/3, accessed 02.12.13).
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International Workshop on Agrometeorology in the 21st Century: Needs and Perspectives, 15–17 February 1999, Accra, Ghana (http://www.sciencedirect.com/science/journal/01681923/103/1-2, accessed 02.12.13).

Glossaries and Dictionaries

- A very useful compilation of glossaries and dictionaries can be found at https://www.meted.ucar.edu/resources_gloss.php (accessed 02.12.13).
- *Glossary of the Australian Bureau of Meteorology*, http://www.bom.gov.au/lam/glossary/ (accessed 02.12.13).
- *The American Meteorological Society's Glossary of Meteorology* (Glickman, 2000).
- *Elsevier's Dictionary of Climatology and Meteorology* (de Lucca, 1994).

Online Teaching Resources

- *Learn about Meteorology*, a web-based platform by the Australian Bureau of Meteorology (http://www.bom.gov.au/lam/, accessed 02.12.13).
- *MetEd* (https://www.meted.ucar.edu/index.php), a free collection of learning resources operated by The Comet® Program (http://www.comet.ucar.edu/) in the context of the University Corporation for Atmospheric Research (UCAR) (http://www.ucp.ucar.edu/) (all links accessed 02.12.13).

See also: Animal Welfare: Stress, Global Issues, and Perspectives. Climate Change: Agricultural Mitigation. Climate Change and Plant Disease. Climate Change: Animal Systems. Climate Change: Cropping System Changes and Adaptations. Climate Change: Horticulture. Climate Change: New Breeding Pressures and Goals. Climate Change, Society, and Agriculture: An Economic and Policy Perspective. Computer Modeling: Applications to Environment and Food Security. Ecoagriculture: Integrated Landscape Management for People, Food, and Nature. Food Security: Postharvest Losses. Food Security: Yield Gap. Plant Abiotic Stress: Temperature Extremes. Plant Abiotic Stress: Water. Simulation Modeling: Applications in Cropping Systems

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World Water Supply and Use: Challenges for the Future

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Glossary

Climate change Refers to any change in climate over time, irrespective of whether it is due to natural variability or as a result of human activity. This usage differs from that in the United Nations Framework Convention on Climate Change, which defines 'climate change' as: "a change of climate which is attributed directly or indirectly to human activity that alters the composition of the global atmosphere and which is in addition to natural climate variability observed over comparable time periods."

Climate variability Refers to variations in the mean state and other statistics (such as standard deviations, statistics of extremes, etc.) of the climate on all temporal and spatial scales beyond that of individual weather events. Variability may be due to natural internal processes within the climate system (internal variability) or to variations in natural or anthropogenic external forcing (external variability).

Drought A drought can be meteorological, hydrological, agricultural, or even socioeconomic. A meteorological or climatological drought is defined with respect to departures from the normal and the duration of the event. An agricultural drought is defined as the deficit in soil moisture. A hydrological drought is the result of decreasing precipitation on surface and subsurface water supply. A socioeconomic drought is the effect of meteorological, agricultural, and hydrological drought(s) on the supply and demand of economic goods.

Groundwater Water beneath the earth's surface, often between saturated soil and rock, which supplies wells and springs.

Transboundary waters Sources of freshwater that are shared among multiple user groups, with diverse values and different needs associated with water use. Water thus crosses boundaries, which can be different economic sectors, legal jurisdictions, or political interests.

Introduction

Water, the liquid of life, like air and soil has no substitute. Life, as one knows it, would not exist without water. The geosphere, atmosphere, and the biosphere are all linked to, and by, water. Water interacts with solar energy to determine climate and it transforms and transports the physical and chemical substances necessary for all kinds of life on the earth. Although 70% of the planet's surface is covered by water, most of which is saltwater, freshwater is limited and is not always in the right place, at the right time, or of the right quality. Water, on the earth, exists in several states: water vapor and clouds in the sky, seawater in the oceans, icebergs in the polar oceans, glaciers in the mountains, freshwater lakes, rivers, and fresh and saline water in aquifers. There are significant continental and country differences in the availability of freshwater.

Over the last 25 years, these differences and the importance of water has grown to occupy national and international agendas. Many international organizations, such as the United Nations, the World Bank, the World Health Organization, the World Meteorological Association, and the Stockholm International Water Institute, hold conferences related to water issues. Awareness among scientists, political leaders, and citizens of the connections between climate change, the hydrologic cycle, food production, environmental services, infrastructure needs, and sustainable water resource management increases every year. The message highlighted by all these efforts is that water is an increasingly scarce resource and that it is important to recognize and accept that there is a finite supply of water. Competition among agriculture, industry, and cities for limited water supplies is already constraining development efforts in many countries. At first glance, most of these water problems do not appear to be directly related to the agricultural sector. Yet, by far, agriculture has the largest demand for the world's water. Approximately 70% of the water withdrawn from the earth's rivers, lakes, and aquifers is used for food and fiber production. Of increasing concern is the rapid depletion of fossil water in the limited recharge aquifers in many regions of the world. Water in these aquifers accumulated over thousands of years and cannot be readily recharged. Regions of concern include the Western United States, Northern China, Northern and Western India, Egypt, and North Africa (Pearce, 2006). As competition, conflicts, shortages, waste, overuse, and degradation of water resources grow, policymakers look increasingly to agriculture for solutions.

Water stress is highlighted by drought. Of all the hydrological hazards, drought has historically impacted the largest number of people because they are more geographically widespread. Droughts are insidious because they do not have a clear beginning like floods. They start slowly and their effects are not apparent for weeks, months, or even years. The southern plains drought of the 1930s in the United States often described as the 'dust bowl' lasted about a decade and was an agricultural, environmental, and human disaster. John Steinbeck in his 1939 novel '*The Grapes of Wrath*' chronicled the human suffering and migration of farmers fleeing the southern plains for California. More recently, a devastating spring 2010 drought in Southwestern China affected 60 million people and caused livestock and crop losses totaling approximately $5 billion. Ironically, in that same year floods in Northwest China impacted 300 million people, killed more than 3000, and caused more than $40 billion in damages. Correspondingly, Texas in 2011 experienced a major drought resulting agricultural losses of nearly $9 billion dollars

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(Combs, 2012). Although floods and droughts have always plagued mankind and agriculture, they serve to heighten awareness on water issues and the need to wisely use and manage water resources.

As a prelude to sustainable water management for agriculture and food systems, this article briefly outlines water supply and use factors and challenges for the future. It begins by briefly providing an overview of the physical and chemical uniqueness of water before discussing water location, availability, and uses. A section on 'virtual water' provides information on the amount of water embedded in food, fiber, and products. Impacts of drought and climate change on water availability are outlined. Before the conclusion, issues with transboundary surface and groundwater resources sharing and management are highlighted. These issues will become increasingly complex as the climate changes.

Physical and Chemical Properties of Water

Water (H_2O) has a very simple atomic structure, which consists of one oxygen atom and two hydrogen atoms bonded together by shared electrons. The hydrogen side of each water molecule carries a slight positive electric charge, whereas the oxygen side carries a slight negative electric charge. This molecular polarity gives water its unique physical and chemical properties. Thus, water occurs naturally as a liquid, a solid, and a gas.

The 'bipolar' nature of water molecules gives water its special adhesion and cohesion properties. Hydrogen bonds cause water molecules to cohere and stay together and form high surface tension. Surface tension allows water droplets to form when placed on a dry surface or allows substances to float on water, while adhesion allows water to stick to other substances. These cohesive and adhesive forces play an important role in the movement of water from the soil matrix in the root zone to the leaves of plants. The forces create a pull as water molecules evaporating from leaves try to cling to water molecules below them. This movement of water across the plant also helps transport of dissolved minerals that plants need in order to grow.

The polarity of water makes it a good solvent allowing it to dissolve other polar substances. Hydrophilic (water loving) substances such as salts, acids, and alcohols dissolve in water and hydrophobic (water fearing) substances such as oils and fats do not mix well in water and are not dissolved. These properties affect the interaction of water molecules with other substances and thus every living organism on Earth. Water, as it flows through the air, the ground, or our bodies, carries valuable chemicals, minerals, and nutrients and helps sustain life.

Water has a unique thermal behavior. It has a high specific heat, which means that it can absorb a large amount of energy before it gets hot and it also releases heat slowly. It is both a heat-transfer medium and a temperature regulator. It heats and cools more slowly than soil and is thus, able to buffer large fluctuations in temperature which helps moderate the climate. An example of the influence of water on the climate can be felt on areas near large water bodies. They tend to have warm autumns and cool springs because of the differential heating and cooling between land and water.

Water expands anomalously when heated, between 0 and 4 °C; water contracts and becomes denser, unlike most substances, which expands and becomes less dense as their temperature rises. Water is densest at 4 °C, and becomes less dense when the temperature either increases or decreases with respect to this temperature.

Ice is therefore less dense than cold water and hence floats over water. Floating ice slows the freezing process and acts as a blanket insulating water found underneath. This ice layer further prevents the whole lake from freezing and fish and other organisms are able to survive through winters.

Global Distribution of Water

The water paradox is that although 70% of the 'blue planet' is covered by water, freshwater resources are very limited. Approximately 97% of the world's water is saltwater, undrinkable and unusable without expensive and energy-intensive desalination techniques. Only 3% is freshwater, and only a relatively small portion is readily available to sustain human, plant, and animal life. Slightly more than two-thirds of this 3% is ice, located in the polar ice caps, glaciers, and permafrost and is not readily available for human use (**Table 1**). Although melting of polar ice caps may not increase the flow of freshwater, melting of interior glaciers may. The Himalayas contain the greatest area of glaciers and permafrost outside of the poles and are melting (Gardner *et al.*, 2013). Most of Asia's largest rivers flow from there and slightly more than a billion people rely on river flow from this glaciated area. Of the remaining 30% that is not frozen, most is groundwater. Only approximately 1.2% of the earth's freshwater is surface water found in lakes, rivers, and streams. Although the 0.49% of surface freshwater that is in rivers is a tiny amount, it provides significant water for agriculture and domestic use.

The amount of water that is accessible for direct human consumption is minute (slightly $<1\%$) compared to the total volume of water on Earth. This water is found in surface water bodies such as lakes, rivers, and stored in man-made reservoirs, and in underground aquifers shallow enough for easy and affordable retrieval. Most of these water sources are

Table 1 Global water distribution

Source	*Water volume (km^3)*	*% Freshwater*	*% of total water*
Oceans	1 338 000 000	–	96.5
Ice caps	24 064 000	68.7	1.74
Permafrost	300 000	0.86	0.022
Groundwater	10 530 000	30.1	0.76
Lakes/Marshes	187 870	0.30	0.008
Soil moisture	16 500	0.04	0.001
Atmosphere	12 900	0.03	0.001
Rivers	2 120	0.006	0.0002

Note: % are rounded, so will not add to 100.

Source: Reproduced from Shiklomanov, I., 1993. World fresh water resources. In: Gleick, P.H. (ed.), Water in Crisis: A Guide to the World's Fresh Water. New York, NY; Oxford: Oxford University Press, pp. 13–24.

Table 2 Richest countries in terms of water resources

Country	*Total water available per inhabitant (km^3 $year^{-1}$)*
Brazil	8233
Russia	4507
Canada	2902
Indonesia	2838
China	2830
Columbia	2132
USA	2071
India	1897

Source: Reproduced from Food and Agriculture Organization, 2003. Review of World Water Resources by Country, Rome: FAO.

renewed by precipitation and can, to a certain extent, be considered renewable. Climate and the geology affect the distribution of water on Earth; hence the uneven availability.

The total renewable water resources in the world on an annual basis are estimated in the order of 43 750 km^3 $year^{-1}$. At the continental level, America has the largest share of the world's total freshwater resources of 45%, followed by Asia with 28% share, Europe with 15.5%, and Africa with 9% (Food and Agriculture Organization, 2003).

On a worldwide basis there are water-rich and water-poor countries. The eight richest countries in terms of water resources, listed in **Table 2**, account for 60% of the world's natural freshwater resources (Food and Agriculture Organization, 2003). The ten poorest countries in terms of water resources per inhabitant are Bahrain, Jordan, Kuwait, Libyan Arab Jamahiriya, Maldives, Malta, Qatar, Saudi Arabia, the United Arab Emirates, and Yemen. The difference between water resources per inhabitant for water-rich and water-poor countries can be explained with the help of an example: Brazil, a water-rich country, has 8223 km^3 of water resources per year per inhabitant, whereas Jordan, a water-poor country, has only 0.75 km^3 of water resources $year^{-1}$ per inhabitant.

Groundwater

Groundwater percolating beneath the earth's surface as soil moisture and contained in aquifers represents approximately one-third of all the world's freshwater resources. The area extending from the top of the land surface through the unsaturated soil to the top of the saturated water table is called the vadose zone. Soil moisture in the upper part of the vadose zone, which is the root zone of plants, is critical for food and fiber production. A very small part of the planet's freshwater is contained in this area (**Table 1**).

Water percolating through the soil may eventually fill all voids to the point that the soil is totally saturated. The upper surface of this zone of saturation is called the water table. The saturated zone beneath the water table is called an aquifer. Aquifers are huge storehouses of groundwater. There are two types of aquifers: unconfined and confined. Unconfined aquifers are those into which water seeps from the ground directly above the aquifer. Confined aquifers are those in which an impermeable layer exists above the aquifer that prevents water from seeping into the ground from the surface directly above. Instead, water seeps into confined layers from recharge zones located farther away where the impermeable layer does not exist. Aquifers are also classified on the basis of their size and the volume of water that can be extracted on an annual basis.

Approximately 35% of the earth's land area contains major groundwater aquifers and basins. Examples include the Ogallala in the United States, the Guarani in South America, the Great Artesian Basin in Australia, the Nubian in Africa, the Western Siberian in Russia, and the North China Plain Basin in Central China. In addition to these major aquifers approximately half of the continents have minor or near-surface aquifers (**Table 3**). Many aquifers exist under deserts where there is little precipitation. The water stored in these aquifers is geologically old water. Recently, satellite imagery and drilling helped to discover the Lotikipi Basin Aquifer – which by one estimate is roughly the size of Rhode Island – and the smaller Lodwar Basin Aquifer in Kenya. These aquifers contain an estimated 250 billion cubic meters of water (Kulish, 2013).

Freshwater Lakes

Most freshwater lakes are located at high altitudes, with nearly 50% of the world's lakes located in Canada alone. Lakes vary by area and volume. Following are some statistics of the freshwater lakes of the world:

- The Caspian Sea is the largest enclosed interior lake but it is saline and not freshwater (Leeden *et al.*, 1990).
- The ten largest lakes by area are given below (Downing and Duarte, 2009).

1. Caspian Sea	Asia	371 000 km^2
2. Lake Superior	North America	82 100 km^2
3. Lake Victoria	Africa	68 800 km^2
4. Lake Huron	North America	59 600 km^2
5. Lake Michigan	North America	57 800 km^2
6. Lake Tanganyika	Africa	32 900 km^2
7. Great Bear Lake	North America	31 328 km^2
8. Baikal	Asia	30 500 km^2
9. Lake Malawi (Lake Nyasa)	Africa	30 044 km^2
10. Great Slave Lake	North America	28 568 km^2

- The ten largest lakes by volume are given below (Downing and Duarte, 2009).

1. Baikal	Asia	23 600 km^3 (~ 20% of the world's freshwater)
2. Tanganyika	Africa	18 900 km^3
3. Superior	North America	11 600 km^3
4. Lake Malawi (Lake Nyasa)	Africa	7 725 km^3
5. Lake Michigan	North America	4 900 km^3
6. Lake Huron	North America	3 540 km^3
7. Lake Victoria	Africa	2 700 km^3
8. Great Bear Lake	North America	2 236 km^3
9. Issyk Kul (Ysyk Kol)	Asia	1 730 km^3
10. Lake Ontario	North America	1 710 km^3

Table 3 Storage of water in groundwater basins by continent

	Major groundwater basins		*Minor groundwater basins*	
	Volume (million km^3)	*% of land*	*Volume (million km^3)*	*% of land*
Africa	13.5	45	13.2	44
Asia	14.5	32	23	51
Australia	2.6	32	2.5	31
Europe	5.1	53	2.7	28
North America	3.2	15	12.4	58
South America	8.3	45	8.1	44

Source: Reproduced from BGR, 2008. Groundwater Resources of the World 1: 25 000 000, Statistics. Paris: BGR Hannover/UNESCO. Available at: http://www.whymap.org/whymap/EN/Statistics/statistics_node_en.html (accessed 20.01.14).

- The Great Lakes – Superior, Michigan, Huron, Erie, and Ontario – located in the Midwest of the United States and shared with Canada are the largest surface freshwater system on the earth. They contain approximately 21% of the world's surface water supply and 84% of North America's surface freshwater (US Evironmental Protection Agency, 2012).
- Lake Baikal in Asia is the largest freshwater lake holding some 23 600 km^3 of water, which is approximately 20% of the earth's total freshwater (Downing and Duarte, 2009).

Rivers

Rivers are the arteries of the planet, delivering most of the fresh surface water that people use. An estimated 263 international river basins cover approximately 50% of the earth's surface, yet by volume they carry approximately 2120 km^3, or 0.006 of 1% of total water (Table 1). The territory of 145 countries straddles international river basins. Some countries share their territory/boundary with only one other country while others may share it/them with several countries – 13 basins are shared between 5 and 8 countries, and 5 basins (the Congo, Niger, Nile, Rhine, and Zambezi) are shared between 9 and 11 riparian nations. Transboundary river basins are home to approximately 40% of the world's population (United Nations, Department of Economic and Social Affairs, 2014).

At least 33 countries depend on other countries for more than 50% of their renewable water resources. These countries include the following: Argentina, Azerbaijan, Bahrain, Bangladesh, Benin, Bolivia, Botswana, Cambodia, Chad, Congo, Djibouti, Egypt, Eritrea, Gambia, Iraq, Israel, Kuwait, Latvia, Mauritania, Mozambique, Namibia, the Netherlands, Niger, Pakistan, Paraguay, Portugal, the Republic of Moldova, Romania, Senegal, Somalia, the Sudan, the Syrian Arab Republic, Turkmenistan, Ukraine, Uruguay, Uzbekistan, Vietnam, and Yugoslavia (Food and Agriculture Organization, 2003).

Dams and Reservoirs

The flow of water in a river is not constant. It is influenced by seasons and hydrometeorological changes in the watershed. Dams are an efficient way to store water to meet demands during low rainfall seasons or periods of drought. Dams, diversions, and canals, are present on about 60% of the world's largest rivers. The 45 000 largest dams around the world have a combined storage capacity of 6000 km^3. These dams provide water for agricultural, irrigation, domestic, and industrial water use, hydropower generation, and for flood control. Dams help irrigate nearly 40% of agriculture around the world and 19% of the world's electricity is generated from water stored in dams. A third of countries rely of hydropower for their electricity needs (World Commission on Dams, 2000).

Although dams provide numerous benefits, they may also negatively impact river flow, existing water rights and access to water, the ecosystem (both aquatic and riparian), and even the livelihood of communities, especially downstream, striving on the river ecosystem for survival. Thus, the construction of new dams are often contested by funding and environmental organizations. Nonetheless, the construction of new dams continues: 46 new dams are planned for the Yangtze River basin in China, 27 in the La Plata basin in South America, 26 in the Tigris and Euphrates basin (Wong *et al.*, 2007).

Water Use

Agriculture is the largest consumer of water. It consumes 70% of the total water withdrawn, compared to only 19% for industrial use and 11% for municipal use. This ratio is skewed by a few countries with high water withdrawals. On an average, the ratio of agricultural to municipal and industrial use is 59%, 23%, and 18% respectively (Food and Agricultural Organization, 2012). It is believed that irrigation started along the Tigris and Euphrates Rivers in what is now Iraq, in the desert valley along the Nile River in Egypt, and the Indus River in Pakistan. The Native Indians, in what is now Mexico and the southwestern United States, also used irrigation to support food production. Irrigated agriculture has expanded tremendously and currently supports 40% of crop production around the world. Table 4 gives the water use for agriculture, domestic, and industry across each continent. Except for Australia, agricultural water use dominates other uses on every continent.

Asia, home to most of the world's population, is also the most irrigated. China, India, and the United States, the three most populous countries, have the largest areas under irrigated agriculture (Table 5), followed by Pakistan, Mexico, and Egypt. A number of countries located in the arid region of the world (e.g., Saudi Arabia, Iran, Iraq, Israel, etc.) and central

Table 4 Water use by continent

Continent	*Agriculture (%)*	*Domestic (%)*	*Industry (%)*
Africa	88	7	5
Asia	86	6	8
Europe	33	13	54
North and Central America	49	9	42
Australia	34	64	2
South America	59	19	23

Source: Reproduced from Food and Agriculture Organization, 1996. Report of the World Food Summit. Available at: http://www.fao.org/docrep/003/w3548e/w3548e00.htm#Annex1 (accessed 20.01.14).

Table 5 Leading irrigation countries

Country	*Irrigated area (1000 km^2)*	*Irrigated land (% of cropland)*	*% of water withdrawals for irrigation*
China	2300	19	87
India	513	29	93
USA	490	11	42
Pakistan	163	80	97
Mexico	62	25	86
Egypt	33	100	86

Source: Reproduced from Gleick, P.H., 2000. The world's waters 2000–2001. The Biennial Report on Freshwater Resources. Washington, DC: Island Press.

Asia are highly dependent on irrigation for their food and fiber needs.

The world's population is projected to increase by an additional 2–3 billion in the next 40 years. This will result in an increase in the demand of food supply and subsequently in the demand for water. With climate change, precipitation and hence water availability is expected to decrease, especially in the lower latitudes. Regions that are likely to be affected by climate change are also the most vulnerable in terms of water availability. In order to meet the food demand for the growing population, water use for irrigation is estimated to increase by about 19% by 2050. Technological (e.g., more efficient irrigation demand) and policy (e.g., use of genetically modified crops) interventions may, however, reduce pressure on agricultural water demands.

Virtual Water and Water Footprint

Production of food is extremely water intensive. The virtual water content, which represents the volume of water content the product has consumed throughout its growth cycle, gives an interesting perspective of the flow of water from major agricultural countries in terms of production to those relying mostly on import.

The production of 1 ton of grain, on an average, requires 1000 m^3 of water, whereas the virtual water content of livestock product is much larger, as it includes the virtual water content of the feed crops consumed, the water that animal drank over its whole lifetime, and the water used in the production of the final product. The production of 1 ton of beef thus requires approximately 15 500 m^3 of water (Hoekstra and Hung, 2002).

A country producing and exporting an array of food product is, in fact, exporting the water embedded in them beyond its boundaries, whereas a country at the importing end is actually importing that embedded water and thus saving its own water, which can be put to other uses (Allan, 1997). **Figure 1** shows the international virtual water flows and virtual water balances for all countries in the world. From 1996 to 2005, the volume of international water flows related to agricultural and industrial products averaged 2320 billion cubic meters. The main virtual water gross exporters were the United States, China, Canada, Brazil, Argentina, and Australia, whereas main gross virtual water importers were the United States, Japan, Germany, China, Italy, and Mexico (Mekonnen and Hoekstra, 2011).

Reliance on food import can be an attractive option for water-poor countries, whereas water-rich countries may produce and efficiently export more virtual water to other regions, thus replicating the logic of economies of scale (Mekonnen and Hoekstra, 2011). Virtual water could advocate for water conservation by discouraging the production of high water-embedded products from water-scarce regions and encouraging the water-dependent economic activity in water-rich regions. The decision-making process of international trade does not seem to drive water efficiency use or water conservation efforts (Black and King, 2009; Ercin and Hoekstra, 2014). Food independence drives large-scale agricultural production and no country is willing to rely solely on import to meet its food needs. This sociopolitical need can easily lead to the misuse of limited available freshwater resources.

Climate

Local hydrometeorological variables (temperature, humidity, sunshine, atmospheric pressure, wind velocity, precipitation, etc.), and hence water availability, are influenced by the climate. Climate (or climatological normal) is a measure of the average pattern of the meteorological variables over a particular region and over a time period, usually 30 years. Discussions on the climate, in the context of water availability, include climate variability and climate change (or global warming). Climate variability pertains to the way the climate fluctuates around the long-term mean, whereas climate change refers to the long-term continuous change to a long-term statistically significant variation in either the mean state of the climate or its variability.

Climate Variability

The common drivers of climate variability are large-scale circulation patterns, sunspots, and volcanic eruptions. The former, however, is the most important one and can dramatically alter the climate, weather, and hydrometeorological variables around the world. The time period of the resultant change can be in terms of months, years, or even decades.

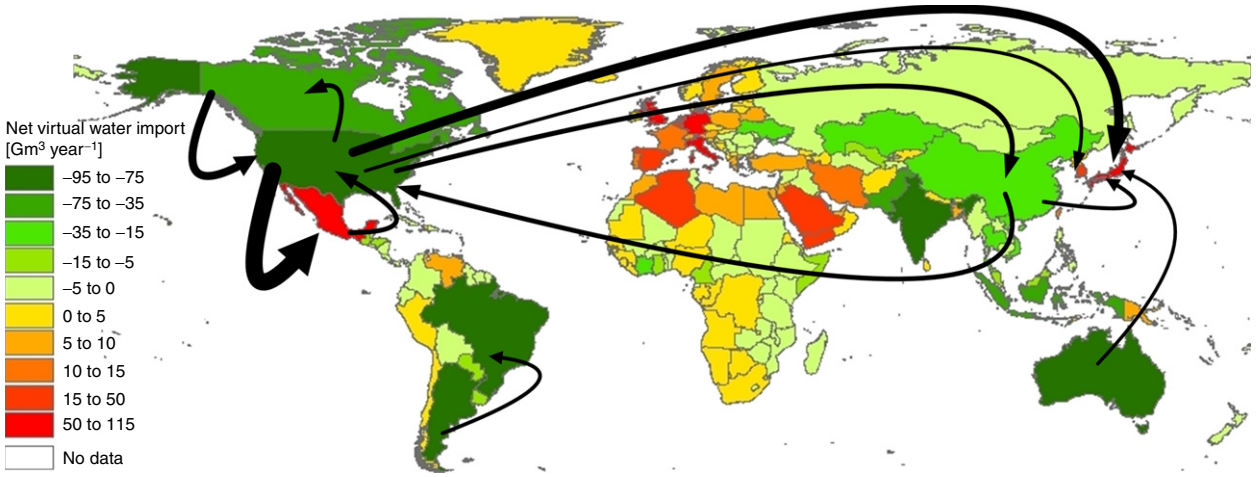


Figure 1 Virtual water balance and direction of gross virtual water flows over the period 1996–2005. Reproduced with permission from Hoekstra, A.Y., Mekonnen, M.M., 2012. The water footprint of humanity. Proceedings of the National Academy of Sciences 109 (9), 3232–3237.

El Niño–Southern oscillation

There are a number of climate variability patterns that influence local hydrometeorological conditions. The most important one is the El Niño–Southern Oscillation (ENSO). ENSO is a coupled ocean–atmosphere phenomenon related to sea surface temperature (SST) anomalies in the Central and Eastern Equatorial Pacific and the associated sea-level pressure difference, the Southern Oscillation (SO) (Rasmusson and Carpenter, 1982). The SO is the fluctuation in air pressure between Tahiti and Darwin, Australia. Negative (positive) pressure is accompanied by sustained warming (cooling) in the Central or Eastern Pacific. ENSO has a recurrence pattern of 3–6 years and every event normally lasts for approximately a year. El Niño events are often, but not always, followed by La Niña events, also referred to as the cold phase of ENSO (Trenberth, 1997). They have a direct effect on the hydrologic cycle both regionally and globally, especially on precipitation patterns (e.g., Khedun *et al.*, 2012; Piechota and Dracup, 1996; Regonda *et al.*, 2005; Ropelewski and Halpert, 1987).

Regional effect of El Niño–Southern oscillation

The effect of ENSO is distributed uniformly neither across the globe, not even across a single continent, nor in time during its period of occurrence (Lyon, 2004). As ENSO cycles through its different phases (El Niño, La Niña, and neutral), its impacts vary both spatially and temporally (**Figure 2**).

Africa

The effect of ENSO is mostly felt in the southeastern part of Africa and Madagascar and the eastern part along the equator. Dry and warm (wet and cool) conditions are felt during El Niño (La Niña) during December through February in the southeastern part, whereas the eastern part benefits from higher (lower) precipitation. ENSO conditions influence the ecosystem and may affect rainfed agriculture and yield. Remote sensing studies on ecosystem variables confirm ENSO's influence; above normal normalized difference vegetation index were noted, indicative of a high biomass content, during the 1997/98 El Niño event in the eastern equatorial region along with wetter than normal conditions in the southeastern region while the southwestern region was dry (Anyamba *et al.*, 2001; Anyamba *et al.*, 2002).

Asia and Australia

El Niño causes abnormally warm and dry conditions during December through February over the region encompassing Southern Asia to Northern Australia. By June and August, the dry conditions extend to most of the eastern part of Australia, leading to an increase in the risk of bush fires (Fuller and Murphy, 2006; Williams and Karoly, 1999). Some 1.75 million hectares of land was destroyed by bush fire in January and February 2003, an El Niño year (Bear and Pickering, 2006).

The relationship between ENSO and the Asian-Australian and Indian summer monsoon is well established (Charles *et al.*, 1997; Kirtman and Shukla, 2000; Kumar *et al.*, 1999; Yoo *et al.*, 2010). The monsoon is associated with the biannual complete reversal of lower atmosphere wind regime over the Indian Ocean, which results from the differential heating between the land and sea surfaces and the presence of the Himalayas (Cadet, 1979). There is a negative correlation between ENSO and the Indian summer monsoon (weak monsoon arising from El Niño events). It causes a change in the precipitation pattern and has a strong impact on glacier-fed rivers. Ice cores from the Himalaya indicate that snow accumulation in the region is sensitive to the changes in the South Asian Monsoon (Thompson *et al.*, 2000). These glaciers are the headwaters of several major rivers (e.g., the Huang He (Yellow) and Yangtze rivers in China, the transboundary Mekong, Ganges-Bhramaputra-Meghna, Indus, etc.) and they sustain the lives and economy of nearly 1.5 billion people in 9 Asian countries – the most populous region of the world.

Europe

The influence of ENSO does not extend into Atlantic Europe, but its impact on Atlantic storm tracks can impact European weather (Schär *et al.*, 1998). It is important to note that the geographical distance separating Europe and the Central Pacific Ocean, where fluctuations in SST lead to ENSO, may

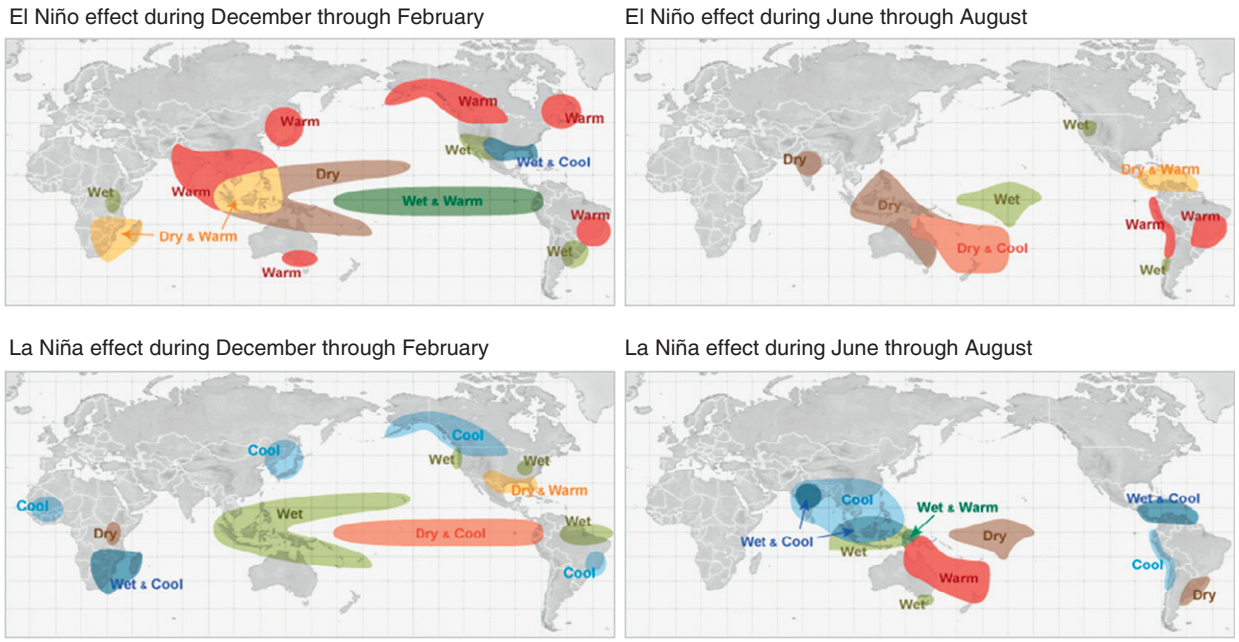


Figure 2 Effect of El Niño and La Niña around the world. Reproduced from National Oceanic and Atmospheric Administration, National Weather Service, 2012. Weather impacts of ENSO. Available at: http://www.srh.noaa.gov/jetstream/tropics/enso_impacts.htm (accessed 28.01.14).

make it hard to detect any association between ENSO and European weather using simple linear correlation techniques (Fraedrich, 1994). Warm (cold) ENSO episodes have been associated with enhanced cyclonic (anticyclonic) activities (Fraedrich, 1990). Warm events have been observed to produce more variable winter conditions, whereas cold events have had a more uniform response. The influence of ENSO on the glaciers of the European Alps, surface water reservoir for a number of important rivers, is almost negligible at the yearly timescale (Durand *et al.*, 2009), but weak correlations may be detected on a multidecadal scale (Efthymiadis *et al.*, 2007). Hence, the influence of ENSO should not be ignored in the water resources planning for the region.

North America

ENSO alters the path of the jet stream and hence affects the weather and storm tracks on the North American continent. El Niño causes a dip in the position of the jet stream in the Eastern Pacific, which results in warmer winters in Western Canada, Southern Alaska, and Northeastern United States, whereas the Southern United States has cooler and wetter weather. During the summer the southern part of Mexico becomes warm and dry. During La Niña the dip in the jet stream shifts west of its normal position toward the Central Pacific. It causes cooler winters in Eastern Canada, whereas the Southern United States becomes warm and dry.

The shift in the jet stream, during warm ENSO events, forces storms south of their normal position in the Pacific Northwest into California. Stronger El Niño events can force storms even further south into Southern California and the Pacific Northwest becomes drier as the moisture flux is transported southward. California thus benefits from above average precipitation during El Niño and flash floods are very common (Mo and Higgins, 1998; Schonher and Nicholson, 1989). This influx of moisture also increases snowfall in the Sierra Nevada mountain range (Kunkel and Angel, 1999). In the Rocky Mountains, the effect of ENSO varies with opposite effects at the northern and southern ends (Baker, 2003). The Rockies can be divided into three sections: the northern Rocky Mountains in Montana, the central Rocky Mountains extending from southern Montana into central Wyoming, and the southern Rocky Mountain stretching from southern Wyoming into New Mexico and Arizona. El Niño (La Niña) winters bring higher (lower) snowfall in the southern Rockies (Kunkel and Angel, 1999). The effect of ENSO on the central and northern Rockies is less pronounced. In its cold (warm) phase ENSO brings higher (lower) snowfall over the Pacific Northwest in early winter and midwinter and over the northern Rocky Mountains in midwinter (Patten *et al.*, 2003; Smith and O'Brien, 2001). The central Rockies receive 30% less heavy precipitation events (Gershunov and Barnett, 1998a).

South America

El Niño is associated with severe drought in Mexico and most of Brazil, whereas Argentina, Paraguay, and Uruguay benefit from increased precipitation. The coastal areas of Ecuador, Northern Peru, and Southern Chile also benefit from increased rainfall, but the mountainous Andes region suffers from drought, which causes the glaciers to retreat. In La Niña conditions, however, this region receives a fourfold increase in heavy storm events as compared with non-ENSO years (Grimm *et al.*, 2000; Haylock *et al.*, 2006). ENSO events have also been found to influence extreme precipitation events in South America (Grimm and Tedeschi, 2009). This is an important observation as hydrological hazards are often associated with changes in extreme events associated with climate variability.

Other large-scale circulation patterns

Even though ENSO is the most well-known large-scale climate variability pattern, there are a number of other climate teleconnection patterns that affect, to varying degrees, local weather conditions and hence water availability. Their influence, either alone or in conjunction with ENSO, should not be discounted. Some of the most common ones include the following: the Pacific Decadal Oscillation (PDO), the North Atlantic Oscillation (NAO), the Atlantic Multidecadal Oscillation, the Quasi Biennial Oscillation, the El Niño Modoki, etc.

In the United States, for example, it has been found that PDO may modulate the effect of ENSO; El Niño (La Niña) during the positive (negative) phase of the PDO, and lead to stronger climate responses than when they are evolving in opposite phases (Gershunov and Barnett, 1998b). There is, however, a possibility that stronger El Niño and La Niña events result from random decadal variation of ENSO and may even be responsible for the PDO (McPhaden *et al.*, 2006; Rodgers *et al.*, 2004). Irrespective, knowledge of all the climate variability patterns that influence local climate conditions is important and can help in the forecasting of precipitation and other climate variables that affect water availability (Chowdhury and Sharma, 2009; Devineni *et al.*, 2008; Khedun *et al.*, 2014).

Climate Change

The earth's climate is constantly changing. The change can be due to natural causes, such as changes in the earth's orbit, changes in solar activity, or volcanic eruptions, or can be anthropogenic, resulting from a change in the composition of the earth's atmosphere. Since the beginning of the Industrial Era, human activities have led to an increase in the concentration of heat-trapping greenhouse gases in the atmosphere, which has led to an increase in atmospheric temperature. In fact, the most likely reason for the recent observed warming, since the mid-twentieth century, is anthropogenic greenhouse gas emissions.

The greenhouse effect

According to the recent Fifth Assessment Report (AR5) from the International Panel on Climate Change (IPCC; Stocker *et al.*, 2013), the global mean surface temperature has been increasing, and each of the past three decades has been successively warmer (**Figure 3**). A linear trend, fitted to global average combined land and ocean temperatures, reveals a 0.85 (0.65–1.06) °C increase over the period 1880–2012.

The temperature on the earth depends on the balance between energy entering and leaving the atmosphere. Incoming energy from the sun can be either reflected back into the space or absorbed by the earth's surface. Some of the energy absorbed is released back into the atmosphere (infrared radiation). Greenhouse gases (water vapor, carbon dioxide, methane, etc.) absorb some of this energy and thus keep the atmosphere warm. The earth's average surface temperature, without the greenhouse effect, would be 255 °K (− 18 °C), instead of the current 288 °K (15 °C), which enables life to thrive. Paleoclimatological records from ice cores, corals, lake sediments, tree rings, etc. reveal that the concentration of greenhouse gases, especially carbon dioxide and methane, has fluctuated naturally over geological times, thus causing the climate to fluctuate between ice ages and interglacial periods. In recent decades, however, a marked increase in the concentration of carbon dioxide has been recorded. This increase has been attributed mostly to human activities, such as burning of fossil fuels, clearing of forests, and the use of gasoline-dependent modes of transportation. The global monthly average concentration of carbon dioxide in the atmosphere has increased from a preindustrial level of approximately 280 ppm (parts per million; pre-1750 tropospheric concentration) to 395.92 ppm (November 2013 (note that June 2013 concentration was higher at 398.58 ppm)) (Blasing, 2013; Tans and Keeling, 2014). The resulting increase in temperature is having a significant impact on the planet, affecting its land and marine ecosystems, the hydrologic cycle, sea level, weather extremes and weather-related hazards, water availability, food and fiber supply, human health, and the economy among others.

Impact on the hydrologic cycle

As the climate changes, the amount of energy on the earth's surface is expected to increase, which shall result in an intensification of the hydrologic cycle. A warmer planet implies that the water-holding capacity of the atmosphere will increase; thus leading to an increase in evapotranspiration. Higher evaporation from the soil implies less water for plants and a decrease in the recharge of groundwater aquifers and may result in a decrease in baseflow and hence less water in streams and rivers, lakes, and wetlands. An increase in evaporation from large water bodies, such as lakes and the ocean, implies more water in the atmosphere and an increase in global precipitation.

According to the IPCC (Stocker *et al.*, 2013), precipitation across the globe is projected to gradually increase at a rate of approximately 2% K^{-1}. This increase in global precipitation, however, will not be equally distributed, neither spatially nor temporally, across the planet; some regions may experience an increase in overall precipitation, whereas others may suffer a decrease, and still other regions may not register a notable change (**Figure 4**). High-latitude regions are likely to experience greater precipitation volumes as a result of the additional water-carrying capacity of the warmer troposphere. Midlatitude and subtropical arid and semiarid regions, however, will likely experience a decline. Similarly, a decrease in runoff in Southern Europe, the Middle East, and North Africa is likely, whereas northern latitude countries will experience an increase. IPCC AR 5 further states that even though global-scale projections of the impact of climate change on soil moisture and drought are not as obvious as that on other variables of the water cycle, drying in the Mediterranean region, the Middle East, Southwestern United States, and Southern Africa can be expected.

Effect on extreme events

An intensification of the hydrologic cycle due to climate change implies that the frequency, intensity, spatial extent, duration, and timing of extreme precipitation events, evapotranspiration, tropospheric water content, and runoff may

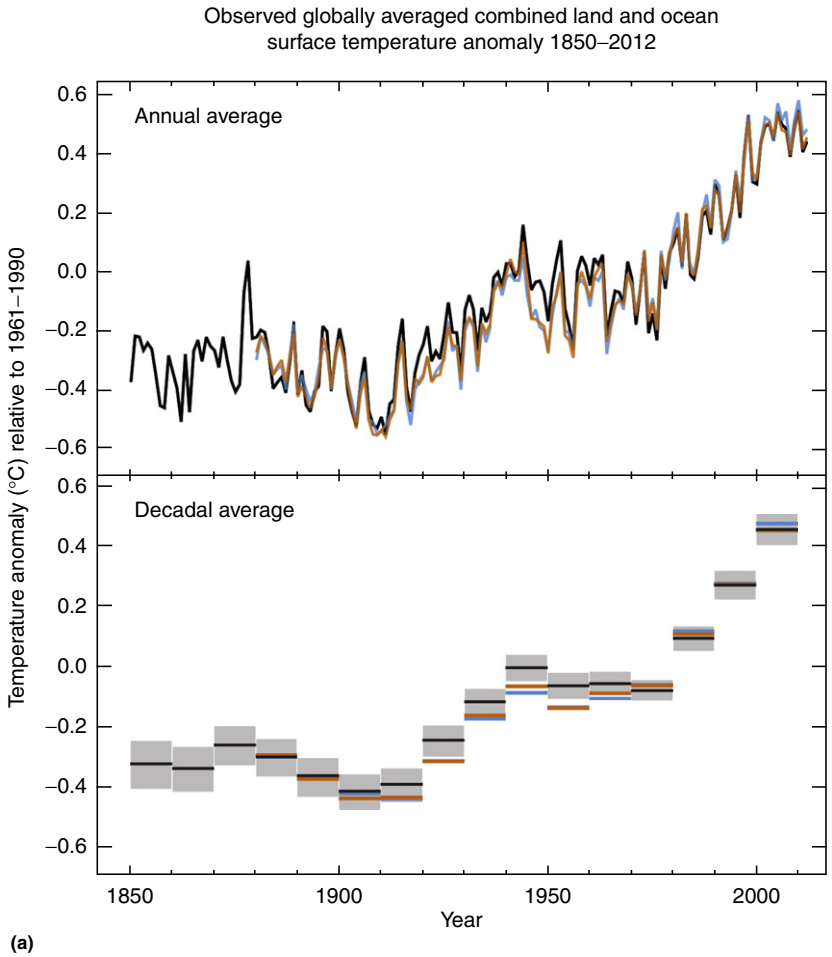


Figure 3 (a) Observed annual and decadal global mean surface temperature anomalies from 1850 to 2012. (b) Map of the observed surface temperature change from 1901 to 2012. Reproduced from IPCC, 2013. Summary for policymakers. In: Stocker, T.F., Qin, D., Plattner, G.-K., *et al.* (Eds.), Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, UK; New York, NY: Cambridge University Press.

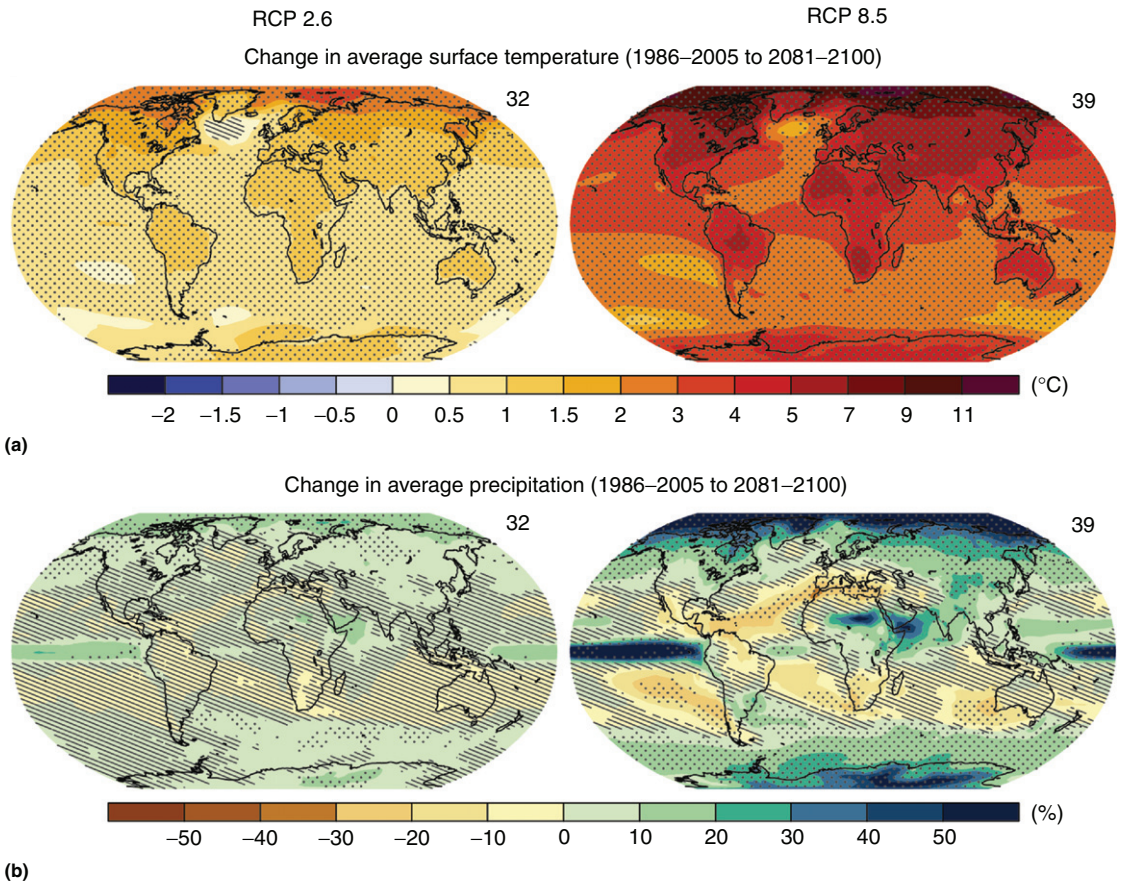


Figure 4 Maps of (a) projected late twenty-first century annual mean surface temperature change and (b) annual mean precipitation change. Reproduced from IPCC, 2013. Summary for policymakers. In: Stocker, T.F., Qin, D., Plattner, G.-K., *et al.* (Eds.), Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, UK; New York, NY: Cambridge University Press.

change (National Research Council, 2011), thus influencing the occurrence, nature, and return period of extreme events. Changes at both the lower (e.g., reduction in precipitation leading to droughts) and the upper tails (e.g., high-intensity rainfall resulting in floods) of range of observed values can be expected. These changes may be in the following three ways: (1) a shift in the mean that will result in less low-magnitude events and more high-magnitude events; (2) an increase in standard deviation and thus variability that equates with more low- and high-magnitude events; and (3) a change in the shape of the distribution where low-magnitude events remain almost constant but high-magnitude events increase (IPCC, 2012).

Water and Biofuel Production

Biofuel has often been touted as a panacea for climate change. It is a vital part of the renewable energy family. Biofuels are gaseous or liquid transportation or heating fuels derived from biological sources, such as grains, sugar crops, starch, cellulosic materials, and organic waste (De Fraiture *et al.*, 2008). Biofuels include bioethanol and biodiesel. Bioethanol is produced by fermentation of sugar from plants, such as sugarcane, or from starch crops, such as corn, whereas biodiesel is made from vegetable oils or animal fats through a transesterification process.

Global biofuel production has been increasing steadily over the last decade – production rose from 16 billion liters in 2000 to more than 100 billion liters in 2011, and today biofuel provides approximately 3% of road transport fuel globally (on an energy basis) (International Energy Agency, 2013). The transportation sector is a major consumer of petroleum fuels, hence substituting biofuel for fossil fuel offers several advantages – it is a renewable energy source, provides energy security by lessening dependence on foreign oil supply, allows a fair trade balance by reducing the financial burden, is less polluting than petroleum fuel (less sulfur, carbon monoxide, and particulates), and reduces greenhouse gas (GHG) emissions; moreover, biofuel, usually used in a local industry, promotes rural economic and social development. These benefits have driven many countries to adopt policies that encourage local biofuel production (De Fraiture *et al.*, 2008; Demirbas, 2007).

In the United States, the Energy Independence and Security Act of 2007 mandated the annual production of 56.8 billion

Table 6 Major biofuel-producing countries, source of biofuel, and current and projected percentage of total water and irrigation water used for biofuel production

Country	*Biofuel (billion liters)*	*Main biofuel crop*	*% of total crop water used for biofuel*		*% of irrigation water used for biofuel*	
	2030		*2005*	*2030*	*2005*	*2030*
USA and Canada	51.3	Maize	4	11	2.7	20
European Union	23.0	Rapeseed		17		1
China	17.7	Maize	1.5	4	2.2	7
India	9.1	Sugarcane	0.5	3	1.2	5
South Africa	1.8	Sugarcane	2.8	12	9.8	30
Brazil	34.5	Sugarcane	10.7	14	3.5	8
World	141.2		1.4	3	1.1	4

Source: Adapted from de Fraiture, C., Giordano, M., Liao, Y., 2008. Biofuels and implications for agricultural water use: Blue impacts of green energy. Water Policy 10, 67–81.

liter of ethanol from corn by 2015 and an additional 60.6 billion liter of biofuels from cellulosic crops by 2022 (Dominguez-Faus *et al.*, 2009). Around the world, Brazil already fuels a quarter of its ground transportation using ethanol derived from the fermentation of sugarcane sugar (Somerville, 2006). India, driven by environmental and rural development considerations, hopes that biofuels will account for at least 20% of its diesel and gasoline consumption by 2017. However, increasing biofuel production raises several concerns, among which exacerbating the stress on water demand, which is already a scarce resource in many countries, is a major one.

Biofuel production impacts water in many ways – enormous amount of water is required to irrigate feedstock crops, water is used during processing in biorefineries, and the quality of water bodies is affected by increased agricultural activities. These combined effects can be referred to as the water footprint of biofuel (Dominguez-Faus *et al.*, 2009). The water requirements for biofuel production depend on the type of feedstock used and on the geographic and climatic variables. Common crops that are used for biofuels production are the following: corn and soybeans (primarily in the United States), flaxseed and rapeseed (Europe), sugarcane (Brazil), and palm oil (Southeast Asia). The most water-intensive aspect of biofuel production is the water used in irrigating feedstock crops, whereas the water used by biorefineries is generally similar to that for oil refining (US Department of Energy, 2006). However, because water use in biorefineries is concentrated into a smaller area, the effects locally can be substantial. A biorefinery that produces 100 million gallons (378 541 m^3) of ethanol per year, for example, would use the equivalent water supply for a town of approximately 5000 people (National Research Council, 2008).

The water consumption of ethanol derived from corn grain is approximately 28 gallons per mile (66 l km^{-1}) (King and Webber, 2008). This is in strong contrast with the water consumption for conventional petroleum gasoline and diesel, which is 0.07–0.14 and 0.05–0.11 gallons per mile (0.16–0.33 and 0.12–0.26 l km^{-1}), respectively. Algae, another source of biofuel, is gaining much attention as, unlike corn or soybean, it does not compete with agricultural land for food crops and may produce 10 times more fuel per hectare. From a water requirement standpoint, however, it is not as efficient. Water consumption can vary anywhere between 3.15 and 3650 l of water for the amount of algal biofuel equivalent to 1 l of gasoline (National Research Council, 2012). The production of 39 billion liters a year, to meet a mere 5% of US transportation fuel needs, is currently unsustainable from a water requirement perspective. **Table 6** shows some major biofuel-producing countries, biofuel crop, and current and projected percentage of crop water used and percentage of irrigation water used for biofuel production. It is clear that production of biofuel will divert more and more of the water currently being used for food production, thus putting additional pressure on water allocation. More efficient irrigation techniques may reduce water consumption and mitigate the effect of biofuel production.

The production of biofuels not only affects water quantity but also affects water quality. Converting grassland to farmland requires both fertilizer and pesticide input and converting existing crops to biofuel will lead to an increase in nitrogen application (National Research Council, 2008). Water quality impacts of various crops can be compared based on fertilizers and pesticides application per unit of the net energy gain captured in a biofuel. Fertilizer requirement varies based on crop type. Corn requires the greatest amount of both fertilizer and pesticides. Between 24% and 36% of the nitrogen fertilizer applied to corn and soybean may be lost through runoff, sediment transport, tile drainage, and subsurface flow. This fraction may be a mere 5% during drought and as high as 80% during floods (Dominguez-Faus *et al.*, 2009). Thus, if proper farm practices and management plans are not implemented, the chemicals can negatively impact neighboring rivers and lakes and hence affect water quality.

Transboundary Water

According to the United Nations, there are 276 international rivers shared by two or more countries and 200 identified transboundary aquifers (UNESCO, 2013). Transboundary river basins cover 50% of the earth's surface (excluding Antarctica) and channels 60% of global streamflow (Biswas, 1999). Some 40% of the world's population lives within transboundary lake and river basins and two billion people depend on more than 300 transboundary aquifer systems (Du and Zhong, 2011).

Transboundary Waters and the Role of the State

Worldwide, countries have found more cost-effective methods to exploit water sources within their jurisdiction than to invest on water management strategies. The only remaining sources of water that can now be developed are mostly transboundary in nature (Biswas, 1999; Black and King, 2009).

Countries manage their shared watercourses considering their own national priorities, commonly overlooking water needs up- or downstream (Kreamer, 2012; Zeitoun, 2013). As this tendency grows, pressure over management enhancement and institutional governance at national and international level challenges the state accountability to cope with contemporary transboundary issues and future threats (Suhardiman and Giordano, 2012; Tarlock, 2000). Even though the role of state actors as the key players in international water affairs is not questionable, it is agreed that their role has been insufficient to understand actual challenges of transboundary water management. There is recognition of participation of nonstate networks, institutional soft power alliances on decision-making processes, and the existence of the scalar relationships and interactions between regional, national, subnational, and local influences (Sanchez and Kaiser, 2011; Zeitoun, 2013). The case of international organizations as key player in negotiators between coriparian river basins and the development of new governance scheme is well documented. The World Bank was mediator in the signing of the Indus River Basin treaty between India and Pakistan; the United Nations Environmental Program on the Zambesi River agreement between its riparians; and the United Nations Development Program (UNDP) over the Mekong River Basin agreement (Biswas, 2011b; Eckstein, 2011).

Water Interdependency: Conflict Versus Cooperation

Management of transboundary water is very complex, and so far only one-third of the transboundary river basins have a cooperative management framework. A transboundary basin can be a source of conflict and represent the potential for water wars or can represent an opportunity for cooperation among neighboring countries (Wolf *et al.*, 2005). Despite the fact that water scarcity may give rise to tension over shared water resources (Kreamer, 2012), international cooperation has been more often the rule than the exception (Giordano and Wolf, 2003; UNESCO, 2013). Black and King (2009) noted that between 1948 and 2008, 42 events related to transboundary river basins have led to hostile or military attacks, but 1743 events have resulted in verbal discussion; cultural, economic, technical, and scientific cooperation; and, in some cases, the signature of an international water treaty.

Even though it is clear that cooperative action may benefit transboundary neighbors, power asymmetry between parties has often been the impediment for effective cooperation over transboundary waters, which compromise water supplies and peaceful relations among parties (Ohlsson, 1995; Sanchez and Kaiser, 2011). Of the world´s 276 international basins, 166 do not have any treaty provisions covering them whatsoever. Only one-third of the multilateral basins are entirely covered by a treaty provision and most of those are limited to bilateral agreements (Biswas, 2008; Subramanian *et al.*, 2012). The United Nations International Convention on the Law of the Non-Navigational Uses of International Watercourses (1997) has only received 31 ratifications of the 35 required (McCaffrey, 2001; United Nations, 2005), which restricts this instrument from international commitment and subordinates it to existing bilateral and multilateral allocation treaties (McCaffrey, 2001; Tarlock, 2000).

Climate Change and Transboundary Water Management

Climate change will only exacerbate present water disputes between countries as water availability and quality changes (Khedun *et al.*, 2009; McCarthy *et al.*, 2007; Nordas and Gleditsch, 2005). Thus, recognizing climate change as one of the challenges for transboundary water management, the actual international legal framework (bilateral and multilateral agreements) will also be adversely affected. Generally, transboundary agreements have not been designed to cope with increased climate variability, as they are often restricted by rigid definitions of water allocation rather than percentages. The certainty of climate variability results in an increased pressure over alternative governance structures, potentially diminishing the legitimacy of weak international agreements (Suhardiman and Giordano, 2012). The declaration of the United Nations in 2013 as the International Year of Cooperation, which fosters states and other nonstate actors to promote actions to achieve cooperation in water related goals, aims the international need for new transboundary governance assessments.

Examples of Transboundary Water Management around the World

There are numerous examples of transboundary basins that represent valuable examples of the challenges pertaining to transboundary water management. Examples include the following:

The Jordan River basin

The classic case of the Jordan River basin is constantly referred to as the most securitized water region in the world (Biswas, 2011a; Wolf, 2001). The Jordan River is shared by Israel, Lebanon, Syria, Jordan, and the Palestinian Authority. Aside from being the most water-scarce region in the world, the Middle East represents a region where political and ideological conflict has been permanently ruling the relationships among its coriparians. For Israel, adequate access to water to support a growing population that has increased six times since 1949 (Gleick, 2000), and an agriculture highly dependent on irrigation, has been a constant concern over water resources allocation since the establishment of the nation (Giordano *et al.*, 2002; Wolf *et al.*, 2005). Likewise, high birth rates among Palestinians and Jordanians have put severe pressure on the already scarce water resources. In Gaza and the West Bank, the annual water availability per capita is below 100 m^3 (Israel less than 300 and Jordan approximately 100 m^3; Wolf *et al.*, 2005). With rising demand and water constraints, conflicts between Israel and its riparian neighbors have oscillated from verbal exchanges to hostile armed conflicts over proposed

water development projects (Wolf, 2000). However, even though historically Israel has been a permanent state of conflict (sometimes at war) with its Arab neighbors, there are examples in which water has constituted the singular bond among them. The 1990 Treaty of Peace between Israel and Jordan described substantial provisions, principles, and cooperative mechanisms over their shared waters. Alternatively, the 1995 Israeli–Palestinian Interim Agreement on the West Bank and Gaza Strip also entails cooperative mechanisms over the Jordan River basin. However, considering power asymmetry between Israel and Palestine, Israel tends to dominate the water situation in the region.

The Mekong River basin

The Mekong River basin is shared by six countries: China, Myanmar, Laos, Thailand, Cambodia, and Vietnam. The magnitude of its challenging interdependency relies mostly on the fact that it is the major water supply in Southeast Asia, source of food and transport to more than 70 million people and home of the most diverse inland fisheries in the world (Black and King, 2009; Houba *et al.*, 2012; Sneddon and Fox, 2006). To cope with the challenges of population growth, expanding irrigation, and hydropower generation, the Mekong River Commission was formed in 1995 between Cambodia, Laos, Thailand, and Vietnam, with the godfathering effort of the UNDP (Biswas, 1999). Even though this Commission highlights the effort toward a cooperation scheme among coriparians to avoid water conflict, the fact that China, the most powerful country in the basin located upstream of the river, is not a signatory of the agreement. In fact, China voted against the resolution to establish the 1997 Convention on the Law of Non-Navigational Uses of International Watercourses (Biswas, 2011a). The expectations regarding the improvement of sustainable water use in the Mekong basin are not high, and the potential for conflict threaten the stability of the region (Biswas, 2011a; Houba *et al.*, 2012). China, pressured by rapid population growth and water for all uses, has already started the construction of series of dams on the upper reaches without consultation with the Commission, thus threatening water supply for downstream users (Black and King, 2009; Sneddon and Fox, 2006). The magnitude of power asymmetry between China and its coriparians does not offer high possibilities to avoid Chinese priorities to rule the basin's water agenda, despite the negotiation and mediation efforts of the UNDP.

The Rio Grande/Río Bravo Del Norte river basin

The Rio Grande river basin, shared by Mexico and the United States, is the most water-stressed region in the continent (UNESCO, 2013). Population growth and extensive and intensive water use for irrigation, combined with drought persistence as climate change imposes new precipitation regimes in the region, are also identified as common challenges (Castro-Ruiz and Gonzalez-Avila, 2012). However, the particularity of this case relies in the fact that despite power asymmetry between the two riparian countries, Mexico and the United States have cooperated intensively and reasonably since the beginning of the 1900s to efficiently and equitably share the waters of the Colorado and the Rio Grande basins (Mumme, 2003; Sanchez-Munguia, 2011). Nevertheless, since the 1980s and more permanently since the 1990s, drought conditions and climate variability have exposed the limitations of the 1944 US–Mexico Treaty. Industrialization and immigration to the region incentivized by the North America Free Trade Agreement of 1994 have accelerated population growth (quadrupled since 1945) and overallocation of water rights in the region has reached its limits (Biswas, 2011b). The treaty (as most treaties around the world) does not contain provisions on water allocation considering climate variability scenarios (Hurd, 2012) and the treaty provision in which timing of water deliveries (5-year cycles) from Mexican tributaries to the United States (Texas) facing a rather constant drought period, do not seem enough to satisfy current water demands (Castro-Ruiz and Gonzalez-Avila, 2012). Further, transboundary groundwater, which is primary source of water for approximately 12 million people, is not even considered in the 1944 treaty (Eckstein, 2011; Mumme, 2000; Sanchez, 2006). Climatologic, hydrologic, but more importantly, institutional and legal challenges govern the US–Mexican conflict/cooperation relationship over shared waters of the Rio Grande and expose the need to evaluate the adequacy of the 1944 Treaty under actual and future conditions (Mumme, 2003; Mumme, 2000).

Conclusions

Providing water to growing areas with limited supplies is a daunting challenge. Climate change further exacerbates water scarcity challenges, especially region that are expected to receive less rainfall (Khedun and Singh, 2013a). Although distributional scarcity is a new reality, there is still time to adopt a new paradigm based on 'sustainable' water management practices. Practices must shift from supply development to demand and supply management incorporating more efficient agricultural irrigation, conservation, reuse, new technologies for water purification, smart improvements to infrastructure, water planning integrating economic, equitable use, and environmental factors with real participation by the widest realm of water users and communities (Brooks, 2005; Kaiser, 1996; Kaiser and Skillern, 2001; Khedun and Singh, 2013b; Wolf and Gleick, 2002). Like most paradigm shifts the practice of 'sustainable water management' will move slowly until accelerated by drought, real climate change, and long-term water scarcity.

See also: Agroforestry: Hydrological Impacts. Climate Change: Horticulture. Land Use: Catchment Management. Virtual Water and Water Footprint of Food Production and Processing. Water: Advanced Irrigation Technologies. Water Use: Recycling and Desalination for Agriculture. Water: Water Quality and Challenges from Agriculture

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Z

Zoonotic Helminths of Livestock

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Glossary

Cestode Hermaphroditic flatworms that are segmented and are commonly known as 'tapeworms.'
Definitive host The host in which sexual reproduction occurs.
Helminth Worms, including roundworms (nematodes) and flatworms (trematodes and cestodes).
Intermediate host A host in which a stage of the parasite grows and develops, but no sexual reproduction occurs.
Nematode Roundworms that have a cylindrical shape and can range in size from microscopic to several meters in length.
Paratenic host A transport host in which a stage of the parasite does not grow and develop, and no sexual reproduction occurs. It is used to bridge an ecological gap.
Trematode Hermaphroditic flatworms that are unsegmented and are commonly known as 'flukes.'

Introduction

The term parasite is derived from the Latin term *parasitus*, which literally means one who dines at another's table. In veterinary medicine, parasites are typically defined as eukaryotic organisms that are single- or multicelled and live within or on the host. Major parasites can be helminths, protozoa, or ectoparasites, which are arthropods, primarily insects or arachnids. Leeches and pentastomes are two other classes of parasites that are less commonly encountered. Parasites from each of these classes can infect humans (Bowman, 2009). The human can be the definitive host, that is the host in which sexual reproduction occurs, or can be an intermediate host, which is a host in which a stage of the parasite grows and develops but no sexual reproduction occurs. In many situations, humans are not the intended intermediate host, but rather are accidently infected. This is particularly true in the case of parasitic zoonoses.

Zoonotic transmission of parasites can be derived from either agricultural or food animals (i.e., sheep, goat, cattle, swine, and poultry) or companion animals (i.e., dogs and cats). There are some common protozoal diseases that affect both livestock and companion animals, most notably toxoplasmosis and cryptosporidiosis (Bowman, 2009). Although protozoal diseases are quite important, helminth zoonotic diseases will be the focus of this article, specifically parasitic zoonoses derived from domesticated agricultural animals. There are a great number of parasites that deserve inclusion in this article; however, examples primarily from swine are detailed. The physiology of pigs is relatively close to that of humans when compared to other domestic animals, which most likely explains why quite a few parasites go between swine and humans. Many of the basic principles from the parasites described below can be applied to other zoonotic parasites.

The Basics of Helminth Life Cycles

The three major types of helminths of zoonotic importance are the nematodes, trematodes, and the cestodes. Knowledge of the parasite life cycle is absolutely imperative if one is to appropriately treat, prevent, and diagnose parasitic diseases. Although life cycles are extremely varied in the exact details, the general features of the life cycles are quite similar.

Nematodes

Nematodes are commonly known as roundworms due to their cylindrical shape and can range in size from microscopic to several meters in length (Gibbons, 2002). They are pseudocoelomates, which means that although they have a complete digestive tract, they do not have a complete body cavity or coelom. Literally, they are a tube within a tube (Gibbons, 2002). They are dioecious, and with rare exceptions, males and females must mate to produce offspring (Bowman, 2009). During their development to adulthood, nematodes will molt four times to the juvenile adult stage, which is also known as the L5 or fifth-stage larva. This juvenile adult will then mature into an adult without molting. Mature males and females will then mate. Females will then typically shed one of the following: (1) live offspring, (2) eggs containing fully developed

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larvae, or (3) eggs containing an undeveloped embryo. These stages will then follow one of the following strategies in order to gain entrance into the definitive host: (1) ingestion by an arthropod intermediate host through the taking of a blood meal from the definitive host, (2) subsequent ingestion of an arthropod or mollusk intermediate host or larvae shed in the feces, (3) ingestion of a larvated or nonlarvated egg, (4) ingestion of a paratenic (transport) or intermediate host that contains larvae in their musculature or organs, or (5) penetration of the skin by the larvae (Lee, 2002). Although this list does not include all life strategies employed by nematodes, it does include the majority.

With very few exceptions, parasitic nematodes are internal parasites. Once inside the host, the infectious stages normally migrate in complicated pathways through a variety of organs. These migrations vary by family, and even genus and species. The end result of these migrations is that a male and female worm will be present in a location that will allow mating and the subsequent shedding of either eggs or larvae. These infectious stages will then infect an intermediate or definitive host as described by one of the strategies described above.

Trematodes

The phylum Platyhelminthes contains the class Trematoda, more commonly known as the trematodes. Most of the common zoonotic trematodes are digenetic, which means these worms require a minimum of two hosts to develop into the adult stage (Nithiuthai *et al.*, 2004). Asexual and sexual reproduction normally occur in an invertebrate and vertebrate host, respectively (Roberts *et al.*, 2013a). Trematodes are primarily hermaphroditic with the family Schistosomidae being a notable exception (Mone and Boissier, 2004). Adult worms live in a variety of locations in the definitive host, including the lungs, liver, and stomach (Bowman, 2009). Regardless of location, operculated eggs are shed in the feces of the definitive host. After a designated time period, which is dependent on temperature, oxygen tension, and pH, the eggs will develop into a miracidium. The miracidium is a ciliated free-living organism, which upon hatching from the egg, enters a mollusk – the intermediate host (Roberts *et al.*, 2013e). The hatching process can occur in water or after ingestion by the requisite intermediate host. In the case of certain species such as *Fasciola hepatica*, light facilitates hatching (Wilson, 1968).

Once inside the intermediate host, usually a snail, the miracidium undergoes a complex series of morphological changes to the saclike sporocyst. Inside this sporocyst, other sporocysts, known as daughter sporocysts, may develop. Alternatively, another intermediate stage, the redia or germinal sac, may develop. Rediae normally exit the sporocyst in a dramatic manner, rupturing the membrane, after which they begin a wandering migration around the host. Rediae can then either develop into daughter rediae or into the next stage, which is the cercaria. The cercariae leave the host and can infect a definitive host in the case of the family Schistosomidae. In other trematodes, the cercariae will either infect a second intermediate host, where they may enter a dormant stage known as the metacercariae (Roberts *et al.*, 2013e). Alternatively, the cercariae of some trematodes, such as the family Fasciolidae, will remain in the environment where they encyst as metacercariae (Olsen, 1947). The life cycle is completed when the definitive host ingests either the second intermediate host containing the metacercariae or the encysted metacercariae in the external environment. As with nematodes, the trematodes undergo complex migrations within the host, after which they arrive at the designated tissue (Nithiuthai *et al.*, 2004; Roberts *et al.*, 2013e). The life cycle and biology described above is what would be considered a classic trematode life cycle. As with all organisms, there are notable exceptions.

Cestodes

There are two major classes of cestodes: the psuedophyllideans and cyclophyllideans, also known as the true tapeworms (Raether and Hänel, 2003). This article focuses mainly on cyclophyllidean tapeworms.

Almost exclusively, adult cestodes live within the gastrointestinal tract of the definitive host, and are divided into hermaphroditic segments called proglottids. The cestodes discussed below are polyzoic – that is they possess multiple proglottids. These proglottids are uniform in structure, but increase in size proximally to distally as the worm grows. The worms will attach to the wall of the intestine via suckers or hooks, which are on the most proximal segment, or scolex, of the tapeworm. It is from the 'neck' area of the scolex that proglottids are formed by a process known as strobilation. Eggs are produced in the proglottids, and depending on the species, the egg-containing proglottids or eggs are shed in the feces (Bowman, 2009; Roberts *et al.*, 2013d). As compared to some nematode species and trematodes, these eggs are directly infective. In other words, these eggs require no time for development outside the host, in order to become infective to the intermediate host (Nithiuthai *et al.*, 2004). After ingestion of the egg, the embryophore or hexacanth embryo hatches from the egg (Bowman, 2009; Roberts *et al.*, 2013d). After hatching, the hexacanth embryo migrates to a locale in the host that was designated by evolution tens of thousands of years ago. In its final location within the intermediate host, the scolex will develop into what can be described as a capsular structure or cyst, whose morphology varies by parasite species. The stages within the intermediate host are known as metacestodes, and will normally contain a scolex (Roberts *et al.*, 2013d). These intermediate stages are so distinct from the adult worms that it was previously thought that they were a separate species of parasite versus an intermediate stage within an intermediate host. For the parasites discussed, the parasites are transmitted from the intermediate host to the definitive host by means of a predator–prey relationship. Once inside the host, the scolices will attach inside the intestine and begin to grow.

Zoonotic Nematodes

There are many zoonotic nematodes, but some of the most well-known ones (such as the canine roundworm *Toxocara*

canis and the canine hookworm *Ancylostoma caninum*) are transmitted from domesticated canines to humans. However, there are some excellent examples of zoonotic nematodes that are transmitted from domesticated food animals to humans. Two of the most well-known species, the pig roundworms *Ascaris suum* and *Trichinella spiralis*, are discussed below.

Ascaris suum

Ascaris suum is the large roundworm of the pig (*Sus scrofa*) and can easily infect humans. This should come as no surprise, because previously *A. suum* and the human roundworm, *Ascaris lumbricoides*, have been considered the same species (Rogers, 1956). This debate is ongoing with some more recent paleoparasitological and genetic evidence supporting the assertion that the two species are indeed one (Leles *et al.*, 2012). Regardless of the species debate, one would not want to ingest the infectious eggs of *A. suum*, which is what happened when Eric Kranz put *Ascaris* eggs in the food of his roommates when he was asked to leave the premises for failure to pay his share of the rent (Carus, 2001). The roommates developed a rather nasty infection as a result (Phills *et al.*, 1972). The bottom line is that cross-infection can result, and precautions should be taken to prevent human infection with *A. suum* (Crewe and Smith, 1971).

Biology

Ascaris suum is currently classified in the infraorder Ascaridiomorpha, family Ascarididae (Roberts *et al.*, 2013b). The ascarids, as they are commonly known, tend to have complex life cycles that can involve relatively complicated migrations through the intermediate/paratenic host or the definitive host (Lee, 2002; Bowman, 2009). For *A. suum*, and its human counterpart, *A. lumbricoides*, the life cycle occurs almost exclusively in the definitive host, with the exception that some larval development inside the eggs occurs while the eggs are in the environment (Dold and Holland, 2011). Adult worms inhabit the small intestine and can grow to a length of 31 and 49 cm, for males and females, respectively (Roberts *et al.*, 2013b). The females are prodigious egg layers, producing up to 200 000 eggs a day, which are shed into the environment in the feces (Sinniah, 1982). This level of production practically ensures that another host will become infected. The outside of the eggs contain a sticky saccharide coating, which surrounds an extremely resilient membrane (Nansen and Roepstorff, 1999; Quiles *et al.*, 2006). The result of this combination is an egg that is both extremely difficult to kill, as well as remove, since the eggs survive quite well in a variety of temperatures and solutions (O'Donnell *et al.*, 1984). These eggs are shed unembryonated, and are not immediately infective. Depending on the temperature, eggs will be infective 2–4 weeks after being excreted into the environment. At this point, they contain the infective third-stage larvae (L3) (Geenen *et al.*, 1999). Eggs can survive for quite some time, although extreme heat and prolonged exposure to sunlight will kill the larvae (Gaasenbeek and Borgsteede, 1998; Quiles *et al.*, 2006). Once ingested by the definitive host, or a suitable paratenic host, these eggs will hatch and the L3 will be released into the intestine (Dold and Holland, 2011). After entering the intestine, the L3 will penetrate the intestine and travel via the blood to the liver, after which the larvae will migrate via the blood vessels to the lungs (Murrell *et al.*, 1997; Roepstorff *et al.*, 1997). Once in the lungs, the larvae will literally burst out of the alveoli. After entering the alveolus proper, the L3 will then travel up the trachea in a process known as tracheal migration. After rising up the trachea, the larvae are swallowed, and travel to the intestine, where they will mature to adults (Roepstorff *et al.*, 1997). This process takes approximately 60–65 days from ingestion of egg to maturation of the adult (Roberts *et al.*, 2013a).

Epidemiology

As mentioned above, the females are prodigious egg layers, producing large numbers of environmentally resistant eggs (Sinniah, 1982). In commercial swine operations, most of the transmission occurs between the sow and the piglets in the farrowing house. The sticky eggs that are in the surroundings and adhered to the sow are inevitably ingested in large numbers by piglets (Nansen and Roepstorff, 1999). Transmission can also occur among other age groups as well, since there is little evidence of age-related immunity to the parasite (Eriksen *et al.*, 1992). In areas where pigs are not raised in confinement, the infective eggs can be present in the soil. Animals can ingest these eggs as they root and forage for food (Roepstorff and Murrell, 1997). Also, pigs that are reared outdoors can become infected by ingestion of paratenic hosts. It is important to remember that pigs are omnivores, not herbivores, and do not hesitate to eat rodents, which could be harboring encysted or migrating *A. suum* L3. This is potentially a means of transmission in underdeveloped countries.

Clinical signs/pathology

Clinical signs and the associated pathology can vary depending on the number of worms that are present, as well as the stage of the parasite. A few adult worms will not result in any observable clinical signs. Typical signs can include diarrhea and a failure to gain weight (Stewart and Hale, 1988). However, a large number of worms can result in intestinal blockage. In extremely severe cases, worms have migrated into the bile duct, although this is a rare occurrence (Bowman, 2009).

Migrating larvae can also result in clinical signs (Spindler, 1947). As the larvae migrate through the lungs, they release antigen. The body responds to this insult with a myriad of inflammatory cells. The inflammation eventually heals resulting in lung fibrosis (Bowman, 2009). This makes it difficult for the animals to breathe, resulting in a condition commonly known as 'thumps' (Spindler, 1947). The migrating larvae can also cause damage to the liver, through which they migrate prior to migration through the lungs. After the initial damage, the liver, like the lungs, responds with an initial inflammatory response, followed by fibrosis. These fibrotic spots are known as 'milk spots' and can result in the condemnation of the liver at slaughter (Sanchez-Vazquez *et al.*, 2012). Other than the condemnation at slaughter, there are no major clinical manifestations associated with migration of the larvae through the liver.

Control/prevention

If the egg-contaminated feces is removed before the development of the infectious L3 within the egg, then theoretically, transmission from one pig to another could be prevented. However, this solution is far from practical, and not a realistic possibility. Although this control measure is feasible for control of dog ascarid infections, it is not in any way possible for control of *A. suum*. In both indoor- and outdoor-reared pigs, the feces can be spread throughout a pen, making it difficult to remove the feces immediately after contamination. Periodically steam-cleaning pens will remove and kill the larvae inside the infective eggs. Since eggs are not immediately infective, cleaning the pen or area every few weeks should decrease transmission (Bowman, 2009). Also, preventing access of pigs to paratenic hosts, with rodents being the most likely, should also decrease transmission.

Zoonotic potential

As stated above, the life cycle of *A. suum* in the human host is almost identical to that of the human roundworm, *A. lumbricoides* (Rogers, 1956). In fact, there has been some debate about whether the two are the same parasites (Leles *et al.*, 2012). Genetically, there have been some studies that seem to indicate that there is some difference, although this debate is still ongoing (Anderson *et al.*, 1993; Dold and Holland, 2011; Leles *et al.*, 2012). Regardless of the scientific debate, *A. suum* can mature in humans, and causes almost identical signs as it does in pigs. Mild infections are well tolerated, whereas heavy infections can result in the signs described above (Crewe and Smith, 1971; Carus, 2001; Dold and Holland, 2011).

Trichinella spiralis

Trichinella spiralis is described as the worm that would be a virus, due to its unique biology (Despommier, 1990). At one point during its life cycle it will inhabit and take over the host cell (Wu *et al.*, 2013). Trichinellosis also has an important place in history – the reason that certain religions do not consume pork, because it is an important source of infection (Murrell and Pozio, 2011). It has been debated that Amadeus Mozart died as a result of *Trichinella*-infected pork (Dawson, 2010). Although some argue he died of the disease, others argue that the reported signs and symptoms would not meet the clinical definition of trichinosis. One key point in the debate is that Mozart would not have been able to compose his famous *Requiem* mass due to the extreme muscle pain, or myalgia, which can be present with the disease (Dupouy-Camet, 2002). Regardless of whether trichinosis killed Mozart, the importance of *Trichinella* as a zoonosis cannot be overstated. It also has one of the simplest solutions for prevention of transmission, which is not ingesting undercooked meat. For this disease, the bottom line is to cook meat to the appropriate temperature, till it is free from *Trichinella*.

Biology

Trichinella spp. are nematodes in the family Trichinellidae. There have been debates about the speciation of *Trichinella*, but it is agreed the primary species is *T. spiralis*, with *T. nativa* playing an important role in transmission in Arctic areas (Murrell *et al.*, 2000; Larrat *et al.*, 2012). *Trichinella pseudospiralis* also plays a role in infection, but is of limited importance when compared to *T. spiralis* (Murrell *et al.*, 2000). Further discussion focuses primarily on *T. spiralis*.

The host range of *T. spiralis* is quite large, as many mammals can become infected with the parasite. However, the major point to remember about the *T. spiralis* life cycle is that transmission is based on carnivorism, so herbivores rarely become infected (Bruckner, 1999). The life cycle is divided into two separate stages: enteral and parenteral cycles.

The enteral stage

Animals become infected by eating the infected muscle of other animals (Bruckner, 1999; Roberts *et al.*, 2013c). The first-stage larvae are encysted in the muscle cells. On ingestion by a mammalian host, the larvae are released from the muscle during digestion in the stomach (Bowman, 2009). The larvae then enter the small intestine, where they travel in between the villous crypts in the small intestine. In 30–32 h following ingestion, the larvae become sexually mature adults, which then release newborn larvae within 5 days (Gardiner, 1976; Bowman, 2009). Perhaps the most fascinating aspect of the *T. spiralis* life cycle is that every animal can serve as a definitive host. One must remember that a definitive host is one in which sexual reproduction of the parasites can occur. Because the worms mature and reproduce in each infected host, each infected animal, by definition, is a definitive host.

Parenteral stage

After birth the newborn larvae penetrate the intestine and then enter the lymphatics, where they migrate via the bloodstream to the musculature (Ali Khan, 1966). Once they reach the muscle, the larvae then literally invade the cell. Hence the description of *T. spiralis* as the worm that would be a virus, since viruses also invade cells (Despommier, 1990). During a 2- to 3-week period, the larva changes the cell into what is known as a 'nurse cell' (Bowman, 2009). Many physiologic changes occur in the cell, as the parasite adapts the cell for its needs (Despommier, 1990). At this point in the infection, the larva can remain alive within the cell for literally years, without causing a significant immune reaction or pathology (Dabrowska, 2013; Roberts *et al.*, 2013a). However, large numbers of nurse cells within a particular muscle group can cause clinical signs and pathology (see Section Clinical signs/pathology of animals). Once the muscle is ingested by a suitable host, the larvae are released from the muscle and the life cycle is completed (Roberts *et al.*, 2013c).

Epidemiology

Some of the greatest stories about public health involve trichinellosis, the condition that occurs when one is infected by *Trichinella* spp. Trichinellosis has historically been associated with pigs. Typically, pigs are infected by cannibalizing other pigs or ingesting rats (Hanbury *et al.*, 1986; Leiby *et al.*, 1990). Pigs also become infected when they are fed 'garbage.' Garbage in this case is defined as undercooked meat scraps. Pigs will ravenously consume this mixture, because of their tendency to consume a variety of food, due to their ominivorous nature. Although commercial swine operations typically do not engage in the practice of garbage feeding, many smaller farms do

(Zimmerman, 1968). When humans ingest the meat of infected pigs that has not been properly cooked, they become infected.

Whereas pigs are domestic animals that are considered the most likely source of infection for humans, other domestic animals that cause infection also have been documented. Certainly consumption of undercooked infected meat of domestic carnivores, such as dogs or cats, could result in human infection. Counterintuitive to the normal infection paradigm for trichinosis, infection of herbivores has been reported (Moorhead *et al.*, 1999). One of the most famous cases involved an outbreak among humans in France, due to ingestion of infected horse meat. Since horses are herbivores, one would logically assume they should not be infected with *T. spiralis*. It is hypothesized that an infected rat actually fell into the grinder when the horse feed was being produced. The larvae would have been in the nurse cells at this point, and would have become activated on exposure to the gastric fluids in the horse's stomach. The horse would have then become infected (Laurichesse *et al.*, 1997). This case drives home an important point regarding trichinellosis. While carnivores and omnivores are more likely to be infected than herbivores with the parasite, it is due to a difference in consumption habits, not due to physiology. Remember, any mammal can become infected with *Trichinella* spp.

The last point of discussion is regarding trichinellosis epidemiology, which is unrelated to agriculture. In the United States, the primary means of infection for trichinellosis is actually ingestion of undercooked wildlife, not infected commercially raised pork (Moorhead *et al.*, 1999). Currently, there is a USDA program in place to certify pork *Trichinella*-free, thus reducing the need to cook the meat at as high temperatures as previously recommended. Pork from wild pigs, and other carnivores, such as bear and cougar, needs to be cooked thoroughly (Dworkin *et al.*, 1996; Kennedy *et al.*, 2009). Also, meat from herbivores, such as deer needs to be cooked thoroughly. As was described for the case above involving the ingestion of horse meat, deer meat can be contaminated if it is ground using a grinder that was previously used to grind contaminated boar, or other wild animal (Moorhead *et al.*, 1999). The bottom line is that if one is unsure of the source of the pork or wildlife, then one should assume that it is infected with *T. spiralis* and cook it using the appropriate precautions (Pozio, 2001).

Clinical signs/pathology of animals

Signs associated with human infection are much better documented than in animals (Murrell and Pozio, 2011). The clinical signs in animals typically associated with infection may include diarrhea during the enteral phase. Invasion of the muscle may or may not result in clinical signs, such as myalgia and fever. It must be noted that if the diaphragm is one of the muscles that is heavily infected, dyspnea (difficulty breathing) and even death could result. On histologic examination of infected muscle, microscopic cysts representing the nurse cells may be observed (Bowman, 2009).

Control/prevention

Control of trichinosis can be achieved at two points: (1) preventing ingestion of contaminated feedstuffs or meat by animals and (2) preventing ingestion of contaminated meat by humans (Bruckner, 1999; Pozio, 2001).

For prevention in animals, focus shall be on prevention in swine. Prevention in animals is theoretically simple, but practically difficult to achieve. First, one needs to prevent cannibalism between pigs. This can obviously be difficult when animals are grouped housed. Also, removing any dead animals as soon as possible after discovery is a prudent measure (Hanbury *et al.*, 1986). The second is to prevent access of pigs to infected rodents. Again, this is a difficult proposition. In commercial operations, standard biosecurity and rodent control measures should be employed (Leiby *et al.*, 1990). In outdoor operations, this will be near impossible. Finally, cooking garbage (i.e., meat scraps) is paramount to preventing infection (Zimmerman, 1968; Leiby *et al.*, 1990).

For humans, preventing ingestion of *Trichinella* spp. can be accomplished by two ways: (1) prevent infected animals from entering distribution channels and (2) eliminate the infective larvae in the meat. To prevent infected meat from entering the human food chain, the meat needs to be screened in order to confirm that it is not infected. In Europe, this is accomplished through use of what are known as trichinoscopes. Slices of diaphragms, where encysted *T. spiralis* larvae in nurse cells can be present in high numbers, are placed on a slide and visually examined (Bowman, 2009). The meat from negative animals, or more appropriately those where no parasites are observed, is allowed to enter the food chain, whereas those from positive animals is discarded. This is a somewhat outdated method, and certainly animals with a low larval burden might not be detected. The other method is by use of enzyme-linked immunosorbent assay (ELISA), which is used much more frequently today (Gajadhar *et al.*, 2009).

In the United States, routine screening methods are not used for pork, much less wild game. Instead proper cooking or freezing of the meat is relied on. Meat must be uniformly cooked to an internal temperature of 77 °C, or alternatively frozen for several weeks. Curing, smoking, or other preparations that do not meet the criteria will not eliminate the larvae (Gajadhar *et al.*, 2009). Furthermore, freezing will not work on the cold-adapted *Trichinella* species, *T. nativa*. Therefore, while ingesting arctic game, such as polar bear, one must make sure to cook rather than freeze the meat (Skirnisson *et al.*, 2010).

Zoonotic potential

As one can see, the zoonotic potential for *Trichinella* spp. is quite large. Over the years, there have been multiple outbreaks in multiple countries (Murrell and Pozio, 2011). Normally, when humans are infected, there could be some diarrhea associated with the enteral phase. This can be mild to severe depending on the parasite load. Two to three weeks post-infection, myalgia may be associated with the parenteral phase (El-Beshbishi *et al.*, 2012). Also, periorbital edema can occur. Normally, this is the extent of the disease. However, if there is a large worm burden, and there are a large number of larvae localized in the heart or diaphragm, then significant problems can occur, either due to inhibition of cardiac function, or a result of respiratory distress secondary to a loss of diaphragm function. In summary, there can be minor morbidity

associated with trichinosis in many cases. In the few cases where there are severe clinical signs, mortality can result (Murrell and Pozio, 2011).

Zoonotic Cestodes

There are quite a few zoonotic cestodes of significance. Arguably, the most significant of these are cyclophyllidean tapeworms in the family Taeniidae (Raether and Hänel, 2003). Two of the most interesting tapeworms are the *Taenia saginatta* and *Taenia solium*. Both use man as the definitive host, and use cows and pigs as intermediate hosts, respectively (Bowman, 2009). As with many tapeworms, the pathology to the definitive host is minimal. For both these species, the pathology to the intermediate host is also minimal. However, there is a unique aspect to the biology of *T. solium*, which makes this tapeworm a very important zoonosis, especially in developing countries (Raether and Hänel, 2003).

Taenia saginata

Biology

As stated above, *T. saginata* uses man as the definitive host. Humans become infected with *T. saginata* when cow muscle containing the cysticercus is ingested (Bowman, 2009). The cysticercus is the intermediate form of the tapeworm, and is best described as small fluid-filled sacs (up to 10 mm in diameter) that contain an invaginated scolex. These cysticerci, which are infective within 2 months, are located within the fibers of striated muscles (Roberts *et al.*, 2013a). When the beef is ingested by the definitive host, man, the cysticercus becomes activated by the digestive juices and devaginates. These scolices then attach to the small intestine after which time the tapeworm will start to elongate as the number of proglottids increases (Bowman, 2009; Roberts *et al.*, 2013d). As stated above, tapeworms are hermaphroditic. Although they can mate with other proglottids of the same tapeworm, they prefer to mate with proglottids of different tapeworms. The proglottids are gravid after 2–12 weeks, and the tapeworm normally reach a length of 3–5 m, but some of over 20 m in length have been documented (Roberts *et al.*, 2013a).

With some tapeworms, the eggs (which are technically oncospheres because of a lack of a defined shell) are shed in the feces, whereas in other species (Raether and Hänel, 2003), the eggs are contained within the proglottid proper. In the latter instance, and in the case of *Taenia* spp., when the proglottid is damaged, eggs are released in the feces. When these eggs are ingested by cattle, the eggs will hatch in the intestine, and the scolex will devaginate, and then migrate through the mucosal wall of the intestine. They will then be carried by the bloodstream where they will lodge in the striated muscle, and form a cysticercus. When a human ingests a cysticercus, the life cycle is complete (Bowman, 2009; Roberts *et al.*, 2013a).

Epidemiology

Taeniasis, as a result of *T. saginatta* is rare in the United States and is more prevalent in Latin America, Africa, and Eastern Europe/Russia (Raether and Hänel, 2003; Ito *et al.*, 2004). Typically transmission occurs in areas where cattle are concentrated, such as feedlots. People will either defecate in the area of the cattle or proglottids will fall out of people's pants. Cattle will then ingest the eggs and the life cycle is complete (Bowman, 2009).

Clinical signs/pathology of animals

There are minimal signs in both the animal intermediate host and the human definitive host. The cysticerci are apparent on eating the meat. Also, the cysticerci or 'beef measles' can be seen during meat processing and can result in condemnation of the carcass (Bowman, 2009). Infestations rarely cause clinical signs in humans with the exception of heavy infections, which could cause gastrointestinal signs including upset stomach .

Control/prevention

Control measures include not ingesting 'measly beef,' containing cysticerci. Alternatively, if the meat is thoroughly cooked then transmission will not occur, as the cysticerci will be killed by cooking to an internal temperature of 56 °C. Humans who are infected should be treated and not allowed around areas such as feedlots and pastures. Cattle will often eat human feces, so prevention of pasture contamination is absolutely essential (Silva and Costa-Cruz, 2010; Roberts *et al.*, 2013a).

Zoonotic potential

The zoonotic potential is self-explanatory as humans are the definitive host.

Taenia solium

Biology

The life cycle of *T. solium* is quite similar to *T. saginata* except that the pig is the intermediate host instead of the cow. As with *T. saginata*, man is the definitive host for *T. solium*. Also similar to *T. saginata*, people become infected when they ingest pork muscle containing, the cysticerci. After the requisite growth, an adult *T. solium* is present in the intestine of the human. However, there is one very crucial difference in this life cycle and it is a potentially deadly one. Man can not only serve as the definitive host, but can also serve as the intermediate host. When this situation occurs, humans do develop cysticerci. Normally, these cysticerci do not cause overt disease. However, when cysticerci occur in the brain, a condition known as neurocysticercosis can result and the parasite can incapacitate or kill the intermediate host (Raether and Hänel, 2003). There are differing sizes of cysticerci, and the relatively large ones could be 20 cm in diameter. When an object of this size is in the brain the result can be catastrophic, with clinical signs ranging from impaired balance to paralysis (Roberts *et al.*, 2013d). This is why prevention of this disease is paramount.

It is important to remember the primary means by which humans develop neurocysticercosis is to ingest an egg, which is shed by another human. Once ingested, this egg undergoes the same migration pathway as in the pig intermediate host, exiting the intestine and accessing the bloodstream. Via the

bloodstream, these eggs can travel to a variety of locations, including the brain. This is a dead-end pathway for the life cycle. Formation of the cysticercus is the same in the pig as in the cow with *T. saginata* (Roberts *et al.*, 2013d).

Epidemiology

Taeniasis, as a result of *T. solium*, like *T. saginata*, is not that common in the US population except among immigrants from Latin America, where it is prevalent. Also, human *T. solium* infection occurs in India, Asia, Eastern Europe, and sub-Saharan Africa. Typically, transmission occurs in areas that are underdeveloped and where people ingest undercooked pork, which results in infection with adult tapeworms (Raether and Hänel, 2003; Del Brutto, 2012).

For neurocysticercosis, the epidemiology is a bit more complex. Typically, infected humans are in more underdeveloped areas, where sanitation may not be a priority, or sanitation measures are unavailable. If handwashing cannot be accomplished easily for either of these reasons, then the possibility exists that feces containing infective eggs may still be present underneath the fingernails or on the hands. Consequently, food for human consumption may become contaminated during preparation. If these eggs are then ingested, then the humans become the intermediate host (Del Brutto, 2012).

The general public was introduced to the disease neurocysticercosis in Robert Desowitz's book, *New Guinea Tapeworms and Jewish Grandmothers* (1981). However, one of the most famous outbreaks occurred in the early 1990s in an Orthodox Jewish community in New York City. Briefly, multiple members of the Orthodox Jewish community developed neurocysticercosis. The members of this community consumed no pork for religious reasons, and therefore most likely would not be infected with adult tapeworms. The source of outbreak was traced back to an active infection with *T. solium* in a Latin American housekeeper who had recently entered the United States. Food for consumption become contaminated with *T. solium* eggs during preparation, and as a result, the members of the community became infected. This case reinforces the necessity of handwashing in prevention of *T. solium* infection (Schantz *et al.*, 1992).

Clinical signs/pathology of animals

There are minimal signs in the swine intermediate host. Similar to *T. saginata*, the cysticerci are apparent on eating the meat, and can also be observed during meat processing (Roberts *et al.*, 2013d).

As compared to *T. saginata*, and as stated above, infections can be deadly in humans when we are the intermediate host. Neurocysticercosis can result in cavitated lesions in the brain, which causes seizures, or other neurological signs and symptoms in the host. The disease can progress to coma and death. Treatment with praziquantel will kill cysts, however, the death of the cyst can result in inflammation, which will either cause or further exacerbate neurologic signs and symptoms. Therefore, praziquantel must be used with caution in cases of active cysticercosis (Del Brutto, 2012). As with *T. saginata*, infections with adult *T. solium* rarely cause disease, with the exception of the occasional gastrointestinal signs (Roberts *et al.*, 2013d).

Control/prevention

Control measures include not ingesting pork containing cysticerci. This includes condemning carcasses containing cysticerci at slaughter. Alternatively, if the pork is thoroughly cooked then transmission will not occur, as the cysticerci will be killed by cooking to proper temperatures. Infected humans should be very careful not to contaminate foodstuffs. Also, if individuals do know that they have an active infection with adult *T. solium*, they should make every effort to get treated. Finally, individuals traveling to endemic regions should make sure that pork is thoroughly cooked (Del Brutto, 2012).

Zoonotic potential

As detailed above, the zoonotic potential is quite high, especially when humans ingest eggs. Although ingesting meat results in infections with adult worms, ingestion of eggs can result in neurocysticercosis (Raether and Hänel, 2003; Del Brutto, 2012).

Conclusion

Zoonotic diseases of livestock can be fairly benign, as with adult tapeworms in the intestine, or quite severe, as when humans are the intermediate hosts. Most zoonotic helminth infections acquired from livestock can be eliminated by combining three simple strategies:

1. Cook meat to a suitable temperature. An internal temperature of 77 °C kills most infectious stages of parasites. Complete recommendations may be located in the USDA website.
2. Wash vegetables: This should remove any infectious stages that have been deposited in the soil, either by humans or animals. Washing should include soap, as well as water, when possible. Also, washing is different from rinsing, so try to remove as much dirt as possible.
3. Wash hands: This will remove any contaminated fecal matter and prevent transmission to other humans or animals, depending on the parasite. The washing of hands means different things to different people. Especially when preparing food, scrub the hands vigorously for at least 20 s. Also, make sure there is no dirt or debris underneath the fingernails. The CDC website has an excellent summary of proper handwashing technique.

Possessing knowledge of the life cycle of the zoonotic helminths in this article, as well as others not discussed, will allow one to implement prevention measures that are best suited to the prevention of potentially devastating and debilitating diseases.

See also: Beef Cattle. Food Safety: Emerging Pathogens. Food Safety: Food Analysis Technologies/Techniques. Food Safety: Shelf Life Extension Technologies. Organic Livestock Production. Safety of Street Food: Indonesia's Experience. Slum Livestock Agriculture. Swine Diseases and Disorders

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Notes
Cross-reference terms in *italics* are general cross-references, or refer to subentry terms within the main entry (the main entry is not repeated to save space). Readers are also advised to refer to the end of each article for additional cross-references – not all of these cross-references have been included in the index cross-references.

The index is arranged in set-out style with a maximum of three levels of subentry heading. Major discussion of a subject is indicated by bold page numbers. Page numbers suffixed by *T* and *F* refer to Tables and Figures respectively. *vs.* indicates a comparison.

Subentries (or subsubentries) to a specific index entry having the same page number, have been included to indicate the breadth of the discussion (as opposed to just the location), as additional assistance to the reader.

This index is in letter-by -letter order, whereby hyphens and spaces within index headings are ignored in the alphabetization (e.g. 'RICEPEST model' precedes 'Rice stripe virus'). Prefixes and terms in parentheses are excluded from the initial alphabetization.

Abbreviations:

GHG greenhouse gases
GM genetically modified

A

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